

# DROSOPHILA INFORMATION SERVICE

## 56

### March 1981

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Artefact Nerds Score Advantage

Scatiopigus males  
 it turns out  
 have got a better shot  
 at mating with caliopigus females.  
 Darwin was confused.  
 It's not the fittest pig  
 but the ugliest.  
 Even the Drosophila women  
 flock and mob  
 nerd male heterosexual fruit flies.



... a noble storie  
And worthy for to drawn to memorie

Larry Sandler

Contemporary Drosophila geneticists feel that Drosophila studies occupy a position close to the cutting edge of modern biology, a conviction which must be evident to participants of recent Annual Drosophila Conferences. This feeling can be objectively validated. A comparison of the material presented one year ago in Bloomington with that reported this year in Salt Lake City shows very rapid progress in many aspects of the genetic biology of Drosophila.

A second striking feature of Drosophila studies that has been amply illustrated in recent Drosophila Conferences is the exploitation for experimental purposes of multiple biological aspects of the fly. From the classical role of Drosophila as a mere vehicle for its chromosomes and its traditional use as a manipulable object in population genetics, Drosophila studies now include biochemical, developmental, neurobiological, and behavioral attacks. The depth and sophistication of this exploitation of the biology of Drosophila is shown by the range of material now considered in the specialized concurrent workshops held during Drosophila Conferences of recent years.

This sense of vitality and centrality that has animated the Conferences lately, as well as the contemporary use of Drosophila in all of its important biological aspects, were not prominent features of the earliest Drosophila Conferences. Indeed, the Drosophila Conferences mirror precisely the renaissance in, and the evolution of, Drosophila studies themselves. Today the meetings are characterized as useful, perhaps even as important. But they started as small get-togethers that could have been called "genetic analysis for fun and recreation". The very first Drosophila Conference, which took place in Madison, Wisconsin in the fall of 1958, was not a formal conference, nor did anyone there at that time imagine that it would give rise to a tradition which has now continued for over twenty years.

In 1958 Dan Lindsley, who was then at the Oak Ridge National Laboratories, flew to Chicago and joined Bill Baker, who was at the University of Chicago, and together they drove to the University of Wisconsin in Madison, where I was a postdoctoral fellow in the laboratory of Jim Crow. Ted Pittenger, a Neurospora geneticist now in Manhattan, Kansas, was then at Marquette. Because Ted had been one of the geneticists at Oak Ridge along with Bill and Dan (and, for a time, me), he joined the two of them in Milwaukee and also came to Madison. Thus, the first "Drosophila Conference", which lasted for two days, involved both Drosophila and Neurospora genetics.<sup>1</sup> The meeting, however, consisted primarily of Baker, Crow, Lindsley, Pittenger, and Sandler each speaking--more or less endlessly--about his current research. Of course, other members of Crow's laboratory, his students and postdoctoral fellows, also attended and participated in the sessions. Most notably, from my point of view, was that Yuichiro Hirai-zumi, with whom I was just beginning to collaborate, was present. Also there--this list is from my memory and therefore almost surely incomplete--were Rayla Greenberg (now Temin), Elaine Johansen (now Mange), and Tom Gregg.

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<sup>1</sup>R.A. Brink dropped in one morning to talk about his current studies on maize, and Hiraizumi distinctly recalls an extended discussion about the chromosomal basis of the departure from equality of the human sex-ratio. As can be seen, Drosophilists in those days were rather more tolerant of work on other, less tractable, organisms than they are today.

\*The perspectives provided here are, of course, mine. However, I have included--mostly without specific attribution--current recollections of Bill Baker, Yuichiro Hiraizumi, Dan Lindsley, and Ted Pittenger. To them, my thanks, in part for their help here, but mostly for making me a participant in the events themselves. Those of you who have read any of my scientific works will surely wonder at the quality of the prose in this note. I haven't learned to write, merely to dictate to Ms. Barbara Hlavin, whose typewriter turns gibberish into English. You may ask, if Barbara Hlavin is responsible for the writing, and others have supplied the memories, why am I the author of this note? You may indeed ask.

It was difficult in those days to find people both interested in and able to discuss the intricacies of formal genetic analysis. The whole group of us did nothing else for two whole days, and it was, to say the least, enormous fun. While the meeting could scarcely be characterized as important, there was enthusiastic agreement that we should do the same thing again the following year, and Bill Baker suggested Chicago as the site of that meeting. In 1959, therefore, Bill sent notices to Dan, Jim and me (Neurospora and corn being summarily dismissed as temporary aberrations), to attend the "Little Men's Chowder and Marching Society". Dan, however, both to explain his absence from Oak Ridge and in order to get reimbursed for the trip, adorned the event with the title of "Midwestern Drosophila Conference".<sup>2</sup> Attendance at this "Second Annual Drosophila Conference" at Chicago ballooned to about 15 or 20 (according to my best recollection), as there were rather a lot of Drosophilists at Chicago and some other workers had heard casually about the projected meeting during the year. This meeting followed the same format as the one at Madison, with individuals speaking whenever they felt they had something relevant to say.

The Chicago meeting was quite as much fun as the earlier one, but it created a considerable furor as news of its existence spread through the Drosophila community, both by word of mouth and through the medium of the bulletin put out by the Oak Ridge National Laboratories. The Christmas edition of that bulletin was received by most laboratories in the country, and contained a notice that Dan Lindsley had attended the Midwest Drosophila Conference. Ed Novitski (learning of the meeting from his new position in Eugene, Oregon) asserted that since Hawaii had become a state, Oregon was in the midwest, and he should therefore have been invited. H.J. Muller was angry that he had not been informed about it, when, after all, he worked in Bloomington, Indiana which was archetypically midwestern, while Dan Lindsley worked in Tennessee, which was the south.

In general, there developed a strong feeling about the impropriety of "exclusive congresses", like those of 1958 and 1959 (although, of course, neither had been congresses in any real sense), so that in 1960 the Third Annual Drosophila Conference, which was held in Bloomington, Indiana, had an enrollment open to anyone who knew of it and wished to come. It was, however, another year before the idea of Drosophila meetings as annual events, with all Drosophila workers formally invited, originated.<sup>3</sup>

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<sup>2</sup>This story appears in Human and Mammalian Cytogenetics, An historical perspective by T.C. Hsu (1974). It is interesting that the Drosophila Conferences took on an official name, and, concomitantly, a certain measure of independent reality, in order to satisfy ORNL's bureaucracy!

<sup>3</sup>It is probably worth reprinting here a section of the letter Dan Lindsley sent out on September 19, 1961 as the invitation to the Fourth Annual Drosophila Conference held at Oak Ridge:

"Three years ago Bill Baker and I got together with Larry Sandler and Jim Crow in Madison and spent two days informally telling each other of our recent experimental results. This meeting was so successful that we decided to repeat it the following year in Chicago. In Chicago we were joined by George Brosseau and Stan Zimmering among others. Last year the meeting was held in Bloomington and the attendance was again higher than the year before.

In previous years we have had no formal program and no official invitations; people simply agreed verbally to meet, and we took turns presenting material. I think that this year the group will be quite large, but we plan to follow much the same procedure as in previous discussions. In view of the annual increase in attendance, the time has come to make a decision whether we wish to formalize an annual Drosophila genetics meeting open to all investigators in the field or whether it would be preferable to disband into the originally conceived, small, regional, bull sessions."

On the copy sent to Bill Baker, Dan appends (by hand): "I decided this year we have to invite everyone--as they all know about it and want to come--or be chicken--I chose the former."

At that conference, as well as at the next several following, the format was still primarily free-form. The entire group met in a single room, and there was no fixed program. People spoke as the spirit moved them, though, as enrollment grew, it became necessary to sign up to speak just before a session was held. However, by 1962 at the latest, enrollment had grown to a point where concurrent sessions had to be scheduled, although free-form plenary sessions were still the norm. At the 1965 Seattle meeting, for example, there was only one afternoon with concurrent sessions (cytogenetics, evolutionary genetics, and physiological genetics).

Following is a list of the Conferences from 1958 through 1980, as reconstructed in 1979 in Bloomington, Indiana and put together and spot-checked by Adelaide Carpenter. There are included, parenthetically, some highlights of early meetings. Also note that the first five meetings, from 1958 through 1962, were held in the fall; afterwards they were held in the spring, and one year (1963) was skipped in the change-over.

1. 1958 Madison I
2. 1959 Chicago I
3. 1960 Bloomington I
4. 1961 Oak Ridge
5. 1962 St. Louis
6. 1964 Madison II [There was a dinner honoring A. H. Sturtevant as he approached his 75th birthday]
7. 1965 Seattle [There was a first general showing of several films depicting courtship and mating in Drosophila, including that classic example of erotica, "I Am Curious Yellow Forked"]
8. 1966 Chicago II
9. 1967 Texas [A eulogy to H. J. Muller, who had recently died, was delivered by C. P. Oliver]
10. 1968 Yale
11. 1969 Iowa
12. 1970 Pasadena
13. 1971 Ithaca College
14. 1972 North Carolina State (Raleigh)
15. 1973 DeKalb
16. 1974 Banff
17. 1975 Louisiana State University
18. 1976 Tempe
19. 1977 La Jolla
- 1978 No meeting--no coal
20. 1979 Bloomington II
21. 1980 Salt Lake City

The next (by true count, the 22nd) conference will be held in Chicago at the Center for Continuing Education on the University of Chicago campus on the weekend of April 24-26, 1981. Save this date and enter it onto your 1981 desk calendar! The first notices will be mailed in mid-autumn. If you have not previously attended or received mailings of earlier conferences, and wish to hear about this one, please contact: Janice Spofford, Dept. of Biology, University of Chicago, 1103 East 57th Street, Chicago IL 60637.

#### 1980 DROSOPHILA RESEARCH CONFERENCE REPORT

Following are abstracts of a few of the talks given at the Drosophila Research Conference in Snowbird, Utah, in May 1980.

##### Sex and the Single Cell

Bruce Baker

(Studies in collaboration with J. Belote and K. Ridge,  
research supported by USPHS grant GM23345)

Sex determination in *D. melanogaster* is under the control of the X chromosome: autosome ratio and at least five major regulatory genes: transformer (*tra*), transformer-2 (*tra-2*), doublesex (*dsx*), intersex (*ix*), and Female lethal (*Fl*). Since sex determination affects the developmental fate of numerous primordia, information about the genetic events involved in the regulation of sex should help elucidate the mechanisms by which eukaryotes effect the expression of alternative developmental pathways.

Our studies on mutations that affect sex determination have focused on the *tra*, *tra-2*, *dsx* and *ix* loci. A comparison of the phenotypes produced in mutant/deficiency and homozygous mutant bearing flies shows that the *dsx*, *tra-2* and *tra* mutants result in a loss of wild type function and probably represent null alleles at these genes. By examining the sexual phenotype of clones of homozygous mutant cells produced by mitotic recombination in flies heterozygous for a given recessive sex-determination mutant it was shown that the *tra*, *tra-2*, and *dsx* loci determine sex in a cell-autonomous manner. These experiments also allowed us to determine when the *tra-2*<sup>+</sup>, *tra*<sup>+</sup> and *dsx*<sup>+</sup> loci had been transcribed sufficiently to support normal sexual development. The wild-type alleles of all three loci are needed into the early pupal period for normal sex determination in the cells that produce the sexually dimorphic (in pigmentation) cuticle of the 5th and 6th abdominal tergites. *tra*<sup>+</sup> and *tra-2*<sup>+</sup> cease being needed shortly before the termination of cell division in the abdomen. *dsx*<sup>+</sup> is required at least until the end of division. In contrast, in the foreleg the wild-type alleles of *tra*<sup>+</sup> and *tra-2*<sup>+</sup> have functioned sufficiently for normal sexual differentiation to occur by about 24-48 hrs prepupariation, but *dsx*<sup>+</sup> is required in the foreleg at least until pupariation.

The time(s) at which the product of the *tra-2* locus was needed for normal sexual development was investigated by means of temperature shift experiments with *ts* alleles at this locus. These experiments demonstrated that *tra-2*<sup>+</sup> function is required at several different times within one tissue for normal sexual differentiation to ensue. For example, in the sex comb region of the foreleg that is sexually dimorphic in bristle number and morphology the product of the *tra-2* locus is required at different times for the determination of bristle number and bristle morphology. Multiple times of action were also strikingly evident in the genital disc.

All possible homozygous double mutant combinations of *ix*, *tra*, *tra-2*, and *dsx* have been constructed and reveal a clear pattern of epistasis: *dsx* > *tra*, *tra-2* > *ix*. It is concluded that these genes function in a single pathway that determines sex. The phenotypes and interactions of these sex determination mutants suggests that *dsx*<sup>+</sup> is a bifunctional locus that in males acts to repress female sexual differentiation whereas in females it functions to repress male sexual differentiation. The *tra*<sup>+</sup> and *tra-2*<sup>+</sup> are suggested to act in concert in chromosomally female individuals to let *dsx*<sup>+</sup> be expressed in the female mode. The *ix*<sup>+</sup> gene functions subsequent to *dsx*<sup>+</sup> in females.

Finally whether there is a time during development by which the X:autosome ratio has acted to irreversibly determine sex was investigated by genetically removing an X chromosome from abdominal cells of 2X2A females at various times during development. The removal of X chromosomes was brought about by (1) induced mitotic recombination in females heterozygous for a T(X:A) and (2) temperature pulses to mutants that affect mitotic chromosome stability.

When an X was removed during the early embryonic period, a 1X2A cell was produced that developed into a healthy clone of phenotypically male cells in the adult. Removal of an X during the larval/pupal period yielded very small clones that appeared to be phenotypically female. The small size of these clones suggests to us that the hypothesis that the determination by the X/A ratio of X chromosome transcription rate has occurred in these cells prior to the time an X was removed and that once set the X chromosome's transcription rate is not reversible. Thus although these cells have a normal male chromosome complement (1X2A) their single X is being transcribed at the rate of a single X in a female which is half that of the single X in a normal male.

These observations suggest that early in development the X/A ratios function in an irreversible manner in both dosage compensation and sex determination. We view the  $tra^+$ ,  $tra-2^+$ ,  $dsx^+$  and  $ix^+$  loci as being the means by which the decision of the X/A ratio with respect to sex is effected. Implications of these observations for the understanding of other homeotic loci were discussed.

#### Of Flies and Men: Human Blood and Enzyme Variation in Drosophila

Jerry Coyne

(Study in collaboration with J.A.M. Ramshaw and R.C. Lewontin,  
supported by Public Health Service Grant GM-24849 to R.C. Lewontin)

Standard methods of electrophoresis in *Drosophila* fail to detect a large number of genetic variants at certain allozyme loci. These variants can only be seen with the application of sequential electrophoretic methods, including varied pH's and gel concentrations. The patterns of gene frequencies, polymorphism, and heterozygosity emerging from these new studies may substantially alter some of our conclusions about the genetics of natural populations.

In an attempt to calibrate the power of such methods, we performed sequential electrophoretic analysis of many human hemoglobin variants with known amino acid sequences.

Our study was divided into three parts. The first experiment was a sequential electrophoretic analysis of 20 hemoglobin variants which fell into only three charge classes. The standard electrophoretic condition used in many previous surveys resolved eight of these variants; and sequential analysis resolved 17, yielding a detectability of 85%.

The second experiment compared groups of hemoglobins, each of which consisted of identical amino acid substitutions occurring in different positions in the molecule. Sequential electrophoresis was able to distinguish 90% of these chemically identical substitutions.

Finally, we examined 5 pairs of substitutions, each of which was a charge-equivalent pair of substitutions occurring at the same position in the molecule. Four of these 5 pairs were distinguishable by our methods.

Using computer-generated pictures of the hemoglobin molecule, we examined the relationship of the position of specific substitutions with the electrophoretic mobility of the resulting variants. We concluded that, in general, substitutions occurring in the interior of the molecule do not express as much of their charge as those on the surface and, in addition, substitutions which appear spatially equivalent can nevertheless show different electrophoretic mobilities. The complexity of interactions between residues seems to be such that almost any genetic variant can be distinguished from any other by electrophoresis.

If hemoglobin is a valid model, then, standard and sequential electrophoresis are obviously capable of detecting much more than simple classes of variants with identical nominal charges. If these conclusions are confirmed in calibration studies using other molecules, we may conclude that sequential electrophoresis has detected a large fraction of the allozyme variation present in natural populations of *Drosophila*.

#### Regulatory Genes in Hawaiian *Drosophila*

W. J. Dickinson

In my laboratory, and several others, natural genetic variants that alter the tissue and stage specific pattern of expression of selected enzymes have been sought and investigated in hopes that they would provide insight into the mechanisms of gene regulation in eukaryotes. During the last several years, there has been increasing interest in the possibility that

changes in regulatory genes (affecting the time, place and quantity of production of proteins) may be more important in adaptive evolution than changes in structural genes (affecting the functional properties of proteins). The intra-specific regulatory variants that we and others have been studying could be the raw material on which selection would act to produce novel patterns of regulation. It therefore seemed relevant to ask how much divergence in patterns of enzyme expression has taken place during the evolution of a phylogenetically well studied group and, if possible, to investigate the nature of the genetic changes that lead to new patterns of regulation.

The tissue and stage specificity of expression of five enzymes was examined by electrophoretic analysis of relative enzyme levels in extracts of 13 larval and adult tissues in 27 species of Hawaiian picture-winged *Drosophila*. The developmentally regulated patterns of enzyme expression thus characterized were compared to a modal standard phenotype. About 30% of the pattern features analyzed differed significantly from the standard in one or more species. Many of these regulatory differences are essentially qualitative, with tissue specific differences in enzyme activity in excess of 100 fold for some species pairs. The adaptive significance of these pattern differences is unknown, but the results provide strong direct evidence for rapid evolution of new patterns of gene regulation in this group of organisms.

Several cases where closely related, hybridizable species pairs differ dramatically have been selected for genetic and molecular analysis. Both cis- and trans-acting elements have been recognized, and both can be involved in producing the pattern differences affecting a single enzyme in one pair of species. Some of the cis-acting elements appear to be complex, with different tissues affected to different extents or even in opposite directions. Where investigated, the cis-acting elements affect the number of enzyme molecules present, not the catalytic properties. As expected, they are linked to the corresponding structural gene.

A hybridization probe derived from a cloned *D. melanogaster* ADH gene has been used to investigate the molecular basis of a qualitative difference in the tissue distribution of ADH in *D. grimshawi* and *D. orthofascia*. The former species had ADH in both larval fat body and midgut but the latter has detectable activity only in fat body. Total RNA was prepared from both tissues of each species, electrophoresed in methyl mercuric hydroxide - agarose gels and blotted to "Northern" paper. Hybridization to the *melanogaster* probe revealed a major RNA species indistinguishable in molecular weight from the ADH mRNA of *melanogaster*. This RNA was present in both tissues of *grimshawi* and in *orthofascia* fat body but was undetectable in *orthofascia* gut, corresponding to the absence of ADH from that tissue. Nor was there any trace of homologous RNA of a different size. Thus, this cis-acting element controlling tissue specificity of ADH expression appears to control mRNA synthesis, apparently at or very close to the transcriptional level. Investigations into the evolution of new patterns of gene expression may prove to be a powerful way to gain insight into the normal operation of regulatory mechanisms.

References: Dickinson, W.J. and H.L. Carson, Proc. Natl. Acad. Sci. USA 76:4559-4562; Dickinson, W.J., Science 207:995-997; \_\_\_\_\_, Devel. Gen. (in press); \_\_\_\_\_, J. Mol. Evol. (in press).

#### ERRATA

DIS 55: January, 1980

Bibliography Item No. 4266: Volume 19, not Volume 119. [p. 239]

#### Corrections to M. Ashburner's Report:

Df(3L)st<sup>SS103</sup>: The breakpoints of this deficiency are 73A3.4;74A6, and not as stated. [p. 196].

DTS-5 (and not DTS-3, as stated): see this DIS. [p. 196]

Su(H): Within bands 35B8.9 to 35C1 and not as stated. [p. 196]

T(Y;2)D6: The Y;2 breakpoint is at 25D6.7 and not 25D2.3 as stated. [p. 196]

cu: Within bands 86D1.2;86D4, and not as stated. [p. 196]

Sixth European Drosophila Research Conference: The Sixth European Drosophila Research Conference has been organized by the Association of Yugoslav Genetic Societies in Kupari - Dubrovnik, between 16-20th September 1979. The Conference was attended by 215 participants from 22 countries, including USSR (12), USA (8), Egypt (2), Israel (2), Canada (1) and Japan (1). A total of 140 reports were submitted at three parallel scientific sessions, (1) biochemical and cytogenetics, (2) developmental genetics, and (3) population and evolutionary genetics. Fourteen of these papers were presented as the plenary reports, such as: "The role of satellite DNA sequences in speciation" (F.J. Ayala), "Genetic instability in *D. melanogaster*" (B. Rasmussen), "Gene versus gene regulation polymorphisms" (J.R. Powell), "Which part may *Drosophila* play in solving the problem of the genetics of aging?" (F.A. Lints), "How many genes are involved in sexual isolation" (C. Petit), "Inversion, allozyme and lethal frequencies in natural populations of *D. subobscura*" (D. Sperlich), and others. A few round-table discussions were held during the Conference, among them on the genetics of sex determination (pres. R. Nöthiger), and on the problems of *Drosophila* taxonomy and evolution (pres. G. Bächli and S. Lakovaara).

The general meetings involved information about the *Drosophila* stock center in Umeå, discussions about the cooperation on common research projects, a consideration of possibility of organizing the international *Drosophila* research conference which will involve also scientists from other continents. The final decision about such proposals should be given at the Seventh European *Drosophila* Research Conference in Finland, which will be organized by Prof. S. Lakovaara, Dept. of Genetics, University of Oulu, in June 1981. [--Prof. D. Marinković]

The Johns Hopkins University Schools of Medicine and Arts & Sciences announce a new collaborative predoctoral training program in Human Genetics leading to a Ph.D. degree in Biology. Broad training will be offered in aspects of human biology (cell biology, biochemistry, anatomy, pathology, pathophysiology) with a special focus and research training in modern human genetics. Write to: Dr. Barbara R. Migeon, Genetics Unit, Dept. of Pediatrics, CMSC 1004, Johns Hopkins Hospital, Baltimore MD 21205.

Genetics & Biology of Drosophila price increases: Drosophilists concerned about the ridiculously high price of the latest volume in this series (volume 2d, \$124.50 US dollars) should definitely communicate their unhappiness to Mr. Fred Haight, National Sales Manager, Academic Press Inc., 111 Fifth Ave., New York NY 10003. Mr. Haight has already received a few complaints and seems very willing to pass along all letters to the British Office where the prices for these volumes are set. Strongly worded letters from both buyers and authors of this series should help keep the prices of future volumes down. [--W.H. Petri, Boston College, Chestnut Hill MA]

The card catalog of the world's Drosophilidae begun by E.B. Basden (DIS 45:171, 46:75) has been taken over by me. When Mr. Basden retired in 1975, he had already abstracted all relevant papers in the Univ. Texas Publications and some of Duda's. This catalog will be continued in a modified way. Successful tests have been made with a computer based Data Retrieval System. I would be grateful for any reprints on drosophilid taxonomy, evolution, ecology, faunistics and related topics. Please put my address on your mailing list. [G. Bächli, Zoologisches Museum, Universität Zürich-Irchel, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland]

Winifred W. Doane and Lynda G. Treat-Clemons have updated the biochemical genetics map of *D. melanogaster* to include published material, notes, and personal communications available up to Dec. 1, 1980. The revised map, entitled Biochemical Loci of the "Fruit Fly" (*Drosophila melanogaster*), will appear in the January 1981 issue of the Isozyme Bulletin (No. 14), edited by G.S. Whitt. It includes an alphabetical list of all loci known to affect specific enzymes, proteins or nucleic acids. A genetic map of loci for which recombination data are available is included, as well as information on cytological mapping and a bibliography of 350 references. Loci mapped by segmental aneuploidy and/or by in situ hybridization are included. For the first time, loci for which there are physical mapping data from restriction enzyme and/or nucleotide sequencing studies are referenced.

For further information about this revised map, please write to: Dr. W.W. Doane, Dept. of Zoology, Arizona State University, Tempe AZ 85281.



Drosophila bottles: There seems to be a chronic shortage of the standard milk bottles traditionally used for culturing *Drosophila*. Inquiries among workers in the field indicate little interest by glass manufacturers in producing these bottles particularly when the number of potential sales is not clearly known but likely to be small by their usual standards. I have offered to coordinate the gathering of information about the consolidated need for bottles. With that information there may be the possibility of gaining the interest of a company to provide them. Please answer the following questions by letter within 30 days of its publication. Although it may appear in more than one journal, answer only once. The questions are: (1) how many bottles would you buy immediately at a reasonable price? and (2) assuming that need is met how many would you buy two years hence?

Suggestions and ideas are welcome. Address replies to: David J. Remondini, Ph.D., Genetics Study Section, Division of Research Grants, SRB, National Institutes of Health, Westwood Bldg., Room 349, Bethesda MD 20205.

Shell vials (33 mm x 100 mm) are now available through the Arthur H. Thomas Co. These shell vials are made of clear autoclavable glass and for a limited time are available for 25¢ each. Send requests to: The Arthur H. Thomas Co., P.O. Box 779, Philadelphia PA 19105, Attention: John Domalewski.

Materials requested: The *Drosophila* cytogenetics group in Novosibirsk (USSR) deals with the organization of two X-chromosome regions: the puff 2B and the "vermillion" band 10A1-2. The first results are published in the following papers: (2B region) Belyaeva et al. 1980, Chromosoma v. 81 & 82, in press; (10A1-2 region) Zhimulev et al. 1981, Chromosoma v. 81 & 82, in press, and DIS 56, in press. We would be glad to receive from drosophilists any stock carrying a mutation or a chromosome rearrangement tentatively affecting 2B (genetic position 0.2-0.6 map units) or 10A (genetic position 32.0-34.0) region. Any such stock will be acknowledged with gratitude. They should be sent to: Igor F. Zhimulev & Elena S. Belyaeva, Institute of Cytology & Genetics, Siberian Division of USSR Academy of Sciences, Novosibirsk 630090, USSR.

Materials requested: We have lost our source of non-absorbent cotton in rolls (Rock River in Wisconsin). Does anyone know where this can now be purchased? Please send information to: William M. Hexter, Webster Center for Biological Sciences, Amherst College, Amherst MA 01002.

"The Genetic Variations of *Drosophila melanogaster*" Revision

Dear Colleagues:

We are embarking on a revision of "The Genetic Variations of *Drosophila melanogaster*", and we wish to enlist your aid. We are soliciting material for inclusion in the forthcoming edition. We would be most grateful if *Drosophila* workers would submit to us the following: (1) corrections of all errors in the current volume that have come to their attention; (2) additions to current entries organized according to the categories of information as used in the format of the current edition; and (3) new entries prepared according to the format of the current volume. We are especially anxious to be as complete and as current as possible in the cytological and genetic mapping information included; thus, we are interested in information on recombination, complementation, and deficiency mapping, on the positions of breakpoints of chromosome rearrangements, and on the sites of in situ hybridization of cloned DNA sequences.

We are anxious to receive suggestions from users as to how the revised version can be made more useful, and we will be receptive to suggestions regarding format, nomenclature, and contents of the volume.

As we proceed with the revision, we propose to send selected copy to workers with expertise in different areas for approval and we sincerely request cooperation in attending to these requests with dispatch.

Dan L. Lindsley & Georgianna Zimm  
Dept. of Biology, B-022  
University of California, San Diego  
La Jolla, California 92093



Herman T. Spieth  
University of California, Davis, California

The Hawaiian Drosophila Project was initiated by D. Elmo Hardy (University of Hawaii) and Wilson Stone (University of Texas) in 1963. The following accepted their invitations to participate in the Project: H.L. Carson, University of Washington, St. Louis; Frances Clayton, University of Arkansas; W.B. Heed, University of Arizona, H.T. Spieth, University of California, Riverside; H.D. Stalker, Washington University, St. Louis; H.L. Throckmorton, University of Chicago. This group began investigations in Hawaii in June 1963.

The overriding immediate problem was the development of methods of rearing the endemic species in the laboratory. Several investigators, including Curt Stern during the 1930's and Gordon Mainland during the late 1940's, had been unable to rear any of the Hawaiian species in the laboratory. As a result the National Science Foundation funded the Project for only a single year and suggested that if successful rearing methods were devised then consideration would be given for extended support.

We quickly became aware that there also existed other refractory related problems. These can be categorized as follows: (1) collections of adequate numbers of flies; (2) successful transportation of captured flies to the laboratory in Honolulu and shipment of living specimens to Texas; (3) maintenance of the flies in healthy condition in the laboratory; and (4) identification of the individuals.

Hardy quickly educated us to the unwelcome fact that the baiting techniques used in other parts of the world were relatively useless for collecting the endemic Hawaiian species. His technique and that of other collectors was to use sturdy insect nets which they swung vigorously through the thick vegetation close to the substrate. Such a method often injured the flies and the specimens were still suitable for pinning but not for rearing. Since the flies would not come to any of the "standard" baits we perforce had to use nets.

Further, we found that the bulk of the native flies were restricted to the cool, moist-to-wet native rain forests which grow on the slopes of the volcanic cones at elevations of 600-1500 meters, with the 900-1200 meter zone containing the majority of the populations. Essentially no humans dwell in the rain forests, and few people enter them other than foresters, water officials, pig hunters, the military in some areas, and scientists. Access to the forests is under the control of private owners, State Foresters, water officials and in some areas the military. Permission to enter must be secured from one to three different agencies and the access routes or roads typically require the use of a four-wheel-drive vehicle. The volcanic terrain of the forest is rough, the footing treacherous and the vegetation often extremely dense. Fortunately, rough narrow trails have been developed for the use of foresters and the water service personnel. Nevertheless, until one has personally engaged in collecting in the rain forests it is difficult to appreciate how large an expenditure of time, energy and money is necessary.

Fortunately, there exist a few collecting sites that can be reached via paved public roads and which have living accommodations nearby. These are Kokee State Park, Kauai; Volcanoes National Park, Hawaii; and the Saddle Road area between Mauna Loa and Mauna Kea, also on Hawaii. On Oahu, with the permission of the military and the use of a four-wheel vehicle, the Mt. Kaala summit can readily be reached. The Tantalus area at the head of Manoa Valley just a few miles from the University of Hawaii campus had been during the early part of this century a major spot for collecting endemic Drosophila. It was here that Mainland and others had collected numerous species. By 1963 the majority of the species had been exterminated, apparently by the intrusion of exotic vegetation and the introduction of ants. Whenever ants, which were totally lacking in the native fauna, are introduced into Hawaii, they quickly exterminate most if not all of the native Drosophila.

We concentrated our collecting efforts during the summer of 1963 on Kokee, Tantalus, Mt. Kaala and the Volcanoes National Park. Our most productive results were achieved in Kipuka Ki and Kipuka Puaula (Bird Park) which are located in the National Park on Hawaii. Both of these kipukas have a rich and abundant Drosophila fauna. Kipuka is the Hawaiian word for "opening" and is used to designate an area that is surrounded by recent lava flows. It is thus a small area or island of relatively rich and deep soil on which the forests are older and more mature than those found on the surrounding younger lava. In a real sense a kipuka is an experimental plot on the volcanic terrain.

We followed the standard technique of placing captured flies in small vials which had a layer of food medium on the bottom. Unlike mainland species the Hawaiians often become stuck to the walls or food of the vials. Since the Hawaiian flies cannot tolerate temperatures above 20°C, we had to transport the vials back to the laboratory in insulated boxes which were cooled with containers of frozen artificial ice. This invariably resulted in some condensation in the vials and accentuated the "sticking" problem. This problem was not solved until about a year later when I developed the sugar vial technique.

Wheeler and Clayton remained in Hawaii during 1963-64, both on sabbatical leave, but the others returned to their home institutions at the beginning of the fall semester. Our achievements had been minimal but we had come to understand some of the problems we faced. During the summer of 1963 Throckmorton was able to study the reproductive anatomy and ova of a number of species. Heed had found the larvae of one species breeding in the leaves of the araliad *Cheirodendron gauchichaudi*. This was the compass sign that led to the solving of the larval substrate problem that Heed successfully pioneered and to which Steven Montgomery later contributed.

During their sabbaticals Wheeler and Clayton vigorously pursued their attempts to devise successful rearing techniques. They prepared and tested a large number of different media, but none was really adequate although they did manage to induce a few field-captured females to oviposit in the laboratory but the resulting larvae died. One morning Wheeler's young daughter refused to eat the prepared dry cereal her mother had purchased. Wheeler took the box of Kellogg's Special K to the laboratory, moistened the cereal and presented it to freshly captured *Drosophila mimica* from Bird Park. The females oviposited avidly and the larvae developed. From this clue the Wheeler-Clayton food was developed.

Several years later I observed that field-captured females which I was using for sexual behavior observations became lethargic when kept on the standard Wheeler-Clayton food. I instructed the food technician to omit the brewer's yeast from the Wheeler-Clayton food that he was preparing for my use. The effect was dramatic and today yeastless Wheeler-Clayton food is the standard medium for the Hawaiian species.

Wheeler and Clayton found that the mature larvae refused to pupate in the rearing vials. Insead they bored through the cotton plugs, wandered about and died. Wheeler remembered that Kenneth Frisk had solved a similar problem with *Agromyzidae* larvae by placing the larvae on a layer of sand. This clue led to the sand jar technique; i.e., when larvae in a food vial are almost mature, the cotton plug is removed and the vial is dropped into a large jar which has a 2-3" layer of moist, sterile sand and the jar is then tightly closed with a piece of cloth. The mature larvae leave the food vial, wander about for a considerable period of time but finally burrow into the sand and pupate. The emerging teneral adult wriggles back to the surface and then expands its wings and matures.

Throughout the life of the project undergraduates have served an important and valuable role in the conduct of the research; approximately 150 of them have participated. A large percentage of them have eventually received advanced degrees in zoology, genetics, botany, medicine, dentistry, veterinary medicine and the paramedical field. One of these undergraduates, Kenneth Kaneshiro, then a sophomore, joined the project in October 1963. Today he is Dr. Kaneshiro and a senior investigator. Ken is a superb field man, a gifted systematist, and an insightful experimentalist. I am sure that other senior investigators in the project will agree that Kaneshiro's overall intellectual grasp and knowledge of Hawaiian *Drosophila* are more comprehensive than that of anyone else who has participated.

In 1964 various types of fruits, vegetables and other substances were tested as baits and all were indifferently effective. Carson concentrated on this problem and found a surprising behavioral trait. On the mainland we place bait in the bottom of a bucket or similar container and collect the flies that come to feed by disturbing the container and netting the flies as they fly upward and out of the bucket. When the Hawaiian flies are similarly disturbed, they fly downward and become enmeshed in the bait. Carson therefore began to smear bait on boards or heavy cardboard which were hung vertically on tree trunks and other objects.

Throckmorton vigorously pursued his anatomical studies and by the end of the summer he was able to identify and delimit the major species groups.

Harua Tokada of Kushiro Women's College, Hokkaido, Japan, joined the project for the summer of 1964 and studied the male genitalia of 55 species of drosophiloids involving both

drosophilids and scaptomyzids. His efforts complemented Throckmorton's studies and helped to elucidate the relationships between the various species groups. Further, he concluded that all the numerous drosophilid species had descended from a single ancestral population and further that the genus *Scaptomyza* probably also arose from the same ancestral population.

Heed systematically searched for ovipositional sites, i.e., larval substrates. None of the native plants produces fleshy fruits so he concentrated on leaves, bark and other possible types of substrates. The two dominant trees of the forest, *Matrosideros collina* polymorpha (Ohia) and *Acacia koa* (Koa), occasionally develop slime fluxes, but proved not to be prime larval substrates.

Less numerous but rather uniformly distributed throughout the forest are individuals of the evergreen deciduous tress and shrubs of the araliads (*Cheirodendron*, *Reynoldsia* and *Tetraplasandra*) and the lobeliads (*Clermontia* and *Cyanea*). In the fermenting fallen leaves, rotting bark, and slime fluxes of these Heed found the larvae of many species. These discoveries led to the finding of other less frequently used substrates and today more than 35 families of plants are known to serve as larval substrates for one or more species of the native *Drosophila*. Most of the species are monophagic, some oligophagic and a few polyphagic.

The Wheeler-Clayton food and sand jar techniques enabled them to rear a number of species, especially some of those that belong to the picture-winged species group. The species belonging to this group are large spectacular flies and Carson found that they had large salivary gland chromosomes. He therefore took this group as his province. Clayton was also able to study the cytology of these and other species. They were both aided by the fact that field-captured females would often lay fertile eggs on Wheeler-Clayton food and from these mature larvae could be reared and used for study. Typically, however, the F<sub>1</sub> adults which emerged from such larvae died young or if they survived refused to oviposit--thus the stock died out.

In the fall of 1964 I was on sabbatical leave, so I remained in Hawaii after other investigators had departed at the end of the summer. During the summer I had made observations on the courtships of several species and was frustrated because, although the males might court vigorously, the females were almost all uniformly recalcitrant and refused to copulate. This occurred with both field-captured and laboratory-reared virgin females. Some species simply refused to engage in sexual activity in the laboratory. I also observed that the flies, especially the males of most species, showed intense antagonism toward each other, engaging in behavior that could only be described as fighting. This occurred also in the rearing vials, and the large picture-winged flies often broke each others' wings.

Since I knew that mainland flies engage in courtship and copulations on the feeding sites in the field, I decided to spend most of the fall in searching for feeding sites as well as collecting flies, etc. I chose three places: Kokee on Kauai, Waikamoi on East Maui, and Bird Park at Volcano, Hawaii, each known to have populations of several species.

At Kokee I was able to collect flies but could find no feeding sites. Therefore, ground-up *Cheirodendron* leaves and other baits were used and observed for long periods of time. To my surprise the flies approached the baits in a quite different fashion than expected. Mainland species fly to the baits, often buzzing and circling before landing. In comparison, the Hawaiian species approach cautiously and slowly; they make quick, short darting flights, land, sit immobile for a period of time, then walk slowly forward and finally after many minutes reach the bait. Once there they feed quietly, engaging in no sexual or antagonistic activities. After feeding for a time, they depart by a quick downward flight and disappear.

At Waikamoi on Maui I searched for food sites and came across a spot where a number of tree ferns had been cut down a few days previously, and the stumps were covered with sap. A number of *Clermontia* shrubs had also been broken and cut with the result that the milky sap was exuding. Large numbers of flies of several species were ravenously feeding on these saps. Again, it was the same behavior as at Kokee. The quiet, cryptic behavior of the flies was amazing. I observed no courtships or antagonistic behavior by the flies when they were feeding. Neither did I find any courtship sites.

At Kipuka Ki, Volcano, a large limb bearing fungi had fallen and here the flies were also quiet, but as soon as they moved off the fungus food site they became antagonistic. I observed males sitting on the upper surface of nearby leaves. Whenever another individual

alighted, the male approached and courted. In another part of Kipuka Ki a large Polyporus fungus was found and again the pattern of behavior was similar to that found on the other fungi. Thus, the flies separate feeding and courtship; i.e., they engage in lek type courtships.

On the lek the males are aggressive, defending it vigorously if another male enters it. The females are extremely choosy in the selection of a male. Even when they are sexually ready and enter a lek, they will often allow a male to court for long periods and then depart without copulating.

In 1965, John Murphy came from Texas to serve as the operational manager of the project. Intelligent, tactful, and with a vivacious personality, he quickly became the individual to whom everyone turned for logistic planning and execution, both in the laboratory and in the field.

Malcolm Brown, a graduate student specializing in microbiology in the Botany Department at Texas, arrived in Hawaii in June of 1965 and began an investigation of the yeasts and other microorganisms found associated with the native vegetation and especially those found on or in the decomposing substrates in which the Drosophila larvae were living or upon which the adults fed, especially Cheirodendron and Clermontia. He isolated a number of the favored yeasts and collectors then began to hang petri dishes which had been inoculated with these yeasts in the field as baits.

The Hawaiian species are cryptic, in both their coloration and behavior. The adults often sit motionless on the vegetation for prolonged periods, especially in the areas surrounding a natural food source. If disturbed they typically fly or dive downwards. Kaneshiro and Jack Fujii exploited this behavior of the flies. They searched the vegetation, moving cautiously and deliberately. Finding a specimen on the underside of a limb or leaf or on the trunk of a tree, they slowly thrust the open end of an 8-dram glass vial over the fly. Invariably the specimen then dove to the bottom of the vial. This technique became known as the "pick off" method. Later the use of glass tube aspirators was introduced and today these two techniques are the standard methods for collecting those species that are attracted to baits as well as those individuals sitting on the vegetation. For those species for which we have as yet no effective baits, sweeping with nets is still mandatory.

Brown isolated a species of yeast from rotting Clermontia. Kaneshiro inoculated Gerber's baby banana with this yeast and then used the fermenting banana to smear on the trunks and under surfaces of limbs of trees and shrubs. Such bait proved attractive to a considerable number of species, especially the picture-winged flies. It was easy to use in the field and the method of application allowed the pick-off technique to be employed. This then became the standard baiting and collecting procedure. A number of species, however, especially those that oviposit on Cheirodendron leaves, only occasionally come to this bait.

Two persistent problems continued to exist in the rearing of the flies: (1) the food in the large shell vials known as Texas vials became moldy and this smothered the eggs which had been deposited into them and also debilitated the adults; (2) the adults tended to "stick" to the food or the walls of the vials. Our normal practice was to insert into the food a small amount of loosely folded Kleenex tissue, with the major part of the paper extending upward above the food; i.e., this portion served as material for the flies to sit on, thus preventing them from becoming "stuck".

Kaneshiro developed the method of folding a small piece of Kleenex into a rectangular pad of about 1 x 2 inches, moistening this with a sterilized solution of yeast, sugar water, and propionic acid. This pad was then pressed against the inside wall of a vial and almost in contact with the food at the bottom. The food vial was then laid on its side with the pad on the "bottom". Thus, the adults could sit on the pad and feed when they desired on the vertically oriented food.

At Texas, Stone with the aid of Kathleen Resch was engaged in building up stocks of the Hawaiian species. Suffice it to say that if Resch cannot keep a species alive and healthy in the laboratory, no one can. Her skill has been invaluable in making it possible for various investigators, especially those at Texas, to study and publish findings on species and species groups that otherwise would not have been available. Kathleen spent the period of February-July 1966 in the laboratory at Honolulu. She had earlier determined that by immersing fresh Cheirodendron leaves in distilled water soluble fungistatic sub-

stances escaped from the leaves. This became known as Cheirodendron "tea". She also suggested that dampened Tomac tissues be used for making the pads rather than Kleenex.

Kaneshiro methodically made teas from the leaves and stems of all of the various native plants that we knew were used as ovipositional substrates. Not surprisingly, at least in retrospect, he found that all of these contained fungistatic substances and also that the teas provided ovipositional stimulus to the females. Cheirodendron tea proved to be the least effective and the many species that use Cheirodendron leaves as their ovipositional sites still remain recalcitrant to oviposition in the laboratory. Clermontia tea is the most effective and broad spectrum for mold control and ovipositional stimulation. Another advantage of the pads is that the females prefer to oviposit in the paper. When the larvae emerge they migrate to the food.

Forbes Robertson of Edinburgh, who had had considerable experience in the area of Drosophila nutrition, joined the group from May to late August of 1966. He chose to investigate *D. waddingtoni*, then known as *D. disticha*, which uses decaying Cheirodendron leaves as its larval substrate and whose eggs, larvae and adults can be readily collected in numbers at Waikamoi, East Maui. Robertson made the significant discovery that while the adults use yeasts, the larvae of *waddingtoni* feed exclusively on bacteria. He was, however, unable to rear stocks of the species in the laboratory. Even today, 14 years later, we still cannot maintain stocks of the varied and numerous species which use Cheirodendron as a larval substrate. During the late afternoon of the day that the Robertsons were to depart for Scotland, the laboratory personnel had a picnic for them at Hanauma Bay, and I took the opportunity to talk with him about his investigations on *waddingtoni* and other Hawaiian species. He ended the discussion by saying: "It will be really pleasant to get back to Edinburgh and work with normal Drosophila for these Hawaiian species literally make one psychotic."

Joseph Grossfield came to Hawaii at the same time as Kathleen Resch. He investigated the field biology of the flies with emphasis on their responses to different light intensities. In doing so he made the valuable discovery that the Hawaiian species are light dependent, i.e., they do not mate in darkness.

The period from 1967 to 1970 was one of great achievements by the various investigators. Carson pursued his studies on the polytene chromosomes of the picture-winged species. Clayton methodically and effectively studied the cytology of many species, concentrating especially on the picture-winged flies. Heed pursued the difficult and often frustrating investigations of the ovipositional substrates and also began his studies on the populations of various kipukas on the big island of Hawaii.

Because the Cheirodendron species, i.e., those whose larvae developed on some part of the trees, were so resistant to laboratory rearing it was suggested that perhaps there was some peculiar characteristic in the biochemistry of Cheirodendron that was responsible for their behavior. Heed had earlier solved a somewhat similar problem with *D. pachea* which uses the Senita cactus. He therefore joined with Henry Kircher, a biochemist at the University of Arizona, in an intensive analysis of Cheirodendron. Unfortunately, they did not solve this particular problem but they did learn a great deal about the biochemistry of Cheirodendron.

In 1967 Mike Kambysellis arrived in Hawaii. He and Heed soon joined together to investigate what can be broadly described as the reproductive strategies of the species of various species groups. A senior investigator of the project once remarked to me that Heed was probably the one member of the group who had not received adequate recognition for his contributions to the project, and there is substance to this evaluation. All of the problems to which Heed devoted his efforts were complex, elusive, time consuming, and often frustrating--but in every instance he achieved significant and basic information which he analyzed with skill and clarity.

At Texas Mrs. Yang and Wheeler investigated the problem of hybridization, using numerous species of the picture-wingeds. Their valuable studies complemented the work of Carson and gave us an understanding of the relationship of the various species, as well as helping to further delimit the parameter of the species group.

Hardy and Kaneshiro described numerous new species that continued to appear in the collections constantly being made. They also determined the geographical ranges, identified sibling species, and gave insight into the speciation process, especially within the picture-winged flies.

Kaneshiro completed his undergraduate studies in 1966, became a graduate student and functionally a senior investigator as well as the prime field collector and skilled rearer of species in the Honolulu laboratory. His studies on the male genitalia enabled him to delineate clearly the subgroups within the picture-winged flies. This investigation plus data from Carson's studies showed that the species of the genus *Idiomya* really constitute a subgroup of the picture-winged species group. *Idiomya* has now been synonymized with *Drosophila*. Kaneshiro also studied the anomalous species group known as the crassifemur group, showing that it constitutes an intermediate unit between the genus *Scaptomyza* and the genus *Drosophila*.

Two young investigators broke "new" ground: Carmen Kanapi and Susan Rockwood, both graduate students at the University of Texas, were the first to use allozyme procedures on the Hawaiian species.

Although Stalker did not return to Hawaii after 1963, he did use the salivary chromosomes to elucidate the relationship of the picture-winged flies to the mainland robusta species group, thus giving a clue to the relationship of the Hawaiian flies to their ancestors.

Yeastless Wheeler-Clayton food is excellent for maintaining adults and many, but not all, species will oviposit in the Tomac pads that have been moistened with *Clermontia* "tea", commonly also called "juice". The young larvae migrate to the W-C food but it is a rather Spartan larval substrate. Resch therefore formulated a cornmeal food that is much richer and the standard procedure today is to allow the young larvae first to thoroughly "work over" the W-C food. Then a generous amount of cornmeal food is added to the vials. This technique allows a large number of larvae to be reared to maturity in a single vial. The resultant adults from such larvae are healthy and robust individuals. The rearing techniques for the Hawaiian flies are thus more complicated and time-consuming than those used for melanogaster and other mainland species. Further, the life cycle is long; typically each full generation, from oviposition of the egg to the sexually mature adult, spans a period of at least 40-60 days.

Although the years from 1966-70 were years of accomplishment, there was also tragedy. Wilson Stone died in 1968. His slipping away deprived us of his wisdom, understanding support, and advice. For myself it was not only the loss of a scientific colleague of great stature but also the loss of one of my closest personal friends. No one is indispensable but Wilson Stone certainly approached being that not only for the *Drosophila* Project but also for his department at the University of Texas.

A considerable number of investigators from various institutions located in diverse parts of the world have participated in the efforts of the Project during the period from 1970-80; some for short periods, others for prolonged stretches. Their individual efforts in the main complement and extend those of the various investigators who had originally founded the Project. In a brief history it is not feasible to comment on their contributions and areas of study. Their names are included in an addendum. Hopefully a full bibliography of the Project will be published, thus enabling their individual contributions to be specifically identified.

John Murphy resigned in 1970 when he accepted a responsible position with the Texas Department of Health Resources. The day-to-day management of the laboratory then fell upon Kaneshiro, a position which he still occupies. Busy as his days had been, they became even busier and his responsibilities more demanding.

At about the same time that Murphy departed, Steven Montgomery (then an undergraduate) began to work with Heed and others in investigating the ovipositional substrates of the picture-winged flies. This species group consists of over 100 species and although Heed had found the substrates of a goodly number of the species, there were many he had not discovered. Montgomery, a superb field investigator, made invaluable additions to Heed's earlier studies.

In 1970 Carson joined the Genetics faculty at the University of Hawaii, a move which vastly improved his effectiveness in his research for now he not only was constantly in Hawaii but also he was able to have his graduate students and postdoctoral fellows cooperate more fully in the investigation of the Hawaiian species. He continued his studies on the salivary chromosomes and expanded into allozyme investigations and intensively into the problem of the dynamics of speciation, concentrating on closely related species of the picture-wingeds. In these speciation studies he and Kaneshiro have cooperated closely and effectively.



Recently he has turned his attention to the courtship behavior and the role that it serves in speciation and phylogeny of closely related species.

Heed has turned his attention primarily to the study and identification of the wild yeasts that the larvae use in their substrates as well as to the competition between larvae in the substrates, such as a single decomposing leaf of *Cheirodendron*. These studies of Heed and his graduate students have involved both desert species of Southwestern North America and the Hawaiian species. During a 1972-73 sabbatical at Davis he, in cooperation with Herman Phaff and Martin Miller, investigated various yeasts. He and Francisco Ayala also developed a technique which enabled them to begin to effectively quantify the biology of leaf breeding Hawaiian species.

At Texas Richard Richardson, Wheeler and Yoon, assisted by Kathleen Resch, have studied the salivary chromosomes and the evolution of the crassifemur, antopocerus and part of the modified-mouthparts species groups. Although all of these are exceedingly difficult to handle in the laboratory, they have been able to elucidate the relationships and evolutionary histories of the crassifemur and antopocerus species groups and also to determine the relationships of the modified-mouthparts to other species groups. Their findings have filled large lacunae in our ignorance.

Hardy and Kaneshiro continued their basic studies on the systematics of various species groups. By now large collections have been accumulated and Hardy has revised the antopocera and split-tarsi species groups. They are in the process of revising several other groups, basic information which is mandatory for further investigation into the evolutionary dynamics, biology and ecology of the various species groups.

Kipuka Puau, known as Bird Park because of the considerable number of native birds that dwell therein, has been an important research area for the Drosophila Project as well as for other scientific investigations. It is approximately 56 acres in extent. Until it was incorporated into Volcanoes National Park during the second decade of this century, it was used as a fattening pen for cattle. It is still recovering from the evil effect of such usage and is a prime example of the necessity of the maintenance of preserves which cannot be decimated by the short-sighted activities of human society.

Richardson, aided by his students and associates, intensively investigated a number of problems in Bird Park and nearby Kipuka Ki which receives less precipitation than does Bird Park.

In 1964 Heed and I observed *Drosophila engyochracea*, a large picture-winged species which has its geographical range limited to the two kipukas and the immediately surrounding area. During daylight hours the flies hide away in the moss found on the trunks of trees. We found that during darkness the flies ascend into the foliage and sit on the undersides of leaves. Spencer Johnston investigated this behavior and found that the flies move to considerable heights and scatter through the forest--indicating how movements in the population occur.

Richardson then investigated in detail the movements of *D. mimica*, a modified-mouthparts species. The adults typically hide in the litter on the forest floors but under appropriate conditions do move; he was able to elucidate these movements and the environmental factors bearing upon such activities. He and his students have also directed their efforts towards understanding the dynamics and possible sympatric nature of speciation that may have occurred. They intensively studied three species that dwell in Bird Park and Kipuka Ki. Their conclusions have attracted attention, including considerable skepticism, but above all they have stimulated others of us to rethink and re-evaluate our ideas as to how speciation may have occurred in the exceedingly rich and complex Hawaiian drosophilid fauna.

Kambysellis continues his excellent and unique studies on the reproductive strategies of the flies, currently concentrating on allozyme investigations of the eggs of numerous species.

Clayton, despite a long period of debilitating illness, continues to provide new and important cytological data.

I was able to study with the cooperation of Heed, who spent a sabbatical year in Davis in 1972-73, two mainland species, *D. pinicola* and *D. flavopinicola*, which are restricted to the Pacific coastal area. We concluded that they are, on the basis of morphology, physiology and behavior, more closely related to the Hawaiian species than are species of the robusta species group. Since these species oviposit on mushrooms and the adults feed on mushrooms,

I concluded that perhaps rotting domestic mushrooms might serve as a bait to attract the species of the Hawaiian light-tipped scutellar group, often called the fungus feeders. We knew that one of the species, *fungiperda*, was attracted to large *Polyporus* fungi and used such fungi for a larval substrate.

I therefore went back to Hawaii and, although I was myself somewhat dubious about the outcome, my colleagues were downright skeptical about the use of mushrooms as bait. A trial run on Kauai, however, even under adverse conditions, was highly successful. Not only do the fungus feeders come in large numbers to the bait, but also all of the antopocerus, the crassifemur, and the majority of the picture-winged species are attracted in numbers. In typical fashion Kaneshiro quickly improved my original technique of using mushrooms impaled in twigs; i.e., he soaked thin cellulose sponges in "juice" of the rotting mushrooms and then attached them to tree trunks, etc.

The mushroom bait gives us a reliable method of capturing large numbers of individuals of at least 200 species. Unfortunately, mushrooms attract very few of the *Cheirodendron* leaf breeders nor most species of the modified-mouthparts and ciliated-tarsi species group. This last group is probably the most primitive species group of the Hawaiian fauna and we essentially know nothing about its biology, behavior or evolution at this point in time. The mushroom technique enabled Hardy, Kaneshiro, Ayala and myself to join together in a study on the systematics, allozymes and behavior of the crassifemur, fungus-feeder and picture-winged species groups--a project now under way and yielding considerable new data.

Kaneshiro continued to shoulder the main responsibility for the day-to-day operation of the laboratory, the organization and logistics of field collecting, and the maintenance of relationships with the various organizations whose help and permission we constantly need--doing all of this in addition to pursuing his own extensive research program. Fortunately, the project acquired in 1976 the services of Mrs. Joyce Karihara. Earlier as an undergraduate Joyce, then Miss Sato, had served as a student assistant. She proved to be competent, resourceful, and responsible. Upon graduation she had become a public school teacher, but after being assaulted and badgered by students, she quit teaching. The Project was fortunate to have her back with it because student assistants, although quite capable and responsible, work only a few hours a week and each deals with only a limited number of species. Joyce, however, provided continuum and oversight for the laboratory.

During the entire period 1963-80 the National Science Foundation provided funds for the support of the Hawaiian Drosophila Project. The major portion of these funds was used to support the specialized "low-temperature" laboratory (which is necessary for maintaining and rearing the Hawaiian species), for media preparation, and for salaries paid to the undergraduate and non-academic staff that cared for the numerous *Drosophila* stocks, etc. As of this year (1980) this support has been discontinued, despite the fact that the last review visitation team indicated that at least another decade of support was justified. Thus, in a real sense the Hawaiian Drosophila Project as conceived by Hardy and Stone now belongs to history.

This is not to say that research on the Hawaiian Drosophila fauna has ceased. A number of investigators have grants in their own names, and the specialized laboratory still exists. By making contributions from their grants the laboratory is operating, albeit at a reduced level. Investigators in various parts of the world are now able to maintain stocks in their own facilities. Thus, research is still continuing on some aspects of the fascinating, unique and complex Hawaiian Drosophila fauna.

In no sense is this a complete history of the Hawaiian Drosophila Project. What I have tried to do is (1) to show how two intelligent and thoughtful scholars, Hardy and Stone, assembled a group of investigators in order to solve a seemingly intractable problem, (2) how the answers to at least some of the major problems were developed, and (3) the role that serendipity plus that elusive ingredient called insight contributes to the solutions.

#### Senior Investigators of the Hawaiian Drosophila Project

Jayne N. Ahearn	University of Hawaii
Francisco Ayala	University of California, Davis
Visut Baimai	Mahidol University, Thailand
Stephen M. Beverley	Stanford University
*R. Malcolm Brown	(Unavailable)



Peter J. Bryant	University of California, Irvine
*Hampton L. Carson	University of Hawaii
*Frances E. Clayton	University of Arkansas
W. Joseph Dickinson	University of Utah
*Theodosius Dobzhansky	Deceased, 1976
Antonio Fontdevilla	University of Santiago, Spain
Helen Gelti-Douka	Athens University, Greece
*Joseph Grossfield	City College of New York
*D. Elmo Hardy	University of Hawaii
*William B. Heed	University of Arizona
Lewis Held	University of California, Irvine
Ralph J. Hodosh	University of Maine
John A. Hunt	University of Hawaii
Duane E. Jeffrey	Brigham Young University
Walter E. Johnson	Case Western University
J. Spencer Johnston	Texas A&M
*Michael P. Kambysellis	New York University
Elysse (Craddock) Kambysellis	New York University
*Carmen G. Kanapi	University of Santa Tomas, Philippines
*Kenneth Y Kaneshiro	University of Hawaii
*Henry W. Kircher	University of Arizona
Karen Loeblich	University of California, Davis
Terrence W. Lyttle	University of Hawaii
Robert Mangan	Pennsylvania State University
George Miklos	Australian National University, Canberra, Australia
*Puliyampetta S. Nair	Southern Illinois University, Carbondale
Alan T. Ohta	University of Hawaii
*Toyohi Okada	Tokyo Metropolitan University, Japan
Rody Raikow	University of Pittsburgh
Richard Richardson	University of Texas
John M. Ringo	University of Maine
*Forbes W. Robertson	University of Aberdeen, Scotland
Fabio de Melo Sene	University of São Paulo, Brazil
Susan Rockwood Sluss	University of Arizona
Eliot Spiess	University of Illinois, Chicago Circle
*Herman T. Spieth	University of California, Davis
*Harrison D. Stalker	Washington University
William T. Starmer	Syracuse University
William W. Steiner	University of Illinois, Urbana
*Wilson S. Stone	Deceased, 1968
W. Dorsey Stuart	University of Hawaii
*Haruo Takada	Sapporo University, Japan
Alan T. Templeton	Washington University
*Lynn H. Throckmorton	University of Chicago
John Tonzetich	Bucknell University
Francisca C. do Val	University of São Paulo, Brazil
Graeme Watson	University of Melbourne, Australia
*Marshall R. Wheeler	University of Texas, Austin
Thomas Wolfe	Washburn University
Hei Yang	California Academy of Science
Jong Sik Yoon	Bowling Green University

\*Those whose names are marked with an asterisk began their participation in the Project prior to 1970.

#### Graduate Students

Lorna Arita	Wayne Ibara
Elizabeth Thomas Arthur	Melanie Kam
Patrick Conant	Jeremy Montague
Tina Dellas	Steven Montgomery

Band, H.T. Michigan State University, East Lansing, Michigan. *Chymomyza amoena* - not a pest.

The genus *Chymomyza* in the family *Drosophilidae* is of world-wide distribution (Throckmorton 1975). In North America they are typically regarded as forest or woodland species and are generally considered to be sap feeders (Wheeler 1963, 1965,

1970). As late as 1952 *Chymomyza amoena* in Michigan was still being collected around the cut ends of trees (Steyskal 1952) while Sturtevant (1921) reported that this species had been bred from walnut and butternut husks and acorns.

*C. amoena* in Michigan has now been found to be breeding in fallen apples in abandoned, remnants of abandoned and in commercial apple orchards. Both adults and larvae are able to use fresh apple as a food source. However, adults require a break in the skin in order to feed, and at the study sites outside East Jordan, Michigan eggs have only been found on apples on the ground, especially those which have been nibbled on by small animals or pecked by birds. Hence although individuals can be found in the trees, the MSU Pesticide Center does not consider *C. amoena* to be a pest.

Wheeler (1965) has commented that although economic pests in the family *Drosophilidae* are rare, some species may act as vectors for the transmission of plant diseases. Judging from the diseases manifest by the fruits on these long unattended trees at the East Jordan study sites, *C. amoena* may be such a species. Males are territorial, aggressive, and spar vigorously since lek behavior has not evolved. In the trees individuals may sit quietly wing-waving (a genus characteristic) on apples, but if challenged, chase one another over stems, leaves, branches and attached apples. Certainly they may transport mites; newly established mini-cages (small glass jars placed horizontally from which food dishes may be removed and inserted with forceps) may sometimes contain as many as 3 species of mites and several transfers of *C. amoena* larvae are required to get rid of them.

References: Steyskal, G. 1952, letter to Dr. Marshall Wheeler (courtesy of Dr. Wheeler); Sturtevant, A.G. 1921, Carn. Inst. Publ. 301, Carnegie Inst., Washington, D.C.; Throckmorton, L.H. 1975, Handbook of Genetics (R.C. King, ed.) 3:421-469; Wheeler, M.R. 1952, Univ. Texas Publ. 5204, pp. 162-180; \_\_\_\_\_ 1965, USDA, Ag. Res. Serv., Ag. Handbook No. 276, pp. 760-772; \_\_\_\_\_ 1970, Catalogue of the Diptera of the American South of the U.S., Museu de Zoologica, Universidade de Sao Paulo, part 79, pp. 1-65.

Band, H.T. Michigan State University, East Lansing, Michigan. Ability of *C. amoena* preadults to survive -2°C with no preconditioning.

*Chymomyza amoena*, a member of the Family *Drosophilidae*, in Michigan is now living in apple orchards where it can overwinter in some pre-adult stage, presumably the late larval stage. Development of a media for growing this species in the laboratory has enabled experimental work

on the mechanism of cold hardiness. In the process of determining that neither larvae nor pupae accumulate glycerol or other polyols when stored for 4 or more weeks at -2°C, late instar larvae--when disturbed--were found to have a tendency to leave the media en masse. This migratory tendency is not abated by mere transfer to 10°C for preconditioning at a low non-freezing temperature prior to subzero treatment.

Therefore larvae and pupae have been transferred directly from room temperature (22°C) to -2°C. The following data have been accumulated on the subsequent ability of either phase to complete development. Larval size is approximately 1 mg in weight.

Table 1. Emergence time following storage at -2°C for *C. amoena* larvae and pupae--no preconditioning.

Source	Stage	Days at -2°C	No. larvae or pupae	No. to emerge	No. days to emerge after -2°C
E. Jordan '78	larvae	3	7	6	14 days minimum
E. Jordan '79	larvae	3	4	4	14 days minimum
E. Jordan '78	larvae	8		larvae dead	
Grand Rapids	larvae	7		larvae reactive but not motile	
Lansing	pupae	1	5	5	3 days
E. Jordan '78	pupae	5	20	1	7 days
E. Jordan '79	pupae	4	20	2	12 days
E. Jordan '78	pupae	8	5	5	no record

Under random photoperiod in the laboratory, all larval stages and pupae can endure 24 h at -2°C. Late instar larvae (1 mg or larger) can resume development, pupate and emerge after 72 h at -2°C, but by 7 days are per-

manently injured if not preconditioned at a low nonfreezing temperature. Emergence records from pupae after 48 h at  $-2^{\circ}\text{C}$  are variable, may depend upon the stage at which pupae encounter the subzero temperature, and imagoes from cold-treated pupae are often weak, fail to unfold their wings and their appearance would offer no support to an hypothesis that the pupal stage is the overwintering stage for *C. amoena*.

However, the ability of the larvae to survive 72 h at mild subzero temperatures without injury indicates that the freeze resistance factor(s) is(are) present despite maintaining cultures at room temperature. Zachariassen and Hammel (1976) found that freeze tolerant tenebroid beetles lost this capacity upon warm acclimation; Duman (1977a,b) discovered that the thermal hysteresis factor in a tenebroid larva disappeared only after a 16 h photoperiod and short daylength, low relative humidity or low temperature could all induce production of the thermal hysteresis factor. These insects within the continental United States are not relying on the accumulation of glycerol or other polyols for freeze resistance but on proteins. Thermal hysteresis factors lower the supercooling point in a freeze susceptible insect; cryoprotectants enable an insect to freeze without injury; some contain both (Duman 1979) although diptera investigated (Duman 1979) did not show evidence of thermal hysteresis. Further work on the effects of photoperiod and on the mechanism by which *C. amoena* larvae survive subzero conditions in winter is planned.

References: Duman, J.G. 1977a, J. Exp. Zool. 201:85-92; \_\_\_\_\_ 1977b, J. Exp. Zool. 201: 333-337; \_\_\_\_\_ 1979, J. Insect Physiol. 25:805-810; Zachariassen, K.E. and H.T. Hammel 1976, Nature 262:285-287.

Band, H.T. Michigan State University, East Lansing, Michigan. Duplication of the delay in emergence by *C. amoena* larvae after subzero treatment.

*Chymomyza amoena* is a cold-hardy drosophilid that now can be grown in the laboratory. Emergence time from field-collected apples in summer versus spring indicates that the overwintering stage is the late larval stage. Experiments subjecting larvae and pupae to  $-2^{\circ}\text{C}$  have shown

that all stages can be stored at that temperature for 24 h and recover, but only the late instar stage can withstand prolonged storage at this mild subzero temperature provided the larvae are preconditioned first at a low nonfreezing temperature. Timed emergence tests after storage at  $-2^{\circ}\text{C}$  and  $-5/6^{\circ}\text{C}$  have now been carried out.  $-2^{\circ}\text{C}$  is achieved in the freezing compartment of a refrigerator,  $-5/6^{\circ}\text{C}$  in a Labline incubator in which the temperature fluctuated between  $-5^{\circ}\text{C}$  and  $-6^{\circ}\text{C}$  during the time cultures were kept in it. For  $-5/6^{\circ}\text{C}$  preconditioning intervals at  $10^{\circ}\text{C}$  and  $-2^{\circ}\text{C}$  varied, and larvae were transferred from room temperature appropriately to fresh media so that all were subjected to  $-5/6^{\circ}\text{C}$  and postconditioning temperatures simultaneously.

Table 1. Emergence data on *C. amoena*, field collections + laboratory.

Source	No. Collections	Emergence period after maintenance at $22^{\circ}\text{C}$
Field collected apples		
Spring (March, April, May)	4	15-23 days
Summer-Fall	7	22-49 days
Laboratory		
apples	Oct. '78 F <sub>2</sub> S	26-52 days
media	3	20 days minimum
oviposition to pupa		10 days
pupa to imago		10 days

Table 1 summarizes the emergence data on *C. amoena* obtained from field-collected fallen apples, from apples in the laboratory and from *C. amoena* media. Duration of larval and pupal stages on media have been the same for *C. amoena* populations from Northern Lower (East Jordan) and mid-Michigan (Lansing, Grand Rapids).

In the larval stage, the last 3 days the larvae are equivalent in size to *D. m.* 3rd instars, i.e., 1 mg or greater in weight. This is the size which has been stored successfully 28-33 days at  $-2^{\circ}\text{C}$  and which was used in the experiments reported here. Table 2 gives the days stored at the specified temperatures, the number of larvae recovered from the media and transferred again to fresh media, number pupating and number of imagoes as well as duration of the larval and pupal stages after subzero treatment.

Table 2. Emergence data on *C. amoena* larvae after subzero treatment.

Source	Days at specified t°				Numbers			Days			
	10°C	-2°C	-5/6°C	-2°C	10°C	l	p	i	l-p	p-i	T
E.J.	7	7				2	2	1	5	10	15
E.J.	7	8	5	8	1	7	6	4	5-10	11-15	16-20
G.R.	-	-	22h	-	-	5	1	0	no emergence		
G.R.	3	-	5	8	1	6	0	0	reactive		
G.R.	7	1	5	8	1	5	0	0	reactive		

As shown in Table 2, successful emergence after -5/6°C requires at least several days pre-conditioning at 10°C and -2°C before-

hand. This is similar to the previous discovery that storage at -2°C a week or longer requires preconditioning at 10°C and is therefore equivalent to what botanists call "hardening". Whatever changes are occurring are necessary to withstand successive lower temperatures, which in Michigan may be well below -6°C when there is no snow cover.

After both -2°C and -5/6°C larvae require at least 5 days to reach the pupal stage again. Emergence data are comparable, 15-16 days, and compare favorably to emergence data for *C. amoena* from spring-collected apples kept in the laboratory at 22°C.

As a check that the 3rd or late instar is the overwintering stage for *C. amoena*, apples were collected from a nearby orchard in early March after a period of very cold weather in a winter of little snow cover. They were held at 10°C overnight, then inspected for *C. amoena* larvae. Five were found; one 2nd instar was dead, three of those actively mobile and feeding were late instars, and one was borderline late instar in size. The apples were quite soggy after defrosting, which suggests that *C. amoena* larvae may be freeze tolerant rather than freeze-susceptible with a very low supercooling point (Zachariassen and Hammel 1976a,b).

References: Zachariassen, K.E. and H.T. Hammel 1976a, *Norw. J. Zool.* 24:349-352; \_\_\_\_\_ and \_\_\_\_\_ 1976b, *Nature* 262:285-287.

Beck, A.K., R.R. Racine and F.E. Würgler.

Institute of Toxicology, Swiss Federal Institute of Technology, and University of Zürich, Switzerland. Primary nondisjunction frequencies in 7 chromosome substitution stocks of *D. melanogaster*.

In continuation of the work by Racine, Beck and Würgler (1979) a number of chromosome substitution stocks were studied for the frequency of primary nondisjunction in females. The balancer stock contained the following chromosomes: Cy = In(2LR)SM5, a1<sup>2</sup> Cy 1t<sup>v</sup> cn<sup>2</sup> sp<sup>2</sup>; Pm = In(2LR)bw<sup>V1</sup>;

Ubx = In(3LR)Ubx<sup>130</sup>; Sb = In(3R),Sb; pol = spa<sup>Pol</sup>. H indicates unmarked chromosomes from a Hikone-R stock, P unmarked autosomes from a stock containing the attached-XY chromosome Parker 110-8 and A the autosomes with inversions (balancer stock). Since all chromosome substitution stocks contain identical X-chromosomes (from the Hikone-R stock) and identical 4th chromosomes (pol from the A stock) the abbreviations used indicate only the stock constitution with respect to chromosomes 2 and 3 (see the table).

In the nondisjunction tests we studied the meiotic segregation of the sex-chromosomes in the females of the chromosome substitution stocks. We crossed 1-2 day old males of the

Female stock	Total progeny	Normal progeny		Nondisjunctional progeny		
		F	M	F	M	ND %
AA	48577	18994	29575	4	4	0.02
HA	20383	9645	10722	9	7	0.08
AH	22787	9591	13183	8	5	0.06
HH	24139	10007	14073	3	56	0.24
PA	24056	9573	14456	12	15	0.11
AP	25207	10339	14834	17	17	0.13
PP	22022	8434	13573	9	6	0.07

F = females, M = males, ND % = nondisjunctional progeny in percent of total progeny.

males of the genotype Y<sup>SX</sup>·YL, In(1)EN, y B to 1 day old females. Three pairs were used per vial. After 3 days the parents were discarded. The progeny were classified according to sex and phenotype. Two types of males could not be distinguished by phenotype: Y<sup>SX</sup>·YL, In(1)EN,y B/O (resulting from primary nondisjunction in XX females) and Y<sup>SX</sup>·YL, In(1)EN, y B/Y (resulting from secondary nondisjunction in XXY females). These males were crossed to C(1)DX, y

f / y<sup>+</sup> Y B<sup>S</sup>; bw; st pP females and surviving C(1)DX progeny indicated the presence of a free Y chromosome in the male tested, because C(1)DX, y f contains a Y-suppressed lethal.

The results with the numbers of progeny scored and the observed frequencies of primary nondisjunction are shown in the table. With all crosses more male than female progeny were obtained. The frequencies of primary nondisjunction show some variation. In particular the HH stock displayed an unexplained high number of exceptional males. But all the nondisjunction frequencies are within the range found with wild type stocks. This demonstrates that no meiotic mutants are present in the chromosome substitution stocks studied.

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Reference: Racine, Beck and Würgler 1979, Mutation Res. 63:87-100.

Batterham, P. and G.K. Chambers\*. Monash University, Clayton, Victoria, Australia; \*Australian National University, Canberra, A.C.T., Australia. The molecular weight of a novel phenol oxidase in *D. melanogaster*.

PHOX, a newly discovered form of phenol oxidase (O-diphenol: O<sub>2</sub> oxidoreductase E.C. 1.10.3.1.) encoded by the Phox locus (II 80.6) in *D. melanogaster* has been described by Batterham and McKechnie (1980). To firmly establish the novelty of this enzyme it was important to devise a test to distinguish it from A component phenol oxidases (see Seybold et al. 1974). We report here

determination of the molecular weight of this new enzyme by Sephadex G-150 gel filtration. *D. melanogaster* pupae (48 hours old) from the Silvan (Victoria) population were homogenized (6 g pupae/4 ml buffer) in ice cold 50mM Tris/HCl buffer pH 8.3 containing 10% (w/v) sucrose and 2M urea. The homogenate was centrifuged at 10,000g for 30 min at 4°C. The supernatant (6.0 ml)

was applied to a Sephadex G-150 column (5.0 x 75 cm) equilibrated with homogenization buffer lacking sucrose and urea. Fractions (15 ml) were collected at a flow rate of 40-45 ml/hr. Effluent was monitored for absorbance at 280nm, MDH activity (malate dehydrogenase: internal standard) after McReynolds and Kitto (1970) and polyacrylamide gel electrophoresis to detect phenol oxidase (after Batterham and McKechnie, 1980). The column was calibrated with chymotrypsinogen ( $\alpha$ -CT: 25,000), ovalbumin (OA:45,000) and bovine serum albumin (BSA monomer: 68,000; BSA dimer 136,000).

The molecular weight of MDH was taken as 71,500 (G.K. Chambers unpublished). The elution position of the PHOX enzyme was judged to be  $44.5 \pm 0.5$  fractions, from which we calculated a molecular weight of  $108,000 \pm 4,000$  for the PHOX oligomer---see Fig. 1. Electrophoretic evidence (Batterham 1980) suggests that the Phox gene product is a dimer and hence we deduce the subunit molecular weight to be 54,000. From such evidence we cannot discount the possibility of higher order aggregates (e.g., a tetramer that hybridizes as pairs of dimers in heterozygotes). However, it is certain that PHOX is non-identical to the A1 phenoloxidase components described by Seybold et al. (1974) as a monomer of subunit molecular weight 77,000.

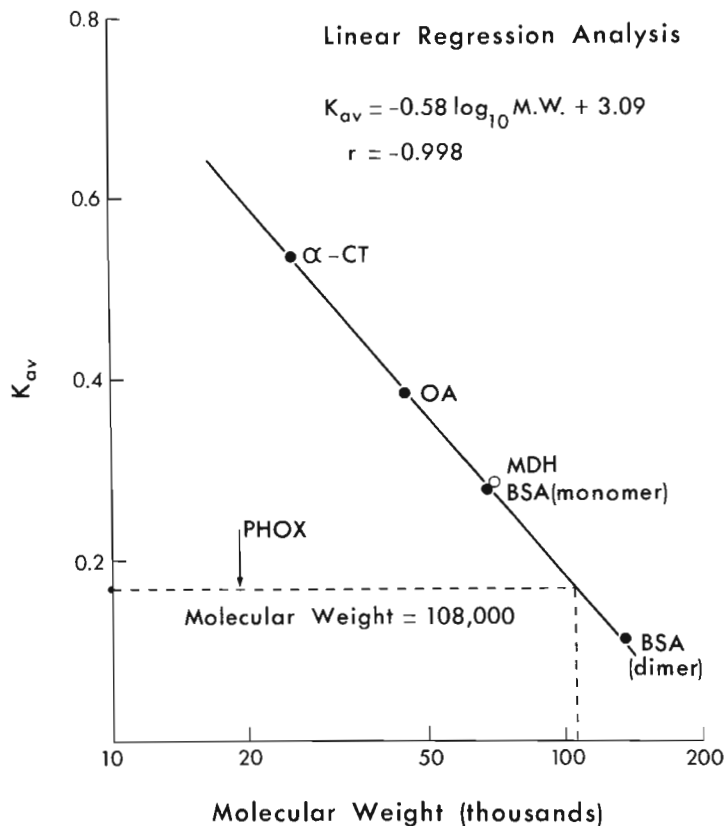


Fig. 1. Calibration of Sephadex G-150 column and calculation of the molecular weight of PHOX.

We would recommend this experimental approach to other workers involved in allozyme surveys of natural populations in view of recent suggestions that enzyme variability is correlated with subunit size (e.g., Nei et al. 1978).

We are indebted to Dr. J.B. Gibson in whose laboratory this work was carried out.

References: Batterham, P. and S.W. McKechnie 1980, submitted to *Genetica*; McReynolds, M.S. and G.B. Kitto 1970, *Biochim. Biophys. Acta.* 198:165-175; Seybold, W.D., D.S. Meltzer and H.K. Mitchell 1975, *Biochem. Genet.* 13:85-108; Nei, M., P.A. Fuerst and R. Chakraborty 1978, *Proc. Nat. Acad. Sci.* 75:3359-3362.

Bewley, G.C. and S. Lubinsky. North Carolina State University, Raleigh, North Carolina. Thermal stability of catalase during development in *Drosophila*.

An analysis of the thermal stability of the enzyme catalase ( $H_2O_2:H_2O_2$  oxidoreductase, E. C. 1.11.1.6) during *Drosophila* development was conducted on crude extracts of an Oregon-R-6 strain and the results are illustrated in Figs. 1 and 2.

The optimum temperature for this study was considered to be 56°C since about half the activity decayed in 5 min (Fig. 1). In extracts from each developmental stage, there is a break in the semilog plot at 5 min, with a half-life of 6.5 min in adult and pupal extracts and 14 min in larval extracts (Fig. 2). Similar results have been obtained in screening 20 different wild type laboratory stocks. Such a bimodal curve indicates the possibility that more than one molecular form of the enzyme exists, although isozymic patterns are not yet evident on electrophoretic gels. Multiple forms could arise by one or more of the following mechanisms, although none of these have been rigorously ruled out in our current studies: (1) isozymes coded for by different structural genes, although only a single enzyme dosage-sensitive region has been identified by segmental aneuploidy (Lubinsky and Bewley 1979); (2) post-translational modification of a primary gene product leading to conformational alterations; (3) the partitioning into compartmentalized and soluble fractions of the enzyme; and (4) dissociation of the enzyme into enzymatically active subunits.

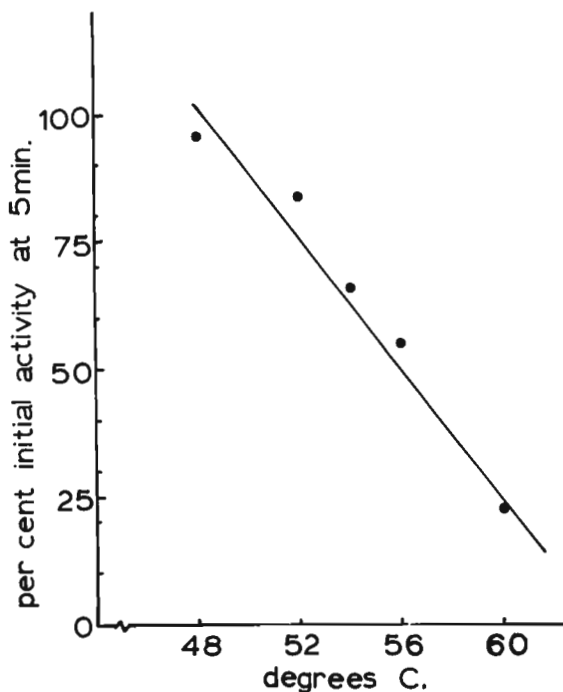


Fig. 1. The effect of increasing temperature on the thermal stability of catalase in adult crude extracts incubated for a period of 5 min.

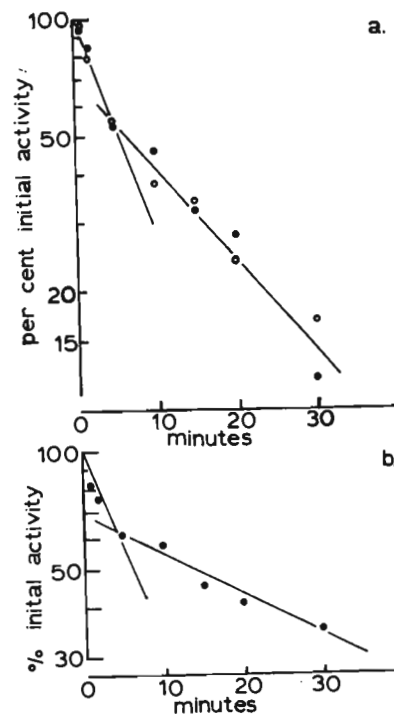


Fig. 2. Thermal denaturation at 56°C of catalase activity in crude extracts. a. Crude adult (○) and crude pupal (●) extracts. b. Crude larval extracts.

It has previously been demonstrated that a fraction of catalase is compartmentalized in the glyoxosomes of maize (Scandalios 1974) and the liver peroxisomes of mammals (Holmes 1971). In our studies, the use of triton X-100 increased the amount of soluble extracted enzyme by 1/3 in adult extracts and by two-fold in larval extracts. These results may indicate that a fraction of the catalase activity is compartmentalized or membrane-bound to sub-cellular organelles in *Drosophila*.

Supported by NIH Grants GM-23617 and AG-01739.

References: Holmes, R.S. 1971, *Nature* N.B. 232:218-219; Lubinsky, S. and G.C. Bewley 1979, *Genetics* 91:723-742; Scandalios, J. 1974, *J. Heredity* 65:28-32.

Biémont, C. Université Lyon I, Villeurbanne, France. Parental effect and inbreeding depression in *D. melanogaster*.

Natural populations of *Drosophila* carry genetic loads consisting of deleterious variants which reduce the viability of their carriers when homozygous as a result of inbreeding (see Lewontin 1974). Dying of inbred offspring ranges from early embryogenesis to larval and pupal stages. Recently, in *D. melanogaster*, I interpreted such effects in terms of a single gene hypothesis (Biémont 1978, 1979). An *Is* (inbreeding sensitivity) gene, located on chromosome III, with alleles *Is*<sup>-</sup> and *Is*<sup>+</sup> is involved in morphogenetic events. Its expression in homozygous (*Is*<sup>-</sup>/*Is*<sup>-</sup>) embryos depends on the presence in one parent of an *Is*<sup>+</sup> allele which promotes embryogenesis. Crosses between *Is*<sup>-</sup>/*Is*<sup>-</sup> sibs produce embryonic deaths, of a level that varies according to the regulation of the expression of the *Is*<sup>-</sup> allele. We now report further evidence supporting the parental control of expressivity of the gene involved.

Brother-sister couples which laid eggs showing blocking in development were selected and the male and female separated. Once females from these couples of presumed *Is*<sup>-</sup>/*Is*<sup>-</sup> constitution were no longer producing fertilized eggs, they were crossed with *Cy*/*Pm* *H*/*Sb* males. *Is*<sup>-</sup>/*Is*<sup>+</sup> *Cy* *Sb* flies from different sibships were then intercrossed leading to four classes of offspring with phenotypes

+

Fig. 1. Egg-to-adult survival of wild type offspring from the + class, versus egg-to-adult survival of wild type offspring from the *Cy* class. For comparison between the two classes, values of the *Cy* class were multiplied by 4 since only 1/4 of the flies were theoretically expected to be wild type.

eggs laid by the sibs. Therefore, to each *Is*<sup>-</sup> *Is*<sup>+</sup> *Cy* *Sb* x *Is*<sup>-</sup> *Is*<sup>+</sup> *Cy* *Sb* parental couple, is associated the inbreeding response of the four classes of their offspring. Since our study is based on the egg-to-adult survival of wild type flies, I have eliminated the *Cy* *Sb* class in the progeny of which only 1/16 of wild type flies is expected; the number of such flies obtained was too small for valuable statistical analysis. The rank correlation coefficient of Spearman reveals a significant link between the values of the + and *Cy* classes (Fig. 1) ( $r = 0.57$ ;  $t = 2.5$ ;  $P < 0.05$ ). This correlation was not significant either between

$$+ : \left( \frac{++ \ +Is^-}{++ \ +Is^-} \right), \quad Cy : \left( \frac{Cy \ + \ +Is^-}{++ \ +Is^-} \right),$$

$$Sb : \left( \frac{++ \ +Is^-}{++ \ Sb \ +} \right) \quad \text{and} \quad Cy \ Sb : \left( \frac{Cy \ + \ +Is^-}{++ \ Sb \ +} \right).$$

In each class, brothers and sisters were mated and viability of their offspring was evaluated as the proportion of wild type individuals (all *Is*<sup>-</sup>/*Is*<sup>-</sup>) obtained from the

classes + and Sb ( $r = -0.019$ ;  $t = 0.63$ ;  $P > 0.05$ ) nor between classes Cy and Sb ( $r = 0.14$ ;  $t = 0.53$ ;  $P > 0.05$ ). Consequently, inbreeding depression is similar in the + and Cy classes but independent of that in the Sb class. As a result of our experimental scheme, all wild type individuals descending from the brother-sister matings were homozygous Is-/Is-. So, the difference between the +, Cy and Sb classes seems associated with the homozygous Is-/Is- constitution of the flies of the + and Cy class as compared with the Is-/Is<sup>+</sup> heterozygous state of the flies of the Sb class. This observation suggests that the proportion of wild type flies, therefore the mortality rate during development, depends on the genomic constitution of the parents. The extent of inbreeding depression appears to characterize the parental couple, thus suggesting regulation by cytoplasmic factors, as previously inferred (Biémont 1978).

Such a parental effect has to be taken into account when inbreeding effects with different mating systems, or various natural populations, are compared. Indeed, whatever the nature of the implied gene, variation of its frequency in populations may influence the extent of viability depression after inbreeding and thus estimate of genetic load.

I thank R. Grantham and C. Gautier for their help with the manuscript.

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Bishop, C.P. and A.F. Sherald\*. University of Virginia, Charlottesville, Virginia; \*George Mason University, Fairfax, Virginia. Isolation of two third chromosome mutants conferring resistance to  $\alpha$ -methyl dopa.

$\alpha$ -methyl dopa ( $\alpha$ -MD) is an in vitro inhibitor of dopa decarboxylase (DDC) and it was originally thought that  $\alpha$ -MD might be used to screen for mutants with altered levels of the DDC enzyme. Although the original screen for resistance to  $\alpha$ -MD produced two strains with elevated levels of DDC (Sherald and Wright 1974), screens for sensitivity to the inhibitor

produced mutants with no effect on the enzyme (Sparrow and Wright 1974). Furthermore, it has been subsequently shown that the greater the number of DDC gene copies, the greater the sensitivity to  $\alpha$ -MD (Wright, unpublished). Sensitivity to  $\alpha$ -MD, it was discovered, was due to a locus, 1(2)amd, other than the structural locus for DDC (Wright et al. 1976a, 1976b). Since the 1(2)amd locus maps very close to the structural gene for DDC, the mutants with both elevated resistance and enzyme activity may be control mutants (Marsh and Wright 1979).

The two  $\alpha$ -MD resistant mutants we report here were isolated from a total screen of 1,715 EMS mutagenized (Lewis and Bacher 1968) progeny from a lethal free third chromosome bw; st stock. They were isolated by survival on 0.8 mM DL  $\alpha$ -MD, well above the concentration that is lethal to wild type flies (less than 0.4 mM). A total of 80 putative resistant mutants were recovered, 18 of which showed resistance upon retesting and two (PR40 and PR45) of these were selected for further study.

Table 1 shows that the locus responsible for resistance clearly segregates with the mutagenized third chromosome. Preliminary mapping of one of the mutants, PR45, places the locus between hairy (3-26.5) and thread (3-43.2) (Lindsley and Grell 1968). Using the L form of  $\alpha$ -MD, which is roughly twice as lethal as the DL form, the LD<sub>50</sub> for the two mutants has been established at 0.325 mM L  $\alpha$ -MD for PR40 (bw; Tm3 Ser Sb/st\*40) and 0.35 mM L  $\alpha$ -MD for PR45 (bw; Tm3 Ser Sb/st\*45). The LD<sub>50</sub> for control stocks was below 0.1 mM L  $\alpha$ -MD.

In addition to showing dominant resistance to  $\alpha$ -MD, these mutagenized third chromosomes are recessive lethal. During preliminary mapping of PR45, replacement of large portions of the third chromosome did not permit construction of a homozygous resistant stock. Crosses between the two resistant mutants produced very few flies (roughly 5% of expected) carrying both resistant chromosomes, indicating that the two chromosomes fail to complement. The fact that the two independently isolated mutants are lethal in trans configuration and that a homozygous resistant stock could not be established even after replacement of significant portions of the third chromosome suggests that dominant resistance and recessive lethality may be due to hits in a single locus.

It is not surprising that more than one locus can affect resistance to a lethal substance. The function of the 1(2)amd locus and the locus reported here are unknown. The sites of possible action could include uptake or detoxification of the compound or alterations in the target protein. The genetic relationship between 1(2)amd locus and the third chromosome



locus is being explored as is the relationship of the other 16 putative resistant mutants.

Table 1. Segregation of resistance to  $\alpha$ -MD with the mutagenized third chromosome.<sup>1</sup>

PR45 (bw; Tm3 Ser Sb/st* <sup>45</sup> ) X Con B (bw; Tm3 Ser/st <sup>B</sup> ) <sup>2</sup>				
Conc. L $\alpha$ -MD	#eggs hatched	bw; Tm3 Ser/st* <sup>45</sup>	bw; st* <sup>45</sup> /st <sup>B</sup>	bw; Tm3 Ser Sb/st <sup>B</sup>
0 mM	271	50	63	63
.1mM	257	71	58	26
.2mM	241	60	61	7
.3mM	265	50	43	0
.4mM	178	11	12	0

PR40 (bw; Tm3 Ser/st* <sup>40</sup> ) X Con #1 (bw; Tm3 Ser Sb/st* <sup>#1</sup> ) <sup>3</sup>				
Conc. L $\alpha$ -MD	#eggs hatched	bw; Tm3 Ser/st* <sup>#1</sup>	bw; st* <sup>40</sup> /st* <sup>#1</sup>	bw; Tm3 Ser Sb/st* <sup>40</sup>
0 mM	249	62	53	63
.1mM	276	2	61	78
.2mM	286	0	37	56
.3mM	287	0	12	41
.4mM	121	0	0	8

- 1) Data from reciprocal crosses were pooled since no maternal effect was found.
- 2) Con B was a control stock which had been through the same crosses as PR40, except that it was not mutagenized.
- 3) Con #1 was a mutagenized control stock isolated from the screen and carried through the same crosses as PR45.

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Beckenbach, A.T. Simon Fraser University, Burnaby, B.C., Canada. Map position of the esterase-5 locus of *D. pseudoobscura*: a usable marker for "sex-ratio".

Recently, Anderson and Norman (1977) published a map of *D. pseudoobscura* mutants. The purpose of this note is to add the esterase-5 (*est-5*) locus to that map. The primary impetus for the work was to determine whether the *est-5* alleles would provide usable markers for the "sex-ratio" (SR) X-chromosome in laboratory population studies.

Efforts to obtain recombinants between *est-5* and SR have thus far failed (Beckenbach, unpubl.; Curtsinger and Feldman 1979). However, Sturtevant and Dobzhansky (1936) have provided a recombination map relating the SR and standard (ST) chromosomes for a number of visible markers. Thus by localizing *est-5* with respect to the visibles on the ST chromosome, it was hoped to obtain a better estimate of the linkage relationship between that locus and the SR inversions.

Stocks used: (1) A marker strain of *D. pseudoobscura* carrying the visible mutants yellow (*y*), singed (*sn*), vermillion (*v*), compressed (*co*) and short (*sh*) was obtained from Dr. W.W. Anderson. This stock was found to be homozygous for the 1.07 allele of *est-5*. (2) A strain of the species, homozygous for the 0.85 allele, was obtained from Dr. G.A. Cobbs. This strain was originally derived from an isofemale line from a citrus grove in Riverside, California, and was made homozygous by recurrent inbreeding. Both strains carried the ST arrangement of the X-chromosome. Virgin females of the marker stock were crossed to *est-5* males. A total of 887 F<sub>2</sub> progeny (431 females, 456 males) were examined for the presence of the visible markers and then tested for *est-5* genotype, using polyacrylamide vertical slab gel electrophoresis and the technique described by Cobbs (1976).

Region	Number Observed	Frequency
non-recombinants	297	0.335
<i>y</i> - <i>sn</i>	103	0.116
<i>sn</i> - <i>v</i>	18	0.020
<i>v</i> - <i>co</i>	194	0.219
<i>co</i> - <i>est-5</i>	54	0.061
<i>est-5</i> - <i>sh</i>	418	0.471

Results: The results are given in the table. Esterase-5 maps to the position 111.8, just distal to *co* on the right arm of the X-chromosome. Graphic representation of the map of part of the X-chromosome, with comparison to recombination values in SR/ST heterokaryotypes (from Sturtevant and Dobzhansky 1936) is given in Fig. 1.

Curtsinger and Feldman (1979) have placed the upper limit (95% confidence interval) of recombination between *est-5* alleles and the SR chromosome in SR/ST heterokaryotypes at 1.5%. That value is based on 0 recombinants in 240 males examined. The

results of this study suggest that their value is quite conservative. Comparison to Sturtevant and Dobzhansky's map suggests an upper limit of 0.5%. This value, too, may be excessive. SR differs from ST by three non-overlapping inversions and a considerable homosequential length of chromosome exists between the proximal pair of inversions and the distal one (Dob-

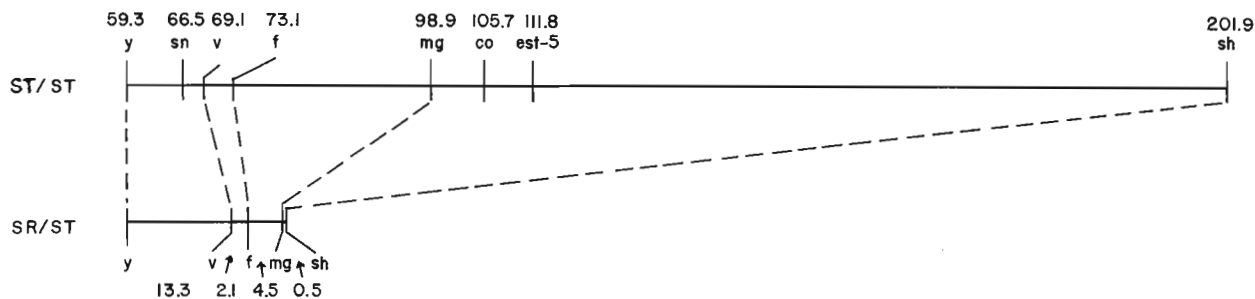


Fig. 1. Map positions for the visible markers and esterase-5 in the ST/ST homokaryotype and recombination frequency in the SR/ST heterokaryotype. Map positions (upper figure) are taken from Anderson and Norman (1977), Sturtevant and Tan (1937) and this study. The symbol *f* refers to "forked"; *mg* refers to "magenta"; other symbols are defined in the text. Recombination values (lower figure) are taken from Sturtevant and Dobzhansky (1936).

zhansky and Epling 1944). Recombinants between SR and ST are known from that region (Wallace 1948; Anderson, pers. comm.), isolating the small distal inversion. The "sex-ratio" phenotype is carried in the proximal pair of inversions (Wallace 1948). It is quite likely that the recombination in the homosequential region accounts for much of the recombination found by Sturtevant and Dobzhansky. Since over 90 map units separate est-5 from sh, it is likely that most recombinants occur distal to est-5, beyond the region conferring the "sex-ratio" phenotype.

References: Anderson and Norman 1977, DIS 52:11-12; Cobbs 1976, Genetics 82:53-62; Curtsinger and Feldman 1979, Genetics, in press; Dobzhansky and Epling 1944, Carnegie Inst. Wash. Publ. 554, Part II, Plate 4; Sturtevant and Dobzhansky 1936, Genetics 21:473-490; Sturtevant and Tan 1937, J. of Genetics 34:415-432; Wallace 1948, Evolution 2:189-217.

Carton, Y., J. Roualt and H. Kitano.  
 Lab. Gén. Evolutive C.N.R.S., Gif-sur-Yvette, France. Susceptibility of the seven sibling species of sub-group melanogaster infected with a Cynipide parasite.

Specific parasites are an important component of the niche and it has been assumed that development of genetic defense mechanisms could play a role during the speciation process. The seven sibling species of the melanogaster sub-group appear to originate from West Africa where speciation process occurs (Tsacas 1979). The existence in this area of parasitic Cyni-

pidae specific to Drosophila (Barbotin et al. 1979) might play a role in this process. *Cothonaspis boulardi* is a solitary, endophagous parasite (parasitoid) that oviposits into larvae of several species of Drosophila. We have tried to estimate the differential susceptibility of the seven sibling species of Drosophila towards this parasite. For this purpose we retained the following experimental procedure. Females of this solitary parasite lay their eggs (at 25°C) in the second instar larvae of the host; consequently, the exposure of host larvae to the parasite was limited to 24 hrs. Ten wasp females were introduced into a plexi-

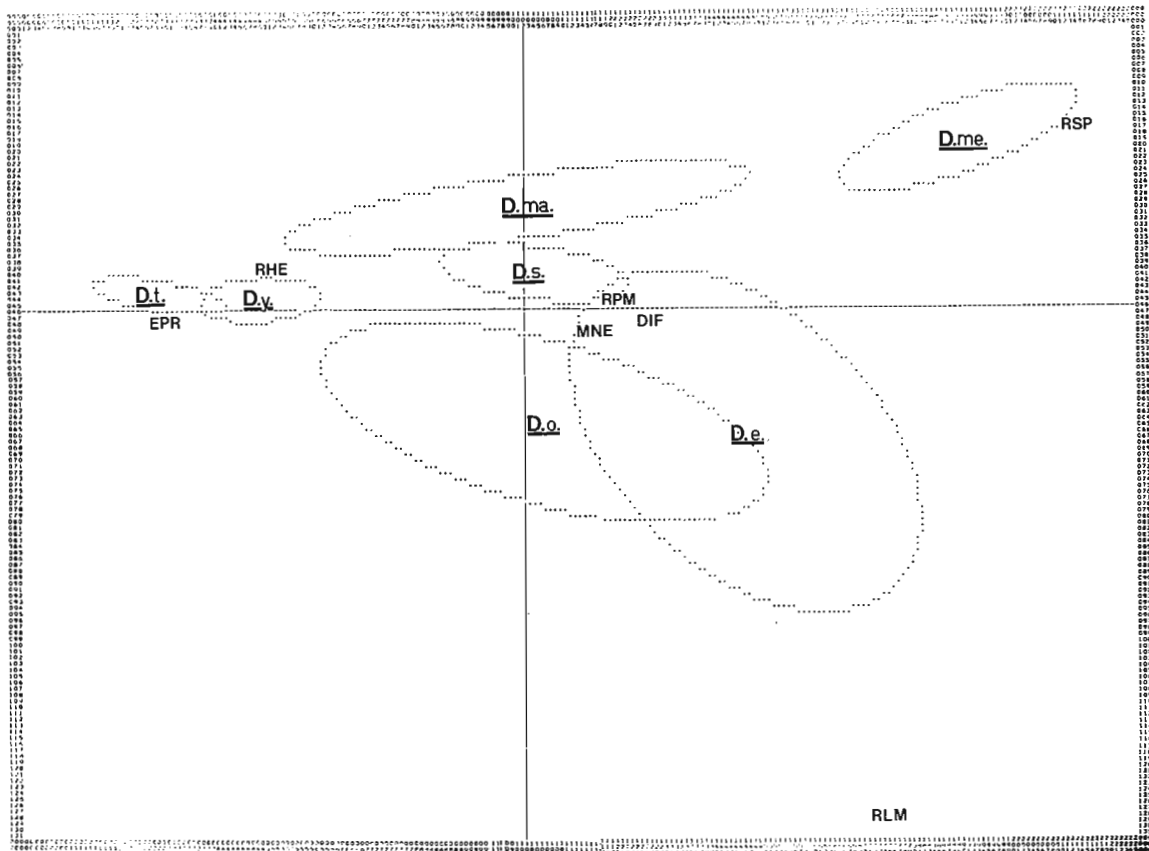


Fig. 1

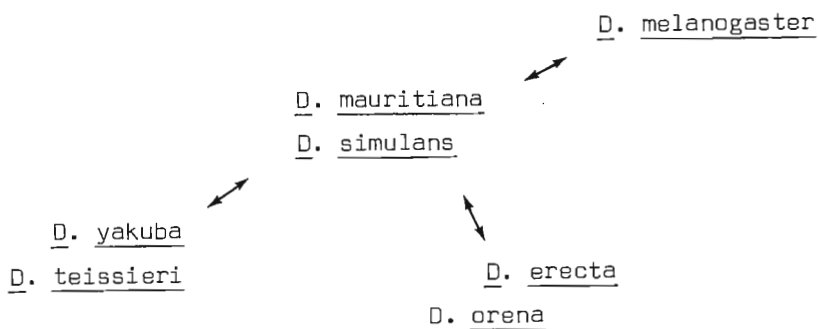
glas box containing 40 second instar larvae deposited on a thin disc of medium. 24 hrs. later, the larvae were collected and divided into two equal batches. The first replicate batch was dissected 48 hrs. after the beginning of infestation; we were able to estimate the experimental mortality (RLM), the degree of infestation (DIF), the average number of parasite eggs per parasitized larva (MNE) and the encapsulation rate (EPR), i.e., the intensity of cellular immunity of *Drosophila* species against the parasite (% of larvae which encapsulated all the parasite eggs).

For the second replicate batch, observed on the 21st day, information was obtained on the following: number of hosts surviving (RHE: rate of host emergence) comprising non-infested hosts plus infested hosts with successful immune reaction, experimental pupal mortality (RPM: rate of pupal mortality) including the hosts with remains of developing parasites, nonemerged fully developed parasites, and "mummified" pupae where no distinguishable parasite or fly remains were evident, and number of hosts producing parasite progeny (RSP: rate of successful parasitism). We must point out that the values for RLM and RPM were obtained from the experimental mortality subtracted from mortality obtained in controls. For each *Drosophila* species, the test was replicated eight times (i.e., 640 larvae).

The data were treated by a multivariate analysis. The analysis of correspondence has the advantage of allowing the simultaneous study and projection of the experimental results ( $n = 56$ , since eight experiments at least were performed for each *Drosophila* species) and of the seven variables (DIF, MNE, EPR, RHE, RSP, RLM and RHM). To each group of experimental results showing the same characteristics (i.e., the same species of *Drosophila*) it is possible to associate a gravity center and an equidensity ellipse (50%) (Fig. 1). In the same figure, we can observe the repartition of the different species, the localization of the different variables and the degree of association between the last two. It is therefore interesting to point out the main physiological features which characterize *Drosophila* species in response to *C. bouvardi*.

Concerning defense capacity, *D. yakuba* and *D. teissieri* are the most effective (association with EPR); consequently these two species have the highest rate of host emergence (association with RHE). On the contrary, *D. melanogaster* has no encapsulation reaction; this species is the best host for *C. bouvardi* (association with RSP on the graph). The other species present an intermediate position. *D. erecta* and *D. oreana* are more susceptible to infestation; there is a good association on the graph between the two species and RLM. On the contrary, *D. simulans* presents susceptibility only at the pupal stage.

In this representative graph (Fig. 1) we observe the following correlations:



This representation, in some way, parallels the phylogenetic relationships established by chromosomal analysis (Lemeunier et al. 1976). This parallelism strongly suggests that such specific host divergences played a role in the present situation. In other words, differences in susceptibility to the parasite would require long evolutionary periods and would be genetically stable.

References: Tsacas, L. 1979, C.R. Soc. Biogeogr. Paris 480:29-51; Barbotin, F., Y. Carton and S. Kelner-Pillault 1979, Bull. Soc. Ent. Fr. 84:20; Lemeunier, F. and M. Ashburner 1976, Proc. Roy. Soc. Lond. B 193:275.

Chadov, B.F. Institute of Cytology and Genetics, Siberian Branch of the USSR Academy of Sciences, Novosibirsk 630090, USSR. Effect of aberrant Y chromosomes on X chromosome nondisjunction.

It is known that structural mutations of X chromosomes and autosomes change considerably the frequency of secondary nondisjunction of X chromosomes. The latter changes with the age of the females, but to a lesser degree.

The effect of aberrant Y chromosomes on the secondary X chromosome nondisjunction was studied in order to obtain some lines contrasting for this character (Chadov 1971). The following Y chromosomes have been used: Y (structurally normal from Berlin wild stock), y<sup>+</sup>Y, BSy<sup>+</sup>Y, YL.sc<sup>V1</sup>, R(Y)L bb<sup>+</sup>, R(Y)L, YS.YS, YS, sc<sup>V1</sup>.YS. Every Y chromosome was introduced into the genome of y sc<sup>V1</sup>In 49 v sc<sup>8</sup>/y v (female I), In(1)d1-49+BM1, y<sup>2</sup> sc wa v BM1/y v f (female II), and In(1)d1-49+BM1, sc v BM1/sc v f (female III). The females were crossed to yellow males and the frequency of X chromosome nondisjunction in each of 27 stocks was determined (see table).

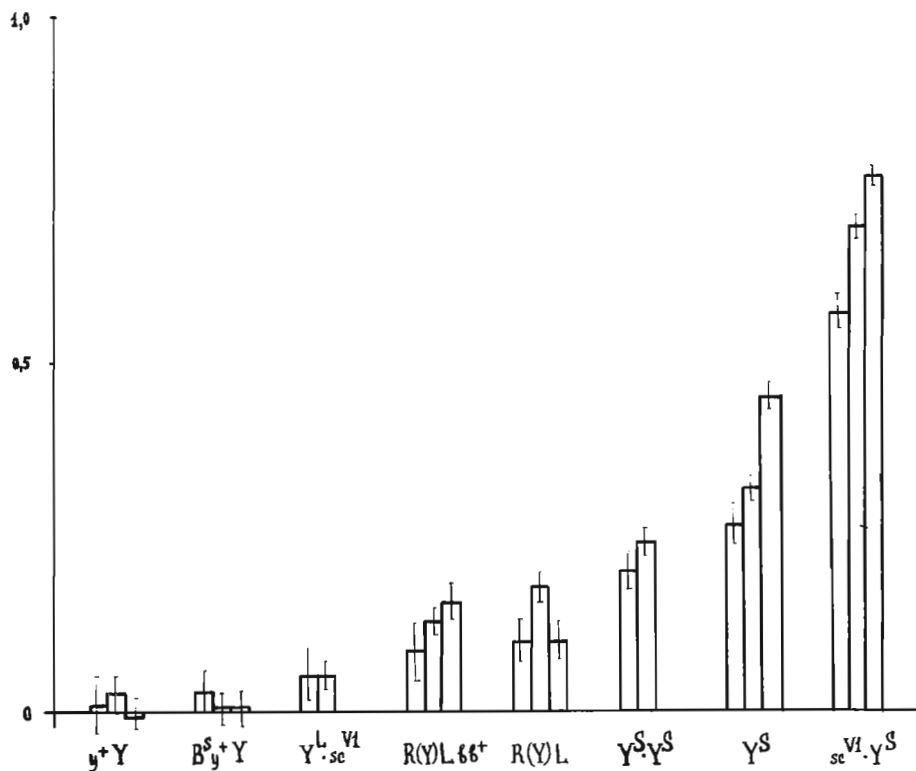
Frequency of secondary nondisjunction (%)

	Female I	Female II	Female III
Y (normal)	54.2 ± 2.2	70.9 ± 2.0	69.6 ± 2.3
y <sup>+</sup> Y	53.5 ± 2.2	68.5 ± 1.2	71.7 ± 0.5
BSy <sup>+</sup> Y	52.8 ± 1.5	70.7 ± 2.0	70.0 ± 2.4
YL.sc <sup>V1</sup>	51.3 ± 1.9	67.2 ± 1.7	---
R(Y)L bb <sup>+</sup>	49.9 ± 1.9	59.8 ± 2.0	60.6 ± 2.2
R(Y)L	48.6 ± 1.5	58.5 ± 1.8	62.6 ± 1.9
YS.YS	43.2 ± 1.5	---	52.7 ± 1.5
YS	39.6 ± 1.8	48.3 ± 1.6	37.7 ± 1.6
sc <sup>V1</sup> .YS	20.8 ± 1.4	21.8 ± 1.3	15.8 ± 1.3

This table shows that the stocks studied had different frequencies of X nondisjunction. To elucidate to what degree these differences depend on the Y chromosome structure or on the genetic background of the lines, the relative effect of each Y chromosome was determined by the formula

$$\frac{f_o - f_n}{f_n}$$

where f<sub>o</sub> stands for nondisjunction frequency in the line containing structurally normal Y chromosome (control) and f<sub>n</sub> represents the frequency in the line containing an aberrant Y chromosome. These values determined in each of the three lines for eight Y chromosomes are shown in the histogram. Each Y chromosome is presented as a triad of columns, YL.sc<sup>V1</sup> and YS.YS as diads. It is evident that the aberrant Y chromosome effect doesn't depend considerably on the background of the line in which it was determined. The main tendency is that the smaller the Y chromosome size, the smaller is the frequency of X nondisjunction. The Y chromosomes deleted for the long arm (sc<sup>V1</sup>.YS and YS) reduce a control frequency in the greatest degree, followed by YS.YS



chromosome; Y chromosomes deleted for the short arm (YL.sc<sup>V1</sup>, R(Y)L bb<sup>+</sup>, R(Y)L) have a lesser effect; and "whole" Y chromosomes (y<sup>+</sup>Y and BSy<sup>+</sup>Y) have the least effect.

Thus, the data obtained strongly suggest that the secondary X nondisjunction is a result of X-Y pairing and the frequency of this pairing depends on a correspondence of X and Y sizes, in agreement with Grell's rule for nonhomolog pairing (Grell 1964).

References: Chadov, B.F. 1971, *Genetica (Rus)* 7(2):117-127; Chadov, B.F. and S.N. Davidova 1971, *Genetica (Rus)* 7(5):87-94; Grell, R.F. 1964, *Proc. Nat. Acad. Sci. USA* 52:226-232.

Chadov, B.F. and E.V. Chadova. Institute of Cytology and Genetics, Siberian Branch of the USSR Academy of Sciences, Novosibirsk 630090, USSR. Nonhomologous pairing and spontaneous interchange in *D. melanogaster* males.

It may be concluded from Moore's cytological data that nonhomolog pairing takes place in mitosis of *D. melanogaster* males (Moore 1971). Inasmuch as nonhomolog pairing is usually accompanied by spontaneous interchanges in *D. females* (Chadov 1975, 1977), it was supposed that nonhomologous pairing and interchanges between C(2L) and C(2R), C(2L) and Y, C(2L) and

X chromosomes took place in mitotically divisioned spermatogonial cells of sc<sup>8</sup>.Y/y;C(2L)RM, b pr;C(2R)RM,cn males bearing autosomal compounds C(2L)RM, b pr and C(2R)RM,cn. The appearance of chromosomes 2L.2R,b pr cn with the standard order of genes was expected as a result of interchanges between the compounds in their centromeric regions, and the appearance of half-translocations Y.2L,b pr or X.2L,b pr, containing arm 2L with b and pr genes, as a result of interchanges C(2L)-Y and C(2L)-X.

In experiments the males mentioned above were mated to C(1)DX,y;b j pr cn/T(Y;2)C and C(1)DX,y;+T(Y;2)C females. These females produce several types of gametes: some of them are euploid and complementary to sperm cells with new arising chromosome 2L.2R,b pr cn; others are aneuploid and complementary to sperm cells with half-translocations Y.2L or X.2L. The progeny of females in three crosses constituted 225 individuals. Judging by phenotypes, 156 individuals contained chromosomes 2L.2R and 12 individuals, half-translocations bearing arm 2L. As the subsequent analysis showed, some of the 225 individuals were sterile, 123 individuals contained chromosome 2L.2R,b pr cn and 5 individuals, half-translocation Y<sup>S</sup>.2L,b pr. 35 individuals arose from sperm and egg cells with nondisjunctional autosomes 2. The progeny with interchanged chromosomes arose in clusters. The data obtained have shown that in spermatogonial cells of *Drosophila* males nonhomologous pairing and interchanges take place.

References: Chadov, B.F. 1975, *Genetica (Rus)* 11(1):80-100; \_\_\_\_\_ 1977, *DIS* 52:79; \_\_\_\_\_ and E.V. Chadova 1977, *Genetica (Rus)* 13:477-489; Moore, C.M. 1971, *Genetica (Ned)* 42:445-456.

Chadov, B.F. Institute of Cytology and Genetics, Siberian Branch of the USSR Academy of Sciences, Novosibirsk 630090, USSR. Nonhomologous X-2 pairing in females containing structurally normal X chromosomes.

Phenomena of nonhomolog pairing usually arise in genotypes in which a conjugation of no less than two chromosome pairs was purposely disturbed or some supernumerary chromosomes were introduced into the genome. One may suppose, however, that the nonhomolog pairing is not restricted to the above mentioned range of genotypes, but can take place in any genotype,

if two nonhomologs don't conjugate for some reason. I have observed two cases when chromosomes, whose conjugation was not purposely disturbed, participated in nonhomologous pairing.

(1) Females with structurally normal X chromosomes and heterozygous SMI, al<sup>2</sup> Cy cn<sup>2</sup> sp<sup>2</sup> inversion were tested for formation of oocytes aneuploid for autosomes 2 and X's (Chadov et al. 1970). In mating with C(2L)RM,b pr;C(2R)RM,cn males they produced progeny arising from the following oocytes:

Oocyte type	XX	XX22	2-2	0	X22	X
Number	20	-	41	-	39	63

Double aneuploid oocytes, i.e., oocytes aneuploid both for the X's and autosomes 2, constituted 55% of all oocytes. The double aneuploid oocytes were of two types only: XX and 2-2. Based on these data, it may be supposed that X-2 pairing takes place and X and 2 dis-

join after the nonhomologous pairing. If X-2 pairing did not take place and autosomes 2 and the X's were distributed independently, the double aneuploid oocytes would rarely arise and four types of such gametes instead of the two types observed would be formed.

(2) Females  $y/y;C(2L)RM4,dp;C(2R)RM4,px$  were crossed to  $C(2L)P4,+;C(2R)Pr,+$  males (Chadov and Podoplelova, in press). They produced, among others, 123 individuals resulting from the nondisjunction of matroclinal  $dp$  and  $px$  compounds. 49 of them arose from double aneuploid oocytes: 32 of XX type and 17 of  $C(2L);C(2R)$  type. Oocytes of  $XX;C(2L);C(2R)$  and 0 types were absent. One can suppose that the formation of double aneuploid oocytes is a result of pairing between the autosomal compounds and X's.

In both cases the conjugation of the X chromosomes was not purposely disturbed, but a part of them was involved in pairing with autosomes. The frequency of X-2 pairing is nearly 1% in the first genotype and 8% in the second. According to Weinstein's data nearly 5% of X's are non-crossovers even if they are structurally normal (Weinstein 1936). Probably, these X's have taken part in the nonhomologous pairing. However, in the second genotype the frequency of nonhomolog pairing is higher than the 5% level. It is not ruled out that some crossover X's could be involved in nonhomologous pairing with autosomal compounds. Recent data concerning spontaneous formation of half-translocations in  $y/\overline{XY};C(2L);C(2R)$  females showed that some of them arising as a result of  $\overline{XY}-C(2L)$  interchanges are X crossovers (Chadov and Podoplelova, in press).

The data obtained, from the methodical point of view, show that the registration of double aneuploid gametes is a simple and sufficiently sensitive test for the presence of non-homolog pairing. In principle, it makes possible the study of this process also in structurally normal genotypes.

References: Chadov, B.F., E.V. Chadova and A.K. Gaponenko 1970, *Genetica (Rus)* 6(10): 79-91; Chadov, B.F. and M.L. Podoplelova, *Genetica (Rus)* in press; Weinstein, A. 1936, *Genetics* 21:155-199.

Charton-Strunk, U. and W.-E. Kalisch.  
Ruhr-Universität Bochum, Germany.  
Intrachromosomal effect of a heterozygous tandem duplication.

The tandem repeat chromosome  $Dp(1;1)Gr, y^2 sc (w^- spl sn^3)(w^c sn^3)$ , which duplicates approximately one quarter of the euchromatic part of the X-chromosome (3A2-3;8B4-C1), was checked for an introchromosomal effect (reviewed by Lucchesi 1976) on the  $v - f$  and  $f - car$  region.

$Dp(1;1)Gr$  is homozygously and hemizygotously lethal (Kalisch 1973). Crossover values are decreased within and adjacent to the duplication (Kalisch 1975). Exceptions come from patroclicious males and intrachromosomal exchanges between the two parts of the tandem repeat after double loop pairing (Kalisch 1976).

Data of experiments no. 3 and 4 in Table 1 show that the crossover decrease in region 1 is accompanied by a significant crossover increase in regions 2 and 3. The long distance between vermilion (33.0) and forked (56.7) as well as the values of regions 1 and 3 suppose that the crossover value of region 2 could be composed of a decreased value near vermilion and an increased one in the rest of the region. Table 2 shows a comparison of the intrachromosomal effect in different X-chromosomal chromosome mutations on the  $f - car$  region. Surprisingly there is neither a correlation between the genetic length nor between the crossover reduction in the distal part ( $y-v$  region) and the strength of the intrachromosomal effect on the proximal part of the euchromatic chromosome region ( $f - car$  region). The simultaneous effects of the heterozygous  $Dp(1;1)Gr$  chromosome (intrachromosomal effect) and of two heterozygous inversions in the autosomes (interchromosomal effect) on the  $f - car$  region have also been tested. The data of the experiments no. 2, 4, 5 and 6 in Table 1 show that the simultaneous effects are in the range of the summation of the two separate effects ( $90.63 \pm 47.98 : 157.51$ ).

**Table 1.** Intrachromosomal effect of heterozygous Dp(1;1)Gr females. Exceptions among the F<sub>1</sub> males (patroclinous males and intrachromosomal exchanges; Kalisch 1976) are not listed, but included in the data. The numbers in parentheses are quotients obtained by dividing the finding for that region by the finding for that region in the control.

No.	Genotype of P-generation*	Number counted	Crossover units		
			Region 1 y - v	Region 2 v - f	Region 3 f - car
1	y v f/+ x y v f/Y	5,078	23.95 ± 0.59	22.65 ± 0.58	
2	f car/+ x f car/Y	9,290	---	---	6.19 ± 0.25
3	Dp(1;1)Gr, y <sup>2</sup> sc/v f car x y v f/Y	1,439**	9.68 ± 0.77 (40.41)	29.27 ± 1.19 (129.22)	11.19 ± 1.33*** (180.77)
4	Dp(1;1)Gr, y <sup>2</sup> sc/f car	4,803**	---	---	11.80 ± 0.46 (190.63)
5	f car/+;SM1/+;TM2/+	3,567**	---	---	9.16 ± 0.48 (147.98)
6	Dp(1;1)Gr, y <sup>2</sup> sc/f car;SM1/+;TM2/+	1,286**	---	---	15.94 ± 1.01 (257.51)

\* Dp(1;1)Gr chromosomes are additionally marked by (w<sup>-</sup> spl sn<sup>3</sup>)(w<sup>c</sup> sn<sup>3</sup>) within the duplication. Females of exp. no. 4-6 were crossed to v f<sup>36a</sup> car males.

\*\* Data collected from single and mass cultures.

\*\*\* From 554 F<sub>1</sub> males.

**Table 2.** Comparison of the intrachromosomal effect by two heterozygous X-chromosomal inversions (data from Grell 1962) and by heterozygous Dp(1;1)Gr females (Table 1, exp. no. 4) in the f - car region.

	Cytological position and length	Map length*	Region**	
			y - v	f - car
In(1)sc <sup>7</sup> /+	1B4-6;5D3-6	~ 13.7 %	23.2 %	144.0 %
In(1)65/+	1C;10B	~ 34.0 %	0 %	140.5 %
Dp(1;1)Gr/+	3A2-3;8B4-C1	~ 26.0 %	40.4 %	190.6 %

\* Within the limits of the chromosome mutation in normal sequence X-chromosomes.

\*\* Percent value for each region is the quotient obtained by dividing map length for that region in heterozygous females by map length for that region in the control with normal X-chromosomes.

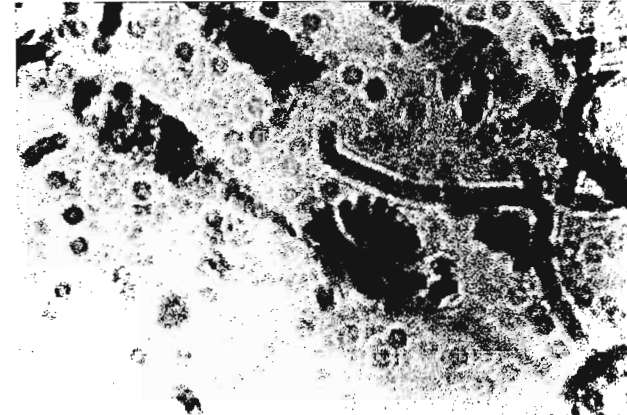
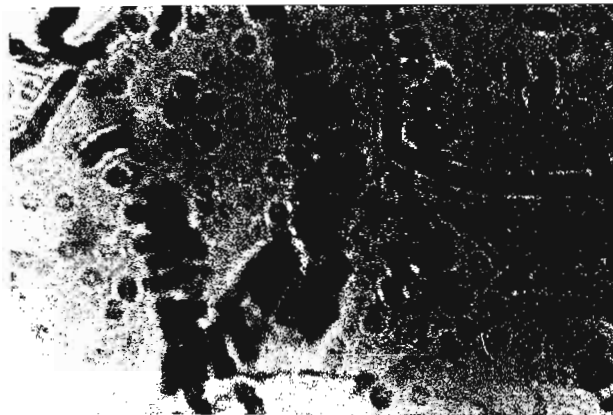
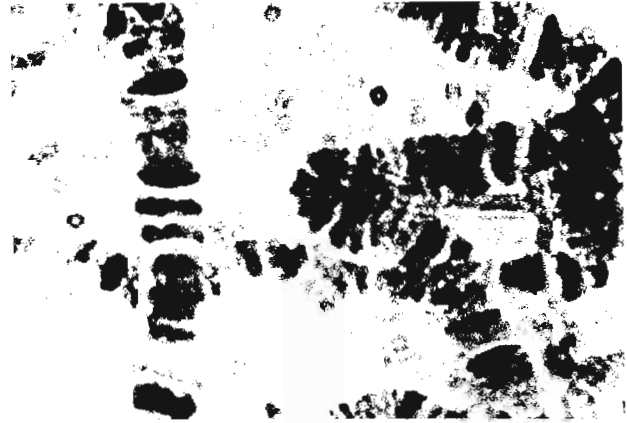
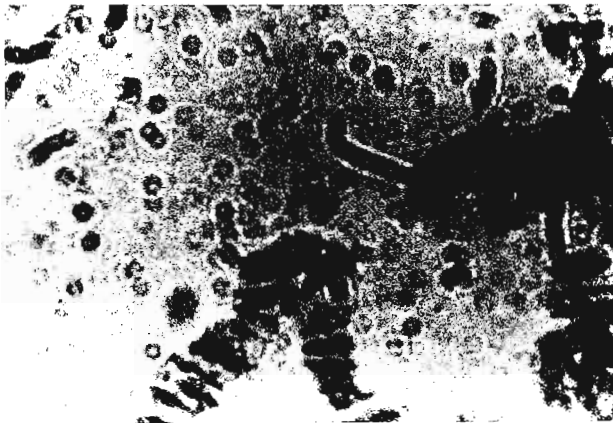
References: Grell, R.F. 1962, *Genetics* 47:1737; Kalisch, W.-E. 1973, *Chromosoma* 41:237; \_\_\_\_\_ 1975, *Theoretical & Applied Genetics* 46:169; \_\_\_\_\_ 1976, *Genet. Res., Camb.* 26:275; Lucchesi, J.C. 1976, In: *The Genetics & Biology of Drosophila*, Vol. 1a:315 (Academic Press, New York).



Chenevix Trench, G. Trinity College, Dublin, Ireland. An endemic inversion in the X-chromosome of *D. melanogaster*.

An endemic paracentric inversion has been found in the X-chromosome of *D. melanogaster*. 35 progeny from a multiple mating (12 virgin females from a wild population, Dahomey, mated with 5 males of the Oregon-K inbred strain) were examined cytologically by salivary gland preparation. In addition, 2 or 3 larvae from each of 5 single crosses were examined. This new inversion, which has been named In(1)A, was found in 20 of the 47 individuals examined. It is a small paracentric inversion with break-points at 16D and 18D, and was always observed to form an inversion loop in salivary gland cells of female larvae.

This discovery is particularly interesting in view of the rarity of X-chromosome inversions. Dahomey is a wild type stock, collected in West Africa in 1969 and maintained in large cage populations in Edinburgh, whence this population came. It is noted for the high level of genetic variation which it has retained in the laboratory.



Chernyshev, A.I. and B.A. Leibovitch. Institute of Molecular Genetics, USSR Academy of Sciences, Moscow, USSR. The effect of temperature during development on the amount of heterochromatin DNA fractions in *D. melanogaster*.

It has been shown earlier by cytophotometry that low temperature may cause underreplication of heterochromatin in a number of different organisms (Evans 1956). Heterochromatin DNA in *Drosophila* basically consists of ribosomal DNA and highly reiterative DNA. The latter contains two fractions: satellite and rapidly renaturing DNA. Satellite DNA consists of long blocks of simple repeats which differ from the main DNA fraction in buoyant density and are localized, with a few exceptions, in centromeric heterochromatin (Peacock et al. 1974). The rapidly renaturing DNA fraction consists of short blocks of simple repeats which do not differ from the main fraction in buoyant density (Hearst et al. 1974) and are localized in centromeric heterochromatin and some other loci, as follows from in situ hybridization (Fig. 1).



Fig. 1. Hybridization of  $^3\text{H}$  RNA synthesized on rapidly renaturing DNA with *D. melanogaster* polytene chromosome. The intensive labeling of centromeric heterochromatin and some other loci is clearly visible. Note regions 39D-E where histone genes are localized.

To find out whether the amount of heterochromatin DNA depends on the conditions of the flies' growth, we determined the amount of ribosomal, rapidly renaturing and satellite DNA in larvae and flies of the wild Oregon-RC stock which had been kept at  $16^\circ\text{C}$  for two generations and in control flies permanently kept at  $25^\circ\text{C}$ . For this purpose RNA was hybridized, in the presence of excess RNA, with  $^3\text{H}$  ribosomal RNA and with  $^3\text{H}$  complementary RNA synthesized by *E. coli* RNA polymerase on the total satellite DNA (a mixture of satellites I, II and IV) and on the rapidly renaturing DNA. The satellite DNA was isolated in a CsCl gradient with actinomycin D (Peacock et al. 1974) and the rapidly renaturing DNA with Cot 10-1 was obtained from the main band DNA fraction by fractionating on hydroxyapatite (Hearst et al. 1974).

The low temperature during development was found not to cause any decrease in the amount of the above heterochromatin DNA fractions either in larvae or in adult males (Table 1). Moreover, the amount of rDNA and rapidly renaturing DNA was the same in adult females reared at  $16^\circ\text{C}$  and  $25^\circ\text{C}$ . A significant difference was observed only with respect to satellite DNA in adult females reared at  $16^\circ\text{C}$  as compared with the control females ( $25^\circ\text{C}$ ). If the amount of ribosomal DNA and rapidly renaturing DNA is invariable, it is unlikely that the increase in satellite DNA content should be due to a relative decrease of the main DNA fraction. Since a large part of female DNA is constituted by oocyte DNA and that of the polytene nurse cells, the underreplication of satellite DNA at  $25^\circ\text{C}$  may be due to a greater polyploidy of the nurse cells at normal temperature. But there is a reverse situation in the case of *Drosophila* salivary glands (Hartmann-Goldstein and Goldstein 1979). Another possible explanation of the cold-induced increase in the proportion of satellite RNA may be an increase in the amount of unfertilized eggs at  $16^\circ\text{C}$ , the proportion of satellite DNA in them being as high as 80% of total DNA (Travaglini et al. 1972).

The above suppositions may explain the lack of excess satellite DNA in males unlike females. At the same time we cannot exclude the possibility that the highly heterochromatinized Y chromosome in males affects the heterochromatin of the autosomes. This seems to be suggested by the fact that the introduction of an additional Y chromosome into the *Drosophila* genome causes a smaller increase of satellite DNA than could be expected from the satellite DNA content in the Y chromosome (Wollenzien et al. 1977). However, all these are suppositions that must be tested.

It is remarkable that adult females have twice as much satellite DNA as larvae, whereas the amount of ribosomal and rapidly renaturing DNA differs only slightly (Table 1). The excess of satellite DNA in flies corresponds to a smaller proportion of polytene tissues as compared with larvae. Meanwhile satellite DNA is more underreplicated than ribosomal DNA in larval salivary glands. The salivary glands of *D. melanogaster* contain 100 to 200 times less satellite DNA than the diploid tissues (Gall et al. 1971) but only 4 to 6 times less genes for rRNA than the diploid tissues (Spear and Gall 1973). The differences observed are probably due to this selective underreplication.

Lately it has been hypothesized that the amount of satellite DNA is unstable, for it may vary in closely related species (Gall et al. 1974) and in different tissues within one organism in the course of aging (Prashad and Culter 1976). Our data on the effect of temperature during development upon the satellite DNA content in *Drosophila* possibly support this hypothesis.

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Biophys. Acta 418:1-23; Spear, B.B. and J.G. Gall 1973, Proc. Natl. Acad. Sci. USA 70:1359-1363; Travaglini, E.C., J. Petrovic and J. Schultz 1972, Genetics 72:431-445; Wollenzien, P., P. Barsanti and J.E. Hearst 1977, Genetics 87:51-65.

Table 1. The amount of different fractions of heterochromatin DNA in larvae and flies reared at 25°C and 16°C.

DNA source	t°C during development	Ribosomal DNA				Rapidly renaturing DNA				Total satellite DNA			
		% of total DNA	16°C in % of 25°C*	♀ larvae & ♂ imago		% of total DNA	16°C in % of 25°C*	♀ larvae & ♂ imago		% of total DNA	16°C in % of 25°C*	♀ larvae & ♂ imago	
				in % of ♀ imago	N			in % of ♀ imago	N			in % of ♀ imago	N
♀ larvae	25	0.254	(100)	82	2	5.87	(100)	95	2	3.6	(100)	62	2
	16	0.262	103±2	84	2	5.93	101±1.6	94	2	3.67	102±1.3	54	2
♀ imago	25	0.310	(100)	(100)	14	6.2	(100)	(100)	6	5.8	(100)	(100)	17
	16	0.313	101±1	(100)	14	6.32	102±3	(100)	6	6.84	118±1	(100)	17
♂ imago	25	0.350	(100)	113	3	6.95	(100)	112	5	7.43	(100)	128	6
	16	0.364	104±2.2	116	3	7.29	105±1.9	115	5	7.01	95±4	102	6

The hybridization of DNA immobilized on nitrocellulose filters was carried out with an excess of labeled RNA. 1 to 2 µg of DNA deposited on a 5mm HAWP filters was annealed in 25 µl of 4 SSC for 18 hours at 66°C in the presence of 0.1 µg of <sup>3</sup>H rRNA or 1-2 µg of <sup>3</sup>H RNA complementary to the satellite or rapidly renaturing RNA. After annealing the filters were treated with RNAase and counted by a scintillation counter.

N = the number of experiments.

\* Results expressed as mean ± standard deviation.

Curtsinger, J.W. Stanford University, Stanford, California. [Present address: North Carolina State University, Raleigh, North Carolina] Embryonic lethality associated with multiple inversion heterozygosity in *D. pseudoobscura*.

In several species of *Drosophila* females heterozygous for two or more unlinked inversions produce high frequencies of inviable embryos (Riles 1965 and references therein). Intense selection against multiply heterozygous females can result: Terzaghi and Knapp (1960) reported 95%, 93%, 79% and 59% egg hatchability among progeny of *D. pseudoobscura* females heterozygous for zero, one,

two, and three unlinked inversions respectively. The resulting selection might account for the restriction of inversion polymorphism mostly to one chromosome: once an inversion system is established, the increase of new inversions (initially present only in heterozygous condition) on nonhomologous chromosomes would be inhibited by reduced fitness of some carriers.

In *D. pseudoobscura* the X-linked "Sex-Ratio" inversions are the only widespread structural polymorphisms other than the extensive system of inversions on III. Anderson et al. have investigated possible selective interactions between the X chromosome and third chromosome inversions by measuring egg-to-adult viability among progeny of females jointly heterozygous for "Sex-Ratio" and third chromosome inversions. They found no reduced fitness compared to progeny of singly heterozygous or doubly homozygous females. However, the method of fitness estimation employed confounds embryonic mortality with larval and pupal viability. Direct measures of embryonic mortality among progeny of females heterozygous for inversions on III and either homozygous on the X chromosome are presented here.

Maternal genotype <sup>1</sup>	Total eggs	Percent hatch	t-test	Probability <sup>2</sup>
X/X ST/ST	225	.964	t=0.11	p=0.912
X/SR ST/ST	186	.962		
X/X AR/ST	231	.978	t=2.99	p=0.003
X/SR AR/ST	206	.917		
X/X TL/ST	196	.990	t=3.10	p=0.002
X/SR TL/ST	202	.936		
X/X PP/ST	186	.946	t=2.17	p=0.030
X/SR PP/ST	150	.880		
X/X CH/ST	227	.991	t=4.52	p<0.001
X/SR CH/ST	215	.907		
All single hets.	1026	.974	t=5.85	p<0.001
All double hets.	773	.912		

<sup>1</sup> X = Standard (X) TL = Tree Line (III)  
 SR = "Sex-Ratio" (X) PP = Pikes Peak (III)  
 ST = Standard (III) CH = Chiricahua (III)  
 AR = Arrowhead (III)

<sup>2</sup> Two-tailed test.

"Sex-Ratio" stocks were collected at Jasper Ridge Biological Preserve in San Mateo County, California. Third chromosome stocks were obtained from Dr. W. Anderson. Stocks were maintained on Carolina Instant Medium at approximately 21°C. Groups of ten 3-day-old females of each of the 10 genotypes shown in the table were mated with X/Y ST/ST males. Eggs were collected for 24 hours on day 5 and scored for hatching for 3 days. Dead embryos turn brown, while unfertilized eggs (two observed) remain white.

Results of the zygotic mortality observations are shown in the table. Standard X homozygotes and Sex-Ratio heterozygotes produce indistinguishable proportions of inviable embryos, provided individuals are also homozygous for inversions on III. However, among third chromosome heterozygotes, X chromosome heterozygotes consistently produce more inviable embryos than X chromosome homozygotes. Thus the deleterious effect of multiple inversion heterozygosity in *D. pseudoobscura* is confirmed for the two sets of inversions which are widespread in natural populations.

While the pertinent pair-wise comparisons of embryonic mortality shown in the table are statistically significant, the resulting selection differentials are small compared to those reported by Terzaghi and Knapp (1960) for other inversions. Excessive embryonic mortality among progeny of multiply heterozygous females might result from meiotic mis-pairing and subsequent production of aneuploid gametes. Sex-Ratio heterozygotes could be less sensitive to mis-pairing as a result of the unique inversion arrangement, consisting of three non-overlapping inversions which preserves chromosome "flexibility". On the other hand, the proportions of inviable embryos observed in this study show no obvious relation to the length of third chromosome inversions carried by double heterozygotes.

The selection differentials reported here are small compared with other modes of selection associated with Sex-Ratio, which can include strong viability, fertility, and sexual selection (Wallace 1948, Policansky 1979, Curtsinger and Feldman 1979). Thus these data confirm the assertion of Anderson et al. that third chromosome heterozygosity is unlikely to significantly influence the geographical distribution of Sex-Ratio inversions through increased embryonic mortality among progeny of multiple inversion heterozygotes.

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Eckstrand, I.A. and R.H. Richardson.  
University of Texas at Austin, Austin,  
Texas. Comparison of water balance  
kinetics between laboratory-reared and  
field-caught *D. mimica*.

*Drosophila mimica* are found on the island of Hawaii in a variety of habitats, ranging from rain forests to arid regions. The species is usually associated with the soapberry tree, *Sapindus saponaria*, and the flies are usually found courting, feeding, or fighting on the leaf litter. Although *D. mimica* are easily

captured, they require special conditions to rear in the laboratory. However, the *Drosophila* Species Resource Center at the University of Texas maintains several stocks, including K85P1, which is the "standard" line.

The ability to remain in water balance is probably a highly selected character (Eckstrand 1979), and physiological, morphological, and behavioral adaptations are all important to survival in field animals. It is likely, however, that the fitness components of water balance control differ between field and laboratory flies. To test differences between field and laboratory flies, transpiration and sorption rates for each group were determined by using tritiated water to measure net water uptake and loss. The techniques for this procedure are found in Eckstrand (1979).

Table 1. Comparison of transpiration rate constants and sorption rates in laboratory and field-caught *D. mimica*.

$a_v$	Sex	K85P1		Field	
		$k_T$ (%/hr)	$m_S$ (mg/hr)	$k_T$ (%/hr)	$m_S$ (mg/hr)
0.99	F	-0.068	0.179	-0.328	0.838
	M	-0.094	0.168	-0.249	0.419
0.70	F	-0.165	0.273	-0.177	0.301
	M	-0.150	0.201	-0.229	0.279

Table 1 gives the net transpiration rates  $k_T$  or % body water lost each hour) and the net sorption rates ( $m_S$  or the mg of water taken up each hour) for laboratory-reared and field-caught flies tested at either 0.99  $a_v$  or at 0.70  $a_v$  ( $a_v$  = relative humidity/100). Laboratory animals have lower transpiration and sorption rates than do field-caught flies, especially at the high  $a_v$ . Culture conditions select for inactivity, and because laboratory flies expend little energy searching for food and mates, they probably have lower metabolic rates than do their wild counterparts. Field flies are noticeably more active than

those reared in the laboratory. Their high activity level is probably supported by high metabolic rate which requires that the flies open their spiracles to obtain oxygen. This would result in increased transpiration. Sorption across the tracheal surfaces or the rectal pads might be enhanced to compensate for the increased water loss. At the low humidity, both field and laboratory *D. mimica* are less active, and their transpiration and sorption rates are similar. Field flies may additionally rely on behavioral adaptations and habitat selection to reduce water loss. Therefore, they may not require strict physiological regulation of water loss at low  $a_v$ 's. However, laboratory animals, which cannot reduce water loss by habitat selection, may depend relatively more on physiological control of water balance.

References: Eckstrand, I.A. 1979, Ph.D. dissertation, The University of Texas at Austin, 190 pp.

Engels, W.R. and C.R. Preston. University of Wisconsin, Madison, Wisconsin: Characteristics of a "neutral" strain in the PM System of hybrid dysgenesis.

The great majority of *D. melanogaster* strains can be classified by sterility tests as either paternally-contributing (P) or maternally-contributing (M) in the PM system of hybrid dysgenesis (Kidwell et al. 1977). A few strains, however, appear to be neutral ("Q strains") by

their lack of sterile offspring when crossed to either P males or M females (Kidwell 1979). One such strain, designated  $v_6$ , is an inbred line derived from a Madison wild population in 1975. The neutrality of  $v_6$  was demonstrated as follows: Under conditions restrictive for sterility (Engels and Preston 1979) a large number of crosses between single  $v_6$  males and females from the M strain, *bw;st*, were performed. Sterility tests of the daughters by the tissue culture plate method of Engels and Preston (1979) yielded less than 1% sterility (4/427), which is indistinguishable from background effects. This lack of sterility cannot be attributed to a suppressor of sterility in the  $v_6$  genome, as shown by tests of each of the  $v_6$  major chromosomes in the absence of the others. The procedure was similar to that reported previously (Engels 1979a) for  $\pi_2$ , a typical P strain. Sterility frequencies from the lone action of the X, second, and third chromosomes of  $v_6$  were respectively 1/103, 1/91, and 0/93. Therefore,  $v_6$  lacks the potential for sterility when crossed to M females. To determine the cytotype of  $v_6$  (see Engels 1979a), 133  $v_6$  females were crossed individually to  $\pi_2$  males under restrictive conditions. None of these crosses produced an appreciable proportion of sterile daughters, with the overall sterility frequency being less than 1% (14/2071). We may therefore say that  $v_6$  has the P cytotype, which confers immunity to the sterilizing action of the  $\pi_2$  chromosomes (Engels 1979a).

There is a strong correlation among wild genomes between their ability to cause sterility and their ability to bring about male recombination when in the M cytotype (Engels and Preston 1980). One might therefore expect  $v_6$  to produce little or no male recombination in its dysgenic hybrids. This was not the case, however, as shown by experiments measuring male

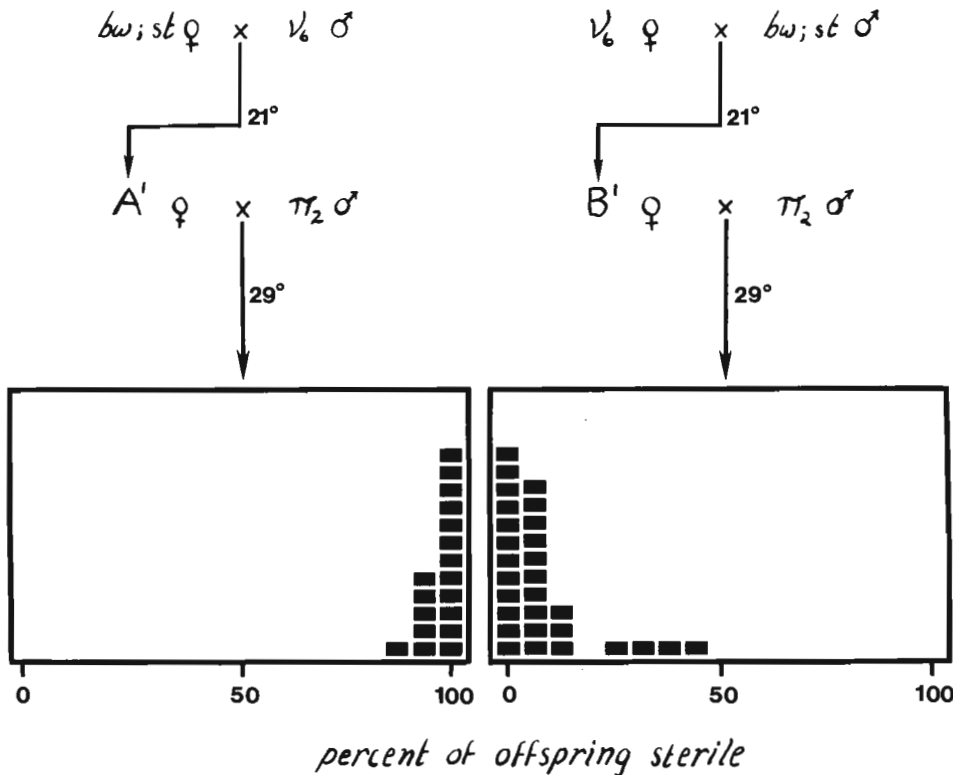


Fig. 1. Determination of cytotype for two reciprocal types of hybrids between  $v_6$  and *bw;st*. Each block represents sterility tests of 16 daughters of a single  $A^1$  or  $B^1$  female.

recombination between *cn* and *bw*, and also segregation distortion at chromosome 2 in the two reciprocal kinds of hybrids involving  $v_6$  and M strain (see Engels 1979b for stocks and procedures). Among approximately 200 progeny from each of 40 males (20 of each reciprocal type) the recombination frequency was  $0.3\% \pm 0.1$  for the dysgenic class, and 0 for the reciprocal class. The transmission frequencies of the  $v_6$  second chromosome were 50% and 54% (both  $\pm 1\%$ ) respectively. (See Engels 1979c for the method of calculating standard deviations when clustering is present.) Treating the progeny of each male as an independent observation, the difference between the two reciprocal crosses was significant at  $p < 0.01$  by the Rank Sum test for both comparisons. Thus  $v_6$  behaves like a typical P strain regarding male recombination and segregation distortion.

Finally, the following set of experiments shows that the cytotype of  $v_6$  as well as its chromosomal determinants are essentially identical to those of  $\pi_2$ . Genetically-identical females from the two reciprocal crosses between  $v_6$  and *bw/st* were grown in permissive conditions, then mated to  $\pi_2$  males under restrictive conditions to determine their cytotype. The results are in Fig. 1. It is clear that the cytotype of  $v_6$  is transmitted matroclinously through two generations, and is therefore not determined by strictly Mendelian factors or simple maternal effects. A self-replicating property of the cytoplasm (or nucleoplasm) which was previously demonstrated (Engels 1979a) is again indicated. To continue substituting the  $v_6$  genome into *bw;st* cytoplasm, the  $A^1$  females were backcrossed to  $v_6$  males for several generations to produce  $A^2$ ,  $A^3$ , etc., females. Each generation about 100 of these females were crossed to  $\pi_2$  to determine their cytotype as above. We see (Fig. 2) that with each successive generation, more of the females have switched their cytotype from M to P. By comparing these results to Fig. 2 in Engels (1979a) it is clear that the ability of the  $v_6$  genome to switch the cytotype is at least equal to that of  $\pi_2$ .

We may conclude that  $v_6$  is neutral for gonadal dysgenic sterility, but it behaves like a typical P strain regarding its influence on cytotype and on the production of some other dysgenic traits. These observations imply that the determinants of cytotype and other traits,

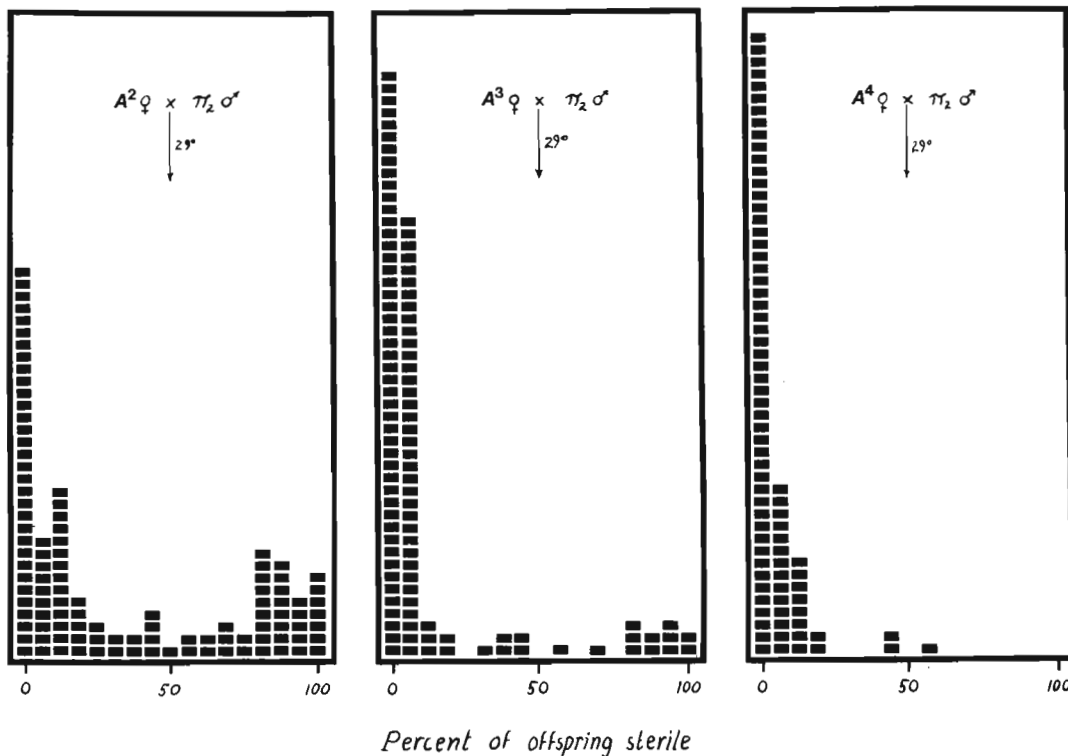


Fig. 2. Determination of cytotype after each successive backcross generation of genomic substitution. Each block represents sterility tests of 16 daughters of a single  $A^1$  female.



are separable from those of sterility. One possibility is that  $v_6$  carries a P factor (presumed to be a movable, multicopy genetic element [Engels 1980]) which lacks its usual sterility function but retains its other capabilities.

This work was done in the laboratory of J. F. Crow, University of Wisconsin, supported by grants 5T32 GM 07133-03, 22038, and 07131 from the National Institutes of Health.

References: Engels, W.R. 1979a, *Genetical Research* 33:219-236; \_\_\_\_\_ 1979b, *Genetical Research* 33:137-146; \_\_\_\_\_ 1979c, *Environmental Mutagenesis* 1:37-43; \_\_\_\_\_ 1980, *C.S.H.S.Q.B. Vol. 45* (eds. A. Bukhari and J. Hicks), in preparation; Engels, W.R. and C.R. Preston 1979, *Genetics* 92:161-174; \_\_\_\_\_ and \_\_\_\_\_ 1980, *Genetics* 95 (in press); Kidwell, M.G., J.F. Kidwell and J.A. Sved 1977, *Genetics* 86:813-833; Kidwell, M.G. 1979, *Genetical Research* 33:105-117.

Falk, R. The Hebrew University, Jerusalem, Israel, and University of Oregon, Eugene, Oregon. Somatic mosaics produced by a loss of a centric fragment.

Developmental analysis in *Drosophila* depends heavily on the ability to induce genetically labeled clones at predetermined times during embryonic and larval development. Such clones have been produced mainly through chromosome nondisjunction and loss and through induced

mitotic recombination events. Here we report on still another method to obtain marked clones, namely by nondisjunction of free chromosome fragments with appropriate markers.

Novitski and Puro (1978) derived a small free ring chromosome from the second autosome, bearing the dominant bristle morphology mutant Bl: Dp(2;f)Bl. Flies with two wild type alleles on their chromosomes and with the mutant allele on the ring are Bl in phenotype. The spontaneous loss of the ring during development can be observed by the appearance of non-Bl bristles on the thorax and the head. We followed seven macrochetæ on the dorsal side of the head, the two major humeral bristles and 13 macrochetæ on the thorax (including two sternopleurals). 213 out of 1070 scored flies had non-Bl spots (19.9%); of these 193 had one spot, 18 had two spots and 2 had three spots each. This is in good agreement with the expectation of random distribution of independently originating spots ( $X^2_{(3)}=0.86$ ). The size of the spots ranged from those of single bristles to one comprising half the thorax and head:

No. of bristles	No. of flies	No. of bristles	No. of flies
1	131	10	2
2	52	11	1
3	16	:	
4	9	13	2
5	6	14	1
6	7	15	3 (half thorax)
7	2 (half head)	:	
:		22	1 (half body)

Only 6 single non-Bl bristles were found in 715 flies of two different Bl/+ laboratory stocks. The frequency of spots can be increased by taking flies with spots as parents for the next generation. Of 114 progeny of such mosaic flies 33 had one spot and 4 had two spots each (32.5%). Thus the non-Bl spots in the free-ring stock appear to be due to genuine fragment losses rather than to variations in the expression or the penetrance

of the mutant character.

The distribution of spots of all sizes indicates that fragment loss may occur at any time during development, being merely a function of the number of cells at each stage that undergo cell division, starting with few large clones induced at early stages of embryogenesis to many small ones shortly before puparium formation. However, the distribution of the spots may depend also on the presence of borderlines for developing clones and on the denseness of the bristle pattern at each site. Thus of the 10 large clones comprising most of the mesothorax only one included also the head disc, while 8 included also the humeral disc; two of these included both left and right humeral discs. These clones were obviously established even before the imaginal disc borders were determined, some even before the midline was laid down (note that the humeral focus is nearer to the midline on the blastoderm fate map than are the mesothoracic foci). In two flies an anterior dorso-central bristle was included in half-thorax clones of the "other side". It could be that these clones too were established before midline determination. Only three of the small clones crossed disc border lines (one 3-bristle spot crossed from head, through humerals to mesothorax). It is possible that these were also large early clones that extended mainly to the inside of the animal.

The scutum-scutellum separation occurs quite late in larval development (Garcia-Bellido 1975) and indeed, of 43 scutellar clones, 15 included only one bristle, 14 included both bristles and another 14 extended into the scutum.

There is no distinct pattern of spot distribution within the head and thorax (besides contingency); spots partially overlap in all possible directions, thus confirming the absence of cellular determination within the disc until late in development (Sturtevant 1929). However, a nonrandom rate of cell division at the late larval development is indicated by the distribution of single bristle spots: Of the 131 single bristle spots, 37 affected the anterior and posterior verticals on the head, 11 the posterior humerals, 13 the anterior notopleurals and 15 the posterior dorso-centrals. The same bristles were also frequently involved in larger spots (though they were not the most frequently involved ones in these spots). The remaining 17 bristles were affected 55 times in single bristle spots. This would indicate a higher rate of cell division at the posterior zones of all three imaginal discs as well as at the antero-lateral zone of the mesothorax at late larval development.

In summary, the loss of a small free chromosome fragment, carrying genes of interest, could become a useful tool in developmental genetics of *Drosophila*. The random loss of such a fragment throughout development may prove useful for the study of the kinetics of determination and of cell multiplication.

Work supported by NIH grants GM 18678 to E. Novitski and GM 24182 to J.H. Postlethwait.

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Fogleman, J. and W. Heed. University of Arizona, Tucson, Arizona. A comparison of the yeast flora in the larval substrates of *D. nigrospiracula* and *D. mettleri*.

Two cactiphilic *Drosophila* of the Sonoran Desert, *nigrospiracula* and *mettleri*, exhibit a larval niche separation (Heed 1977). *D. nigrospiracula* breeds mainly in the necrotic tissue of cardon (*Pachycereus pringlei*) on the Baja peninsula and saguaro (*Carnegiea gigantea*) on mainland Mexico. *D. mettleri* breeds in the soil saturated with the fermenting juices of these cacti. The niche separation certainly acts to eliminate interspecific larval competition. The mechanism through which the niche separation is maintained has yet to be fully elucidated, but laboratory experiments have shown that *nigrospiracula* larvae are more adapted to relatively "fresh" cactus substrates (Mangan 1978). Previous studies (Heed et al. 1976; Starmer et al. 1976) have analyzed the yeast flora associated with cactiphilic *Drosophila* and their host plants. They reported little overall difference between saguaro and soaked soils with one yeast, *Pichia membranaefaciens*, being predominant in both. They speculated that competition for this yeast could be one of the factors that led to the spatial isolation of the larvae. Since then, it has been shown that their isolates designated *P. membranaefaciens* were really several new species of yeast distinct from

Table 1. Comparison of Larval Substrates

Parameter	Cactus Rots	Soaked Soils	Significant Difference?
Log Average Concentration*			
<i>Pichia opuntiae</i> (var. <i>thermotolerans</i> )	7.860	7.920	no
<i>Pichia cactophila</i>	7.282	7.669	no
<i>Pichia heedii</i>	7.099	7.528	no
<i>Pichia amethionina</i> (var. <i>pachycereana</i> )	6.797	6.744	no
<i>Candida sonorensis</i>	3.163	7.406	P<0.1
<i>Cryptococcus cereanus</i>	2.219	6.053	--
<i>Candida ingens</i>	4.902	5.423	--
<i>Candida</i> species "K"	--	6.125	--
<i>Pichia</i> species "M"	--	5.247	--
Avg. Freq. of Isolation	0.65	0.60	no
Log Avg. Concentration (All Yeasts)	7.198	7.341	no
Shannon-Weaver Diversity Index ( $H'$ ) (previous estimate)	0.433 (0.590)	0.630 (0.568)	--
Evenness ( $J'$ )	0.512	0.660	--
Avg. Number of Yeast Species Per Sample $\pm$ SE (previous measurement)	4.57 $\pm$ 0.48 (1.88 $\pm$ 0.33)	5.43 $\pm$ 0.57 (2.00 $\pm$ 0.38)	no
Average % (Wt./Wt.) Moisture $\pm$ SE	82.3 $\pm$ 1.3	13.5 $\pm$ 1.0	P<<0.001

\*Average of seven samples collected over a 10-month period.

*P. membranaefaciens* (Starmer et al. 1980). In addition, new techniques have been developed which provide for the quantification of the yeast flora through the use of selective media (Starmer et al. 1980). This report is a reinvestigation of the larval substrates in the light of this new information.

Seven samples of each substrate, saguaro rots and soaked soils, were collected over a 10-month period starting in January 1979. The results are shown in Table 1. Yeast concentrations are expressed as the log of the average number of cells per milliliter of available water. That is, an adjustment was made to compensate for the differences between substrates in percent moisture content. Statistical comparisons between substrates represent *t*-tests of arc sin  $\sqrt{\text{relative percent transformed data}}$ .

The bottom four species in Table 1 were not used in the comparison of substrates since they represent less than 1% of the total yeasts and were infrequently encountered. The concentration of only one, *C. sonorensis*, of the remaining five species was significantly different between substrates. The high concentration of this species in soils, however, is due to one collection in which it occurred with abnormally high frequency. There are noticeable increases in the diversity index for soils and in the average number of yeasts per sample for both substrates over previous reports of these parameters. These increases are most likely due to the split of *P. membranaefaciens* into the four new species: *P. opuntiae*, *P. cactophila*, *P. heedii*, and *P. amethionina*. It is evident from the data that no major differences exist between the substrates with respect to yeast species. Seasonal variation in yeast flora may, however, have masked significant differences between substrates. Seasonal variation in yeast flora has been shown to exist in *Opuntia* rots of the Australian desert (H. J. Phaff, pers. communication).

The techniques employed in this study provide a more accurate characterization of the yeast flora than previously possible. This is especially true with respect to yeasts that occur in low concentrations. The conclusions remain essentially unchanged: there are several predominant yeasts which could be considered common resources and the basis of competition if the larvae of the two species were to live together and feed exploitatively. The only physical parameter measured for which major and consistent differences exist between substrates is percent moisture content (Table 1). It is possible that females of the two *Drosophila* species use this as a cue for oviposition site separation.

This work was supported by an NIH postdoctoral fellowship (GMO6807) awarded to J.F.

References: Heed, W.B., W.T. Starmer, M. Miranda, M.W. Miller and H.J. Phaff 1976, *Ecology* 57:151-160; Heed, W.B. 1977, *Proc. Entomol. Soc. Wash.* 79:649-654; Mangan, R. 1978, Ph.D. Dissertation, Univ. of Arizona; Starmer, W.T., W.B. Heed, M. Miranda, M.W. Miller and H.J. Phaff 1976, *Microbial Ecology* 3:11-30; Starmer, W.T., H.J. Phaff, W.B. Heed, M. Miranda and M.W. Miller 1980, *Am. Nat.* (submitted).

Fujikawa, K. Hiroshima University, Hiroshima, Japan. Pilot experiments involving visible mutations induced in immature *Drosophila* oocytes by  $\gamma$ -rays at low dose rate.

In an attempt to obtain more information on factors which alter the incidence of genetic radiation damages induced in meiotic germ cells corresponding to prophase I, the dose-rate effect of  $\gamma$ -rays on the frequency of visible mutations induced in immature *Drosophila* oocytes was in-

vestigated in the experiments described herein.

Females of *D. melanogaster* carrying X-chromosomes marked with *sc*<sup>S1</sup> B InS *sc*<sup>8</sup> were collected within 4 h of eclosion and then irradiated with 3000 rad of <sup>60</sup>Co  $\gamma$ -rays either at 3000 rad/min or at 30 rad/min. The irradiated females were aged for 24 h and mass mated with *y w m f/B<sup>S</sup> Y sc<sup>8</sup>*; *dp* males (40 females to 120 males per culture bottle). Six successive daily brood changes were made. All the F<sub>1</sub> progeny were examined for dumpy mutations, and the recovered mutants were classified according to their phenotypes (*olv*, *ov*, *ol*, *lv*, *o*, *v* and *cm*; see Carlson and Oster 1962). The yellow and Minute exceptions were scored in the F<sub>1</sub> female count. Although these three kinds of exceptions are detectable as either whole-body or mosaically expressed changes, the mosaic-individuals for any of them were seldom recovered in the present experiments. Therefore, data pertaining to mosaic-types are not discussed in this report.

The results obtained are summarized in Table 1. Since the number of any kind of exceptions isolated in each brood was not large, the mutation frequencies in this table are given as average of those obtained in six broods. As shown in Table 1, the frequencies of yellow and Minute

Table 1. Frequencies of yellow, Minute and dumpy mutations observed after irradiation of immature oocytes with 3000 rad of  $\gamma$ -rays at 3000 rad/min and at 30 rad/min.

Dose rate (rad/min)	Mutation frequency (%)		
	yellow	Minute	dumpy
Control	0.0000 (0/13587)	0.0442 (6/13587)	0.0000 (0/24113)
3000	0.2254 (15/6654)	0.7364 (49/6654)	0.1023 (12/11733)
30	0.0781 (9/11529)	0.2342 (27/11529)	0.0894 (18/20141)

involve minute deficiencies (see Frye 1961, and Lindsley and Grell 1968). An association of yellow mutations with minute deletions was confirmed in the present study. Almost all of the yellow mutants recovered after irradiation either at 3000 rad/min or at 30 rad/min were male lethals in the progeny test. On the other hand, it was found that 9 out of 18 dumpy mutants isolated in the low dose-rate series and 5 out of 12 in the high dose-rate series were the (ol, lv, o, v) types, a class of dumpy mutations which are usually free from aberration phenomena (Carlson and Southin 1962; Fujikawa and Inagaki 1979). The remainder were the olv types, which often originate from deficiencies or rearrangements. However, no Minute bristles were observed in the olv mutants, although a locus whose deficiency results in a Minute phenotype lies close to the dumpy locus (see Carlson and Southin 1962).

Acknowledgements: I express my sincere thanks to Dr. E. Inagaki for stimulating interest and to Dr. K. Takeshita for providing the facility of  $\gamma$ -ray irradiation.

References: Carlson, E.A. and I.I. Oster 1962, *Genetics* 47:561-576; Carlson, E.A. and J.L. Southin 1962, *Genetics* 47:321-336; Frye, S.H. 1961, *Genetics* 46:865-866; Fujikawa, K. and E. Inagaki 1969, *Mutation Res.* 63:139-146; Kastenbaum, M.A. and K.O. Bowman 1970, *Mutation Res.* 9:527-549; Lindsley, D.L. and E.H. Grell 1968, *Genetic Variation of D. melanogaster*.

Futch, D.G. San Diego State University, San Diego, California. Crossing over in a hybrid *D. ananassae*-*D. pallidosa* X-chromosome.

species. The chromosome is marked with the three mutations yellow, forked, and white and has been integrated by repeated (13 generations) backcrossing into otherwise normal strains of *ananassae* and *pallidosa*.

This particular chromosome was obtained from F<sub>1</sub> interspecific hybrid females heterozygous for an *ananassae* X-chromosome marked with yellow and a *pallidosa* X-chromosome marked with forked and white and resulted from a single crossover between y and f. Several genetic maps have been constructed for the *ananassae* X-chromosome with these three mutations arranged in the sequence y f w (see Moriwaki and Tobar 1975). The three alleles in this hybrid chromosome, y<sup>d</sup> (*ananassae*) and f and w (*pallidosa*), were reported by me in DIS 50 (1973). The forked mutant which has a very strong bristle effect was mistakenly identified as a singed mutant in that report because of its phenotypic resemblance to singed and because it seemed to complement another allele of forked (probably f<sup>49</sup>) carried in one of my *ananassae* stocks. However, mapping results have subsequently placed this mutant at the forked locus and closer inspection of hybrid females heterozygous for the two alleles in trans-position has revealed a very mild forked phenotype expressed by one or two bristles in most of them. Claude Hinton (pers. communication) has noticed a similar relationship between a pair of *ananassae* forked alleles in his possession, one of them being f<sup>49</sup>.

The hybrid composition of this synthesized X-chromosome and estimates of the approximate physical locations of the three mutant genes have been determined by observing how the chromo-

mutations are considerably lower after irradiation at 30 rad/min than after irradiation at 3000 rad/min. Statistical tests by the use of Kastenbaum and Bowman's tables (1970) showed that such differences were highly significant, but the difference observed for dumpy mutations was far from significant. The simplest, although not only, interpretation for the relative lack of dose-rate effect on dumpy mutations may be ascribed to the fact that these mutations originate from point mutational events as well as from breakage events (Carlson and Southin 1962; Fujikawa and Inagaki 1979), while the majority of the yellow mutations induced in scute<sup>8</sup> chromosome (the one used) and Minute mutations are known to

In the course of my studies on the comparative genetics of the two interfertile sibling species, *D. ananassae* and *D. pallidosa*, I have found a certain synthesized X-chromosome to be very useful, especially as a marker chromosome in the analysis of parthenogenic strains of the two

some crosses over in a variety of genetic backgrounds. The chromosome which is identically submetacentric in both species has a left arm which is largely ananassae containing the mutant allele  $y^d$  and the standard ananassae gene sequence rather than the standard sequence of pallidosa with the fixed inversion ln (1) LA. The right arm is mainly pallidosa containing the two mutant alleles f and w from pallidosa.

Table 1. X-Chromosome Inversions

Inversion	Break points		Approximate proportion of chromosome arm
	Hinton's Map	Seecof's Map	
ln (1) LA	4A; 8C	5.7; 16.0	40%
ln (1) LB	9A; 11B	16.7; 20.3	25%
ln (1) RA	14B; 17A	8.5; 2.3	50%

Table 1 provides a description of three naturally occurring inversions in pallidosa and ananassae X-chromosomes. ln (1) A is a fixed sequence in pallidosa and two strains of ananassae from Papua, New Guinea (Futch 1966). Fig. 1 represents a photomicrograph of synapsed polytene salivary gland X-chromosomes from a female larva heterozygous for ln (1) LA and ln (1) RA and the standard ananassae gene sequence. Break points

Table 2.

Exp. No.	Structural karyotype of female parent			No. progeny	% Recombinant between	
	Chromosome				y - f	f - w
	X = 1	2	3			
	L . R	L . R	L . R			
1	$\frac{+ . +}{+ . +}$	$\frac{+ . +}{+ . +}$	$\frac{+ . +}{+ . +}$	1992	42.8	20.4
2	$\frac{+ . +}{+ . +}$	$\frac{A . +}{+ . +}$	$\frac{A . +}{+ . +}$	2216	43.2	27.8
3	$\frac{A . +}{+ . +}$	$\frac{(C;D), B. (A;B)}{(C;D), B. (A;B)}$	$\frac{+ . B}{+ . B}$	2193	9.5	22.3
4	$\frac{A . +}{+ . +}$	$\frac{(C;D), B. (A;B)}{+ . +}$	$\frac{+ . B}{+ . +}$	1795	11.1	34.6
5	$\frac{A . A}{+ . +}$	$\frac{C, (E;B)F. (A;C), D}{+ . +}$	$\frac{C . (B;C)}{+ . +}$	1222	13.7	1.6
6	$\frac{A, B . A}{+ . +}$	$\frac{C, (E;B)F. (A;C), D}{+ . +}$	$\frac{C . +}{+ . +}$	1391	1.4	2.9

of each of the 3 X-chromosome inversions are given relative to two different cytological maps (Hinton from Hinton and Downs 1975, and Seecof from Stone et al. 1957). Approximate percentages of euchromatic portions of each arm occupied by each inversion as determined from polytene chromosomes are also given.

Table 2 presents recombination data for crossovers between y and f and between f and w involving the hybrid X-chromosome in combination with various

hybrid karyotypic conditions. The two major autosomes of both species are metacentric. The letter designations of autosomal inversions are from my earlier study (Futch 1966) as are the X-chromosome inversions; +'s indicate standard ananassae arrangements. Centromere positions are indicated by dots. Parentheses surrounding two letters, e.g., (C/D) in chromosome 2L, identify instances of overlapping inversions; in this instance ln (2) LC and ln (2) LD occur together and overlap one another in this particular pallidosa chromosome.

The data in Table 2 clearly show the relationship of y with ln (1) LA. This agrees with Hinton's observation (pers. communication) that the locus of y is between the left and right break points of ln (1) LA. Crossing-over between y and f is even further reduced by the presence of ln (1) LB which has its right-hand break point very near to the right end (proximal end) of the euchromatic portion of XL. The effect of ln (1) RA on crossing over between f and w is also very clear showing that w is located in the medial to distal part of XR, very likely within the break points of ln (1) RA. The location of f is certainly very close to the centromere end and, based on these data, probably in the proximal part of XR.

Reductions in crossing over between genes located in an X-chromosome heterozygous for structural rearrangements are very obvious here. Also of significance are increases in crossing over associated with structural heterozygosity in other chromosomes. This interchromosomal, Schultz-Redfield effect (Schultz and Redfield 1951) is particularly apparent in Experiment No.



Fig. 1. Photomicrograph of synapsed polytene X-chromosome of a *D. ananassae* female larva heterozygous for *ln* (1) LA in the left arm (XL) and *ln* (1) RA in the right arm (XR).

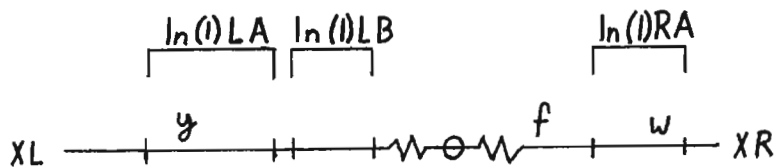


Fig. 2. Diagram of *ananassae-pallidosa* X-chromosome showing approximate locations of break points of three inversions and genes *y*, *f* and *w*.

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Galus, H.M., I.B. Perelle and L. Ehrman.  
SUNY College at Purchase, Purchase, New York. The heritability of egg length in *D. paulistorum*.

employed hatchability as the criterion of fitness and found that hatchability was higher from intermediate-sized eggs. Studies of artificial selection for egg length have also been undertaken utilizing this same species (Bell, Moore and Warren 1955; Parsons 1964). In these instances artificial selection for egg length resulted in the culling of both large- and small-sized lines diverging from unselected control lines. Maximum divergence occurred by the tenth generation of selection after which regression toward the unselected mean appeared to take place.

Research published by Perelle, Daniels and Ehrman (1980) indicates that egg length heritability is low in the Mesitas strain of *D. paulistorum*. A bimodal distribution resulted when

4 where the crossover frequency between *f* and *w* is 34.6% compared to 22.3% in Experiment No. 3, a highly significant difference ( $\chi^2 = 73.12$ ,  $p < .001$ ). A similar interchromosomal effect resulting in the enhancement of crossing over between *f* and *w* was found when Experiments 1 and 2 were compared ( $\chi^2 = 30.18$ ,  $p < .001$ ). The possibility of an interbrachial effect in the X-chromosome was also investigated but with no clear-cut results. The difference in crossing over between *y* and *f* in Experiments 4 and 5 ( $\chi^2 = 4.30$ ,  $p < .05$ ) is quite possibly due only to additional autosomal inversions while that between *f* and *w* in Experiments 5 and 6 ( $\chi^2 = 3.92$ ,  $p < .05$ ) could be interbrachial caused by the addition of *ln* (1) LB.

Fig. 2 presents a schematic representation of the X-chromosomes of *ananassae* and *pallidosa* showing the suggested locations of the three genes, *y*, *f* and *w*, and the three inversions, *ln* (1) LA, *ln* (1) LB, and *ln* (1) RA. The hybrid X-chromosome that it represents has been of considerable value to me since it has allowed me to examine aspects of chromosome behavior in two very closely related species using essentially the same chromosome in each species.

References: Futch, D.G. 1966, Univ. Texas Publ. 6615: 79-120; Hinton, C.W. and J.E. Downs 1975, *J. Heredity* 66: 353-361; Moriwaki, D. and Y.N. Tobar 1975, *Handbook of Gene-*

Research done by Curtsinger (1976a,b) indicates that egg length in the Oregon-R *D. melanogaster* strain is influenced by stabilizing selection. This is a type of natural selection in which intermediate phenotypes are favored. Curtsinger



a graph was constructed of measured egg lengths versus frequency or number of eggs deposited. The midpoint of depressed frequency of eggs was found at approximately the mean length of the eggs. Hatchability of all measured eggs was then derived. Upon comparison among egg lengths, frequencies and hatchability, it was discovered that eggs of the mean length--that of depressed frequency--had a higher hatchability than any other egg length measured. From these results it was concluded that heritability of egg length must be low in this strain. If egg length was indeed substantially heritable then the point of highest hatchability--in this case the mean--would represent the modal egg length. Initially one would suspect a larger number of assorted lengths would be produced, but a significantly higher percentage of mean-lengthed eggs would hatch. The resulting adults would then be likely to produce more eggs of approximately the same mean lengths, and this mean would have eventually become the most common, modal egg length. Therefore when the graph of eggs deposited versus egg lengths was constructed, a unimodal distribution would have resulted with its point of highest frequency at the modal length, rather than the bimodal distribution which was actually found.

A more direct approach to heritability estimates was taken in our present study. This was done by measuring and comparing eggs from which larvae eclosed to produce  $P_1$  and  $F_1$  generations, i.e., over a three generation level. Once more the *D. paulistorum* strain used originated in Mesitas, Colombia and belonged to the Andean-Brazilian semi-species.

Eggs were chosen at random from cultures of this strain, measured, and then "bottled" according to their individual egg lengths. Measurements were taken on microscope slides aided by a 12 x 10 cm microscope screen (Hudson Photographic Ind. Inc., Irvington-on-Hudson, NY 10533, model #325), which was attached to a compound microscope. A 20X objective lens was used and magnification contributed by the screen was adjusted to give a total magnification of 100X. The image of eggs were then measured with a metric ruler on this screen; once measured, they were divided into groups of 0.005 mm egg length intervals. Then, each group was gently placed into half-pint culture bottles which held cardboard spoons containing fresh medium (Carolina Biological Supply, Burlington, NC 27215, Formula 4-24) seeded with yeast. To this substrate a 0.01 percent solution of crystal violet was added to impede bacterial growth and provide background pigment.

In approximately 10-12 days, with the appearance of imagoes, crosses between parental flies were made. Such crosses were initiated both between imagoes hatched from eggs of the same lengths, and between imagoes hatched from eggs of different lengths. These parents were then placed in fresh half-pint culture bottles outfitted as described earlier, and allowed to breed. After approximately 2-3 days, eggs from these bottles were removed from the spoons and measured, using the same technique described above. The results from these crosses are listed in Table 1. Statistical analyses are provided in Tables 2 through 4.

$t$ -tests were performed for each "within cross" to determine the relationship between the  $F_1$  means ( $\bar{X}_2$ ) and the  $P_1$  means ( $\bar{X}_1$ ). For crosses numbered 1, 3, 4, 6 and 9,  $\bar{X}_1$  was found to be significantly different from  $\bar{X}_2$  at  $p < 0.01$ . For crosses numbered 2 and 5,  $\bar{X}_1$  was significantly different from  $\bar{X}_2$  at  $p < 0.05$ . Only cross number 6 provided a nonsignificant  $t$ -value.  $t$ -values obtained for  $F_1$  means with mothers' egg lengths and fathers' egg lengths showed essentially the same results (see Table 1). Comprehensively, these tests indicate that the  $P_1$  and  $F_1$  eggs within each cross do have significantly different egg length means.

The critical statistic for heritability is the regression line of  $F_1$  values on parent values (Curtsinger 1980). Using standard regression techniques it was determined that the

Table 1. Results of crosses made between  $P_1$  eggs of Mesitas *D. paulistorum*.

Cross no.	Mother's egg length (mm)	Father's egg length (mm)	Parents' mean egg length (mm)	Number $F_1$ eggs	$F_1$ 's egg length means (mm)	Standard error
1	.445	.450	.447	19	.480	0.003
2	.470	.470	.470	14	.484	0.006
3	.480	.480	.480	23	.467	0.004
4	.485	.485	.485	12	.454	0.008
5	.455	.455	.455	12	.442	0.005
6	.500	.505	.502	17	.466	0.004
7	.460	.450	.455	7	.441	0.006
8	.435	.390	.412	22	.456	0.005
9	.505	.505	.505	9	.471	0.002

Table 2. t-tests: Mesitas D. paulistorum egg lengths.

cross no.	df	<u>t</u> values of F <sub>1</sub> 's mean egg length with mother's egg length	<u>t</u> values of F <sub>1</sub> 's mean egg length with father's egg length	<u>t</u> values of F <sub>1</sub> 's mean egg length with parents' mean egg length
1	18	12.73	10.93	11.83
2	13	2.27	2.27	2.27
3	22	-3.35	-3.35	-3.35
4	11	-4.11	-4.11	-4.11
5	11	-2.61	-2.61	-2.61
6	16	-9.11	-10.46	-9.78
7	6	-3.23	-1.49	-2.36
8	21	3.96	12.30	8.13
9	8	-15.62	-15.62	-15.62

Table 3. One-way analysis of variance: Mesitas D. paulistorum egg lengths.

Source	df	Sum of squares	Mean squares	F ratio
between groups	8	23.064	2.883	7.74
within groups	126	46.949	.372	
total	134	70.013		

$F_{.01}(8,126 \text{ df}) = 2.65$

Table 4. Multiple range test--Scheffé procedure: Mesitas D. paulistorum egg lengths.

Subset 1		Subset 2	
Cross no.	F <sub>1</sub> mean (mm)	Cross no.	F <sub>1</sub> mean (mm)
7	.441	4	.454
5	.442	8	.456
4	.454	6	.466
8	.456	3	.467
6	.466	9	.471
3	.467	1	.480
9	.471	2	.484
1	.480		

regression of F<sub>1</sub> egg lengths on mothers' egg lengths is  $.425 + 0.084m$ ; the regression of F<sub>1</sub> egg lengths on fathers' egg lengths is  $.420 + 0.096f$ . It is apparent that heritability is extremely low, 0.084 and 0.096 of mothers' and fathers' egg lengths, respectively. It must be noted that even though heritability was extremely low the apparent similarity of maternal and paternal effect is almost certainly due to the mating of flies artificially selected from identical or very similar length eggs ( $r = 0.93$ ,  $p < 0.001$ ).

A one-way analysis of variance was conducted on this data (Table 3). An F ratio of 7.74 was obtained, which is much higher than  $F_{.01}(8, 126 \text{ df}) = 2.65$ . This shows that a significant difference does exist between the mean F<sub>1</sub> egg lengths of the crosses. A multiple range test (Scheffé procedure) was calculated with these means and homogeneous subsets were derived (Table 4).

In conclusion, this study found low heritability existing in the Mesitas strain of D. paulistorum for egg length. This was shown most dramatically by the regression lines of F<sub>1</sub> egg lengths on mothers' and fathers' egg lengths and by the t-tests, which show significant differences existing between P<sub>1</sub> and F<sub>1</sub> egg lengths both within crosses and over all of the crosses.

References: Bell et al. 1955, Cold Spring Harbor Symp. Quant. Biol 20:197-212; Curtsinger 1976a, J. Hered. 67:59-60; \_\_\_\_\_ 1979b, J. Hered. 67:246-247; \_\_\_\_\_ 1980, pers. communication; Parsons 1964, Genetics 35:175-181; Perelle et al. 1980, Univ. Texas Publ., Studies in Genetics (in press).



Das Mohapatra, D.P., N.K. Tripathy and C.C. Das. Berhampur University, Orissa, India. Distribution of different species of *Drosophila* in Khallikote Ghats, Ganjam District, Orissa, India.

The genus *Drosophila* has a wide range of distribution covering entire India. The available data on field collection cover most parts of the country, but there still remain large regions lacking dependable data on the *Drosophila* fauna. In this

Species	No. of flies collected			Percentage
	Male	Female	Total	
Subgenus: <i>Sophophora</i>				
<i>D. malerkotliana</i>	245	189	434	58.25
<i>D. kikkawai</i>	78	50	128	15.83
<i>D. takahashii</i>	23	55	78	10.45
<i>D. rajasekari</i>	8	31	39	5.23
<i>D. bipectinata</i>	8	27	35	4.69
<i>D. melanogaster</i>	4	14	18	2.41
<i>D. suzukii</i>	1	1	2	0.26
Subgenus: <i>Scaptodrosophila</i>				
<i>D. nigra</i>	3	8	11	1.46

short communication we wish to report the *Drosophila* fauna from the Khallikote Ghats, Orissa, India, which are about 60 km to the north-east of Berhampur at 19°15' and 19°5' N latitude and 84°20' and 85°15' E longitude. This mountain range has woody plants at its foot while teak plantation and thick bushy vegetation occur in its upper ranges. The table gives the different species of *Drosophila* collected on banana bait during several collection trips conducted between the months of January and March, 1980. The average temperature during this period was 27°C. A total of 745 flies were collected

which included eight different species belonging to two subgenera.

The dominant species in the collection belonged to *melanogaster* species group (especially *D. malerkotliana* and *D. kikkawai*) with males outnumbering the females; the sex ratio, however, was reversed in the case of *D. takahashii*, *D. rajasekari*, *D. bipectinata* and *D. melanogaster*.

Gilbert, D.G. Indiana University, Bloomington, Indiana. Effects of CO<sub>2</sub> vs. ether on two mating behavior components of *D. melanogaster*.

Various effects of two anesthetics, carbon dioxide and ethyl ether, on *Drosophila* have been reviewed by Ashburner and Thompson (1978). These authors indicate that carbon dioxide treatment can markedly reduce survival and fertility of adults if administered up to 3 hours post-eclosion,

but shows no toxic effect if used 5 or more hours after eclosion. Light ether treatment does not produce similar toxic effects. Bingo (1971) found ether to have slighter effects on behavior of *D. grimshawi* than cold or carbon dioxide when flies were tested a few hours after anesthetization. To determine whether the type of anesthesia used in virgin collection had any long-term effects on reproductive behavior in *D. melanogaster*, virgin males and females were collected with carbon dioxide or ether and were paired 3 days later in a 2 x 2 factorial experiment. Latency to mounting and copula durations were measured.

Table 1. Analysis of variance in mating behavior components due to female and male anesthetic treatment 3 days previously.

Term	Mounting latency			Copula duration		
	Df	Ms	F	Df	Ms	F
Female treatment	1	0.6022	4.65*	1	0.00883	1.99
Male treatment	1	0.3554	2.74	1	0.00222	0.50
Interaction	1	0.0906	0.70	1	0.00047	0.11
Error	56	0.1294		49	0.00444	

\* p < 0.05

The *D. melanogaster* stock tested was a strain homozygous for esterase 6 Slow derived from flies trapped in Bloomington, Indiana, and free of extreme CO<sub>2</sub> sensitivity associated with viruses. The stock was maintained in half-pint bottles of well yeasted cornmeal-molasses-agar media at 25±1°C, 60±10% humidity, on a 12:12 hour light/dark cycle. Eight hours after clearing the stock bottles of adults, newly eclosed flies were sexed and separated by first shaking flies into a transfer bottle. They were then either anesthetized on a CO<sub>2</sub> diffusion pad for the duration of sexing, up to 5 minutes, or anesthetized with ether until their surface clinging response was lost, about 30 seconds. Twenty males or females were housed per vial for 64 to 76 hours at 25°C.

Light ether treatment does not produce similar toxic effects. Bingo (1971) found ether to have slighter effects on behavior of *D. grimshawi* than cold or carbon dioxide when flies were tested a few hours after anesthetization. To determine whether the type of anesthesia used in virgin collection had any long-term effects on reproductive behavior in *D. melanogaster*, virgin males and females were collected with carbon dioxide or ether and were paired 3 days later in a 2 x 2 factorial experiment. Latency to mounting and copula durations were measured.

All collected flies were alive and appeared vigorous at this time, 3 days after the ether or CO<sub>2</sub> anesthetization. Male and female pairs were aspirated from their holding vials into observation vials containing media seeded with liquid yeast two days previously. A block of pairings consisted of an ether-treated male with an ether-treated female, an ether male with a CO<sub>2</sub> female, a CO<sub>2</sub> male with an ether female, and a CO<sub>2</sub> male with a CO<sub>2</sub> female. Two blocks were started at each observation period by adding all males, then all females within 5 min of each other, or the reverse order. The time of initial pairing, time of male mounting female and time of dismounting were recorded for each pair to the nearest half-minute.

The factorial analysis of variance for latency to mounting and copula duration are presented in Table 1. These two measures were transformed to their common logarithms for analysis to reduce the correlation of group means with variances. Within group variances are homogeneous, as determined by an F<sub>max</sub> test (F<sub>max</sub> = 1.45, Df = 4,14 and F<sub>max</sub> = 2.26, Df = 4,13 for mounting latency and copula duration, respectively). Female anesthetic treatment significantly affected latency to mounting, and had the largest, but nonsignificant effect on copula duration. Male treatment and the interaction of treatments are nonsignificant components of variance.

Table 2. Mean effects of female anesthetic treatment on mating components.

Treatment	Mounting latency	Copula duration
Ether	11.5 min	22.21 min
CO <sub>2</sub>	18.2 min	20.93 min

The effect of carbon dioxide treatment on females is to increase latency to mounting and decrease copula duration relative to ether treatment, as indicated in Table 2. These effects suggest that carbon dioxide use in virgin collecting may have a long-term effect on reproductive responses of females. Supported by NIH AG02035.

References: Ashburner and Thompson 1978, in: The Genetics and Biology of *Drosophila*,

v. 2a (Ashburner and Wright, eds.), pp. 1-109; Ringo 1971, DIS 47: 118.

Gilbert, D.G. Indiana University, Bloomington, Indiana. Sperm counts and initial sperm storage in *D. melanogaster*.

males differing in their esterase 6 genotype. This note describes the methods used for counting sperm and the major results for 47 matings of 3 to 5 day virgins of the Oregon-R strain.

The dissection methods reported here are modified from those described by Fowler (1973) in two important respects. Female reproductive tracts are dissected directly in aceto-orcein stain rather than in Ringer's saline, avoiding a saline-stain reaction which destroys the specimen within a week. Specimens dissected in the stain and sealed under coverslips preserve for several months. Secondly, the spermathecae are dissected from the uterus, pared of their surrounding fat which inhibits staining, and squashed under a separate coverslip. With this method, sperm heads in the densely packed mass of spermathecal sperm stain deeply enough to count the preparations accurately.

Materials used in dissections are two fine forceps, two tungsten dissecting needles, a dissecting microscope, slides and coverslips, and nail polish for sealing slides. The orcein stain used is the salivary chromosome "dissecting" solution described by Strickberger (1962). Viewing specimens with phase optics at 1000X, the stained 10 micron long sperm heads of *D. melanogaster* can be readily counted with a hand held counter.

The uterus, with attached ventral receptacle, dorsal spermathecae and parovaria, along with the lower portion of the common oviduct, are simply dissected from the female. A mated, etherized female is placed in a drop of orcein stain on a slide. Squeezing the abdomen with the left forceps, the extruded ovipositor is grasped with the right forceps and pulled posteriorly until the reproductive tract is out of the abdomen. Any exterior chitin and digestive tract are dissected away. To obtain clear counts of spermathecal sperm, these paired organs are dissected from the uterus by severing the spermathecal ducts. The fat is dissected away, and the spermathecae are transferred to a second drop of orcein stain on the slide. After applying coverslips to both spermathecal and uterine preparations, the spermathecae are squashed with a hard pressure that expels the sperm mass entirely from its opaque capsule. The uterus-receptacle is squashed gently to flatten it for phase optics without disrupting receptacle integrity.

In the course of investigating reproductive functions of the male anterior ejaculatory duct enzyme esterase 6 (Richmond et al. 1980), I have examined the number of sperm initially stored by *D. melanogaster* females from ejaculates of

Females were dissected at intervals ranging from 10 minutes to 50 hours after mounting of the female by the male, which included interrupted copulations. Details of these results will be reported elsewhere. There is a high degree of individual variation in the sperm storage process; the results reported here are in terms of least squares regression estimates of the population values and individual values. Uteral sperm numbers, when greater than 300, were estimated by measuring the area covered by the uteral sperm mass with an ocular micrometer and counting sperm density at random points in the mass. Receptacle and spermathecal sperm were counted directly. The entire counting time for a specimen ranged from 15 to 45 minutes. Only specimens for which two complete replicate counts could be obtained ( $N = 47$ ) were analyzed. Counting error (mean coefficient of variation  $\pm$  SEM) for the combined classes of receptacle, spermathecal and uteral sperm was  $2.7 \pm 0.91\%$  per individual, after logarithmic transformation of counts. Table 1 lists the maximums and times of maximum sperm numbers for these sperm classes.

Table 1. Initial sperm storage parameters for Oregon-R matings, in terms of regression estimates of population values and individual observed values.

Sperm class	Maximum number		Hour* of maximum	
	Estimated	Observed	Estimated	Observed
Transferred sperm:				
Uteral sperm	5800	4690	0.28	0.25
Stored sperm:				
All organs	1120	1032	5.1	5.3
Receptacle	670	767	4.0	0.9
Spermathecae	390	449	7.0	5.3

\*Hour post mounting of female by male.

of stored sperm, as well as transferred sperm (approximately 10% of transferred may ultimately fertilize eggs), suggests that sperm selection may be an important component of natural selection in *D. melanogaster*, particularly if sperm genotypes within or between ejaculates differ in their functional abilities.

Supported by NIH AG02035.

References: Fowler 1973, *Adv. in Genetics* 17:293-360; Gilbert et al. 1981, *Evolution*, in press; Kaplan et al. 1962, *DIS* 36:82; Richmond et al. 1980, *Science* 207:1483-1485; Strickberger 1962, *Experiments in Genetics with Drosophila*, p. 103, Wiley.

Goncharenko, G.G. and I.K. Zakharov. Institute of Cytology and Genetics, Novosibirsk, USSR. A phosphoglucomutase locus in *D. virilis*.

Polymorphism at the locus phosphoglucomutase (Pgm) has been extensively studied in may *Drosophila* species. The genetic localization of this structural locus was determined for some species (Hjorth 1970, Trippa et al. 1970, Lako-vaara and Saura 1972, Charlesworth et al. 1977).

The total of 20 lines from seven members of the virilis group of *Drosophila* (*D. virilis*, *D. americana texana*, *D. littoralis*, *D. ezoana*, *D. novomexicana*, *D. lummei*) was included in this study. The genetic variability of phosphoglucomutase has been studied using starch gel electrophoresis. Each fly was homogenized in 0.025 ml double distilled water on the rough surface of a slide. The starch gel electrophoresis was performed vertically using 12-13% starch and 10% sucrose in medium containing 0.045M TRIS, 0.025M boric acid and 0.001M EDTA. The electrode buffer had 0.18M TRIS, 0.1M boric acid, 0.004 EDTA (anodal) and 0.13M TRIS, 0.07M boric acid, 0.003M EDTA,  $10^{-5}$  NADP (catodal) (Porter et al. 1964). The electrophoresis took 4-5 hours at 5-10°C with a voltage of 320-360v and current intensity of 60-80 ma. Staining mixture as in Ayala et al. (1972).

The electrophoresis of Pgm revealed the presence of three variants, called Pgm<sup>0.80</sup>, Pgm<sup>1.00</sup> and Pgm<sup>1.20</sup> on the basis of their mobilities (see Fig. 1). The data from different crosses indicate that these three variants are coded by three codominant alleles at one locus.

An important aspect of these results is that the maximum storage of sperm greatly exceeds the commonly referred to value of 750 for maximum storage capacity (Kaplan et al. 1962, based on examination of 8 females). This high amount of storage appears to be balanced by a high degree of sperm waste (loss from the reproductive tract without fertilization) during the first 3 days after mating (Gilbert et al. 1981), causing progeny to stored sperm ratios of approximately 50%. Such an inefficient use

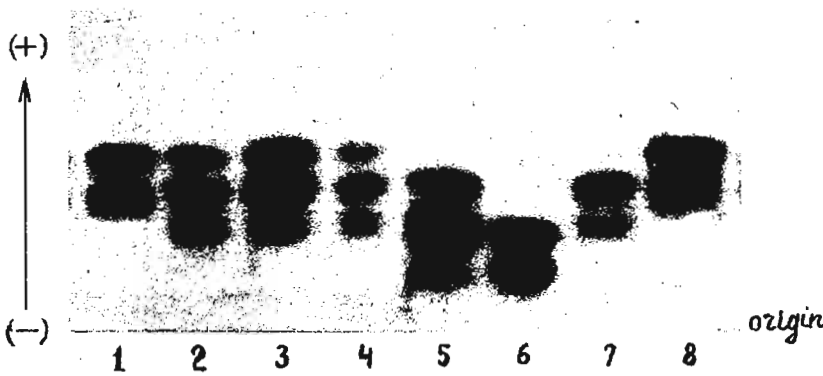


Fig. 1. Starch gel electrophoretic pattern of one fly homogenates of *D. virilis*. The following genotypes are shown:

$$\begin{aligned}
 1, 8 & - \frac{\text{Pgm } 1.20}{\text{Pgm } 1.20}; & 2, 3, 4 & - \frac{\text{Pgm } 1.20}{\text{Pgm } 1.00}; & 5 & - \frac{\text{Pgm } 1.00}{\text{Pgm } 0.80}; & 6 & - \frac{\text{Pgm } 0.80}{\text{Pgm } 0.80}; \\
 7 & - \frac{\text{Pgm } 1.00}{\text{Pgm } 1.00}
 \end{aligned}$$

$$\begin{aligned}
 \text{♀♀} & \left( \frac{\text{Pgm } 1.00}{\text{Pgm } 1.20} \right) \frac{\text{sv t tb gp}}{+ + + +} \times \text{♂♂} \left( \frac{\text{Pgm } 1.00}{\text{Pgm } 1.00} \right) \frac{\text{sv t tb gp}}{+ + + +}
 \end{aligned}$$

According to the result of such crosses the recombination frequency between sv and t genes was 27.8%; between t and tb, 33.0%; and between tb and gp, 13.6%. This is in agreement with the position of the loci on the standard genetic map of *D. virilis* (Alexander 1976). In the *D. virilis* map four visible markers have the following localization: sv (shot veins, 3-24.5); t (telescoped, 3-57.5), tb (tiny bristles, 3-104.0), and gp (gapped, 3-118.5) m.u.

Table 1. Localization of Pgm locus.

Parent	Offspring maternal chromosome	Pgm 1.20	Pgm 1.00
		Pgm 1.00	Pgm 1.00
♀ $\left( \frac{\text{Pgm } 1.20}{\text{Pgm } 1.00} \right) \frac{+ + + +}{\text{sv t tb gp}}$	+ + + +	14	0
	sv t tb gp	0	13
	+ t tb gp	2	0
	sv + + +	0	4
	+ + tb gp	4	0
♂ $\left( \frac{\text{Pgm } 1.00}{\text{Pgm } 1.00} \right) \frac{\text{sv t tb gp}}{\text{sv t tb gp}}$	sv t + +	0	4
	+ + + gp	3	0
	sv t tb +	0	3
	+ t	41	2
	sv +	4	65

It is necessary to note that under the electrophoresis method used the homozygous variants were always revealed by two bands. The discussion of the causes of this phenomenon is beyond the scope of this report; further details will be published elsewhere.

The examination of the offspring from the backcross

$$\begin{aligned}
 \text{♀♀} & \left( \frac{\text{Pgm } 1.00}{\text{Pgm } 1.00} \right) \frac{\text{b, gp, cd, pe, gl}}{\text{b', gp', cd', pe', gl}} \times \\
 \text{♂♂} & \left( \frac{\text{Pgm } 1.00}{\text{Pgm } 1.20} \right) \frac{\text{b, gp, cd, pe, gl}}{+ + + +}
 \end{aligned}$$

demonstrated that the Pgm gene is linked to the gp (gapped, 3-118.5) locus and therefore located in the third chromosome. For a more definite localization of the locus Pgm the following crosses were carried out:

From Table 1 it is evident that 6/112 of crossovers occurred in the course of recombination between sv and Pgm genes and 106/112 between Pgm and t genes. Therefore, Pgm is placed at 26.3± on the genetic map of the third chromosome of *D. virilis*.

References: Alexander, M.L. 1976, *in*: The Genet. and Biol. of *Drosophila*, Vol. 1c:1365-1427, Academic Press; Ayala, F.J., J.R. Powell, M.L. Tracey, C.A. Mourao and S. Perez-Salas 1972, *Genetics* 70:113-119; Charlesworth, B., D. Charlesworth and M. Loukas 1977, *DIS* 52:133; Hjorth, J.P. 1970, *Hereditas* 64:146-148; Lakovaara,

S. and Saura 1972, *DIS* 48:93; Porter, J.H., S.H. Boyer, E.J. Watson-Williams, A. Adam, A. Szienberg and M. Siniscalco 1964, *Lancet* 1:895; Trippa, G., C. Santolamazza and R. Scozzari 1970, *Biochem. Genet.* 4:665-667.

Grace, D. University of Oregon, Eugene.  
The Ubx/bx transvection effect in the entire compound chromosome C(2;3)EN.

In Ubx/bx flies, the phenotype is enhanced when one of the chromosomes is involved in a rearrangement which has a break in 3R between the locus of bx and the centromere (the transvection effect,

Series	Progeny	Exceptions	Transmitted	% tr.	0	4
A	1718	37 (2.2%)	11	29.7	11	0
B	1638	34 (2.1%)	9	26.4	7	2
C	1878	28 (1.5%)	15	53.5	14	1
D	1545	20 (1.3%)	8	40.0	7	1
E	1189	32 (2.7%)	11	34.4	11	0
F	1783	41 (2.3%)	27	51.2	21	0
G	1052	19 (1.8%)	4	21.1	4	0
H	1642	26 (1.6%)	10	38.5	8	2
I	2241	39 (1.7%)	18	46.2	16	2
J	1107	21 (1.9%)	7	33.3	7	0
K	3322	33 (1.0%)	12	36.4	11	1

Lewis 1954). In the entire compounds now available, the 3L arm is placed between the locus of bx and the centromere (composition: 3R3L·2L2R), and it is of interest to know whether breaks in 3R under these conditions can also exaggerate the Ubx/bx phenotype.

Flies carrying C(2;3)EN, Ubx chromosomes were irradiated with 3000 r and mated to flies with normal meta-centric third chromosomes

carrying bx<sup>34e</sup>. Following the numerical scale of 0-4, most of the progeny had a transvection score of 3; the exceptions fall into two distinct categories, those with a score of 0 or a weak 1 and those with a score greater than 3.

The table is a summary of the data. Over 90% have a score of 0. Since they occurred singly, in most cases, and in subsequent crosses appear to be the result of changes on the third chromosome, it seems likely that these represent induced changes of some sort. Some other exceptions also enhance or reduce the haltere effect. Mosaic and complete somatic and gonadal mutants were observed. Cytological analysis of these exceptions will be undertaken.

Gromko, M.H. Bowling Green State University, Bowling Green, Ohio. An attempt to reduce population size through extensive trapping.

Only one attempt to manipulate a local population of *Drosophila* through extensive trapping is reported in the literature (Dobzhansky and Wright 1943). One possible reason for the failure of extensive trapping to reduce population size in that experiment is that adults may have been im-

migrating to the study area from the large continuously wooded surrounding area. *Drosophila* have been demonstrated to show bait-directed movement (Johnston and Heed 1975) and to be capable of long distance migration. Here I report an attempt to reduce population size of *D. affinis* in an isolated woodlot. Although migration from other woodlots is not impossible, the frequency of such events is limited by the woodlot's island nature.

The study area, Carter Woods (Wood County, Ohio), is a small (6.3 acre) woodlot dominated by oak and hickory. It is surrounded by fields usually planted in corn. The nearest neighboring woodlot is 1.5 km distant, with no fence rows or migratory corridors of any kind between.

Sixty-four baits (old banana and yeast) were placed in the woodlot at 15.2 m (50 ft) intervals in a rectangular grid. The bait-grid was situated centrally, and occupied approximately 60% of the total wooded area. Collections were made in all activity periods in which it was not raining, and were carried out over a period of 18 consecutive days in August, 1979. Temperature, humidity, approximate wind speed and degree of cloud cover were recorded at the beginning of every collection period. Baits were removed and replaced with previously unused baits so that no bait was left in the woodlot for more than nine days.

8,157 individuals of 19 species of *Drosophila* were removed from the woodlot over the 18-day trapping period. The most abundant species and their approximate relative frequencies in the collections were *D. putrida* (0.35), *affinis* (0.25), *tripunctata* (0.11), *falleni* (0.09), *robusta* (0.06), and *algonquin* (0.05). The daily relative abundance data were analyzed using factor analysis and multiple regression (SPSS). Of the large number of data manipulations tried, the outcome that explained the largest amount of variability gave the following results. For the fungus-feeding species (predominantly *D. putrida*, *tripunctata*, and *falleni*), the regression of abundance on time was positive, large and highly significant. The increase in population size was not unexpected for these species as the experiment was carried out in late

summer when large numbers of mushrooms were evident throughout the woods. For *D. affinis*-- which has a population flush much earlier in the year--the regression of abundance on time was in fact negative in sign, but not significantly different from zero.

Thus, extensive trapping has failed to reduce population size of *D. affinis* significantly despite the fact that flies were probably not immigrating in numbers large enough to replace the trapped individuals. Apparently, replacements are abundantly available from within the small isolated woodlot.

This work was supported by the Faculty Research Committee at Bowling Green State University.

References: Dobzhansky, Th. and S. Wright 1943, *Genetics* 28:304-340; Johnston, S. and W.B. Heed 1975, *Am. Nat.* 109:207-216.

Gupta, J.P. Banaras Hindu University, Varanasi, India. A list of drosophilid species so far known from India.

There has always been a conspicuous gap in our knowledge of world distribution of *Drosophila* where India is concerned. Although a beginning of such study in the subcontinent of India was made as early as 1920, only about a decade ago

have workers shown renewed interest in such study. During these years several collections undertaken by various workers in different parts of the country have yielded considerable data on Indian species. Recently our extensive surveys in different localities of northeast India have uncovered several interesting new species inhabiting this region. A few of them have already been published; manuscripts for those remaining are in preparation and have also been included in this list. In this report an attempt is made to include all species so far described and recorded from India. However, the final picture of the Indian drosophilid species seems to be far from complete. There are undoubtedly more species awaiting discovery.

Genus <i>Amiota</i> Loew	1. <i>shillongensis</i>	Singh & Gupta (in press)
Genus <i>Cacoxenus</i> Loew	2. <i>punctatus</i>	Duda 1924, Syn. of <i>Gitonides perspicax</i> Knab 1914. Ref. McAlpine 1968, <i>Canad. Entomol.</i> 100(5):514.
Genus <i>Chymomyza</i> Czerny	3. <i>vaidyai</i>	Okada 1976, Nom. nov. for <i>Chymomyza pararufithorax</i> Vaidya & Godbole 1973, DIS 50:71.
Genus <i>Curtonotum</i> Macquart	4. <i>neoangustipennis</i>	Dwivedi & Gupta (in press)
Genus <i>Gitonides</i> Knab	5. <i>perspicax</i>	Knab 1914
Genus <i>Hypselothyrea</i> de Meijere	6. <i>guttata</i>	Duda 1926
Genus <i>Leucophenga</i> Mik	7. <i>varanasiensis</i>	Gupta 1974
	8. <i>albicineta</i>	(de Meijere 1908)
	9. <i>flavicosta</i>	Duda 1926
	10. <i>guttiventris</i>	(de Meijere 1911)
	11. <i>interrupta</i>	Duda 1924
	12. <i>neoangusta</i>	Vaidya & Godbole 1976
	13. <i>shillongensis</i>	Dwivedi & Gupta (in press)
	14. <i>subpollinosa</i>	(de Meijere 1914)
Genus <i>Liodrosophila</i> Duda	15. <i>angulata</i>	Dwivedi & Gupta (in press)
	16. <i>okadai</i>	Dwivedi & Gupta (in press)
	17. <i>penispinosa</i>	Dwivedi & Gupta (in press)
	18. <i>rufa</i>	Okada 1974
Genus <i>Lissocephala</i> Malloch	19. <i>metallescens</i>	(de Meijere 1914)
	20. <i>sabroskyi</i>	Wheeler & Takada 1964
Genus <i>Microdrosophila</i> Malloch	21. <i>purpurata</i>	Okada 1956
Genus <i>Mycodrosophila</i> Oldenberg	22. <i>gratiosa</i>	(de Meijere 1911)
Genus <i>Paraleucophenga</i> Hendel	23. <i>invicta</i>	(Walker 1857)
Genus <i>Scaptomyza</i> Hardy	24. <i>cristata</i>	Singh 1976
	25. <i>graminum</i>	(Fallén 1823)
	26. <i>pallida</i>	(Zetterstedt 1847)
	27. <i>plumata</i>	Singh 1976

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|--|----------------------------|---|
| Genus <i>Sinophthalmus</i> Coquillett                              | 28. <i>creberii</i>        | Singh 1976  |
| Syn. of subgenus <i>Erima</i> Kertész of genus <i>Amiota</i> Loew. | 29. <i>pictus</i>          | Coquillett 1904   |
| Ref. Okada 1971, Kontyû 39:83.                                     |                            |   |
| Genus <i>Stegana</i> Meigen  | 30. <i>subexcavata</i>     | Vaidya & Godbole 1976   |
| Genus <i>Zaprionus</i> Coquillett                                  | 31. <i>indiana</i>         | Gupta 1970  |
|  | 32. <i>multistriata</i>    | Sturtevant 1927   |
|  | 33. <i>paravittiger</i>    | Godbole & Vaidya 1972   |
|  | 34. <i>striata</i>         | Nirmala Sajjan & Krishnamurthy 1975   |
| Genus <i>Drosophila</i> Fallén                                     | 35. <i>albomicans</i>      | Duda 1924   |
|  | 36. <i>ananassae</i>       | Doleschall 1858   |
|  | 37. <i>andamanensis</i>    | Gupta & Ray-Chaudhuri 1970  |
|  | 38. <i>andamanensis</i>    | Parshad & Singh 1971. Syn. of <i>D. andamanensis</i> Gupta & Ray-Chaudhuri 1970. Ref. Gupta 1980, DIS 55.         |
|  | 39. <i>annulipes</i>       | Duda 1924   |
|  | 40. <i>anomelani</i>       | Reddy & Krishnamurthy 1973  |
|  | 41. <i>bambuphila</i>      | Gupta 1971  |
|  | 42. <i>birarmipes</i>      | Malloch 1924  |
|  | 43. <i>bicolovittata</i>   | Singh 1974  |
|  | 44. <i>bifasciata</i>      | Pomini 1940   |
|  | 45. <i>bipectinata</i>     | Duda 1923   |
|  | 46. <i>brachynephros</i>   | Okada 1956  |
|  | 47. <i>brevis</i>          | Parshad & Singh 1971; Homonym   |
|  | *48. <i>brindavani</i>     |   |
|  | 49. <i>brunettii</i>       | Ray-Chaudhuri & Mukherjee 1941  |
|  | 50. <i>bryani</i>          | Malloch 1934  |
|  | 51. <i>busckii</i>         | Coquillett 1901   |
|  | 52. <i>chamundiensis</i>   | Nirmala Sajjan & Krishnamurthy 1975   |
|  | 53. <i>chandrprabhiana</i> | Gupta & Ray-Chaudhuri 1970  |
|  | *54. <i>charmadiensis</i>  |   |
|  | 55. <i>coei</i>            | Okada 1966  |
|  | 56. <i>confusa</i>         | Staeger 1844  |
|  | 57. <i>coonorensis</i>     | Reddy & Krishnamurthy 1973  |
|  | 58. <i>coracina</i>        | Kikkawa & Peng 1938   |
|  | 59. <i>curviceps</i>       | Okada & Kurokawa 1957   |
|  | 60. <i>daruma</i>          | Okada 1956  |
|  | 61. <i>ebonata</i>         | Parshad & Duggal 1966   |
|  | 62. <i>emulata</i>         | Ray-Chaudhuri & Mukherjee 1941. Syn. of <i>D. melanogaster</i> Meigen 1830. Ref. Parshad, Narda & Paika 1964.     |
|  | 63. <i>epiobscura</i>      | Parshad & Duggal 1966   |
|  | 64. <i>eugracilis</i>      | Bock & Wheeler 1972. Nom. nov. for <i>D. (Tanygastrella) gracilis</i> Duda 1926, not <i>gracilis</i> Walker 1853. |
|  | 65. <i>ficuspila</i>       | Kikkawa & Peng 1938   |
|  | 66. <i>fusciostata</i>     | Okada 1966  |
|  | 67. <i>giriensis</i>       | Prakash & Reddy 1977  |
|  | 68. <i>gundensis</i>       | Prakash & Reddy 1977  |
|  | 69. <i>guptai</i>          | Dwivedi (in press)  |
|  | 70. <i>helvetica</i>       | Burla 1948  |
|  | 71. <i>hoozani</i>         | Duda 1923   |
|  | 72. <i>hypocausta</i>      | Osten Sacken 1882   |
|  | 73. <i>immacularis</i>     | Okada 1966  |
|  | 74. <i>immigrans</i>       | Sturtevant 1921   |
|  | 75. <i>jambulina</i>       | Parshad & Paika 1964 (identified in error as <i>seguyi</i> Smart in Gupta & Ray-Chaudhuri 1970c:59).              |
|  | 76. <i>kikkawai</i>        | Burla 1954  |
|  | 77. <i>krishnamurthyi</i>  | Nirmala Sajjan & Reddy 1975   |

Genus *Drosophila* Fallén  
(continued)

78. <i>kurseongensis</i>	Gupta & Singh 1977
79. <i>lacertosa</i>	Okada 1956
80. <i>latifshahi</i>	Gupta & Ray-Chaudhuri 1970
81. <i>lucipennis</i>	Lin 1972
82. <i>malerkotliana</i>	Parshad & Paika 1964
83. <i>maryensis</i>	sp. nov.
84. <i>mediobandes</i>	sp. nov.
85. <i>meijerei</i>	Wheeler 1959
*86. <i>meijerei indicus</i>	
87. <i>melanogaster</i>	Meigen 1830
88. <i>mercatorum</i>	
<i>pararepleta</i>	Dobzhansky & Pavan 1943
89. <i>minima</i>	Okada 1966
90. <i>montium</i>	de Meijere 1916
91. <i>multispina</i>	Okada 1956
92. <i>mundagensis</i>	Nirmala Sajjan & Reddy 1975
93. <i>mysorensis</i>	Reddy & Krishnamurthy 1970
94. <i>nasuta</i>	Lamb 1914
95. <i>neoelegans</i>	Gupta & Singh 1977
96. <i>neokuntzei</i>	Singh & Gupta (in press)
97. <i>neonasuta</i>	Nirmala Sajjan & Krishnamurthy 1973
*98. <i>neotruncata</i>	
99. <i>nepalensis</i>	Okada 1955
100. <i>notostriata</i>	Okada 1966
101. <i>novaspinofera</i>	Gupta & Singh (in press)
102. <i>novazonata</i>	sp. nov.
103. <i>obscuricornis</i>	(de Meijere 1915)
104. <i>orissaensis</i>	Gupta 1972
105. <i>parabipectinata</i>	Gupta & Ray-Chaudhuri 1970
107. <i>parazonata</i>	sp. nov.
108. <i>penidentata</i>	Singh & Gupta (in press)
109. <i>penispina</i>	Gupta & Singh (in press)
110. <i>pentaspina</i>	Parshad & Duggal 1966
111. <i>pentavittata</i>	Gupta & Ray-Chaudhuri 1970
112. <i>prashadi</i>	Brunetti 1923
113. <i>prolongata</i>	Singh & Gupta (in press)
114. <i>prostipennis</i>	Lin 1972
115. <i>pulchrella</i>	Tan, Hsu & Sheng 1949
116. <i>punjabiensis</i>	Parshad & Paika 1964
117. <i>pseudoananassae</i>	Bock 1971
118. <i>quadrilineata</i>	(de Meijere 1911)
119. <i>rajasekari</i>	Reddy & Krishnamurthy 1968
120. <i>ramamensis</i>	Dwivedi (in press)
121. <i>raychaudhurii</i>	Gupta 1969. Syn. of <i>D. rajasekari</i> Reddy & Krishnamurthy 1968. Ref. Bock & Wheeler 1972.
122. <i>repleta</i>	Wollaston 1858
123. <i>rhopaloa</i>	Bock & Wheeler 1972
124. <i>riverata</i>	Singh & Gupta 1977
125. <i>rufa</i>	Kikkawa & Peng 1938
126. <i>setaria</i>	Parshad & Singh 1971
127. <i>setitarsa</i>	sp. nov.
128. <i>silvalineata</i>	Gupta & Ray-Chaudhuri 1970
129. <i>subtilis</i>	Kikkawa & Peng 1938
130. <i>suzukii indicus</i>	Parshad & Paika 1964
131. <i>takashii</i>	Sturtevant 1927
132. <i>testacea</i>	van Roser 1840
133. <i>tricornbata</i>	Singh & Gupta (in press)
134. <i>trilutea</i>	Bock & Wheeler 1972
135. <i>trisetosa</i>	Okada 1966



Genus <i>Drosophila</i> Fallén	136. <i>tristipennis</i>	Duda 1924
(continued)	137. <i>trizonata</i>	Okada 1966
	138. <i>truncata</i>	Okada 1964
	139. <i>varietas</i>	Singh 1972

\*Indicates names were reported for new species, but no description of these supposedly new species has been published so far.

Gvozdev, V.A., T.I. Gerasimova, G.L. Kogan, Ya.M. Rosovsky, S.G. Smirnova.  
Institute of Molecular Genetics, USSR Academy of Sciences, Moscow 123182, USSR. A collection of G6PD mutations which suppress the lethal effect of mutations affecting 6-phosphogluconate dehydrogenase in *D. melanogaster*.

We have obtained 39 mutations in the *Zw* locus (1-63) (Lindsley and Grell 1968) of *D. melanogaster*. 32 mutations were induced with ethylmethane sulfonate (EMS), one with  $\gamma$ -irradiation as described earlier (Gvozdev et al. 1977), and six were selected as spontaneous mutations. All the mutations were selected as recessive X-linked suppressors which corrected the lethal effect of mutations inactivating 6-phosphogluconate dehydrogenase. The amount of protein product of

the gene as assessed by immunochemical techniques remained unchanged in all cases. Meanwhile if mutant individuals kept an active enzyme its properties usually differed from the wild type enzyme. These results suggest that all the mutations affect the structural part of the locus. The frequency of mutations affecting G6PD was evaluated by comparing the number of sisters and revertant brothers in the progeny of the cross between C(1)RM, *ywf* females and mutagen-treated *Pgd<sup>-</sup> pn/w<sup>+</sup>Y* males (no treatment in the case of spontaneous mutagenesis). The frequency came to  $6.6 \times 10^{-5}$  for EMS-induced mutations and about  $0.6 \times 10^{-6}$  for spontaneous mutations. Both figures accord with other people's data (Green 1977; Mukai and Cockevham 1977; Schalet 1957, 1978; Simmons and Crow 1977). The mutants showed a broad range of G6PD activities as assessed under optimum conditions for the wild type: from complete inactivity (17 mutations) to the normal level.

A study of mutant G6PD activity in *Drosophila* extracts revealed considerable activity oscillations probably due to the high and uncontrollable lability of the mutant enzyme. In some cases the G6PD activity in mutant extracts exceeded the G6PD activity in wild type *Drosophila* extracts, which shows that mutations may increase the maximum rate of the reaction catalyzed by G6PD.

In accordance with the proposed biological mechanism of suppression (Gvozdev et al. 1977) all null-mutations proved to be good suppressors, i.e., the number of males in the progeny which carried a lethal mutation and a suppressor did not differ from the number of normal sisters carrying linked X chromosomes. Most of the mutants keeping some level of G6PD activity also showed a good suppression of the lethal mutations, although this group included some weak suppressors (5,12,15,23,26,28,47).

The table shows that in most of the mutants that keep G6PD activity the enzyme is different from normal G6PD. It is not always possible, however, to establish a correlation between the degree to which the enzyme is changed and the level to which viability is restored. This is not surprising since the data on G6PD activity in vitro do not necessarily reflect its activity in the cell (Olaniyi et al. 1976). A similar situation has been described for mutant forms of human G6PD when the emergence of a chronic haemolysis of erythrocytes could not be related to specific changes in the enzyme's functional properties (Johnson et al. 1977).

A comparison of the viability of heterozygotes for various mutant alleles of the *Zw* gene with the viability of the corresponding homozygous stocks revealed the possibility of inter-allelic complementation, but only for combinations of (*su*)14 with three other suppressors (2,9 and 12). The number of *su*2/*su*14 and *su*9/*su*14 heterozygotes was decreased 5 to 50 times as compared with the corresponding males and their development was considerably delayed. The number of *su*2/*su*14 females was halved.

References: Green, M.M. 1977, Proc. Nat. Acad. Sci. USA 74:3490; Gvozdev, V.A., T.I. Gerasimova, G.L. Kogan and Ya.M. Rosovsky 1977, Molec. gen. Genet. 153:191; Johnson, G.J., M.E. Kaplan and E. Beutler 1977, Blood 49:247; Lindsley, D.L. and E.H. Grell 1968, Carnegie Inst. Wash. Publ. 627; Mukai, T. and C.C. Cockevham 1977, Proc. Nat. Acad. Sci. USA 74:2154; Olaniyi, A., G. Babalola, J.G. Beetlestone and L. Luzzatto 1976, J. Biol. Chem. 251:2993; Schalet, A.P. 1957, Genetics 42:393; \_\_\_\_\_ 1978, Mutation. Res. 49:313; Simmons, M.J. and J.F. Crow 1977, Ann. Rev. Genet. 11:49.

No. of mutation	Mutagenized X chromosome	Mutagen	G6PD activity in % of norm*	$K_m^{\text{NADP G6PD}}$ $\times 10^5 \text{M}^*$	$K_m^{\text{G6P G6PD}}$ $\times 10^5 \text{M}^*$	Maximum rate (V)*	Electrophoretic mobility of G6PD (in respect to Zw <sup>A</sup> and Zw <sup>B</sup> )	Thermo-sensitivity of G6PD
Wild type				0.6-1.5	4.7-11.8	37-51		
(Zw <sup>A</sup> )								
6**	139pnZw <sup>A</sup>	EMS						
7**	"	"						
8**	"	"						
10	"	"						
11	"	"						
13	"	"						
14	"	"						
16	"	"						
17	"	"	0.5-1					
18	"	"						
20	"	"						
21	"	"						
22	"	"						
24	135pnZw <sup>A</sup>	"						
31	"	Co <sup>60</sup> ( $\gamma$ -irrad.)						
34	139pnZw <sup>A</sup>	spontaneously						
36	"	"						
15	"	EMS	2-5					normal
23	"	"	7				adjacent to B	
27	"	"	4-10	46	40	11		
32	"	spontaneously	1-7					
33	"	"	2-6				A <sup>+</sup>	
44	171pnZw <sup>B</sup>	EMS	2-10		280			
45	"	"	4-10	10	430		A <sup>+</sup>	
1**	"	"	10-20	14.9 <sup>+</sup>	260		intermediate	
2**	"	"	4-20	23.7 <sup>+</sup>	360		"	
5**	"	"	3-20	33.0 <sup>+</sup>	590		"	
9	135pnZw <sup>A</sup>	"	90-130	11			"	increased
12	139pnZw <sup>A</sup>	"	90-140	1.2	15		"	"
19	"	"	30-60	2.9	280		"	

(continued)

(continued)

No. of mutation	Mutagenized X chromosome	Mutagen	G6PD activity in % of norm*	$K_m^{\text{NADP G6PD}}$ $\times 10^5 \text{M}^*$	$K_m^{\text{G6P G6PD}}$ $\times 10^5 \text{M}^*$	Maximum rate (V)*	Electrophoretic mobility of G6PD (in respect to $Zw^A$ and $Zw^B$ )	Thermo-sensitivity of G6PD
25	139pnZw <sup>A</sup>	EMS	30-70		11		A	increased
26	"	"	40-70	increased	increased		A <sup>+</sup>	
28	"	"	20-40	"	"		A	
29	"	"	70-130	1.8	86		A	increased
30	"	"	30-70	18	47	29	A	
35	"	spontaneously	20-180	9.0	130			increased
40	135pnZw <sup>A</sup>	EMS	20-130	2.0	2300	150	A	decreased
43	171pnZw <sup>B</sup>	"	7-20				intermediate	
47	139pnZw <sup>A</sup>	spontaneously	30-110	1.7	1300	120	A	decreased

\* The norm is the stock with the  $Zw^A$  isozyme.  $K_m^{Zw^A}$  and  $Zw^B$  coincide with regard to coenzyme and substrate. The mean activity of the normal stock is 60 nmol of reduced NADP/min/mg of protein. V is expressed in the same units.

\*\* G6PD mutations described earlier.

+ The staining intensity of the G6PD band is very low.

† To determine these values of  $K_m^{\text{NADP}}$  the extracts were obtained in a homogenization buffer without NADP. In this case the value of  $K_m^{\text{NADP}}$  for normal G6PD was  $7.4 \times 10^{-5} \text{M}$ .

Hägele, K. and W.-E. Kalisch. Ruhr-Universität Bochum, Germany.  $^3\text{H}$ -thymidine labeling intensity over a prominent band group prior to and during puffing.

$^3\text{H}$ -thymidine labeling experiments on polytene chromosomes of *D. melanogaster* have been made in order to check whether or not an alteration in the morphology of a chromosome section is correlated with a change in the amount of silver grains over it. In late third instar larvae (115 h after egg deposition) and white prepupae (0-2 h after puparium formation) region 61A-64C of chromosome arm 3L was analyzed autoradiographically at the discontinuously labeled end phases of the replication cycle. Especially section 63E1-5 was studied because the prominent band group of this region forms a large puff in prepupae.

Table 1. Silver grain labeling intensities over puffed and non-puffed 63E1-5 sections compared to reference sections.

	Ratios of silver grain numbers over sections		
	63E1-5/62C1-2	62A1-2/62C1-2	63A1-3/62C1-2
Puff 63E1-5 present	1.26	0.18	0.84
Puff 63E1-5 absent	0.64	0.22	0.85

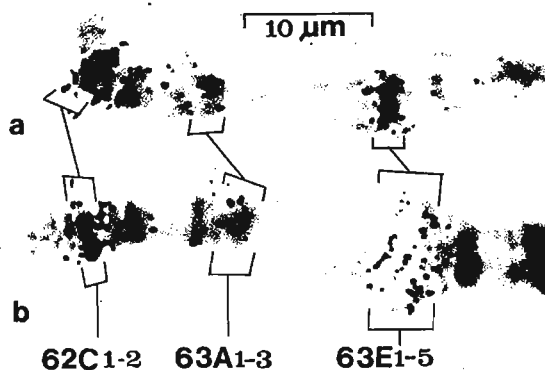


Fig. 1 a and b. Autoradiographs at the late replication phase of region 62C-63E in a late third instar larva (a) and a prepupa (b). Labeling intensities over 62C1-2 and 63A1-3 correspond with each other in (a) and (b). The puffed 63E1-5 section shows approximately twice as much silver grains as the 63E1-5 bands in (a).  $^3\text{H}$ -thymidine incubation of the excised salivary glands 10 min (50  $\mu\text{Ci}/\text{ml}$ ; spec. activity 24.0 Ci/m mol), exposure time 11 days, Giemsa stained. Autoradiographic methods and background determination have already been published (Hägele and Kalisch 1974; Kalisch and Hägele 1973, 1977).

The ratios of silver grain numbers over the puffed and non-puffed 63E1-5 sections and the reference sections 62A1-2 and 63A1-3 to those over section 62C1-2 were determined (Table 1). In 53 chromosomes, silver grain ratios between the reference sections correspond with each other during late third instar larvae and prepupae. However, the ratios of the 63E sections show that the labeling intensity over the puffed 63E1-5 section is twice as high as over the non-puffed 63E bands. Fig. 1 gives an example for labeling distributions over the 62B-64A region in a late third instar larva and a prepupa.

Our data do not agree with those of Zhimulev and Belyaeva (1975), which claim that the amount of silver grains over the 63E1-5 section does not de-

pend on whether the puff is present or not. Experimental methods used in this study, however, are quite different from ours. After hatching, larvae were incubated up to the 0 h and 1 h prepupa stage in a medium containing the radioactive precursors. In our experiments, pulse labeling with  $^3\text{H}$ -thymidine was only allowed to take place before (late third instar larva) or during (prepupae) puff formation of 63E. Furthermore, Zhimulev and Belyaeva (1975) have used a "correction factor" for silver grain calculations which is thought to correct region geometry and self-absorption of  $\beta$ -particles (Holmquist 1972). We have omitted this correction because the factor does not deal with the increase of a region's volume in the special case of puffing of a condensed band.

With regard to our results it could be argued that the molecules, necessary for DNA synthesis, more easily reach the DNA in the puffed state than in the condensed situation because of the less dense packing of the DNA protein complex in the puff (Berendes 1966). This would imply that replication in the puffed 63E1-5 section could proceed faster and that, therefore, the labeling intensity after  $^3\text{H}$ -thymidine application is higher than in the condensed 63E section. However, replication duration of 63E remains unchanged whether this region is puffed or not (Hägele and Kalisch, in press). Thus, an increased labeling intensity of the puffed 63E section, based on a faster replication, can be excluded. It seems more likely that in a

labeled puff section the changed conditions in comparison to the non-puffed state have an increasing effect on the silver grain numbers. In the transcriptionally active, puffed situation there is a greater area of chromosome contact with autoradiographic emulsion, a decreased clustering of the precursors incorporated and, presumably, a lowered self-absorption of  $\beta$ -particles on the basis of the changed DNA histone (nucleosome) configuration.

References: Berendes, H.D. 1966, *Chromosoma* 20:32; Hägele, K. and W.-E. Kalisch 1974, *Chromosoma* 47:403; \_\_\_\_\_ and \_\_\_\_\_, *Chromosoma* (in press); Holmquist, G. 1972, *Chromosoma* 36:413; Kalisch, W.-E. and K. Hägele 1973, *Chromosoma* 44:265; \_\_\_\_\_ and \_\_\_\_\_ 1977, *DIS* 52:127; Zhimulev, I.F. and E.S. Belyaeva 1975, *Chromosoma* 49:219.

Hankins, G.R. and A.F. Sherald. George Mason University, Fairfax, Virginia. Hydroypyrimidine hydrase in *D. melanogaster*.

The black mutation (2-48.5) of *Drosophila* is the result of a partial deficiency in beta-alanine synthesis (Hodgetts and Choi 1974); however, the specific enzymatic lesion is still unknown. Beta-alanine can be synthesized via a number of pathways including direct decarboxylation of aspartate, or by synthesis and degradation of uracil. In *Musca*, the major biosynthetic pathway proceeds through uracil (Ross and Monroe 1972), and in *Drosophila*, Jacobs (1974) found that, like beta-alanine, exogenous uracil, dihydrouracil and beta-ureidopropionate promoted normal coloration in black adults; and label from both orotate and uracil was incorporated more strongly into black than wild type cuticles. These data would suggest that black causes a partial metabolic lesion in the pathway via uracil, possibly prior to orotate. However, studies of several gene-

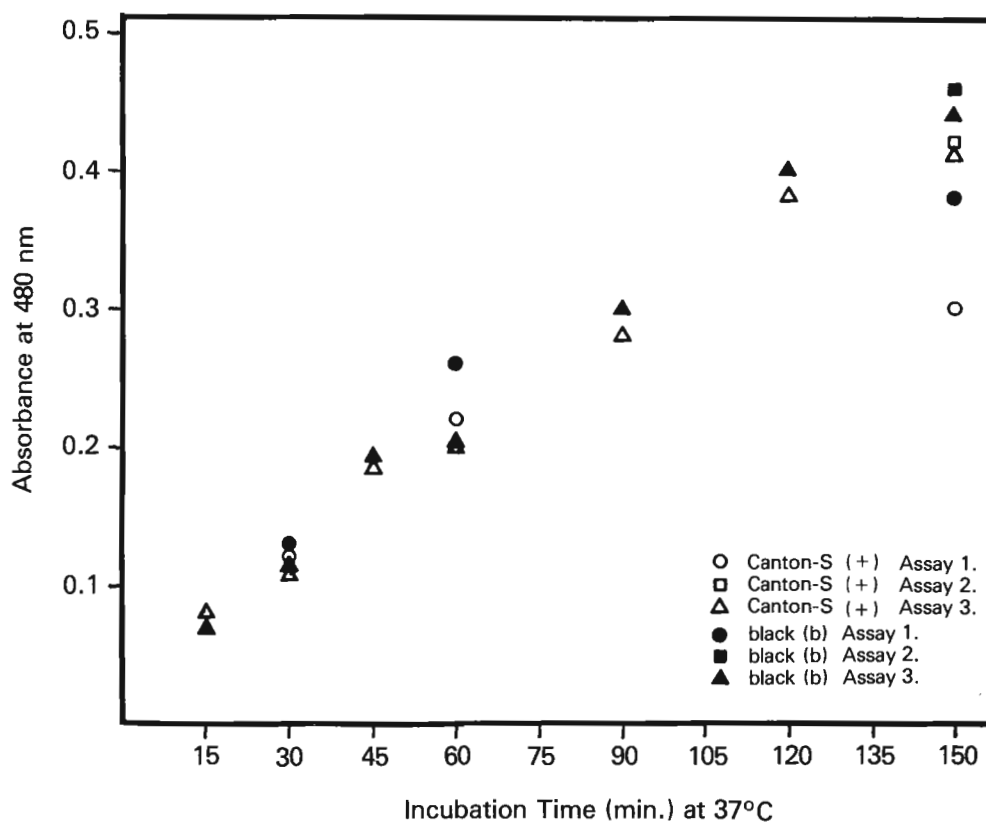


FIGURE 1. Hydroypyrimidine Hydrase Activity in Canton-S and black *Drosophila*.

Assays were performed using crude *Drosophila* supernatant of 100 flies/ml. Protein determinations were performed for assay no. 3 and no significant difference was found between black and Canton-S supernatants. Flies were usually no older than 9 hours.

enzyme systems are in complete contradiction to this interpretation. The first three enzymes in orotate synthesis are reduced by various of the alleles of rudimentary (Rawls and Fristrom 1975) and the last two by rudimental (Lastowski, pers. comm.). None of these mutations show a black phenotype, nor does suppressor of rudimentary which blocks the first step in uracil catabolism (Stroman et al. 1973). Therefore, if the black lesion does occur in the pathway via uracil, it must affect either of the final enzymes; hydroxypyrimidine hydrase or beta-ureidopropionase.

We have assayed hydroxypyrimidine hydrase EC 3.5.2.2. which catalyzes the conversion of dihydrouracil to beta-ureidopropionate. The spectrophotometric method described by Dudley et al. (1974) was used except that buffer was substituted for ethanol to attain better solubility of the substrate. Protein was determined by the method of Lowry et al. (1951). Canton-S was used as the wild type control and the black strain was back bred to Canton 11 times prior to the assays.

The results given in Fig. 1 fail to show any difference in activity between black and wild type for this enzyme. While beta-ureidopropionase remains to be tested, it appears more likely that black is a lesion in aspartate decarboxylase. Jacobs (1974) found a slight but significant decrease in  $^{14}\text{CO}_2$  excretion from black flies injected with labeled aspartate. Since a heterozygous deficiency of the wild allele also produces a black phenotype (Lindsley et al. 1972) suggesting that black homozygotes could have enzyme levels as high as 50% or more than wild type; and the available black alleles are leaky, homozygotes producing as much as 50% of normal levels of beta-alanine (Hodgetts 1972); more definitive results might be obtained with a direct in vitro assay for aspartate decarboxylase using either stronger black alleles or flies that are heterozygous for black and a deficiency of the wild allele. While the pathway through uracil is capable of compensating for black when supplied with exogenous substrates, it appears that the increased amounts of beta-alanine needed during puparium formation and eclosion are normally supplied by aspartate decarboxylase.

This research was supported in part by George Mason University Research Grant to A.F.S. The authors wish to thank Dr. George Andrykovitch, Ms. Martha Corjay, Mr. Thomas Hundley and Ms. Nancy Meinecke for their expert advice and assistance.

References: Dudley, K.H. et al. 1974, *Drug. Metab. Disp.* 2:103; Hodgetts, R. 1972, *J. Insect Physiol.* 18:937; Hodgetts, R. and A. Choi 1974, *Nature* 252:710; Jacobs, M.E. 1974, *J. Insect Physiol.* 20:859; Lindsley, D.L. et al. 1972, *Genetics* 71:157; Lowry, O.H. et al. 1951, *J. Biol. Chem.* 193:265; Rawls, J. and W. Fristrom 1975, *Nature* 233:738; Ross, R. and R. Monroe 1972, *J. Insect Physiol.* 18:1593; Stroman, P. et al. 1973, *Hereditas* 73:239.

Hartmann-Goldstein, I.J. Sheffield University, England. DNA-content of Malpighian tubule nuclei from white-variegated larvae.

In *D. melanogaster* the main segment of larval Malpighian tubules consists of two readily distinguishable cell types (Wessing and Eichelberg 1978): the numerous type I cells are relatively large, yellow in  $w^+$  tubules and in white-variegated strains may be colorless; the small and

flattened type II cells are colorless, generally occur singly, and tend to decrease in number towards the proximal end of the segment. To establish whether there are consistent differences in the degree of polyteny in these cell types, I used a Barr and Stroud GN2 integrating microdensitometer to measure the Feulgen-DNA content of formalin-fixed cells in one anterior tubule from each of four female  $T(1;4)w^m258-21$  prepupae reared at  $14^\circ\text{C}$ . In the squash preparations used, the relative positions of the cells in the tubule were largely preserved. Of 384 nuclei measured (Fig. 1; Table 1) all but 12 fell into 3 discrete DNA classes, with mean values of approximately 9, 36 and 70 arbitrary units. Presumably the class with the smallest mean differed from the other two classes by two and three replication steps respectively. The remaining 12 nuclei (shown on the histogram as unshaded areas, and not included in the tables) were, with only one exception, grouped between the two smaller classes and had a mean value of 19.2; they may represent the "missing" replication step.

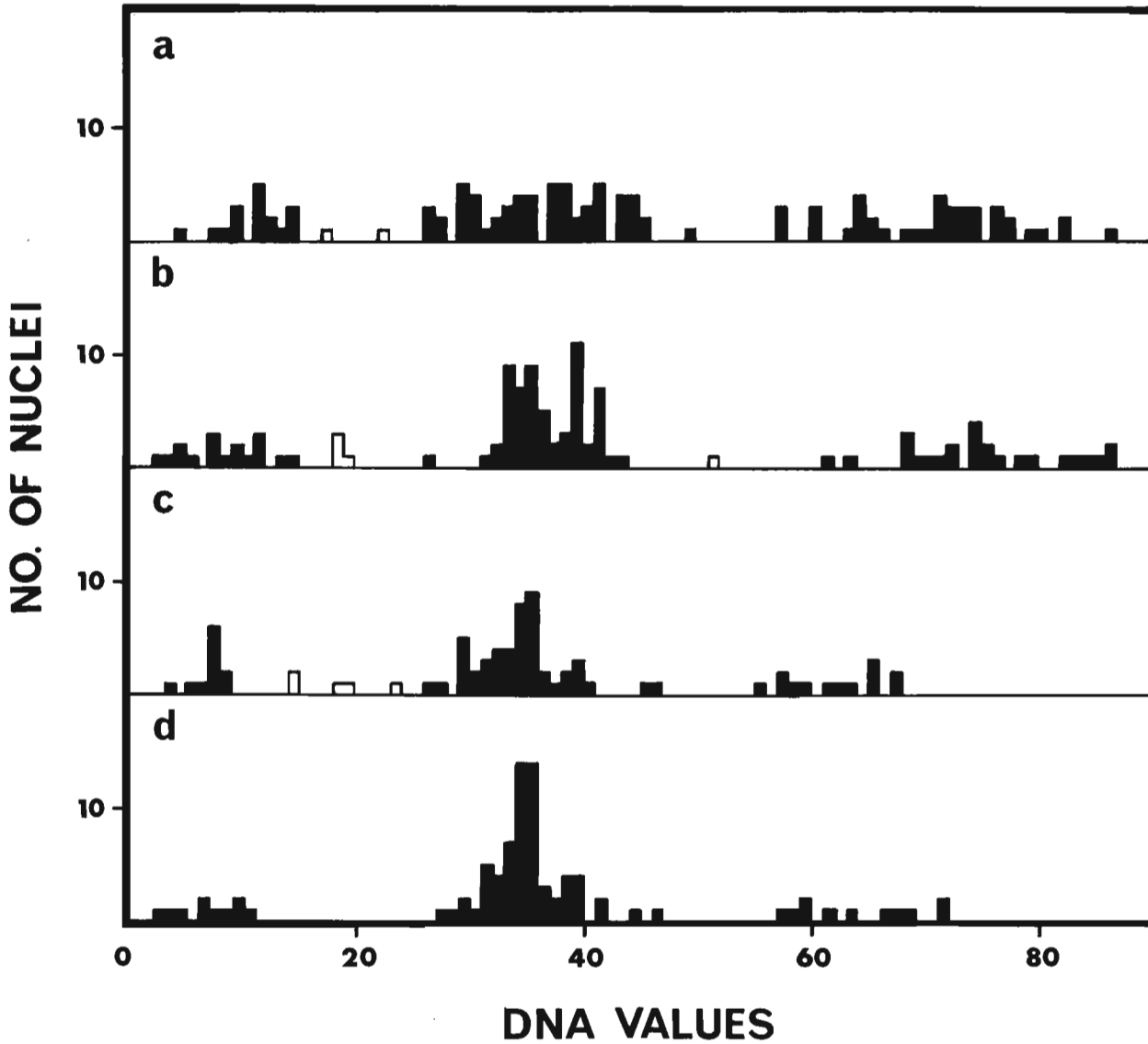
Nuclei falling into the lowest DNA class were usually distributed singly and were somewhat more numerous toward the distal end of the tubule. It seems probable, therefore, that they belong to type II cells. Nuclei in the highest class were most numerous in the proximal regions while those in the next lower class predominated near the distal end. In the intermediate regions these two classes were represented in approximately equal numbers, and nuclei

Table 1. Mean Feulgen-DNA values, in arbitrary units, of Malpighian tubule nuclei in three DNA classes.

Prepupa	N	$\bar{M}$	SE
a	17	11.40 ± 0.65	
	59	36.96 ± 0.76	
	40	71.03 ± 1.15	
b	18	8.28 ± 1.03	
	58	37.31 ± 0.45	
	25	75.92 ± 1.40	
c	13	8.69 ± 0.86	
	49	34.73 ± 0.61	
	13	63.0 ± 1.26	
d	10	7.40 ± 0.86	
	59	35.86 ± 0.45	
	11	64.64 ± 1.57	

Table 2. Comparison of mean Feulgen-DNA values in pigmented and unpigmented cells.

Prepupa	N	$\bar{M}$	SE
c unpigmented	13	8.69 ± 0.86	
	27	32.93 ± 0.72	
	3	64.0 ± 3.0	
c pigmented	-	-	-
	22	36.96 ± 0.81	
	10	62.70 ± 1.45	
d unpigmented	10	7.40 ± 0.86	
	24	35.13 ± 0.48	
	5	61.0 ± 0.89	
d pigmented	-	-	-
	35	36.37 ± 0.67	
	6	67.67 ± 2.11	



of a given class occurred either singly or in groups of two or three. This distribution pattern is reminiscent of white-variegation, since those type I cells which are colorless usually occur singly or in small groups, and are frequently more common towards the distal than the proximal end of the tubule.

Two of the tubules (c and d in the illustrations) had been pre-fixed in 2% mercuric chloride (which preserves the pigmentation and improves the contrast between pigmented and unpigmented cells), and photographed before being fixed and stained. The DNA-content of individual cells could therefore be correlated with presence or absence of pigment. To investigate the possibility that degree of polyteny and variegated position effect are related, the DNA-content of pigmented and unpigmented cells was compared (Table 2). Cells with the lowest DNA content were always unpigmented, confirming the conclusion that they are of type II; the absence of pigment in this cell type is not related to variegation, since type II cells are colorless even in wild-type strains. All 12 unclassified nuclei belonged also to unpigmented cells, which suggests that they too may be of type II. The nuclei in the two highest DNA classes were found in similar proportions in pigmented and unpigmented cells; in neither tubule was the difference statistically significant ( $\chi^2 = 0.421$  and  $0.086$  respectively in c and d). Thus in larval Malpighian tubules the absence of pigment associated with variegated position effect does not appear to be related to degree of polyteny.

Reference: Wessing, A. and D. Eichelberg 1978, in: *The Genetics and Biology of Drosophila* (Ashburner, M. and T.R.F. Wright, eds., Academic Press) Vol. 2c:1-41.

Heed, W.B. University of Arizona, Tucson, Arizona. Central and marginal populations revisited.

*D. mojavensis* appears to be an exemplary species with which to study the ecology and life history strategies of populations containing substantial amounts of inversion heterozygosity ("central populations") and those with little or none ("marginal populations") chiefly because the geographic areas containing each kind of population are approximately equal in size and the host plants are well known in each case. Furthermore, detailed field studies may be accomplished on a year-round basis.

Central populations are considered by many investigators to be (1) geologically older and to live under conditions considered to be (2) spatially more heterogeneous and (3) temporally more predictable. The question arises whether all three conditions are necessary for the origin and maintenance of inversion heterozygosity. Our preliminary studies are demonstrating that increased trophic resource predictability is a characteristic feature of areas in which *D. mojavensis* maintains inversion heterozygosity while increased niche diversity or breadth is not immediately evident. The question of geologic age is at least not disputed.

*D. mojavensis* spends its entire life cycle on chiefly two host plants. In Baja California, the islands in the Gulf and in the Desemboque Region of Sonora, *mojavensis* utilizes agria cactus, while in the remainder of Sonora and in northern Sinaloa and southern Arizona, the species switches to the organ pipe cactus. Of special interest is the fact that all inversion heterozygosity on chromosome 2 (4 common gene arrangements and 3 rare gene arrangements) and the major portion of the heterozygosity on chromosome 3 (2 gene arrangements) are restricted to populations living in agria cactus. Furthermore, while there are areas in Baja California which have lower heterozygosities than other areas, none of the more than 30 localities sampled were completely monomorphic for gene arrangements. By contrast populations living in organ pipe are invariably monomorphic in the northern half of their distribution and three localities where heterozygous in chromosome 3 in the south. In general then, and as a first approximation, populations living in agria cactus are considered to be central or subcentral while those living in organ pipe are called marginal or submarginal populations. The data on the inversions was kindly supplied by William R. Johnson.

*D. mojavensis* spends its entire life cycle on chiefly two host plants. In Baja California, the islands in the Gulf and in the Desemboque Region of Sonora, *mojavensis* utilizes agria cactus, while in the remainder of Sonora and in northern Sinaloa and southern Arizona, the species switches to the organ pipe cactus. Of special interest is the fact that all inversion heterozygosity on chromosome 2 (4 common gene arrangements and 3 rare gene arrangements) and the major portion of the heterozygosity on chromosome 3 (2 gene arrangements) are restricted to populations living in agria cactus. Furthermore, while there are areas in Baja California which have lower heterozygosities than other areas, none of the more than 30 localities sampled were completely monomorphic for gene arrangements. By contrast populations living in organ pipe are invariably monomorphic in the northern half of their distribution and three localities where heterozygous in chromosome 3 in the south. In general then, and as a first approximation, populations living in agria cactus are considered to be central or subcentral while those living in organ pipe are called marginal or submarginal populations. The data on the inversions was kindly supplied by William R. Johnson.

Trophic resource predictability is being measured by three different methods: (1) surveys of the host plant density and density of the necrotic tissue, (2) correlations of the variation in biotic and abiotic factors in the necrotic tissue and (3) comparison of yeast species diversity in both host plants. A total of 13 plant censuses have been conducted throughout the Sonoran Desert to date. Nine of these were made in agria cactus and four were made on organ pipe cactus (data kindly supplied chiefly by Robert L. Mangan, Jean S. Russell and William T. Starmer). The areas surveyed varied in size from 3 to 62 acres. In one area of 54 acres both agria and organ pipe were scored. The mean number of organ pipe plants per



acre was 11.6 with a range of 2.4 to 21.7. The agria cacti averaged 46.9 plants per acre with a range of 4.3 to 167.1. The latter figure represents a survey of about 4 acres in southern Baja California. These occasional thickets are produced vegetatively and are probably nurtured by the decaying stems themselves as they bend down and take root. We can tentatively state that agria cactus is generally more abundant than organ pipe even though it is not as large. The mean frequency of rotting plants among all plants scored was 13.5% of 4,100 agria cacti compared to 6.1% of 286 organ pipes. The biological difference is even greater, however, since many organ pipe rots do not contain *D. mojavensis* larvae while the majority of agria rots do.

The second method for measuring resource predictability was attempted by correlating the variation in concentration of yeasts, low molecular weight volatiles, and abiotic factors such as pH and temperature, with each other, and with the presence or absence of adult *D. mojavensis* (information kindly supplied by Don C. Vacek). Four significant correlations were found in agria rots while only one was found in organ pipe rots. Therefore, a *D. mojavensis* female can better assess an agria rot for both feeding and egg laying. For instance, there is a positive correlation between the concentration of ethanol, 2-propanol and other volatiles with the presence of adult *D. mojavensis* and a negative correlation between the concentration of these volatiles and the concentration of yeasts in the substrate. As the necrotic tissue advances, the yeasts increase in density, at least in part, at the expense of the volatiles and subsequently for the benefit of the maturing larvae. In the case of organ pipe necrotic tissue, the only significant correlation found was a negative one between pH and volatile concentration. No correlations were detected for temperature in either host plant.

Yeast species comparisons among host plants showed agria rots to be more predictable because they are less variable (data kindly offered by William T. Starmer). There were 4 effective species out of 12 species recovered in this host compared to 5.4 effective species out of 9 species recovered in organ pipe. On a per-plant basis, agria averages 1.8 species of yeast while the organ pipe average is 2.2. Furthermore, on a per-isolate basis, the yeasts from agria utilize an average of 8.5 compounds for growth (N=183) while those from organ pipe utilize an average of 10.1 compounds (N=83). Since the variance of these means is twice as high in organ pipe (31.0 vs 16.5) it means this plant is a more variable environment. The most notable evidence we have for this lies in the presence or absence of *Pichia cactophila*, probably the most important yeast for *D. mojavensis* since it is a good indicator of the presence or absence of larvae. This yeast was recovered in 73% of 105 agria rots sampled compared to 59% of 41 organ pipe rots. The difference is marginally significant.

In summary, central populations live in a more predictable environment than marginal populations because of the greater abundance of rots which have higher resolving power for the flies and which are more suitable (chemically stable?) for the growth of the nutritionally favored yeast. The first and last points may be a reflection of the asexual reproduction periodically exhibited in agria cactus.

Hilliker, A.J. University of British Columbia, Vancouver, British Columbia.\* Heterochromatic duplications and the meiotic segregation of compound second autosomes during spermatogenesis of *D. melanogaster*.

It is well documented that in *D. melanogaster* females bearing compound second or third autosomes (and no additional structural heterologues or supernumerary chromosomes) that the complementary compound autosomes regularly disjoin from each other at meiosis (Holm 1969; Grell 1970; Holm and Chovnick 1975). That this segregation was not dependent on heterochromatic

homology between the two compound autosomes was clear as it could be easily perturbed by the introduction of a Y chromosome, by the substitution of an attached X chromosome for the two free X chromosomes or by structural heterozygosity for the other autosome.

The present of meiotic pairing sites active during spermatogenesis and responsible for the meiotic segregation of the X and Y chromosomes (reviewed in Peacock and Miklos 1973) led to the speculation that analogous sites may exist in the autosomal heterochromatin. Nevertheless, Holm (1969; Holm and Chovnick 1975) in the analysis of compound third autosomes

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found that they behaved as nonhomologous chromosomes during spermatogenesis. As recent work has demonstrated that compound autosomes arise by a translocation mechanism (reviewed in Holm 1976; Hilliker 1978), any pair of compound autosomes share heterochromatic homology and, hence, one would expect some pairs of compound third autosomes to exhibit non-random segregation during male meiosis given the existence of pairing sites in the autosomal heterochromatin.

Holm (1969) in examining the meiotic segregation during spermatogenesis of compound second autosomes in several *Drosophila* strains found that none of the compound second autosomes examined segregated randomly, that is, there was a smaller proportion of sperm recovered nonsegregational for the compound autosomes than would be predicted from a model of random segregation. However, such departures from random segregation are minor and may be the consequence of elimination of one compound autosome from a proportion of diplo-2 spermatid nuclei (see Hardy 1975).

Sandler et al. (1968) found a C(2R) chromosome which apparently segregated in males with relatively high efficiency from any C(2L) chromosome with which it was tested in combination. The segregational properties of this chromosome, C(2R)cn, were further analyzed by Evans (1971) and Gethmann (1976). C(2R)cn carries a 2L duplication extending from the centomere to 38 or 39 (E.B. Lewis, unpubl., cited in Gethmann 1976) and is, therefore, duplicated for the 2L heterochromatin as well as 2L proximal euchromatin. Gethmann (1976) suggests that the relatively efficient segregation of C(2R)cn from C(2L) is due to the 2L duplication and specifically to the duplication of pairing sites in the heterochromatin. Equally likely is that C(2R)cn is duplicated for a pairing site in the 2L proximal euchromatin. Yamamoto's (1979) cytological analysis of the meiotic segregation of C(2R)cn from a complement C(2L) during spermatogenesis led him to conclude that these chromosomes segregated randomly; however the data in support of this conclusion are not presented in sufficient detail to allow statistical evaluation.

In our laboratory a number of compound autosomes carrying heterochromatic duplications of a portion of the complementary arm have been constructed. For example, C(2L)SH1+ carries a duplication of 2R extending from the centomere to a point distal to the *rl*<sup>+</sup> locus within the 2R heterochromatin. Our previous analysis of the second chromosome proximal heterochromatin (Hilliker and Holm 1975; Hilliker 1976) has enabled us to set limits on the extent of the duplications associated with compound second autosomes. C(2L)SH1+ and C(2L)VH1 lt, which bear *rl*<sup>+</sup> duplications of 2R, are duplicated for at least half of the 2R heterochromatin and C(2R)VK2bw is duplicated for most of the 2L heterochromatin.

In order to examine the role, if any, of heterochromatin homology in meiotic pairing in males, the segregation of compound autosomes bearing duplications for heterochromatic material of the complementary compound autosomes was assayed. Segregation was assayed by crossing males of the selected compound-second autosome bearing strains to differentially marked compound-second autosome bearing females possessing a Y-chromosome. These BSY; C(2L)P,b; C(2R)P,px females give, as first demonstrated by E.H. Grell (1970) for BSY; C(2L); C(2R) bearing females in general, a high frequency of compound-second autosome nonsegregation. Female gametes nonsegregational for the compound second autosomes will result in a viable zygote only if fertilized by a sperm nonsegregational for the paternal compound-second autosomes. Thus a strain in which compound-second autosomes partially segregate in males when crossed to BSY; C(2L)P,b; C(2R)P,px females will give a lower frequency of progeny completely matroclinous or patroclinous for the two compound-second autosomes than will a strain in which C(2L) and C(2R) segregate at random in the male.

Therefore, males of the C(2L)SH3+;C(2R)SH3+ strain, one in which nearly equal frequencies of C(2L); C(2R); diplo-2; and nullo-2 sperm are produced (Holm 1969), and of several other strains in which one or both compound autosomes bore heterochromatic duplications of the other arm were crossed singly in shell vials to BSY;C(2L)P,b;C(2R)P,px virgin females. The results are presented in Table 1 and in summary form in Table 2.

Since there is no significant reduction in the frequency of nonsegregation in those crosses involving males carrying C(2L) and C(2R) chromosomes with extensive heterochromatic homology (Table 2), it is probable that heterochromatic homology per se is not a major factor in the meiotic segregation of autosomes in male *D. melanogaster*. Further, in conjunction with the compound third chromosome studies, as well as studies involving autosomes (and autosomal derivatives) heterozygous for heterochromatic deletions (Yamamoto 1979; Hilliker 1980), these data provide evidence for the absence of male meiotic pairing sites in the bulk of the autosomal heterochromatin.

The foregoing data have been abstracted from Hilliker (1975).

Table 1. Progeny of B<sup>SY</sup>; C(2L)P,b; C(2R)P,px females and various compound second autosome bearing males.

Male genotype	Chromosome from mother						B <sup>SY</sup>	0	Total
	B <sup>SY</sup>	B <sup>SY</sup>		B <sup>SY</sup>		B <sup>SY</sup>			
	C(2L)P,b; C(2R)P,px	C(2L)P,b; C(2R)P,px	C(2R)P,px	C(2R)P,px	C(2L)P,b	C(2L)P,b			
C(2L)SH3,+ C(2R)SH3,+	1	462	300	273	204	279	247	5	1771
C(2L)SH1,Dp(2R)r1+ C(2R)SH1,+	1	567	395	365	286	383	447	4	2448
C(2L)SH1,Dp(2R)r1+ C(2R)SH3,+	0	57	39	46	31	47	44	0	264
C(2L)SH3,+ C(2R)VK2,Dp(2L)1t+,bw	0	127	153	146	122	174	215	3	940
C(2L)VH1,Dp(2R)r1+,1t C(2R)VK2,Dp(2L)1t+,bw	1	122	127	102	80	146	163	1	742

Table 2. Frequency of progeny nonsegregational for compound-second autosomes from B<sup>SY</sup>; C(2L)P,b; C(2R)P,px virgin females crossed to various strains of compound-second autosome bearing males.

C(2L)	C(2R)	Percent nonsegregational progeny	N
SH3+	SH3+	40.4	1771
SH1+*	SH1+	41.6	2448
SH1*	SH3+	38.3	264
SH3+	VK2bw**	36.7	940
VH11t*	VK2bw**	38.7	742

\* Bears a r1+ duplication of 2R.

\*\* Bears a 1t+ duplication of 2L.

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Hilliker, A.J.\*, A. Chovnick and S.H. Clark. Univ. of Connecticut, Storrs, Connecticut. The relative mutabilities of vital genes in *D. melanogaster*.

In recent years, several chromosomal regions of *D. melanogaster* have been subjected to intensive analysis. Most of these studies have focused primarily on the identification of genes capable of mutating to a lethal or semi-lethal state within a short, defined chromosome segment. How-

ever, the screens employed were generally competent to detect genes whose mutant alleles exhibit a recessive alteration in visible phenotype.

If all vital genes in a given region were equally mutable, then it would be possible to employ the Poisson distribution to determine the number of unmutated genes remaining after completion of a mutagenesis study. Cohen (1960) has discussed such methods for truncated Poisson distributions. It is, however, generally appreciated that vital genes within a given chromosomal interval are not of equal mutability, a point we herein substantiate and document for several regions of the *Drosophila* genome that have been extensively analyzed.

Since the Poisson distribution has only one parameter, the mean ( $m$ ), which is equal to the variance, it is possible to determine if a given distribution of counts differs from a Poisson distribution by use of the variance ratio,  $s^2/m$ , where the sample mean square,  $s^2$ , estimates the variance of the distribution, and where  $m$  has infinite degrees of freedom (see discussion in Gilbert 1973). The variance ratio test of significance for deviation from the Poisson distribution is preferable to the chi square test in that it is more readily applicable to smaller data samples. Moreover, even in situations where one can apply the chi square test, the variance ratio test is associated with a greater number of degrees of freedom. Where the variance ratio is not significantly different from one, indicating possible agreement with a Poisson distribution, it is possible that the count distribution does differ from a Poisson distribution. Such cases would be better revealed by the chi square test which examines the entire distribution. However, this issue is irrelevant with respect to the present analysis since (1) the sample counts are too small to employ the chi square test, and (2) none of the 11 data sets examined are in good agreement with a Poisson distribution by the variance ratio test.

Table 1 summarizes a series of mutagenesis experiments that are competent to determine if vital genes within a given region are equally mutable by a given mutagen. Each entry represents a mutagenesis screen in which lethal mutations for all genes within a region are detected following treatment of sperm with the indicated mutagen. The data for the regions defined by Df(3R)ry<sup>614</sup> (Df(3R)87D2-4; 87D11-14) and Df(3R)ry<sup>619</sup> (Df(3R)87D7-9; 87E12-F1) were obtained in this laboratory as part of a larger analysis of the chromosome interval adjacent to the rosy locus (Hilliker et al. 1980).

The six regions included in the analysis of Table 1 involve both euchromatic and heterochromatic segments of the *Drosophila* genome. In no instance are the vital genes within a segment of equal mutability. Of the 11 experiments examined in Table 1, only the analysis of fourth chromosome spontaneous mutations failed to show a significant deviation from the Poisson expectation. The P value for this count distribution is greater than 0.05 but less than 0.10.

On the basis of these data, we are led to conclude that *Drosophila* vital genes within a defined chromosome segment are not of equal mutability. Hence, one cannot use the Poisson distribution to estimate the number of remaining unmutated vital genes within such an extensively analyzed segment.

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Table 1. Variance ratio analyses for the 11 indicated mutagenesis experiments involving six chromosomal intervals in *D. melanogaster*.

Region analyzed	No. of lethal complementation groups	Mutagen	Mean no. of alleles per complementation group	Variance	Variance ratio	Reference
Chromosome 4	36	Spontaneous	0.806	1.190	1.477 <sup>†</sup>	Hochman 1973
		X-rays	0.833	2.486	2.983***	
		EMS	3.111	18.273	5.873***	
		ICR-170	0.306	0.733	2.397***	
2R Heterochromatin	6	EMS	14.000	202.800	14.486**	Hilliker 1976
2L Heterochromatin	7	EMS	4.000	20.000	5.000**	Hilliker 1976
Df(3R)ry <sup>614</sup>	9	EMS	3.778	23.444	6.206**	Hilliker et al. 1980
Df(3R)ry <sup>619</sup>	15	EMS	4.933	20.210	4.097**	Hilliker et al. 1980
Zeste-white	15	EMS	5.533	53.552	9.678***	Lim & Snyder 1974
		TEM	1.800	10.029	5.571***	
		MMS	7.000	37.286	5.327***	

<sup>†</sup> 0.05 < P < 0.10

\*\* P < 0.01

\*\*\* P < 0.001

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Hilliker, A.J.\*, S.H. Clark, W.M. Gelbart\*\* and A. Chovnick. University of Connecticut, Storrs, Connecticut. Cytogenetic analysis of the rosy micro-region, polytene chromosome interval 87D2-4; 87E12-F1, of *D. melanogaster*.

Figure 1 presents a summary of our cytogenetic analysis of the rosy micro-region. A total of 153 recessive lethals falling into this region were subdivided by inter se complementation, and complementation tests with rosy region deficiencies, into 20 lethal complementation groups. Adjacent complementation groups illustrated within parentheses in Fig. 1 have not

been separated by deficiency from one another, hence their relative left-right order is unknown.

The recessive lethals employed in this study are listed in Table 1 according to complementation group (beginning with the most proximally located and continuing through to the most distal). Each listed recessive lethal mutation is accompanied by a description of its source, the mutagen used and, where possible, the isogenic third chromosome on which it was constructed (designated by the specific ry<sup>+</sup> allele carried on that chromosome).

A majority of the 153 recessive lethals listed in Table 1 were synthesized by Hilliker and Clark (120) as lethal alleles of Df(3R)ry<sup>614</sup> (34), Df(3R)ry<sup>619</sup> (83) and Df(3R)ry<sup>75</sup> (3) (see Table 2). These recessive lethals were recovered from the treatment of iso-3 males with either 0.025M EMS (Lewis and Bacher 1968) or gamma radiation (2000 to 4000 rads).

Since the majority of recessive lethals were synthesized as alleles of Df(3R)ry<sup>614</sup> or Df(3R)ry<sup>619</sup>, the region encompassed by these deficiencies, 87D2-4; 87E12-F1, defines the rosy micro-region.

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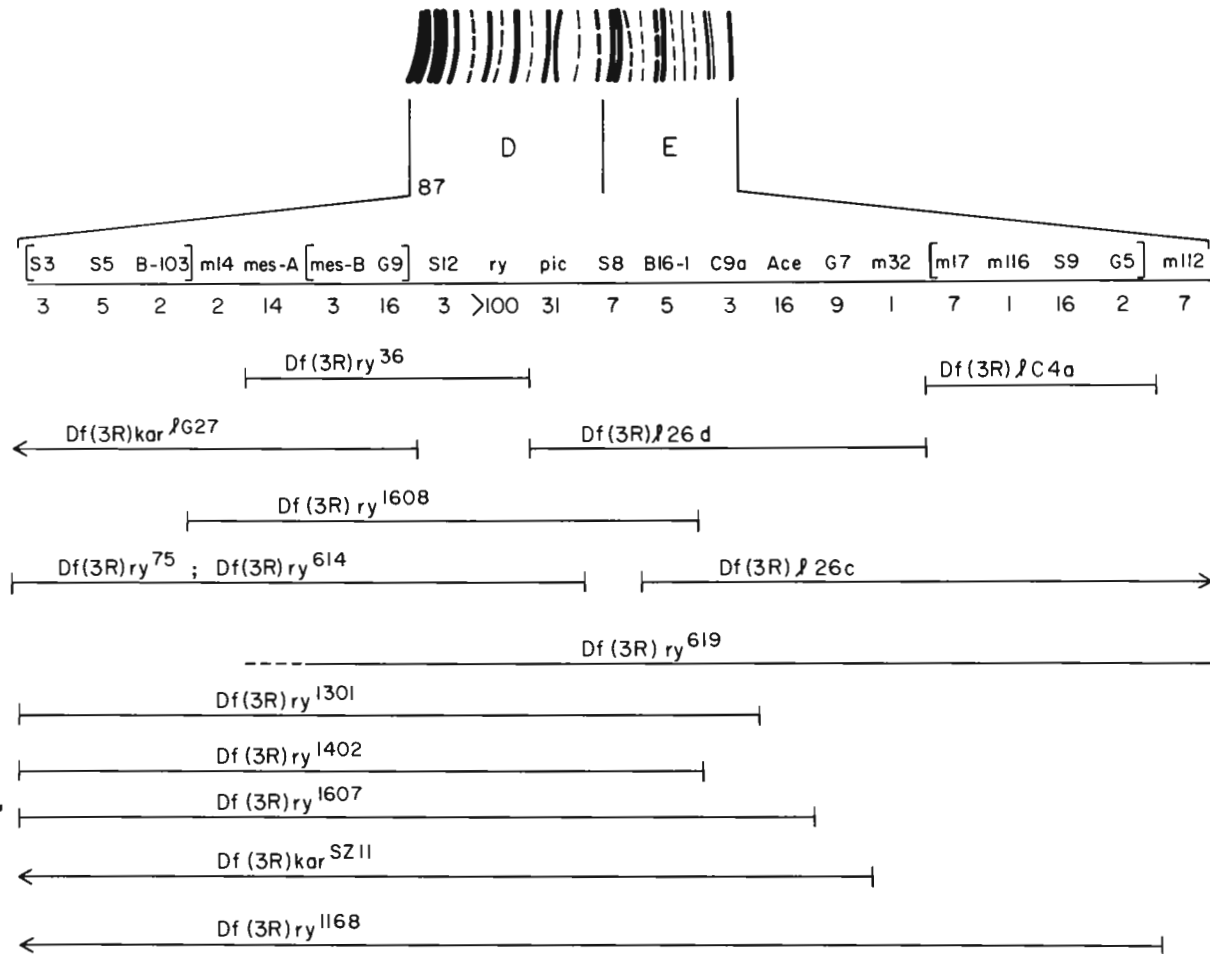


Figure 1. Summary of the cytogenetic analysis of polytene chromosome region 87DE.

The rosy region recessive lethals synthesized by Gelbart, by Schalet and by Deland (Table 1) were selected as lethal alleles of larger deficiencies which encompassed the entire 87D2-4; 87E12-F1 interval. Further details on the synthesis of the recessive lethals provided by Schalet and by Deland may be found in Schalet, Kernaghan and Chovnick (1964) and Deland (1971).

Each rosy region recessive lethal was subsequently tested for complementation with the rosy region deficiencies listed in Table 2.

On the basis of complementation tests with rosy region deficiencies, the recessive lethals fell into 14 clusters. Within each cluster, ALL inter se combinations of recessive lethals were examined for complementation. Further, when the recessive lethals within each cluster were resolved into complementation groups, each recessive lethal within each cluster was tested for complementation with a representative allele of each of the complementation groups defining the immediately adjacent clusters. Finally, most recessive lethals were tested for complementation with a representative allele of each complementation group within the rosy micro-region.

Let us now consider, briefly, each functional group in terms of phenotype and complementation pattern, beginning with the most proximally located.

The 1(3)S3 complementation group is associated with two additional, semi-lethal alleles, 1(3)A34-1 and 1(3)A46-1. The 1(3)A46-1 allele is associated with a mean viability of approximately 15% when heterozygous with 1(3)S3. Both alleles, when heterozygous with 1(3)S3, are associated with variation in dorsocentral bristle number and length. Further, among heterozygotes for the semi-lethal alleles and 1(3)S3, females greatly outnumber males. The 1(3)A34-1/1(3)A46-1 heterozygotes are associated with about 75% viability and normal bristle morphology and sex ratio.

Table 1. Recessive lethals listed according to complementation group.

Lethal allele	Isogenic third chromosome	Mutagen	Source	Lethal allele	Isogenic third chromosome	Mutagen	Source
1(3)S3	--	X-rays	Schalet	1(3)A39-2	ry+4	EMS	Hilliker, Clark
1(3)A34-1	ry+4	EMS	Hilliker, Clark	1(3)B10-1	ry+11	EMS	Hilliker, Clark
1(3)A46-1	ry+4	EMS	Hilliker, Clark	1(3)B13-2	ry+11	EMS	Hilliker, Clark
1(3)S5	--	X-rays	Schalet	1(3)B13-3	ry+11	EMS	Hilliker, Clark
1(3)C8a	--	X-rays	Chovnick	1(3)B23+1	ry+11	EMS	Hilliker, Clark
1(3)E4a	--	X-rays	Chovnick	1(3)B25-1	ry+11	EMS	Hilliker, Clark
1(3)G12	ry+2	EMS	Gelbart	1(3)H37	ry+11	EMS	Hilliker, Clark
1(3)9-13	ry+11	EMS	Hilliker, Clark	1(3)H73	ry+11	EMS	Hilliker, Clark
1(3)B-103	ry+11	EMS	Hilliker, Clark	1(3)H2	ry+11	Gamma	Hilliker, Clark
1(3)A6-1	ry+4	EMS	Hilliker, Clark	1(3)H23	ry+11	Gamma	Hilliker, Clark
1(3)m14	--	EMS	Deland	1(3)S12	ry+11	X-rays	Schalet
1(3)10-194	ry+11	EMS	Hilliker, Clark	1(3)G1	ry+2	EMS	Gelbart
1(3)mes-1A	--	X-rays	Schalet	1(3)B21-4	ry+11	EMS	Hilliker, Clark
1(3)G2	ry+2	EMS	Gelbart	1(3)pic21	--	X-rays	Schalet
1(3)G3	ry+2	EMS	Gelbart	1(3)m10	--	EMS	Deland
1(3)G8	ry+2	EMS	Gelbart	1(3)G23	ry+4	EMS	Gelbart
1(3)G19	ry+2	EMS	Gelbart	1(3)G26	ps612	Gamma	Gelbart
1(3)A27-2	ry+4	EMS	Hilliker, Clark	1(3)8-107	ry+11	EMS	Hilliker, Clark
1(3)10-140	ry+11	EMS	Hilliker, Clark	1(3)12-196	ry+11	EMS	Hilliker, Clark
1(3)2-34	ry+11	EMS	Hilliker, Clark	1(3)A34-3	ry+4	EMS	Hilliker, Clark
1(3)8-9	ry+11	EMS	Hilliker, Clark	1(3)33-1	ry+4	EMS	Hilliker, Clark
1(3)A13-1	ry+4	EMS	Hilliker, Clark	1(3)D-64	ry+11	EMS	Hilliker, Clark
1(3)13-62	ry+11	EMS	Hilliker, Clark	1(3)A3-3	ry+4	EMS	Hilliker, Clark
1(3)4-22	ry+11	EMS	Hilliker, Clark	1(3)A112	ry+11	EMS	Hilliker, Clark
1(3)B26-1	ry+11	EMS	Hilliker, Clark	1(3)A80	ry+11	EMS	Hilliker, Clark
1(3)A12-2	ry+4	EMS	Hilliker, Clark	1(3)A19-1	ry+4	EMS	Hilliker, Clark
1(3)mes-4B	--	X-rays	Schalet	1(3)A42-1	ry+4	EMS	Hilliker, Clark
1(3)34-2	ry+4	EMS	Hilliker, Clark	1(3)3-119	ry+11	EMS	Hilliker, Clark
1(3)B14-1	ry+11	EMS	Hilliker, Clark	1(3)A12-3	ry+4	EMS	Hilliker, Clark
1(3)G9	ry+2	EMS	Gelbart	1(3)A19-2	ry+4	EMS	Hilliker, Clark
1(3)G15	ry+2	EMS	Gelbart	1(3)8-181	ry+11	EMS	Hilliker, Clark
1(3)G21	ry+2	EMS	Gelbart	1(3)A111	ry+11	EMS	Hilliker, Clark
1(3)6-120	ry+11	EMS	Hilliker, Clark	1(3)B2-4	ry+11	EMS	Hilliker, Clark
1(3)2-228	ry+11	EMS	Hilliker, Clark	1(3)H10	ry+11	EMS	Hilliker, Clark
1(3)11-147	ry+11	EMS	Hilliker, Clark	1(3)H49	ry+11	EMS	Hilliker, Clark
				1(3)H51	ry+11	EMS	Hilliker, Clark
				1(3)H59	ry+11	EMS	Hilliker, Clark
				1(3)H72	ry+11	EMS	Hilliker, Clark

Table 1. [continued]

Lethal allele	Isogenic third chromosome	Mutagen	Source	Lethal allele	Isogenic third chromosome	Mutagen	Source
1(3)H19	ry+11	Gamma	Hilliker, Clark	1(3)G7	ry+2	EMS	Gelbart
1(3)H22	ry+11	Gamma	Hilliker, Clark	1(3)B1-3	ry+11	EMS	Hilliker, Clark
1(3)C-9-2	ry+11	Gamma	Hilliker, Clark	1(3)B9-1	ry+11	EMS	Hilliker, Clark
1(3)C-17-3	ry+11	Gamma	Hilliker, Clark	1(3)B13-1	ry+11	EMS	Hilliker, Clark
1(3)C-18-1	ry+11	Gamma	Hilliker, Clark	1(3)B30-2	ry+11	EMS	Hilliker, Clark
1(3)H54	ry+11	EMS	Hilliker, Clark	1(3)H34	ry+11	EMS	Hilliker, Clark
1(3)S8	--	X-rays	Schalet	1(3)H91	ry+11	EMS	Hilliker, Clark
1(3)B21-2	ry+11	EMS	Hilliker, Clark	1(3)H75	ry+11	EMS	Hilliker, Clark
1(3)B30-1	ry+11	EMS	Hilliker, Clark	1(3)H20	ry+11	Gamma	Hilliker, Clark
1(3)H79	ry+11	EMS	Hilliker, Clark	1(3)m32	--	EMS	Deland
1(3)B13-4	ry+11	EMS	Hilliker, Clark	1(3)m17	--	EMS	Deland
1(3)H66	ry+11	EMS	Hilliker, Clark	1(3)B1-1	ry+11	EMS	Hilliker, Clark
1(3)H9	ry+11	Gamma	Hilliker, Clark	1(3)B11-1	ry+11	EMS	Hilliker, Clark
1(3)B16-1	ry+11	EMS	Hilliker, Clark	1(3)B16-3	ry+11	EMS	Hilliker, Clark
1(3)B16-4	ry+11	EMS	Hilliker, Clark	1(3)B26-3	ry+11	EMS	Hilliker, Clark
1(3)B27-2	ry+11	EMS	Hilliker, Clark	1(3)H45	ry+11	EMS	Hilliker, Clark
1(3)H13	ry+11	EMS	Hilliker, Clark	1(3)H77	ry+11	EMS	Hilliker, Clark
1(3)H69	ry+11	EMS	Hilliker, Clark	1(3)m116	--	EMS	Deland
1(3)C9a	--	X-rays	Chovnick	1(3)S9	--	X-rays	Schalet
1(3)B2-6	ry+11	EMS	Hilliker, Clark	1(3)m102	--	EMS	Deland
1(3)B26-2	ry+11	EMS	Hilliker, Clark	1(3)B1-2	ry+11	EMS	Hilliker, Clark
1(3)26	--	X-rays	Schalet	1(3)B1-5	ry+11	EMS	Hilliker, Clark
1(3)m15	--	EMS	Deland	1(3)B2-3	ry+11	EMS	Hilliker, Clark
1(3)B2-5	ry+11	EMS	Hilliker, Clark	1(3)B8-1	ry+11	EMS	Hilliker, Clark
1(3)B4-2	ry+11	EMS	Hilliker, Clark	1(3)B8-4	ry+11	EMS	Hilliker, Clark
1(3)B8-2	ry+11	EMS	Hilliker, Clark	1(3)B12-2	ry+11	EMS	Hilliker, Clark
1(3)B15-2	ry+11	EMS	Hilliker, Clark	1(3)B15-1	ry+11	EMS	Hilliker, Clark
1(3)B22-1	ry+11	EMS	Hilliker, Clark	1(3)21-3	ry+11	EMS	Hilliker, Clark
1(3)B22-2	ry+11	EMS	Hilliker, Clark	1(3)B26-4	ry+11	EMS	Hilliker, Clark
1(3)B27-1	ry+11	EMS	Hilliker, Clark	1(3)B28-1	ry+11	EMS	Hilliker, Clark
1(3)B29-1	ry+11	EMS	Hilliker, Clark	1(3)H9	ry+11	EMS	Hilliker, Clark
1(3)B29-2	ry+11	EMS	Hilliker, Clark	1(3)H30	ry+11	EMS	Hilliker, Clark
1(3)H36	ry+11	EMS	Hilliker, Clark	1(3)H32	ry+11	EMS	Hilliker, Clark
1(3)H41	ry+11	EMS	Hilliker, Clark	1(3)H57	ry+11	EMS	Hilliker, Clark
1(3)H89	ry+11	EMS	Hilliker, Clark	1(3)G5	ry+2	EMS	Gelbart
1(3)B21-5	ry+11	EMS	Hilliker, Clark	1(3)B4-1	ry+11	EMS	Hilliker, Clark
1(3)H15	ry+11	EMS	Hilliker, Clark				



Table 1. [continued]

Lethal allele	Isogenic third chromosome	Mutagen	Source	Lethal allele	Isogenic third chromosome	Mutagen	Source
1(3)m112	--	EMS	Deland	1(3)H21	ry+11	EMS	Hilliker, Clark
1(3)B9-2	ry+11	EMS	Hilliker, Clark	1(3)H24	ry+11	Gamma	Hilliker, Clark
1(3)B16-2	ry+11	EMS	Hilliker, Clark	1(3)H25	ry+11	Gamma	Hilliker, Clark
1(3)B17-1	ry+11	EMS	Hilliker, Clark				

Table 2. Deficiencies employed in this analysis and their breakpoints.

Deficiency	Breakpoints	Synthesis	Cytology
Df(3R)ry <sup>36</sup>	No visible deletion	Schalet	Gelbart, Hilliker, Lefevre
Df(3R)ry <sup>75</sup>	Df(3R)87D1-2; 87D14-E1	Schalet	Gelbart, Lefevre
Df(3R)ry <sup>81</sup>	Df(3R)87C1-3; 87D14-E2	Schalet	Gelbart, Lefevre
Df(3R)ry <sup>614</sup>	Df(3R)87D2-4; 87D11-14	Gelbart	Gelbart, Hilliker
Df(3R)ry <sup>619</sup>	Df(3R)87D7-9; 87E12-F1	Gelbart	Gelbart, Hilliker
Df(3R)ry <sup>1168</sup>	Df(3R)87B15-C1; 87E9-12	Hilliker	Gelbart
Df(3R)ry <sup>1301</sup>	Df(3R)87D2-4; 87E1-2	Gelbart	Gelbart
Df(3R)ry <sup>1402</sup>	Df(3R)87D2-4; 87D14-E2	Gelbart	Gelbart
Df(3R)ry <sup>1607</sup>	Df(3R)87D3-4; 87E2-3	O'Donnell	Gelbart
Df(3R)ry <sup>1608</sup>	Df(3R)87D4-6; 87E1-2	O'Donnell	Gelbart
Df(3R)kar <sup>1G27</sup>	Df(3R)87B3-5; 87D6-12 In(3R)87B-D, 99E1-F1	Gelbart	Gelbart, Hilliker
Df(3R)kar <sup>SZ-11</sup>	Df(3R)87C7-8; 87E5-6	Gausz et al. (1980)	
Df(3R)1C4a	Df(3R)87E5-7; 87E11-F1	Chovnick	Gelbart
Df(3R)126c	Df(3R)87E1-2; 87F11-12	Chovnick	Gelbart, Lefevre
Df(3R)126d	Df(3R)87D11-13; 87E3-5	Chovnick	Gelbart, Hilliker, Lefevre

The 1(3)S5 associated complementation group is represented by four other alleles (Table 1). All allele combinations are completely lethal.

The 1(3)B-103 complementation group is associated with two alleles (Table 1).

The foregoing three lethal complementation groups have not been separated from one another by deficiency or by recombination analysis, thus their relative left/right order is not defined.

The next complementation group, 1(3)m14 (Fig. 1), has two alleles and is separable by deficiency from adjacent complementation groups. Df(3R)ry<sup>1608</sup> separates 1(3)m14 from the complementation groups to its left while Df(3R)ry<sup>36</sup> separates it from mes-A.

The next complementation group is that associated with mes-1A. The deficiency, Df(3R)ry<sup>36</sup> (Fig. 1, Table 1) separates mes-1A from 1(3)m14, the proximally flanking complementation group. Further, 1(3)mes-1A was separated from the distally flanking complementation group associated with 1(3)mes-4B by Df(3R)ry<sup>74</sup> (Schalet, Kernaghan and Chovnick 1964), a deletion which has been lost. All of the 14 mes-A alleles are semi-lethals associated with a visible mutant phenotype when hemizygous and in mutant allele heterozygous combinations. The visible phenotype is characterized by extra head and thoracic bristles; especially marked is duplication of the anterior scutellar bristles. Surviving mutant allele heterozygotes uniformly express the mes-A phenotype. Although mes-A alleles were tested for complementation with 1(3)m14, all mes-B alleles and three alleles of the 1(3)G9 group [1(3)G9, 1(3)G15 and 1(3)G21]. All heterozygotes exhibited full complementation.

The next complementation group, mes-B (Fig. 1), has three alleles and is similar to the mes-A group in that alleles are semi-lethal and associated with a recessive visible phenotype; namely, outspread wings, held at about a 45° angle to the body, and a dark trident-like crown on the dorsal thorax. The penetrance of this phenotype is excellent. (Occasionally, thoracic bristle duplication reminiscent of that associated with mes-A alleles is observed.)

The adjacent lethal complementation group, the 1(3)G9 complex, is associated with 16 alleles (Fig. 1), one of which, 1(3)H23, is semi-lethal. Although the 1(3)G9 complementation group has not been separated by deficiency from the mes-B group, all combinations of mes-B alleles with 1(3)G9 alleles complement fully. Thus, we conclude that these two complementation groups represent separate gene loci. The order of 1(3)G9 and mes-B is unclear. We infer that 1(3)G9 is to the right of mes-A from the following observations: Df(3R)ry<sup>619</sup> appears to have its left breakpoint in the immediate vicinity of mes-A for although heterozygotes for Df(3R)ry<sup>619</sup> and alleles of the mes-A complementation group exhibit a mes-A phenotype, they have much greater viability than is ordinarily the case for mes-A allele hemizygotes, suggesting that the mes-A locus on the Df(3R)ry<sup>619</sup> chromosome is partially functional; whereas, Df(3R)ry<sup>619</sup> is completely lethal in combination with 1(3)G9 alleles.

The next complementation group (Fig. 1), that associated with 1(3)S12, consists of three alleles and is separated from 1(3)G9 and mes-B by Df(3R)kar<sup>1G27</sup>. We observed that 1(3)S12 fully complemented with 1(3)G1. However, neither allele complemented with 1(3)B21-4. Since all three recessive lethals mapped by deficiency analysis immediately adjacent to the rosy locus we concluded that the complementation map observed was a function of allele complementation. Although 1(3)S12 and 1(3)B21-4 are completely lethal when hemizygous, 1(3)G1 is associated with low hemizygous viability. Surviving hemizygotes for 1(3)G1 uniformly express a phenotype of very thin and short thoracic bristles. Although 1(3)S12 has not been separated by deficiency from the rosy locus, recombination experiments have demonstrated that 1(3)S12 maps to the left of all rosy locus variants which have been assigned positions in the rosy locus genetic map (Chovnick et al. 1976; McCarron et al. 1979).

The next complementation group is that associated with the rosy locus (ry: 3-52.0), a genetic unit containing the xanthine dehydrogenase structural element and adjacent cis-acting regulatory sequences (Chovnick et al. 1976; McCarron et al. 1979).

The next complementation group is that associated with the previously described piccolo (pic) locus, which has been separated from the rosy locus by deficiencies and recombination (Schalet, Kernaghan and Chovnick 1964; Fig. 1). Df(3R)ry<sup>36</sup> serves to place pic to the right of ry; Df(3R)ry<sup>614</sup>, to place pic to the left of 1(3)S8. A total of 32 recessive lethal and semi-lethal alleles of this locus were available for analysis. Unlike all other complementation groups, not all inter se allele combinations of pic variants were tested for complementation (185 of 496 possible allele combinations were tested). Of the pic alleles listed in Table 1, all allele combinations involving the 19 alleles from 1(3)pic<sup>21</sup> to 1(3)A111 inclusive were tested for complementation. Of the 19 alleles extensively analyzed, 6 alleles exhibited, in combination, heterozygous surviving progeny--1(3)pic<sup>21</sup>, 1(3)m10, 1(3)A42-1,

1(3)A12-3, 1(3)A33-1 and 1(3)A3-3. The heterozygous surviving progeny were of reduced viability and uniformly exhibited a pic phenotype, namely, short, fine bristles and abnormal tergite morphology. Thus interallelic complementation extending to the visible phenotype was not observed among alleles of the pic locus.

The next complementation group, that associated with 1(3)S8, consists of 7 alleles (Fig. 1; Table 1), all combinations of which exhibit complete lethality. Df(3R)126c places 1(3)S8 to the left of 1(3)B16-1.

The next complementation group, associated with 1(3)B16-1, consists of 5 alleles (Table 1) and on the basis of its localization by complementation with rosy region deficiencies almost certainly corresponds to the previously described 1(3)S6 locus (Schalet, Kernaghan and Chovnick 1964), the sole representative allele of which was lost prior to the present analysis. All allele combinations were lethal save two. Heterozygotes for 1(3)H69/1(3)B16-1 and for 1(3)H69/1(3)B27-2 were of 4% and 15% viability, respectively. Surviving heterozygous progeny were of normal phenotype.

The 1(3)C9a complementation group consists of three hemizygous lethal alleles which exhibit limited allele complementation. The heterozygotes, 1(3)C9a/1(3)B2-6, 1(3)C9a/1(3)B26-2 and 1(3)B2-6/1(3)B26-2, were of 8%, 14% and 2% mean viability, respectively. Surviving heterozygous progeny are somewhat reduced in size relative to wild type. Df(3R)ry1402 and Df(3R)ry1608 place 1(3)C9a to the right of 1(3)B16-1.

The next complementation group, Ace, associated with 1(3)26 (Schalet, Kernaghan and Chovnick 1964), consists of 16 alleles (Table 1). All allele combinations are lethal save two, both involving 1(3)B15-2. The heterozygotes 1(3)m15/1(3)B15-2 and 1(3)B15-2/1(3)B22-1 are of 5% and 12% viability, respectively. This locus has been the focus of a recent analysis (Hall and Kankel 1976) which presents strong evidence that the locus associated with the 1(3)26 complementation group is the site of the structural gene for acetylcholin-esterase. Hence, following the suggestion of Hall and Kankel (loc. cit.) it is renamed Ace, although 1(3)26 must remain a synonym. Df(3R)ry1607 places Ace to the left of 1(3)G7, the next complementation group.

The 1(3)G7 complementation group is represented by 9 alleles (Table 1); all allele combinations exhibit complete lethality.

The next complementation group is associated with only one allele, 1(3)m32. A second allele, 1(3)J38, has been generated by J. Hall. The two alleles are completely noncomplementary. Df(3R)kar<sup>SZ11</sup> places 1(3)m32 to the right of 1(3)G7 and Df(3R)126d separates 1(3)m32 from the cluster of lethal loci to the right (Fig. 1).

The next four complementation groups, associated with 1(3)m116, 1(3)m17, 1(3)S9 and 1(3)G5 have not been separated by deficiency.

The 1(3)m17 group includes 7 alleles and exhibits limited allele complementation as outlined in Fig. 2. One allele combination shown as noncomplementary in Fig. 2 does exhibit weak viability. This heterozygote, 1(3)H45/1(3)H77, is associated with a mean viability of 11%.

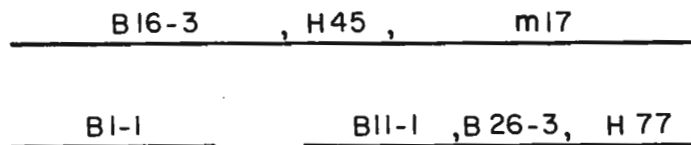


Fig. 2. Complementation map of the 1(3)m17 group.

The 1(3)m116 complementation group is associated with only one allele.

The 1(3)S9 complementation group is associated with 16 alleles and exhibits limited allele complementation as indicated in Fig. 3. All complementing allele combinations involve 1(3)B8-4. Three allele combinations indicated as noncomplementary in Fig. 3 do, in fact, exhibit weak complementation, all involving 1(3)B8-4. The heterozygotes 1(3)B8-4/1(3)B2-3, 1(3)B8-4/1(3)B15-1 and 1(3)B8-4/1(3)B12-2 are of 14%, 13% and 22% mean viability, respectively.

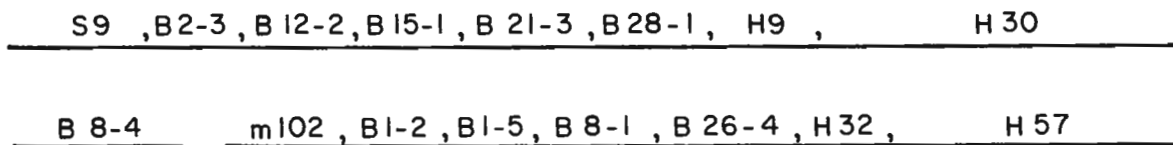


Fig. 3. Complementation map of the 1(3)S9 group.

The fourth member of this cluster of complementation groups is that associated with 1(3)G5 which has two alleles (Table 1).

The most distal complementation group in the 87D2-4-87E12-F1 interval is that associated with 1(3)m112. The complementation map of the alleles of this group is presented in Fig. 4. Although 1(3)H24 and 1(3)H25 are indicated as noncomplementary to 1(3)m112, they do, in fact, weakly complement. The heterozygotes 1(3)H24/1(3)m112 and 1(3)H25/1(3)m112 are of 40% and 24% mean viability, respectively; however, unlike other complementing allele combinations of this locus, surviving heterozygotes are associated with a mutant visible phenotype of short, very thin bristles and irregularly arranged ommatidia. Df(3R)ry<sup>1168</sup> separates 1(3)m112 from the complementation groups to the left.

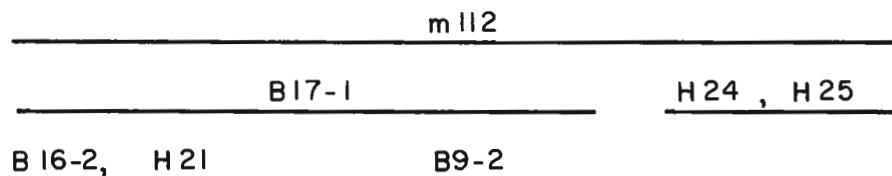


Fig. 4. Complementation map of the 1(3)m112 group.

Overall, we have observed 21 complementation groups within the 87D2-4 to 87E12-F1 interval, a polytene chromosome segment of 23 or 24 chromomeres.

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Hilliker, A.J. Univ. of British Columbia, Vancouver, British Columbia. Meiotic effects of second chromosome heterochromatic deletions.

It has been suggested by a number of authors (reviewed in Yunis and Yasmineh 1971) that centromeric heterochromatin may promote the initiation of meiotic pairing of homologous chromosomes and, further, protect the centromere from the "rigors of meiosis"--presumably the terminalization of

chiasmata and subsequent reductional segregation of homologous dyads. These hypotheses suggested the following experiments, as they predict that heterozygosity for second chromosome heterochromatic deficiencies may result in appreciable second chromosome nondisjunction and/or chromosome loss. The proximal deficiencies studied were Df(2R)M-S210, which is deficient for the 2R heterochromatic block and Df(2L)C', which is undoubtedly deficient for much of the 2L proximal heterochromatin (Hilliker 1976).

Df(2R)M-S210: Virgin females heterozygous for Df(2R)M-S210 and b pr cn were crossed, singly, in vials, to C(2L)VH1,lt; C(2R)P,px males and brooded for six days. As these compound-second autosome bearing males produce nearly equal frequencies of the four classes of C(2L); C(2R); nullo-2; and diplo-2 sperm (Gibson 1977); nullo-2 and diplo-2 female gametes, the consequence of second chromosome nondisjunction or chromosome loss, may be recovered as viable zygotes with 25% efficiency. Thus by the use of control (multiplier) crosses to estimate the total number of fertilized eggs one may assay second chromosome loss and nondisjunction in *Drosophila* females by mating them with compound second autosome bearing males.

From an estimated 4844 fertilized eggs, no nondisjunctional progeny were recovered. Thus neither chromosome loss or nondisjunction of chromosome two is associated with heterozygosity for Df(2R)M-S210. The absence of chromosome loss is in contradiction to the theory of the protection of centromeres by flanking heterochromatin. No newly induced isochromosome bearing exceptions (a possible consequence of chromosome "breakage") or patroclinous progeny were observed. Clearly the M(2)S10 chromosome is stable despite the absence of the 2R heterochro-

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matic block. The upper 95% confidence limit of second chromosome loss, and therefore chromosome instability, is 0.25%.

Nor did M(2)S10/b pr cn heterozygotes prove particularly sensitive to radiation-induced nondisjunction. From mating Df(2R)M-S2<sup>10</sup>/b pr cn females irradiated with 2000 rads of gamma radiation to C(2L)VH,lt;C(2R)P,px males only one matroclinous progeny was observed in an estimated 44,269 fertilized eggs, although 33 patroclinous progeny and 15 newly induced compound second autosome bearing exceptional progeny were recovered. Indeed, M(2)S10 heterozygotes appear to be resistant to radiation induced disjunction. Gibson (1977) found the frequencies of matroclinous progeny from +/lt pk cn females irradiated with 2000 rads to be 0.053%, a frequency an order of magnitude greater than that observed for M(2)S10/b pr cn females.

Second chromosome nondisjunction, and loss, was also assayed in males heterozygous for Df(2R)M-S2<sup>10</sup> and In(2LR)SM1. Df(2R)M-S2<sup>10</sup>/In(2LR)SM1 males were crossed to B<sup>SY</sup>;C(2L)P,b;C(2R)P,px virgin females, singly in vials and brooded for 9 days. B<sup>SY</sup> is a Y-chromosome carrying a small duplication of the X-chromosome including a dominant allele of the Bar (B) locus (see Lindsley and Grell 1968 for further details). B<sup>SY</sup>;C(2L)P,b;C(2R)P,px females produce 40% second chromosome nonsegregational progeny when crossed to compound second autosome bearing males. Thus 20% of the female gametes are diplo-2 and 20% are nullo-2. Consequently, nondisjunction for chromosome 2 may be assayed in males by mating them to B<sup>SY</sup>;C(2L)P,b;C(2R)P,px females.

In order to estimate the number of nondisjunctional female gametes produced per female per vial, a sample of B<sup>SY</sup>;C(2L)P,b;C(2R)P,px virgin females were crossed to C(2L)SH3,+;C(2R)SH3,+ males. As these males produce approximately 25% diplo-2 and 25% nullo-2 sperm (Holm 1969), the nondisjunctional progeny represent 1/4 of nondisjunctional female gametes. Thus, the number of nondisjunctional female gametes per experimental vial may be estimated as 4 times the number of nondisjunctional progeny per multiplier vial. However, in the cross to the Df(2R)M-S2<sup>10</sup>/In(2LR)SM1 males a nondisjunctional (diplo-2 or nullo-2) sperm fertilizing a nondisjunctional female gamete has a 50% chance of resulting in a viable, diplo-2 zygote.

Thus chromosome-2 nondisjunction per experimental vial may be estimated as 2 times the number of exceptional (i.e., nondisjunctional) progeny per experimental vial divided by 4 times the number of nondisjunctional progeny per multiplier vial. In the experimental series, an estimated 8810 nondisjunctional female gametes resulted in no diploid nondisjunctional progeny. (The only exceptional progeny recovered were one triploid female and 2 intersexes.) Thus a 95% upper confidence limit on chromosome-2 nondisjunction in Df(2R)M-S2<sup>10</sup>/In(2LR)SM1 heterozygotes of 0.068% is established. With chromosome-2 nondisjunction and chromosome loss less than 0.1% in males and 0.3% in females heterozygous for Df(2R)MS-10, the loss of the heterochromatic block to the right of the centromere of chromosome-2 clearly does not result in any meiotic instability of the second chromosome.

We do not consider these data to indicate the absence of sites important for meiotic pairing in the 2R heterochromatin. If a number of pairing sites are distributed throughout the second chromosome heterochromatin and/or euchromatin, deleting one or even several sites may not be sufficient to induce nondisjunction.

However, the absence of chromosome loss among M(2)S10 heterozygotes argues strongly that centromeric heterochromatin is not important for chromosome stability.

Heterozygosity for Df(2R)M-S2<sup>10</sup> is associated with a reduction in exchange in 2R. If one examines crossing-over in M(2)S10/b pr cn heterozygotes, where b and pr lie in the proximal euchromatin at 48.5 and 54.5 (Lindsley and Grell 1968) and cn lies in the proximal 2R euchromatin at 57.5, crossing-over is reduced in the pr cn interval nearly fivefold relative to the control. As most crossovers in the pr cn interval occur in proximal 2R euchromatin between stw and cn (T. Yeomans, pers. comm.) and as crossing-over in the b pr interval is not reduced, these data suggested that heterozygosity for M(2)S10 affected exchange in 2R euchromatin. Exchange in 2R was then examined in M(2)S10/cn bw heterozygotes, where bw at 104.5 near the tip of 2R and cn in the proximal euchromatin span most of 2R. Recombinant progeny were recovered at a frequency of 28%, well below that observed in the control (48%). Thus M(2)S10 appears to have a significant effect on meiotic recombination in the 2R euchromatin despite the fact that the region deleted, the 2R heterochromatin, is not a region in which appreciable crossing-over occurs. It should be noted that save for the deletion of 2R heterochromatin the M(2)S10 chromosome is associated with no visible chromosomal aberrations, thus the meiotic effect noted is probably the result of deleting the 2R heterochromatin.

Df(2L)C'. Virgin females heterozygous for Df(2L)C' and b pr cn were mated to C(2L)VH1,lt; C(2R)P,px males and brooded for 6 days. In an estimated 31,200 fertilized eggs, 2 matroclinous and 1 patroclinous progeny were recovered. The frequency of spontaneous second chromosome nondisjunction in Df(2L)C' heterozygotes is  $4 \times 3/31,200$  or 0.038% with 95% confidence limits of 0.008% and 0.112% (Stevens 1942), well within the range observed for *Drosophila* females homozygous for normal second chromosomes (Gibson 1977).

Although Df(2L)C' is deficient for much of the 2L heterochromatin (Hilliker and Holm 1975; Hilliker 1976), cytological analysis of Df(2L)C' found a substantial block of heterochromatin to the left of the centromere, approximately equal in size to that normally associated with the 2L heterochromatin. This can be explained by the following hypothesis. In the construction of Df(2L)C' from the detachment of C(2L)SH3,+;C(2R)SH3,+ the acentric 2L fragment was generated by a break in the distal 2L heterochromatin (that this break was proximal to the secondary constriction at the 2L heterochromatin-euchromatic junction was clear, as Df(2L)C' was not deficient for this constriction) with the centric 2R fragment being generated by a break in the distal heterochromatin of 2R resulting in a centric 2R fragment duplicated for much of the 2R heterochromatin including the rl<sup>+</sup> locus. Df(2L)C' therefore would be a 2L proximal deficiency but a 2R proximal duplication with a rl<sup>+</sup> locus on each side of the centromere.

In order to test the hypothesis I constructed with radiation nonsister 2L compound autosomes (compound autosomes with one 2L chromatid from one second chromosome and the other 2L chromatid from its homolog) from females heterozygous for Df(2L)C' and b pr cn. If Df(2L)C' carries a rl<sup>+</sup> duplication in the left arm then compound left autosomes deriving one arm from the Df(2L)C' chromosome should more frequently carry rl<sup>+</sup> duplications of 2R than do compound lefts derived from normal second chromosomes. Of 21 nonsister compound left autosomes derived from Df(2L)C'/b pr cn heterozygotes, 17 were rl<sup>+</sup> whereas Yeomans (1972) found only 10 of 21 compound left second chromosomes derived from lt stw<sup>3</sup>/b pr cn heterozygous females were rl<sup>+</sup>. Thus Df(2L)C' would appear to be duplicated for rl<sup>+</sup> and, therefore, much of the 2R heterochromatin. Additional genetic evidence is presented in Sandler (1977).

Interestingly heterozygotes for Df(2L)C' and b pr cn show normal levels of recombination in both the b pr and pr cn intervals. Thus unlike Df(2R)M-S210, Df(2L)C' has no marked effect on recombination in adjacent euchromatin. However, in this regard the duplicated 2R heterochromatin may substitute for the deleted 2L heterochromatin.

Further, again unlike Df(2R)M-S210 heterozygotes, Df(2L)C' heterozygous females showed no apparent resistance to radiation induced second chromosome nondisjunction. Df(2L)C'/b pr cn females were irradiated with 2000 rads of gamma radiation and crossed to C(2L)VH1H; C(2R)P,px. Among 56,890 estimated zygotes 27 matroclinous and 71 patroclinous progeny were recovered as well as 73 progeny bearing newly induced compound autosomes. The frequency of recovery of these progeny is similar to that obtained in females with standard second chromosomes given the same irradiation treatment and brooding (Gibson 1977).

The foregoing data have been extracted from Hilliker (1975).

References: Gibson, W.G. 1977, Ph.D. Thesis, Univ. of British Columbia; Hilliker, A.J. 1975, Ph.D. Thesis, Univ. of British Columbia; \_\_\_\_\_ 1976, *Genetics* 83:765-782; \_\_\_\_\_ and D.G. Holm 1975, *Genetics* 81:705-721; Holm, D.G. 1969, Ph.D. Thesis, Univ. of Connecticut; Lindsley, D.L. and E.H. Grell 1968, *Carnegie Inst. of Wash. Publ. No. 627*; Sandler, L. 1977, *Genetics* 86:567-582; Yunis, J.J. and W.G. Yasminch 1971, *Science* 174:1200-1209.

Hunter, A.S. Univ. of the Pacific, Stockton, California. *Drosophila* of Pompano Beach, Florida.

A small collection of *Drosophila* was made in December 1978 in Pompano Beach. The flies were collected by net sweepings over the fallen fruit under various citrus trees. The number of flies of the various species found are as follows:

<i>D. melanogaster</i>	54
<i>D. simulans</i>	12
<i>D. cardini</i>	134
<i>D. acutilabella</i>	5
<i>D. willistoni</i>	26
<i>D. equinoxialis</i>	10
<i>D. sturtevantii</i>	87
<i>D. latifasciaeformis</i>	48

In order to identify the females of the willistoni group, they were each isolated and the genitalia of the male offspring were checked. These data are reported here because I believe that this is the northernmost range of *D. equinoxialis*. Additional collections made in 1979 and 1980 in the same location contained the same species, although in different frequencies. Reference: Spassky, B. et al. 1971, *Evolution* 25: 129.



James, A., M. Bownes\* and S. Glenn\*\*. Sidney Farber Cancer Institute, Boston, Massachusetts; \*Edinburgh University, Edinburgh; \*\*Center for Pathobiology, University of California, Irvine. The re-establishment of pattern elements in regenerating imaginal wing discs of *D. melanogaster*.

We have attempted to analyze how regeneration occurs in imaginal discs by determining the sequence in which pattern elements reappear during regeneration of a fragment of the wing disc.

Late third instar wing discs were cut into a small O2 fragment corresponding to presumptive notum and a large 28 fragment corresponding to the wing hinge and blade (Bryant 1975). The O2 pieces were metamorphosed immediately as controls. The 28 pieces were injected into females and allowed to grow for 1 to 5 days before metamorphosis in a larval host was induced. The metamorphosed implants were scored for the regeneration of the bristles found in the notum.

The process of wound healing and growth observed in the majority of discs can be seen in Fig. 1. Before culture in the adult abdomen the 28 fragment has an exposed surface of cells. After culture for 1 to 2 days these cells have healed together. Maximum growth occurs between 2 and 4 days of culture.

The results of the sequence of regeneration are shown in Table 1. Regeneration in the 28 pieces was measured as an increase in the frequency of those elements expected from the immediate metamorphosis of the O2 controls. Fig. 2a shows the wing disc fate map and the location of the cutting line. The bristles scored were the presutural bristles, the anterior and posterior notopleural bristles, the anterior and posterior supraalar bristles, the anterior and posterior postalar bristles, the anterior and posterior dorsocentral bristles and the scutellar bristles. All of these bristles, with the exception of the presutural bristle, were present at least 75% of the time in O2 control implants.

28 fragments metamorphosed immediately in larvae produced no thoracic bristles. Implants cultured for one day showed very little regeneration. The pattern elements which were regenerated at a low frequency were those structures near to the original O2 cutting line, notopleural bristles, presutural bristles, supraalar bristles, and structures furthest

Fig. 1. Wound healing and growth during culture. (a) 28 fragment immediately after cutting and after (b) 1 day, (c) 2 days, (d) 3 days, (e) 4 days, (f) 5 days of culture in an adult female abdomen. → marks the original wound line.

from the cut edge, the scutellar bristles. Fig. 2b shows the frequency of regenerated elements and three outside markers. By the second day all of the pattern elements of the notum were present at a low frequency except the postalar bristles, which were missing completely. As seen in Fig 2c, the notopleural, supraalar, and scutellar bristles were present in the highest frequencies. Implants cultured for three days had regenerated the notopleural and scutellar bristles more than 20% of the time (Fig. 2d). The dorsocentral and presutural bristles were regenerated with lower frequencies. The notopleural, supraalar, postalar, and scutellar bristles were regenerated at least 70% of the time in pieces cultured for four days (Fig. 2e). The remaining bristle elements were present more than 50% of the time, except for the presutural bristle which was present 20% of the time. However, the presutural bristle is often absent in control implants, being present in only 62% of the O2 control fragments. In

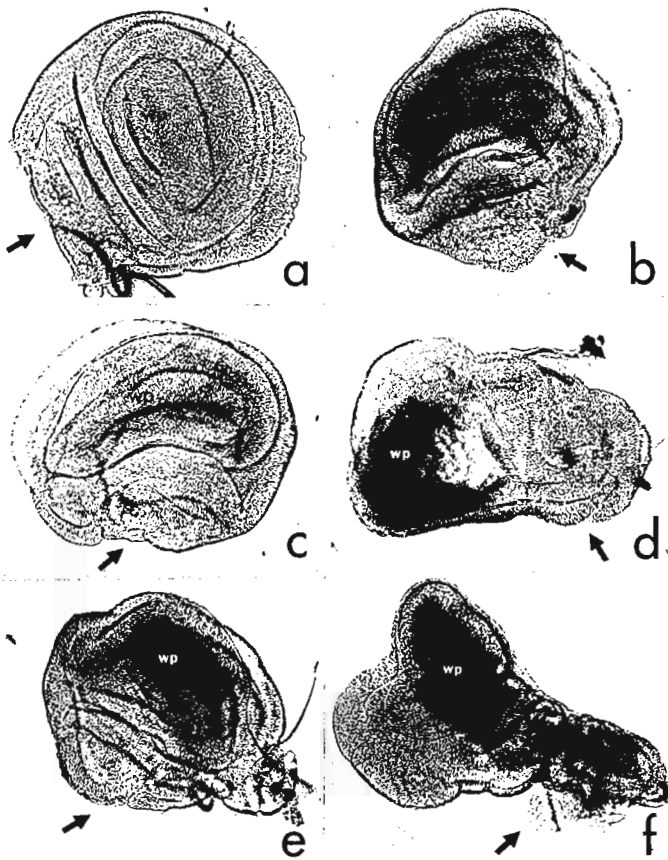


TABLE 1.

Structures identified in regenerating fragments of wing discs

Element scored	control 0 Day 02	control 0 Day 28	experimental 1 Day 28	experimental 2 Day 28	experimental 3 Day 28	experimental 4 Day 28	experimental 5 Day 28
Presutural Bristles	62		5	4	13	20	26
Notopleural Bristles	81		10	15	57	80	56
Supraalar Bristles	93		5	15	25	85	67
Post alar Bristles	86				30	70	59
Dorsocentral Bristles	86			4	17	55	56
Scutellar Bristles	94		5	8	52	70	63
Anterior notal wing process		46	52	54	96	95	74
Tegula	8	88	81	85	100	100	81
Humeral plate		79	67	92	100	90	81
Unnamed plate		75	48	88	100	100	74
Axillary sclerites							
first	6	96	76	96	100	100	93
second	1	100	95	100	100	100	85
third		92	90	100	78	100	81
fourth	69	33	52	23	35	60	44
Proximal costa		96	67	88	83	95	81
Medial costa		96	86	88	87	100	81
Distal costa		92	71	85	78	90	81
Triple row		100	76	92	96	85	74
Double row		96	52	81	74	60	74
Posterior row		25	38	69	52	95	70
Sc4d		92	52	92	65	80	59
Sc25		100	90	96	87	95	85
Prealar apophysis		21	90	73	74	65	67
Yellow club		88	90	85	91	85	89
Proximal ventral radius		92	67	73	83	90	78
Pleural wing process		71	90	92	96	90	93
Axillary pouch		75	76	77	36	75	89
Total implants	84	24	21	26	23	20	27

All figures refer to the percentage occurrence of each element in the total implants obtained for that series.



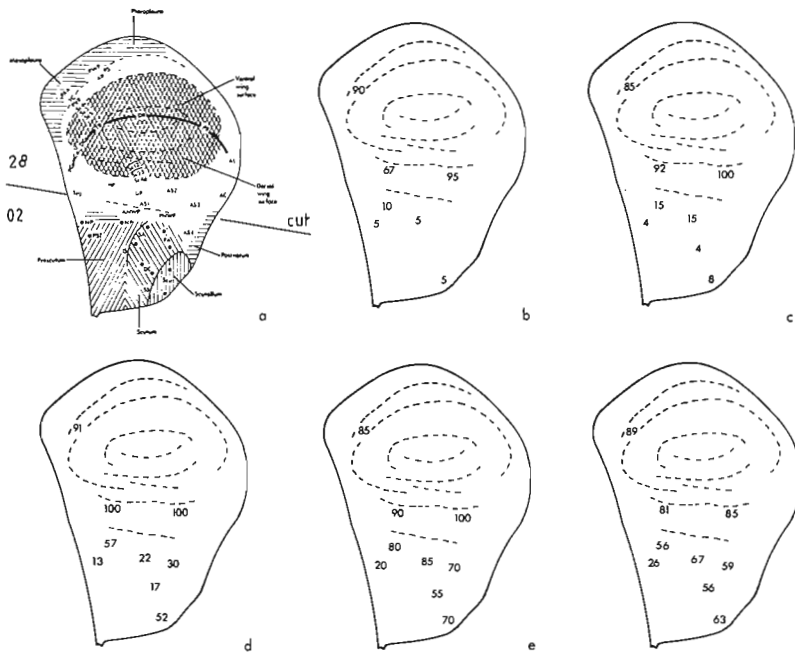


Fig. 2. (a) Fate map of wing disc (after Bryant 1975). Markers used in this study: ANWP, anterior notal wing process; AP, axillary pouch; AS, axillary sclerites, first, second and third; PCO, MCO, and DCO, proximal, medial and distal costa; DC, dorsocentral bristles; HP, humeral plate; NP, notopleural bristles; PS, pleural sclerite; PWP, pleural wing process; PA, postalar bristles; PAA, prealar apophysis; PST, presutural bristles; PVR, proximal ventral radius; TR, OR, and PR, triple row, double row and posterior row of wing margin hairs; Scu, scutellar bristles; Sc4d and Sc25, group of 4 and group of 25 sensilla campaniformia on the dorsal radius; SA, supraalar bristles; Reg, tegula; UP, unnamed plate; YC, yellow club. For rest of abbreviations see Bryant 1975. (b) Frequency of presence of pattern elements in disc fragments cultured for one day. The frequencies of 3 unregenerated markers are given in the 28 piece to contrast with the frequency of markers in the regenerating 02 region. (c) Two-day culture periods. (d) Three-day culture periods. (e) Four-day culture periods. (f) Five-day culture periods.

first in the regenerating disc and the remaining structures are then intercalated.  
 Reference: Bryant, P.J. 1975, J. exp. Zool. 193: 49-78.

Jenkins, J.B. Swarthmore College, Swarthmore, Pennsylvania. Paternal age and mutagen sensitivity.

This study was undertaken to ascertain whether the chronological age of *Drosophila* males was a factor in the sensitivity of germ cells to ethyl methane-sulfonate (EMS) mutagenesis.

Ore-R males of different ages were fed EMS (40 mM for 8 hours) by the Lewis technique, then mated individually to 2 day old ed dp<sup>OV</sup>cl virgin females. The F<sub>1</sub> from post-meiotic male germ cells only (first 6 days of mating) was scored for dp mutations. As can be seen in this preliminary analysis, 27 day old males are substantially more susceptible to EMS mutagenic action than 2 day old males. The basis for

the five day implants all pattern elements of the notum appeared less frequently than in the four day pieces, with the exception of the presutural bristle which now appeared in 26% of the implants.

Using statistics we were able to conclude that the sequence with which the bristles reappeared was: (1) notopleurals, (2) supraalars and scutellar bristles, (3) presuturals, postalars and dorsocentral bristles. It should be noted that presutural bristles are not included in the figures since they are often not differentiated in the controls (Table 1).

During regeneration the cells respond to positional cues which are set up in the growing tissue mass and these in turn define which part of the regenerate the cells will make. Initially there are not enough cells to regenerate the entire thorax and cells must decide which pattern elements to differentiate first. One might have expected a simple sequence beginning close to the cut surface and moving towards the edge of the fate map of the disc until the pattern of the thorax is complete. It appears, however, that regions close to the cut edge, notopleural and supraalar bristles, and those furthest from it, scutellar bristles, are re-established

No. of males	Male age (days)	F <sub>1</sub> scored	dp mutants	Frequency (%)
36	2	7156	40	0.56 ± .03
23	27	5050	54	1.07 ± .04

the increased susceptibility to EMS mutagenesis by aged males is unknown, but may be due to depressed error-free repair functions which normally deteriorate with age.

Kaidanov, L.Z. and E. Hugoto. Dept. of Genetics & Selection, Leningrad State University, USSR. Studies on genetic possibilities of inbred stocks of *Drosophila*.

maintained by closed inbreeding during about 300 generations. After 261 generations lateral branches were founded, which were selected for increasing a number of abdomen bristles. In contrast to HA the LA selection was very effective. There were also some differences between the stocks. The rate of LA and its lateral branches' semi- and sublethal mutations was higher (55-65% for 2 chromosome). When the selection of LA was stopped, the result was gradual clearing of the stock from mutation load. There was no equal distribution of harmful mutations among the LA genome; they have been concentrated in chromosome 2. The reasons for their accumulation were artificial selection and increased rate of spontaneous mutations (Gorbunova and Kaidanov 1975; Kaidanov 1979). The latter probably also was a result of previous selection. The mutable loci have been localized (Kaidanov 1979).

References: Gorbunova, V.N. and L.Z. Kaidanov 1975, *Genetika* (Russ) 11:9; Kaidanov, L.Z. 1979, *Z. ob. biol.* (Russ) 40:6.

This work was aimed at discovering genetic consequences of long-term selection on sexual activity. The concentration of mutations to viability has been studied for selected stocks of flies.

We used the following stocks: LA (low activity) and HA (high activity), produced from the former by reverse selection. Both of these have been

Kaplin, V. and L. Korochkin. Institute of Cytology & Genetics, Novosibirsk, USSR. Histochemistry of the tissue distribution of some enzymes during the development of *D. melanogaster*.

Using histochemical methods we investigated the tissue distribution of some enzymes at the different stages of development in *D. melanogaster*. Two stocks, Canton S and In(3LR)D/Sb with the complicate inversion on the 3rd chromosome, have

been investigated. Embryonic material was synchronized according to Delcour (1969). Two special methods of preparation of sections for the histochemical staining were elaborated by us.

First method: (1) Washing of eggs in some portions of distilled water. (2) Treatment by 2.5% glutaraldehyde prepared using Hanks solution with the addition of a substrate enzyme for a corresponding enzyme, at 4°C.

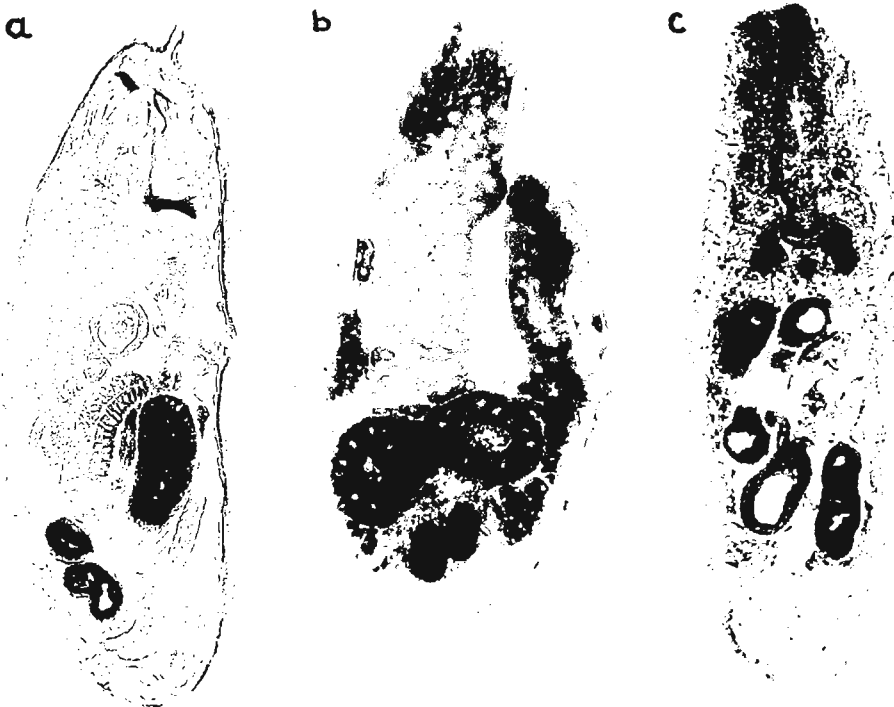


Fig. 1. Sections which were stained histochemically. (a) Alkaline phosphatase; embryo 22 h. (b) Esterase; embryo 22 h. (c) Malic acid; embryo 24 h.

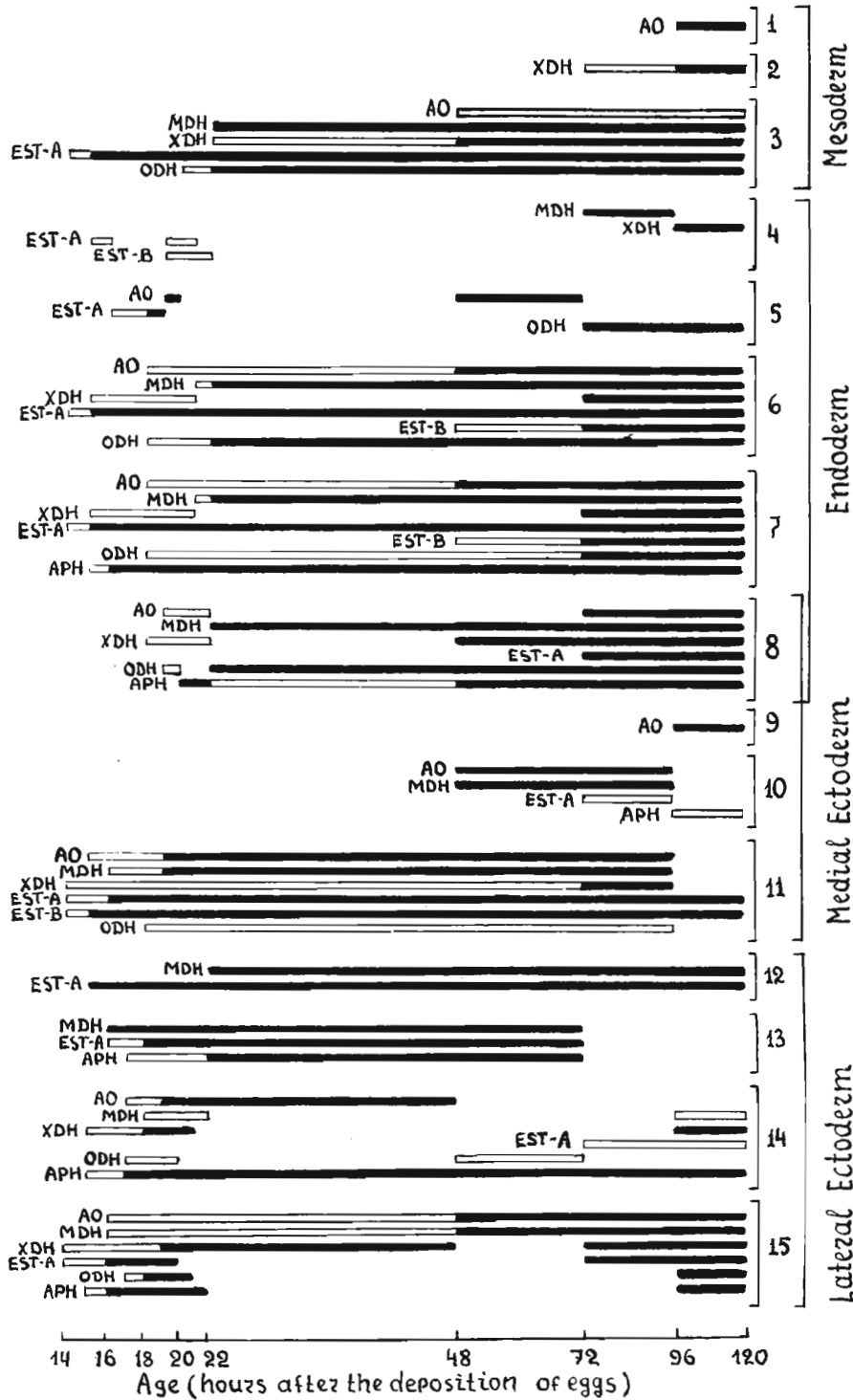


Fig. 2. Results of histochemical investigations of some enzymes in *D. melanogaster*, stock Canton-S. □, the first finding of the activity; ■, the beginning of the increase of histochemical reaction; APH, alkaline phosphatase; EST-A, esterase,  $\alpha$ -naphthyl acetate used as substrate; EST-B, esterase,  $\beta$ -naphthyl acetate used as substrate; ODH, octanol dehydrogenase; XDH, xanthine dehydrogenase; MDH, malic enzyme; AO, aldehyde oxidase. 1-aorta, 2-muscles, 3-fat body, 4-cardia, 5-gastric caeca, 6-ventriculus, 7-midintestine, 8-Malpighian tubules, 9-esophagus, 10-hypopharynx, 11-ganglion, 12-oenocytes, 13-spiracles, 14-salivary glands, 15-hypoderm.

(3) Egg membranes are pierced by a fine needle; fixation 2 h at 4°C. (4) Chorion and yolk membranes are removed by special needle. (5) Washing in cold Hanks solution for 1 h at 4°C. (6) Incubation in the solution for histochemical staining, 5-30 minutes. (7) Hanks solution 30 min. at 4°C. (8) Alcohols (40, 70, 96, 100%) 5 min. in each concentration at 4°C. Alcohol + acetone (1:1), 10 min.; acetone, 10 min. (9) Araldite:acetone 1:3, 2 h; 1:1, 2 h; 3:1, 2 h. Araldite, 15 h. (10) Polymerization of araldite for 1 day at 43°C and 2 days at 60°C. (11) Preparation of sections. This method was used mainly for the staining of histological sections by the usual histological and cytological technique.

Second method (mainly for the histochemical investigations): (1) Washing of eggs (50-100) in some portions of distilled water. (2,3) Same as in the first method. (4) Hanks solution, 30 min. at 4°C. (5) Impregnation by solution of polyacryl amide gel. The solution is prepared by the mixture of 5 parts solution A and 3 parts solution B. Solution A: acryl amide 30 g, bisacryl amide 1 g, TEMED 0.25 ml, Tris-acetic buffer 0.05M, pH 8.2, 10 ml, distilled water 60 ml. Solution B: 2% ammonium persulfate 20 ml, distilled water 15 ml. (6) Polymerization 20-30 min. (7) Freezing of the gel slabs with eggs. (8) Preparation of sections (5-10 micron) in the cryostat. (9) Histochemical staining. We used histochemical methods according to Pearse (1960) and Burstone (1962). Aldehyde oxidase was detected according to Dickinson (1970).

The quality of our histochemical technique is illustrated in Fig. 1a,b,c. Designated on Fig. 2 are the periods of development when some enzymes are detected in the different tissues for the first time and a time when the increase of enzymatic activity is established histochemically. It was shown that alkaline phosphatase has been detected rather early during development (12-14 h of embryogenesis) before histochemical finding of the activity of most other enzymes investigated by us. Traces of aldehyde oxidase can be seen at the earliest stages of development. This activity is a result of the presence of the maternal products in the eggs. Then the activity of aldehyde oxidase in the embryos decreases. The increase of this activity and correspondingly the intense histochemical reaction is established rather late during development (1st-2nd instar larvae).

The increase of histochemical reaction of NADP-dependent malic enzyme takes place before the corresponding increase in activity of aldehyde oxidase. There is some similarity of the histochemical pattern between the organs which are developed from the same embryonic anlagen. It was established that two chains of enzymes are sequentially expressed during development: (1) Alkaline phosphatase → esterase → octanol dehydrogenase → xanthine dehydrogenase. (2) Malic acid → aldehyde oxidase. It is possible that there is a correlation between the sequence of phenotypic expression of some enzymes and the sequence of distribution of genes coded for the corresponding enzymes (Korochkin 1978).

The histochemical pattern in the developing embryos and larvae of the stock with the inversion In(3LR)D/Sb has in general some similarity to the same in Canton-S but there are also some differences in the periods of the first histochemical detection of enzymes in the different tissues.

References: Burstone, M. 1962, Enzyme histochemistry and its application in the study of neoplasms, Academic Press, New York-London; Delcour, J. 1969, DIS 44:133; Dickinson, W. 1970, Genetics 66:487; Korochkin, L. 1978, 13 Internat. Embryol. Conf. Berlin, p. 26; Pearse, A. 1960, Histochemistry J. and Churchill Ltd., London.

Kaurov, B.A. Institute of Medical Genetics, AMS USSR, Moscow, USSR. To the definition of the notion "field of gene activity".

Studying the features of manifestation of mutations that changed the number of bristles on the body of *Drosophila*, Rokizky (1929) established that in any given mutation the reduction or addition of bristles extended over a definite region of the body. This region of visible gene effect was defined "field of gene activity" (Rokizky 1929). In this work special attention was given to the topographic features of gene manifestation, not to explanations concerning the reasons for gene behavior. This question was not well studied and its discussion confined to phenotypic gene manifestation. However, lately the data on the interaction of genes have been obtained which permit the attachment of new importance to this notion.

Studying the interaction of homoeotic mutations *Ns* and *ss<sup>a</sup>* (transforms antennae to legs of mesothoracic type) with mutation *sn* (twists bristles), as well as homoeotic mutation *pb* (transforms oral lobes of proboscis to legs of prothoracic type) with "antenna" mutations

al and th (decreases the number of arista filaments and the number of claws on the prothoracic legs) and "leg" mutations d and fj (decreases the number of tarsal segments on the prothoracic legs) at 16°C and 29°C in *D. melanogaster*, we found the appearance of essential signs of non-homoeotic mutations on the corresponding homoeotic structures (Kaurov et al. 1976, 1978). In addition, in double mutants pb ss<sup>a</sup> we observed a special manifestation of mutation ss<sup>a</sup> on homoeotic structures, caused by the action of mutation pb (Kaurov et al. 1977). Similar effects were also observed by other authors (Brown 1940, Ouwennell 1970, Lewis 1963, Stepshin and Ginter 1972).

On the basis of the data obtained I suggest defining the notion "field gene activity" as a totality of cells of definite determination, specific for manifestation of activity of a given gene, to which a definite phenotype of definitive structures corresponds. The consequences include application for definition of gene activities, morphogenetic relationship of normal and homoeotic structures and gene activity after the appearance of cells of definite determination, independently of its origin in ontogenesis and localization.

References: Brown, W. 1940, *Genetics* 25:143-149; Kaurov, B.A., V.I. Ivanov and V.A. Mglinetz 1976, *Genetics* (Russ.) 12:75-81; \_\_\_\_\_, \_\_\_\_\_ and \_\_\_\_\_ 1977, *Genetics* (Russ.) 41:1-20; \_\_\_\_\_, \_\_\_\_\_ and \_\_\_\_\_ 1978, *Genetics* (Russ.) 13:76-84; Lewis, E. 1963, *Amer. Zoologist* 3:33-56; Ouwennell, W. 1970, *Genetica* 41:1-20; \_\_\_\_\_ 1970, *Wilh. Roux's Archiv* 166:76-88; Rokizky, P.F. 1929, *Zh. exp. Biol.* (Russ.) 5:182-214; Stepshin, V.P. and E.K. Ginter 1972, *Genetics* (Russ.) 8:67-74.

Kaurov, B.A. Institute of Medical Genetics, AMS USSR, Moscow, USSR. Mutation aristapedia causes the transformation of distal segments of antennae to five-segmented tarsi in *D. melanogaster*.

Despite the fact that homoeotic mutation causing the transformation of distal segments of antennae to the distal structures of mesothoracic legs has been discovered by Balkaschina in 1928 in *D. melanogaster*, there was no information concerning the number of tarsal segments in the homoeotic tarsus up to now. This number is considered to

be equal to four and to correspond to Ta2-Ta4 of the tarsus, which are homologous to AIY-AY of the antenna; Tal of the tarsus is homologous to AIII of the antenna (Postlethwait and Schneiderman 1971). So, the appearance of leg bristles on AIII and four tarsal joints on the homoeotic tarsus will indicate the presence of Tal on it.

Studying the different alleles of the aristapedia locus (ss<sup>ak</sup>, ss<sup>ax</sup> and ss<sup>a40a</sup>) in *D. melanogaster* at 16, 25 and 28°C, we observed the appearance of four tarsal joints on homoeotic tarsi in the mutants ss<sup>a40a</sup> at 16°C and between Tal and Ta2 (Kaurov and Ivanov 1977). The tarsal joints in the mutants ss<sup>a</sup> at this locus have been observed by other authors (Mglinetz 1974). In addition, we observed leg bristles on AIII. The mean number of these bristles varied depending on the temperature (16, 25 or 28°C) and the genotype (ss<sup>ak</sup>, ss<sup>ax</sup> or ss<sup>a40a</sup>) from 1.5±0.1 to 7.4±0.4. It can be noted that leg bristles on AIII in different mutants ss<sup>a</sup> reacted to the change in temperature, as well as the bristles reacted to Ta2-Ta5 of homoeotic tarsus. At 16°C the number of leg bristles on AIII in the mutants ss<sup>ak</sup> and ss<sup>ax</sup> was increased, while in the mutants ss<sup>a40a</sup> it was decreased in comparison with 28°C.

So, the data obtained show that the homoeotic mutation aristapedia causes the transformation of AIII-AY of the antenna to Tal-Ta5 of the tarsus, i.e., the formation of five-segmented homoeotic tarsi.

References: Balkaschina, E.I. 1928, *Zh. exp. Biol.* (Russ.) 4:93-106; Kaurov, B.A. and V.I. Ivanov 1977, *Genetics* (Russ.) 13:70-75; Mglinetz, V.A. 1974, *Genetics* (Russ.) 10:91-97; Postlethwait, J.H. and H.A. Schneiderman 1971, *Develop. Biol.* 25:606-640.

Kidwell, M.G. Brown University, Providence, Rhode Island. The use of pupation height as a method for distinguishing between the sibling species *D. melanogaster* and *D. simulans*.

Although males of the sibling species *D. melanogaster* and *D. simulans* may be readily distinguished by examination of their external genitalia, separation of females is difficult on the basis of morphological differences. We have found that pupation height in shell vial cultures provides a quick and reliable means of

preliminary separation for females of the two species without time-consuming microscopic examination of male progeny.



Fig. 1. Typical shell vial cultures showing a high frequency of pupation above the medium level in *D. melanogaster* (left) but not in *D. simulans* (right).

During the 1977 and 1978 summer seasons, *Drosophila* collections were made at a number of North American locations in order to establish isofemale lines of *D. melanogaster* from widely dispersed geographical areas. The frequency of *D. simulans* at several locations was high, but after some practice it was possible to separate individual female cultures of the two species with a high degree of accuracy according to their pupation pattern in shell vials. It was observed that a majority of *melanogaster* larvae pupated at a level clearly above that of the food medium while *simulans* pupae were only occasionally seen above this level. Typical examples of these two distinct patterns are illustrated in Fig. 1. The fact that similar differences were observed in flies collected in Rhode Island, New Hampshire and Texas suggests that species differences rather than strain differences are involved.

An experiment was designed in order to quantify the observed variation in pupation site. An equal volume of a standard cornmeal-molasses-agar medium was dispensed into sixty

8-dm shell vials and all were seeded with live yeast. The level of the medium in the vials was at a height of 2.5 cm. Into 30 of the vials were placed single gravid *melanogaster* females, aged 4-5 days, which were the progeny of flies collected locally in October 1978. Into the remaining 30 vials were similarly placed *simulans* females, the progeny of flies from the same collection. Development took place at 21° under identical humidity and lighting conditions. All pupation sites located above the initial level of the medium were marked daily on the exterior of the vials with a magic marker. The number of adult progeny were counted on the 22nd day after the start of the experiment. The mean adult production per female at 22 days was 59.3 for *melanogaster* but only 39.9 for *simulans*. The number of pupae located above the 2.5 cm level was 95.4% of the 22 day adult production for *melanogaster* but only 8.9% of that production for *simulans*. This difference in pupation behavior cannot be explained in terms of larval density, however, because the 15 *melanogaster* vials that were ranked lowest for adult production had a higher frequency of pupation above the 2.5 cm level than the 15 vials with the highest production. Close examination of the culture vials indicated that *simulans* tended to pupate on the surface of the medium itself. It was further noted that the medium in *melanogaster* vials was clearly more liquefied by the action of the larvae than in *simulans* vials. Indeed, in most cases, pupation on the surface of the liquefied medium in *melanogaster* vials would likely have resulted in the drowning of the pupae.

These observations of species differences in pupation height are consistent with the previously reported results of Barker (1971) and Markow (1979).

References: Barker, J.S.F. 1971, *Oecologia* 8:139-156; Markow, T.A. 1979, *Behav. Genet.* 9: 209-217.

Liebrich, W. Institut für Genetik, Universität Düsseldorf, F.R. Germany. In vitro differentiation of single cysts of spermatocytes of *Drosophila hydei*.

In this laboratory techniques have been developed to study the in vitro differentiation of single cysts of spermatocytes isolated from testes of *Drosophila hydei* (Fowler and Uhlmann 1974, Fowler and Johannisson 1976). Recently Cross and Shellenbarger (1979) showed that it is possible to

obtain differentiation of isolated cysts of *D. melanogaster*, too.

Improvements of these culture techniques have recently been worked out. A simple culture chamber (details described below) permits the observation of the developing cells even with an oil immersion objective (100x).

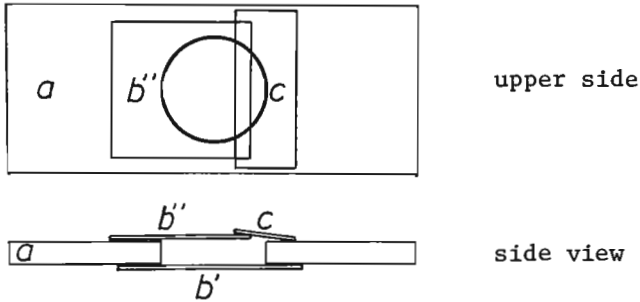


Fig. 1. Culture chamber. The basic part of the chamber is a 3mm thick glass slide. The hole has a diameter of 15mm. First coverslip b' is mounted. If the chamber shall be opened to change the medium, it is better to use a piece of mica or plastic (c) to close the chamber. (A glass coverslip c can cohere to a glass coverslip b.)

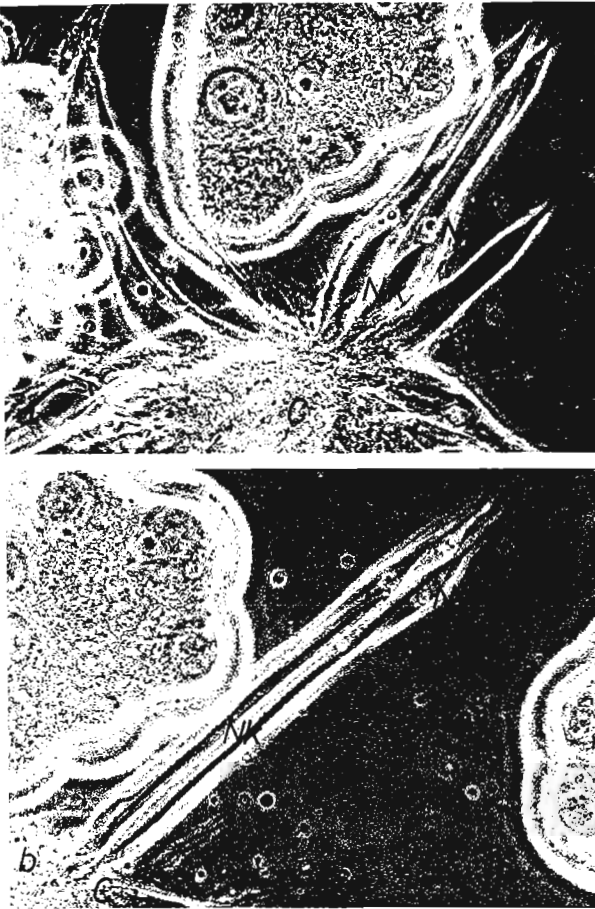


Fig. 2. Burst cyst cell (C) with the freed spermatids (arrow); 2b shows the same cell after 3 hrs of observation. (N = nucleus, Nk = Nebenkern; X 500.)

configuration. The spermatids are connected only terminally in a center which often is covered by the detached cyst cells. Free spermatids elongate continuously, whereas the detached cyst cells do not alter their fibroblast-like shape. Individualization of the spermatids was not

For proper development of the isolated cysts it is important to stage the pupae from where the testes are isolated; the color of the cuticula should be light brown and the contour of the developing embryo should be visible through the transparent cuticula. The eyes should still be white, i.e., they should not yet show the final red color. The testes of these pupae, in general, are ellipsoid and have lose their dense contact to fat-body cells. After collecting pupae of the right stage, the testes are isolated in *Drosophila* Ringer, removed from the Ringer with a Pasteur-pipette, and transferred immediately into Shields and Sang's medium to which 20% fetal calf serum and a mixture of antibiotics are added. After washing the testes a second time in fresh medium, one testis is pipetted into a culture chamber and opened by means of thin glass needles. The culture chamber is filled with medium and closed as described below.

The basic part of the culture chamber is a thick glass slide with a hole of 15mm diameter (Fig. 1). From one side a thin coverslip (Fig. 1, b') is mounted with vaseline. The chamber is filled partly with nutrient medium. The isolated testis is transferred into it and opened. To close the chamber another coverslip (Fig. 1, b'') is mounted leaving a small cleft through which the chamber finally is filled with medium. Thereafter, the cleft is closed with a small piece of coverslip (or mica; Fig. 1, c) using vaseline as a glue. By removing the small coverslip it is very easy to change partly the medium under the stereo microscope with the aid of a Pasteur-pipette or to transfer the cysts with a microliter pipette into a chamber with fresh medium. Observations are made with the inverted light microscope (Zeiss IM 35) with phase contrast optics.

With this technique it is possible to follow the development of 5-10 cysts up to the "coiling process" (Tokuyasu et al. 1972). When the medium is not changed, the two cysts often detach from their 8 primary spermatocytes or the 32 spermatids. Despite this, it might occur that the "naked" spermatocytes continue meiosis until metaphase I. Spermatids also continue to differentiate (Fig. 2). The apical tips of the spermatids of the burst cyst emanate in all directions thus forming a star-like



observed. However, individualization may sometimes occur also in vitro, since we found a damaged cyst in the coiling stage which contained unconnected spermatozoa. An "individualization cone" as seen in vitro (Tokuyasu et al. 1972) and in vitro (Cross and Shellenbarger 1979) on *D. melanogaster* was not detected. In our preparations coiling occurs even in cysts which are not so much elongated as is expected from in vivo investigation.

The following preliminary conclusions can be drawn from our observations. (1) The elongation of the spermatids is independent of an intact cyst. (2) The elongation of the cyst is more a consequence of the elongation growth of spermatids. (3) Individualization seems to occur only in an intact cyst. (4) Individualization and coiling of spermatids may also occur in completely elongated cysts, or spermatids, respectively.

References: Cross, D.P. and D.L. Shellenbarger 1979, *J. Embryol. exp. Morph.* 53:345; Fowler, G.L. and R. Johannisson 1976, in: *Invertebrate Tissue Culture* (E. Karstak and K. Maramorusch, eds.) p. 161, Academic Press; Fowler, G.L. and J. Uhlmann 1974, *DIS* 51:81; Tokuyasu, K. et al. 1972, *Z. Zellforsch.* 127:492.

Lohs-Schardin, M. Biologisches Institut I, Freiburg, West Germany. A new allele of Ubx causing a strong phenotype.

The allele Ultrabithorax<sup>78</sup> was discovered in a line selected for an embryonic mutation. Recombination experiments demonstrate that the mutation is located in the bithorax region (3-58.8). Flies heterozygous for Ubx<sup>78</sup> are fertile

and show the typical Ubx-phenotype (Lindsley and Grell 1968) which is characterized by enlarged haltere. The homozygous condition is lethal at late embryonic stages or shortly after hatching. In the homozygous state, the Ubx<sup>78</sup> allele has a more extreme phenotype than any other Ubx allele described so far. It resembles the phenotype of larvae homozygous for Df(3)P9, the deficiency of the entire bithorax complex (Lewis 1978). On all segments posterior to the mesothorax the homozygous larvae show morphological structures which are characteristic for the mesothorax (Fig. 1). These characteristics include the thorax-type ventral row of fine denticles with some stronger denticles in the posterior segments. Keilin's organs, "black" sense organs (Lohs-Schardin et al. 1980) and a separate section of the tracheal trunk are found on all segments, but the 8th abdominal segment. However, the phenotype differs from larvae homozygous for Df(3)P9 at the posterior end where the telson appears normal.



Fig. 1. The most posterior series (7th and 8th segments and telson) of a homozygous Ubx<sup>78</sup> larva. The abdominal segments show the thin thoracic-type denticle rows, but some denticles of the 8th segment are slightly stronger. The 7th segment carries two "black" sense organs (Lohs-Schardin et al. 1980) and Keilin's organs.

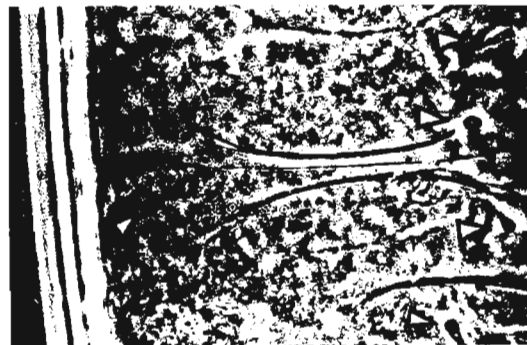


Fig. 2. A series of abdominal segments from a homozygous Pc<sup>3</sup>;Ubx<sup>78</sup> larva. The rudimentary spiracles of four segments and the thin thoracic-type denticles of one of these segments are visible.

Trans-combination between Ubx<sup>78</sup> and other mutations of the bithorax region [bx<sup>3</sup>, pbx, bx<sup>3</sup>pbx, Cbx (Lindsley and Grell 1968)] produce flies with extreme phenotypes; in this respect Ubx<sup>78</sup> is comparable to some other Ubx alleles (Ubx<sup>130</sup>, Ubx<sup>80</sup>) and to deficiencies of the whole bithorax complex [Df(3)P115, Df(3)P9 (Morata 1975)].



In larvae homozygous for  $Pc^3(3-48)$  and  $Ubx^{78}$  each segment posterior to the mesothorax is influenced by both mutations.  $Ubx^{78}$  exerts its effect on the ventral denticle rows which are thorax-like but at the same time  $Ubx^{78}$  enhances the expression of  $Pc^3$ : most segments develop rudimentary posterior spiracles with "Filzkörper" and carry posterior sense organs which decrease in size towards the anterior segments (Fig. 2) while  $Pc^3$  carries these structures only on the posterior 4 segments. This effect is even stronger than in larvae homozygous for  $Pc^3$  combined with 3 doses of the bithorax complex (Lewis 1978).

When exposed to ether vapors at the cellular blastoderm stage,  $Ubx^{78}$  produces in 75% of the treated embryos bithorax phenocopies as compared to 25% phenocopies in the sib controls. The response to ether is known to be higher in embryos carrying bithorax mutations associated with break-points in the bithorax region [ $Ubx^{80}$ ,  $Ubx^{130}$ ,  $Df(3)P9$  (Capdevilla and Garcia-Bellido 1978)]. Cytological analysis of salivary gland chromosomes with the genetical constitution  $Ubx^{78}/Df(3)P9$  [ $Dp(3)P115$  translocated] and  $Ubx^{78}/+$  failed to reveal any deficiency in the bithorax region linked to  $Ubx^{78}$ .

The allele  $Ubx^{78}$  resembles the deficiency of the entire complex by its homozygous phenotype. However in combination with  $Pc^3$  it shows effects ascribed to increased doses of the bithorax complex. Yet the yield of ether phenocopies is increased as in bithorax mutants known to carry a break-point within the bithorax region.

Supported by the Deutsche Forschungsgemeinschaft (SFB 46).

References: Capdevilla, M.P. and A. Garcia-Bellido 1978, Roux's Archives 185:105-126; Lewis, E.B. 1978, Nature 276:565-570; Lindsley, D.C. and E.H. Grell 1968, Genetic Variations of *D. melanogaster*, Publs. Carnegie Inst.; Lohs-Schardin, M., C. Cremer and C. Nüsslein-Volhard 1980, Dev. Biol. 33:239-255; Morata, G. 1975, JEEM 34:19-31.

Loukas, M. Agricultural College of Athens, Greece. A new esterase locus in *D. melanogaster*.

We found that *D. melanogaster* possess the corresponding locus to Est-9 of *D. subobscura*. This esterase is detected only in the adults and only when 1-leucyl- $\beta$ -naphthylamide is used as a substrate together with  $\alpha$ -naphthyl acetate.

(For the technique used for detecting the enzyme, see Loukas and Krimbas 1975.) It is located on the fly's head and migrates in the gel as fast as Est-9 of *D. subobscura*.

In order to locate this gene we performed the following crosses (in all cases we refer to the same Fast and Slow alleles): For chromosome 3: Males of the "curled" strain (cu a recessive mutant located on chromosome 3), homozygous for the Slow allele (SS), were crossed with females of wild type homozygous for the Fast allele (FF).  $F_1$  males were then crossed with females of the curled strain. Half of the wild and half of the curled progeny of this backcross were heterozygous (FS), while the other half were homozygous (SS). So, the esterase gene is not located on chromosome 3. For chromosome 4: Males of the "cubitus interruptus-Dominant" strain ( $ci^D$  a dominant mutant, lethal in homozygotes, located on chromosome 4), homozygous FF, were crossed with females of wild type homozygous SS.  $F_1$  males of phenotype  $ci^D$  were then backcrossed with the females of wild type. Half of the wild and half of the mutant progeny were heterozygous, while the other half were homozygous (SS). So, the esterase gene is not located on chromosome 4. For chromosome 2: Males of the "orange" strain (or, a recessive mutant located on chromosome 2), homozygous FF, were crossed with females of wild type homozygous SS.  $F_1$  males were then crossed with females of the orange strain. All the wild type progeny were heterozygous and all the orange ones homozygous FF. So, the esterase gene is located on chromosome 2.

Taking into consideration all the similarities between this esterase gene and the Est-9 of *D. subobscura* (similar biochemical properties of the enzymes and probably similar physiological role) as well as the fact that Est-9 is located on chromosome E of *D. subobscura* which is homologous to 2R of *D. melanogaster* (Krimbas and Loukas 1980), we suggest that these esterase loci are homologous.

References: Krimbas, C.B. and M. Loukas 1980, DIS 55:55; Loukas, M. and C.B. Krimbas 1975, Genetics 80:331-347.

Loukas, M. Agricultural College of Athens, Greece. Breeding sites of *D. subobscura*.

Until now very little was known of the breeding sites of *D. subobscura*. Decaying Cornus berries in northern Italy (Buzzati-Traverso 1948), diseased Iris root in England (Smart 1945), oak galls of *Biorrhiza pallida* in England (Basden 1952) or slime fluxes, where larvae of other obscure group species are found (e.g., *D. ambigua* by Prevosti 1959) have been advocated as possible breeding sites. Also, *D. subobscura* flies emerged from rowan-berries collected in the field (Begon 1975), from apples (Hummel 1978) and from fruits of *Magnolia grandiflora* (Lachaise 1978). Finally Shorrocks (unp. information) found that the species breeds in England on mushrooms, especially *Amanita phalloides*, and Fontdevila (1978) in northwest Spain (Galicia) in *Amanita rubescens*.

We collected 30 fruits of *Ziziphus jujuba* and 30 orange fruits from the Botanical Garden of Athens. From the *Ziziphus jujuba* fruits 218 *D. subobscura* and 637 *D. melanogaster* flies emerged while from the orange fruits only *D. melanogaster*.

The rarity of all these substrates mentioned above does not seem to justify the great densities of *D. subobscura* at least in the "central" populations (Begon, Krimbas and Loukas in prep.). The situation resembles its North American counterparts, for which we ignore their breeding sites.

References: Basden, E.B. 1952, *Entomol. Monthly Mag.* 88:200-201; Begon, M. 1975, *Oecologia* (Berlin) 20:227-255; Buzzati-Traverso, A.A. 1948, *DIS* 22:69; Fontdevila, A. 1978, *Bul. European Drosophila Pop. Biol. Group No. 2* (Leeds); Hummel, H. 1978, *Bul. European Drosophila Pop. Biol. Group No. 1* (Leeds); Lachaise, D. 1978, *Bul. European Drosophila Pop. Biol. Group No. 1* (Leeds); Prevosti, A. 1959, *DIS* 33:154; Smart, J. 1945, *Proc. Roy. Ent. Soc. (London)* B14:53-56.

Lujan, D. University of California, Santa Cruz. A comparison of TSP's of *Notch<sup>ts1</sup>*, *shibire<sup>ts1</sup>* and the double mutant.

Although a number of mutants affect the disposition of bristles on *Drosophila* none has the extensive pleiotropic effects of *shibire<sup>ts</sup>* (Poodry et al. 1973) and *Notch<sup>ts</sup>* (Shellenbarger and Mohler 1975). The developmental phenotypes

of these two mutants are remarkably similar even though the mutants are located far from each other on the X chromosome and they do not share the phenotype of reversible paralysis. A detailed analysis of the temperature-sensitive periods for each mutant and for the double mutant was undertaken to determine whether the loci interact in any way.

Strains bearing *shibire<sup>ts1</sup>* (*shits<sup>1</sup>*) and *Notch<sup>ts1</sup>* (*wants<sup>1</sup>rb*) and both mutations (*wants<sup>1</sup>rb shits<sup>1</sup>f*) were reared in mass cultures on standard food at 22°. White prepupae were collected at 1 hr intervals, transferred to shell vials and shifted to 29° for 6 hrs then returned to 22° for the remainder of their development. The 6 hr heat pulses were delivered at various times in 1 hr increments from pupariation to 48 hrs after pupariation.

The results confirmed the similarity in phenotypes and temperature-sensitive periods reported previously. The effects causing deletion of structures are more severe in *shits<sup>1</sup>*. The period from pupariation to pupation is lethal at 29° for *shits<sup>1</sup>* but not for *Notch<sup>ts1</sup>*. The deletion of bristles especially macrochaetes is much less severe in *Notch<sup>ts1</sup>*. In contrast, *Notch<sup>ts1</sup>* appears to have a much stronger response to heat pulses causing supernumerary microchaetes. Since the temporal pattern of temperature-sensitive periods is specific to various regions, and even to bristle rows, on the thorax a single 6 hr heat pulse may lead to overlapping phenotypes. That is, supernumerary bristles in one area or row may be near regions where deletion of bristles has begun. *Notch<sup>ts1</sup>* is less effective in deleting bristles so the net result is a more hirsute thorax on *Notch<sup>ts1</sup>* animals given comparable heat pulses to *shits<sup>1</sup>*. The timing, duration and intensity of the effect on bristle shape called "scimitar" is the same in the two mutants.

The phenotype of the double mutant is essentially that of *shibire<sup>ts1</sup>* alone. The presence of *Notch<sup>ts1</sup>* does not enhance or rescue any of the *shibire* effects at the restrictive temperature. Neither does it alter the restrictive temperature.

The similar complex pleiotropic phenotypes of these two non-interacting temperature-sensitive mutants are difficult to explain by a hypothesis of intermittent gene activity. The interpretation we favor is that the temperature-sensitive periods reflect times when the particular cells enter a sensitive stage of their cell cycle or developmental program.

This work was supported by NIH Grant RR 08132.

References: Poodry et al. 1973, *Develop. Biol.* 32:373-386; Shellenbarger and Mohler 1975, *Genetics* 81:143-162.

Lyttle, T.W. University of Hawaii, Honolulu. Segregation in XYY males and XXY females of *D. melanogaster*.

Grell (1958) investigated the pattern of sex chromosome segregation in the progeny of XYY males and recovered XY/Y segregation in excess of the .667 frequency predicted under non-preferential segregation. In addition, there

appeared to be a deficiency of XYY males which Grell attributed to a lowered viability of such aneuploid types. This report presents data which independently supports Grell's speculation.

In the course of our work with a translocation [T(Y;2),SD L<sup>2</sup>] in *D. melanogaster* which has its autosomal break in division 58 proximal to bw<sup>+</sup>, we found it necessary to measure the amount of sex chromosome nondisjunction in X/X/T(Y;2),SD L<sup>2</sup>/CyO females and X/Ybw<sup>+</sup>/y<sup>+</sup>YBS males. Flies hyperplod for the 2R tip survive and carry all the Y fertility factors.

Table 1 shows the resulting progeny when X/X/T(Y;2),SD L<sup>2</sup>/CyO (= Rsp<sup>I</sup>) females are mated to y/y<sup>+</sup>YBS;Rsp<sup>S</sup> cn bw (or Rsp<sup>I</sup>-16 cn bw, kindly provided by B. Ganetzky) males. Here Rsp<sup>S</sup> and Rsp<sup>I</sup> denote the alleles at the Responder locus which are sensitive and insensitive, respectively, to the sperm dysfunction induced by Segregation distorter (SD).

Some progeny classes are lethal and others are confounded, but a reasonable estimate of the overall nondisjunction rate can be obtained by doubling the contribution of the three surviving nondisjunctional classes to the total, to give  $\underline{m}$  = proportion of XX/Y disjunctions = 14/635 = .022. This should be compared to the somewhat higher rate of  $2 \cdot (2404/54070) = .086$  obtained by Bridges (1916,  $\chi^2 = 15.4$ ,  $p < .001$ ). The apparent reduction in secondary nondisjunction may be partially due to a decreased viability of y flies, or may be explained on the basis of a decreased probability of heterosynapsis owing to the interference of the bw<sup>+</sup> material on the Y.

Two classes of progeny males (A and B) were themselves progeny tested in matings to cn bw females in order to further determine the viability of, and segregation in, XYY flies. Tests of B Cy cn males (class A in Table 1) showed 3/21 males were XYY, and their progeny distribution is presented in Table 2. The B L males (class B, Table 1) are all XYY, but some of those (5/14) tested were carrying Rsp<sup>S</sup> and showed segregation distortion, while the remainder were X/y<sup>+</sup>YBS;T(Y;2),SD L<sup>2</sup>/Rsp<sup>I</sup> - 16 cn bw and showed no SD activity. The progeny from these crosses are summarized in Tables 3b and a, respectively.

Several observations can be made from this somewhat heterogeneous mass of information. First, the data from Table 2 include all progeny classes and allow the best estimate of  $\underline{l}$  = proportion X/YY disjunction (summarized in Table 4b). I give a range for  $\hat{l}$  because its value depends critically on whether there is a viability reduction in XYY flies, since  $\hat{l}_1 = (X + YY)/TOTAL$  will then underestimate  $\underline{l}$ . On the other hand,  $\hat{l}_2 = X/(X + Y)$  uses less of the available information and is therefore less precise, though perhaps more accurate. Secondly, the presence of the SD L portion of the T(Y;2) in the B L males allows us to use Table 3a to determine whether the translocation itself affects segregation. Finally, from Table 3b we can determine whether the strength of SD is altered by the presence of the extra sex chromosome.

From Table 3a we first estimate the parameter  $\underline{c}$  = proportion of X ↔ SD segregations, which should be equal to 0.5 if the two chromosomes are assorting independently. Here  $\underline{c} = 167/343 = .487$  with  $\chi^2_1 = .557$ ,  $p \approx .54$ , and we provisionally accept the hypothesis that the translocation is not interfering with sex chromosome disjunction.

Also in Table 3a, we attempt to measure  $\underline{l}$  by first estimating the three missing classes by the observed numbers for their respective complementary classes (immediately right adjacent to each empty box) and summarizing the data in Table 4c. Notice that the range of  $\underline{l}$  here barely overlaps that obtained from the data of Table 2 (see Table 4b). This is primarily because of the zero value for the XYY class in the latter data, which makes  $\underline{l}_1$  extremely low. It should be noted that the pattern of the data and the estimates of  $\underline{l}_1$  vary very little if we ignore the missing or confounded data classes in Tables 2 and 3 and use only the even numbered columns for purposes of estimation. These alternate estimates of  $\underline{l}$  are presented in Table 4 with asterisks.

The overall estimate of  $\underline{l}$  in the current data may also have a slightly upward bias owing to the apparent tendency of y<sup>+</sup>YBS to be involved in a proportionally greater number of heterosynapses in these XYY males, perhaps due to some pairing ability of the X material on y<sup>+</sup>YBS. This shows up in all crosses as an increased tendency for X Ybw<sup>+</sup>/y<sup>+</sup>YBS compared to X y<sup>+</sup>YBS/Ybw<sup>+</sup> segregations. The data from both Tables 2 and 3 are homogeneous in this respect, and when pooled (ignoring the SD L classes) gives an overall  $\chi^2_1 = 15.63$ ,  $p < .001$  for the contingency test for independence of the X and the type of Y chromosome present (89 XYbw<sup>+</sup>:50 Xy<sup>+</sup>YBS:57 Ybw<sup>+</sup>:84 y<sup>+</sup>YBS). If there is an enhanced tendency for Xy<sup>+</sup>YBS synapses, this will increase the proportion of recovered X ↔ YY disjunctions and thus increase  $\hat{l}$  above the level

Table 1 - Progeny from  $X/X/T(Y;2)SD L^2/CyO$  ♀ by  
 $y/y^+YB^S;cn bw^\sigma$ .

GAMETES ♂/♀	X CyO	XYbw <sup>+</sup> CyO	X SDL	XYbw <sup>+</sup> SDL	XX CyO	Ybw <sup>+</sup> CyO	XX SDL	Ybw <sup>+</sup> SDL
y;cn bw	303	cy cn♀	†	97 L♀	+	2y Cy cn	+	1 yL♂
y <sup>+</sup> YB <sup>S</sup> ;cn bw	(A) 160	B Cy cn♂	†	(B) 61 BL♂	4 B Cy ♀	+	+	+

Table 2 - Progeny from  $X/y^+YB^S/Ybw^+;cn bw/CyO^\sigma^\sigma$   
 by  $X/X;cn bw^\sigma^\sigma$ .

♂ GAMETES <sup>†</sup>	XY CyO	XY cn bw	XY <sup>1</sup> CyO	XY <sup>1</sup> cn bw	Y CyO	Y cn bw	Y <sup>1</sup> CyO	Y <sup>1</sup> cn bw	X CyO	X cn bw	YY <sup>1</sup> CyO	YY <sup>1</sup> cn bw
PROGENY	18 <sup>†</sup>	28	8	10	15	9	20	22	8 <sup>†</sup>	12	0	0
PHENOTYPE	Cy ♀	cn ♀	B Cy ♀	B cn♀bw	Cy ♂	Cn ♂	B Cy ♂	cn <sup>B</sup> cn♂bw	Cy ♀	cn bw ♀	B Cy ♀	B cn ♂

<sup>†</sup> based on partitioning 26 Cy♀ progeny according to XY cn bw: X cn bw proportions observed.

\*  $Y = Ybw^+$   
 $Y^1 = y^+YB^S$

Table 3a, b - Progeny from a)  $X/y^+YB^S;T(Y;2),SD L^2/Rsp^I - 16 \text{ cn bw}$   
 or b)  $X/y^+YB^S;T(Y;2),SD L^2/Rsp^S \text{ cn bw}$   $\sigma\sigma$  by  $X/X; \text{cn bw}$   $\text{♀♀}$ .

$\sigma$ GAMETES *	XY SDL	XY cn bw	XY <sup>1</sup> SDL	XY <sup>1</sup> cn bw	Y SDL	Y cn bw	Y <sup>1</sup> SDL	Y <sup>1</sup> cn bw	X SDL	X cn bw	YY <sup>1</sup> SDL	YY <sup>1</sup> cn bw
PROGENY a	39	42	-	26	14	33	-	42	-	30	13	6
b	71	1	-	5	73	0	-	0	-	0	12	1
PHENOTYPE	L ♀	cn ♀	+	cn <sup>B</sup> cn bw ♀	L ♂	cn ♂	+	cn <sup>B</sup> cn bw ♂	+	cn bw ♀	BL ♂	B cn ♂

\*  $Y = Ybw^+$   
 $Y^1 = Y^+YB^S$

Table 4 - Summary of data from Grell (1958) and Tables 2 and 3.

$\sigma$ GAMETES	XY	X	YY	Y	$\hat{l}_1$	$\rightarrow$	$\hat{l}_2$
PROGENY	XXY ♀	XX ♀	XYY ♂	XY ♂			
a	1153	307	207	1155	.182	-	.210
b	64	20	0	66	.133	-	.233
					.148	-	.279*
c	133	60	19	131	.230	-	.314
					.201	-	.286*

\* see text

obtained for normal XYY males. In any case, even if we ignore this potential bias, the various estimates for  $\underline{l}$  tend to argue against nonpreferential segregation (i.e.,  $\underline{l} = .333$ ), and in favor of Grell's conclusion of preferential pairing of the Y chromosomes.

Table 3b can be used to estimate  $\underline{k}$  (= proportion of SD bearing sperm) in these crosses where distortion is active. The estimate obtained is  $\underline{k} = 156/158 = .987$ , indistinguishable from a control value obtained for X;T(Y;2),SD L<sup>2</sup>/Rsp<sup>S</sup> cn bw males of  $6260/6290 = .995$  ( $\chi_1^2 = 1.94$ ,  $p = .173$ ). Therefore, I conclude that the presence of the extra Y is having no significant effect on the strength of distortion.

The low frequency of XYY males among the B Cy cn progeny tested from Table 1 (14% recovered) as well as the disparity in the X versus YY gamete recovery in all data of Table 4 indicates a reduced viability for XYY flies, best estimated from Grell's data alone as a loss of about 0.33 compared to XY males. The viability is further lowered in my data by the fact that the XYY males are often hyperploid for the 2R tip.

The estimates of  $\underline{l}$  differ somewhat, with  $\underline{l}_2$  being most reliable owing to the viability effect. After making allowances for the possible biases discussed, it would seem that  $\underline{l} \sim .2 - .25$  is a reasonable estimate. However, an important inference from the data presented here should be that marked Y chromosomes may introduce considerable bias for segregation studies in *Drosophila*.

References: Bridges, C.B. 1916, *Genetics* 1:1-52; 107-163; Grell, R.F. 1958, 10th Int. Cong. of Genet. (Proc.) p. 105.

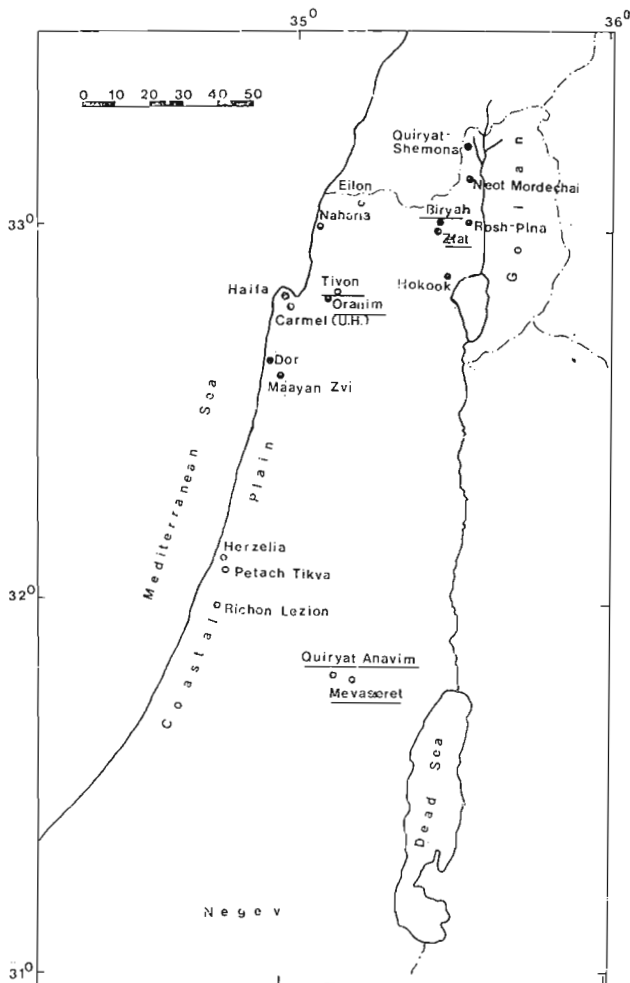
Malogolowkin-Cohen, Ch. and M. Livni. Institute of Evolution, University of Haifa, Israel. A preliminary study on polymorphism and heterozygosity found in *D. subobscura* in Israel.

A genetic analysis, polymorphism and heterozygosity of 16 loci of 12 enzymes of Israeli populations of *D. subobscura* was initiated in our laboratory in 1976. Five collecting sites from three of the four biogeographic regions cited by Malogolowkin-Cohen (1979) and Malogolowkin-Cohen et al. (1979) are used in this

study: (1) mountains - Biryah-Zefat, Carmel and Quiriat Anavim-Mevasseret; (2) foot hills - Tivon-Oranim; (3) coastal plain - Dor (Fig. 1). Males caught at the above mentioned places were pair-mated to virgin females from a stock of inversion-free chromosomes and wild impregnated females caught at the same places were permitted to oviposit in the lab, after which

Locality	$\bar{A}$ (allele frequency)	$\bar{p}$ (polymorphism)	$\bar{H}$ (heterozygosity)
Kiryat Anavim-Mevasseret	1.68	0.37	0.05
Tivon-Oranim	2.19	0.81	0.08
Biryah-Zefat	2.19	0.81	0.05
Dor	2.06	0.62	0.05
Mount Carmel	2.37	0.87	0.09

wild males and wild females were assayed for enzymes. Horizontal starch gel electrophoresis was carried out according to the techniques of Ayala et al. (1972) with modifications and additions made by Saura et al. (1973). The allele frequency,  $\bar{A}$ , polymorphism,  $\bar{p}$ , and heterozygosity,  $\bar{H}$ , are calculated and the results may be seen in Table 1. Polymorphism and allele frequencies are found to be higher in the center (Tivon-Oranim, Mount Carmel and Dor) and in the north (Biryah-Zefat) and lower in the western distribution area of the fly (Quiriat-Anavim-Mevasseret), while no variation is found in heterozygosity (Table 1). The estimates are based on the following loci: acid phosphatase (Acph 1, 2, and 3), aldehyde oxidase (Ao), esterase (Est), fumarase (Fum),  $\alpha$ -glycerophosphate dehydrogenase ( $\alpha$ -Gpdh), hexokinase (Hk), isocitrate dehydrogenase (Idh), leucine aminopeptidase (Lap), malate dehydrogenase (Mdh 2 and R), malic enzyme (Me), phosphoglucumutase (Pgm) and phosphoglucose isomerase (Pgi 1 and 2).



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References: Ayala, F.J., J.R. Powell, M.L. Tracey, C.A. Mourao and S. Perez-Salas 1972, Genetics 70:113-139; Malogolowkin-Cohen, Ch. 1979, DIS 55; Malogolowkin-Cohen, Ch., H. Levene and E. Nevo 1979, Rev. Bras. Genetica (in press); Saura, A., Lakovaara, J. Lokki and O. Lankinen 1973, Hereditas 75:33-46.

Fig. 1. Map of Israel illustrating sites where *D. subobscura* was found by us in 1976. Underlined are the sites used for the present study. U.H. = University of Haifa.

Mather, W.B. and G. Balwin. University of Queensland, Brisbane, Australia. Inversions in three species of *Drosophila* from the River Kwai, Thailand.

June 1978 and January 1979 (Mather et al. 1980; Mather and Balwin 1979 and in press).

Table 1

Inversion	Chromosome	Simple	Complex	Het. %
C	III	X		4.2
E	IIL	X		12.5
G	I	X		4.2
W <sub>2</sub>	III	X		4.2
F <sub>3</sub>	III	X		4.2
A <sub>5</sub>	III	X		91.7
C <sub>5</sub>	IIR	X		45.8
D <sub>5</sub>	IIL		X	25.0

In June 1979 twenty-four isolines of *D. s. albostrigata*, fifteen of *D. albomicans* and three of *D. kohkoa* were established from the River Kwai region of Thailand. The inversions from this region have been reported on three times before from collections made in November 1977,

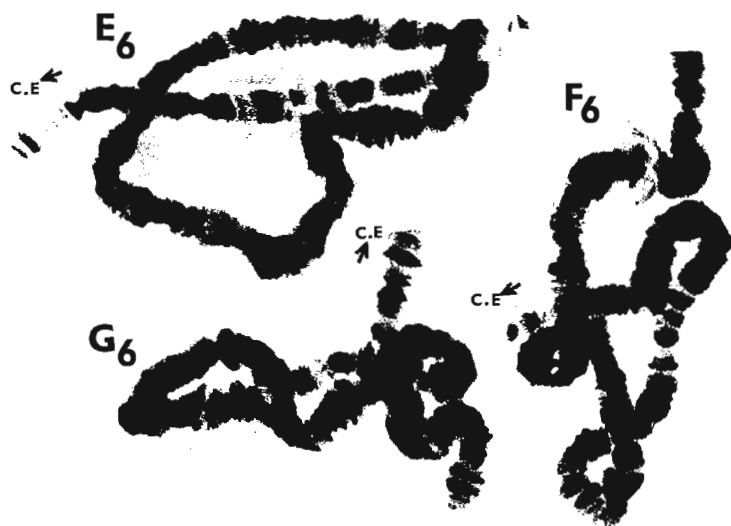
(a) *D. s. albostrigata*. Seven simple and one complex inversions were detected. No new inversions were detected but this is the first time that inversions G and F<sub>3</sub> have been recorded at the River Kwai. Inversion G - Mather, W.B. and P. Thongmeearkom DIS 48:40 previously recorded at Cebu (Phill.), DIS 48:40 and Luzon (Phill.), DIS 50:60. Inversion F<sub>3</sub> - Mather, W.B. and P. Thongmeearkom, M. Clyde and D. Lambert DIS 51:86, recorded at Kuala Lumpur (Malaysia). The heterozygosity frequency of all inversions detected is given in Table 1.

Table 2

Inversion	Chromosome	Table 2		Break Points	Het. %
		Simple	Complex		
C	III	X			33.3
L <sub>3</sub>	III	X			6.6
R <sub>5</sub>	I	X			13.3
S <sub>5</sub>	IIL	X			73.3
U <sub>5</sub>	IIL		X		20.0
W <sub>5</sub>	III	X			13.3
X <sub>5</sub>	III		X		73.3
B <sub>6</sub>	III	X			13.3
C <sub>6</sub>	IIL	X			20.0
D <sub>6</sub>	III	X			20.0
E <sub>6</sub>	III		X	21.6 - 40.0	13.3

(b) *D. albomicans*.

Eight simple and three complex inversions were detected. All inversions except one had previously been detected at the River Kwai. A photograph of the new inversion (E<sub>6</sub>) is presented and break-points assigned (in relation to the standard photographic map - Mather, W.B. and P. Thongmearkom DIS 55:101). See Table 2. The heterozygosity frequency of all inversions detected is given.

(c) *D. kohkoa*. One simple

and one complex inversion were detected. Both inversions F<sub>6</sub> and G<sub>6</sub> are new. Photographs are presented and break points assigned (in relation to the standard photographic map, Mather, W.B. and P. Thongmearkom 1978, DIS 53:150). See Table 3.

The material was collected and the isolines established by W.B.M. The laboratory work was carried out by G.B.

Table 3

Inversion	Chromosome	Table 3		Break Points
		Simple	Complex	
F <sub>6</sub>	III	X		32.9 - 37.0
G <sub>6</sub>	IIL		X	6.6 - 20.3

References: Mather, W.B. and G. Balwin 1980, DIS 55:99 and in press; Mather, W.B., W.R. Knibb and G. Balwin 1980, DIS 55:103; Mather, W.B. and P. Thongmearkom, DIS 48:40, 50:60, 53:150 and 55:101; Mather, W.B., P. Thongmearkom, M. Clyde and D. Lambert, DIS 51:86.

Mather, W.B. and G. Balwin. University of Queensland, Brisbane, Australia. Inversions in the nasuta complex from the River Kwai, Thailand.

Inversions in species of the nasuta complex from the River Kwai region of Thailand have been reported on twice before from collections made in November 1977 and June 1978 (Mather et al. 1980; Mather and Balwin 1980). In January 1979 seventy-one isolines of *D. s. albostrigata* and four isolines of *D. albomicans* were established.

(a) *D. s. albostrigata*. Nine simple and one complex inversions were detected. Seven of these had previously been detected at the River Kwai and one (A<sub>2</sub>) had first been detected elsewhere in Southeast Asia (Mather and Thongmearkom 1973). The remaining inversions Y<sub>5</sub> and Z<sub>5</sub> are new and photographs are presented and break points assigned (in relation to the standard photographic map, Thongmearkom 1977). See Table 1. The heterozygosity frequency of all inversions detected is given and compared with June 1978. It will be noted that there are considerable differences in frequency in some cases. (Seventy-six isolines were analyzed in the June 1978 collection.)



Table 1. *D. s. albostrigata*

Inversion	Type	Chromosome	Break Points	Het. Freq. %	
				Jan. '79	June '78
C	simple	III		5.6	1.3
E	simple	IIL		19.7	14.5
A <sub>2</sub>	simple	III		4.2	--
W <sub>2</sub>	simple	III		9.9	3.9
A <sub>5</sub>	simple	IIL		76.1	55.3
B <sub>5</sub>	simple	III		7.0	7.9
C <sub>5</sub>	simple	IIR		29.6	55.3
D <sub>5</sub>	complex	IIL		16.9	34.2
Q <sub>5</sub>	simple	IIL		--	2.6
Y <sub>5</sub>	simple	III	10.2 - 15.6	1.4	--
Z <sub>5</sub>	simple	IIL	17.0 - 21.4	1.4	--

Table 2. *D. albomicans*

Inversion	Type	Chromosome	Break Points	Inversion Detection	
				Jan. '79	June '78
C	simple	III		+	+
J <sub>2</sub>	complex	IIL		+	-
L <sub>3</sub>	simple	III		+	-
R <sub>5</sub>	simple	I		+	+
S <sub>5</sub>	simple	IIL		+	+
T <sub>5</sub>	simple	IIL		-	+
U <sub>5</sub>	complex	IIL		-	+
V <sub>5</sub>	simple	III		-	+
W <sub>5</sub>	simple	III		-	+
X <sub>5</sub>	complex	III		+	+
A <sub>6</sub>	simple	III	32.4 - 38.8	+	-
B <sub>6</sub>	simple	III	34.2 - 40.1	+	-
C <sub>6</sub>	simple	IIL	1.1 - 10.0	+	-
D <sub>6</sub>	simple	III	1.1 - 7.4	+	-



(b) *D. albomicans*. Eight simple and two complex inversions were detected. Five of these had previously been detected at the River Kwai; four in *D. albomicans* and J<sub>2</sub> in *D. s. albostrigata*. One (L<sub>3</sub>) had been detected previously at Phuket in Thailand (Mather and Thongmeearkom in press). The remaining inversions A<sub>6</sub>, B<sub>6</sub>, C<sub>6</sub> and D<sub>6</sub> are new and photographs are presented and break points assigned (in relation to the standard photographic map, Mather and Thongmeearkom in press). See Table 2. Because only four isolines were established and analyzed heterozygosity frequencies are not given but a comparison between the inversions detected in June '78 and Jan. '79 is given.

The material was collected and the isolines established by W.B.M. The laboratory work was carried out by G.B.

References: Mather, W.B. and G. Balwin 1980, DIS in press; Mather, W.B., W.R. Knibb and G. Balwin 1980, DIS in press; Mather, W.B. and P. Thongmeearkom 1973, DIS 50:60, 1980 DIS in press; Thongmeearkom, P. 1977, DIS 52:154.

(McInnis)

Table 1. *Drosophila* collected in Raleigh, N. C. (1975-1977).

Species	1975				1976													
	Oct.		Nov.		Dec.		Jan.		Feb.		Mar.		Apr.		May		June	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<i>D. melanogaster</i>	30	} 92	21	} 76	3	} 38	0	} 0	1	} 3	12	} 16	14	} 16	6	} 7	33	} 42
" <i>simulans</i>	67		122		69		0		0		0		0		0		0	
" <i>tripunctata</i>	13	9	14	1	16	8	9	1	35	15	133	82	65	45	173	13	326	39
" <i>immigrans</i>	63	31	86	39	28	14	1	0	1	0	9	9	29	14	46	9	55	37
" <i>affinis</i>	16	3	3	0	8	1	6	1	184	32	244	33	126	27	64	3	26	7
" <i>putrida</i>	0	0	0	0	0	0	0	0	0	0	133	82	380	20	348	14	79	5
" <i>robusta</i>	0	1	3	1	1	1	0	0	0	1	34	7	11	0	7	0	9	4
" <i>quinaria</i>	1	1	1	4	0	0	0	0	3	3	0	0	22	38	18	29	11	22
" <i>buskii</i>	0	0	0	0	0	0	0	0	0	0	1	0	6	3	0	0	2	1
" <i>hydei</i>	0	0	2	0	0	0	0	0	1	2	3	3	0	0	0	1	0	0
" <i>nigromelanica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
" <i>micromelanica</i>	5	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
" <i>melanica</i>	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
" <i>falleni</i>	0	0	0	0	0	0	0	0	0	0	0	0	21	8	83	43	69	21
" <i>duncani</i>	2	0	0	0	1	0	12	12	1	6	1	0	0	0	0	0	0	0
# Collections	4		4		6		12		13		29		30		31		26	

Table 1. (cont'd).

Species	1976										1977									
	July		Aug.		Sept.		Oct.		Nov.		Dec.-Feb.		Mar.		Apr.		May		June	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<i>D. melanogaster</i>	59		119		46		11		2		0		0		11		3		9	
" <i>simulans</i>	8	37	62	116	194	148	96	77	53	45	0	0	0	1	0	17	0	1	50	36
" <i>tripunctata</i>	65	20	64	16	42	21	15	2	23	4	1	0	4	12	22	17	36	10	15	7
" <i>immigrans</i>	13	15	2	7	17	13	21	14	24	9	0	0	0	1	12	22	15	17	46	39
" <i>affinis</i>	2	1	29	5	35	2	12	3	2	1	8	3	26	14	22	21	1	1	22	3
" <i>putrida</i>	90	7	84	7	24	0	1	0	2	0	0	1	6	0	74	6	42	1	4	1
" <i>robusta</i>	6	10	6	0	2	1	0	0	1	0	0	2	3	0	0	1	3	2	14	7
" <i>quinaria</i>	3	11	4	6	4	13	0	1	1	2	0	0	0	0	3	5	1	5	3	0
" <i>buskii</i>	1	1	3	0	0	0	0	0	1	0	0	0	16	12	16	13	34	21	9	1
" <i>hydei</i>	0	2	1	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	6	1
" <i>nigromelanica</i>	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
" <i>micromelanica</i>	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0
" <i>melanica</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
" <i>falleni</i>	3	5	3	2	10	5	1	0	4	3	1	1	1	0	5	17	18	20	11	4
" <i>duncani</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
# Collections	10		17		14		8		7		8		11		9		9		7	

McInnis, D.O. Screwworm Research Laboratory, Mission, Texas. *Drosophila* collections from Raleigh, North Carolina.

activity periods *Drosophila* were netted above a bucket containing fermenting banana. Collections were taken at least once a week except for the months of December (1976) and January (1977) when the weather was extremely unfavorable for *Drosophila*. The results of the samples are shown in Table 1 [preceding pages].

Several comments can be made about the seasonal variations in abundance of the 15 species trapped. Typically, the arrival of warm spring temperatures heralded the arrival of large numbers of *Drosophila*, occasionally with suddenness. Populations of the most numerous species, *D. tripunctata*, *D. immigrans*, *D. affinis* appear to increase swiftly during March or April before tapering off gradually into the winter months. Two of these species, *D. tripunctata* and *D. affinis*, seem to have continuity year-round, though their means of overwintering is not known. Interestingly, *D. duncani* was trapped almost exclusively during the winter months, albeit at low numbers. Of the two sibling species, *D. melanogaster* and *D. simulans*, the latter appeared later in the spring yet lasted longer during the fall. However, the spring catch of *D. melanogaster* could have been at least partly due to escaped laboratory flies from a campus building only 1/4 mile from the trap site (known multiply marked laboratory mutants were sometimes trapped). The female members of these siblings are not reliably distinguished on morphological grounds so only a single total is given for them. With the exception of *D. quinaria*, males were consistently trapped in greater numbers than females. *D. putrida* was the most extreme example of this.

McInnis, D.O. Screwworm Research Laboratory, Mission, Texas. The seasonal spread of *D. melanogaster* and *D. simulans* in Raleigh, North Carolina.

A shaded glen on the campus of North Carolina State University at Raleigh, NC provided a suitable and convenient area for *Drosophila* collections. A fixed trap site was the source of data from October 1975 to June 1977. During evening

During the summer and fall of 1977, *Drosophila* were collected at various sites around the city of Raleigh, NC. One site was maintained on the campus of North Carolina State University, another sustained in a residential park, and two others set in suburban pine (Schenck Forest) or

hardwood (Umstead State Park) areas. A difference between the campus and residential park data was noted in the timing of the onset of relatively high frequencies of *D. melanogaster* and *D. simulans*. For the campus site, combined frequencies (ca. 75%) of *D. melanogaster* and *D. simulans* were observed by early June, but at the residential park the peak did not occur until late June or early July. The phenomenon of a gradual spread of "domesticated" species of *Drosophila* from source areas of human habitation into wilder habitats has already been observed for *D. melanogaster*, *D. hydei* and *D. busckii* by McCoy (1962) in Indiana. The relevancy of this notion to the Raleigh area of North Carolina is further strengthened by the Schenck Forest and Umstead Park data. The peak populations of the siblings appeared in August or September at Schenck Forest, sometime after their appearance at the campus and residential park sites. At the most isolated of collecting areas (the experimental field at Umstead Park) the siblings never attained ascendancy over the class of other *Drosophila* combined, while their greatest abundance came in October. As a result of the late arriving pulse of *D. melanogaster* and *D. simulans* in the study areas, the peak populations of the sibling species are correspondingly more short-lived than in the two urban sites. By the end of November, colder temperatures apparently reduced numbers of *Drosophila* to near zero at all four trap sites.

Reference: McCoy, C.E. 1962, Jour. Econ. Ent. 55:978-985.

Miglani, G.S. and F.R. Ampy. Howard University, Washington, D.C. A possible cline between the body weight and altitude in Mexican populations of *D. melanogaster*.

Mean body weight (mg) per 40 males was measured for 12 Adh I/Adh I and 40 Adh II/Adh II isochromosomal lines extracted from 16 Mexican populations of *D. melanogaster* (Pipkin et al. 1976) raised at 25°C. A significant correlation ( $r = 0.627$ ;  $p < 0.05$ ) was observed between the altitude and mean body weight of

the populations representing the Adh II/Adh II lines. The sites located at higher altitudes were in northern Mexico where the mean annual temperatures were low as compared to the sites located at lower altitudes in southern Mexico (Atlas Climatologico de Mexico, 1921-30). This

relationship suggested that the increased body weight at low temperatures may be due to the slower development of the individual. This view was supported by highly significant differences ( $p < 0.001$ ) in mean body weight among three developmental stages (third instar larvae > pre-emergency pupae > adult) raised at 18°C and 28°C. It was also observed that the rate of development at 18°C was approximately one half the rate at 28°C. The above relationship suggested a possible cline between the body weight and altitude in Mexican populations of *D. melanogaster*.

Reference: Pipkin et al. 1976, J. Hered. 67:258-266.

Miglani, G.S. and F.R. Ampy. Howard University, Washington, D.C. ADH denaturation depends on native ADH activity levels in *D. melanogaster*.

Native ADH activity (nM of NADH produced/ml/min/mg of live weight) was determined spectrophotometrically for 12 Adh I/Adh I and 40 Adh II/Adh II isochromosomal lines extracted from 16 Mexican populations of *D. melanogaster* (Pipkin et al. 1976) raised at 25°C. The native

ADH activity was compared with the activity of ADH for each line after treatment with 0.7M guanidine hydrochloride (GuHCl) or 1.0M urea (UR) for 40 seconds or with heat for 15 minutes at 45°C. The relationship between native ADH activity and ADH activity after treatments with denaturants was investigated. A significant correlation ( $r = 0.63$ ;  $p < 0.05$ ) was observed between native ADH activity for the 12 Adh I/Adh I lines and ADH activity after treatment with UR. Significant correlations were observed between native ADH activity for the 40 Adh II/Adh II lines and ADH activity after treatment with GuHCl ( $r = 0.59$ ;  $p < 0.01$ ) and UR ( $r = 0.71$ ;  $p < 0.01$ ). These relationships suggested that the degree of ADH denaturation was possibly dependent on the native ADH activity levels of the strain.

Reference: Pipkin et al. 1976, J. Hered. 67:258-266.

Moss, L.J. and E.A. Carlson. State University of New York, Stony Brook. EMS induced yellow mosaics in *D. melanogaster*.

Wild type Ore-R males were fed EMS (ethyl methane sulfonate) using an 0.0125M concentration for 24 hours. These males were mated to virgin y w f females and the F<sub>1</sub> flies were observed for mutations of yellow body, white eyes, or forked bristles. Altogether 21 yellow, 5 forked (all mosaic), and 5 white (all mosaic, one of which was an apricot) mutations were found among 9638 F<sub>1</sub> progeny.

The yellow mutations were classified as mosaic or complete in phenotype and then mated to y w f males for a test of transmissibility. Of the 21 yellow mutations, 7 were transmitted, 4 were probably gynandromorphs involving (y f) F<sub>1</sub> mosaic phenotypes with non-white head areas. Of these 4 gynandromorphs, 2 were sterile, and the 2 which were fertile segregated the y w f and Ore R wild type X (along with some f crossovers). Of the 17 yellow phenotypes not due to chromosome loss, 6 were sterile. Of the 11 fertile yellow mutants, 10 were mosaic and 1 was complete. The complete transmitted as did 6 of these 10 mosaics.

Table 1. Frequency of mutation chart.

	yellow phenotypes	F <sub>1</sub> females
EMS run #1	3	1235
EMS run #2	11	5162
EMS run #3	3	854
EMS run #4	4*	2387
total	21	9638

\*Includes one yellow complete; all others in runs 1-4 are mosaic.

Total yellow phenotypes =  $(21/9638)(100) = 0.217\%$  frequency of yellow phenotypes.

Total F<sub>1</sub> females =  $(17/9638)(100) = 0.176\%$  frequency of yellow mutations.

The transmissibility data for the yellows are shown in Table 1.

These results show that EMS induces chromosome loss as well as gene mutations affecting yellow (none of the transmitted viable yellows showed achaete or scute mutations in association with the yellow). One of the two lethals is not associated with an lJ1 lethal because

Table 2. Frequency of transmissibility of y mosaics.

	Transmitted	Sterile	Non-transmitted mosaics	Total yellow mosaics
EMS run #1	0	1	2	3
EMS run #2	3	4	1	8
EMS run #3	2**	1	0	3
EMS run #4	$\frac{1}{6}$	$\frac{0}{6}$	$\frac{1}{4}$	$\frac{2}{16}$
total	$\frac{6}{6}$	$\frac{6}{6}$	$\frac{4}{4}$	$\frac{16}{16}$

\*\*Both lethal--no (y) males.

$\frac{\text{Total transmitted}}{\text{Total (y) mosaics}} = (6/16)(100) = 37.5\%$  frequency of transmission.

$\frac{\text{Total transmitted}}{\text{Total fertile (y) mosaics}} = (6/10)(100) = 60\%$  frequency of transmission.

the  $y w f / y^{ems}$  females do not produce (y) sons, indicating the presence of an independent lethal to the right of white. Of 4 surviving stocks carrying the EMS-induced yellow, one shows a (y<sup>2</sup>) phenotype (dark bristles). The others have typical yellow-brown bristle color. Unlike X-rays, which frequently involve the 1J1<sup>+</sup>, ac<sup>+</sup>, or sc<sup>+</sup> regions, none of the transmitted mutants in this series shows evidence of minute structural rearrangements or multiple involvement of these neighboring genes.

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Mukhina, L.I., V.A. Kulitchkov and I.F. Zhimulev. Institute of Cytology and Genetics, Novosibirsk, 630090, USSR. Distribution of chromosome rearrangement breaks along the polytene chromosomes of *D. melanogaster*.

Hannah (1951) described two main characteristics of intercalary heterochromatin in *D. melanogaster*: ectopic pairing and a high frequency of chromosome rearrangement break points. Since then new peculiarities of intercalary heterochromatin have been described: late replication (Arcos-Teran 1972; Zhimulev and Kulitchkov 1977), "weak points" (Zhimulev and Kulitchkov 1977),

and strong homologous synapsis (Kulitchkov and Belyaeva 1975; Polyanskaya 1975). After *in situ* hybridization, bands, having the characteristics of intercalary heterochromatin, preferentially bind labelled nucleic acids, i.e., c-DNA (Rudkin and Tartof 1974), c-RNA (Gvozdev et al. 1980), poly (A<sup>+</sup>) RNA (Spredling et al. 1975; Gvozdev et al. 1980) and also some cloned *D. melanogaster* sequences (Ilyin et al. 1977; Finnegan et al. 1977). In addition, more precise data on the location of the regions of ectopic pairing in the polytene chromosomes (Kaufman and Iddles 1963; Kulitchkov and Zhimulev 1976) and numerous chromosome rearrangements have been published in recent years.

Distribution of chromosome rearrangement breaks along the polytene chromosomes will be described here.

We have chosen to exclude mutations selectively induced in a specific region by investigator and have included only those rearrangements which either were induced in *Drosophila* genome at random or those found in populations (we classify these provisionally as "spontaneous"). Table 1 lists the origin of the rearrangements analyzed.

Data on the localization of break points in F<sub>1</sub> larvae after mating females with irradiated males (Prokofyeva-Belgovskaya and Khvostova 1939; Kaufman 1946) were also used.

The distribution of breaks is shown in Figs. 1-6. Data on translocations and inversions both naturally occurring and induced are presented separately. In the summary histogram as well as the inversions and translocations, all the remaining aberrations listed in Table 1 are included. For the regions adjacent to the centromere: 20A-F, 40A-41F, 80D-81F, the total number of breaks was divided by the number of letter subdivisions of these regions and mean data are shown in Figs. 1, 2 and 4.

Distribution of the breaks in the X chromosome (Fig. 1F) is clearly non-random. In addition to the centromeric region 20A-F such regions as 1B, 2B, 3C, 7B, 11A, 12E, 16F, 19E show marked peaks as well. All these regions are considered to be intercalary heterochromatin re-

Table 1. List of chromosome rearrangements studied.

Nature of rearrangements	Deficiencies	Duplications	Inversions	Translocations and transpositions	Rearrangements with non-precise locations of 1 break	Breaks in the first generation	References	
Spontaneous	28	6	34	1	17		Lindsley, Grell 1968	
			52	8			Yamaguchi et al. 1976	
			43		8		Stalker 1976	
			13		15		Pipkin et al. 1976	
			6		2		Dubinen et al. 1940	
			6				Zacharopoulou 1974a	
			4				Yang et al. 1971	
			3				Zacharopoulou 1947b	
			2				Paik et al. 1969	
			2				Mukai et al. 1970	
			1				21	
	4						Ashburner, Lemeunier 1976	
	1						Choi 1977	
	19						Mettler et al. 1977	
	103	4					Yutaka et al. 1979	
	2			Yamaguchi et al. 1974				
			2			Alahiotis et al. 1977		
Totally spontaneous	29	6	315	13	46			
Induced	9	6	11	309	61		Lindsley, Grell 1968	
			8	269	6		Lindsley et al. 1972	
			25	60	16		Roberts 1970	
				53	1		Stewart, Meriam 1973	
			5	7	17		Valencia 1970	
			1	1	1		Mukhina, Zhimulev 1980	
					7		17	Mamon et al. 1977
			43				1	Lefevre 1974
				14	4		1	Ashburner 1972
					12		3	Denell et al. 1978
					50			Roberts 1972
			1	20	5		6	Woodruff, Ashburner 1978
								170
				1389	Kaufman 1976			
Totally induced	59		86	842	130	1529		
Totally	88	6	401	855	176	1529		

gions. Table 2 shows the correlation coefficients between frequencies of breaks in the regions and the other cytological characteristics of polytene chromosomes. All the coefficients with the exception of the underlined ones are statistically significant ( $P \geq 0.05$ ). It is unlikely that break point frequencies follow the DNA concentration in the region. Although precise estimations of DNA quantities in the lettered subdivisions have not been done, it can be seen that in the regions 9A, 10A and 10B where very large bands are located there are no peaks of break points. This suggests that higher break frequencies in different regions may have structural significance.

Table 2. Coefficients of correlation between the frequencies of breakage in weak points (wp), ectopic pairing (ep), late replication (lr), strong homologous synapse (ss), preferential binding of c-RNA (cR), poly(A<sup>+</sup>) RNA (pR), and chromosomal rearrangements (b).

	ep	lr	cR	pR	b	ss
Chromosome X						
wp	0.77	0.61	0.49	0.48	0.47	0.49
ep		0.65	0.39	0.43	0.55	0.50
lr			0.55	0.58	0.34	0.59
cR				0.77	0.40	0.56
pR					0.36	0.64
b						0.50
Chromosome 2L						
wp	0.72	0.54	--	--	0.21	--
ep		0.62	--	--	0.27	--
lr			--	--	0.24	--
Chromosome 2R						
wp	0.54	0.40	0.33	0.27	0.08	--
ec		0.67	0.53	0.41	0.17	--
lr			0.68	0.67	0.32	--
cR				0.80	0.22	--
pR					0.30	--
Chromosome 3L						
wp	0.83	0.62	--	--	0.24	--
ep		0.59	--	--	0.35	--
lr			--	--	0.20	--
Chromosome 3R						
wp	0.78	0.58	--	--	0.06	--
ep		0.60	--	--	0.16	--
lr			--	--	0.25	--

Data were taken: for weak points, ectopic pairing, late replication from Zhimulev and Kulitchkov (1977), for strong homologous synapsis from Kulitchkov and Belyaeva (1975), for binding of c-RNA and poly(A<sup>+</sup>) RNA from Gvozdev et al. (1980).

-- = No data available.

Some differences are rather clear between the distributions in Figs. 1D and 1E. For example, among rearrangements which are maintained in the stocks (Fig. 1D) the highest peak is located in 3C, and there are also high peaks in 11A, 12E and 20AF. As for the F<sub>1</sub> rearrangements (Fig. 1E), the highest peaks are seen in 20AF, 12E, 11A and 2B.

In the other chromosomes the "peaks" are located in the centromeric regions as well as in the regions 26A, 30B, 34A (Fig. 2), 50A, 56F, 59D (Fig. 3), 61F, 64C, 75C (Fig. 4), 101F (Fig. 6) which with the exception of 26A and 34A are considered to be intercalary heterochromatin (Zhimulev and Kulitchkov 1977).

The data examined show once more that chromosome rearrangement break points are distributed non-randomly among the chromosomes and are predominantly located in the regions of intercalary heterochromatin.

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Stewart, B. and J.R. Meriam 1973, DIS 50:167; Valencia, R. 1970, DIS 45:37; Woodruff, R.C. and M. Ashburner 1978, Amer. Naturalist 112:456; Yamaguchi, O. et al. 1974, Genetics 78:1209; Yamaguchi, O. et al. 1976, Genetics 83:409; Yang, H. et al. 1971, DIS 47:71; Yutaka, I. et al. 1979, Japan J. Genet. 54:69; Zacharopoulou, A. 1974a, DIS 51:110; Zacharopoulou, A. 1974b, DIS 51:52; Zhimulev, I.F. and V.A. Kulitchkov 1977, Genetica (USSR) 13(1):85.

Fig. 1-6: Distribution of chromosome rearrangement breaks along the X chromosome (Fig. 1), 2L chromosome (Fig. 2), 2R chromosome (Fig. 3), 3L chromosome (Fig. 4), 3R chromosome (Fig. 5) and fourth chromosome (Fig. 6).

Abscissa: chromosome regions according to Bridges' revised maps.  
 Ordinate: number of breaks in the letter subdivision of the map.

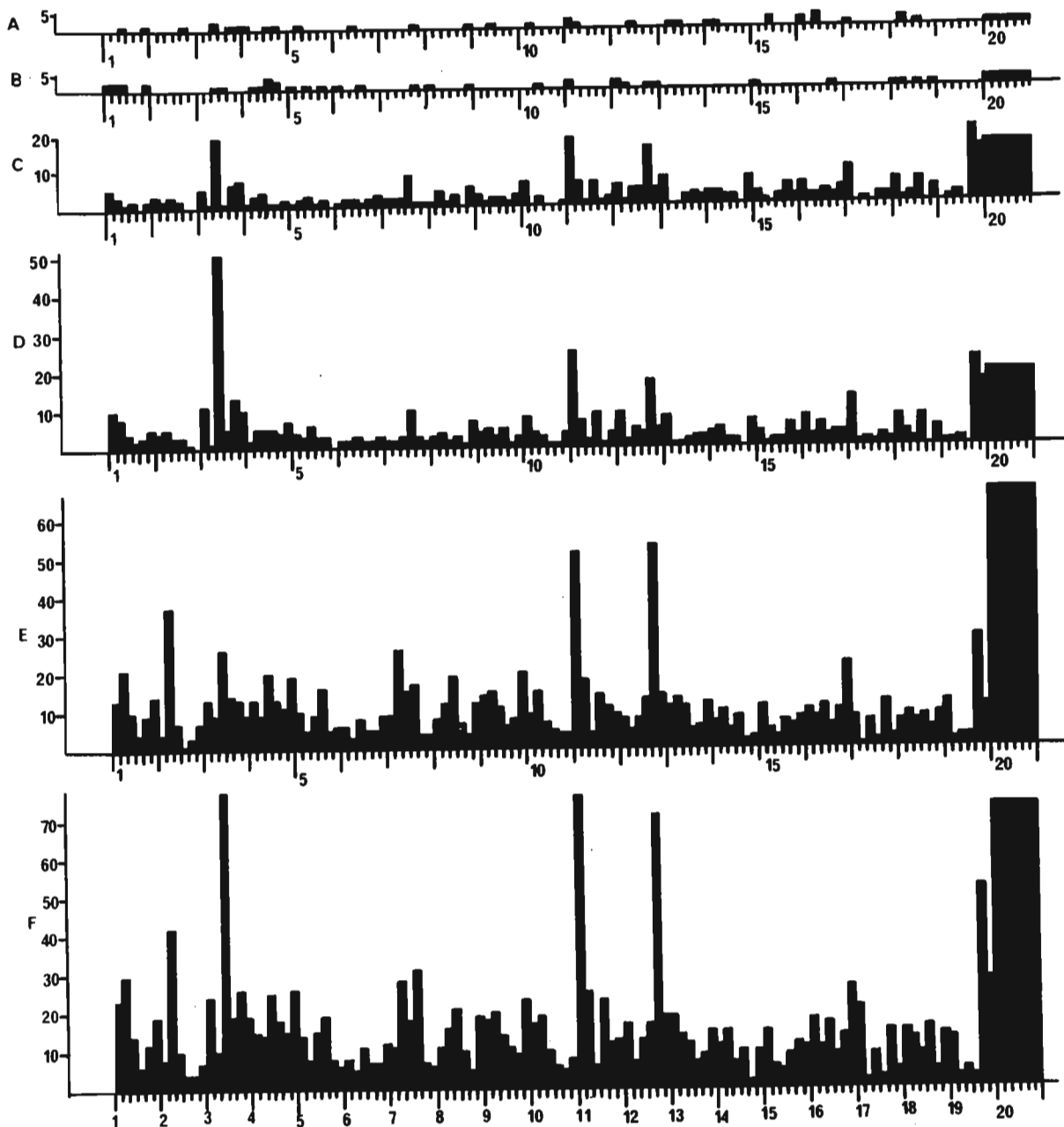


Fig. 1. A=inversions induced, B=inversions spontaneous, C=translocations induced, D= sum of A-C plus deficiencies, duplications and translocations indicated in Table 1. E=sum of the data of Kaufman and Prokofyeva-Belgovskaya and Khvostova, F=sum of D and E.

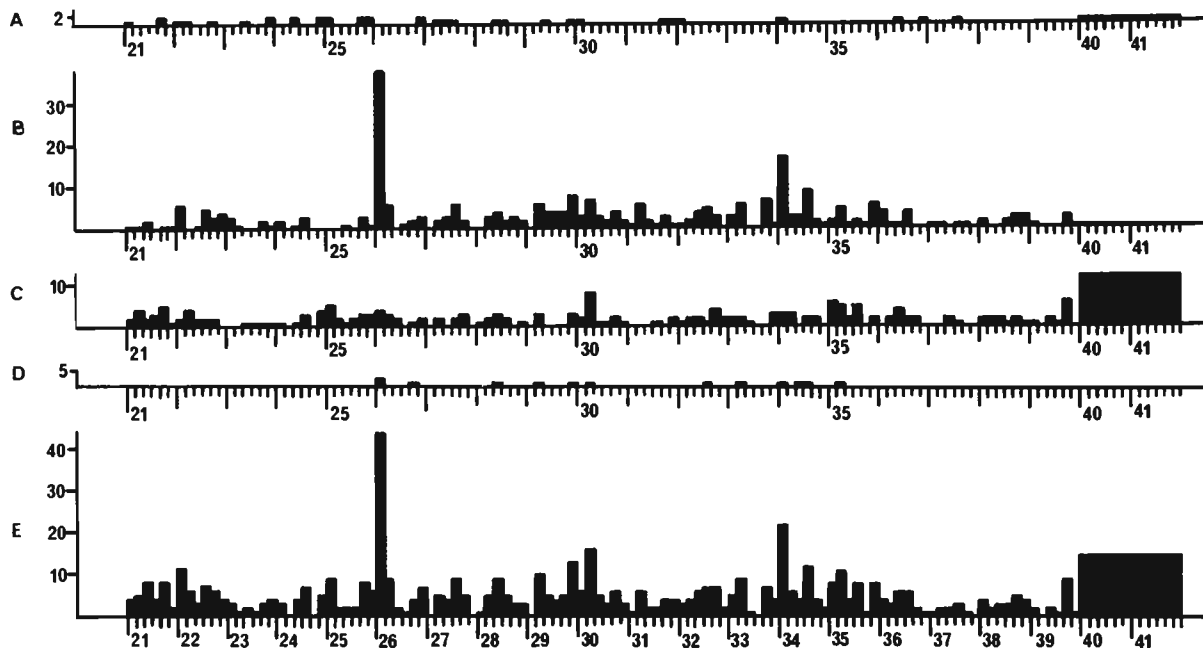


Fig. 2. A=inversions induced, B=inversions spontaneous, C=translocations induced, D=translocations spontaneous, E=sum of A-D plus deficiencies, duplications and transpositions, indicated in Table 1.

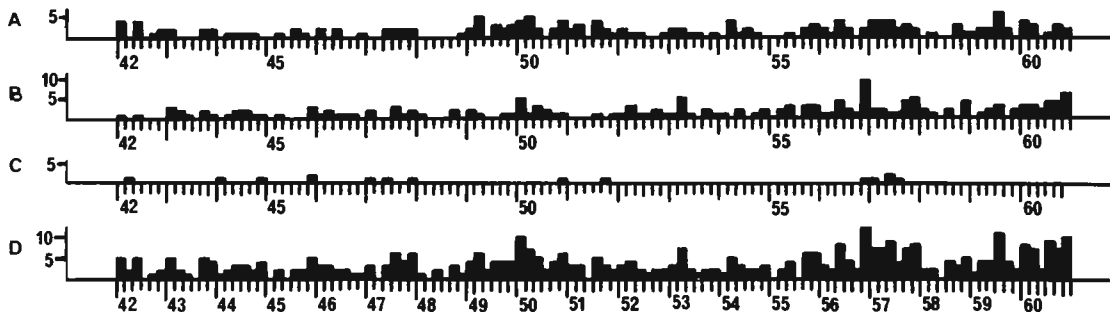


Fig. 3. A=inversions spontaneous, B=translocations induced, C=translocations spontaneous, D=sum of A-C plus deficiencies, duplications and transpositions (Table 1).



Fig. 4. A=inversions induced, B=inversions spontaneous, C=translocations induced, D=translocations spontaneous, E=sum of A-D plus deficiencies, duplications and transpositions, indicated in Table 1.

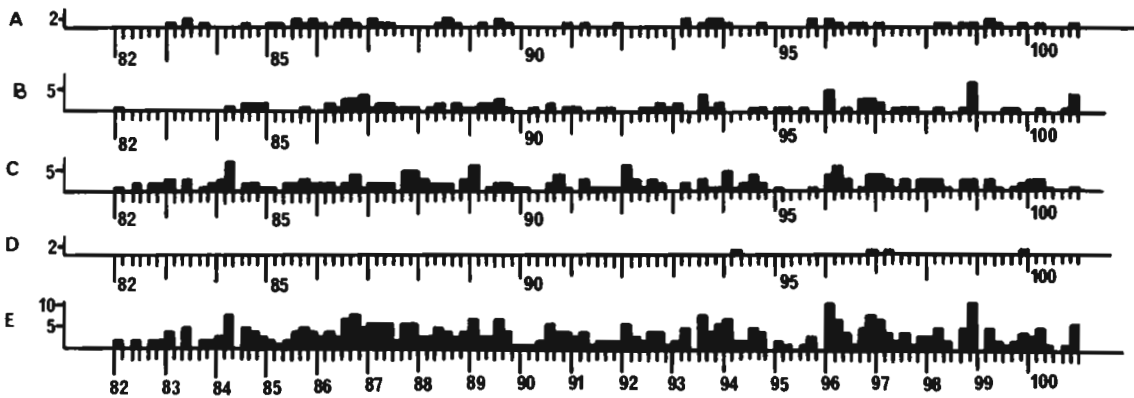


Fig. 5. A=inversions induced, B=inversions spontaneous, C=translocations induced, D=translocations spontaneous, E=sum of A-D plus deficiencies, duplications and transpositions, indicated in Table 1.

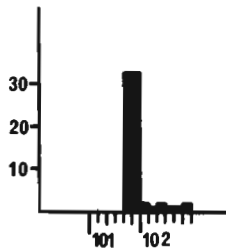


Fig. 6. Sum of all breaks.

Nikoshkov, A.B. and V.T. Kakpakov. Institute of General Genetics, Moscow, USSR. Dosage compensation of sex-linked genes in established cell lines of *D. melanogaster*.

Established cultures of *Drosophila* cells which are homogeneous from caryological point of view and have different ratio between sex chromosomes and autosomes represent an advantageous model for the study of dosage compensation.

Rawls, Jr. 1973) and fumarase (Pipkin et al. 1977), determined by sex-linked structural genes Pgd (1-0.64) and Fuh (1-19.9) and  $\alpha$ -glycerophosphate dehydrogenase (Luccheci and Rawls, Jr. 1973), determined by autosomal structural gene  $\alpha$ -Gpdh (2-20.5) in cell cultures with different ratio between sex chromosomes and autosomes (see Table 1).

We measured the activity of two enzymes, 6-phosphogluconate dehydrogenase (Luccheci and Rawls, Jr. 1973) and fumarase (Pipkin et al. 1977), determined by sex-linked structural genes Pgd (1-0.64) and Fuh (1-19.9) and  $\alpha$ -glycerophosphate dehydrogenase (Luccheci and Rawls, Jr. 1973), determined by autosomal structural gene  $\alpha$ -Gpdh (2-20.5) in cell cultures with different ratio between sex chromosomes and autosomes (see Table 1).

Table 1. Ratio of fumarase and  $\alpha$ -glycerophosphate dehydrogenase activity in cell lines of *D. melanogaster*.

Cell lines	Passage	Caryotype	X:A	Fumarase activity -glycerophosphate dehydrogenase activity	
KcH	(3)	80-100	1X:2A	0.5	0.163 $\pm$ 0.008
KcI	(3)	1-10	2X:2A	1.0	0.175 $\pm$ 0.011
67jDBS	(4)	180-200	2X:2A	1.0	0.151 $\pm$ 0.002
67j25D	(4)	600-620	2X:2A	1.0	0.172 $\pm$ 0.006

Identification of the isozymes of all three enzymes was carried out by means of polyacril amide gel electrophoresis. All cultures showed heterozygosity in three enzymes except Kc cell line cells. We could find only two bands of fumarase in heterozygotes.

The ratio of fumarase and  $\alpha$ -glycerophosphate activity remains approximate-

ly constant in all cell cultures (see Table 1). It means that the cells with one X chromosome have fumarase activity per X chromosome two times higher than the cells with 2X chromosomes. The change of ratio between X chromosomes and autosomes from 1 to 0.5 causes the "switching" of gene activity from the low level to the high which means the existence of dosage compensation on the cell level (see Table 1).

The same data obtained for 6PGD varied greatly from passage to passage and from experiment to experiment. For instance, in 67j25 cell lines and KcH the ratio between 6PGD and  $\alpha$ -GPDH activities was fluctuating from 1.8 to 4 and from 2 to 6.4, respectively.

Detection of dosage compensation on cell level will make it possible to make further investigation of this phenomenon.

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Osipova, N., L. Korochkin, M. Golubovsky, T. Khlebodarova and V. Kulutchkov. Institute of Cytology and Genetics, Novosibirsk, USSR. Biochemical-genetical investigation of the unstable locus lozenge in *D. melanogaster*.

The following stocks of *D. melanogaster* have been investigated: Oregon R - wild type. Lozenge 50 (stable allele) - eye narrower than wild type and ovoid, facets are absent; females are fertile. Lozenge A (unstable allele) - males are characterized by oval small eyes; facets are absent, tarsal claws reduced; females are sterile. Stock A+1 (stable allele

A<sup>+</sup>) - reverse of unstable lzA to wild type (A<sup>+</sup>); phenotype of males is identical to the wild type. Stock B+5 (stable allele A<sup>+</sup>) - revertant of unstable lzA to the wild type; males are phenotypically identical to stocks Oregon R and A+1. In all stocks (except Oregon R and lz50) males cross to females XX (linked X chromosomes) with markers w of ywf. The development of flies was synchronized beginning with the stage of white pupa (the formation of puparium). The pupae have been investigated in different times after pupariation. We detected the activity of phenol oxidase (Mitchell 1966) and pattern of isozymes of this enzyme, using the microelectrophoretic method (Korochkin et al. 1977).

Table 1. Changes of the activity of phenol oxidase during the development of pupae of *D. melanogaster*.

Age of pupae (hours)	Total activity of phenol oxidase (units of act./mg/min)				
	Oregon R	lozenge A	A+1	lz50	B+5
0	43.5±0.5	18.0±1.0	29.5±0.5	34.0±1.0	32.5±1.0
24	17.5±1.1	22.5±1.2	21.0±0.5	16.8±1.0	21.5±1.5
48	23.0±0.5	30.0±1.0	24.5±1.25	17.8±1.0	15.1±1.0
72	26.0±1.0	28.0±1.0	23.5±1.0	23.0±1.0	28.1±1.8
96	17.5±1.0	12.5±0.7	11.5±0.5	17.0±0.2	10.0±0.5

Table 2. Ratio A<sub>2</sub>/A<sub>1</sub> fractions of phenol oxidase during the development of pupae of *D. melanogaster*.

Age of pupae (hours)	Ratio A <sub>2</sub> /A <sub>1</sub>				
	Oregon R	lozenge A	A+1	lz50	B+5
0	0.76±0.07	---	0.71±0.07	0.50±0.05	0.65±0.12
24	1.20±0.04	3.70±0.40	0.78±0.08	1.54±0.02	1.02±0.11
48	0.98±0.10	1.43±0.14	1.28±0.19	1.67±0.30	0.87±0.05
72	0.44±0.14	0.07±0.06	0.83±0.21	2.25±0.30	1.05±0.24
96	2.02±0.31	---	0.61±0.05	1.05±0.24	0.65±0.05

The results of the detection of enzymatic activity are depicted in Table 1. The similarity of changes of enzymatic activity in stocks Oregon R and lz50 can be seen.

The unstable stock lzA is characterized by the low level of enzymatic activity on the stage of white pupae and in 96 h after pupariation and by the high level of the activity of phenol oxidase during the middle pupal period.

It is interesting that the pattern of enzymatic activity during the development of two reversible stocks is different on the stage 48 h after pupariation. In this period the enzymatic activity is higher in stock A+1 in comparison with stock B+5 (see Table 1).

Reversible stocks differ from the unstable stock lzA, which is their ancestor. These differences are especially distinct during pupariation and 48 h later. In the first stage of pupal development the activity of phenol oxidase is higher in reversible stocks in comparison with lzA ( $P > 0.999$ ) but 48 h later the enzymatic activity is higher in stock lzA. The similar pattern of changes of the enzymatic activity in the reversible stock A+1 and Oregon R was established.

After microelectrophoretic investigations and densitometry we determined the ratio  $A_2/A_1$  - fractions of phenol oxidase. The results are shown in Table 2. Stock Oregon R is characterized by the predominance of  $A_1$  fraction (monophenol oxidase). The ratio  $A_2/A_1$  in this time is equal to  $0.76 \pm 0.07$ . Then (24 h after pupariation) the activity of the fraction  $A_2$  (diphenol oxidase) is higher. The total enzymatic activity decreases in this period (see Table 1). Probably this process is caused mainly by the change of activity of monophenol oxidase. However, in the following stages of pupal development (48 h and 72 h after pupariation) the ratio  $A_2/A_1$  decreases again. In this period the total enzymatic activity increases and we suggest that the activity of  $A_2$  fraction is not changed and the activity of  $A_1$  fraction increases. The activity of  $A_2$  fraction is twice that of  $A_1$  at 96 h after pupariation. The total enzymatic activity is relatively low in this period. Probably the predominance of  $A_2$  fraction is explained mainly by the decrease of activity of monophenol oxidase. It can be proposed that the changes of the enzymatic activity and the pattern of phenol oxidase isozymes is caused by the changes of the level of activity of monophenol oxidase.

Unstable stock lz50 is characterized by the specific change of the pattern of isozymes of phenol oxidase during ontogenesis. In this stock diphenol oxidase is absent during puparium formation. Its activity is detected at 24 h after pupariation and is very high at this time (ratio  $A_2/A_1$  is  $3.7 \pm 0.4$ ). Monophenol and diphenol oxidases are present at 48 h after pupariation. However, the activity of  $A_2$  fraction sharply decreases at the end of pupa development. Diphenol oxidase is not detected at 96 h after pupariation. The activity of diphenol oxidase is not detected in the unstable stock lzA during pupariation and 72 and 96 h after pupariation. The pattern of changes of the ratio  $A_2/A_1$  in the unstable stock lz50 is different from Oregon at this time, although the total activity of enzyme is similar. Unlike the Oregon R stock, lz50 is characterized by the predominance of diphenol oxidase at 72 h after pupariation (ratio  $A_2/A_1$  is  $2.25 \pm 0.3$ ), but the activity of monophenol oxidase is higher at 96 h ( $A_2/A_1$  is  $0.61 \pm 0.08$ ). The ratio  $A_2/A_1$  in this case at 72 h after pupariation is intermediate between Oregon and lz50.

We conclude that the unstable stock A has some specific capacities in the pattern of changes of activity of phenol oxidase and pattern of isozymes of phenol oxidase during development and is different from the stable stock lz50, reversible stocks and wild stock Oregon. Probably the instability of locus lz is explained by the insertion and exclusion of a strange segment of DNA into the region of this locus. In this case the regulatory effect of locus lz on the ratio  $A_2/A_1$  is changed.

References: Korochkin, L. et al. 1977, Genetics of Isozymes, Nauka, Moscow (in Russian); Mitchell, H. 1966, J. Insect Physiol. 12:755.

Platt, S.A. Northern Michigan University, Marquette, Michigan and University of Illinois, Champaign, Illinois. Discrimination learning in individual *D. melanogaster*.

By using a unique methodology and a versatile series of choice points in two distinct apparatus, individual *Drosophila* were shown to possess the ability to learn (Platt, Holliday and Drudge 1980). This behavior can be controlled by a discriminative stimulus (substrate texture). Following a correct response in the presence of the discriminative stimulus at a horizontal choice point, *D. melanogaster* bred for negative geotaxis in a Hirsch-type geoselection maze were given the opportunity to ascend a vertical alley leading to another choice point. When cues were consistent reliable learning occurred. When cues were inconsistent learning did not occur. Cue reversal produced the classic temporary increase in "incorrect" responses.

The apparatus is inexpensive and versatile. It is described in a technical note herein (Platt and Holliday). We believe there are several factors responsible for our successful demonstration of discrimination learning in *D. melanogaster*. In general, we took an ethological perspective that the association of a discriminative stimulus with some response pattern would be possible if, and only if, we did not elicit tropistic or escape responses.

Lights and odors tend to elicit an automatic, stereotyped approach response highly resistant to modification. Noxious stimuli (e.g., shock, shaking, sudden movements, sudden strong light) inevitably elicit immediate, and apparently disruptive, flight (escape) responses. We, therefore, allowed the fly to progress from one trial to the next with a minimum of disruption and experimenter interference. Our "reinforcer" for the negative geotaxic strain, the opportunity to ascend a vertical tube, led to the next choice point. At the choice point the presence or absence of paper served as a substrate discriminative cue.

At each of 30 horizontal T-choice points, a correct response was recorded if the fly did not reach the end of the cul-de-sac arm and continued up the vertical alley at the end of the correct arm of the T. An incorrect response was recorded if the fly touched the end cap of the cul-de-sac. Learning was observed in individual flies as an increase in number of correct responses over the 30 choice points. Convincing evidence was noted when the consistent discriminative cue at the first 15 choice points (consistent presence or absence of paper in the arm leading to the next vertical alley) was reversed for the second 15 choice points. Many "incorrect" responses were noted as choice points 16-18 where the previously correct discriminative cue now led to the cul-de-sac.

Using this paradigm and apparatus we are currently attempting to selectively breed for a behavior change over trials--learning.

Reference: Platt, S.A., M. Holliday and O.W. Drudge 1980, J. Exp. Psych: Anim. Beh. Proc. 6(4):in press.

Polivanov, S. Catholic University of America, Washington, D.C. Possibly non-Mendelian factor for stimulation of egg deposition.

We reported recently (Polivanov et al. 1980) that  $lz^{63i}$  males of *D. melanogaster* stimulate egg deposition by  $lz^{63i}/M-5$  females to a greater extent than M-5 males. The original mutant lozenge male was crossed to M-5 females approximately six years before our experiment

began and since that time the lozenge mutant was maintained on M-5 background. Consequently, it is reasonable to assume that the genetic background of the lozenge and M-5 males was largely equalized, and that M-5 and  $lz$  males differed, on the average, from each other only in the X chromosomes. If this is so, then the genetic factor responsible for the increase in egg deposition should be associated with the X chromosomes, containing the mutant lozenge<sup>63i</sup>. In our experiment populations were started with  $lz/M-5$  females and with either lozenge or M-5 males. All populations were started with 100 pairs of flies and were maintained for one generation. Apparently overproduction of eggs in the lozenge-fathered populations led to overcrowding and extremely high larvae mortality. As a result of that, the average size of lozenge-fathered  $F_1$  populations was 529, while that of the M-5 fathered ones was 1041. Checking my old records, I found that I performed a similar experiment in the past but that experiment was initiated for a completely different purpose (Polivanov, unpub.). In that experiment 8 populations were also started with 100  $lz/M-5$  females and with 100 either lozenge or M-5 males. In four of these populations the flies were derived from one subpopulation, while in the other four they were derived from the other subpopulation. These subpopulations were isolated from each other for approximately 12 generations. The total number of adult flies in the  $F_1$  of the eight experimental populations was as follows:

<u>Populations derived from subpopulation 1</u>		<u>Populations derived from subpopulation 2</u>	
Pop. #	Total # of flies	Pop. #	Total # of flies
	<u>lz-fathered</u>		<u>lz-fathered</u>
1	821	5	782
2	848	6	851
	<u>M-5 fathered</u>		<u>M-5 fathered</u>
3	1286	7	838
4	1164	8	827

If the sizes of these populations reflect the stimulating effect of the males, it could be said that in the population derived from Subpopulation 1 there was a difference in the stimulating effects of  $lz$  and M-5 males, while none of such existed in the populations derived from Subpopulation 2. It is interesting to note that visible recombinants between  $lz$  and M-5 X chromosomes were almost completely absent. There was found one recombinant in three out of the eight populations.

It is very probable that the factor for the stimulating male effect behaves similarly with the factor for the female sterility reported by Picard (1979); in other words, it could be transposed from one chromosome to another without classical crossing over. Further investigations of this problem are in progress.

References: Picard, G. 1979, *Genetics* 91:455-471; Polivanov, S., P. Peck and K. Dornan-Kendig 1980, *J. Hered.*, in press.

Pot, W. University of Groningen, Haren (Gr.), The Netherlands. Courtship and mating success in alcohol dehydrogenase genotypes of *D. melanogaster*.

Investigating the role of mating behavior in the maintenance of the alcohol dehydrogenase (Adh) polymorphism, Pot et al. (1980) found large differences in numbers of matings performed by flies having different Adh genotypes. In multiple choice experiments FF males were about five times

as successful as SS males, and FF females were almost three times as successful as SS females, as indicated by the mating chance ratio *r*. This paper describes observations of courtship behavior of individual flies in single pair mating chambers (19 mm diameter, 7 mm deep) which were carried out in order to investigate whether differences in the pattern of courtship were involved in the differential mating success.

Table 1. Numbers of matings and percentages mated in single pair mating chambers.

♀ x ♂	Time (min.)				% mated within 30 min.
	0-10	10-20	20-30	>30	
FF x FF	26	10	4	3	93.0
FF x SS	15	11	7	10	76.7
SS x FF	28	7	2	6	86.0
SS x SS	16	13	4	10	76.7
FF ♂♂	54	17	6	9	89.5
SS ♂♂	31	24	11	20	76.7
FF ♀♀	41	21	11	13	84.9
SS ♀♀	44	20	6	16	81.4

First, mating success in the single pair chambers was measured in 30 min. observation periods (this time limit was also used in the multiple choice experiments). At the time of the experiments the flies were 6 days ± 8 hours old; the sexes had been separated within 8 hours from eclosion. One female and one male were introduced without anaesthesia and the time the copulation started was noted. Table 1 gives the results. The percentages of flies mating within 30 min. were much higher than those in the multiple choice experiments (those were: FF males 54.9%, SS males 14.3%, FF females 46.9%, SS females 22.3%).

Not surprisingly, starting a copulation appears to be much easier when only one male and one female are present. Probably as a consequence of this the differences in mating success between the genotypes were much smaller in the single pair experiments. The difference between the males was still significant (FF vs. SS, mated vs. not mated:  $\chi^2_1 = 5.02$ ,  $P = 0.05$ ) but the difference between the females was not significant any more ( $\chi^2_1 = 0.37$ ). Testing the distribution of matings over consecutive periods of time (0-10 min., 10-20 min., 20-30 min., and >30 min.) yielded a similar result (FF males vs. SS males:  $\chi^2_3 = 13.06$ ,  $P < 0.005$ ; FF females vs. SS females:  $\chi^2_3 = 1.91$ , N.S.).

Table 2. Courtship latency times of FF and SS males with FF females.

	Courtship latency time (min.)					
	0-1	1-2	2-3	3-4	4-5	>5
FF ♂♂	-	4	9	1	1	5
SS ♀♀	1	6	5	2	2	4

For a behavioral observation one female (always FF) and one male (either FF or SS) were introduced into a mating chamber. Twenty replicate observations were carried out for each male genotype. Table 2 gives the distribution of the courtship latency times, that is the time till the first vibration (see below) occurred. No significant difference was found between the distributions of FF and SS (data taken together in three periods: 0-2 min., 2-4 min., and >4 min.;  $\chi^2_2 = 1.35$ , N.S.). The behavior of the

males was recorded on an event recorder during the first 5 min. after introduction. The following elements of courtship were distinguished: orientation (or): the male stands still, facing the female; approaching (ap): the male walks towards the female or follows her if she is moving; wing vibration (vi); licking (li); and attempted copulation (ac). (For a description of the latter three elements, see Bastock and Manning 1955.) The frequencies (number of

times an element was performed) and duration (total time spent performing an element) of the courtship elements were calculated over a period of 30 sec. and a period of 60 sec., both starting with the first vibration. The duration of li and ac could not accurately be recorded as these activities lasted very short. The bout lengths (duration divided by frequency) of

Table 3. Frequencies, duration, and bout lengths of the courtship elements (average values of N observations).

		N <sup>1</sup>	or	ap	vi	li	ac
frequencies:	FF (30)	13	3.9	6.2	6.2	0.8	0.6
	SS (30)	14	4.1	4.2*	4.3*	0.6	0.3
	FF (60)	12	7.3	11.8	11.8	1.8	0.7
	SS (60)	12	7.3	7.4**	6.6**	1.2	0.3
duration:	FF (30)	13	4.3	9.8	12.6		
	SS (30)	14	6.7	7.5	8.2**		
	FF (60)	12	9.0	19.5	22.6		
	SS (60)	12	12.1	17.5	12.8**		
bout lengths:	FF	15	1.2	1.8	2.0		
	SS	16	1.7	2.3	2.0		

Significance of the difference between FF and SS: \*P 0.05, \*\*P 0.02 (Mann-Whitney U test). (30) and (60) indicate values over the first 30 and 60 seconds after the start of the first vibration, respectively.

<sup>1</sup>In a number of observations the courtship period was shorter than 60 sec., or even 30 sec., therefore N is always smaller than 20.

the elements were calculated over the complete courtship periods. Table 3 gives the outcomes. FF males show significantly higher frequencies of ap and vi. The duration of vi is also significantly longer for FF, while its bout length is exactly the same for FF and SS. FF and SS show no significant differences in duration and bout length of or and ap. So FF males show a more active courtship behavior in which especially the element of vibration, which is performed more often, though not in longer bouts, might be responsible for the higher mating success. Vibration has been shown to be very stimulating to the female (Bastock 1956).

It is theoretically possible that the difference

in behavior between the FF and SS males is not an intrinsic quality of the males themselves, but is mediated by the females. Females might be able to distinguish between the genotypes and to exert a differential influence on their courtship, for instance by making more repelling movements (see Bastock and Manning 1955) towards SS males, thus causing more breaks in their courtship.

References: Bastock, M. 1956, *Evolution* 10:421-439; Bastock, M. and A. Manning 1955, *Behavior* 8:85-111; Pot, W., W. van Delden and J.P. Kruijt 1980, *Behav. Genet.* 10:in press.

Rahman, R. and D.L. Lindsley. University of California, San Diego. Ysu(f)<sup>-</sup>, a spontaneous derivative of Ymal<sup>+</sup>.

Ymal<sup>+</sup> is an x-ray induced derivative of YSx<sup>+</sup>y<sup>L</sup>, In(1)EN that arose through the deletion of the majority of the X euchromatin [1(1)Jl<sup>+</sup> through car<sup>+</sup>] (E.H. Grell). Among a number of stocks in which Ymal<sup>+</sup> was being used to cover proximal

lethals induced on the X chromosome by Lifschytz and Falk (1968), one was found that differed from the rest in that the Y, although still covering the proximal lethal in the stock, no longer covered deficiencies for su(f). Tests of this Y in combination with an array of proximal X-linked lethals indicate that it is a derivative of Ymal<sup>+</sup> from which the X-derived segment from 1(1)R10-10 through su(f) has been deleted. This segment includes the loci of lethals designated R10-10, Q463, X4, and X1 by Lifschytz and Falk, as well as that of su(f); the Y carries at least one dose of bb<sup>+</sup> as determined from its phenotype in combination with bb<sup>1</sup>. The constitution of this duplicated Y, which we designate Ysu(f)<sup>-</sup>, may be designated as follows:

KL<sup>+</sup>bb<sup>+</sup>? sw<sup>+</sup>--1(1)Q-56<sup>+</sup> bb<sup>+</sup>? KS



Ramamoorthy, C., N.R. Padaki, S. Nirmala Sajjan and E. Krishnamachari. K.L.E. Society's S. Nijalingappa College, Bangalore, India. Mutagenic activity of quinine in *D. melanogaster*.

Quinine is one of the commonly used antimalarial drugs in India. It has been shown that it forms an intercalated complex with DNA in vitro (cf. Schupbach 1979). But its mutagenicity in higher organisms remains obscure. The mutagenic activity of injectable quinine (each

Table 1. Induction of sex-linked recessive lethals by quinine in *D. melanogaster*.

	Total no. of chromosomes tested	No. of normal chromosomes	No. of lethals	% of lethals
Brood 1	640	639	1	0.15
Brood 2	640	614	26	4.23*
Brood 3	620	619	1	0.17

Index: Brood 1 = mature sperm stage  
 Brood 2 = early spermatid stage  
 Brood 3 = spermatogonial stage

\* $\chi^2 = 47.6$   
 $P < 0.001$

have been tabulated in Table 1. The data given indicate mutagenic effect of quinine in *Drosophila* at different germ cell stages. The incidence of sex-linked recessive lethals is significantly very high in Brood 2, which represents the spermatid stage. Detailed work in this direction is in progress.

Acknowledgments: The authors are deeply indebted to the Principal, S. Nijalingappa College, Bangalore for his constant encouragement. This work is financially supported by U.G.C., India.

References: Schupbach, M.E. 1979, *Mut. Res.* 68:41-49; Vogel, E. and H. Luers 1974, *DIS* 51:113-114; Wurgler, F.E., F.H. Sobels and E. Vogel 1977, *Handbook of Mutagenicity Test Procedures*, ed. Kilbey et al., pp. 335-373.

Rapport, E. and M.K. Yang. University of Toronto, Ontario, and Simon Fraser University, Burnaby, B.C. Effects of food deprivation on larval amino acid pools.

Experimental manipulations often require that fruit fly larvae be removed from the normal complement of food. We wished to determine the effect of an 8-hour period of food deprivation on the free amino acid pool. Oregon-R larvae 36, 56 or 85 hours after hatching were

removed from a yeast seeded cream of wheat-molasses medium. Approximately half the larvae in each age group were placed on paper pulp moistened with water and the remainder were frozen prior to amino acid analysis. After 8 hours, larvae on the paper pulp were also frozen. Amino acids were obtained from supernatants of 80% ethanol homogenates of larvae which had been boiled for 1/2 hour and centrifuged (Rapport and Sing 1971; Rapport and Yang 1974). A Beckman 119 amino acid analyzer was used for quantitative amino acid determinations. Table 1 shows the relative abundance of amino acids in molar percents.

The most striking result is that the relative abundance of alanine diminishes after food deprivation in each age group. It is likely that alanine is deaminated to pyruvic acid for energy metabolism and the amino group is either found primarily as ammonia in the 44-hour larvae or as glutamine in the 64-hour larvae. Other changes less readily interpreted involve a reduction in threonine with "starvation" and an elevation of arginine and a peak identified tentatively as ethanolamine in the two younger age groups. Analysis of the oldest group is complicated by the fact that even under normal conditions feeding is slowing down in this age group as rapid physiological changes occur in preparation for metamorphosis. For example, relative tyrosine levels almost double between 85 and 93 hours and glucosamine was found in the 93 but not 85-hour larvae. The results tend to support the view that certain amino acids like alanine fluctuate in response to physiological stress, perhaps buffering the relative abundance of other amino acids.

ml contains 0.3 gm of quinine dihydrochloride I.P and 0.01 gm of sucrose I.P, manufactured by Bengal Immunity Co., Ltd., India) is tested in *D. melanogaster* at different germ cell stages employing "Basc" test for sex-linked recessive lethals.

Two-day-old male *Drosophila* flies of Oregon-R stock are fed with quinine solution on glass filters for 48 hours following the method described by Vogel and Luers (1974). The brooding pattern (3-2-2) of Wurgler et al. (1977) is followed. The results

Table 1. Percentage (in moles) of free amino acids in Oregon-R larvae at different ages before and after 8 hours of food deprivation.

	36 hr*	36-44 hr H <sub>2</sub> O	56 hr*	56-64 hr H <sub>2</sub> O	85 hr*	85-93 hr H <sub>2</sub> O
Aspartic acid	3.6	1.6	3.4	2.1	2.0	2.4
Threonine	3.3	0.9	3.9	1.7	4.8	2.4
Serine	3.5	2.9	3.1	2.7	2.3	2.2
Asparagine & glutamine	32.9	32.2	30.1	37.1	25.6	27.5
Proline	2.5	3.1	7.6	5.4	12.2	14.2
Glutamic acid	11.5	12.6	8.9	7.8	7.2	9.8
Glycine	4.1	5.1	3.5	3.8	3.5	3.2
Alanine	16.6	5.9	13.3	6.2	10.9	5.6
Valine	1.3	0.8	1.0	0.8	1.0	1.2
Methionine	--	--	--	--	--	0.1
Isoleucine	0.5	0.3	0.3	0.4	0.7	0.7
Leucine	0.7	0.5	0.5	0.6	1.1	1.2
Tyrosine	0.9	0.9	3.4	4.6	7.7	13.3
Phenylalanine	--	0.2	--	0.4	0.6	0.9
β-alanine	3.1	2.3	4.7	3.4	4.6	2.4
Ethanolamine	2.1	5.0	2.3	5.0	0.6	0.3
Ammonia	2.9	11.0	2.2	1.2	2.6	1.6
Lysine	3.1	3.4	4.4	4.0	3.0	2.4
Histidine	4.2	5.3	3.6	6.7	4.6	4.0
Tryptophane	0.1	--	0.2	--	0.4	0.3
Arginine	3.2	6.0	3.6	6.2	4.7	4.2

\*removed from growth media and immediately prepared for analysis

References: Rapport and Sing 1971, Can. J. Genet. and Cytol. 13:822-833; Rapport and Yang 1974, Comp. Biochem. Physiol. 493:165-169.

Richmond, R.C. and M.E. Claerbout. Indiana University, Bloomington. Ratios in crosses segregating for Esterase 6<sup>0</sup> (Null) and Esterase 6<sup>S</sup> alleles.

The presence of a null allele at the esterase 6 locus in *D. melanogaster* was first described in these pages (Johnson et al. 1966). These investigators examined segregation ratios in crosses of Est 6<sup>S</sup>/Est 6<sup>0</sup> x Est 6<sup>0</sup>/Est 6<sup>0</sup> and Est 6<sup>S</sup>/Est 6<sup>0</sup> x Est 6<sup>S</sup>/Est 6<sup>0</sup>. In both cases

a significant deficiency of the Est 6<sup>0</sup>/Est 6<sup>0</sup> genotype was found. This result suggests that the Est 6 locus has an important function which is expressed during the development of flies. These data are suspect, however, since the stock homozygous for the Est 6<sup>0</sup> allele apparently also carried car. We repeated this analysis using esterase 6 stocks which do not carry morphological markers. Our data show no significant deviation from mendelian expectations.

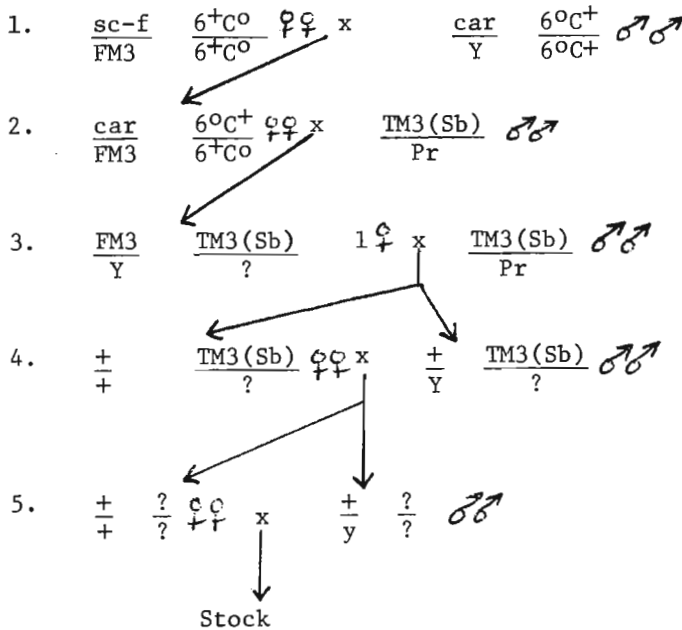
Stocks homozygous for the Est 6<sup>S</sup> and Est 6<sup>0</sup> alleles were obtained by crossing a sc ec cv ct<sup>6</sup> v g<sup>2</sup> f/FM3 y<sup>3</sup>ld sc<sup>8</sup> dm B 1 strain which is also homozygous for a null allele of Esterase C to a car strain which is homozygous for Est 6<sup>0</sup>. F<sub>1</sub> females from this cross were mated to TM3(Sb)/Pr males to begin the series of crosses necessary to extract recombinant third chromosomes. This procedure is summarized on the following page and allowed us to produce four different types of strains each homozygous for the following combinations of alleles at the esterase 6 and esterase C loci: 6<sup>0</sup>C<sup>+</sup>, 6<sup>+</sup>C<sup>0</sup>, 6<sup>0</sup>C<sup>0</sup>, 6<sup>+</sup>C<sup>+</sup> (+ = active allele). These stocks contain no morphological markers.

Approximately 200 #3 crosses were made and strains that proved to have identical Est 6 and C genotypes were combined. Crosses made to determine segregation ratios utilized the 6<sup>0</sup>C<sup>+</sup> and 6<sup>+</sup>C<sup>+</sup> combined stocks.

? = 6<sup>0</sup>C<sup>+</sup> or 6<sup>+</sup>C<sup>0</sup> or 6<sup>0</sup>C<sup>0</sup> or 6<sup>+</sup>C<sup>+</sup>

$\frac{sc-f}{FM3} = sc\ ec\ cv\ ct^6\ v\ g^2/FM3\ y^{3ld}\ sc^8\ dm\ B\ L$

Chromosome: X III X III



Segregation ratios were checked by first crossing 6<sup>0</sup>C<sup>+</sup> ♀♀ to 6<sup>+</sup>C<sup>+</sup> ♂♂. F<sub>1</sub> females and males from this cross were separately backcrossed to the 6<sup>0</sup>C<sup>+</sup> stock. Backcross progeny should exhibit a 1:1 ratio of Est 6<sup>0</sup>/Est 6<sup>+</sup> and Est 6<sup>0</sup>/Est 6<sup>+</sup> genotypes. Since females show low esterase 6 activity, only male progeny from the backcrosses were analyzed using standard starch gel procedures (Richmond 1972). In order to determine if larval density affected genotype ratios, the final crosses were completed under conditions which produce high larval density (10 pairs of adults allowed to lay eggs for 4 days at 25°C in a 1/2-pint bottle) or low larval density (2 pairs of adults allowed to lay for 2 days). Since there were no significant differences between the reciprocal backcrosses, they are combined in the data presented below.

Although there is an absolute deficiency of Est 6<sup>0</sup>/Est 6<sup>0</sup> genotypes at both densities

Density	N	6 <sup>0</sup> /6 <sup>0</sup>	6 <sup>0</sup> /6 <sup>+</sup>	X <sub>1</sub> <sup>2</sup>	P
High	174	81	93	0.83	>0.1
Low	143	63	80	2.02	>0.1

neither case approaches statistical significance as determined by chi-square. A chi-square test of homogeneity of the high and low density crosses is also insignificant (χ<sup>2</sup> = 0.2) indicating little effect of larval density on segregation ratios. The

discrepancy between our results and those of Johnson et al. can likely be traced to the inclusion of morphological markers in the earlier crosses or the presence of a gene affecting viability which was closely linked to the Est 6 locus but which was recombined away in our crosses. The present data demonstrate that the absence of the esterase 6 enzyme has little if any effect on viability.

Acknowledgments to Kathy Sheehan for technical assistance.

References: Johnson, F.M., B.B. Wallis and C.M. Denniston 1966, DIS 41:159; Richmond, R.C. 1972, Genetics 70:87-112.

Ruiz, A. and A. Fontdevila. Universidad de Santiago de Compostela, Spain. Two new chromosome arrangements in *D. buzzatii*.

*D. buzzatii* belongs to the mulleri subgroup of the repleta group of the genus *Drosophila*. Wasserman (1962) has proposed that the chromosomal arrangements of this species are derived from the most primitive chromosomal sequence

of the group by fixing three inversions in the second chromosome (2x<sup>3</sup>, 2k, 2w<sup>3</sup>) and one inversion in the fifth chromosome (5g). In addition, *D. buzzatii* has been reported heterozygous for inversion j, jz<sup>3</sup> and y<sup>3</sup> in the second chromosome (Wasserman 1962; Carson and Wasserman 1965).

We have studied the chromosomal polymorphism of 12 populations and two strains of *D. buzzatii* (Fontdevila et al. 1979) of the Old World. The majority of these samples showed the presence of two new inversions, one in the second and another in the fourth chromosome.

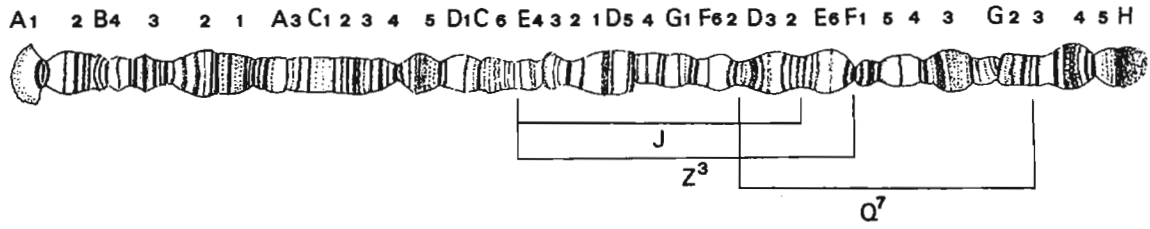


Fig. 1.

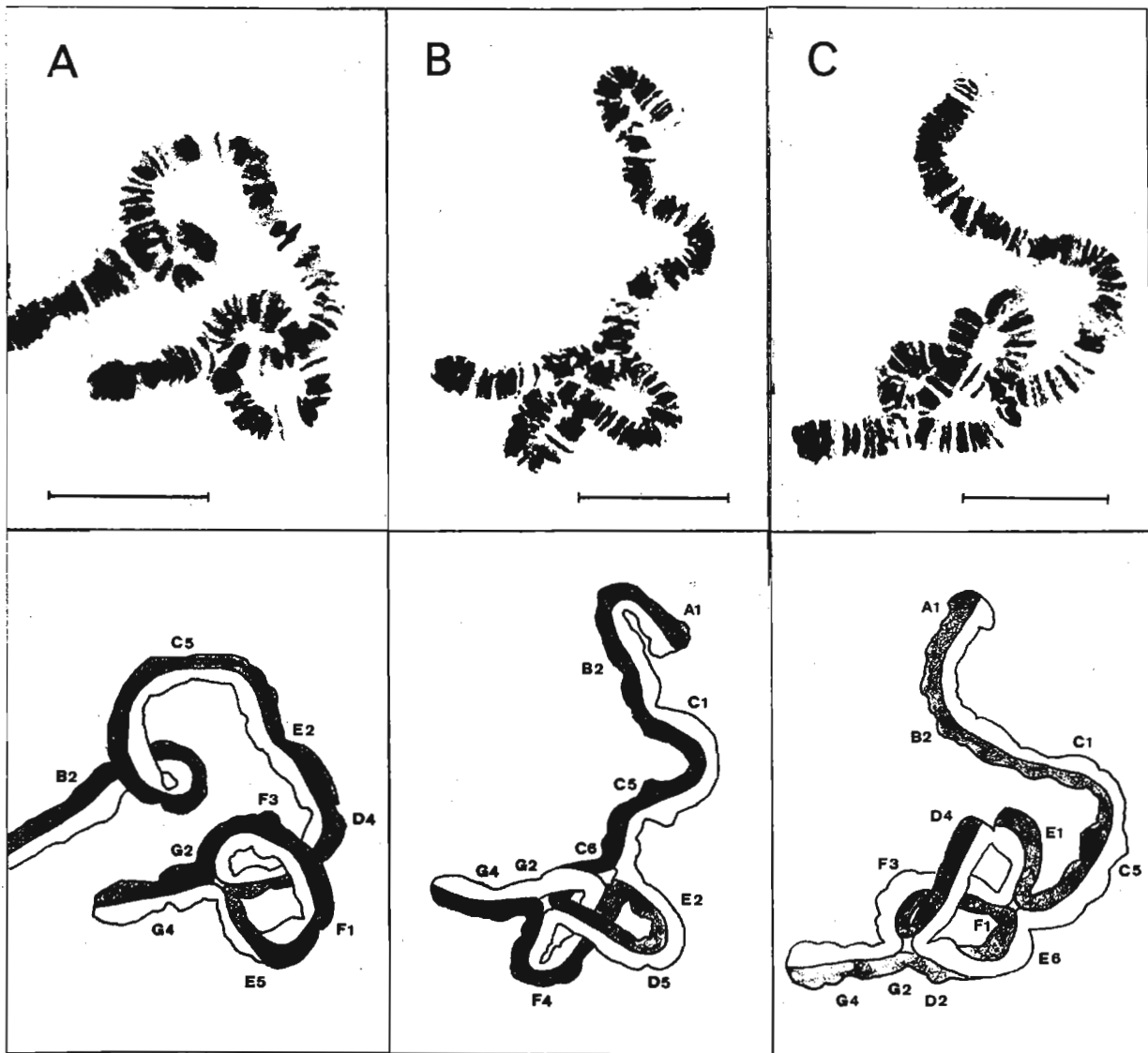


Fig. 2.

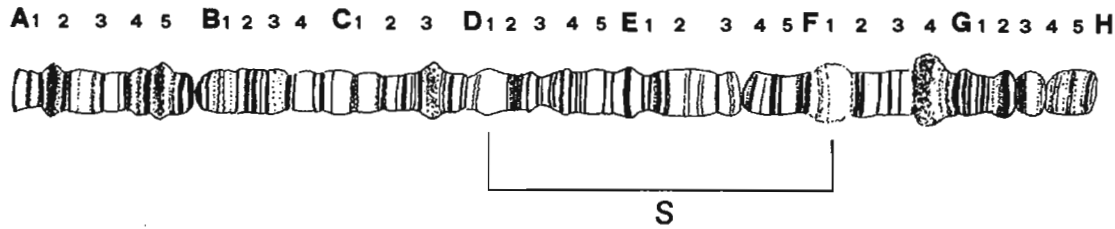


Fig. 3

The second chromosome has been found polymorphic for a new inversion which is always associated with *j* arrangement and it has been named tentatively  $jq^7$ . Its breakage points are D3b and G2f, the former included in inversion *j* region. In Fig. 1 is shown a scheme of both ends of inversion  $jq^7$  in a chromosome *j/j* and also the ends of *j* and  $jz^3$  already described (Wasserman 1962) for comparison.

Fig. 2 shows three microphotographs (A, B, C) of inversion loops formed in polytene chromosomes of three heterokaryotypes for the second chromosome ( $2jq^7/j$ ,  $2jq^7/st$  and  $2jq^7/jz^3$ , respectively), with the interpretative scheme. This inversion was found originally in Carboneras (Spain) and since then it has been found in the great majority of the studied populations of the Iberian Peninsula and Canary Islands. However, it is absent in the Balearic Island, the Madeira Island, Egypt and Dahomey populations. The frequency of  $jq^7$  arrangement ranges from 0.13 to 0.04, which qualifies it as moderately frequent.

Most of the populations and strains studied by us have been found also polymorphic for the fourth chromosome. This chromosome shows two arrangements: the standard (*st*) which is the primitive fourth chromosome of the repleta group (Wasserman 1962), and another arrangement which bears the new inversion extending from D1d to F1c regions. The breakage points are diagrammed in Fig. 3. The *s* inversion had not been detected in all the previous analyses of natural populations (Carson and Wasserman 1965) or laboratory strains (Wasserman 1962, 1954; Mather 1957). Yet, the frequency of this inversion is rather high (between 0.1 and 0.3) in the great majority of populations and strains analyzed by us. Fig. 4 (D) shows a microphotograph of the inversion loop formed in salivary gland chromosome of one heterokaryotype for the fourth chromosome ( $4st/s$ ), with the interpretive scheme.

The origin of these inversions is not known. The species has been given an Argentinian origin (Wasserman 1962; Carson and Wasserman 1965), on the basis of its high chromosomal polymorphism in the populations of S. Luis (Argentina). However, the polymorphism found by us in the Old World is the highest of all studied and poses the problem of its origin. *D. buzzatii* was introduced in the Old World following most probably the spread by man of its host plant *Opuntia ficus-indica* after the discovery of America. The evolutionary implications of this polymorphism, especially on the process of colonization, are discussed elsewhere (Fontdevila et al. 1979) and emphasize the interest for searching these new inversions in the endemic areas of the

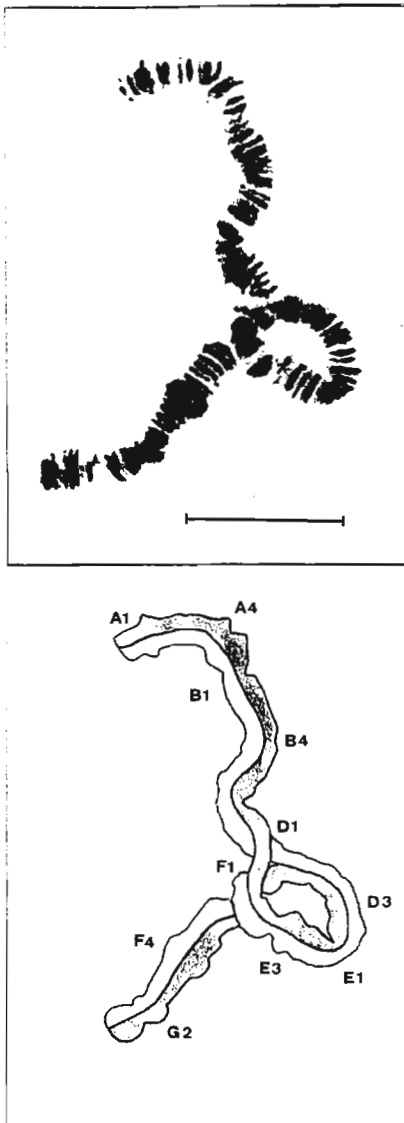


Fig. 4

New World in order to understand the colonizing strategy of this species. The presence of these new inversions in introduced populations of *D. buzzatii* suggests that colonization may not necessarily lead to loss of chromosomal polymorphism when the niche is narrow, although more information is needed from the original populations to further substantiate this point.

References: Carson, H.L. and M. Wasserman 1965, *Amer. Natur.* 905:111-115; Fontdevila, A., A. Ruiz, G. Alonso and J. Ocaña 1979, *Evolution* (submitted); Mather, W.B. 1957, *Texas Univ. Publ.* 5721:221-225; Wasserman, M. 1954, *Texas Univ. Publ.* 5422:130-152; Wasserman, M. 1962, *Texas Univ. Publ.* 6205:85-117.

Sampsell, B. Chicago State University, Chicago, Illinois. Survival differences between *Drosophila* with different ADH thermostability variants.

Temperature has been implicated as a potential selective agent in maintaining the polymorphism at the Alcohol dehydrogenase locus in *D. melanogaster* (Gibson 1970; Vigue and Johnson 1973; Clarke 1975). Two alleles,  $Adh^{Fm}$  and  $Adh^{Sm}$  (see Sampsell 1977 for an explanation of symbols) are

found in most natural populations.  $Adh^{Sm}$  codes for an enzyme,  $ADH^{Sm}$ , that is generally less active, but more heat stable than the  $ADH^{Fm}$  form produced by  $Adh^{Fm}$ . Along the eastern coast of the United States,  $Adh^{Sm}$  increases in frequency from about 60% in Maine to nearly 90% in Florida (Vigue and Johnson 1973; Sampsell 1977). This allelic distribution may be the result of an increasing fitness of flies with  $ADH^{Sm}$  (or conversely a decreasing fitness of flies with  $ADH^{Fm}$ ) with increasing mean temperature.

Numerous laboratory studies have shown that ADH is necessary for survival on various alcohol-supplemented media (the exception involves certain alcohols whose ketone metabolites are extremely toxic). If a significant portion of a fly's ADH enzyme were inactivated by high temperatures without killing the fly outright, the alcohol tolerance and thus survival would be reduced.

In an effort to test this hypothesis, larval viability was observed under various environmental conditions. Four strains have been constructed which are nearly isogenic except for a small region of the second chromosome containing the *Adh* locus. The relative thermostabilities of the allozymes of these strains is  $ADH^{Fr} > ADH^{Sm} > ADH^{Fm} > ADH^{Fs}$  (Sampsell 1978). Three

Table 1. Survival of larvae under various combinations of temperature and ethanol.

Parental genotype	Temp °C	Ethanol conc.	Number of adults emerging				x <sup>2</sup>	Relative survival		
			FF	FS	SS	Total		FF	FS	SS
$FrSm$	20	0%	201	422	179	802	3.31	.25	.53	.22
		5%	185	353	148	686	4.62	.27	.51	.22
		10%	13	17	2	32	7.69*	.41	.53	.06
	29	0%	209	413	171	793	5.01	.26	.52	.22
		5%	168	362	150	680	3.79	.25	.53	.22
		10%	24	50	9	83	8.81*	.29	.60	.11
$FmSm$	20	0%	234	411	186	831	5.69	.28	.49	.22
		5%	177	389	150	716	7.40*	.25	.54	.21
		10%	30	75	12	117	14.25**	.34	.56	.10
	29	0%	190	332	154	676	4.05	.28	.49	.23
		5%	210	406	185	801	1.72	.26	.51	.23
		10%	42	85	15	142	16.01**	.30	.60	.11
$FsSm$	20	0%	190	440	218	848	3.05	.22	.52	.26
		5%	193	405	190	788	0.64	.24	.51	.24
		10%	57	81	22	160	15.34**	.36	.51	.14
	29	0%	179	393	143	715	10.67**	.25	.55	.20
		5%	156	280	128	564	2.81	.28	.50	.23
		10%	32	37	7	76	16.50**	.42	.49	.09

\*  $p < 0.05$

\*\*  $p < 0.01$

different combinations of Adh alleles were studied. Flies homozygous for one of the three fast alleles were crossed to flies homozygous for Adh<sup>Sm</sup>. This is the slow allele which is most common in natural populations. FS heterozygous offspring were inbred, and the females were allowed to oviposit on "apricot-agar" for 18 hours. The egg-covered dishes of agar were incubated at 25°C for 24 hours; then first-instar larvae were collected and transferred to food vials at a density of 50 per vial. Vials contained Instant Drosophila medium (Carolina Biological) made up with an ethanol solution to produce a final concentration by volume of 0%, 5%, or 10% alcohol. Vials were placed at 20°C or 29°C until development was complete. Twenty vials were prepared for each experimental condition making an initial input of 1000 larvae. After the adults emerged, they were electrophoresed using standard procedures for cellulose acetate strips (Sampsel 1977).

If larvae of all genotypes are equally viable, the adults from an FS x FS cross should appear in a ratio of 1 FF:2 FS:1 SS. Table 1 shows the number of flies of each genotype that emerged, as well as the relative survival of each genotype within a specific set of conditions.

From the data, it is clear that increasing temperature and increasing alcohol concentrations reduce survival among virtually all genotypes. Significant deviations from a 1:2:1 ratio are seen primarily when high concentrations of ethanol are present. The survival of SS flies is about 22% on either 0% or 5% ethanol, regardless of temperature. On 10% ethanol, at both 20°C and 29°C, their survival decreases by 50%. On food supplemented to 10% ethanol, FF and FS flies survive in greater than expected proportions in the vials involving the Adh<sup>Fr</sup> and Adh<sup>Fm</sup> alleles; however, with ADH<sup>Fs</sup>, only the FF homozygotes seem to be favored.

Superficially, these results appear to be in agreement with other studies in which flies with the more active forms of ADH have a relatively higher survival rate on higher alcohol concentrations. Spectrophotometric assays of ADH activity levels in the strains with the rare thermostability variants has only just begun in our laboratory. Visual observation of stained strips following electrophoresis confirms that ADH<sup>Fm</sup> and ADH<sup>Fs</sup> are more active than ADH<sup>Sm</sup>. ADH<sup>Fr</sup>, however, is not nearly as active as the other two allozymes with fast mobility; instead its activity level appears very similar to that of ADH<sup>Sm</sup>. Thus the greater survival of FF flies can't be ascribed to higher activity as that of FmFm and F<sup>S</sup>F<sup>S</sup> can.

In the F<sup>m</sup>Sm crosses, there was a significant departure from 1:2:1 on 5% ethanol-supplemented food at 20°C as a result of an excess of FS and a deficiency of SS flies among the emerging adults. At 29°C, the three genotypes are equally viable on 5% ethanol. Although this might reflect a change in the fitness of SS and FS flies caused by the increase in temperature, the relative survival values are not adequate to produce the allele frequencies observed in natural populations. SS need not be the genotype with the highest fitness, but it must be superior to FF if Adh<sup>Sm</sup> is to be the more common allele.

In this experiment, relative survival was clearly a function of the specific environmental conditions, but there was no consistent evidence that flies with the enzymes that have been shown to be more heat-labile in vitro have lower survival rates than ones with the more heat resistant forms when reared at high temperatures. Our failure to observe the kind of differences that would support temperature as a selective agent for this enzyme does not disprove the hypothesis, however. It may well be that a constant temperature of 29°C, while high enough to cause some non-specific mortality, is not a severe enough heat stress to inactivate a substantial fraction of a fly's ADH and thus reduce its alcohol tolerance.

We have recently begun a series of tests in which adult flies are subjected to a heat treatment of 15 min at 40°C. Most adults survive this treatment; however, when F<sup>S</sup>F<sup>S</sup> flies are tested immediately after such a treatment, there is almost no ADH activity detectable on the stained strips. That the living flies' alcohol tolerance has indeed been reduced as well is confirmed by placing them on alcohol-supplemented food as soon as they recover consciousness. Preliminary results indicate that flies with ADH<sup>Fm</sup> show much less loss of alcohol tolerance after this heat treatment than ones with the more heat-labile ADH<sup>Fs</sup>. These experiments are being continued with flies with other ADH variants.

This work was supported by an NSF grant DEB-7911538.

References: Clarke, B. 1975, Genetics 79:101-103; Gibson, J. 1970, Nature 227:959-960; Sampsel, B. 1970, Biochemical Genetics 15:971-988; Sampsel, B. 1978, Biochemical Genetics 16:1139-1141; Vigue, C. and F. Johnson 1973, Biochemical Genetics 9:213-227.

Sapunov, V.B. Dept. of Genetics, Leningrad State University, Leningrad, 199164, USSR. The effect of juvenile hormone analogs on mutation frequency in *D. melanogaster*.

Table 1. The effect of JHA (Entacon) on frequency of dominant lethal mutations.

Line	Variant	n	% mutations
LA	control	7095	1.3 ± 0.13
Canton-S	"	4267	1.0 ± 0.15
LA	treatment	974	3.4 ± 0.58
Canton-S	"	1797	4.4 ± 0.48

Table 2. The effect of JHA (Altozid) on frequency of recessive viability mutations.

Line	Variant	Chromosome	n	% Semilethals	% Lethals
LA	control	X	784	0.8 ± 0.32	0.6 ± 0.35
"	treatment	X	635	1.6 ± 0.50	0.3 ± 0.22
"	control	2	1123	12.0 ± 0.97	2.8 ± 0.49
"	treatment	2	854	21.3 ± 1.40	4.6 ± 0.72
Canton-S	control	2	988	0.2 ± 0.14	0.5 ± 0.22
"	treatment	2	934	3.5 ± 0.60	4.8 ± 0.70

solution). 0.07 µ-liter was applied to pupae at age 135 hours. The data (shown in Tables 1 and 2) suggest that the LA strain has a high rate of mutability in chromosome 2. JHA has no effect on the mutation frequency in the X-chromosome of strain LA, but increased the mutability in chromosome 2 of both lines. Entacon could induce dominant mutations in both strains.

The data suggest that hormones are able to induce some types of mutations. Perhaps the endocrine system is the natural regulator of mutability in living organisms as well.

References: Kaidanov, L.Z. 1978, XIV Internat. Cong. Gen., Symposia 91-92; Kaidanov, L. Z., I.R. Pole and V.B. Sapunov 1978, XIV Internat. Cong. Gen., Contrib. Paper Sessions I:553; Lobashev, M.E. 1947, Vest. Leningrad Univ. 8:10-29; Sapunov, V.B. and L.Z. Kaidanov 1977, Vest. Leningrad Univ. 15:135-142 (Russ.)

Sapunov, V.B. Dept. of Genetics, Leningrad State University, Leningrad, 199164, USSR. The effect of juvenile hormone analogs on reproductive behavior of *D. melanogaster*.

In some insect species the corpus allatum has been shown to affect mating behavior, while in others this gland is less important (Engelmann 1970). To test the effect of juvenile hormone (JH), the secretion of the corpus allatum, on mating behavior in *D. melanogaster*, we have compared the wild strain Canton-S to the LA strain, which has been selected for 10 years for low male mating activity (Kaidanov 1978). In the LA line the corpus allatum contains very small cells, suggesting that corpus allatum function might also be altered (Sapunov and Kaidanov 1977). A third stock was obtained in which the proximal part of the X-chromosome is derived from the LA, but the rest of the genome is from wild strain. This strain, L,y ct, is characterized by males with mating activity lower than of the parent LA stock.

The index of mating activity was the percent of animals engaging in copulation during 0.5 hours after contact with 3-4 virgin flies of the opposite sex. The JH analogs (JHA) Altozid and Entacon (Zoecon Corporation) were topically applied in doses of 0.07 microliter. Altozid was dissolved in water, Entacon in oil. Concentrations are given in the tables. Treatment was performed in white prepupae (Stage I), middle pupae (130-140 hours after hatching of the larvae, Stage II), and some hours (3-5) before hatching of the larvae (Stage III).

The physiological hypothesis of the mutation process (Lobashev 1947) suggests that the endocrine system is able to control mutagenesis. The aim of this work was to study the effects of juvenile hormone analogs (JHA) on mutation frequency in *D. melanogaster*. Two strains were studied: Canton-S (wild strain) and LA. The latter line was selected for the low male mating activity and characterized by a high rate of spontaneous mutations and hypofunction of the gland corpus allatum (Sapunov and Kaidanov 1977; Kaidanov 1978; Kaidanov et al. 1978).

The analogs used were Altozid and Entacon (Zoecon Corporation). Dominant lethal mutations, effective at the end of embryogenesis, were detected by microscope

as eggs which stopped development at the last stages of embryogenesis. Recessive viability mutations were checked by the method of Muller-5 (X-chromosome) and Cy/Pm (chromosome 2).

Analogues were applied in concentrations of 10% (Altozid, water solution) and 20% (Entacon, oil



Table 1. Effects of JH analogs on male mating activity of *D. melanogaster*.

Line	Stage	Variant, analog, concentration %	n	% of ♂♂ engaging in copulation during 30 min.
Canton-S	-	control	86	84 ± 4.0
	III	Entacon, 20	128	81 ± 3.5
LA	-	control	1049	12 ± 1.1
	I	Entacon, 4	122	33 ± 4.2
	I	" 20	129	16 ± 3.2
	II	" 4	265	15 ± 2.1
	II	" 20	158	29 ± 3.6
	III	" 4	107	28 ± 4.3
	III	" 20	158	25 ± 3.4
	III	Altozid, 10	122	25 ± 3.9

I - white prepupae (98 hrs after hatching)

II - middle pupae (130-140 hrs after hatching)

III - old pupae (165-170 hrs after hatching)

Table 2. Effects of JH analogs on female mating activity of *D. melanogaster*.

Line	Stage	Variant, analog, concentration %	n	% of ♀♀ engaging in copulation during 30 min.
Canton-S	-	control	159	84 ± 2.9
	III	Entacon, 20	118	83 ± 3.4
LA	-	control	147	48 ± 2.9
	I	Entacon, 4	77	47 ± 5.7
	I	" 20	91	55 ± 5.2
	II	" 4	117	52 ± 4.6
	II	" 20	108	45 ± 4.8
	III	" 4	141	55 ± 4.2
	III	" 20	142	72 ± 3.8
	III	Altozid, 10	76	59 ± 5.5
	L,y ct	-	control	207
III		Entacon, 20	128	66 ± 4.6

V.B. and L.Z. Kaidanov 1977, Vest. Leningrad Univ. 15:135-142 (Russ.)

Semjonov, E.F. and A.F. Smirnov. Dept. of Genetics & Breeding, Leningrad State University, USSR. Somatic synapsis of *D. melanogaster* chromosomes.

without colchicine and hypotonic treatment. The slides were stained by the C-banding method (Patkin et al. 1978). Tight synapses of homologous chromosomes have been discovered in hetero- and euchromatic regions during interphase-mitosis (prophase-anaphase). The chromocenter-like structure has been shown for heterologous heterochromatic regions until anaphase. The disturbing influence of cochicine and hypotonic treatment has been noted in relation to somatic synapsis of chromosomes (Semjonov and Smirnov 1979). There were tight homologous synapses of chromosome 2 in *Df(2R)MS-2<sup>10</sup>/+*, *Df(2L)C'/+*, *Df(2R)MS-2<sup>10</sup>/Df(2L)C'* and *In(2LR)SMI/+*. However, the frequency of intimic heterozygous SMI inversion of chromosome 2 increased synapses

Table 1 shows that mating activity in the LA line is normally quite low--only 12% of treated imago males engaged in copulation in the half-hour test period. Seven times as many Canton-S males mated in the test period. A treatment with JHA resulted in increasing mating activity in LA but not Canton-S males. The most sensitive stage of treatment was pharate adults.

Females of the LA line also have lower mating activity than Canton-S despite the fact that the line was selected only for low mating activity in males. This trait is also very low in *L,y ct* flies, suggesting that genes responsible for the effect reside on the proximal part of the X-chromosome. JHA application stimulated mating activity in both LA and *L,y ct* lines (Table 2).

Our experiments show that mating activity can be stimulated by JHA in both males and females of a low mating activity strain.

Since the cytology of the corpus allatum is abnormal in LA strain and since JHA increased mating activity, we conclude that JH is the regulator of mating activity in *Drosophila*.

References: Engelmann, F. 1970, Physiology of Insect Reproduction, N.Y.; Kaidanov, L.Z. 1978, XIV Intern. Cong. Gen., Symposia 91-92; Sapunov,

of X chromosomes (Table 1). Sometimes interchromosome connections have been found between heterologous chromosomes.

There were tight homologous and heterologous synapses of chromosomes during practically all the mitotic cycle. We propose that normal homologous synapses have been connected with the intact structure of the common chromocenter.

Table 1. Homologous synapses of chromosomes X and 2 in neuroblasts of *D. melanogaster*.

Chromosome	Tight synapses (%)				
	Canton-S	Df(2R)MS-2 <sup>10</sup> /+	Df(2L)C <sup>1</sup> /+	Df(2R)/Df(2L)	In(2LR)SMI/+
2	73.7	61.3	55.8*	29.3*	51.2*
X	48.0	52.7	51.3	48.9	57.6*

\* significant differences from control (Canton-S),  $P < 0.05$

References: Hilliker, A.J. 1975, *Genetics* 81:705; Hilliker, A.J. and D.G. Holm, *Genetics* 83:765; Patkin, E.L., A.F. Smirnov and M.G. Smaragdov 1978, *Vestn. Ser. Biol. Leningr. Univ.* 15:143; Semjonov, E.P. and A.F. Smirnov 1979, *Genetika (Russ)* 15:12.

Sene, F.M., M.A.Q.R. Pereira, C.R. Vilela and N.M.V. Bizzo. IBUSP, São Paulo, Brazil. Influence of different ways to set baits for collection of *Drosophila* flies in three natural environments.

Bait traps have been used in South America and other parts of the world in most ecological and geographical surveys of *Drosophila*. Dobzhansky and Pavan (1943, 1950), Pavan, Dobzhansky and Burla (1950), Freire-Maia and Pavan (1950), Pavan and Cunha (1947), Peterson (1960), and others have used this technique.

On the other hand, several investigators, especially Dobzhansky and Pavan (1950), Pavan (1959) and Brncic (1957), have pointed out that the results obtained do not always represent natural conditions, since they are affected by many factors: the weather, kinds and conditions of bait, natural foods existing within the surveyed area, feeding and flight activities of the flies, and so on. Da Cunha et al. (1957) show that species of flies are attracted in different frequencies when different yeasts are used as bait.

In the present paper we report the influence of two different types of traps using the same kind of bait, on the attraction of species of *Drosophila*. Beppu and Toda (1976) did a similar study in Japan and conclude that the different ways to set bait cans affect species attraction.

The collections were made in three localities, two of which are adjacent to each other: (1) Mogi-Guacu (41°11'W-22°17'S). The area is covered by cerrado vegetation and is part of a Natural Reserve belonging to the Secretaria de Agricultura do Est. de São Paulo. Four collections were made in January, March, May and June 1978. (2) Peruibe (46°56'W-24°14'S). The area is covered by restinga (or strand) vegetation, which shows a transitional type of vegetation between the dunes and the Atlantic Forest. The place where the collection was made is about 2 km away from the sand beach. Four collections were made in May, July and October 1978 and in February 1979. (3) Peruibe (46°55'W-24°14'S). The area is covered by typical dune vegetation and is situated close to the sand beach. Three collections were made in May and July 1978, and in February 1979.

In all collections, bananas and oranges seeded with baker's yeast were used as bait. The collections were made 2 or 3 days after the baits were set. The bait was placed in two different ways: (1) On the ground--the banana-orange was simply placed on the ground in an area previously cleaned in order to avoid problems of sweeping with the net during collection. The collection was done by sweeping the net over the trap while the fruits were kicked. (2) In hanging cans--the banana-orange was put inside of 1-liter cans, which were hung by wire on trees at about 1.5 meter over the ground. The collection was done by lacing a net on the can's open side. A rubber band was used to keep the net fastened on the can. By carefully tapping the can, all flies can be collected inside the net. With this technique, no flies can escape. In each collection, we have three situations: (a) cans hanging close to the ground baits, never more than 3 meters from each other; (b) ground baits situated at least

SPECIES	CERRADO								RESTINGA								DUNES					
	Jan/78		Mar/78		May/78		Jun/78		May/78		Jul/78		Oct/78		Feb/79		May/78		Jul/78		Feb/79	
	C	G	C	G	C	G	C	G	C	G	C	G	C	G	C	G	C	G	C	G	C	G
Sbg.willistoni	9.8	49.6	10.7	44.6	13.7	19.3	32.4	62.8	46.4	40.5	8.4	36.3	2.3	2.2	9.5	21.8	36.6	23.4	6.5	5.4	3.4	7.0
D.capricorni	-	-	-	-	-	0,1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D.nebulosa	0.3	12.0	0.1	1.5	0.2	3.5	-	1.6	-	0.3	-	-	-	-	0.7	2.7	-	0.3	-	-	0.9	6.1
Sbg.bocainensis	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D.austrosaltans	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D.prosaltans	0.5	-	0.6	0.1	4.9	0.8	1.5	-	0.2	-	0.1	-	-	-	0.1	-	0.1	-	0.1	-	-	-
D.sturtevantii	52.6	0.6	69.4	9.9	37.4	19.4	16.5	2.7	18.1	1.7	41.6	21.3	7.0	0.9	22.7	7.1	14.5	1.3	22.9	4.6	8.9	0.9
D.malerkotliana	1.1	0.4	8.7	14.8	2.3	2.3	0.1	0.4	3.9	7.8	3.3	5.4	0.1	1.8	5.9	15.8	4.6	2.3	3.9	7.2	11.3	22.7
D.simulans	21.3	6.8	1.0	2.0	19.2	15.4	20.2	7.4	16.6	15.9	29.8	12.1	55.4	64.7	31.9	36.2	13.0	14.0	46.3	52.7	45.5	41.5
D.latifasciiformis	0.6	1.7	1.0	6.7	9.0	24.8	0.4	0.6	8.7	26.3	0.8	4.3	1.0	4.0	0.7	1.3	16.7	44.8	1.8	14.4	1.4	3.5
D.immigrans	-	0.2	-	0.1	0.2	0.1	0.3	0.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D.ararama	-	-	-	-	-	0.2	0.1	0.1	-	-	-	-	-	-	-	-	-	-	0.1	-	-	-
Gr.cardini	4.1	15.2	4.6	13.1	4.3	7.7	14.0	14.0	2.1	1.1	3.4	7.2	1.9	2.7	23.3	13.6	3.5	0.3	3.8	2.8	22.3	18.3
D.guaramunu	-	0.8	-	0.2	-	0.3	0.3	1.0	-	-	-	-	-	-	-	0.4	-	-	-	-	-	-
D.guarani	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-
D.pallidipennis	-	-	1.0	0.1	-	-	0.4	-	0.1	0.3	0.2	-	0.4	-	0.6	0.1	0.5	-	0.5	-	0.5	-
Gr.repleta	9.6	0.4	3.4	2.2	9.0	5.1	12.5	1.4	3.6	4.3	12.4	13.0	31.5	22.8	3.3	1.0	10.0	12.3	14.0	12.8	5.3	-
D.griseolineata	-	-	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	0.5	-	-	-	-	-
Gr.calloptera	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-
Gr.tripunctata	-	11.8	0.2	4.6	-	0.5	0.6	6.8	-	-	0.1	0.1	-	0.4	-	-	-	0.6	-	-	-	-
Total	614	474	892	5262	511	1400	1645	482	1118	345	2986	831	1014	223	2380	920	852	299	2775	389	1686	299

C = Cans ; G = Ground

TABLE 1 - Results of collection made using baits setted at differents ways in three environments situation, in differents times.

200 meters away from any can baits; (c) can baits situated at least 200 meters away from any ground baits. Since we found no difference between the ground baits in cases (a) and (b), they are considered together here; the same happens with can baits in cases (a) and (c).

All flies were brought alive to the laboratory and classified. All of the specimens were deposited in the Museum of Zoology, USP. In the classification we placed some species in groups as follows: willistoni subgroup--consisting of the sibling species which were not identified; cardini group--consisting of three species, *D. polymorpha*, *D. cardini* and *D. cardinoides*. The identification of these flies is in progress. As far as we know, *D. cardinoides* is rare in all three areas studied, *D. polymorpha* is more common in cerrado and *D. cardini* is more abundant in restinga and dunes. Repleta group--this group will be the special subject for a future paper and we can say now that *D. mercatorum* is the most common species in the three areas; tripunctata group--the flies belonging to this group were not identified to species level.

The species and number of flies collected at the two different traps in the three ecological situations at different times are presented in Table 1. The preference of the different species to the two kinds of traps was not the same in the three environments analyzed. In the cerrado situation, the following flies show a preference: (a) to ground baits--willistoni subgroup, *D. nebulosa*, *D. latifasciaeformis*, cardini group, *D. guaramunu* and tripunctata group; (b) to can baits--*D. prosaltans*, *D. sturtevanti*, *D. simulans* and repleta group; *D. malerkotliana* show no preference and the other flies were collected in small numbers. In the restinga situation we found: (a) preference for ground baits--willistoni subgroup, *D. nebulosa* and *D. latifasciaeformis*; (b) preference for can baits--*D. prosaltans* and *D. sturtevanti*; *D. malerkotliana*, *D. simulans*, cardini group and repleta group show no preference. In the dunes situation: (a) ground--*D. nebulosa* and *D. latifasciaeformis*; (b) can--*D. prosaltans* and *D. sturtevanti*; no preference--subgroup willistoni, *D. malerkotliana*, *D. simulans*, cardini group and repleta group.

We know from previous studies (cited above) that different kinds of baits attract different species of flies. But in this study we show that the same kind of baits give different results depending on the way they are set. In previous personal observations we have detected that the age of the bait, set on the ground, affects the attraction of different species. The same observation was made by Beppu and Toda (1976). Although we have no systematic data to show this, we have some evidence which seems to indicate that the species that were attracted preferentially by old baits set on the ground are the same as those that are attracted preferentially to baits set in cans. Based on this observation we have the hypothesis that the differences between baits set on the ground and those set in cans are caused by differences in the fermentation process.

As we can see from the results, the influence of the way the baits were set was strong in the cerrado, where 10 "entities" show preference and one was indifferent; in the restinga the effect was less obvious as only five showed preference while four were indifferent; in the dunes we have the smallest effect with four showing preference and five being indifferent.

A possible explanation is that in the dunes, the wind and the salty, dry situation affect the baits more strongly than in the cerrado, and interfere with the fermentation of the baits. Another hypothesis to explain the differences between the environments, that must be checked in the future, is that the species which have been grouped into what we have called the willistoni subgroup or cardini group could be different species in the cerrado and in the restinga or dunes (Dobzhansky and Pavan 1950), and instead of differences due to environmental situations we may have different species in each area. For the repleta group, we know for sure that the dominant species in the three environments was *D. mercatorum*. *D. nebulosa* shows a constant preference for ground baits in spite of the environmental situation; the same happens with tripunctata group species and *D. latifasciaeformis*. The flies of saltans group showed a strong preference for the can baits.

These data increase the problem of conducting a survey of the *Drosophila* fauna by using bait set in only one way for attracting the flies. For instance, the more extreme data found was the collection in the cerrado in January 1978. If we compare the collection made on the ground with the collection made in the can, we would be led to believe that they were made in two different environments and that the faunal composition of each were very different.

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USP 221, Biol. Geral 11:1-81; Pavan, C. and A.B. Da Cunha 1947, Bol. Fac. Filos. Cienc. Let. USP 86, Biol. Geral 7:3-46; Pavan, C., T. Dobzhansky and H. Burla 1950, Ecology 31(8):36-43; Petersen, J.A. 1960, Rev. Bras. Biol. 20(1):3-16.

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Shadravan, F. and J. McDonald. Iowa State University, Ames, Iowa. The effect of environmental 2-propanol on the ability of flies to survive in alcohol environments.

Anderson and McDonald (1980) have recently demonstrated that *Drosophila* exposed to an environment containing 2-propanol undergo (1) a post-translational conversion of their alcohol dehydrogenase, (2) a significant drop in ADH specific activity, (3) an increase in ADH in vivo stability, and (4) a consequent

increase in in vivo levels of ADH. These authors suggest that this phenomena may have adaptive significance for *Drosophila* living in those environments abundant in secondary alcohols (e.g., Heed 1978) by preventing the production of highly toxic ketones. A second prediction which follows from these data is that *Drosophila* exposed to environmental 2-propanol should be more sensitive to the toxic effect of alcohols due to a decrease in ADH specific activity. In this note we present the results of a study designed to test this prediction.

The strains used in this study are F-2 and S-1 as described by McDonald et al., 1980. These flies are completely homozygous (McDonald and Ayala 1978) and are fixed for an ADH-fast (F-2) and ADH-slow (S-2) allele. The relative survivorship of flies pretreated with 2-propanol and non-pretreated were examined at 0, .125, .250, .500, 1.00, 3.00, 5.00 and 8.00% ethanol. For each experiment 6 vials (3 vials of females, 3 vials of males) each containing 10 flies (6-10 days post-eclosion) were set up for each strain and alcohol concentration tested. Flies were allowed to fully recover from very light etherization for a period of 1-2 hours before

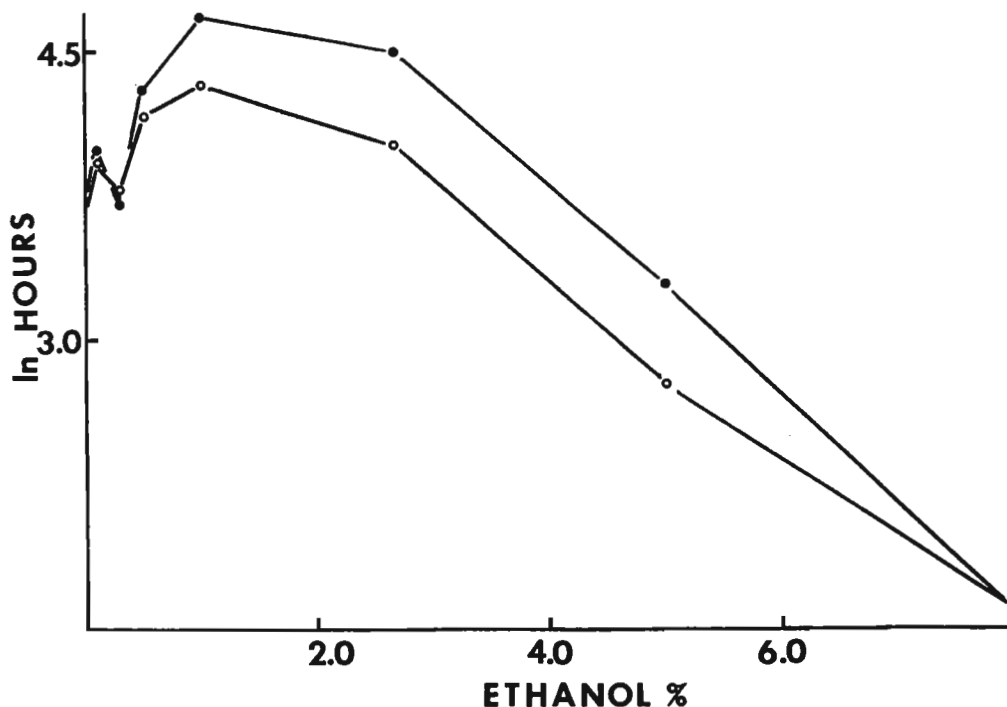


Fig. 1. Mean longevities given in lh(hr) for Fast strain exposed to increasing concentrations of ethanol. Closed circles are control flies and open circles are pretreated flies with 1% 2-propanol for 1 day.

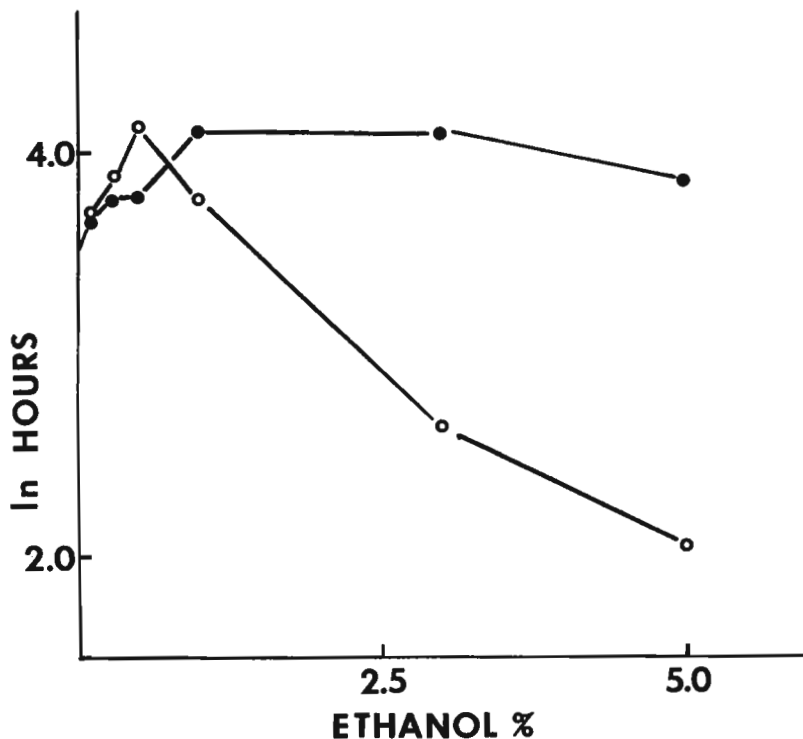


Fig. 2. Mean longevities given in  $\ln(\text{hr})$  for Slow strain exposed to increasing concentrations of ethanol. Closed circles are control flies and open circles are pretreated flies in 1% 2-propanol for 1 day.

absorbed with 1 ml of 1% 2-propanol solution. The results presented in Figs. 1 and 2 demonstrate that 2-propanol pretreated flies are in fact more sensitive to ethanol than non-pretreated flies. These results are analogous to the results recently reported by Papel et al. (1979) which demonstrate that pretreatment with acetone (the oxidized product of 2-propanol) also reduces the viability of *Drosophila* in alcohol stress environments.

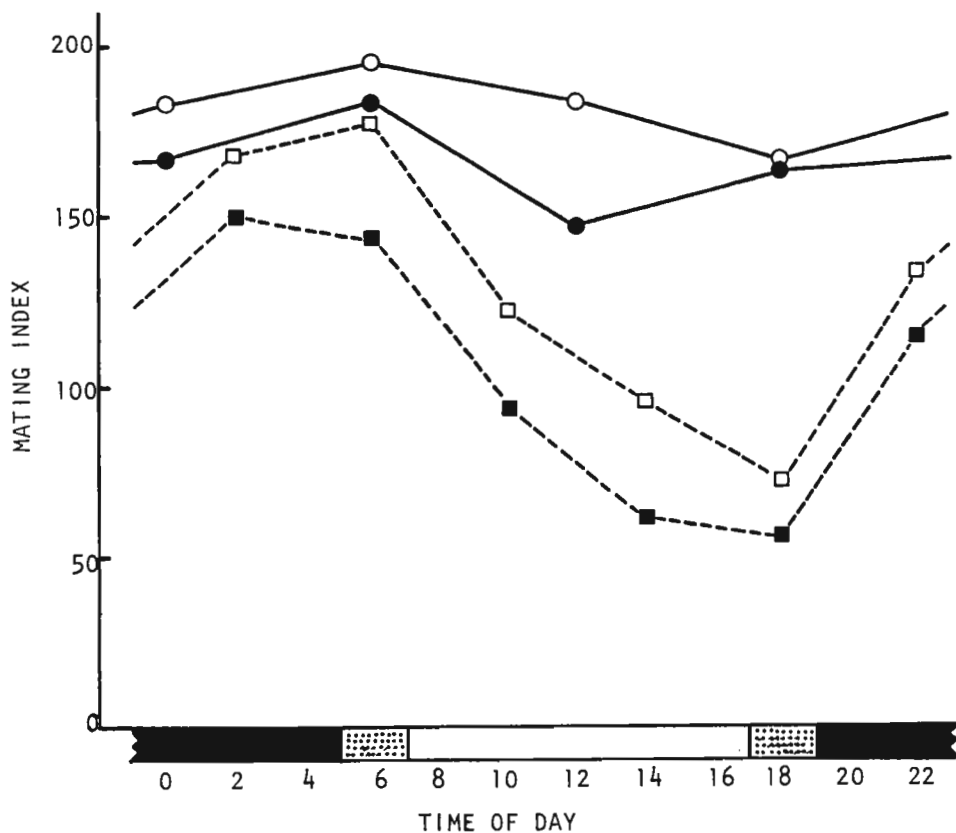
References: Anderson, S.A. and J. McDonald 1980, *Biochem. Genet.* (in press); Heed, W.B. 1978, in: *Ecological Genetics--the Interface*, P.F. Brussard (ed.), Springer-Verlag, New York, p. 109; McDonald, J., M. Santos and S.A. Anderson 1980, *Genetics* (in press); McDonald, J. and F.J. Ayala 1978, *Genetics* 89:371-388; Papel, I., M. Henderson, J. Van Herrewege, J. David and W. Sofer 1979, *Biochem. Genet.* 17:553; Starmer, W.T., W.B. Heed and E.S. Rockwood-Sluss 1977, *Proc. Nat. Acad. Sci. USA* 74:387-391.

Shitamoto, T. and H. Ikeda. Ehime University, Matsuyama, Ehime, Japan. Differences in the diurnal rhythmicity of mating activity in *D. melanogaster*.

Two strains of *D. melanogaster* were compared with respect to the diurnal rhythms of mating activity. Strains used are J<sup>5</sup>, a wild type laboratory strain, and Bw, a brown eye color strain. Flies were reared and aged in the LD cycle, which was set as follows: a light phase (200 lux), 7:00-17:00; a dark phase, 19:00-5:00. Dim light phases were set for two hours between the dark and the light phases both in the late afternoon and in the early morning. Observations of matings were carried out in the light (200 lux) and also in the red light. Fifteen 5- or 6-day-old males and ten 5- or 6-day-old females were introduced into an observation vial. The number of matings per 5 min. interval was scored during a 30-min. observation period. A mating index was calculated by the formula proposed by Spiess et al. (1966), on the basis of data of 3 to 6 runs.

the test was initiated. Initiation of a test consists of adding to each vial a 2.00" x 2.00" filter paper tab (Watman #1) which had been saturated with 1 ml of either H<sub>2</sub>O (control) or a test alcohol-H<sub>2</sub>O solution of a specific concentration. Vials are immediately sealed with parafilm and placed in the incubator (25°C, constant humidity and lighting). The number of flies alive in each vial are observed and recorded (every 5 hours for high alcohol concentrations, every 10 hours for low alcohol concentrations). Mean % survivorship at each alcohol concentration is plotted vs. time. From these "primary plots", we graphically determined mean hrs to 50% mortality at each alcohol concentration and use this information to construct secondary plots ( $\ln$  hrs to 50% mortality vs. alcohol concentration) as devised by Starmer et al.

Figure: Changes in the mating index depending on the time of day at which observations were carried out. —○—,  $J^5$ , in the light; —●—,  $J^5$ , in the red light; —□—,  $bw$ , in the light; —■—,  $bw$ , in the red light.



The figure shows the change of the mating index depending on the time of day. The diurnal rhythmicity in mating was found for the  $bw$  strain, but not for the  $J^5$  strain. This tendency was not affected by the light condition under which observations were performed. However, mating indices obtained in the light are significantly larger than those measured in the red light, except that no difference in the value was found at 14:00 for the  $bw$  strain and at 0:00 and 12:00 for the  $J^5$  strain.

More careful experiments should be carried out to test whether or not the differences in the diurnal rhythmicity in mating between strains depend on the eye color of flies.

References: Spiess, E.B., B. Langer and L.D. Spiess 1966, *Genetics* 54:1139-1149.

Siegel, J.G. Scripps Clinic & Research Foundation, La Jolla, California. Cytological identification of autosomal breakpoints in several T(Y;2) stocks.

near the proximal heterochromatin of 2L, but distal to M(2)H. A second group was also chosen, with reported breakpoints proximal to M(2)H. Polytene chromosomes from each of these stocks

In a series of experiments to analyze the base of 2L, I have made use of segmental aneuploids to generate specific deficiencies, as described in Lindsley and Sandler et al. (1972). One group of T(Y;2)-bearing stocks was selected reported bearing autosomal breakpoints in or

Stock	Reported Autosomal Breakpoint	Observed Autosomal Breakpoint
A87	40	38A-B
L138	39C	39A
B190	40	39C
A107	40	39D-E
B209	40	39D-E
B251	40	39D-E
H54	40	39D-E
B199	40	40
H118*	40	40
H131	40	40
R116	40	40

\*May have free B<sup>Sy</sup>+ element segregating in stock.

cent studies on irradiation-induced lethal mutants mapping to the histone gene locus also suggest that the M(2)H locus may coincide with a part of the histone gene locus.

References: Lindsley, D.L., B. Baker, A.T.C. Carpenter, R.E. Denell, J.C. Hall, P.A. Jacobs, G.L.G. Miklos, B.K. Davis, R.C. Gethmann, R.W. Hardy, A. Hessler, S.M. Miller, H. Nozawa, D.M. Parry and M. Gould-Somero 1972, *Genetics* 71:157; Pardue, M.L., L.H. Kedes, E.S. Weinberg and M.L. Birnsteil 1977, *Chromosoma (Berl.)* 63:135; Wright, T.R.F., R.B. Hodgetts and A.F. Sherald 1976, *Genetics* 81:267.

Simms, R.W., N.D. Bearss and J. Tonzetich. Bucknell University, Lewisburg, Pennsylvania. Transfer RNA resolution in a Minute mutant of *D. melanogaster*.

the Minute class. Atwood argued that the slow rate of development in Minute bearing individuals was consistent with the reduced rate of protein synthesis expected from the decreased

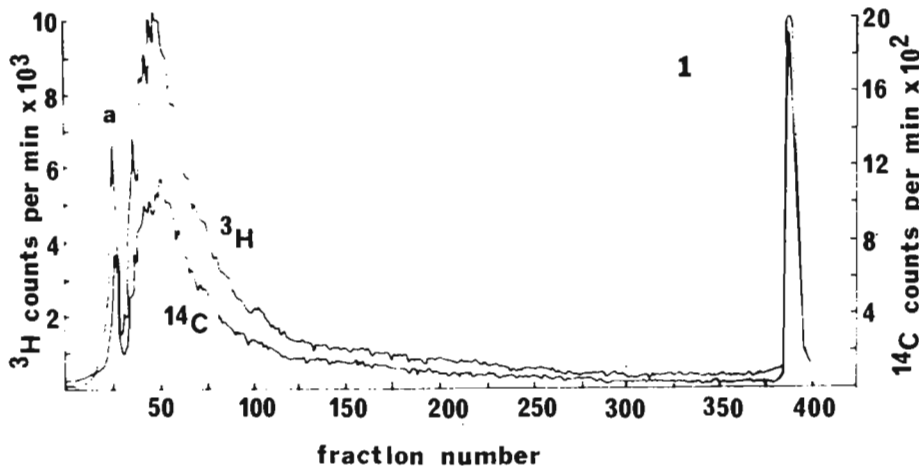


Fig. 1. Elution profiles of M(2)S7-(<sup>3</sup>H)-tRNA and Oregon R-(<sup>14</sup>C)-tRNA from a BD-cellulose column.

were examined to verify the reported breakpoints. Several discrepancies between the reported and observed breakpoints were found.

Table 1 lists the various T(Y;2) stocks examined, the autosomal breakpoints as reported in Lindsley and Sandler et al. (1972), and the observed breakpoints. All stocks with breakpoints reported to be distal to M(2)H carry euchromatic breaks, whereas those reported broken proximal to M(2)H bear heterochromatic breaks. It is of interest that several of the stocks examined are broken between 39D and 39E, the chromosomal region known to include the histone gene sequence (Pardue et al. 1977). Segmental aneuploids deficient for the region between the breakpoint of L138 and the breakpoints of H54, B251, and B209 do not show a Minute phenotype. However, deficiencies carrying more proximal euchromatic breaks are Minute (Wright et al. 1976). It is possible, therefore, that M(2)H may map to the proximal region of the histone gene cluster. My re-

Mutations producing the Minute phenotype in *D. melanogaster* occur in a number of genes on all four chromosomes. It has been proposed by Atwood (Ritossa et al. 1966) that alterations in DNA cistrons which code for transfer RNA are responsible for the characteristic mutations of

availability of a particular tRNA. Several investigators have tested this hypothesis using radioactively labeled tRNA and the method of in situ RNA-DNA hybridization to correlate sites of tRNA binding with genetically established positions of Minute loci (Steffensen and Wimber 1971; Grigliatti et al. 1974). The results, however, have been inconclusive. The present study involves a new preliminary test of the Atwood hypothesis, which utilizes a qualitative comparison of tRNA chromatographic elution profiles from both normal and Minute flies, thus



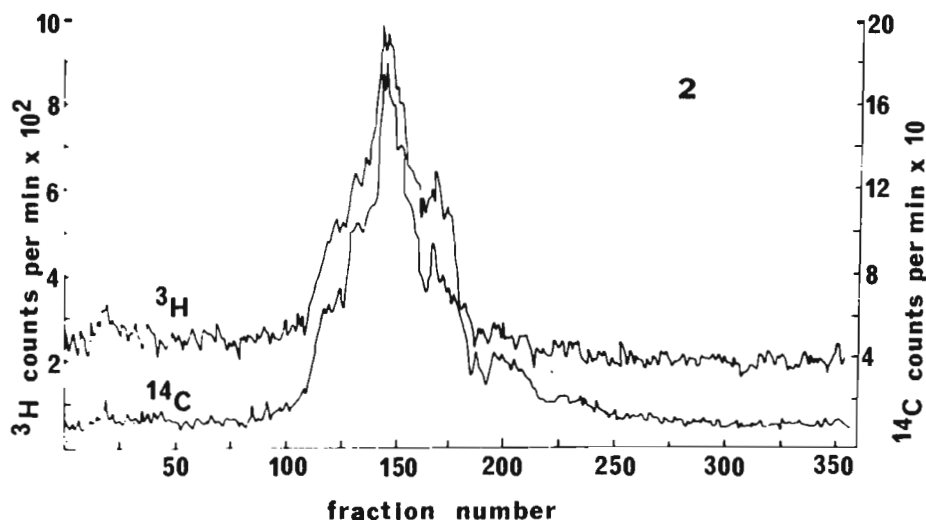


Fig. 2. Elution profiles of M(2)S7-( $^3\text{H}$ )-tRNA and Oregon R-( $^{14}\text{C}$ )-tRNA contained in fractions 20-120 of Fig. 1 from a BD-cellulose column.

mole). Transfer RNA from *Drosophila* was prepared by the method of White et al. (1973). Whole labeled third instar M(2)S7 Minute and Oregon R larvae were homogenized together and the final tRNA preparation was applied to a DEAE-cellulose column for further purification. The chromatography of the labeled tRNA sample follows the general method of Gillam et al. (1967), utilizing BD-cellulose. The sample was applied to a 1 x 90 cm BD-cellulose column previously equilibrated with the starting buffer. The column was then prewashed with buffer and the labeled tRNA was subsequently eluted in 5 ml fractions using a linear NaCl gradient ranging from 0.3 M NaCl to 1.0 M NaCl. Once the gradient was completed, 7 M urea was added to the final NaCl solution. Two ml aliquots of each fraction were added to 15 ml of Biofluor and then assayed for radioactivity in a Packard Tri-Carb liquid scintillation spectrophotometer. Fractions 10-120 from the BD-cellulose column were taken to be the major tRNA fractions as they contained the peaks with the highest number of counts. To further resolve the profile these fractions were pooled, precipitated, and applied to a BD-cellulose column as before with a similar linear NaCl gradient. 2 ml aliquots of each fraction were added to 15 ml of Biofluor and again counted in the scintillation spectrophotometer.

Fig. 1 shows the elution profiles of both M(2)S7 Minute ( $^3\text{H}$ )-tRNA and the wild type Oregon R ( $^{14}\text{C}$ )-tRNA chromatographed simultaneously on a BD-cellulose column. The two curves indicate that the tRNA from both Minutes and wild type are qualitatively very similar. The differences in height are due to the lower specific activity of the  $^{14}\text{C}$  isotope. The major peaks in Fig. 1 occur simultaneously at fractions 30 and 55 and drop off at the same rate through fraction 120. tRNA's in fractions 120-138 are also similar with no major discrepancies and occur in much lesser quantities until the final peak representing the extraction by urea. If the relative peak heights of each profile are compared by dividing the counts per minute of each fraction by the height of peak A for each profile, no significant differences are found.

Fig. 2 shows the elution profile obtained from a rechromatographing of fractions 20-120 on a BD-cellulose column. Both curves exhibit a large peak at fractions 145 and 169 and two small shoulders at fractions 124 and 131. The tRNA constituting the sharp peak at fraction 30 in Fig. 1 is spread over the broad profile ranging from fractions 0-100 in Fig. 2. Thus only one broad peak is observed as opposed to the two sharp peaks seen in Fig. 1. Fig. 2 also shows a significant reduction in the number of radioactive counts detected as compared to the number of counts observed in Fig. 1. A small portion of the tRNA (500 ml) in Fig. 1 was spread over a volume of 2 liters in the latter graph. Thus a substantial loss of quantity is expected. A comparison of relative peak heights of the two profiles in Fig. 2 again shows no significant differences. Further resolution may be achieved by chromatographing the peak material on reverse phase columns as described by Pearson, Weiss and Kilmers (1971).

avoiding the difficulties associated with in situ hybridization.

Labeling of RNA in Oregon R flies was accomplished by growing first instar Oregon R larvae on a low agar medium (0.3%) injected daily with a yeast-water suspension containing a total of 1 mCi ( $^5\text{-}^{14}\text{C}$ )-uridine (New England Nuclear Corp., 51.0 mCi/mole). M(2)S7 Minute RNA was labeled by permitting the first instar Minute larvae to feed on the low agar medium injected daily with a yeast-water suspension containing a total of 1 mCi ( $^5\text{-}^3\text{H}$ )-uridine (New England Nuclear Corp., 28.3 Ci/

References: Gillam, I., S. Millward, D. Blew, M. van Tigerstrom, E. Wimmer and G.M. Tener 1967, *Biochemistry* 6:3043-3056; Gillam, E. and G.M. Tener 1971, in: *Methods in Enzymology*, Vol. XX, K. Moldane and L. Grossman, eds., Academic Press, New York; Grigliatti, T.A., B.N. White, G.M. Tener, T.C. Kaufman and D.T. Suzuki 1974, *Proc. Nat. Acad. Sci. USA* 71:3527-3531; Pearson, R.L., J.F. Weiss and A.D. Kilmers 1971, *Biochem. Biophys. Acta* 228:770-774; Ritossa, F.M., K.C. Atwood and S. Spiegelman 1966, *Genetics* 54:663-676; Steffensen, D.M. and D.E. Wimber 1971, *Genetics* 69:163-178; White, B.N., G.M. Tener, J. Holden and D.T. Suzuki 1973, *J. Mol. Biol.* 74:635-651.

Singh, B.K. and Y.N. Dwivedi. Banaras Hindu University, Varanasi, India. Report on spontaneous occurrence of mosaics in *D. rajasekari* Reddy & Krishnamurthy.

and *D. funebris* (Spencer 1927; Timofeeff-Ressovsky 1928). According to Sturtevant and Beadle in the insects hormonal control of sex and secondary sex characters apparently does not occur, but instead these are controlled by intracellular factors. This is shown in a very simple way in individuals in which part of the body is XX in constitution and the remainder XY or XO. Such individuals, known as gynandromorphs, are mosaic for sex characters. They result in two ways: (1) by elimination from one daughter cell at an early cleavage of one of the two X chromosomes (Morgan and Bridges), or (2) from double nucleus eggs (Doncaster). In the former, all descendants of the cell with a single X chromosome are genetically male while those from the sister XX cell are female. A double-nucleus egg may or may not give rise to a gynandromorph, depending on whether the two nuclei are fertilized by like (X and X or Y and Y) or different (X and Y) sperms. Regardless of origin, gynandromorphs in *Drosophila* usually show autonomy of development with regard to sex characters, i.e., each part develops (with few exceptions) according to its own genetic constitution and without regard to the genetic constitution of adjacent or associated tissues.



Fig. 1

It was Morgan (1914) who reported for the first time the spontaneously arising gynandromorph in *D. melanogaster*. Subsequently, there have been a few reports on gynandromorphs in other species of *Drosophila* also, such as in *D. simulans* (Sturtevant 1921), *D. virilis* (Weinstein 1922)

Recently extensive collections were carried out for *Drosophilid* fauna in the vicinity of Punjim (Goa) which yielded a large number of flies representing several species of the genus *Drosophila*. They are *D. bipectinata*, *D. malerkotliana*, *D. jambulina*, *D. rajasekari*, *D. nasuta*, *D. orissaensis*, *D. eugracilis* and *D. meijerei*.

*D. rajasekari* is an indigenous species which seems to be quite common in certain parts of the Indian subcontinent. The male individual of the species can be easily distinguished from the female in having completely black terminal tergites, apical black patch on wings, metatarsal sex-comb of prothoracic legs. Altogether 50 flies represented this species during the collection. Of these flies, one was found to show the characteristics of a gynandromorph, with half of the body showing male and the other half female characters, especially with respect to wing patch and sex comb. However, this fly was found to be a female with respect to its external genitalia and the abdominal banding pattern (Fig. 1).

The authors wish to express their gratitude to Dr. J.P. Gupta for his guidance and to the University Grants Commission for financial assistance.

Smaragdov, M.G., A.F. Smirnov, A.V. Dukelskaya and A.V. Felcher. Dept. of Genetics & Breeding, Leningrad State University, USSR. Condensation and interchromosomal heterogeneity of *D. melanogaster* heterochromatin.

In relation to the frequency of C and H (Hoechst 33258) banding interchromosomal heterogeneity of heterochromatic regions have been demonstrated in third instar larvae neuroblasts. Both very different methods revealed practically the same results. Heterochromatin of sex chromosomes

Table 1. The frequency of differential staining in *D. melanogaster* heterochromatin (in percentage).

Type of banding	Stock	Chromosome					
		X	Y	2L	3L	3R	4
H band	C-S	97±2	94±3	62±4	66±4	26±4	34±4
	LA	96±1	95±2	47±3	64±3	16±3	29±3
C band	C-S	99±1	95±4	[	66±2	]	35±4
	LA	98±1	99±1	[	79±2	]	44±6

Table 2. Specific decondensation of X chromosome heterochromatin (after 6 hrs Hoechst 33258 treatment, 80) (ml).

Sex	n	Number of decondensed X	Length of decondensed heterochromatic regions
♀	624	41 ± 2.8	0.354 ± 0.0049
♂	189	16 ± 2.5	0.287 ± 0.0021

was stained differentially more frequently than these regions of autosomes (Table 1). Interstock differences have been demonstrated also for chromosome 2 heterochromatin of Canton-S and inbred stock LA (Smaragdov 1977; 1978; Patkin et al. 1978). In respect to specific decondensation heterogeneity of heterochromatin has been shown also by using Hoechst according to the method of Pimpinelli et al. (1975). Besides different intra- and interchromosomal sensitivity of heterochromatin the differences for male and female X chromosomes have been discovered (Table 2). Regarding the nature of interchromosomal heterogeneity of heterochromatin it is possible to imagine different levels of chromosomal DNA packing inside heterochromatin due to various timetables of mitotic condensation. True morphometric analysis revealed definite timetables for heterochromatin of LA and Canton-S.

References: Pimpinelli, S., M. Gatti and A. DeMarco 1975, *Nature* 256:335; Patkin, E.L., A.F. Smirnov and M.G. Smaragdov 1978, *Vestn. Ser. Biol. Leningr. Univ.* 15:143; Smaragdov, M.G. 1977, *Vestn. Ser. Biol. Leningr. Univ.* 15:143; Smaragdov, M.G. 1978, *Zytologia* 11:1278.

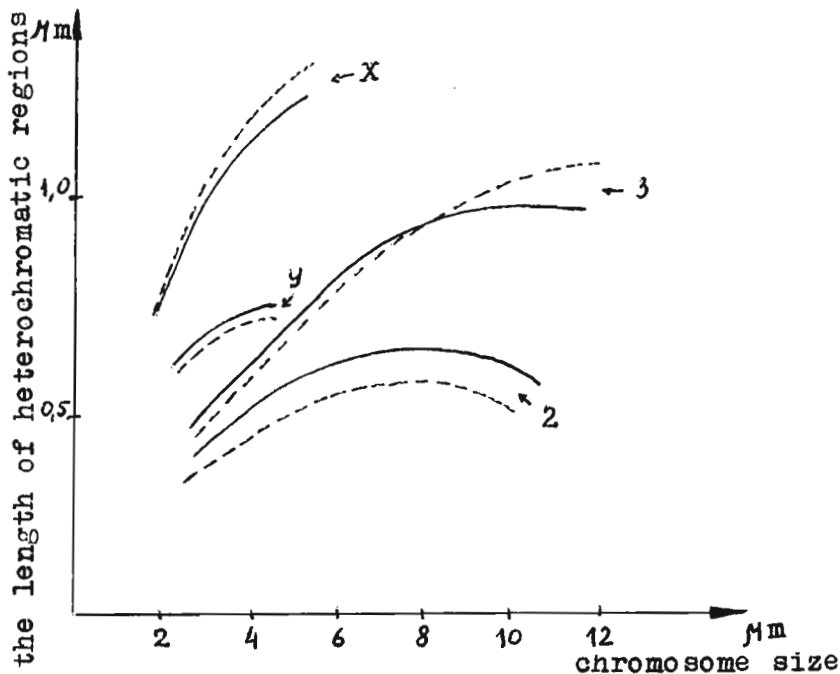


Fig. 1. The length of heterochromatin and chromosome size in *D. melanogaster* mitotic chromosomes from neuroblasts. ----- C-S ——— LA [For the Y chromosome H (LB) region has been measured.]

Sperlich, D. University of Tübingen, Germany. Lack of male recombination in *D. subobscura*.

Rare male recombination has been observed several times in *D. melanogaster* and other *Drosophila* species (for a review see Thompson and Woodruff 1978) including *D. subobscura* (Philip 1944). The phenomenon of male recombination

(MR) is frequently accompanied by segregation distortion, mutator activity and sterility. The final cause for this MR syndrome is not yet clear but it might be due to DNA insertions analogous to IS elements of bacteriophages (Green, Golubowsky and others) or simply to hybrid dysgenesis (Sved, Thompson and others). Whatever the case might be the MR effect seems to become an important factor in population and evolutionary genetics.

Since *D. subobscura* is our favored species for population studies we have made a small experiment in order to investigate whether MR effects can be discovered in our otherwise studied populations. Two different mutant strains, "cn, ma" (most probably homologous to st and se of *D. melanogaster*, respectively) and "vg, pp" (vg = vg of *D. melanogaster*; pp = light red eyes, maybe cn of *D. melanogaster*). According to localization and linkage to a group of enzyme loci cn, ma must be on chromosome I of *D. subobscura* which corresponds to III L of *D. melanogaster*, whereas vg, pp must be on chromosome E of *D. subobscura* which is

vg,pp/vg,pp x vg,pp/+,+ ♂					cn,ma/cn,ma x cn,ma/+,+ ♂				
Wild Chrom. No.	Phenotype of offspring				Wild Chrom. No.	Phenotype of offspring			
	++	vg pp	vg +	+ pp		++	vg ++	vg +	+ pp
2	117	30	-	-	2	106	38	-	-
10	173	61	-	-	9	202	104	-	-
13	222	67	-	-	13	137	66	-	-
14	275	81	-	-	24	182	112	-	-
22	70	24	-	-	27	43	33	-	-
24	237	65	-	-	29	236	135	-	-
29	105	31	-	-	42	34	8	-	-
31	55	11	-	-	46	27	13	-	-
34	138	30	-	-	50	31	16	-	-
42	105	52	-	-	51	99	80	-	-
46	157	82	-	-	53	24	23	-	-
47	96	40	-	-	54	64	50	-	-
50	146	27	-	-	55	56	23	-	-
186	242	52	-	-	60	75	54	-	-
188	48	13	-	-	63	185	116	-	-
189	293	85	-	-	179	96	44	-	-
191	128	54	-	-	186	55	21	-	-
203	157	29	-	-	188	246	126	-	-
310	262	103	-	-					
311	85	21	-	-					
n=20	3111	958	-	-	n=18	1898	1062	-	-

homologous to II R of *D. melanogaster*. A number of wild males from Cinisy (Sicily) were crossed individually to *cn*, *ma* or *vg*, *pp* females. From the offspring heterozygous single *cn ma/++* or *vg pp/++* males respectively were back-crossed to ten or more mutant females in order to get a big enough number of offspring flies to detect any male recombination with a rate higher than 0.5%. The results are shown in the table.

There was not a single male recombination in any of the various wild chromosomes and no segregation distortion could be observed. The predominance of ++ phenotype is due to the poor performance of the double mutant phenotypes. Segregation distortion, however, is expected to be effective against the ++ chromosomes. There is no evidence for such an effect in any of the cultures. The results can certainly not be taken as a general proof of absence of male recombination in *D. subobscura* but might be an indication that the phenomenon is not a general one for all crosses, for all populations and all chromosomes of the genome.

(The technical assistance of Mrs. Stögerer and Miss Kaipf is highly appreciated.)

Stamatis, N.D. University of Patras, Patras, Greece. Male recombination elements in a southern Greek *D. melanogaster* population.

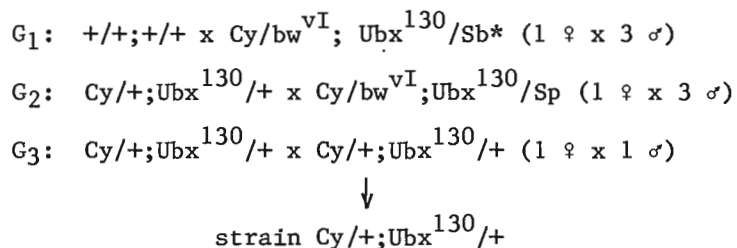
Since 1971 (Hiraizumi), chromosomes associated with male recombination elements have been isolated from natural populations of *D. melanogaster*, covering almost all the world. During the autumn of 1971 and in the course of a study which aimed to detect recessive lethals in a

natural population of southern Greece, one lethal second chromosome (symbol 31.1) was discovered to be associated with male recombination element(s) (Yannopoulos and Pelecanos 1977).

The aim of the present communication which constitutes a part of a much wider investigation is to ascertain whether male recombination elements are still present in the same population and to estimate their frequencies.

Wild flies were collected in June 1977. Captured females were transferred individually on fresh food (consisting of a standard cornmeal medium) and were allowed to lay eggs for five days. All cultures were kept in  $25 \pm 0.5^\circ\text{C}$ .

The progenies of each captured wild female were then crossed in a brother-sister mass mating; thus, a number of wild lines were established. Afterwards, strains *Cy/+;Ubx<sup>130</sup>/+*, bearing one second and one third chromosome from each wild line, were established by the following procedure:



In order to determine whether the wild chromosomes of these strains have the ability to induce male recombination along the second chromosome, males *Cy/+;Ubx<sup>130</sup>/+* were mated with *dp b cn bw;ve* virgin females. The *F<sub>1</sub>* *+/dp b cn bw;+ve* and *+/dp b cn bw;Ubx<sup>130</sup>/ve* sons (at least ten for each case) were then separately selected and individually mated with *dp b cn bw;ve* virgin females (see Table 1; crosses A and B, respectively). The *F<sub>2</sub>* progenies of both crosses were scored for recombinants until the 18th day after setting up the matings.

Among the 23 strains tested 13 (56.52%) have shown an association with MR elements, for they yielded male recombination frequencies higher than those of the control (see Table 1, line 14). Moreover, the spontaneous level of male recombination frequency is known to be 0-8/10,000 (Demerec 1965). For control, *F<sub>1</sub>* Canton/*dp b cn bw* Canton/*ve* males derived from Canton (wild type stock) fathers were mated with *dp b cn bw;ve* virgin females and their progeny were scored for recombinants.

The results show that the presence of the wild third chromosome influences male recombination along the second chromosome.

Our data do not allow us to suggest that one or more of the MR elements are identical

\*For description, see Lindsley and Grell (1968).

Table 1. Male recombination frequencies in +/dp b cn bw;+/ve (A) and +/dp b cn bw;Ubx<sup>130</sup>/ve (B) males. (+ stands for the whole second and third chromosomes.)

Strain	A				B			
	Male recombination frequency (%)	No. of males which produced recombinants (%)	No. of progeny	Average K*	Male recombination frequency (%)	No. of males which produced recombinants (%)	No. of progeny	Average K*
1	4.12	25.00	1844	0.53	0.13	6.67	1707	0.58
2	1.75	65.38	1660	0.46	0.08	6.67	1181	0.59
3	--	---	--	--	0.47	20.00	1909	0.51
4	0.46	13.33	2161	0.49	0	0	1114	0.55
5	0.31	30.77	1923	0.51	0	0	825	0.53
6	0.28	14.29	717	0.57	0.21	8.33	1421	0.57
7	0	0	1719	0.52	0.27	12.50	1100	0.54
8	0.05	6.67	1949	0.51	0.24	25.00	418	0.54
9	0.20	11.11	987	0.47	0	0	772	0.53
10	0.17	10.00	563	0.52	0	0	2250	0.59
11	0	0	1665	0.53	0.16	5.88	1899	0.60
12	0.15	19.19	1370	0.53	0	0	1018	0.55
13	0	0	1082	0.57	0.15	12.50	684	0.54
14	0	0	1835	0.55	0	0	2153	0.56

\*Average K = the proportion of wild-type among total progeny (excluding crossovers).

with the 31.1 MRF, which was found in the same population. Moreover, it is still obscure whether the above mentioned population is polymorphic as regards the male recombination elements. New experiments are needed before jumping to conclusions. Our investigation is still in progress.

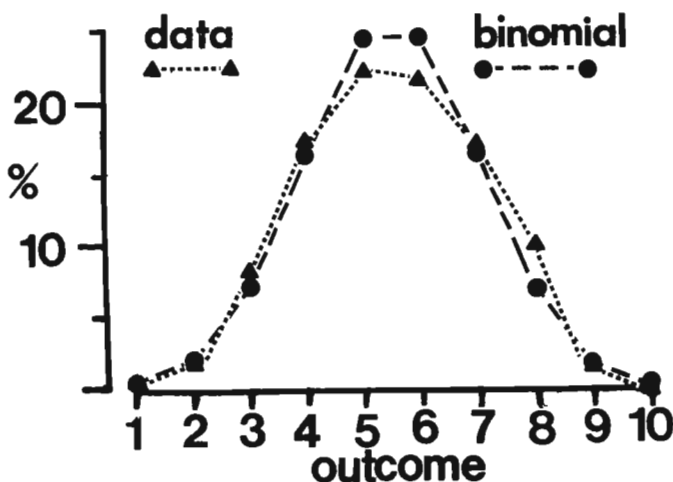
References: Demerec 1965, Hafner Publishing Co.; Hiraizumi, Y. 1971, Proc. Nat. Acad. Sci. USA 68:268-270; Lindsley, D.L. and E.H. Grell 1968, Carnegie Inst. of Wash. Publ.; Yanopoulos, G. and M. Pelecanos 1977, Genet. Res. 29:231-238.

Stark, W.S., K.G. Hu and R.B. Srygley.  
The Johns Hopkins University, Baltimore, Maryland. Comparisons of phototaxis properties in differing mazes.

The purpose of this communication is to dramatize the dependence of phototactic behavior in *D. melanogaster* upon the conditions of the experiment. Specifically, we have found flies to be photoneutral in a 10-outcome Hirsch-Hadler (Hadler 1964) classification maze at an illumina-

tion wavelength and intensity to which flies are highly phototactic in our straight and Y-shaped arenas (Hu and Stark 1977). The accompanying figure plots the outcome placements in the Hirsch-Hadler classification maze of white-eyed *cn bw* *D. melanogaster* ( $N = 339$ ) under medium intensity ( $6.3 \times 10^{13}$  quanta/cm<sup>2</sup>.s) blue-violet light (from a GE ribbon filament bulb, 6V 18A, with Corning filters CS-5-57 and CS-3-75 transmitting from 400 to 500 nm). Outcome 10 is towards light. Under these conditions, unselected flies were photoneutral (mean score = 5.51), consistent with a slight photonegativity greatly lessened by lack of eye color pigment (see Markow and Scavarda, 1977 recently). Even though the subject number,  $N = 339$ , is summed from 7 runs of 26 to 87 flies, the data show a slight flattening from the expected binomial distribution, perhaps due to crowding at early central decision points. On the other hand, the same *Drosophila* are highly positively phototactic in our straight (and Y) arenas: they go in increasing numbers to the brighter side in a choice. This is expressed as a high correlation coefficient (typically  $r = 0.9$ ) in the function relating proportion of flies on one side with the log of the intensity on that side for 7 intensity levels spanning 2 log units. At these illumination levels, phototaxis was found to be dominated by compound eye receptor cells R 7/8 (see Hu and Stark 1977).

The discrepancies in phototactic behavior among different experimental situations are rarely discussed (except see Rockwell and Sieger 1973; Markow and Merriam 1977). Polygenic selection experiments using the classification maze find unselected flies photoneutral while in most studies emphasizing function of compound eye receptors, *Drosophila* are photopositive (Bertholf 1932; Schümperli 1973; Heisenberg and Buchner 1977; Hu and Stark 1977; Jacob et al. 1977). In this study, we compared the same fly strain under similar illumination conditions to reduce the number of variables which differ between most straight, Y or T arena vs. Hirsch-Hadler maze experiments. To this end, we used much dimmer monochromatic light, typical of the receptor input experiments conducted at specific receptor thresholds, rather



than bright white fluorescent lighting used in genetic-selection experiments. Even so, flies were photoneutral. Lewontin (1959) has reported that agitation can increase phototaxis. This could account in part for the clear distinction of phototactic flies from nonphototactic mutants using Benzer's (1967) counter current device (see also Markow and Merriam 1977). Clearly, flies meandering through a classification maze overnight are unagitated. But in some of the receptor-input studies cited (Schümperli 1973; Heisenberg and Buchner 1977; Jacob et al. 1977) flies were also unagitated. Our experiments using straight or Y arenas, as well as the classification maze, would minimize the contribution of the predominant photoreceptor type R1-6, by

adaptation (see Hu and Stark 1977 for arguments), resulting in behavior dominated by R7/8. At lower intensities, selected to be near R1-6 electrophysiological and behavioral thresholds, flies are photoneutral in our straight or Y arena experiments. In these arenas, reasonably light-adapted flies are shaken and given 30 s for a choice. In experiments with less agitated, dark-adapted flies orienting to extremely dim lights at their leisure, flies show strong photopositive phototaxis probably mediated by the sensitive R1-6 photoreceptor system (Schümperli 1973; Jacob et al. 1977). These differing conditions operationally define additional phototaxis variables, namely fast vs. slow phototaxis (see Heisenberg and Götz 1975). In straight, T or Y arenas, R1-6 may mediate positive slow phototaxis near R1-6 threshold while R7/8 mediates fast phototaxis at R7/8 threshold. Phototaxis in a Hirsch-Hadler maze is obviously different. Clearly, numerous variables affect phototaxis under the differing conditions of straight, T or Y arenas vs. Hirsch-Hadler mazes; we have shown that fly strain or illumination condition cannot completely account for these discrepancies.

References: Benzer, S. 1967, Proc. Natl. Acad. Sci. 58:1112-1119; Bertholf, L.M. 1932, Z. vergl. Physiol. 18:32-64; Hadler, N. 1964, Biol. Bull. 126:264-273; Heisenberg, M. and E. Buchner 1977, J. comp. Physiol. 117:127-162; Heisenberg, M. and K.G. Götz 1975, J. comp. Physiol. 98:217-241; Hu, K.G. and W.S. Stark 1977, J. comp. Physiol. 121:241-252; Jacob, K.G., R. Willmund, E. Folkers, K.F. Fischbach and H.Ch. Spatz 1977, J. comp. Physiol. 116:209-225; Lewontin, R. 1959, Am. Naturalist 93:321-328; Markow, T.A. and J. Merriam 1977, Behav. Genetics 7:447-455; Markow, T.A. and N.J. Scavarda 1977, Behav. Genetics 7:139-146; Rockwell, R. and M. Sieger 1973, Am. Scientist 61:339-345; Schümperli, R.A. 1973, J. comp. Physiol. 86:77-94.

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Stark, W.S., R.B. Srygley and R.M. Greenberg. The Johns Hopkins University, Baltimore, Maryland. Analysis of a compound eye mosaic of outer rhabdomeres absent marked with cardinal.

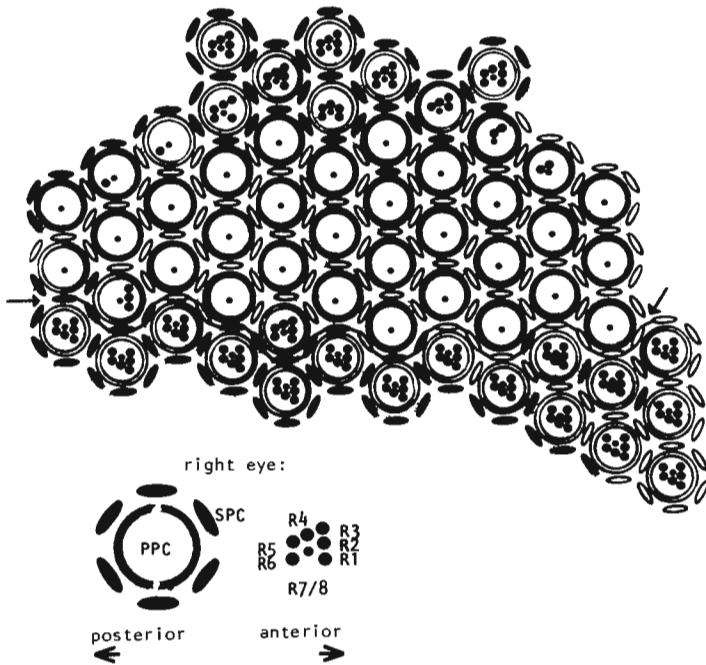
Drosophila with mutant compound eye receptors have been investigated by developmental biologists and vision researchers. Harris, Stark and Walker (1976) introduced characterizations of 3 such mutants, frequently studied since. Two of these mutants, *rdgB* and *sev* (causing degeneration of retinula cells R1-6 and non-

formation of R7 respectively) were shown to be cell autonomous by mosaic studies. The third mutant, *ora*<sup>JK84</sup>, was not studied by mosaic means at that time because its third chromosome location (65.3) made mosaic induction and combination with autonomous markers more difficult. Outer rhabdomeres absent, *ora*, discovered and mapped by Koenig and Merriam (1977) causes non-formation of R1-6 rhabdomeres, i.e., the microvillar photopigment-containing organelles. Here we present a mosaic study of *ora*.

An *ora* stock with eye color markers, *bw*; *ora cd*, was constructed with the aid of microscopic optical techniques and histology (see Harris, Stark and Walker 1976). Brown (*bw*) blocks and red drospterin synthesis while cardinal (*cd*) is an eye-autonomous mutant lowering brown ommochromes to about 15%; *cd* (3-75.7) is near *ora* on the right arm of chromosome 3 (see Lindsley and Grell 1968). The *bw* and *bw*; *ora cd* stocks were crossed to produce heterozygotes which were irradiated at 24 to 75 hours after egg laying (rearing at 24°C) with 1200 r of gamma rays (from <sup>137</sup>Cs source, Gammator) to induce somatic crossing over. Several eyes mosaic for eye color were found. Heads were fixed shortly after eclosion with a hypertonic aldehyde fixative followed by osmium tetroxide (see Stark and Clark 1973) and embedded in Spur, a low viscosity epoxy. One large right eye mosaic was serial sectioned at 1 micron and examined (without staining to enhance eye color pigment contrast) for reconstruction.

The accompanying figure shows reconstruction of much of this large mosaic. The trapezoidally arranged R1-6 rhabdomeres were scored for their presence or absence. The central R7/8 rhabdomeres, not affected by *ora*, were always present and are thus always drawn in. Secondary pigment cells (SPC's), 6 of which surround an ommatidium and are shared between ommatidia, were scored for presence (dark) or absence (clear) of brown pigment granules. Primarily pigment cells (PPC's), 2 of which surround the distal light-focusing pseudocone in each ommatidium, were scored for the presence (dark) or absence (clear) of conspicuous large brown pigment granules. The mosaic patch is located at the eye's equator (shown by a line and arrows).





type) background. Such a mosaic should have a homozygous  $ora^+ cd^+$  twin patch (undetected in the same phenotype heterozygous background) and would be expected from an early somatic cross-over event between the centromere and the closely linked  $ora cd$  vs  $ora^+ cd^+$  in the heterozygotes.

Near the borderline, ommatidia with mixed rhabdomere and pigment cell phenotype were found. The presence or absence of R1-6 rhabdomeres was not consistently correlated with whether nearly neighboring pigment cells were  $bw; ora cd$  or  $bw; ora^+ cd^+$  phenotype. This mosaic thus suggests that  $ora$  and  $cd$  are cell autonomous, i.e., that the mutant phenotypes are determined by the cells themselves, not by any possible interaction between receptor and eye color pigment cells or circulating factors. The pattern of receptor cell autonomy is consistent with other receptor cell mutants (e.g., see Campos-Ortega and Hofbauer 1977).

References: Campos-Ortega, J.A. and A. Hofbauer 1977, Wilhelm Roux's Arch. 181:227-245; Harris, W.A., W.S. Stark and J.A. Walker 1976, J. Physiol. 256:415-439; Koenig, J. and J.R. Merriam 1977, DIS 52:50-51; Lindsley, D.L. and E.H. Grell 1968, Genetic Variations of *Drosophila melanogaster*, Carn. Inst. Wash. Publ. 627; Stark, W.S. and A.W. Clark 1973, DIS 50:105-106.

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Steiner, Th. and F.E. Würigler. Institute of Toxicology, Swiss Federal Institute of Technology & University of Zürich, Schwerzenbach, Switzerland. Oocyte stages in newly hatched females of some  $mus$  and  $mei$  mutants.

cells of such stocks. In order to get comparable results with the different mutants it must be possible to treat and test comparable germ cell stages. Studies on oocytes cannot be ini-

Basically, the ommatidia lacking R1-6 have unpigmented secondary pigment cells and primary pigment cells with large brown granules while ommatidia with normal receptors have pigmented secondary pigment cells and pale primary pigment cells. Most of the rest of the eye's ommatidia not drawn in this reconstruction show this same pattern of normal receptor cells. The apparent reversal from the expected primary pigment cell phenotype is caused by a previously undescribed property of  $cd$ ;  $cd$ , which does not completely eliminate ommochromes, actually increases the size and visibility of primary pigment cell granules. It causes much greater ommochrome loss in secondary pigment cells. Thus, the primary pigment cells scored dark are actually  $cd$  phenotype ( $bw; ora cd$  genotype) and the paler ones (which do, in fact, have smaller brown granules) are actually phenotypically  $cd^+$  ( $bw; ora^+ cd^+$ ). The large mosaic studied is thus a  $bw, ora cd$  patch in a phenotypically  $bw$  (otherwise wild-

A number of *D. melanogaster* stocks are known in which larvae exhibit increased sensitivity to chemical mutagens. Several X-chromosomal loci were identified which lead to mutagen sensitivity ( $mus$ ). In addition to mutagen sensitivity some loci show strong meiotic effects ( $mei$ ). It is a task for the near future to study the mutagen sensitivity of the germ

Table 1. Strains from which females were analyzed.

Abbreviation	Formula	Reference
mus101	w mus(1)101D1	Boyd et al. 1976
mus104	w mus(1)104D1	Boyd et al. 1976
mei-41	w mei-41D5	Boyd et al. 1976
mei-9	mei-9L1	Graf et al. 1979
mei-9/M5	mei-9L1/Basc	Graf et al. 1979
w	w	Boyd et al. 1976
B.w.	Berlin wild	Steiner & Würgler 1979
$\bar{X}\bar{X}$	C(1)RM, y <sup>2</sup> su-w <sup>a</sup> wa bb/ y In(1)d1-49 v . YL/scV1.YS	Steiner & Würgler 1979

tiated without some basic information concerning the kinetics of oogenesis in the various mutants. To this aim we analyzed the ovarioles of freshly hatched females of a few mus and mei mutants and some control strains. Table 1 gives the genetic constitution of the strains used, the abbreviated

name, and references which give further details concerning the particular mutants. The mutagen-sensitive mutants were chosen because they have known DNA repair defects: mei-9 is excision repair deficient (Nguyen and Boyd 1977), whereas mei-41, mus101, and mus104 are postreplication repair deficient (Boyd et al. 1976). The flies were cultured on our standard *Drosophila* medium (Würgler, Sobels and Vogel 1977) at 25°C and 60% rh under uncrowded conditions. Females 2.5 ± 1.5 h old were dissected and the ovaries analyzed as described by Bürki and Würgler (1972). Oocyte stages were classified according to King, Rubinson and Smith (1956). The results of our study are compiled in Table 2. The most advanced stages in all types of female are stage 8 oocytes (S8). Only in a few exceptions were stage 9 or even stage 10 oocytes found. Of the younger oocytes stage 7, stage 5/6 and stage 3/4 are found in slightly increasing frequencies. This unexpectedly good agreement of oocyte stages between females of such divergent genotypes indicates that the mus and mei mutants studied do not alter the kinetics of oogenesis. In addition, because the white stock is the ancestor of the mus101, mus104 and mei-41 females (Boyd et al. 1976), our results also indicate that the mutagenic treatment of germ cells of the white stock did not induce other mutations on the X-chromosome which modify the kinetics of oogenesis in these related mutagen-sensitive stocks. It is important to stress that comparable kinetics of oogenesis does not mean comparable "quality" of the oocytes studied. This is easily seen if we look at the last line of Table 2 in which we report the egg-to-adult survival observed with the oocytes obtained from the different types of females. In contrast to the kinetics of oogenesis these data on spontaneous lethality indicate profound strain differences which seem to be due to the mus and mei mutations.

Table 2. Analysis of ovarioles and oocyte stages in 2.5 ± 1.5 h old females of different *D. melanogaster* strains.

	Genotypes of females							$\bar{X}\bar{X}$
	mus101	mus104	mei-41	mei-9	mei-9/M5	w	B.w.	
No. flies analyzed	20	20	20	20	20	20	18	20
No. ovarioles analyzed	824	784	817	768	786	800	783	748
Mean numbers per female:								
ovarioles	41.2	39.2	40.8	38.4	39.3	40.0	43.5	37.4
S10	--	--	--	0.05	--	--	--	--
S9	--	--	0.2	0.6	--	0.4	0.2	0.2
S8	3.4	1.8	3.8	5.8	3.8	3.2	2.9	3.0
S7	19.6	17.5	20.2	16.4	17.6	18.6	20.5	11.0
S5-6	20.0	21.6	25.1	19.7	17.8	22.6	17.5	14.4
S3-4	27.1	26.6	28.7	24.7	23.0	27.5	n.d.	n.d.
Class B oocytes	43.0	40.9	49.2	42.6	39.3	44.8	41.1	28.5
Egg to adult survival (%)	88.8	n.d.	34.9	23.8*	61.5*	88.1	92.1	33.6

n.d. = not determined

\*from Graf and Würgler 1978

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Stevens, P.G. and E.A. Carlson. State University of New York, Stony Brook. Chromosome mosaics induced in ring-X by ethyl methane sulfonate and by X-rays in *D. melanogaster*.

Chromosomal mosaics were produced by inducing breakage of a ring-X chromosome. When this resulted in the loss of the ring chromosome during one of the early cleavage stages of the zygote, an XX/XO gynandromorph was formed. In some cases the chromosome was repaired or altered without breakage, resulting in a point

mutation rather than chromosome loss. The markers *w*, *m*, *f*, and *B* were used so that the extent of mosaicism could be observed to distinguish point mutations from gynandromorphs.

Table 1. EMS-induced mosaics and their transmissibility.

Transmissibility	Gynandro-morphs	Point mutations			
		<i>w</i> <sup>+</sup> → <i>w</i>	<i>B</i> → <i>B</i> <sup>+</sup>	<i>m</i> <sup>+</sup> → <i>m</i>	
died	1	1	1	0	
nontransmissible	0	4	1	1	
sterile	5	0	0	0	
transmissible	0	0	1	0	
lethal	0	0	2	0	
total	6	5	5	1	

In the first series *Xc*<sup>2</sup> *y B* males were fed ethyl methane sulfonate (0.0125M EMS in 2% sucrose) for 24 hours. They were then mated to *w m f* virgin females and progeny were examined for mosaics (Table 1). The mosaics obtained from among 4787 total progeny consisted of 6 gynandromorphs (0.1%) and 11 point mutations (0.2%). The data sug-

gest that EMS produces more chemical alterations or repaired breaks on the ring-X chromosome, resulting in point mutations, than unrestituted breaks or aneupentric rings leading to loss and gynandromorphism.

In the second series *Xc*<sup>2</sup> *y B* males were exposed to X-rays (2500R) and then mated to *w m f* virgin females. As in the previous series, the progeny were examined for mosaics (see Table 2). The mosaics obtained from among 920 total progeny consisted

Table 2. X-ray induced mosaics and their transmissibility.

Transmissibility	Gynandro-morphs	Point mutations	
		<i>w</i> <sup>+</sup> → <i>w</i>	
nontransmissible	3	0	
sterile	2	1	
total	5	1	

of 5 gynandromorphs (0.5%) and 1 point mutation (0.1%). These X-ray results are consistent with the expectation that breakage of the ring-X chromosome is more likely to occur, producing gynandromorphs, than the induction of point mutations.

The distribution of the 11 gynandromorphs obtained is shown in Table 3. Note that in none of these 11 cases was there mosaicism for all five of the phenotypic characteristics used. Most of the gynandromorphs were genital male or female in phenotype and their sterility is probably due to incompatible head tissue of the opposite sex. The fertility of three gynandromorphs, one with an apparently male head and female genitalia, suggests that her head ganglial tissue was female or that males were successful in overcoming her behavioral barriers to reproduction. In two of the three fer-

tile gynandromorphs, only the w m f chromosome (male tissue) entered the gonads. In those two cases the genitalia of the gynandromorphs was male.

Table 3. Distribution of affected tissue in gynandromorphs

mutagen used	fertile(F) or sterile(S)	eye color		bristles	wing	sex comb		abdomen
		R	L			P=present A=absent		
						R	L	
EMS	S	B <sup>+</sup> w <sup>mos</sup>	B w <sup>+</sup>	f <sup>+</sup>	m <sup>+</sup>	A	A	♀-like
EMS	died	B <sup>+</sup> w <sup>mos</sup>	B w <sup>+</sup>	f <sup>mos</sup>	m <sup>mos</sup>	P	A	♂
EMS	S	B <sup>+</sup> w	B <sup>+</sup> w	f <sup>mos</sup>	m <sup>mos</sup>	P	A	♀
EMS	S	B w <sup>+</sup>	B w <sup>+</sup>	f <sup>mos</sup>	m <sup>mos</sup>	A	P	♂
EMS	S	B w <sup>+</sup>	B w <sup>+</sup>	f <sup>+</sup>	m <sup>+</sup>	A	A	♂
EMS	S	B w <sup>+</sup>	B w <sup>+</sup>	f <sup>+</sup>	m <sup>+</sup>	A	A	♂
X-ray	F*	B <sup>+</sup> w	B w <sup>+</sup>	f	m	P	P	♂
X-ray	F*	B <sup>+</sup> w	B <sup>+</sup> w	f <sup>+</sup>	m <sup>+</sup>	P	A	♂
X-ray	S	B w <sup>+</sup>	B w <sup>+</sup>	f <sup>+</sup>	m <sup>mos</sup>	P	A	♂
X-ray	S	B w <sup>+</sup>	B w <sup>+</sup>	f	m	P	P	♂
X-ray	F**	B <sup>+</sup> w	B <sup>+</sup> w	f <sup>+</sup>	m <sup>+</sup>	A	A	♀

\*=non-transmitted, only (w m f) progeny obtained

\*\*=non-transmitted, (y B) and (w m f) progeny obtained

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Takamura, T., H. Hayashi\*, A. Yokoyama\* and I. Shimada\*. Tokyo Metropolitan University and \*Tohoku University, Japan. *D. melanogaster* can taste amino acids.

Some progress has been made in the genetics of taste perception in *Drosophila* (Isono and Kikuchi 1974a; Falk and Atida 1975). Like other dipterans, the taste-bristle of *Drosophila* contains 4 chemosensory cells (Falk et al. 1976).

One of these is the sugar receptor which reacts specifically with certain sugars. In larger flies such as fleshfly and blowfly, Shiraish and Kuwabara (1970) showed 6 of 19 L-type amino acids could electrophysiologically stimulate the sugar receptor of these flies but there have been no data on *Drosophila*. In this report we show that *D. melanogaster* can also taste certain amino acids dissolved in pH-adjusted phosphate buffer.

A petri dish with 4 glass rings in it was employed for behavioral assay (Isono and Kikuchi 1974b). Two of the 4 rings were filled with  $5 \times 10^{-2}M$  amino acid dissolved in 1/15M phosphate buffer (pH 7.0), while the other 2 were filled with phosphate buffer only. Each solu-

tion contained 2% agar to set it in the ring. Six amino acids which can stimulate sugar receptor of larger flies were used (Shiraishi and Kuwabara 1970). About 100 *D. melanogaster*, 24-48 hours old, allowed to take only water for 24 hours before experiments, were introduced into the petri dish and the distribution of the flies on the rings was examined by photographing them 4 times at 30-minute intervals (for details see Isono and Kikuchi 1974b). Isogenic strain AA75-3 (Isono and Kikuchi 1974b) and wild-type laboratory stock derived from natural populations were used. The results are shown in Table 1.

Table 1. Response of *D. melanogaster* to six L-type amino acids presented at the concentration of  $t \times 10^{-2}M$ .

Amino acid	Strain	Sex	Number of flies observed on the amino acid	Number of flies observed on the phosphate buffer	$\chi^2$	P
L-Leucine	AA75-3	female	103	82	2.38	>0.1
		male	30	38	0.94	>0.7
L-Valine	AA75-3	female	139	45	48.02	<0.001
		male	93	61	6.65	<0.01
L-Methionine	AA75-3	female	276	138	46.00	<0.001
		male	116	79	7.02	<0.01
L-Phenylalanine	Wild	female	219	76	69.32	<0.001
		male	323	103	113.62	<0.001
L-Isoleucine	AA75-3	female	230	92	59.14	<0.001
		male	119	59	20.22	<0.001
L-Tryptophan	AA75-3	female	98	74	3.35	>0.05
		male	37	38	0.01	>0.9

*D. melanogaster* could discriminate L-valine, L-methionine, L-phenylalanine, and L-isoleucine from the buffer control but they did not seem to taste L-leucine and L-tryptophan at the concentration tested. Because  $5 \times 10^{-2}M$  is the concentration at which the magnitude of the electrophysiological responses of larger flies reached maximum and usually behavioral assay is more sensitive than electrophysiological assay, there must be a large difference in stimulating ability between the former four and the latter two amino acids. However, further study is necessary to conclude that *D. melanogaster* is not able to taste L-leucine and L-tryptophan at all. Shimada and Isono (1978) reported two of these six amino acids, L-phenylalanine and L-tryptophan, differed from the other four in such a manner that these two reacted with furanose site of the fleshfly. This classification, however, did not agree with our data here. It would be interesting to know the relationship of these six amino acids and the furanose site in *D. melanogaster* by electrophysiological technique.

Temin, R.G. and R. Kreber. University of Wisconsin, Madison, Wisconsin. A look at SD (Segregation Distorter) in the wild population in Madison, Wisconsin, more than 20 years after its initial discovery there.

Flies were collected in the fall, 1979, for a study of how SD behaves in nature and to understand the factors determining its frequency. With the recent work on hybrid dysgenesis in our laboratory (Engels 1979-1980) and with the more detailed understanding of the substructure of the SD region (Hartl and Hiraizumi 1976; Ganetsky 1977), it became of interest to see

what bearing these might have on the course of SD in wild populations.

There were two trapping sites in Madison, in woods near the homes of R.G. Temin and J.F. Crow. Since the observations, listed below, were similar in the two subpopulations, they have been combined:

1. SD is still present in Madison, in 20 chromosomes among 741 screened. This frequency of 3% is, in fact, the same as it was in 1956 (6/183) and must represent the equilibrium frequency. The average "k" value, representing the degree of distortion, was 0.95, from the

ratio of 1603 + : 86 cn bw progeny from individual test crosses of +/cn bw  $\sigma\sigma$ , where + is derived from a wild-caught male.

2. Cytological analysis revealed that 19 of the 20 SD chromosomes contained the small pericentric inversion In(2LR) 39E1.4-5.8; 42A-B, as well as the large distal Nova Scotia inversion in the right arm. This set of inversions is of the SD-72 type, as designated for the original SD's. The remaining one of the 20 was of the SD-5 type, namely with In(2R)NS and a small proximal inversion also in the right arm, In(2R)45D2-E1; 49 A2-B1, but lacking the pericentric inversion. As controls, 23 SD<sup>+</sup> lines had no second chromosome inversions and two SD<sup>+</sup> lines had In(2R)NS only. (Two of the SD lines from Crow's collection, in addition to being SD-72, had a highly complex set of second chromosome inversions; the more complex of these also showed a reduced k value of 0.66 on further testing.)

Thus, nearly all the SD chromosomes are now SD-72, in contrast to 1956, when five of the six were SD-5 and one was SD-72. This difference in relative frequencies of SD-5 and SD-72 in the two collections was significant at  $p = 0.0005$ , by Fisher's Exact Test. The chromosome with the pericentric inversion has become predominant, maintaining the tight linkage between the SD and Rsp alleles in that region.

Even before the pericentric inversion was discovered by Lewis in 1962, Hiraizumi, Sandler and Crow (1960) predicted, from population cage studies, that SD-72 might replace SD-5. Finding that SD-72 (which was lethal-free) maintained a higher equilibrium frequency than SD-5 (lethal bearing) in cages, they suggested that in nature SD-72 had just arisen as a derivative of SD-5 but had not yet in 1956 had time to replace it. Studies are underway to determine the homozygous viabilities of the newly collected SD's.

3. Male recombination was also detected in the SD screening test crosses of the F<sub>1</sub> +/cn bw dysgenic male, indicating that components of hybrid dysgenesis are present in these populations. Among 27,216 progeny of such heterozygous males, 82 were either cn or bw, a frequency of 0.3% recombinants. These occurred in SD lines as well as in SD<sup>+</sup> lines, in the same approximate frequency. Recombinant progeny from heterozygous fathers continued to appear even in the F<sub>4</sub>. In the SD lines the ratio of bw to cn recombinants (67:10 among 14,536 progeny) was significantly greater than in the non-SD lines (44:33, among 25,523), with  $p = 0.00003$ . This supports the notion that segregation distortion and hybrid dysgenesis can occur simultaneously.

It is interesting to speculate whether male recombination was occurring in the SD screening of the Madison population in 1956. The original isolation of SD by Hiraizumi during a study of lethal heterozygotes (1960) was from +/cn males which would not have revealed this. However, other tests in our laboratory in that era (Mange 1961; Greenberg 1962) to screen wild populations for SD did use +/cn bw dysgenic F<sub>1</sub> males, but recombinants were not reported. We do not know if they were too infrequent or were overlooked, or actually did not occur. However, this raises the question of whether the situation has changed since that time with regard to components of hybrid dysgenesis, either in the cn bw lab stock or in the wild flies themselves.

4. Previous studies have demonstrated suppressors of SD activity, on the X and on other autosomes, as well as on the second chromosome (non-allelic and at the Rsp locus itself). To estimate directly how active SD is in a wild genome, k values were measured for the 20 wild caught males revealed to be harboring SD. This was done by testing a number of F<sub>1</sub> sons (14-45) of each such line. If SD was fully operative in the P<sub>1</sub> male ( $k = 1$ ) then all of the F<sub>1</sub> sons would have inherited SD and themselves have a high k value. If SD was completely suppressed in the P<sub>1</sub> male ( $k = 1/2$ ) then about half of the F<sub>1</sub> sons would have a high k.

SD appeared to be fully active in only about 1/4 of the cases; in fact, there was a wide range of distortion in the wild males. Of the 20 lines, 8 showed no distortion in the P<sub>1</sub> male ( $k$  less than 0.57), 5 showed high distortion ( $k = 0.87$  or greater), 6 showed reduced distortion ( $k$  between 0.63 and 0.77), and one gave too few sons to test.

5. Another approach to the question of how much distortion occurs in nature was to screen SD<sup>+</sup> chromosomes from Madison for sensitivity vs. insensitivity. A strongly distorting SD-5 bw recombinant, provided by Dr. Barry Ganetsky, was used to test 122 non-SD chromosomes, as +/R(SD-5 bw), in the fourth generation after crossing to laboratory stocks, providing an opportunity for some of the unlinked modifiers to be crossed out. Of the 122, approximately 82 were sensitive to SD-5 action ( $k = 0.83$  or greater), 24 had reduced sensitivity ( $k$  between 0.61 and 0.80), and 16 appeared to be in the range of insensitivity ( $k$  less than 0.60). Thus, the maximum frequency of insensitive chromosomes is about 13%; to establish these as having true Rsp<sup>ins</sup> alleles would require further special tests. This figure is substantially lower than the 45% found by Hartl and Hartung (1971) in more specific and thorough testing. This variability among populations with regard to the non-SD chromosome bears further investigation.

References: Hartl, D.L. and Y. Hiraizumi 1976, in: The Genetics of Drosophila, 1, Novitski and Ashburner, eds.; Ganetsky, B. 1977, Genetics 86:321; Engels, W.R. and C.R. Preston 1980, Genetics 95:1 (in press); Hartl, D.L. and N. Hartung 1975, Evolution 29:512; Hartl, D.L. 1970, Can. J. Genet. Cytol. 12:594; Hiraizumi, Y. 1971, PNAS 68:268; Hiraizumi, Sandler and Crow 1960, Evolution 14:433.

Tobari, I. and M. Murata. National Institute of Radiological Sciences, Chiba-shi, Japan. Fertility load and frequency of lethal second chromosome in Drosophila populations with radiation histories.

It has in general been considered that most of the radiation-induced mutations are sooner or later eliminated from a population by the acts of natural selection of the irradiation is suspended. The purpose of this study is to see a recovery of genetic damages caused by the radiation-induced mutations by estimating the amounts of fertility load and the frequency of lethal second chromosomes in the populations with radiation histories. Experimental populations of *D. melanogaster* used in this study were identical with those reported by Murata and Tobari (1973). Three experimental populations, B, C and D, were derived from the irradiated population which had been successively exposed to 5,000r of X-rays in every generation (Tobari and Murata 1970). The populations B, C and D have been subjected to the cumulative radiation exposures of 25,000r, 50,000r and 75,000r, respectively. These populations were maintained for 75-77 generations without X-irradiation before the present experiment was carried out. The frequency of lethal second chromosomes was estimated by the Cy/Pm technique, using about 200 males taken from each of the experimental populations. To estimate the fertility load the homozygous and heterozygous flies for wild-type second chromosomes were reconstituted. For each of approximately 100 chromosomes, in homozygous as well as heterozygous condition, 10 males and 10 females were tested. Each wild-type male (or female) was mated individually to three *cn bw* virgin females (or males). After one week all cultures were examined for evidence of fertility. A vial was classified as sterile (S) if there were no larvae or pupae present and the parents were alive. Cultures bearing progeny were classified as fertile (F). In some of the cultures which contained no progeny, the parent of interest was dead; this type was recorded as D.

The frequency of lethal second chromosomes in a non-irradiated (control) population was estimated to be  $17.8 \pm 1.9\%$ , while it was  $30.7 \pm 3.7\%$ ,  $32.7 \pm 3.8\%$ , and  $32.5 \pm 3.4\%$ , respectively, in populations B, C and D. The difference in frequency between the control populations, A, and the experimental one is statistically significant.

The proportion of fertile cultures among the total fertile and sterile cultures was computed and these fertility ratios,  $F/(F+S)$ , for males and females are given in Table 1. In all

Table 1. The mean fertility ratios,  $F/(F+S)$ , in the irradiated and control populations.

Population		A: Control	B: 25KR-77G	C: 50KR-75G	D: 75KR-75G
<u>Males:</u>					
Heterozygotes	n	99	72	100	117
	$F/(F+S)$	$0.934 \pm 0.016$	$0.957 \pm 0.012$	$0.868 \pm 0.021$	$0.881 \pm 0.023$
Homozygotes	n	101	99	102	105
	$F/(F+S)$	$0.866 \pm 0.020$	$0.892 \pm 0.025$	$0.789 \pm 0.032$	$0.748 \pm 0.031$
Homozygotes excluding complete steriles	n	99	97	94	95
	$F/(F+S)$	$0.884 \pm 0.016$	$0.916 \pm 0.019$	$0.856 \pm 0.023$	$0.856 \pm 0.024$
<u>Females:</u>					
Heterozygotes	n	105	97	101	120
	$F/(F+S)$	$0.969 \pm 0.008$	$0.969 \pm 0.008$	$0.941 \pm 0.011$	$0.961 \pm 0.007$
Homozygotes	n	104	99	100	100
	$F/(F+S)$	$0.909 \pm 0.019$	$0.871 \pm 0.028$	$0.842 \pm 0.026$	$0.817 \pm 0.030$
Homozygotes excluding complete steriles	n	102	95	94	93
	$F/(F+S)$	$0.926 \pm 0.014$	$0.907 \pm 0.022$	$0.896 \pm 0.015$	$0.896 \pm 0.021$

F = fertile, S = sterile, n = number of chromosomes tested



Table 2. Total sterility load (T), partial sterility load (P) and complete sterility load (C) in the irradiated and control populations.

Population	T	P	C	P:C
<u>Males:</u>				
A: Control	0.0755±0.0288	0.0550±0.0250	0.0205±0.0295	2.7
B: 25KR-77G	0.0703±0.0320	0.0438±0.0253	0.0266±0.0352	1.6
C: 50KR-75G	0.0954±0.0465	0.0139±0.0361	0.0815±0.0487	0.2
D: 75KR-75G	0.1636±0.0493	0.0288±0.0282	0.1348±0.0520	0.2
<u>Females:</u>				
A: Control	0.0640±0.0108	0.0454±0.0177	0.0186±0.0168	2.4
B: 25KR-77G	0.1066±0.0332	0.0661±0.0256	0.0504±0.0405	1.6
C: 50KR-75G	0.1112±0.0326	0.0489±0.0205	0.0623±0.0349	0.8
D: 75KR-75G	0.1623±0.0355	0.0700±0.0234	0.0923±0.0437	0.8

the populations the fertility rates are higher for heterozygotes than for homozygotes. Furthermore, in populations C and D, which had been exposed to 50,000r and 75,000r of X-rays respectively, the fertility of both the homozygotes and the heterozygotes is lower than that in the control population. The loads have been computed from the mean fertility ratios by the same method as Temin's (1966). As seen in Table 2, the total load for males and females markedly increases as an accumulated dose of X-rays increases. In populations A and B most of the total load for males and females is due to mutant genes leading to partial sterility. On the other hand, in populations C and D the total load for males is mainly due to mutant genes causing complete sterility and for females the ratio of P:C is approximately 1:1.

The results described above indicate that some of the radiation-induced mutant genes with detrimental effects on viability or fertility are maintained for a number of generations in the populations with radiation histories, although these detrimental genes may partly be eliminated by natural selection in early generations after the irradiation is suspended.

References: Temin, R.G. 1966, *Genetics* 53:27-46; Tobari, I. and M. Murata 1970, *Genetics* 65:107-119; Murata, M. and I. Tobari 1973, *Jap. S. Genet.* 48:349-359.

Traut, H. Institut für Strahlenbiologie, Universität Münster, Münster, Germany. An approximate  $\chi^2$  test as applied to mutation experiments with *D. melanogaster*.

The rapidly increasing interest in the development of methods for the detection of environmental mutagens has been accompanied by an interest in the statistical procedures to be employed by mutation researchers (see e.g., Armitage 1971; Berchtold 1975; Kastenbaum and Bowman

1970; Katz 1978, 1979; Traut, in press; Würigler et al. 1975). One of those procedures is the chi-square ( $\chi^2$ ) test. The following approximation to that test facilitates the computation of  $\chi^2$  considerably and yields nevertheless  $P$  values almost identical with those calculated in the usual way. (Note that by the help of Patau's (1942) graphs the  $P$  values belonging to the calculated  $\chi^2$  values can be obtained.) Although this approximation has already been described (Armitage 1971), it is, as far as I know, not employed to test the significance of the difference between mutation frequencies. The approximate procedure should be applied to low relative frequencies only, amounting to at most a few percent. This requirement, however, is generally complied with in mutation experiments carried out with *D. melanogaster* (main types of mutations studied: recessive sex-linked lethals, autosomal translocations and X-chromosomal aneuploidy). It is true that there are cases allowing the applicaiton of the following approximate formula also to high mutation frequencies (Traut, unpublished). However, it would be difficult to consider this possibility in practice and it seems, therefore, wise to use the approximate formula only when the mutation frequencies are small. As well formulae (1) to (4) presented below as the two examples illustrating the performance of the approximate test consider Yates' correction for continuity.

The following  $\chi^2$  formula is usually applied to test the significance between two mutation frequencies  $x_1/n_1$  and  $x_2/n_2$  ( $x$  = number of mutated units, e.g., cells, chromosomes, loci; and  $n$  = number of units analyzed), where  $x_1(x_2)$  = number of mutated units and  $y_1(y_2)$  = number of non-mutated units of experiment 1 (experiment 2), and  $N = x_1 + y_1 + x_2 + y_2$ . For low mutation frequencies (see above), formula (1)

$$(1) \chi^2 = \frac{([x_1 y_2 - x_2 y_1] - 0.5 N)^2 N}{(x_1 + x_2)(y_1 + y_2)(x_1 + y_1)(x_2 + y_2)}$$



$$(2) \chi^2 \approx \frac{([x_1 - x_1'] - 0.5)^2}{x_1'} + \frac{([x_2 - x_2'] - 0.5)^2}{x_2'}$$

expected absolute frequencies belonging to  $x_1$  and  $x_2$ , respectively. This approximation can be derived as follows. When the formula for  $\chi^2$  is expressed in its extended version instead of by formula (1), we obtain:

$$(3) \chi^2 = \frac{([x_1 - x_1'] - 0.5)^2}{x_1'} + \frac{([x_2 - x_2'] - 0.5)^2}{x_2'} + \frac{([y_1 - y_1'] - 0.5)^2}{y_1'} + \frac{([y_2 - y_2'] - 0.5)^2}{y_2'}$$

where  $y_1'$  and  $y_2'$  are the expected absolute frequencies belonging to  $y_1$  and  $y_2$ , respectively. For low mutation frequencies the contribution to  $\chi^2$  from the non-mutated units,  $y_1$  and  $y_2$ , is so small when compared with the contribution from the mutated units,  $x_1$  and  $x_2$ , that it can be neglected. It is this omission which transforms formula (3) to formula (2). In addition, the numerical computation carried out with formula (2) is facilitated by the fact that in formula (2),  $([x_1 - x_1'] - 0.5)^2 = ([x_2 - x_2'] - 0.5)^2$ , as can be shown by a simple consideration. Furthermore, when formula (2) but not when formula (1) is used, one automatically learns whether there is an expected absolute frequency ( $x$ ) smaller than 5, and, therefore, whether the application of the  $\chi^2$  test is legitimate. Formula (2) could be expressed also in other ways; however, the numerical computations are carried out best when this formula is used as it stands.

Example illustrating the application of formula (2):

- $x_1/n_1 = 100/1000 = 10.0\%$  (experiment 1)
- $x_2/n_2 = 40/50 = 8.0\%$  (experiment 2)
- (a)  $x_1' = 1000([100 + 40]/1500) = 93.3$
- (b)  $x_2' = 100 + 40 - 93.3 = 46.7$
- (c)  $([x_1 - x_1'] - 0.5)^2 = ([x_2 - x_2'] - 0.5)^2 = 6.2 = 38.4$
- (d)  $\chi^2 \approx 1.24$  [The exact value, computed with formula (1) or (3), amounts to  $\chi^2 = 1.36$ .]

When the two frequencies to be compared with each other (e.g., one belonging to the treated, the other belonging to the control sample) are based on equal (or almost equal) sample sizes ( $n_1 = n_2$ ), formula (2) can be simplified, because in this formula both  $x_1'$  and  $x_2'$  can now be substituted for  $\frac{1}{2}(x_1 + x_2)$ . We then obtain formula

$$(4) \chi^2 \approx \frac{([x_1 - x_2] - 1)^2}{x_1 + x_2}$$

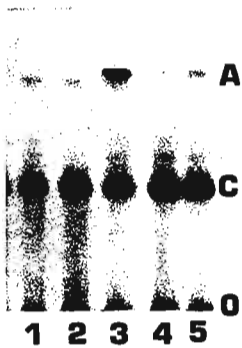
Example illustrating the application of formula (4):

- $x_1/n_1 = 30/5000 = 0.600\%$  (treated sample)
- $x_2/n_2 = 5/5000 = 0.100\%$  (control sample)
- $\chi^2 \approx ([30 - 5] - 1)^2 / (30 + 5) = 16.46$  (The exact value, computed with formula (1) or (3), amounts to  $\chi^2 = 16.52$ .)

References: Armitage, P. 1971, *Statistical Methods in Medical Research*, Blackwell Scientific Publ., Oxford, London, Edinburgh, Melbourne, pp. 138-140; Berchtold, W. 1975, *Arch. f. Genetik* 48:151-157; Kastenbaum, M.A. and K.O. Bowman 1970, *Mutation Res.* 9:527-549; Katz, A.J. 1978, *Mutation Res.* 50:301-307; \_\_\_\_\_ 1979, *Mutation Res.* 64:61-77; Patau, K. 1942, *Zeitschr. Abst. Vererb. lehre* 80:558-564; Traut, H. (in press), *Biometrical Journ.*; Würzler, F.E., U. Graf and W. Berchtold 1975, *Arch. f. Genetik* 48:158-178.

Triantaphyllidis, C.D. Aristotelian University of Thessaloniki, Greece. The esterase-A of *D. auraria*.

In three laboratory strains of *D. auraria*, an enzyme polymorphism of esterase A (Est-A) could be detected by means of starch gel electrophoresis. There exist two variants of Est-A with different electrophoretic mobility, which were called Fast and Slow (Fig. 1). To analyze the genetic basis of these electrophoretic variants, homozygous stocks for each of them were constructed. Then single-pair matings in many combinations were performed. The hybrids resulting from these crosses as well as the progenies resulting from the backcrosses and from  $F_1 \times F_1$  crosses were analyzed electrophoretically. The results showed that the two esterase A variants were controlled by codominant alleles at an autosomal gene. Heterozygous individuals show two electrophoretic zones, and there is no indication for the formation of a hybrid enzyme. As far as substrate specificity is concerned the two Est-A variants showed an  $\alpha$ -naphthyl acetate specificity in an  $\alpha$ - $\beta$  mixture. Furthermore the Est-A zones show increased activity in the presence of 10 ml n-propanol in 100 ml



$\alpha$ - $\beta$ -naphthyl acetate staining mixture. Also it is interesting that the Est-A zones have greater activity in the females than in the males (Fig. 1, no. 3).

Acknowledgements: I would like to thank Mr. A. Svinios for his technical assistance.

Fig. 1. Electrophoretic variants for the Est-A locus in *D. auraria*. 1-2: Est-A<sup>S</sup>. 3-5: Est-A<sup>F</sup>. 0 = origin, C = Est-C, A = Est-A.

Triantaphyllidis, C.D. Aristotelian University of Thessaloniki, Greece. Genetic localization of Est-C, Acph and w genes of *D. auraria*.

It has been established earlier that the esterase-C (Est-C) and acid phosphatase (Acph) variants of *D. auraria* are under the control of autosomal loci (Triantaphyllidis and Kastritsis 1976; Triantaphyllidis 1978). These two genes as well as the white eyes gene are unplaced on the chromosomes of *D. auraria*. For this reason crosses were made for their chromosomal localization. The results of crosses ♀ w x +w ♂ and ♀ +w x w ♂ showed that the w allele is recessive and sex-linked. On the other hand, in order to find if the Est-C and Acph loci are independent or linked, homozygous females of the form Est-C<sup>S</sup> Acph<sup>3-5</sup> were crossed with homozygous males of the form Est-C<sup>F</sup> Acph<sup>1-3</sup>. Then heterozygous males or females Est-C<sup>S</sup> Acph<sup>3-5</sup>/Est-C<sup>F</sup> Acph<sup>1-3</sup> were backcrossed to Est-C<sup>S</sup> Acph<sup>3-5</sup> females or males respectively. In the progenies of the first backcross only flies of the phenotypes Est-C<sup>S</sup> Acph<sup>3-5</sup> and Est-C<sup>F</sup> Acph<sup>1-3</sup> were found. Thus, the Est-C and Acph loci are linked in the same autosomal chromosome. In the progeny of the second reciprocal backcross 101 out of 254 offspring were recombinants (39.8%). Hence, the Est-C locus is about 40 map units away from the Acph locus. The existence of similar gene-enzyme systems in *D. melanogaster* (O'Brien and MacIntyre 1971) located in the third chromosome (positions 49.0 and 101.1 respectively) is a good indication that the Est-C and Acph loci are probably located in the same chromosome in *D. auraria* and the genes retained their ancestral position during the phylogeny of the two species. The difference between the two species with respect to the relative distances between the similar genes may depend on many factors. Work is now in progress in order to map the position of the cistron which codes for other gene-enzyme systems in *D. auraria*.

Acknowledgements: I would like to thank Mr. A. Svinios for his technical assistance.

References: O'Brien, S. and R.I. MacIntyre 1971, DIS 46:89-93; Triantaphyllidis, C.D. 1978, DIS 53:118; Triantaphyllidis, C.D. and C. Kastritsis 1976, *Experientia* 32:1277-1278.

Tribe, J. and I.R. Bock. La Trobe University, Melbourne, Australia. *Drosophila* collections in southeastern Australia.

Collections were made during December 1979 at several wineries and orchard areas in inland southeastern Australia. The localities sampled are shown in Fig. 1; the numbers represent

Mourquong orchard (1), flies swept over fresh fruit; Mildura winery (2), flies collected on old filters outside the winery; Mildara winery (3); Ettiwanda fruit juice factory (4), flies swept from orange skins; Sarnia fruit juice factory (5), flies swept from mixed fruit skins; Lake Boga winery (6); Best's winery (7); and Bridgewater winery (8). Flies collected at localities 3, 6, 7 and 8 were aspirated directly from fermentation vats. Ambient maximum temperatures on all collection days exceeded 30°C.

Results are given in Table 1. Only cosmopolitan species were found, and indeed only two of the eight cosmopolitan *Drosophila* species (*anassae* and *repleta*) were not collected. *D. anassae* occurs in Australia but is restricted to the Northern Territory and northern Queensland, while *D. repleta*, although known from southern localities, is very rare. The large numbers of *melanogaster* collected in the wineries are not surprising; the ability of this species to utilize ethanol is well known and widely documented.



Fig. 1. *Drosophila* collection areas in southeastern Australia.

Table 1. *Drosophila* collections in southeastern Australia. Species numbers are given as males, females.

Locality	<i>melanogaster</i>	<i>simulans</i>	<i>busckii</i>	<i>immigrans</i>	<i>hydei</i>	<i>funnebris</i>
1	4, 2				70, 3	
2	0, 2				6, 3	
3	65, 65				48, 21	
4	31, 76	3, 1			44, 52	
5	36, 21			0, 1	15, 26	
6	15, 27		1, 0	0, 1	8, 2	
7	7, 2					
8	67, 48			1, 0		2, 0

Perhaps of greater interest is the collection of large numbers of *hydei* in one of the wineries (3) as well as at several other sites. *D. funnebris* has previously only been recorded within Australia from Sydney.

Acknowledgments: The assistance of Ms. Lesley Anderson and the wine and fruit producers at the localities sampled is gratefully acknowledged.

Tripathy, N.K., D.P. Dasmohapatra and C.C. Das. Berhampur University, Orissa, India. Chromosomal polymorphism in *D. ananassae*.

Abundant evidence now exists to prove that differential gene arrangements have evolved in many species of *Drosophila* to meet the adaptive needs in a dynamic environment. Inasmuch as

Table 1. Inversion frequencies.

Type of inversion	Jan.	Feb.	Mar.	Apr.	May	Percentage
3LA	35	30	27	23	34	29.8
3RA	3	2	2	2	5	2.8
2LA	4	7	11	10	11	8.6
XLA	1	-	-	-	-	0.2

the adaptive values of different genomes differ considerably, the fitness of certain kinds of gene arrangements may, therefore, increase or decrease with fluctuation in environmental milieu. *D. ananassae*, a cosmopolitan domestic species, is known to exhibit nearly 50 different inversions in different natural populations. Of the several paracentric inversions, 3LA, 3RA and 2LA are common to all populations while the rest of the inversions are selectively restricted to these populations. From their studies on *D. willis-toni*, da Cunha et al. (1950) postulate a close correlation of chromosomal polymorphism with environmental conditions. In an attempt to assess the correlation, if any, between the different inversions and the environmental temperature, the present study has been undertaken on the natural population of *D. ananassae* of Gola-bandha, situated at an altitude of 17.5 m and about 6 km to the south of the university campus, during the months of January

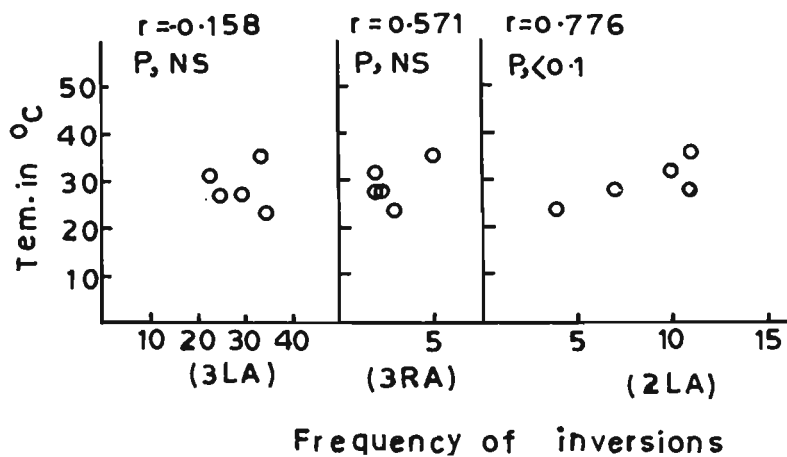


Fig. 1. Correlation between frequency of inversions (3LA, 3RA and 2LA) and environmental temperature in °C.

through May, 1980. The temperature during these months was recorded as 24°C in January, 28°C in February and March, 32°C in April and 36°C in May.

Collections were made in the first week of every month and the naturally inseminated gravid females were isolated. Individual flies were transferred to independent vials with wheat cream agar medium. 100 larvae were used in studying the inversions every month. Table 1 lists the inversion frequency data during the different months of study.

The correlation graphs of the frequency of inversions, coextensive with the species, and the temperature fluctuation during these months are represented in Fig. 1. As can be seen there is no significant correlation between the frequency of these inversions and the environmental temperature in the investigated population of *D. ananassae*.

Reference: da Cunha, A.B., H. Burla and Th. Dobzhansky 1950, *Evolution* 4:212.

Trippa, G., A. Loverre and M. Lepore. Università di Roma, Italy. Segregation distortion of second chromosomes by a wild third chromosome in *D. melanogaster*: modifier or Sd gene?

Samples of wild populations of *D. melanogaster* from southern Italy have shown a frequency of 1 to 10% of second SD chromosomes (Trippa et al. 1972) and about 70% of third chromosomes carrying a dominant Sd modifier (Trippa and Loverre 1975). The characterization of Italian natural populations as regards frequency of

meiotic drive systems utilizes a cross scheme which makes it possible to follow the segregation of both second and third chromosomes. F<sub>1</sub> +/bw-5; +/-st-5 males from the cross between wild males and y; bw-5; st-5 females are backcrossed with y; bw-5; st-5 females to permit a first count of k<sub>1</sub> and k<sub>2</sub> at F<sub>2</sub> (k<sub>1</sub> for segregation of second chromosome = bw<sup>+</sup> individuals/

total progeny;  $k_2$  for segregation of third chromosomes =  $st^+$  individuals/total progeny). A further count of  $k_1$  and  $k_2$  in the progeny of  $F_2$  males makes it possible to evaluate the degree of distorted segregation of chromosomes 2 and 3 and their reciprocal effects on segregation.

A study on two wild populations collected in October 1978 in northern Italy (Mareno, Veneto) and in southern Italy (Nardò, Puglia) has led to the recovery of a third chromosome,  $III^{Nr}$  ( $III^{Nardò}$ ) which alters the segregation of second chromosomes (Table 1). This chromosome normally segregates in  $III^{Nr}/st$  heterozygous males ( $n = 41$ ;  $k = 0.53$ ). As things stand at present, two general hypotheses can be put forth to interpret the results obtained: (1)

Table 1. Effect of the  $III^{Nr}$  chromosome on the segregation of second chromosomes.

Cross	$\sigma \frac{+}{bw-5} \frac{st-5}{st-5} \times \text{♀ } bw-5; st-5$			$\sigma \frac{+}{bw-5} \frac{+}{st-5} \times \text{♀ } bw-5; st-5$		
	n	tot. prog.	$k \pm S.E.$	n	tot. prog.	$k \pm S.E.$
#13	13	1100	$0.51 \pm 0.06$	41	3885	$0.96 \pm 0.05$

there may be an Sd-like factor acting like other Sd factors so far detected on the second chromosome but located on the third chromosome; (2) there may be on chromosome 3 an Sd modifier (enhancer?) acting on the  $II^+$  Nardò chromosome (which is actually an SD chromosome, despite the fact that in the  $+/bw-5; st-5/st-5$  heterozygous males  $k = 0.51$ ) thus causing segregation distortion of second chromosomes. The frequency of genotypes with the SD trait which is a consequence of the interaction of wild chromosomes II and III is in the Mareno population 0.00% (0/137 chromosomes) and in the Nardò population about 0.03% (3/108 chromosomes). In the Nardò population, besides #13, there are two examples of SD with  $k$  value equal to 0.67 in  $+/bw-5; st-5/st-5$  males and 1.00 in  $+/bw-5; +/st-5$  males. These data indicate that there is a significant difference ( $P \gg 0.001$ ) in the  $k$  values of the two genotypes and that this difference depends on the presence of wild third chromosomes which enhance distortion by the wild second chromosome.

It is interesting to note that while the Nardò (South Italy) population shows an SD frequency of about 3% (a very similar value to those observed in wild populations from many parts of the world), the Mareno population (North Italy) shows no cases of SD. This is the second example of a wild population with no cases of SD, after that extensively examined in Austin, Texas (see Hartle and Hiraizumi 1976). If it is true that one of the mechanisms contrasting the spread of SD in populations is the appearance and increase of normal chromosomes resistant to Sd, it would be particularly stimulating to test the degree of sensitivity to distortion by Sd of the second chromosomes of these two populations.

References: Hartl and Hiraizumi 1976, in: Genetics and Biology of Drosophila (Ashburner and Novitski, eds.) vol. 1b; Trippa et al. 1972, DIS 49:81; Trippa and Loverre 1975, Genet. Res. 26:113.

Tsakas, S.C. Agricultural College of Athens, Athens, Greece. Chromosomal breaks and alteration in staining observed in vitro after ultrasonication of salivary glands of *D. subobscura* species.

It is known that many chemical agents and physical factors produce chromosomal breaks and aberrations. The purpose of this work was to discover if ultrasonics also have an effect of this kind in vitro.

Salivary glands of the "Küsnacht" strain, first pupal stage, were used. This strain has a standard/standard chromosomal structure for the five long chromosomes, X, O, U, E, and J. Tap water was used as dissecting solution; its chemical analysis is as follows: pH = 7.2;  $SO_4^{--} = 30$  mg/l;  $NO_3^- = 2$  mg/l;  $Cl^- = 34$  mg/l;  $HCO_3^- = 150$  mg/l;  $Ca^{++} = 60.1$  mg/l;  $Fe^{++} = 0.2$  mg/l;  $Mg^{++} = 29.4$  mg/l;  $Cl_2$  free = 0; hardness:  $CaCO_3 = 150$  mg/l, the remaining = 32 mg/l; total = 182 mg/l. The staining solution was composed of 2 g of synthetic orcein (Edward Gurr, Ltd., London) dissolved into 50 ml hot glacial acetic acid, plus 50 ml of 85% lactic acid after removing from heat (Strickberger 1962).

Immediately after dissection of eight pairs of salivary glands, four of these pairs were placed on one slide and four on another. Each slide contained one drop of dissecting solution. One slide was kept as a control and the other was placed under the sonicator's microphone. A TECH Ultrasonicator (company, Japan) was used, with a crystallic twiter microphone.

Conditions were: (a) distance between the slide and the microphone, 6.0 cm; (b) sine waves; (c) frequency, 40,000 cps, first harmonic waves at 120,000 cps; (d) power,  $N = 0.3$  watts; (3) time, 30 min; (f) temperature, 19°C.

After sonication each pair of salivary glands was placed on a slide containing a drop of staining solution. So, there were four slides produced from the control slide and four from the treated. After a 10 min. interval for staining, a cover slip was placed without applying pressure on top of each slide. The first observation then took place using a magnification of 100X. After this, the cover slide was pressed slightly until the point enabling magnification of 700X and another observation was made.

The above procedure was performed six times, so the total number of slides observed was 24 control and 24 treated. In every slide of treated glands a significant number of chromosomal breaks appeared as well as a significant alteration in the effectiveness of staining by orcein, whereas the control slides showed chromosomes without breaks and clear and sharp staining. Figs. 1 and 2 are presented as an example of these findings. The only difference between the two figures is that ultrasonication was applied to the glands in Fig. 2; all other conditions from dissection through the development of the photograph were the same.



Fig. 1. Partial view of a control slide of salivary chromosomes of *D. subobscura* (1000X).



Fig. 2. Partial view of a treated slide (ultrasonication) of salivary chromosomes of *D. subobscura* (1000X).

Since ultrasonication is used to break the bodies of cells such as chloroplasts, it was probable that it also would produce chromosomal breaks in salivary chromosomes *in vitro*. This work gave evidence that this does occur. The unexpected finding was the alteration of staining after ultrasonication with the white bands taking on some color and the dark bands appearing more faint. This resulted in such a difference in the appearance of the chromosome as to render it virtually unidentifiable. If staining is the result of chemical reactions between orcein and chromosomal DNA, then after ultrasonication these reactions take place in

in a different way from the usual. One possible explanation for this could be that ultrasonication alters the chemical and/or physical properties of the chromosomal DNA structure or composition.

Although this work took place in vitro and salivary glands were used, these findings require further attention because ultrasonics are utilized in research and applied science such as obstetrical medicine.

Reference: Strickberger, M.W. 1962, in: Experiments in Genetics with *Drosophila*, ch. 18, p. 103, John Wiley & Sons, Inc., New York-London.

Turner, M.E. University of Georgia, Athens, Georgia. A laboratory overwintering experiment with *D. montana* and *D. pseudoobscura*.

*Drosophila* which live at high elevations are subject to low temperature extremes during the winter months. At elevations 7000 ft. and above low temperatures and/or snow cover may last six months or longer. For these populations of *Drosophila* to persist either some

stage (or stages) of the life cycle must overwinter or a new population must be founded each spring from lower elevation populations of the same species. *D. montana* and *D. pseudoobscura* were tested to determine their ability to endure cold temperatures for an extended period of time. *D. montana* were obtained from the University of Texas Stock Center (#1218.8d); this strain was originally captured from Ogden, Utah and has been in the laboratory since 1941. The *D. pseudoobscura* were collected from American Fork Canyon, Utah (elev. 7550) in 1976.

Flies were kept in half-pint milk bottles containing cornmeal-molasses medium. Approximately 50 adults were put in a bottle and allowed to reproduce at 15°C; when pupae appeared the bottles including the parents were put in an incubator at -2°C.

After eight days all *D. pseudoobscura* adults were dead. These bottles were moved to 15°C and no progeny from the original adults appeared; apparently the cold temperature had also killed eggs, larvae and pupae. *D. pseudoobscura* can be kept at 5°C for long periods of time with larvae, pupae and adults surviving.

After six months (184 days) the montana bottles (adults still alive) were removed from the incubator, adults were separated by sex and put in new bottles at 15°C. No flies had hatched from the original bottles after one month at 15°C and no living larvae were observed. The other life stages (eggs, larvae, and pupae) had been killed by the cold temperature. Additionally no larvae appeared in the bottles containing surviving females after one month at 15°C. The sexes were combined in a new bottle and larvae, and eventually adult progeny, appeared. The time at the cold temperature had despoiled the "overwintering" females, but had not, at least grossly, affected their fertility.

The ability of montana adults to survive this temperature (-2°C) for an extended period of time (6 months) would seem to imply that adults can and probably do overwinter. The death of the pseudoobscura individuals does not demonstrate that they do not overwinter, but only that they may overwinter where temperatures do not get this cold. In many forest environments at or above 7000 ft. elevation both montana and pseudoobscura live in the same area and are attracted to the same banana baits. The greater cold temperature tolerance of montana adults should allow them to survive in the more exposed and colder areas of this environment.

Valente, V.L.S., C.C.R. Saavedra, A.M. de Araújo and N.B. Morales. Universidade Federal do Rio Grande do Sul, Porto Alegre, R.S., Brasil. Observations on the attraction of *Drosophila* species for different baits and chromosomal polymorphism in *D. willistoni*.

Present data were obtained in three days of collection from October to November 1978, in the locality of Estação Experimental Agrônômica de Guaíba, Guaíba County, 40 km from Porto Alegre, the capital of the State of Rio Grande do Sul, Brasil. The studied place is a brushwood enclosed in a capon, with some watersheds. Five fermented banana baits were used besides natural available baits: fer-

mented fruits fallen around the original plant, the native palm-tree *Arecastrum romanzoffianum* (Palmae), which fruit is commonly called "coquinho".

The collection methods were: (1) capture of adults with nets over the two types of baits; (2) collection of two samples of 100 fruits individually placed in tubes with cultural medium in a controlled temperature chamber at  $25^{\circ}\text{C} \pm 1^{\circ}\text{C}$  for 15 days until metamorphosis of the pre-adult forms from nature was completed. In each of these samples, only 19 and 15% of the fruits were not colonized by *Drosophila* species.

Table 1. Numbers and percentage of *Drosophila* species from Guaíba.

Species	Collection method							
	Net (flying adults)				Rotting fruits (pre-adults)			
	Banana		"Coquinho"		"Coquinho"		Total	
N	%	N	%	N	%	N	%	
<i>D. willistoni</i>	51	8.02	574	21.87	169	14.54	794	17.95
<i>D. simulans</i>	477	75.00	1515	57.71	622	53.53	2614	59.10
<i>D. griseolineata</i>	17	2.67	226	8.61	-	-	243	5.49
<i>D. guaranunu</i>	14	2.20	88	3.35	-	-	102	2.31
<i>D. polymorpha</i>	34	5.35	108	4.11	8	0.69	150	3.39
repleta group	6	0.94	60	2.29	354	30.46	420	9.50
Others*	37	5.82	54	2.06	9	1.42	100	2.26
Total	636		2625		1162		4423	

\*These numbers are relative to species whose frequencies were less than 1% individually as: *D. cardinoides*, *D. bandeirantorum*, *D. immigrans*, *D. nebulosa* and *D. fumipennis*.

illustrates clearly the difference between oviposition site and the feeding sites of adults.

In order to test the homogeneity of the species distribution of flying adults, two types of baits - banana and "coquinho" - a chi-square test was made. The differences between the two samples were highly significant, with a value of  $\chi^2 = 110.88$  ( $P < 0.001$ ); this was due mainly to the different attractivity exerted by the two types of baits on *D. willistoni*, *D. simulans* and *D. griseolineata*, as far as food source is concerned.

Differences between fauna eclosed from "coquinho" and that captured with nets on the same trophic resource were compared by using the Kolmogorov-Smirnov test since there were null classes in the sample eclosed from "coquinho".

The maximum deviation between these two samples reached a value of 0.2837 which is highly significant ( $P < 0.001$ ). This result points out that not all the females attracted by the fermentation of "coquinho" actually oviposit in the fruits, which can probably be attributed to genetic differences. Another explanation for this situation would be the occurrence of high selective pressures at the larval phase, the exploration of food resource being one of

the more effective. Nevertheless we believe we attenuated the conditions for food competition by putting each fruit individually in a tube with culture medium and dilute bread yeast.

As was previously stated, *D. willistoni* is one of the most abundant species and also presents differences concerning attraction for the different baits. That is why it has been chosen

Table 2. Statistical significance of the differences in chromosomal rearrangements of *D. willistoni* among samples collected in banana baits, and those attracted and eclosed from *Arecastrum romanzoffianum* fruits ("coquinho").

Samples	II L rearrangements		III rearrangements	
	single	complex	single	complex
	P	P	P	P
banana x "coquinho" (collected with nets)	N.S.	<0.05	N.S.	N.S.
"coquinho" x "coquinho" (eclosed from rotting fruits and attracted from the same fruit)	N.S.	N.S.	N.S.	<0.01

P = probability; N.S. = not significant



for the evaluation of genotypical differences through the chromosomal polymorphisms, as had already been described by Dobzhansky (1950), da Cunha (1957), Cordeiro (1954) and others.

The progeny of each female captured in nature was analyzed in relation to the larval salivary gland chromosomal rearrangements, by the technique of Ashburner (1967); the same was applied to the progeny of females eclosed from "coquinho" fruits fecundated by males eclosed from the same fruit.

The analysis of 363 individuals showed that of the five chromosome arms, X L, X R and II R were homozygous. As for the left arm of the second chromosome (II L), the Kolmogorov-Smirnov test showed that the differences between the  $F_1$  of females collected from banana and "coquinho" baits were significant ( $P < 0.05$ ) for combined rearrangements (two to four inversions together). For the third chromosome (III) there were significant differences between the offspring of females captured with nets over the fruits of *Arecastrum romanzoffianum* and the offspring of females eclosed from these fruits in the laboratory, when combined rearrangements were considered (two to three inversions).

The results of the statistical test to the chromosomal rearrangements are summarized in Table 2. The total number of rearrangements observed for II L chromosome was 17, 6 of which were single rearrangements (only one inversion) plus the homozygous; 11 were combined rearrangements (two to four inversions together), with a frequency different from those of each inversion separately, although most of these inversions being located far enough in the chromosome as to permit the occurrence of crossing over between them.

Four single rearrangements were found for the third chromosome, including the homozygous, as well as four complex rearrangements, representing two and three inversions. Among the combined rearrangements of II L, for example, whereas D, E, B/d, e, b reached a frequency of 54.1% in banana baits, it was not found in larvae of females eclosed in "coquinho" and attained 45.8% in larvae from females attracted by the fruit; F, D, E, B/f, d, e, b reached 77% in banana baits, 22% in the natural one as was not found in larvae of females eclosed from the native fruit.

Among the third chromosome complex rearrangements, J, B/j, b was 22.3% in larvae from females attracted by banana, 2.12% in larvae from flies eclosed from "coquinho" and 75.5% in larvae attracted by this same fruit; the B, C/b, c rearrangement reached 0%, 41.6% and 58.3%, respectively, in the offspring of the same samples and the J, B, C/j, b, c rearrangement was exclusive of larvae from flies eclosed from "coquinho" fruits. This indicates a clear association of certain types of rearrangements with the kind of explored trophic resource.

References: Ashburner, M. 1967, *Chromosoma* (Berl.) 21:289-428; Cordeiro, A.R. 1954, *Bol. Instituto de Ciências Naturais* 1:5-54; da Cunha, A.B. 1957, *Bol. Fac. Fil. Ciên. e Letr. Univ. São Paulo* #220, *Biologia Geral* 10:1-56; Dobzhansky, Th. 1950, *J. Heredity* 41:156-158.

van Delden, W. and A. Kamping. University of Groningen, The Netherlands. Selection against an Adh null allele.

Several null mutants of the alcohol dehydrogenase (Adh) locus in *D. melanogaster* are known. Homozygotes for these mutants, which lack detectable ADH activity, can be maintained as laboratory strains without culture

problems when kept on regular food. On ethanol-supplemented medium, however, they lack detoxification ability and die quickly compared to ADH-positive flies. As we have found (van Delden et al. 1978) that selection occurs also on regular food in populations polymorphic for the naturally occurring Fast (F) and Slow (S) alleles we studied whether in populations polymorphic for a null mutant and either F or S alleles, selection would occur against the null allele. For this purpose the Adh<sup>nl</sup> (0) mutant (Grell et al. 1968) was introduced into the background of the Groningen population, whereafter 0 x S and 0 x F crosses were made with S and F strains possessing the same background. The offspring of these crosses ( $F_1$ ) were put in population cages at 25°C. The populations were continued in time and allele frequencies were determined at intervals beginning with the  $F_2$  generation. Populations were started both on regular and ethanol-supplemented food. Table 1 lists the observed null allele frequencies, populations indicated as S0 and F0 are polymorphic for the null allele and S and F alleles respectively. To study the importance of strain effects, five S0 and five F0 populations were started, both on regular and ethanol-supplemented food. Populations numbered up to four inclusive each contained two S or F lines which differed from the lines used in the other three populations; populations numbered five contained all eight lines S or F lines used in the other four populations of the same type.

Table 1. Frequencies of null-alleles in the course of time (initial frequency: 0.50).

Populations	Regular food					Ethanol-supplemented food				
	F <sub>2</sub>	Time (weeks)				F <sub>2</sub>	Time (weeks)			
		8	14	26	38	52		8	14	26
SO 1	0.50	0.45	0.44	0.37	0.35	0.22	0.23	0.06	0.01	0
SO 2	0.49	0.45	0.46	0.40	0.37	-	0.20	0.05	0.02	0
SO 3	0.49	0.44	0.38	0.36	0.33	0.31	0.18	0.05	0.01	0
SO 4	0.48	0.42	0.43	0.31	0.34	0.28	0.18	0.05	0.01	0
SO 5	0.49	0.46	0.40	0.33	0.28	0.24	0.23	0.05	0.01	0
SO	0.49	0.44	0.42	0.35	0.34	0.26	0.22	0.06	0.01	0
FO 1	0.46	0.42	0.42	0.33	0.33	0.30	0.26	0.01	0	0
FO 2	0.44	0.41	0.40	0.33	0.28	0.27	0.24	0.02	0	0
FO 3	0.49	0.44	0.41	0.38	0.36	0.23	0.23	0.03	0	0
FO 4	0.50	0.43	0.38	0.35	0.32	0.22	0.20	0.03	0	0
FO 5	0.50	0.42	0.37	0.24	0.28	0.28	0.20	0.01	0	0
FO	0.48	0.42	0.39	0.32	0.31	0.26	0.23	0.02	0	0

From Table 1 it is clear that, as has been expected, a rapid decrease in frequency of the 0 allele has occurred on ethanol food: frequency of the 0 allele had dropped to 0.01 after 14 weeks (approximately 4 generations) in the SO populations and the 0 allele was even lost in the FO population. Also on regular food the frequency of the 0 allele decreased considerably: to 0.26 in 52 weeks (approximately 26 generations). It appears that the decline in 0 frequency is very similar in all populations of the same type: line effects are therefore small. We conclude that also on regular food the absence of ADH activity has detrimental effects and lowers the fitness of the homozygotes for the null allele; whether the fitness of the heterozygotes is also lowered is the object of further study.

References: Grell, E.H., K.B. Jacobson and J.B. Murphy 1968, Ann. New York Acad. Sci. 151:441-455; van Delden, W., A.C. Boerema and A. Kamping 1978, Genetics 90:161-191.

van Dijk, H. University of Groningen, The Netherlands. The relationship between ADH activity and body weight in *D. melanogaster*.

When measuring ADH-activity in larvae and flies of *D. melanogaster* it is important to take body weight into account. The parameter activity per mg is strongly positively correlated with body weight. The most likely explanation is the deposition of relatively large amounts of

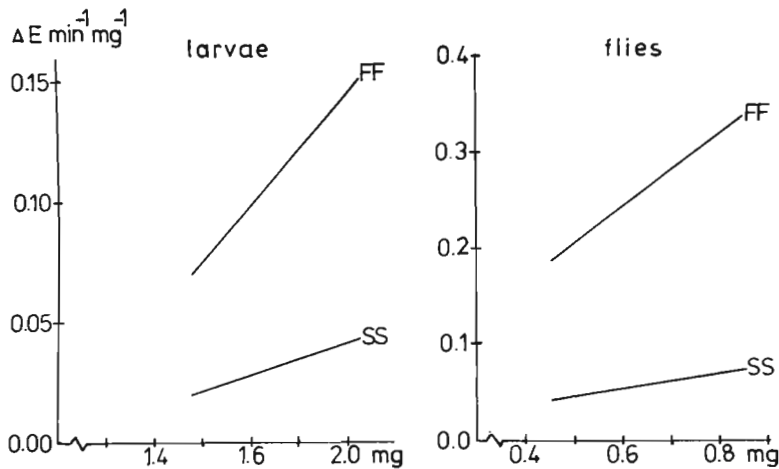
fat after reaching the critical weight. It is known (Ursprung et al. 1970) that fat bodies have a high ADH activity.

In this experiment done for the Groningen population (see Bijlsma-Meeles and Van Delden 1974) ADH activity was measured according to Van Delden et al. (1975) both in larvae showing the first signs of pupation and in 7-day-old male flies. Differences in individual weights were induced by varying the level of crowding. For ADH activity per mg ( $\Delta E \text{ min}^{-1} \text{ mg}^{-1}$ ) = y and body weight (mg) = x, the following relationships were found (see figures on following page):

Larvae ADH<sub>FF</sub> y = 0.1144 x - 0.0829  
 " ADH<sub>SS</sub> y = 0.0355 x - 0.0255  
 Flies ADH<sub>FF</sub> y = 0.3765 x + 0.0181  
 " ADH<sub>SS</sub> y = 0.0776 x + 0.0089

The larger ADH activities of larvae when ethanol is present in their food can be completely explained by this relation: body weights increase with increasing ethanol concentration. Selection experiments for increase of ADH activity will lead to selection for body weight when no precautions are made to keep body weight at a constant value.

All regression coefficients were significant (P < 0.001).



Our *Drosophila* cultures were kept at 25°C. At lower temperatures body weight increases. The described relationship with ADH activity does not hold in this case. ADH activity per mg is then even somewhat reduced with increasing body weight.

References: Bijlsma-Meeles, E. and W. van Delden 1974, *Nature* (Lond.) 247:369; Ursprung, H., H. Sofer and N. Burroughs 1970, *Wilhelm Roux' Archiv* 164:201; van Delden, W., A. Kamping and H. van Dijk 1975, *Experientia* 31:418.

Vasudev, V. and N.B. Krishnamurthy. University of Mysore, India. Effect of Dithane M-45 on rate of development and viability in *D. melanogaster*.

Rate of development and viability are the two parameters by which toxicity of a chemical is measured. Such parameters were used to test the effect of Dithane M-45 on *D. melanogaster* (Oregon-K). Eggs of the same age ( $\pm 4$  hours) were collected following the procedure of Delcour (1969). 35 eggs were then placed into each 3" x 1" vial containing chemical-supplemented media and normal medium and permitted to develop at a constant temperature of  $23 \pm 1^\circ\text{C}$ . Concentrations of 2, 5, 10, 15, 20, 25 and 30 mg of the chemical were thoroughly mixed in 100 ml wheat cream agar medium. The normal medium was used as control. The flies were scored each day from the time of emergence up to the end of eclosion. The pattern of emergence of flies in the control and in different concentrations of Dithane M-45 is depicted in Fig. 1 (see following page). It is clear from this graph that in the control the emergence of flies started on day 9 with a peak on day 11 and terminated on day 17. In contrast to this, the rate of development is prolonged in different concentrations of the chemical, thus affecting the time of emergence. In the lowest concentration (2 mg/100 ml food medium) eclosion commenced on day 11 and ended on day 22 with a peak on day 14. On the other hand, in the highest concentration (30 mg/100 ml) emergence began on day 19 and terminated on day 29. Here the peak of emergence was confined to day 25. The effect of Dithane M-45 on viability was measured by the number of flies emerged in each group. Thus the number of flies obtained in the control is 93.57%, while in the lowest concentration it is 82.14%; in the highest, 3.57%. From these results it is clear that Dithane M-45 has a significant toxic effect at higher concentrations.

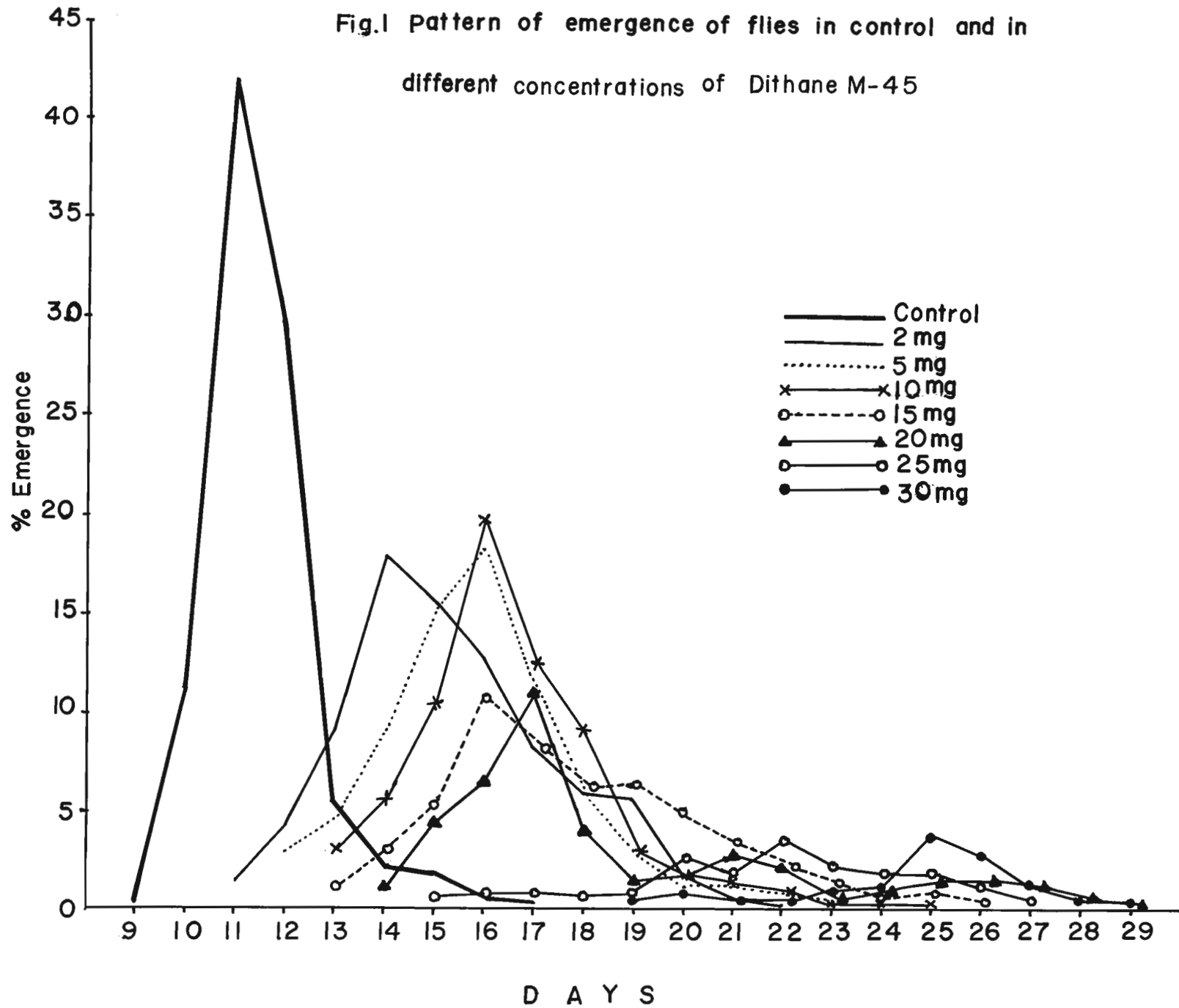
Acknowledgements: The authors are grateful to Dr. M.R. Rajasekarasetty for his constant encouragement and valuable suggestions, and to the UGC for financial assistance.

Reference: Delcour, J. 1969, DIS 44:133-134.

Vasudev, V. and N.B. Krishnamurthy. University of Mysore, India. Effect of aspirin on *D. melanogaster*. II. Non-induction of sex-linked recessive lethals.

Acetyl salicylic acid, marketed under the name "Aspirin", is well known for its antipyretic, analgesic and anti-inflammatory activity. It has been convincingly shown that aspirin produces drastic changes in experimental animals and plants. It is reported by Vasudev et al. (1978) that aspirin has a pronounced effect on the rate of development and viability in *D. melanogaster*. So far, there are no mutagenic reports of this drug. Hence, the authors tested the mutagenic property of this drug by scoring sex-linked recessive lethals in *D. melanogaster*.

Oregon-K and M-5 of *D. melanogaster* formed the materials for the present study. Aspirin was fed to *D. melanogaster* larvae in concentrations of 300 and 350 mg per 100 ml of food



medium. The procedure for scoring sex-linked recessive lethals is described in detail by Abrahamson and Lewis (1971). In the present experiments two-day-old treated males were used to test for the induction of sex-linked recessive lethals.

Table 1. Frequency of sex-linked recessive lethals induced by aspirin in *D. melanogaster*.

Concentration	No. of chromosomes tested	No. of lethals produced	% lethals
Control	895	1	0.11
300 mg/100 ml	850	2	0.24
350 mg/100 ml	615	2	0.33

Table 1 incorporates the data on the frequencies of sex-linked recessive lethals in controls as well as in the chemical-treated series. From this it is clear that both the concentrations tested were unable to induce a significant percentage of lethals compared to controls. By this, it can be concluded that these concentrations of aspirin are non-mutagenic to *D. melanogaster*. Consistent with this non-mutagenic nature of the drug, Maner et al. (1970) have reported that aspirin is unable

to induce chromosomal aberrations in human leukocytes. In contrast to these results, Jarvik and Kato (1968a,b) and Loughman (1971) in human leukocytes and Sen et al. (1975) in *Allium cepa* have shown significant chromosomal aberrations from aspirin and concluded it to be mutagenic. In the light of these highly contradicting results, more investigations on other animals and plants are necessary even though it is non-mutagenic in *D. melanogaster*.

Acknowledgements: The authors are grateful to Dr. M.R. Rajasekarasetty for his constant encouragement and valuable suggestions, and to the UGC for financial assistance.

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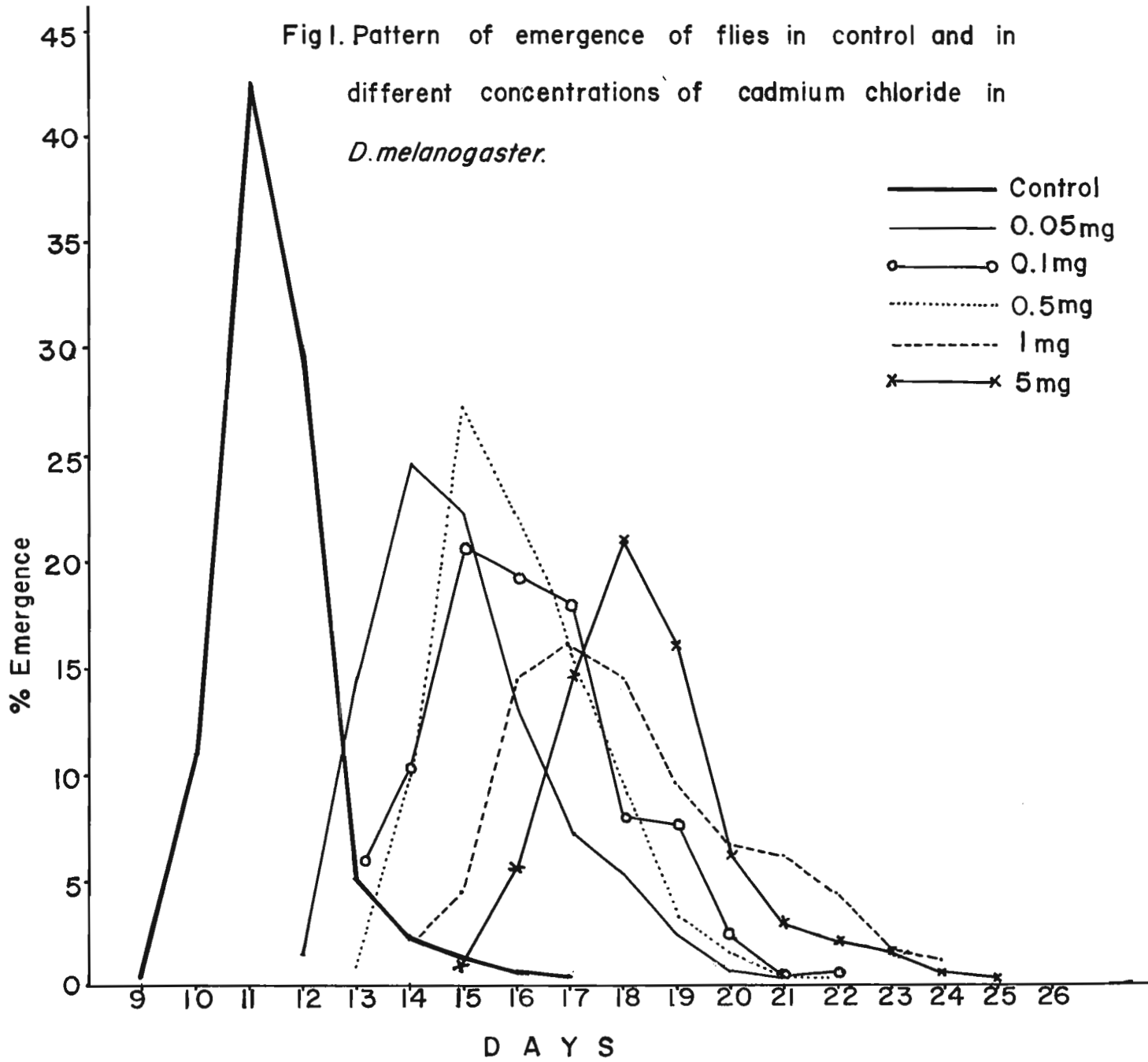
Vasudev, V. and N.B. Krishnamurthy. University of Mysore, India. Preliminary studies on the effects of cadmium chloride on *D. melanogaster*.

Cadmium pollution is increasing day by day due to its extensive use in industries and its existence as an impurity in zinc products. Cadmium has been demonstrated to induce drastic effects in experimental animals (Gunn and Gould 1970; Fowler et al. 1975; Tiggler et al. 1976;

Kumaraswamy and Rajasekarasetty 1976). Further, the disease "Ouchi-Ouchi" has been shown to be due to cadmium poisoning (Lucas 1975). Lucas (1975) has pointed out that no conclusive evidence links cadmium as a mutagen, carcinogen or teratogen for man. An attempt is made by the authors to investigate the effects of cadmium on the somatic and genetic systems of *Drosophila* and the preliminary results are presented.

*D. melanogaster* (Oregon-K) formed the material for the present study. Cadmium in the form of cadmium chloride was fed to larvae in concentrations of 0.05, 0.1, 0.5, 1.0 and 5.0 mg per 100 ml food medium. Normal medium was used as control. The eggs were collected following the procedure of Delcour (1969) and 35 eggs per vial were placed in each of the above concentrations. Flies were counted from the first day of eclosion to the last day of emergence. From the data, the rate of development and viability were estimated.

Fig. 1 (see following page) presents the pattern of emergence in different concentrations and in control. It is clear from this graph that the pattern of emergence is very much altered by the chemical. Developmental time is a fairly good indicator of various somatic effects caused by the chemical in the test substrate (Luning 1966). Hence, mean developmental time in control and in different concentrations of cadmium chloride has been estimated and presented in Table 1. Perusal of this table indicates that the rate of development is prolonged even at the lowest concentration tested. Prolongation of the mean developmental time becomes significant as compared to control ( $P < 0.05$ ). This is in line with the findings of Sorsa and Pfeifer (1973), wherein more than 1.25 mg CdCl<sub>2</sub>/1 substrate is known to cause significant prolongation in the rate of development.



Vijayan, V.A. and N.B. Krishnamurthy. University of Mysore, Manasagangotri, Mysore, India. Reduction of oviposition by a polycyclic hydrocarbon in *D. melanogaster*.

Chlorinated naphthalenes are industrially important polycyclic hydrocarbons used in electrical industry, cable covering compositions and storage batteries. 2,4-Dichloro-1-naphthol is one such chemical employed here to find out its effect on fecundity in *D. melanogaster*. 30

mg/100 ml food medium is found to be the LC50 of this chemical on melanogaster (Krishnamurthy and Vijayan 1978).

20 and 30 mg/100 ml food media represent the concentrations of the above chemical used to feed the larvae of Oregon-K strain of the said test system. Normal food medium was used as a control. Twenty virgin females and 20 bachelor males from each concentration were isolated, aged for five days and used for making crosses. The egg laying was calculated continuously for 10 days for each of the batches and compared with that of the control. All the experiments were carried out at  $24 \pm 1^\circ\text{C}$ .

Table 1. Fecundity of chemical-treated and control *D. melanogaster* flies.

Concentrations	Total number of eggs	Number of eggs/female/day
Control	6910	34.55
20 mg	3666	18.33*
30 mg	2648	13.24*

\*P < 0.05, by analysis of variance

The results are presented in Table 1 and the daily pattern of egg laying is graphically represented in Fig. 1. In control the total eggs laid were 6910, whereas in 20 and 30 mg concentrations the totals were 3666 and 2648 eggs, respectively. This shows significant decline in fecundity in both the concentrations employed compared to the control.

The life span and the fecundity of *Drosophila* are extremely sensitive to a great variety of environmental conditions like temperature, light, crowding, presence or absence of the opposite sex, and so on. Gruwez et al. (1971) have reported that photoperiodicity rhythm considerably influences the rate of eclosion in melanogaster. In our experiment all the above conditions were stable; the decline in oviposition must have been brought about by the chemical only. The effect may be in the number of ovariole production or in the speed of growth of the successive stages of the egg chambers. So here the authors opine that the chemical might have interfered and affected the oviposition and hence a reduction in fecundity. Higher concentration induced more damage to fecundity than lower concentration (Table 1). The nature of genetic damage that

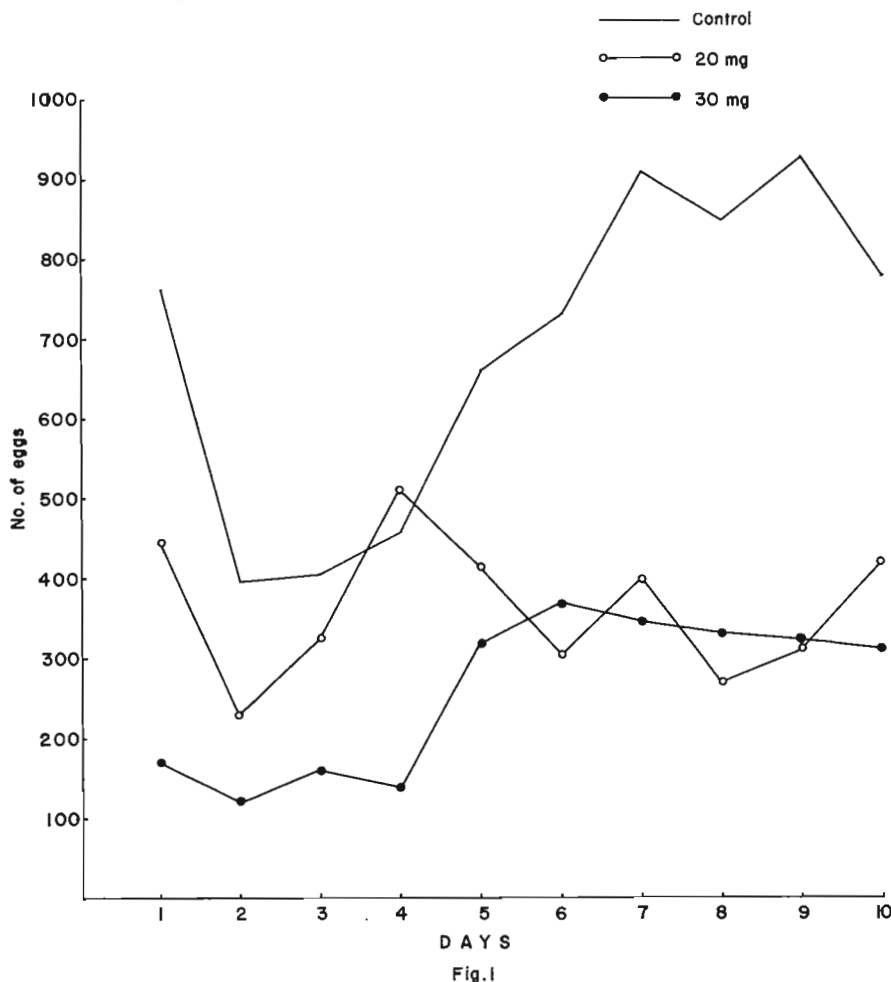


Fig. 1. Pattern of egg-laying by treated *D. melanogaster* with 2,4-dichloro-1-naphthol and control.

2,4-dichloro-1-naphthol could cause is being analyzed.

The authors are grateful to Dr. M.R. Rajasekarasetty for his constant encouragement and valuable suggestions. Financial aid by the Dept. of Atomic Energy, Government of India, is greatly acknowledged.

References: Gruwez, G., C. Hoste, C.V. Lints and F.A. Lints 1971, *Experientia* 27(12): 1414-1416; Hardie, D.W.F. 1964, *in* Encyclopedia of Chemical Technology, Vol. V (2nd ed.), pp. 302-304; Krishnamurthy, N.B. and V.A. Vijayan 1978, *Entomon* (in press).

Villa, T.G. and W.T. Starmer\*. University of Salamanca, Salamanca, Spain, and \*Syracuse University, Syracuse, New York. Some carbohydrases present in axenic larvae of *D. mojavensis*.

Most *Drosophila* species feed on yeasts, which supply vitamins, sterols, proteins and other nutritional requirements of the larvae and adults. Since yeasts are known to have a complex cell wall composed of glucans, mannans, chitin, protein and lipids (Pfaff 1971), it was of interest to assay *Drosophila* larvae

for activity of carbohydrases which could function in degrading the yeast cell wall.

The larvae of an axenic strain of *D. mojavensis* were collected, washed and homogenized in 0.05 M sodium succinate buffer (pH 5.5) for 10 minutes (10 ml volume). The homogenate was centrifuged at 10,000 g for 15 minutes; the pellet was re-extracted and centrifuged in the same manner. Both supernatants were combined and brought down to 5 ml by ultrafiltration on an amicon ultrafiltration cell using PM-10 membranes. This solution of "soluble" enzymes was assayed for activity on the following carbohydrate substrates obtained from the carbohydrate collection of the Dept. of Food Science and Technology, University of California, Davis: laminarin, pustulan, xylan,  $\alpha$ -(1-3)-glucan, CM-chitin, CM-cellulose and starch. The unit of enzyme activity was defined as the amount of enzyme which catalyzed the release of 1 nmol of D-glucose or equivalent reducing power (Villa et al. 1975) per minute at 30°C from each of the substrates given above. Total protein in the sample (4 ml) was determined by the Lowry method to be 20 mg.

Table 1. Summary of some carbohydrases found in cell-free extracts of axenic larvae of *D. mojavensis*.

Substrate <sup>1</sup>	Enzyme activity units/ml	Associated enzyme activity
Laminarin	3.1	$\beta$ -(1-3)-Glucanase (EC 3.2.1.6)
Pustulan	4.1	$\beta$ -(1-6)-Glucanase (EC 3.2.1.75)
Xylan	22.5	$\beta$ -(1-4)-Xylanase (EC 3.2.1.32)
- (1-3)-Glucan	18.5	$\alpha$ -(1-3)-Glucanase (EC 3.2.1.59)
CM-Chitin <sup>2</sup>	10.3	$\beta$ -(1-4)-Chitinase (EC 3.2.1.14)
CM-Cellulose <sup>3</sup>	2.3.	$\beta$ -(1-4)-Cellulase (EC 3.2.1.4)
Starch	131.2	$\alpha$ -(1-4)-Glucanase (EC 3.2.1.3)

<sup>1</sup>All substrates were prepared at a final concentration of 0.5% in 0.05 M sodium succinate buffer (pH 5.5)

<sup>2</sup>CM-Chitin = Carboxy-methyl chitin

<sup>3</sup>CM-Cellulose = Carboxy-methyl cellulose

Table 1 lists the enzyme activities for the various carbohydrases found in the axenic larvae. It is apparent that  $\alpha$ -amylase accounts for most of the activity (68%) while xylanase,  $\alpha$ -(1-3)-glucanase and chitinase together account for 27% of the activity. The remaining activity (5%) is due to the enzymes  $\beta$ -(1-3)-glucanase,  $\beta$ -(1-6)-glucanase and cellulase. These preliminary results indicate that the cell-free extracts of axenic larvae possess the enzymatic potential to partially

hydrolyze the cell wall of yeasts found in the natural diet of the fly (Starmer et al. 1976). It is noteworthy that several hydrolases, xylanase,  $\alpha$ -(1-3)-glucanase and chitinase are present in the larvae but the total enzyme complement necessary for the complete degradation of the yeast cell envelope is not present, otherwise the activities of  $\beta$ -(1-3) and  $\beta$ -(1-6)-glucanases would be higher since it is well established that these enzymes are directly related to yeast cell wall hydrolysis (Pfaff 1977). This may indicate that the larvae only "weaken" the wall, rendering the cell more susceptible to extraction of the necessary nutritional factors for the development of the fly. It is known that the fecal pellet of adult *Drosophila* contains "ghost" cells and the yeast cell wall is left at least partially intact (Shehata et al. 1951). The



reason for the lack of total cell wall hydrolysis is not clear but it might be due to a biologically improbable adaptation or a coevolutionary condition of the yeast and the *Drosophila*.

References: Phaff, H.J. 1971, in *The Yeasts* (eds. A.H. Rose and J.S. Harrison), pp 133-210; \_\_\_\_\_ 1977, in *Food Proteins, Advances in Chemistry Series No. 160* (eds. R.E. Feeney and J.R. Whitaker), pp. 244-282; Shehata, A.M. El Tabey et al. 1951, *Amer. Natur.* 85:381-383; Starmer, W.T. et al. 1976, *Microbial Ecology* 3:11-30; Villa, T.G. et al. 1975, *Arch. Microbiol.* 104:201-206.

Wheeler, M.R. University of Texas, Austin, Texas. Are the new species described in DIS validly published?

A number of new species of *Drosophila* and related genera have been described in DIS, but their validity and recognition in scientific nomenclature has never been clear. To be valid, new names must be "published" in accordance with

the International Code of Zoological Nomenclature, as adopted by the International Congress of Zoology and administered by the International Commission on Zoological Nomenclature (ICZN). The question of whether DIS is a publication has been debated often--see for example DIS 30: 6a, 33:7, 34:164, 36:8. Earlier issues of DIS, up to No. 29 of 1955, carried the front cover statement "This is not a publication." Beginning with No. 30 (1956) the statement was dropped. The current statement, "Material presented here should not be used in publications without the consent of the author", does nothing to help determine whether new names are validly published or not.

The question, then, is not whether the editor(s) of DIS consider it to be a publication, but whether it is a publication in the sense of the Code. To (hopefully) settle this matter, I quote opinions from E.B. Basden of Scotland, who has been very active in *Drosophila* systematics, Curtis Sabrosky of the Systematic Entomology Laboratory, USDA, a well known Dipterist and long-time member of the ICZN, and Richard Melville, permanent Secretary of the ICZN, at the British Museum (N.H.), London.

They are unanimous in their opinions, with which I concur: New taxa described in DIS since 1955 should be considered as having been validly published. Here are a few of their comments:

Basden: "I have always thought that it [DIS] was a publication according to the Rules, p. 7, Art. 8, and I think that it should be accepted as such, in spite of Recommendation 8A [i.e., it is best not to use mimeographing, etc., for a publication - MRW]. It's a regular scientific periodical."

Sabrosky: "...now that I have seen [DIS] I am inclined to agree with Melville that it is indeed a publication... It seems obvious that the editors also realized that when they dropped the statement 'This is not a publication.' And unless DIS is copyrighted, they might as well drop the requirement about getting the author's consent. ...I have no doubt that some of the research notes are mere progress reports, which some journals would not accept. But some notes seem pretty complete in themselves, such as pp. 71-72 in DIS 50, where types and paratypes are specified. One very unfortunate aspect of all this is that taxonomic papers in DIS will probably not be picked up by Zoological Record or Biological Abstracts. And ordinary libraries--museums for example--will not have DIS on their shelves."

Melville: "It seems clear that the production satisfies all the mandatory requirements of Art. 8: (a) it is produced in ink on paper in numerous identical copies--No. 38 was issued in 1100 copies, which far exceeds the edition of many learned journals whose status as publications is not questioned merely because their editions are small; (b) some of the material in it is clearly published for the purpose of permanent, public record in the science; (c) it is obtainable by purchase; (d) it is not reproduced by a forbidden method."

The number of new names is, fortunately, fairly small. Only one appeared before 1956: Nolte and Stoch, DIS 24:90 (1950) described a new *Drosophila* from Africa; it has since been named *D. yakuba* (Burla 1954). Following is a list of the new taxa described in DIS since 1955. I consider them to have been validly published, and I am sending a statement to this effect to Zoological Record.

*Chymomyza pararufithorax* Vaidya and Godbole 1973. DIS 50:71-72  
*Drosophila chamundiensis* Sajjan and Krishnamurthy 1972. DIS 48:56-57  
*Drosophila charmadensis* Gwoda and Krishnamurthy 1972. DIS 48:38  
*Drosophila ezoana* Takada and Okada 1957. DIS 31:164\*

*Drosophila mojavensis* baja Mettler 1961. DIS 38:57-58  
*Drosophila neonasuta* Sajjan and Krishnamurthy 1972. DIS 48:56-57\*  
*Leucophenga neoangusta* Godbole and Vaidya 1977. DIS 52:24  
*Stegana subexcavata* Vaidya and Godbole 1977. DIS 52:55-56  
*Zaprionus paravittiger* Godbole and Vaidya 1972. DIS 48:135-136

\*Starred species were later described again in another journal.

In my opinion, *Drosophila* taxonomists should not publish new species descriptions in DIS--at least until it is formally recognized as a "publication". Further, it is not wise to include new names in articles of a non-taxonomic nature. The Code provides that a new name may be valid if accompanied by a "description"; but a complete, thorough description is not required--the simplest descriptive remark may be enough to validate a new name (e.g., describing the chromosomes, some electrophoretic patterns, etc.). *Drosophila* workers have a rather poor reputation in systematic circles, having used new, unpublished names without regard to the International Code.

Regretfully, the writer is an expert on this subject, having made more than a few of such errors!

Wijsman, E.M. University of Wisconsin, Madison, Wisconsin. The effect of ether on mating behavior in *D. simulans* y w.

In setting up some experiments which involved matings between virgin females and their brothers in *D. simulans* y w, I encountered considerable difficulty with sterility. I decided to test the possibility that the ether that I

was using as an anesthetic was causing this sterility.

I established pair matings using virgin females and their brothers separated by ether, CO<sub>2</sub>, or aspirator (no anesthesia), and placed the vials at 25°C. Two weeks later I scored the vials as fertile or sterile. As can be seen in Table 1, ether had a very strong effect on fertility. The hypothesis that anesthesia had no effect on fertility was tested using a 1-tailed Fisher's exact test. Comparison of ether and no anesthesia gave  $p < 0.000001$ . CO<sub>2</sub> vs. no anesthesia gave  $p = 0.18$ , which is not significant.

Table 1. Number of vials which were either fertile or sterile when parents were exposed to different types of anesthesia.

Anesthesia	Fertile	Sterile
Ether	4	56
CO <sub>2</sub>	18	8
None	21	4

To determine which of the two sexes was sterilized I repeated the experiment using only one sex which had been exposed to ether. When only the male had been anesthetized high sterility resulted. Anesthetized females mated to non-anesthetized males were fertile.

To determine the cause of sterility I dissected the testes to check for motile sperm and watched the males court females. Males were isolated for 3-4 days after collection with either ether or an aspirator and then placed in empty vials with 3 aged virgin females. Those which had been collected without ether showed normal courtship behavior;

those which had been exposed to ether showed virtually no courtship behavior. Dissection of the testes showed motile sperm. Thus in this strain of *D. simulans*, ether seems to produce almost complete, permanent, behavioral sterility in the males.

Williams, J.M. University of California, Santa Cruz, California. Tumorigenesis in *D. melanogaster* bearing the temperature-sensitive mutation *shibire*<sup>ts1</sup>.

The imaginal discs of *Drosophila* are single-layered secretory epithelia (Bodenstein 1950; Poodry and Schneiderman 1970) which resemble the ascinar units of vertebrate exocrine glands. This feature has been exploited along with the convenience of in vivo culturing meth-

ods (Hadorn 1963) to characterize the initial morphological and ultrastructural changes occurring in the eye-antenna imaginal disc of *D. melanogaster*.

A temperature-sensitive mutation, *shibire*<sup>ts1</sup> (Poodry et al. 1973) in *D. melanogaster*

was used to generate information concerning the timing of initiation of tumorous growth and the pattern of cellular proliferation in the neoplasm. Neoplasia in *Drosophila* is well documented (Gateff 1977, 1978); however, none of the previously defined neoplasms of genetic or epigenetic origin have yielded satisfactory data concerning the initial stages of tumorigenesis. The fact that the eye-antenna disc of *shit<sup>ts1</sup>* is temperature sensitive, transplantable, displays autonomous growth and loss of differentiation capacity has augmented its usefulness in documenting patterns of neoplastic change.

*Shit<sup>ts1</sup>* eye-antenna discs were dissected from mature third instar larvae and implanted into the hemocoel of mated 3-4 day old Ore-R female hosts (Ursprung 1967). Host flies were incubated at 29°C (the mutant restrictive temperature) in shell vials containing standard medium. In some experiments these flies were cultured for two weeks. After this time the eye disc had tumorized and began to fill or filled completely the abdominal cavity. The tumorous growth was dissected from the abdomens in buffered ringer solution, fragmented with tungsten needles and reimplanted for second generation growth (one generation = two weeks). Wild-type eye discs do not tumorize or behave similar to *shit<sup>ts1</sup>* when treated in an identical fashion.

Other eye-antenna discs from *shit<sup>ts1</sup>* third instar larvae were incubated in vivo for periods ranging from 16 to 22 days. These implants were cultured at 29°C for period between 2 and 10 days and then maintained at 22°C for the remainder of the incubation period. After dissection from the abdomens these implants were measured with a stage micrometer and examined for gross morphological features. Data summarized in Table 1 show that tumorigenesis is initiated within a 48 hour period in these tissues and that continued heat stimulation is not required to maintain tumorous growth. These data indicate that tumorigenesis in this tissue is irreversible. Furthermore, it is noted that the tumors grew to about the same size irrespective of the time cultured at 29°C. This indicates that a maximum pattern of proliferation was established concomitant to the initiation of tumorigenesis. Thus, the neoplasms behave autonomously. This expression is initiated via temperature sensitivity to yield information concerning regulation of gene expression in normal vs. tumorous tissue.

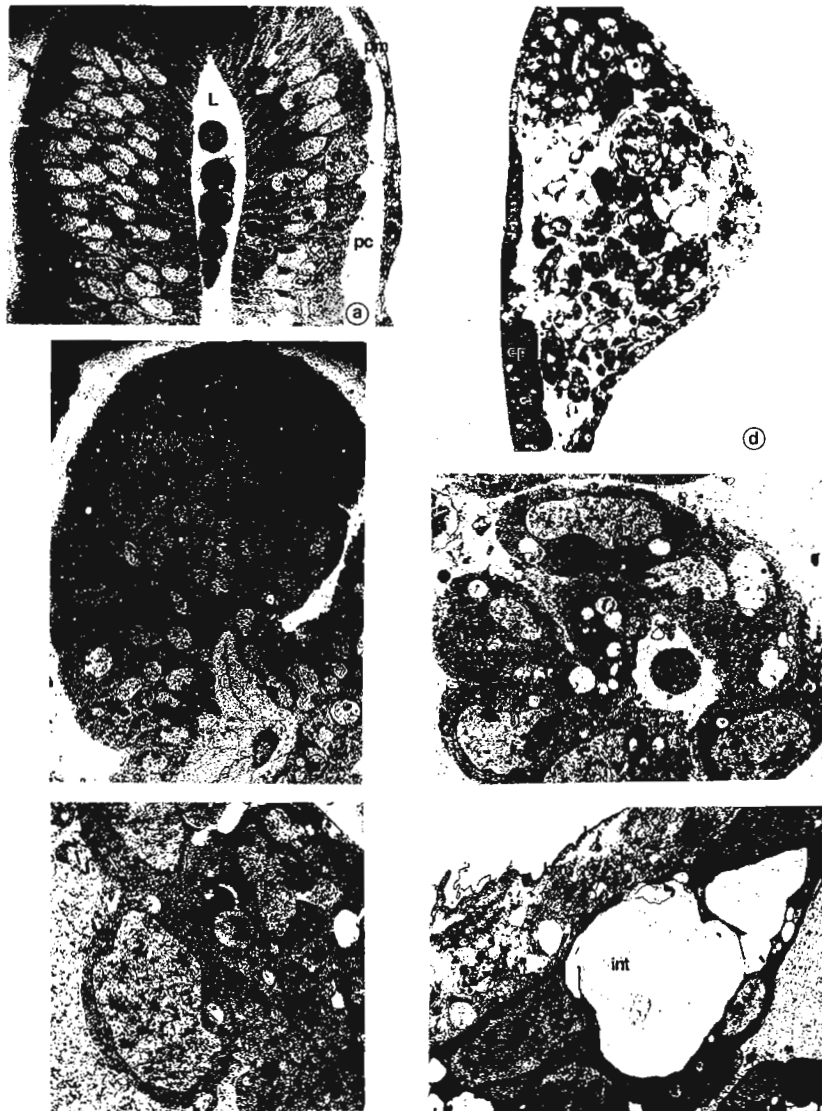
Table 1.

	Group I	Group II	Group III	Group IV	Group V
Days at 29°C	8	10	8	4	2
Days at 22°C	14	10	10	13	14
Total days in culture	22	20	18	17	17
Size* in mm <sup>2</sup> x 10 <sup>-3</sup>	1.2	1.08	1.138	1.21	1.2

\*Size of control disc is  $\sim 0.85 \text{ mm}^2 \times 10^{-3}$ .

Implants ranging from 6 hours to 4 weeks were used in histological and ultrastructural studies. The study of 1  $\mu\text{m}$  sections and thin section electron micrographs reveal that structural changes occur in the disc epithelium within the first 6 hours of in vivo culture. Regions of the epithelium bulge in what appears to be a solid mass of cells. The arrangement of the monolayer becomes contorted resulting in irregular folds and projections. Some cells lose contact with the basement membrane in areas and aggregate in groups. The predominant columnar appearance of the epithelial cells seen in wild-type discs is not visualized in temperature-sensitive disc epithelia cultured for 6 hours. Instead they become more cuboidal and irregular in shape and show modification to the apical border. The microvilli become shortened and irregular with disorderly microtubular arrangement. Cell-to-cell contacts are interrupted by intercellular spaces and membrane-bound undersides appear intracellularly. The cytoplasm contains numerous ribosomes; many rough ER are present and possibly more mitochondria are present in these cells than in the controls.

Many of the initial morphological aberrations are detectable in implants cultured for longer periods and other abnormalities result as well. The basal lamina of these tumors often form pockets filled with amorphous material, vesiculate particles and dead cell debris. It is often thrown into irregular projections extending beyond the basal surface of the epithelial cells. Multiple cell layers are seen and membranes of juxtaposed cell layers often appear fused. Cells with picnotic nuclei increase in number with continued in vivo cultures as well as cells containing virus-like particles.



- a. The cross section of third larval instar eye disc appears as a pseudostratified single layered epithelium with distinct microvillar and basal surfaces. PM, peripodal membrane; PC, peripodal cavity; dv, dividing cell; L, lumen; MC, macrophage-like cells. (1300X)
- b. A section of eye-antenna disc tumors cultured for 6 hrs at 29°C. A mass of epithelial cells infiltrated with dead cells (dc) protrudes into the lumen of the disc. (1000X)
- c. Epithelium with virus-like particles (vlp) present. Intercellular spaces and a cell elaborating microvilli on two opposite sites is seen. (10,000X)
- d. The epithelium (ep) which makes up the cortex varies in thickness but seems to be single-layered. Aggregations of cells and cells organized in monolayers around a central lumina (arrows) are found in the medulla (M). (200X)
- e. An aggregate of cells reminiscent of the ommatidial precursor clusters. No apical/basal distinction is apparent. (5000X)
- f. The basement membrane (bm) is not in contact with the basal surface of the epithelial cells. A massive amount of mitochondria (arrows) and amorphous debris is present between them. Atypical cell morphology and large intercellular spaces (int) are evident. (3300X)

After one generation in vivo the monolayer of epithelial cells becomes rearranged. It appears sponge-like due to intercellular spaces; it also lacks cellular continuity in areas. The basal lamina is often the only structure maintaining the sac-like appearance. In these tumors the outer portion of termed the "cortex" and is comprised of a remnant population of epithelial cells. These cells surround a "medulla" region which is composed of cells arranged in sperical configurations. The cell number in these spheroids vary but are reminiscent of the ommitidial precursor cluster found in the developing eye disc of the wild-type (Waddington and Perry 1960). Thus, it is possible that tumorigenesis did not affect the determined state of this cell population, but did interfere with the differentiation process. A considerable amount of cell debris and amorphous material is found in the medulla.

Autoradiographic studies of tumors incubated with <sup>3</sup>H-thymidine for 48 hours showed differential incorporation in areas of the tumor whre masses of cells bulge in the epithelium. This indicates that proliferation continues in the epithelium (cortex region) as opposed to the medulla. These features are important in determining basic kinds of cellular interactions which occur in other tumors arising from secretory epithelia and are indicative of a certain pattern of neoplastic change.

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Wu, C.K. and P. Smith. Adrian College, Adrian, Michigan. Calcium cyclamate induced lethal effect and genetic damage in spermatocytes of Drosophila.

In determining the lethal effect of calcium cyclamate on development, v w f females of the same age were mated individually with three males into five different series according to the concentrations of calcium cyclamate solution in the food media. It is assumed

that, on the average, one female would lay the same number of eggs during the same period of time. It was found that in the treated series, the survival rates were decreasing with increasing concentrations of calcium cyclamate solution in the media, or in other words, the higher the concentration of calcium cyclamate in the medium causes the higher rate of lethality (Table 1). It clearly suggests that calcium cyclamate causes lethal effect on the early development of D. melanogaster.

Table 1. Average number of progeny, survival rate and lethality rate from a single female Drosophila in media with different concentrations of calcium cyclamate.

	Control	Cyclamate media			
		0.625%	1.25%	2.5%	5%
Male	46.3 ± 9.8	27.2 ± 4.3	27 ± 2.5	10.2 ± 11	0
Female	56.7 ± 4.3	37.2 ± 2.7	35.6 ± 13.2	15.8 ± 9.8	0
Total	103 ± 14.1	64.4 ± 3.8	62.6 ± 13.0	28.6 ± 18.4	0
Survival rate	1.00	0.63	0.61	0.28	0
Lethality	0	0.37	0.39	0.72	1

To estimate the chromosomal damage induced by calcium cyclamate, a doubly marked Y chromosome was used in the experiment. Males of the composition ywf/B<sup>S</sup>.Y.y<sup>+</sup> (y= yellow body; w=

white eyes; f= forked bristles; B<sup>S</sup>= Bar eyes of Stone, which is a marker on the long arm of the Y chromosome; y<sup>+</sup>= normal allele of yellow, which is attached to the tip of the short arm of the Y chromosome) were used in this study. Day-old males were collected and transferred to a treatment chamber in which medium mixed with 1.25% calcium cyclamate for about 2 days. Then, the treated males were mated individually with three virgin females of the composition ywf/ywf for a period of 9 days; males treated with 1.25 sucrose mated in the same manner served as the control.

The regular offspring from these crosses are phenotypically yellow, white, forked females and Bar, white forked males. An exchange between the X chromosome and Y<sup>L</sup> (the long arm of the Y chromosome) proximal to the B<sup>S</sup> marker generates an X chromosome with Y<sup>S</sup> and the appended y<sup>+</sup> marker attached proximally and is recoverable as a phenotypically white, forked female (ywf.

y+/ywf). The reciprocal product is a centric fragment carrying the B<sup>S</sup> marker, recovered as Bar, yellow, white, forked male (ywf/FR Y·B<sup>S</sup>). An exchange between X and Y<sup>S</sup> (the short arm of the Y chromosome) proximal to the y+ marker generates an X chromosome with Y<sup>L</sup> and the appended B<sup>S</sup> marker attached proximally and is recoverable as a phenotypically Bar, white, forked female (ywf·B<sup>S</sup>/ywf) and the reciprocal product is also a centric fragment, carrying the marker y+ (FR Y·y+) recovered as a white, forked male (ywf/FR Y·y+). These exceptional males may also arise from the deletion of one of the two markers. From the recovery of both X and Y chromosomes following nondisjunction phenotypically Bar, white, forked females (ywf/ywf/B<sup>S</sup>·Y·y+) are obtained. The reciprocal product is recovered as yellow, white forked males (ywf/0). Such a male may also arise from loss of both markers.

Table 2. Progeny from crosses of ywf females, mated with ywf/B<sup>S</sup>·Y·y+ males. Treated (T) or not treated (C) with 1.25% calcium cyclamate medium (frequency x 10<sup>-4</sup>).

Series	Regular		X-Y Exchange		Nondisjunction	
	Female	Male	Female	Male	Female	Male
C	10907	9022	0	1	4	6
			-	(1±1)	(3.5±1.8)	(6.6±2.7)
T	39449	32172	1	6*	9	1
			(.25±.25)	(10±5.5)	(2.3±.76)	(1.6±.7)

\*In one vial there were 7 exceptional males; the event probably occurred in the spermatogonia stage. It was scored as a single event.

calcium cyclamate to the disjunction of X and Y chromosomes.

In line with the findings in the first experiment, these data suggest that the calcium cyclamate not only inhibits the early developmental stages to cause lethality, but also causes chromosomal breakage during spermatogenesis of *D. melanogaster*.

The results are given in Table 2. The information from the exception flies of X-Y exchange class indicates that the frequencies in the treated series exceed those in the control series. Turning to the class of nondisjunctional, it may be seen that there is no harmful effect of

Xamena, N., R. Marcos and A. Creus.  
Autonomous University of Barcelona  
Bellaterra, Spain. Effect of mating  
system on disruptive selection.

Among the different effects that disruptive selection can produce on a population, the increase in the phenotypic variability and consequently, the divergence between the extreme phenotypes is generally accepted.

See Thoday (1972) for a review. However,

there is not agreement about other effects that disruptive selection can produce, as well as the effectivity of different mating systems used.

In order to check the effect that the different mating systems can produce on the divergence of extreme phenotypes we have carried out a disruptive selection experiment using two mating systems: quasi-random and mating-choice.

With the quasi-random mating the gene flow in any generation depends only on the probability that the "hybrid" individuals will be included in the selected sample. With mating-choice is also depends on the probability that "hybrid" matings will occur, and on their success relative to the "non-hybrid", that is, assortive matings that occur.

The experiment has been carried out during 15 generations and the trait selected has been the interocellar bristles in *D. melanogaster*. All the experiments were done at 25±1°C with a selection intensity of 20%.

For each kind of mating two lines were set up. Figs. 1 and 2 show the divergence between extreme phenotypes in the two mating systems. From these figures we can conclude that while mating-choice mating does not produce divergence (neither MCh1 nor MCh2), in one line of quasi-random (QR1) there is a clear divergence (2.04% of overlap at 15 generations) although in the other the divergence is practically null.

These results seem to show that quasi-random mating is more effective; but something striking in these results is the resistance to divergence of this population, which con-

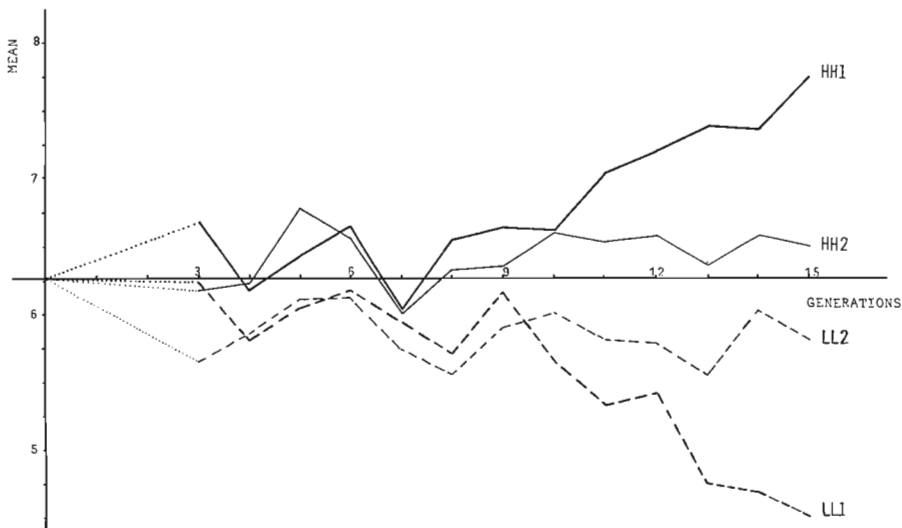


FIG. 1 (QUASI-RANDOM)

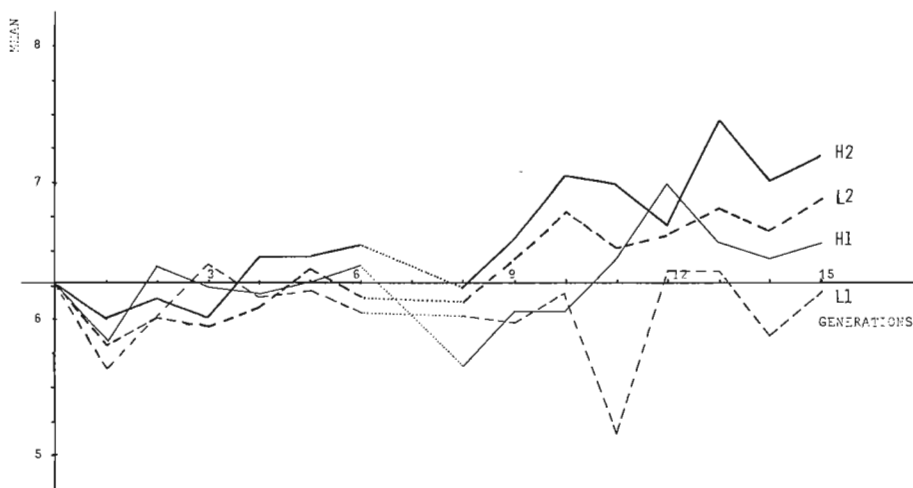


FIG. 2 (MATING-CHOICE)

trasts with the results obtained on the same population in front of directional selection (Marcos 1977). This resistance may indicate a decrease in the genetic additive variance of the population although the phenotypic variance has been kept without variation.

References: Thoday, J.M. 1972, Proc. R. Soc. Lond. B. 182: 109-143; Marcos, R. 1977, DIS 52:61.

Yoo, B.H., J.J. Moth and J.S.F. Barker. University of Sydney, Australia. Abdominal bristle numbers and sex-dimorphism ratios in different *Drosophila* species.

The number of bristles on abdominal sternites has been used as a model character in many experimental quantitative genetic studies. However, the functional role of the bristles and adaptive significance of the variation in number are not well understood, although this

character was described as being peripheral to reproductive fitness (Robertson 1955), and of ancient phylogenetic origin (Robertson and Reeve 1952). Mather (1941) observed enormous variation in abdominal bristle number, particularly in the ratio of numbers in the two sexes, among 4 species of *Drosophila*, and suggested the action of selection for this character in the process of speciation.

With this background in mind, bristle numbers on the 4th abdominal sternite were scored in small samples (20-40 pairs) of 13 *Drosophila* species. These flies (except for *D. repleta*) were caught using banana baits in Sydney suburbs and cactus-infested areas of N.S.W., mostly in 1972-73. Wild-caught flies were bred on a dead yeast fortified medium, first under crowded conditions and then under "optimal" conditions, except for *D. brunneipennis*, which could not be cultured easily in the laboratory; wild-caught flies only were scored for the latter. The crowded culture conditions reduced bristle number in some species, but hardly influenced the sex dimorphism (SD) ratio, viz. male score to female score ratio. Hence, SD ratios are perhaps comparable under quite diverse conditions.

Mean bristle numbers under "optimal" conditions and SD ratios averaged over the two culture conditions are presented in Table 1. To indicate the extent of variation among different populations within a species, the mean and standard deviation of averages for 8 strains of *D. melanogaster* from literature (Reeve and Robertson 1954; Clayton et al. 1957; Sheldon 1963; Sheridan et al. 1968) and our observations were calculated as follows:

	Male	Female	SD Ratio
Mean	18.12	22.30	0.811
Std. deviation	2.37	2.24	0.033

The large variation in SD ratio among species (0.77-1.72), considering the extent of changes produced by artificial selection (Frankham 1968) and of within-species variation, might not have been possible without selective forces being involved. This, together with

the general similarity among species within subgenera, suggests that abdominal bristle number was perhaps an adaptively important character in the phylogenetic history as previously conjectured.

Table 1. The number of bristles on the 4th abdominal sternite and SD ratio in different *Drosophila* species (mean  $\pm$  S.E.).

Subgenus	Group	Species	Male	Female	SD Ratio
Sophophora	melanogaster	simulans	15.2 $\pm$ 0.4	19.5 $\pm$ 0.5	.770 $\pm$ 0.020
		melanogaster	15.4 $\pm$ 0.3	19.6 $\pm$ 0.5	.782 $\pm$ 0.022
		ananassae	20.6 $\pm$ 0.3	23.1 $\pm$ 0.4	.910 $\pm$ 0.017
		serrata	16.7 $\pm$ 0.3	17.9 $\pm$ 0.3	.926 $\pm$ 0.020
		obscura	subobscura*	15.4 $\pm$ 0.3	16.6 $\pm$ 0.3
Scapto- drosophila		lativittata	22.4 $\pm$ 0.5	24.5 $\pm$ 0.5	.916 $\pm$ 0.029
		brunneipennis	26.9 $\pm$ 0.7	29.1 $\pm$ 0.5	.924 $\pm$ 0.029
Drosophila	immigrans	immigrans	26.5 $\pm$ 0.4	23.3 $\pm$ 0.3	1.135 $\pm$ 0.023
		funnebris	39.2 $\pm$ 0.9	31.8 $\pm$ 0.7	1.235 $\pm$ 0.026
		repleta	45.4 $\pm$ 0.5	36.3 $\pm$ 0.6	1.251 $\pm$ 0.024
	virilis	repleta**	56.8 $\pm$ 0.8	42.1 $\pm$ 0.4	1.351 $\pm$ 0.023
		aldrichi	28.7 $\pm$ 0.5	26.0 $\pm$ 0.5	1.106 $\pm$ 0.028
		buzzatii	42.5 $\pm$ 0.5	29.0 $\pm$ 0.3	1.466 $\pm$ 0.023
		virilis*	59.9 $\pm$ 0.8	34.9 $\pm$ 0.4	1.716 $\pm$ 0.032
Dorsilopha		buskii	25.3 $\pm$ 0.6	17.0 $\pm$ 0.3	1.487 $\pm$ 0.033

\*From Mather (1941)

\*\*A laboratory stock from Texas, USA

This work was supported by a University of Sydney Studentship to BHY.

References: Clayton, G.A., J.A. Morris and A. Robertson 1957, *J. Genet.* 55:131-151; Frankham, R. 1968, *Aust. J. Biol. Sci.* 21:1225-1237; Mather, K. 1941, *J. Genet.* 41:159-193; Reeve, E.C.R. and F.W. Robertson 1954, *z. Vererbungslehre* 86:269-288; Robertson, A. 1955, *Cold Spring Harb. Symp. Quant. Biol.* 20:225-229; Robertson, F.W. and E.C.R. Reeve 1952, *J. Genet.* 50:414-448; Sheldon, B.L. 1963, *Aust. J. Biol. Sci.* 16:490-515; Sheridan, A.K., R. Frankham, L.P. Jones, K.A. Rathie and J.S.F. Barker 1968, *Theor. Appl. Genet.* 38:179-187.



Young, D.J., D.C. Vacek and W.B. Heed. University of Arizona, Tucson, Arizona. The facultatively anaerobic bacteria as a source of alcohols in three breeding substrates of cactophilic *Drosophila*.

Knowledge of the microbial ecology of the necrotic tissues of columnar cacti, the breeding substrates of cactophilic *Drosophila* of the Sonoran Desert, is very important in elucidating the ecological niche of these *Drosophila*. The saprophytic yeast flora is probably important as a concentrated protein source and

attractant for *Drosophila* (Starmer et al. 1976). However, very little is known about the bacterial flora; *Erwinia carnegieana* is believed to be the causal agent of the necrosis (Lieghtle et al. 1942), and at least eight genera of bacteria can be found in *Pachycereus pringlei*, cardon cactus, and *Carnegiea gigantea*, saguaro cactus (Graf 1965).

Gas chromatography studies have shown that several alcohols are present in necrotic cacti (Heed 1978). Anaerobic bacteria probably play an important role in alcohol production because the only two saprophytic yeasts which ferment, *Torulopsis sonorensis* and *Candida tenuis*, produce only ethanol and are not found in all necrotic samples containing alcohol. Knowledge of alcohol variability as a function of the microflora is necessary for an understanding of the variability at the ADH locus in *D. mojavensis* (Heed 1978). Here we report the results of a preliminary analysis of the distribution and alcohol production of the facultatively anaerobic bacteria inhabiting the soft rots of three species of giant cacti.

Samples of necrotic tissue of one *Carnegiea gigantea* (saguaro cactus), two *Lamaireocereus thurberi* (organ pipe cactus), and two *Machaerocereus gummosus* (agria cactus) were appropriately diluted and plated on the following three media: (1) 0.3% yeast extract, 0.3% Bacto peptone, 1.5% Bacto agar; (2) tryptic soy agar; (3) nutrient agar (all components and media were from Difco). One set of plates was incubated microaerophilically with CO<sub>2</sub> and another set aerobically at 24°C and 30°C for the initial isolation. Standard microbiological techniques were used for maintenance of the isolates. Identification was made with the aid of the API 20E System (Analtab Products), a miniaturized version of conventional procedures for bacteria identification, and other tests as indicated in Bergey's Manual (Buchanan and Gibson 1974). Although the API 20E System is designed for the identification of clinical isolates in the family Enterobacteriaceae, it can be very useful as a quick screening method in other studies where small, Gram-negative, facultatively anaerobic rods are present. The GasPak anaerobic system (BBL) was used to test for anaerobic growth. Gas chromatography

Table 1. The concentration of each bacteria species in the substrates and the amount of ethanol produced by each species in pure culture.

Bacteria		Colony forming units/cc of sample*					EtOH Production	
Species	No. of isolates	Saguaro (77-30)	Organ pipe (77-31)	(77-32)	Agria (77-33)	(77-34)	No. tested	% EtOH**
<i>Bacillus laterosporus</i>	3	10 <sup>5</sup>	10 <sup>7</sup>				2	0-3
<i>Citrobacter</i> sp. A	2			10 <sup>7</sup>			2	31-34
<i>Citrobacter</i> sp. B	5		10 <sup>7</sup>			10 <sup>8</sup>	0	
<i>Enterobacter aerogenes</i>	1		10 <sup>6</sup>				1	55
<i>Enterobacter agglomerans</i>	1				10 <sup>7</sup>		0	
<i>Enterobacter cloacae</i>	1					<10 <sup>2</sup>	1	29
<i>Erwinia carnegieana</i>	2		10 <sup>7</sup>				0	
<i>Escherichia coli</i>	3		10 <sup>4</sup>	10 <sup>7</sup>			2	31-40
<i>Klebsiella ozaenae</i>	2	10 <sup>3</sup>				<10 <sup>2</sup>	1	94
<i>Klebsiella pneumoniae</i>	13		10 <sup>8</sup>				6	45-91
<i>Leuconostoc</i> sp.	2		10 <sup>7</sup>			10 <sup>7</sup>	2	2-3
<i>Staphylococcus</i> sp.	6	10 <sup>5</sup>		10 <sup>7</sup>			4	0
<i>Yersinia enterocolitica</i>	1				<10 <sup>2</sup>		0	
Unknown A	2			10 <sup>4</sup>			0	
Unknown B	1				10 <sup>7</sup>		0	
Unknown C	1				10 <sup>8</sup>		0	

\*One saguaro sample, 77-30 (Arizona no.), and two organ pipe samples, 77-31 and 77-32, collected at Sil Nagya, Arizona in September 1977; and two agria samples, 77-33 and 77-34, collected at Punta Arenas in Sonora, Mexico in November 1977.

\*\*Expressed as % ethanol (v/v) x 10<sup>3</sup>, minimum value-maximum value.

(1/8 inch x 5 foot stainless steel column packed with Poropak Q at 140°C and 170°C oven temperatures) was used to determine if methanol, ethanol, acetone, 2-propanol, and 1-propanol were produced both in the rot pockets and by the isolates (grown in 0.5% glucose fermentation broth for 3-4 days).

Forty-six isolates representing 9 genera, 13 species, and 3 unknowns were obtained from the 5 samples of necrotic cactus (Table 1). The majority are in the family Enterobacteriaceae and are true phytobacteria. *Yersinia enterocolitica*, *Escherichia coli*, and *Klebsiella ozaenae* are not true phytobacteria. *Klebsiella pneumoniae*, previously associated only with inflammations of the respiratory tract, has recently been found in the heartwood and sapwood of living redwood trees (Bagley et al. 1978). *Enterobacter aerogenes*, *E. cloacae*, and *Erwinia carnegleana* are the only species from our study that were isolated from saguaro and cardon by Graf (1965).

Of the volatiles tested, only ethanol was produced in detectable quantities by the bacterial isolates. This corroborates White and Starr (1971) who found that 65 of 71 strains of Enterobacteriaceae produced ethanol. The cacti contained not only ethanol but also the other four volatiles as well.

Three conclusions can be made. First, the diversity of genera is high when compared with the yeasts which are represented by only four genera (Starmer et al. 1976) in the cactus substrates. Given the small sample size of five reported here, this is a minimum estimate of the diversity. Secondly, there is less similarity within than among substrates, i.e., the two agria samples have no species in common but share three species with saguaro and organ pipe, and the two organ pipe samples have only one species in common and share five species with saguaro and agria. Thirdly, the facultative anaerobes contribute only to the ethanol content. Alcohols are also produced by bacteria (i.e., obligate anaerobes) not isolated in this study (unpublished data). This investigation is a first approximation of the facultative anaerobes and suggests a much higher diversity of these bacteria than yeasts.

References: Bagley, S.T., R.J. Seidler, H.W. Talbot, Jr., and J.E. Morrow 1978, *Appl. Environ. Microbiol.* 36:178-185; Buchanan, R.E. and N.E. Gibson (co-eds.) 1974, *Bergey's Manual of Determinative Bacteriology*, 8th ed., Williams & Wilkins; Graf, P.A. 1965, Master's Thesis, Univ. of Arizona; Heed, W.B. 1978, *in* Proceedings in the Life Sciences (Symposia on Genetics and Ecology: The Interface), P.R. Brussard (ed.), Springer-Verlag (in press); Lieghtle, P.E., E.T. Standring and J.G. Brown 1942, *Phytopath.* 32:303-313; Starmer, W.T., W.B. Heed, M. Miranda, M.W. Miller and H.J. Phaff 1976, *Microb. Ecology* 3:11-30; White, J.N. and M.P. Starr 1971, *J. Appl. Bacteriol.* 34:459-475.

Zacharopoulou, A., G. Yannopoulos and N. Stamatis. University of Patras, Patras, Greece. Cytological localization of the "cn" (cinnabar) locus in *D. melanogaster*.

For localizing cytologically the "cn" locus we have used the deficiencies induced by a wild lethal chromosome II (Symbol 23.5). The previously mentioned chromosome was isolated from a female captured in 1978 from the same natural population of Southern Greece (Peloponnesse-Patras) where the male recombination

factor 31.1 MRF was found by Yannopoulos and Pelecanos (1977). Wherever heterozygous F<sub>1</sub> 23.5/dp b cn bw sons of the cross ♀♀ dp b cn bw; ve x 23.5/CyL<sup>4</sup> ♂♂ were individually mated with dp b cn bw; ve virgin females, high frequencies of cn individuals were observed, sometimes reaching up to 2.50%. Moreover, the 23.5 chromosome was found to induce sterility, male recombination, etc. (Stamatis, in preparation). Ten cn individuals derived from different F<sub>1</sub> 23.5/dp b cn bw males were separately mated with dp b cn bw; ve virgin females. Salivary chromosomes from third instar larvae were then examined for deficiencies. Eight out of the ten males tested have shown detectable deficiencies in the 2R chromosome, namely: (1) Df(2R)43C;44C, (2) Df(2R)42E;43F, (3) Df(2R)43D;44A, (4) Df(2R)43B;44D, (5) Df(2R)43C;44C, (6) Df(2R)42E;44A, (7) Df(2R)43D;43E, (8) Df(2R)43E. The breakpoints were recognized on the basis of photographic maps of Lefevre (1976).

An approximate estimation of the distribution of the breakpoints on the chromosome is presented in Fig. 1. The figure shows that all eight deficiencies include the region 43E<sub>3</sub>-E<sub>14</sub>. This finding strongly suggests that the "cn" locus is located in this region.

References: Lefevre, G., Jr., 1976, *in* The Genetics and Biology of *Drosophila la* (A. Ashburner and E. Novitski, eds.); Yannopoulos, G. and M. Pelecanos 1977, *Genetical Research* (Cambridge), 29:231-238.

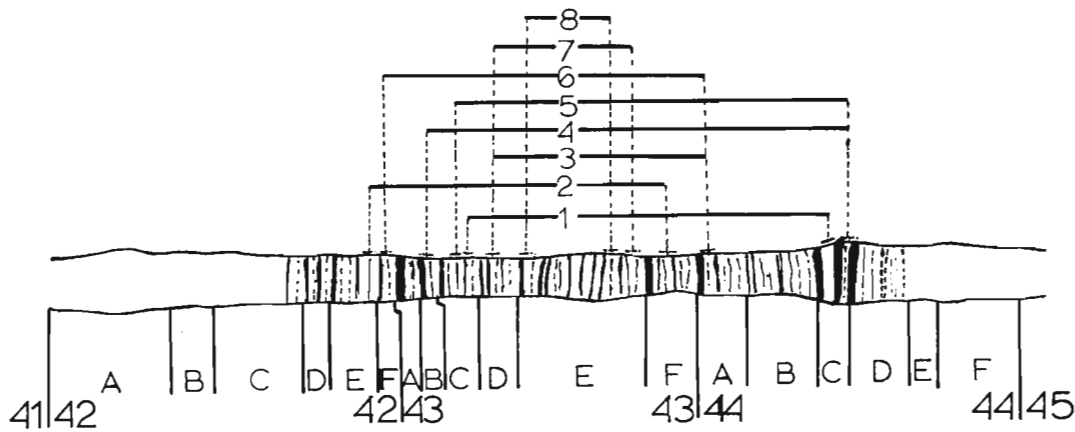


Fig. 1

Zouros, E. Dalhousie University, Halifax, Nova Scotia, Canada. An autosome-Y chromosome combination that causes sterility in *D. mojavensis* x *D. arizonensis* hybrids.

The sibling species *D. arizonensis* and *D. mojavensis* can be crossed and produce hybrids which, with the exception of males from the cross ♀ *arizonensis* x ♂ *mojavensis*, are fertile. The two species show partial ethological isolation.

To study the chromosomal basis of this isolation I established two stocks of *arizonensis* and two stocks of *mojavensis* each of which was homozygous for an electrophoretic marker at each of the four autosomes (no marker was available for the fifth dot-like autosome). The *arizonensis* markers had different electrophoretic mobilities than the *mojavensis* markers. The loci-markers are: ODH, ADH, PGM, and Amy. These four loci reside each at a different autosome. Using inversions as markers it was found that ODH is on chromosome II (chromosome designation of Wasserman 1962), and ADH is on chromosome III. PGM is either on chromosome IV, in which case Amy is on V, or on V, in which case Amy is on IV. The fact that the two species bear no cytological differences at these two chromosomes makes it impossible to distinguish between the two possibilities.

Table 1. Combinations of autosomes that show no sperm motility of  $Y_a/X_m$  flies.

Chromosome combination			Sperm motile	Sperm immotile
II <sub>m</sub> /m	III <sub>m</sub> /m	PGM <sub>m</sub> /m	0	7
II <sub>m</sub> /m	III <sub>m</sub> /m	PGM <sub>m</sub> /a	3	0
II <sub>m</sub> /m	III <sub>a</sub> /m	PGM <sub>m</sub> /m	0	3
II <sub>m</sub> /m	III <sub>a</sub> /m	PGM <sub>a</sub> /m	6	0
II <sub>a</sub> /m	III <sub>a</sub> /m	PGM <sub>m</sub> /m	0	2
II <sub>a</sub> /m	III <sub>a</sub> /m	PGM <sub>a</sub> /m	3	0

$F_1$  males from the cross ♀ *mojavensis* x ♂ *arizonensis* were backcrossed to females *mojavensis* and the sperm motility of the resulting males was examined. It was found that half the males had immotile sperm and that this phenomenon has a single chromosomal basis. In Table 1 the chromosomal constitution of 24 males is shown together with the information about sperm motility. These males were not

scored for Amy, so information about one autosome is missing. With regard to sex chromosomes all males were  $Y_a/X_m$  (a = *arizonensis* origin, m = *mojavensis* origin). It is seen that PGM<sub>a</sub>/m males have motile sperm, whereas PGM<sub>m</sub>/m males have immotile sperm. Subsequent crosses have shown that this phenomenon is strain-independent. To establish that presence or absence of sperm motility in  $Y_a/X_m$  males depends solely on the PGM-marked autosome, I derived a line through repeated backcrosses to *mojavensis* females in which all autosomes were m/m, except the PGM-marked autosomes for which males were either m/m or m/a. Of these, those of the first type had immotile sperm, those of the second type had motile sperm.

The observation is of some interest because it points to an interaction between an autosome and the Y chromosome: when the Y is of *arizonensis* origin then at least one PGM-autosome of *arizonensis* origin is required for sperm motility. It may be coincidental that the auto-

some involved is the same one that in other species of *Drosophila* (e.g. *pseudoobscura*) has fused with the X arm to produce a metacentric X chromosome. If the same phenomenon were observed in *pseudoobscura* it would appear as an X/Y interaction.

Males of immotile sperm are capable of mating and transmitting sperm into female receptacles as the following experiment showed. Single pairs consisting of a *mojavensis* female and a Ya/Xm male were kept for 24 hours and the females were examined for presence of sperm. Out of 87 such pairs 40 showed sperm. Of these in 32 cases the male was PGMa/m, and in 8 cases it was PGMm/m; the latter are males with immotile sperm. Of the 47 females that showed no sperm 12 had been kept with PGMa/m males, and 35 with PGMm/m males. If presence or absence of sperm corresponds to copulation or no copulation, then these data suggest that PGMm/m males are only 30% as successful in mating as are PGMm/a. Females involved in such matings lay unfertilized eggs.

#### Drosophila Ramblings

It started with Mendel<sup>1</sup>  
 a horny old monk  
 his un-natural relationships with pea-pods.  
 New mendels tap away on calculators  
 learn about floppy disks<sup>2</sup>  
 and hurry over to hear about meaningful relationships.  
 New mendels like to believe in choices  
 thus oocytes appear to be non-binding.  
 They watch the *Drosophila*  
 hoping to see something good enough  
 for an article  
 and maybe a better college town  
 like San Francisco, or Boston<sup>3</sup>.  
 We are watching the *Drosophila* Studiers.  
 We grade them by weight, color, sex, etc.  
 We pick only the strongest and most fit  
 for the very best paying *Drosophila* slots<sup>4</sup>.  
 We consider sex linked middle factors<sup>5</sup>,  
 interrupted mitosis, anaphase mypths,  
 metaphase farce, etc.  
 All these inputs are calculated and weighed  
 until we determine which *Drosophila* Researcher  
 is the most fit.  
 Those with the brownest noses have been  
 traditionally chosen,  
 Although ability to plagiarize has become  
 a significant middle factor.  
 This could be a trend in *Drosophilan* Behavioral evolution.  
 A recent journal article predicted that the next  
 PRESIDENT will be a retired *Drosophila* freak,  
 not from Georgia, but from Salsalito<sup>6</sup>.

#### Footnotes

1. Life With Mendel, Miss Sing Link, Jean Press, 1902, pp. 6.
2. IBID, pp. 964.
3. OPSIT, pp. 1148, V. 2.
4. BUF (Big Upfront Swingers), February 1979, pp. 40D.
5. Sex Linked Middle Factor Quarterly, Spring 1888, pp. 6.
6. National Enquirer, May 10, 1980, "Marta Madel reveals sex linked predictors in Presidential selection using demografic quantifiers", pp. 86.

Allemand, R., J. Biston and P.M. Mallet.  
 University of Lyon I, Villeurbanne Cedex,  
 France. An apparatus for recording free-  
 running oviposition rhythm in *Drosophila*.

To measure the oviposition rhythm in *Drosophila*, several devices have already been constructed. In these apparatuses the medium on which the flies lay their eggs is moved at a constant speed so that placement of the eggs corresponds to time of deposition. This was achieved ei-

ther by sliding the medium under the flies (David and Fouillet 1973) or by shifting the cage with the flies over the medium (Jungen and Locher 1970). In both kinds of apparatuses, the food-bearing plates must be changed every day and this change acts as an external synchronizer. Free-running experiments, in which conditions must be kept absolutely constant, are thus impossible with these devices.

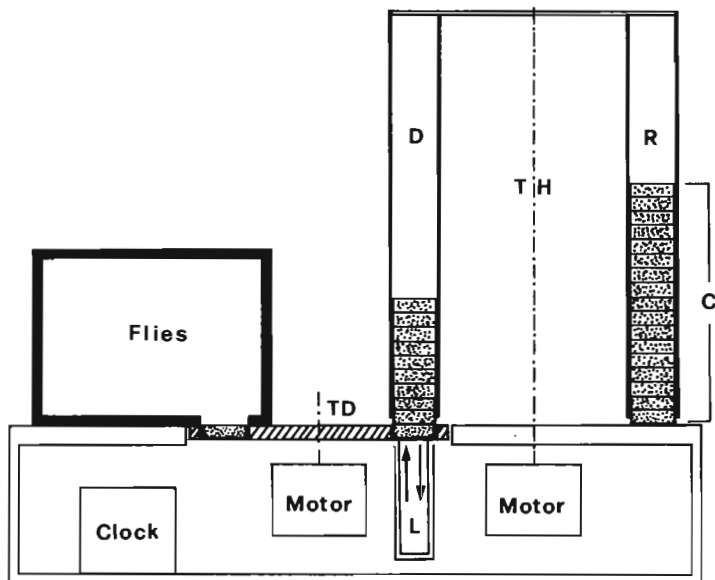
The apparatus which is described here allows free-running experiments since no handling of the flies is needed. The principle idea is to collect the eggs on small plates which are periodically changed automatically. Every hour a cup containing fresh medium is taken from a distributor, given to the flies for one hour and then put into storage in which the order corresponds to oviposition time.

**Description:** (Fig. 1) The cage containing the flies (200 cm<sup>3</sup>) is made of plastic (methacrylate) which a circular hole through the floor (diameter 2 cm) adapted to the size of the cups containing the medium. The cups (C) are plastic, cylindrical plates (diameter 2 cm, height 0.5 cm, depth 0.4 cm). The surface of medium is 2 cm<sup>2</sup>. The transferring-disc (TD) is of duraluminium and is pierced by two holes (diameter 2 cm) in order to transfer

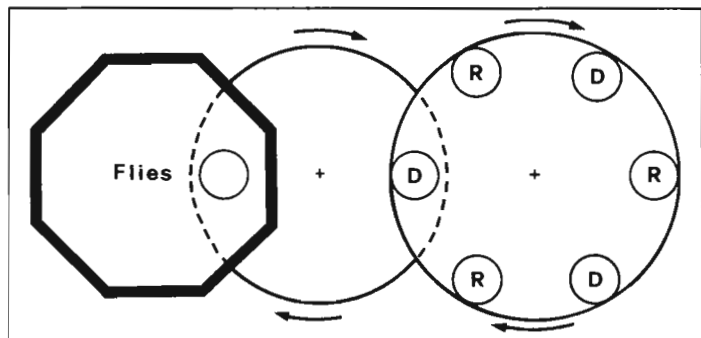
the cups. Its thickness is the same as the height of the cups (0.5 cm). The tube-holder (TH) bears six store-tubes consisting of three distributors (D) and three alternated recuperators (R). Each tube can contain 35 stacked cups, this disposition preventing the dessication of the medium.

**Functioning:** Every hour an electric pulse given by the clock causes the change of the laying plate. This change is obtained by successive linked movements which occur in the following order:

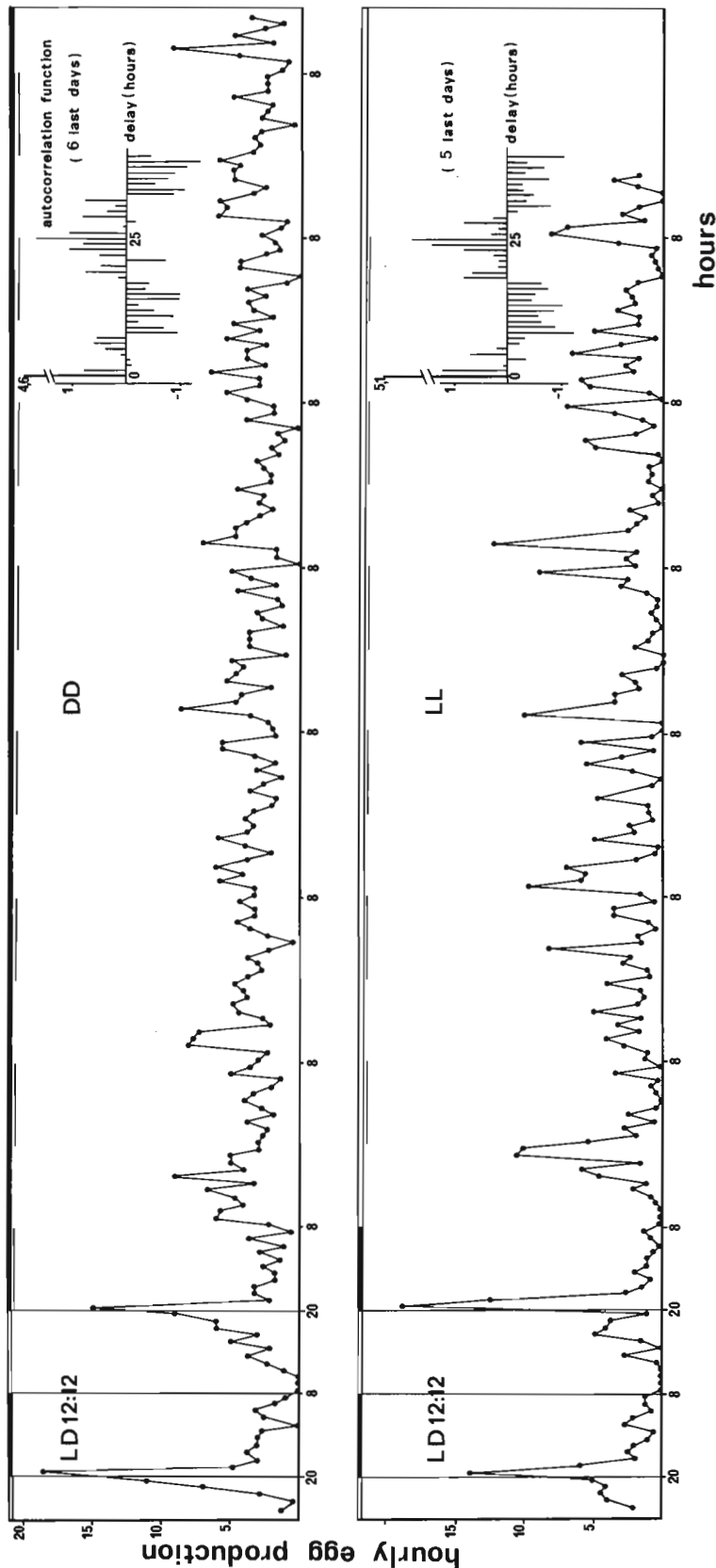
1. A distributor-tube (D) being above the transferring-disc (TD), a downward movement of the lift (L) causes the lower cup to enter a hole of the transferring disc.
2. The transferring disc turns (180°) until the fresh plate reaches the hole at the bottom of the cage. Simultaneously the plate used by the flies during the previous hour is transferred by the same movement under the tube holder (TH).
3. The tube-holder turns 60° so that a recuperator-tube (R) comes above the lift.
4. The lift which was in the lower position is moved upward and pulls up the plate into the recuperator tube. The lift then stays in the upper position.



Side-view



Top-view



5. The tube-holder turns and stops when the next distributor tube is just above the lift (60°). The apparatus has then returned to starting position.

The onset of each movement is electrically dependent on the completion of the former one, making the apparatus more reliable. When the cup is transferred from the cage to the recuperator tube, glycerol (50%) is poured over the medium in order to avoid its dessication and to prevent embryo development. The autonomy of the apparatus is 4 days (about 100 cups) but longer experiments can be carried out since the tube-holder can be changed without disturbing the flies, even in darkness.

**Results:** Fig. 2 shows two examples of oviposition rhythms in *D. melanogaster* studied during 7 days in free-running conditions. In both cases the flies lived under a LD 12:12 photoperiod and then were transferred under constant darkness or constant light. Under LD 12:12 a peak of egg deposition occurs after the light-off (Allemand 1976a). Upon suppressing the light cycle, the oviposition pattern is modified: there are no more large peaks but only small peaks. A statistical analysis showed that in both cases a free-running rhythm remained with a period of about 25 hours (see autocorrelation functions, Fig. 2), a weak amplitude and a maximum during the virtual photophases. This oviposition rhythm in free-running conditions seems to correspond to endogenous ovarian rhythm of vitellogenesis (Allemand 1976b).

**References:** Allemand, R. 1976a, *J. Insect Physiol.* 22: 1031-1035; 1976b, *J. Insect Physiol.* 22:1075-1080; David, J. and P. Fouillet 1973, *Rev. Comp. Anim.* 7:197-202; Jungen, H. and R. Locher 1970, *DIS* 45:201.

Fig. 2.

Band, H.T. Michigan State University, East Lansing, Michigan. A method for growing *Chymomyza amoena* in the laboratory.

Two behavioral traits, wing waving and aggression, seem to pose obstacles to the maintenance of *Chymomyza amoena* in the laboratory in the manner traditional for *Drosophila*. Therefore, pint-sized canning jars have been employed, tipped sideways, and capped with kleenex se-

cured by a rubber band. These are referred to as "minicages". Kerr canning jars work best since three of the four sides are clear glass. Each pint-sized jar will hold two media-filled stendor dishes (5 cm wide by 2.5 cm deep) or two or more apple quarters, which are inserted and removed with teetted forceps. Territorial defense in this species is very strong. A watercolor brush is useful for sweeping away the flies from the dishes or from the apple pieces. This method is useful for maintaining stocks, for collecting eggs, larvae or pupae and for doing feeding choice experiments.

Before media-filled stendor dishes are added, a freshly cut apple piece (skin still attached) is inserted into the media. Newly emerging flies have a prefertile period lasting about a week, so the initial dish(es) is (are) discarded, after which oviposition may be allowed to continue for another week in cages of 20-25 adults, then dishes removed, inserted into a clean jar to which is also added a piece of moist paper toweling or kleenex. Dessication is a problem but the paper also provides a pupation surface for those larvae that leave the medium to pupate. If undisturbed, most larvae pupate on the media surface or in the apple piece. Developmental time varies since egg hatchability, duration of the larval and pupal phases all vary. Minimum egg-eclosion time on the applesauce/protein/cream-of-wheat media devised for Michigan *C. amoena* seems to be 20 days.

The media has a tendency to mold. This may be cut away from the remaining surface or else larvae and pupae transferred to new dishes to continue development.

Band, H.T. Michigan State University, East Lansing, Michigan. A medium for growing *Chymomyza amoena* in the laboratory.

In Michigan, *Chymomyza amoena* adults and larvae have been found to be able to use apple as a food source. Maintenance in the laboratory on apple alone results in a decline in fertility after two generations. However, the feeding activity of the females tends to

produce a wet surface which presents another hazard when depending on laboratory media to maintain the species.

A medium developed from that devised by Wheeler and Clayton (1965) for the Hawaiian *Drosophila* and the cream-of-wheat medium developed by Spassky (1943) has worked well. The following recipe yields just over a liter of food, enough for 34-36 stendor dishes (5 cm wide x 2.5 cm deep) for use in glass "minicages":

8 gms Bacto-agar	600 ml distilled water	Blend the Hi-Pro, wheat germ, and Concentrate in a Waring blender for several minutes, add the applesauce and blend 5 min. more. Boil 400 ml water in
15 gms Gerber's Hi-Pro	500 ml Spartan applesauce (no corn products)	
15 gms Kretschner's wheat germ	3 ml propionic acid	
5 gms Kellogg's Concentrate	9 ml 95% ethyl alcohol	
45 gms Quick Cream-of-Wheat		

a large pot, add agar, stir till dissolved. Add in the applesauce-protein mixture; rinse the blender with 100 ml water and add to the food mixture. Add the remaining 100 ml water to the cream-of-wheat and stir into the food mixture as it begins to boil. Reduce heat and stir until thickened, usually about 5 minutes. Remove from heat, stirring to cool. Add the ethyl alcohol and propionic acid. The medium can then be poured into a 500 ml beaker, 300 ml at a time, for filling the stendor dishes. These are then cooled, capped and refrigerated until ready to use. No yeast is added. This medium can also be used for *D. melanogaster*, yeasted or unyeasted.

References: Spassky, B. 1943, DIS 17:67-68; Wheeler, M.R. and F.E. Clayton 1965, DIS 40:98.

Baumann, J.L. and W.L. Bischoff. University of Toledo, Toledo, Ohio. A rapid reliable assay for glucose and fructose specific hexokinases in crude extracts of *D. melanogaster*.

The initiation of a series of experiments designed to cytologically localize the hexokinase loci in *D. melanogaster* necessitated the development of a satisfactory spectrophotometric assay for this system of enzymes. Published methods designed for use with various mammalian systems proved to be unreliable due to a lack

of linearity attributable primarily to inappropriate substrate concentrations and pH optima. These problems have been overcome in our laboratory through the use of the assay procedure described below.

A. Preparation of extracts: Three to ten adult males or females aged 5±1 day post-emergence are ground in 2 ml glass microhomogenizers containing 0.05 ml of 0.03 M tris-HCl buffer at pH 8.5/fly. Homogenates thus prepared are centrifuged at 12,000 xg in the cold for 20 minutes, the supernatant fraction serving as a source of enzyme. Assays were performed within three hours of homogenization. Storage of extracts even at -70°C results in a total loss of activity after 48 hours.

B. Assay: 0.56 ml of a reaction mixture composed of 0.015 M glucose or fructose, 0.02 M MgCl<sub>2</sub>·6H<sub>2</sub>O, 0.00013 M NADP, 0.00001 M EDTA (disodium salt) and 0.12 units of glucose-6-phosphate dehydrogenase in 0.02 M tris-HCl at pH 8.5 is mixed with 0.02 ml of the above enzyme extract in a 0.75 ml Helma quartz cuvette and gently agitated. After 1 minute 0.02 ml of 0.03 M ATP is added to initiate the reaction. To assay fructose phosphorylating activity 0.12 units of phosphoglucose isomerase are added to an otherwise identical reaction mixture. Reference cuvettes contain reaction mixture, enzyme, and 0.02 ml of tris-HCl buffer in place of the ATP. The reduction of NADP is monitored at 340 NM, and under the above condition is proportional to enzyme concentration. This assay is linear for at least 30 minutes and has been successfully utilized for the cytological localization of two hexokinase loci. The results of these studies will be reported elsewhere.

Boulétreau, M. and P. Fouillet. University of Lyon, Villeurbanne, France. An accurate and reliable olfactometer.

A new olfactometer was developed in order to measure the behavioral response of flies to various odoriferous substances. The greatest concern was to allow flies to move and fly freely in a sufficient space during the exper-

iment, to prevent the olfactory cue from interfering with other directional signals such as light, drafts or gravity, and to provide an accurate control of the composition and the concentration of the odor to be tested. The device has two main originalities: the use of a large, well aerated cage in which adults can fly and exhibit normal behavior towards an odoriferous source; the use of a gas mixing pump (Wüsthoff) which mixes gases in definite ratios and delivers mixtures of reliable composition.

The cages (Fig. 1, 6) are made up of clear plastic boxes (23 x 17 x 10 cm) with large gauze panels arranged on the top and the walls. The traps (Fig. 1) are fitted on the sides of the cages and can be renewed at given intervals without disturbing the flies. Traps are fed with gas mixtures to be tested. The whole arrangement is drawn in Fig. 1: atmospheric air is compressed with a diaphragm pump (1) and dried on silica gel columns (2). It is divided into two flows respectively saturated with vapors of substances A and B in convenient saturators (3) before reaching the pump (4). The pump mixes flows (a) and (b) in the required ratios and delivers two mixing ratios M1 and M2 each of which feeds two traps. The flow in each line is regulated using a flowmeter (5) and a needle valve so as to provide 25 ml/min to each trap.

The reliability of the device was tested by measuring the response of a wild strain of *D. melanogaster* to various concentrations of ethanol. Flow (a) is first saturated with ethanol vapor by bubbling twice in 100% ethanol and then conveniently diluted with flow (b), which is kept pure. The pump delivers two concentrations of M1 and M2 of ethanol vapor which are expressed as a percentage of concentration in flow (a), which is considered as saturated. Standardized flies, 6 days old and starved for 24 hours on water + agar are put in lots of 500 (250 of each sex) in each cage. Each cage is fitted with only one trap, so that four tests are run simultaneously. The cages are 1.5 m below two 40 W fluorescent lamps, and are kept at 25° and 30% R.H.



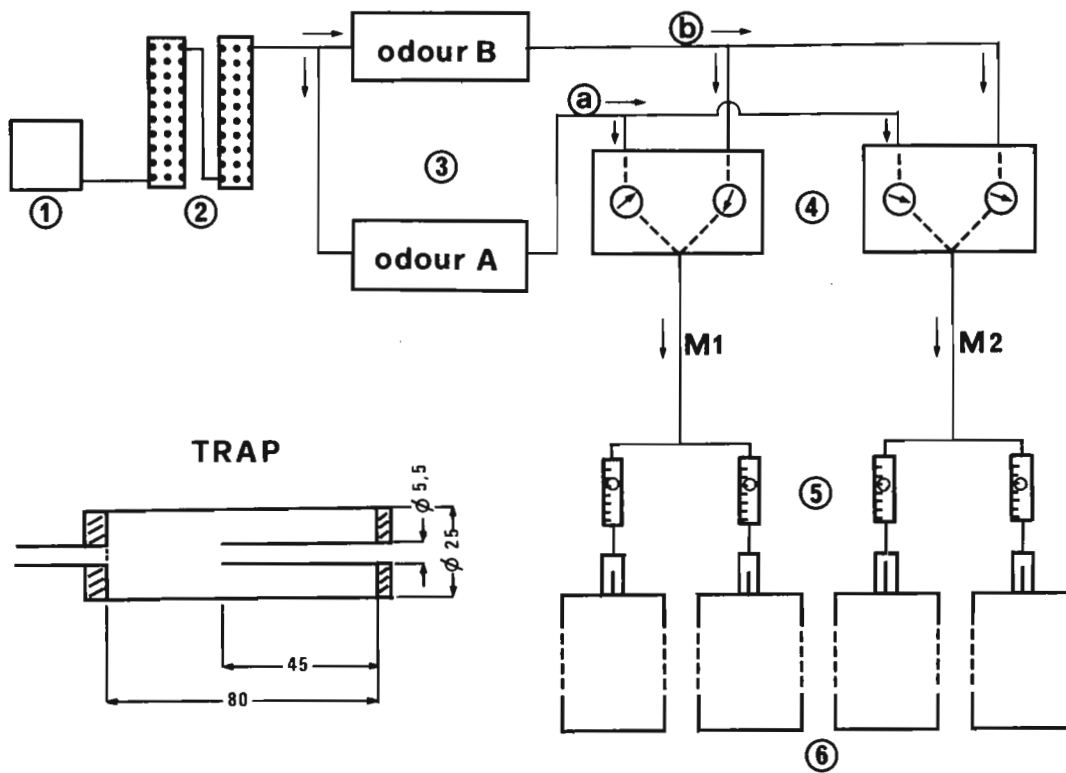


Fig. 1. Connection of the olfactometer with the air-delivery system (see text).

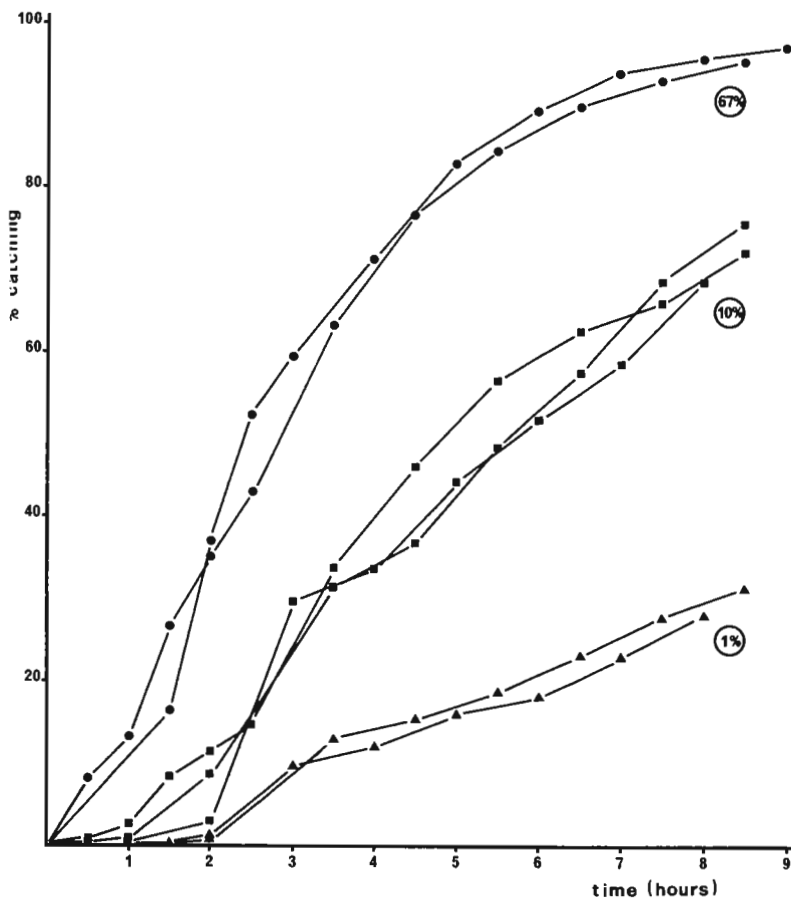


Fig. 2. Response of D.m. (wild strain) to various concentrations of ethanol vapor in dry air (1%, 10%, 67%).

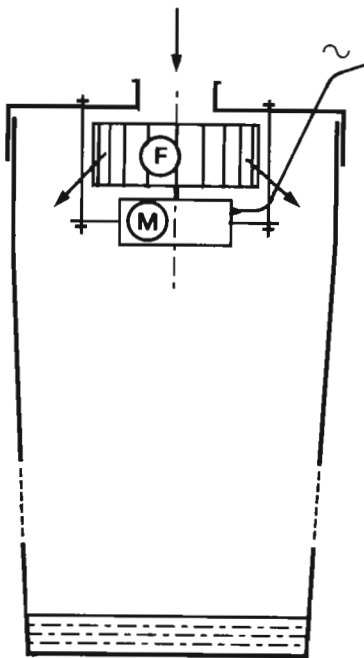
Fig. 2 gives the kinetics for three concentrations of ethanol. Each curve corresponds to the mean of two parallel boxes and is based on 1000 flies. The different curves given for each concentration were obtained in different experiments. Their similarity demonstrates the reliability of the device. The curves fit well with an exponential model, thus indicating the constancy of individual response throughout the experiment. Each concentration can thus be simply characterized by the proportion of flies which enter the trap per unit of time. No decrease in ethanol attraction occurs at higher concentrations. This observation is opposite to previous results (Fuyama 1976; Carton 1977). This difference is likely to result from the quite different methods: our device allows the humidity to be kept constant (here: 0%) whatever the concentration of ethanol. The only effect to be measured is that of ethanol. Other methods

lead necessarily to a simultaneous variation of ethanol and water contents in the tested air flow. Since in these experiments flies had to choose between this air flow and a control saturated with water, the authors actually measured some interaction between the response of flies towards ethanol and their response towards humidity. High concentrations of ethanol probably act as air dessicators, which could explain the observed repulsion.

Choice experiments can also be carried out with this olfactometer: by adjusting pump inputs and fitting two traps to each box, flies can be given a choice either between two different concentrations, or between two odor mixtures.

References: Carton, Y. 1977, Coll. Int. CNRS Tours (Fr.) 285-303; Fuyama, Y. 1976, Behavioral Genetics 6:407-420.

Boulétreau, M. and O. Terrier. University of Lyon, Villeurbanne, France. A device for getting rid of excess adult flies.



Routine rearings or experimental plans often require the daily destruction of large numbers of flies. A simple device was developed to prevent flies from escaping in the lab and to avoid disadvantages of traditional devices.

A weak electric motor (M), fitted with a plastic fan (F), hangs on the cover of a cylindrical plastic spice jar (1.5 liter). A 30 mm hole is pierced through the wall of the jar, 10 cm above the bottom. 100 ml water, added with a few drops of household detergent, are poured into the device.

By gentling drumming inverted vials or tubes above the upper hole, flies are allowed to be sucked down by the air swirl. They immediately sink to the bottom. None escape or float on the surface, thus allowing the quick drowning of next victims and making the capacity unlimited.

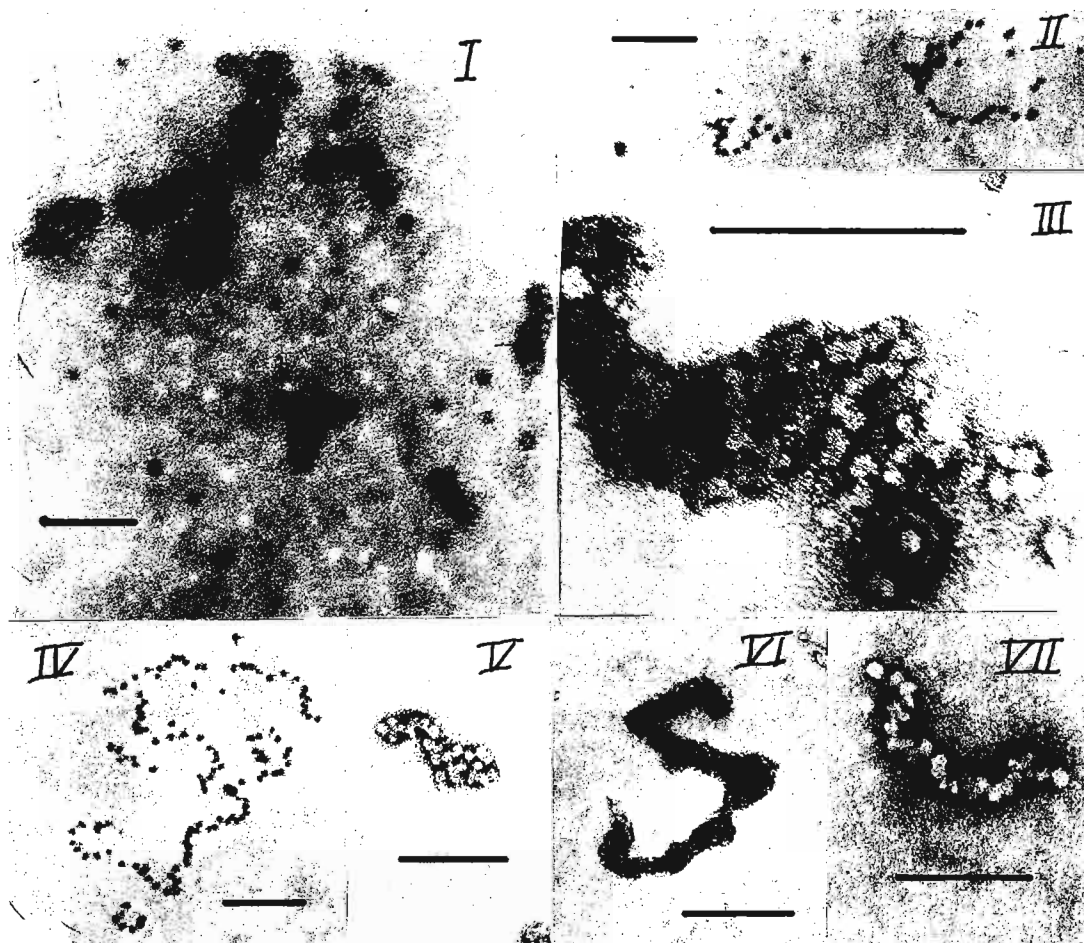
Once the daily holocaust is completed, the cover is removed, the jar is water rinsed and provided again with water + detergent. Years of daily use proved the device to be very efficient and suitable.

Crespí, S. and O. Cabré. Autonomous University of Barcelona, Bellaterra, Barcelona, Spain. A simple method for electron-microscope visualization of *D. melanogaster* embryo polysomes.

of the traduction complex. Here, we propose a very simple analytic method, with mild conditions, and material proceeding from only one egg. It allows the study by electron microscopy of processes related to translation, with minimum interference between the experimental treatment and its visualization.

The method consists of dechorionizing one egg in the embryonic stage that is to be studied. The egg is disrupted in 50  $\mu$ l of Na borate buffer  $\mu$ M pH 8.5, and left 10 min. at room temperature. 20  $\mu$ l of the sample is placed on a carbon-coated grid (300 mesh), and

The common techniques of polysome and ribosome preparation are based on relatively complex methods in which tissue homogenates, gradient centrifugations, etc., are used. These preparative methodologies are characterized in subjecting the samples to drastic treatments which can alter the native stage



Note the length of some polysomes and the apparent ribosome disposition in doublets, or the polysome in helix.

allowed to adsorb for a few minutes. The excess is removed with a lens tissue. Immediately, the grid is dipped in absolute ethanol, then in 0.5% Photo-fl6 and air dried. Finally the preparation is dyed with an ethanolic solution (70%) of uranile acetate 2%, for 30 seconds.

The micrographies shown were obtained with a transmission electron microscope Hitachi at 70 KV at different magnifications. Pictures II and IV present positive staining and the others, negative. (Bar = 250 nm).

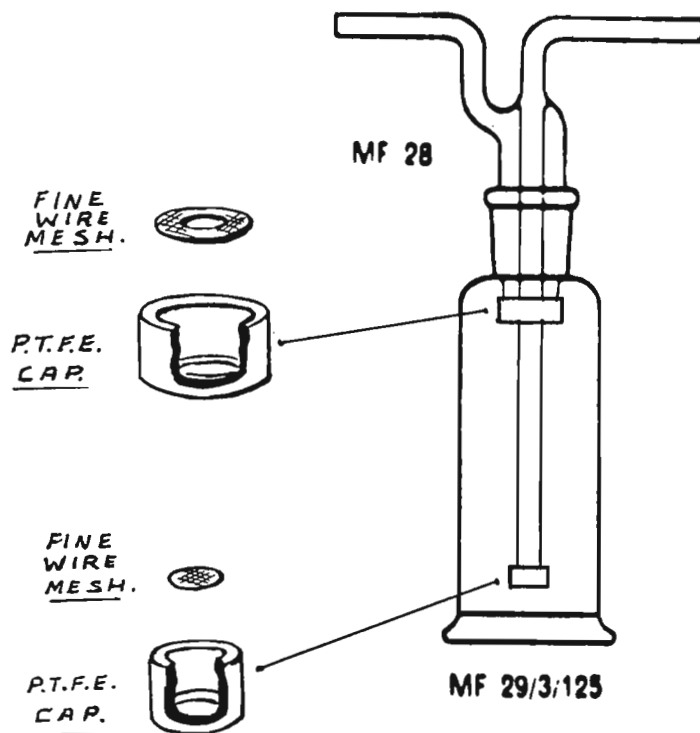
Done, J.N. and D.B. McGregor. Inveresk Research International, Ltd., Musselburgh, Scotland. A simple device for Drosophila containment during exposure to gases or vapors.

The apparatus is simply a modified Dreschel bottle. Inlet tubes on Dreschel bottles now have scintered glass discs fused into them to facilitate dispersion of the incoming gas to the washing medium. This disc must be cut off. The only other modifications necessary are those which prevent the flies from escaping.

Containment could be done by plugging inlet and outlet tubes with cotton wool or, if preferred, glass fiber. Plugging in this way does impede the flow of gases or vapors through the apparatus. With certain atmospheric analytical techniques such impediment may cause problems (e.g., infrared absorption analysis). We have, therefore, elected to prevent fly escape by closing the inlet and outlet apertures with stainless steel mesh.

A disc of the mesh is cut so as to fit the outlet aperture. Into the middle of this disc is punched a hole which is the same diameter as the external diameter of the inlet tube. The smaller mesh disc punched from the large disc is used to cover the inlet tube aperture. These mesh discs are held in their correct positions by teflon sleeves (Fig. 1).

This simple device allows the flies to be observed during exposure to dynamic test atmospheres passing through the bottle at 3-5 l/min. Following exposure, the bottle may be flushed with air then the flies lightly anesthetized with carbon dioxide before they are re-



turned to their culture vials. Temperature control, by immersion in a water bath, is also possible.

This work was supported by NIOSH Contract No. 210-78-0026.

Graf, U. Institute of Toxicology, Swiss Federal Institute of Technology and University of Zurich, Schwerzenbach, Switzerland. An easy way to test for ring configuration of ring-X-chromosomes in *D. melanogaster*.

In experiments for mutagen-induced ring-X losses there is a permanent need for verification of the ring structure of the commonly used R(1)2 chromosome. There are several ways of doing this (Leigh 1976). Since cytological analyses may be misleading (Moore 1971), the most common way is to record crossing-over in ring-X/rod-X females. In a recent series of experi-

ments we have found that this type of female produces enhanced rates of nullo-X eggs which lead to XO-male progeny. Six males from a R(1)2, y B/y<sup>+</sup>Y·B<sup>S</sup>; bw; st pP strain and five males from an identical strain with a spontaneously opened ring-X were crossed individually to virgin y cv v f females. The heterozygous F<sub>1</sub> females were then mated individually to Berlin wild males. In the F<sub>2</sub> only the male progeny were classified and counted; the bristle phenotype (forked) was not recorded. The results are shown in the table. It is evident that the females heterozygous for a ring-X chromosome produce one order of magnitude more XO-male progeny than those heterozygous for an open ring-X (5.5% and 0.1%, respectively). The presence of the ring-X is further demonstrated by the reduced frequency of females of recombinants in the progeny: The females heterozygous for the ring-X give rise to only 4.4% (57/1297) recombinants whereas the corresponding frequency of females heterozygous for the open ring-X is 35.6% (535/1503). In order to verify that the wild type male progeny are really XO, 30 of these males have been crossed to virgin w females. None of these crosses proved to be fertile.

The experiment has been repeated with the same procedure but using y w females to produce ring/rod heterozygous females. The results were essentially the same (104/2709 = 3.8% XO-males). It is therefore concluded that the registration of phenotypically distinguishable XO-males in the progeny of ring-X/rod-X females is an easier way to check for the ring structure than the laborious registration of crossing-over phenotypes.

[See table on following page.]

References: Leigh, B. 1976, Genetics and Biology of *Drosophila*, Vol. 1b, pp. 505-528; Moore, C.M. 1971, Can. J. Genet. Cytol. 13:164-166.

Supported by the Swiss National Science Foundation, Project No. 3.156-0.77.

Male No.	Yellow males									Wild type X0-males (%)	Total
	cv v +	++ B	cv v B	+++	cv + B	+ v +	cv ++	+ v B			
<u>Ring-X males</u>											
1	127	167	2	3	3	4	4	1	17 (5.2)	328	
2	147	163	1	4	1	3	3	1	17 (5.0)	340	
3	86	113	2	2	1	0	0	0	15 (6.8)	219	
4	60	66	1	4	2	1	2	2	9 (6.1)	147	
5	85	113	1	2	0	2	2	0	10 (4.7)	215	
6	61	52	0	0	0	3	0	0	8 (6.5)	124	
Sum	566	674	7	15	7	13	11	4	76 (5.5)	1373	
<u>Open ring-X males</u>											
7	91	72	18	21	22	28	0	2	0	254	
8	120	132	15	28	35	38	1	5	1 (0.3)	375	
9	77	96	18	20	26	27	0	2	0	266	
10	114	114	31	35	32	46	1	4	0	377	
11	76	76	21	17	23	15	3	1	0	232	
Sum	478	490	103	121	138	154	5	14	1 (0.1)	1504	

Gupta, A.P.<sup>†</sup> Harvard University, Cambridge, Massachusetts. [Present address: Cidade Universitaria UFRJ, Rio de Janeiro, Brazil.] A new technique for collecting *Drosophila* eggs.

Generally, *Drosophila* eggs are collected by having flies oviposit in bottles on spoons containing food medium or in petri dishes on colored food medium. The well fed adults are usually allowed to oviposit 24 to 48 hours to collect an adequate egg sample. It is difficult to collect eggs of sufficient sample size from a number of crosses or strains simultaneously. To facilitate collecting large egg samples from a number of crosses simultaneously over a short period of time, I modified the prevailing techniques with excellent results. The success of this technique depends upon starving the flies shortly before permitting them to oviposit.

25-30 pairs of newly emerged *D. pseudoobscura* were allowed to mate in vials for 5-10 days at 24°C under optimal rearing conditions. They were then transferred to empty half-pint milk bottles for 45-90 minutes at room temperature. The time of starvation is determined by noting when the activity of the flies diminishes. At this time, a teaspoon containing Carpenter's medium with food coloring and covered with a tin layer of dead or live Fleishmann's yeast suspension is put into the bottle. If dead yeast is used, prepare the solution 2-3 days before use. The thin layer of yeast suspension is allowed to dry before the spoon is put into the bottle. The back of the spoon must fit firmly against the side of the bottle to prevent females ovipositing between the spoon and the bottle. The spoons with large numbers of eggs are removed after 6-14 hours.

It would appear that the starved females retain their eggs until they once again are able to feed. At that time they lay their eggs in profusion. For a research project, I had to collect 1800 fertile eggs for each of two parental and two F<sub>1</sub> classes, for a total of 7200 eggs, to be tested simultaneously. Using this technique, I had no trouble in collecting the required number of eggs in a short period of time. The technique was further tested using 25-30 pairs of *D. melanogaster*. Approximately 1000-2000 eggs were collected in 1-3 hours. Thus this method is probably useful for collecting large numbers of eggs in a number of species in a short period of time.

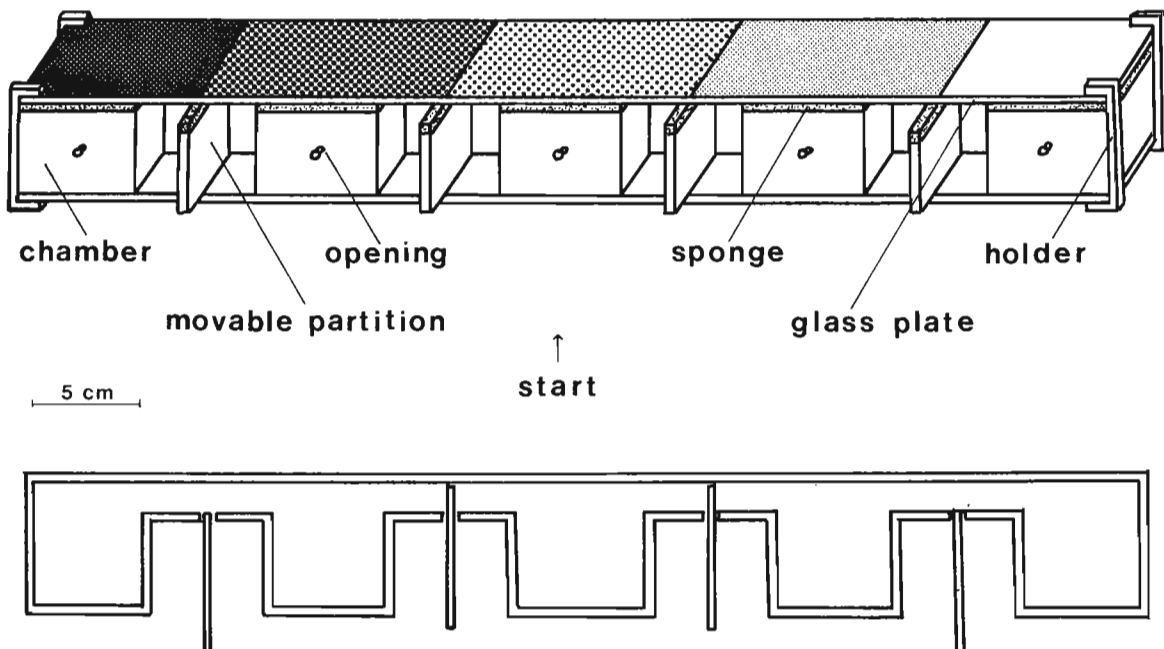
This work was supported by NIH Grant GM 21179 to R.C. Lewontin.

<sup>†</sup>In memory of Prof. Th. Dobzhansky

Kekić, V. Institute of Zoology, University of Belgrade, Beograd, Yugoslavia. Maze for the study of phototactic behavior in *Drosophila*.

In 1971 we described in DIS a maze in which it is possible to regulate, observe and measure the phototactic behavior of *Drosophila* flies in laboratory conditions. It was composed of five interconnected chambers each lighted by different light intensity. The phototactic behavior of each individual was measured by the light intensity of the chamber in which that individual was at the end of the test. By using somewhat modified version of this maze, we succeeded in completing a very successful selection of *D. subobscura* individuals for preference of "low" (30-300 lux), "medium" (1300-3200 lux) and "high" (6500 lux) light intensities. In such a way we obtained three laboratory strains of *D. subobscura* which were very different regarding their distribution in this maze (Kekić and Marinković 1974). The modified maze which we want to describe now, although not basically different from the previous two, makes a study of phototactic behavior faster and easier to a great extent.

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The maze is composed of five 5 x 5 x 2 cm chambers, which are connected by 5 x 1 x 2 cm corridors (see diagram). In the middle of each corridor there is a movable partition by which we can permit or stop the free movement of *Drosophila* individuals between chambers. In each of the chambers there is an opening through which it is possible to manipulate flies in the chamber (to introduce, to etherize, etc.). This part of the maze is made out of wood. The maze is covered by an 0.5 cm glass plate, fastened by holders. As light sources, the 20 W neon tubes are used, and gradient of light intensity is realized by the paper cover of different thickness which is put on the glass plate.

As all students of phototactic behavior of *Drosophila* well know, their behavior is always to a great extent a function of the experimental procedure. In our experiments, using the following procedure, we noticed a high percentage of repetition. At the beginning of the experiment we introduced about 100 individuals in the middle ("start") chamber of the maze. At that time the corridor partitions were closed. After 15 minutes the corridors were opened and in the following hour a free movement through the maze was permitted. After one hour the partitions between chambers were closed and the flies etherized and counted.

In Table 1 the distribution of several *Drosophila* species is shown, when the light intensity was the same in each chamber (0 or 300 lux).

It can be seen that at 300 lux the distribution of all individuals, regardless of species, is uniform, and that at 0 lux the distribution is normal, with more or less positive excess. [See table on following page.]

Table 1. The distribution of *Drosophila* species in a maze when the light intensity was the same in each chamber (300 or 0 lux).

Species	Chamber					N
	I	II	III	IV	V	
<u>300 lux</u>						
<i>D. funebris</i>	36	38	46	42	38	200
<i>D. testacea</i>	36	40	50	44	30	200
<i>D. kuntzei</i>	32	42	42	48	36	200
<i>D. melanogaster</i>	34	46	40	38	42	200
<i>D. subobscura</i>	36	44	44	40	36	200
<u>0 lux</u>						
<i>D. funebris</i>	2	20	140	30	8	200
<i>D. testacea</i>	6	26	122	36	10	200
<i>D. kuntzei</i>	10	30	122	24	14	200
<i>D. melanogaster</i>	10	20	132	28	10	200
<i>D. subobscura</i>	14	24	116	28	18	200

References: Kekić, V., D. Marinković, N. Tucić and M. Andjelković 1971, DIS 46:148; Kekić, V. and D. Marinković 1974, Behav. Genet. 4:285-300.

McInnis, D.O. Screwworm Research Laboratory, Mission, Texas. Estimation of the attractive radius for a *Drosophila* collection trap.

A vital factor in some estimates of density and dispersal rate in field populations of *Drosophila* is the attractive radius of a standard trap containing a fairly fixed amount of bait. Each trap here consisted of a 2-gallon wax-paper bucket containing two fermenting bananas as bait.

Several experiments run at Schenck Forest, a pine forest in Raleigh, North Carolina, early in the summer of 1977, were directed toward estimating the attractiveness of individual traps used in a study of dispersal rate in *Drosophila*. The procedure involved marking and releasing flies at various distances (10 meter intervals out to 50 meters) from a central point, such that at each distance flies were marked with a differently colored dust (a micronized fluorescent pigment from Helecon Industries, U.S. Radium Corp.). An attempt was made to minimize overcrowding by releasing small numbers of flies at each of several points (at least four) around concentric circles at the specified distances (Fig. 1). Then, after one full day of elapsed time, flies were collected by swinging a net above a trap located at the center. After returning

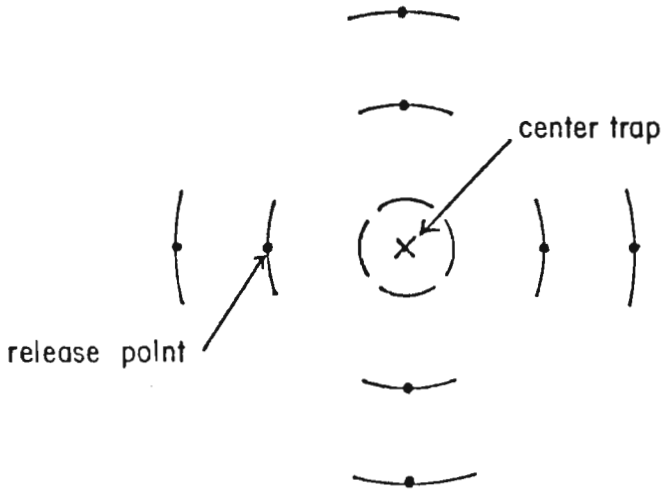


Fig. 1. Design for attractive radius determination.

to the lab, marked flies were separated from unmarked flies after shining a U.V. lamp upon the samples. The proportion of released flies from a certain distance trapped at the center is illustrated in Fig. 2. A trap placed in a relatively sheltered site yielded a greater percentage of recaptured *Drosophila* at all distances compared to a trap placed in a more open area. For both traps the distances at which a trap's power to attract reaches zero (i.e., the attractive radius) is estimated to be approximately 60 meters from the best fitting lines of linear regression.

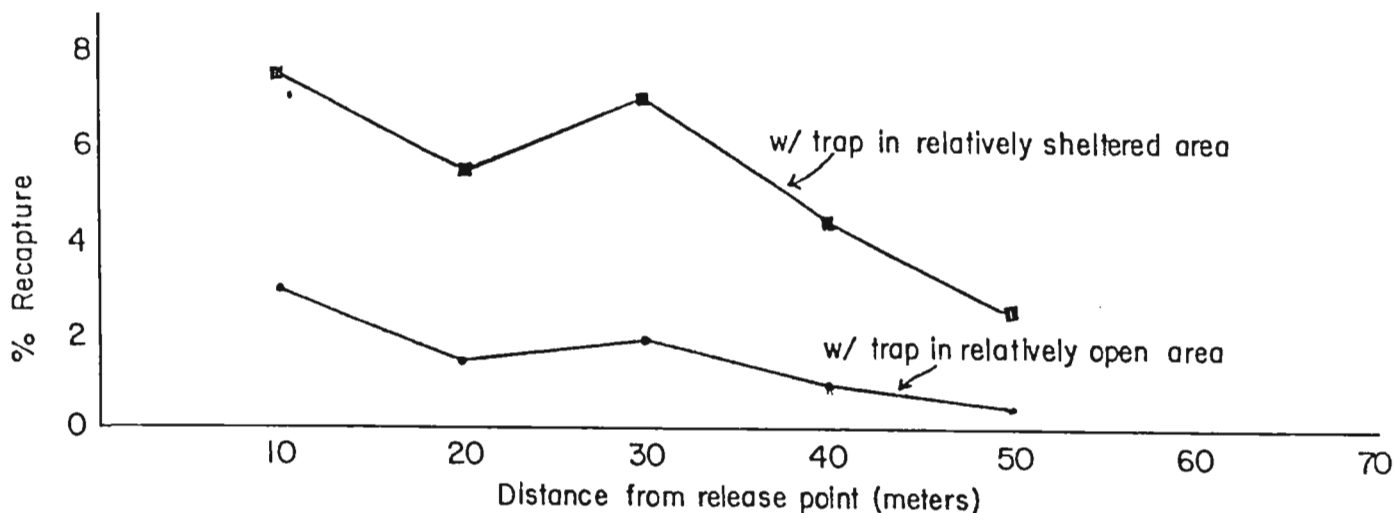


Fig. 2. Attractive radius experiments.

Platt, S.A. and M. Holliday. University of Illinois, Champaign, Illinois. A versatile apparatus for the demonstration of and selective breeding for discrimination learning in individual *D. melanogaster*.

Once instrumental learning has been demonstrated in individual *Drosophila* (Platt, Holliday and Drudge 1980), many questions concerning the parameters of the learning behavior can be investigated (e.g., what are the effects of delay of reinforcement; what is the duration of retention and memory) and the proposed components of learning might be teased apart by

selective breeding and a behavior-genetic analysis. The apparatus we are currently using to attempt to selectively breed for learning is versatile, inexpensive and easily adaptable to various critical control procedures to insure that learning is, in fact, occurring and selection is being carried out on the behavior change (learning) and not upon some stereotyped or biased response pattern.

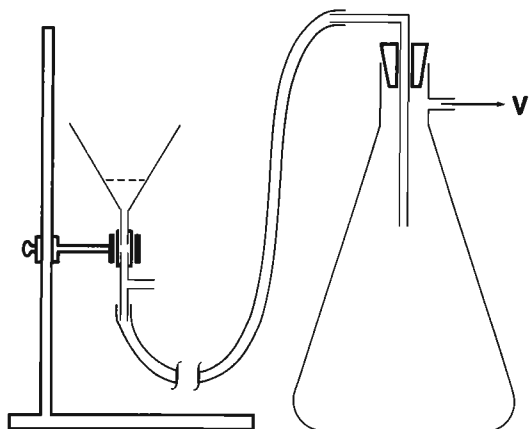
Our apparatus is constructed of modified Beral dropping pipets (Stock #B-75-100). Horizontal arms of the choice points were made by cutting the straight tubing section from the pipet and drilling a small hole in the center for receiving a pipet tip (the pipet tip was cut back about 1 cm to permit the fly to move through). In pipets to be used for the vertical alleyways, a hole was cut near the bottom to insert one arm of the T. A perforated cap cut from a pipet bulb was placed over the other arm of the T to form the cul-de-sac.

Recently we have made several useful refinements. A small ring of vinyl tubing is slid over each end of the horizontal arm. The outside diameter of the tubing ring matches the inside diameter of the cut bulb and cap. This prevents escape of the subjects and facilitates the rapid reversal of the choice point arms. About one-half of the bulb at the bottom of the vertical alley is cut off, perforated and inserted inverted. This prevents the occasional fly from descending into the bulb. We now use two different textures of white paper inside each arm of the choice points. Therefore, it is no longer possible for a fly to avoid exposure to the discriminative stimulus at the choice point. In addition, we now introduce each fly to a brief maze pre-exposure of choice points and vertical alleys all leading to the first choice point with discriminative stimuli. The pre-exposure is thought to acclimate the subject to the apparatus and reduce excessive initial choice point exploration.

Reference: Platt, S.A., M. Holliday and O.W. Drudge 1980, *J. Exp. Psych: Anim. Behav. Proc.* 6(4): in press.



Seecof, R.L. City of Hope National Medical Center, Duarte, California. An apparatus for rinsing *Drosophila* eggs.



A large quantity of eggs can be dechorionated conveniently in a beaker. The eggs can then be rinsed in a funnel with attached T connecting tube. This apparatus is small, so it can be used within a sterile hood, and the level of rinse fluid can be controlled easily so that the eggs do not dry.

Attach a funnel (Hirsch type with coarse fritted disc) to a T-shaped connecting tube (O.D., 1/4") by rubber tubing. Attach the opposite end of the connecting tube to a trap, using flexible tubing, and attach the trap to a vacuum source. Support the funnel with a ring-stand and clamp(s). Place the trap out of the working area.

Activate the vacuum. Pour the eggs into the funnel. Control the vacuum by touching a fingertip to the open end of the connecting tube. Follow with several rinses, controlling the vacuum so that eggs are not sucked dry. To prevent drainage over a long period of time, use a pinch clamp between the funnel and the connecting tube.

Partially supported by NSF Award No. PF78-09625 to R. Seecof.

#### ACCUSED PROFESSOR CLONES DEFENDANT

PALO ALTO, Calif. (DIS) Officials in this university town are shocked and confused by the latest development in a trial that began in Recommit County Court Friday. Dr. Seamon Bullvard is accused of fabricating data on a research project. It is a felony in California to fabricate data on a state-funded project. Monday prosecutor Milford Delbert told the court that he believed that the defendant was a clone. Delbert said that Dr. Bullvard was actually working in her lab while her clone sat through boring courtroom sessions and faculty and Departmental meetings. DIS reporters swarmed around the alleged clone after Wednesday's session,

See Clone Seeks Tenure, page 4

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Wild stocks

W10 Canton S  
W20 Karsnäs 51  
W30 Oslo  
W40 Sevelen

330 In(2L)Cy In(2R)Cy, Cy pr cn<sup>2</sup> sp/  
In(2LR)Gla, Gla  
340 In(2L)Cy In(2R)Cy, S2 Cy pr B1  
cn<sup>2</sup> L<sup>4</sup> bw sp<sup>2</sup>/In(2L)NS In(2R)NS,  
px sp  
350 vg

Chromosome 1 stocks

10 BSY/w mei-41D5  
20 Basc = Muller 5 = In(1)sc<sup>S1</sup>Lsc<sup>8R+S</sup>,  
sc<sup>8</sup> sc<sup>S1</sup> wa B  
30 C(1)DX, y f/y<sup>2</sup> sc ec ct<sup>6</sup> v f<sup>5</sup>  
40 Dp(1;1)sc<sup>V1</sup>, y<sup>2</sup> y<sup>+</sup> sc sc<sup>V1</sup> ec ct<sup>6</sup>  
v f<sup>5</sup>  
50 Dp(1;1)sc<sup>V1</sup>, y<sup>2</sup> y<sup>+</sup> sc sc<sup>V1</sup> ct<sup>6</sup> v  
f<sup>5</sup>/FM7c, y<sup>31d</sup> sc<sup>8</sup> wa sn<sup>X1</sup> v B  
1(1)TW-24  
60 Dp(1;1)sc<sup>V1</sup>, y<sup>2</sup> y<sup>+</sup> sc sc<sup>V1</sup> ec  
ct<sup>6</sup> v mei-218 car/FM7c, y<sup>31d</sup>  
sc<sup>8</sup> wa sn<sup>X1</sup> v B 1(1)TW-24  
70 A, B Dp(1;1)sc<sup>V1</sup>, y<sup>2</sup> y<sup>+</sup> sc sc<sup>V1</sup> mei-9b  
ct<sup>6</sup> v f<sup>5</sup>/FM7c, y<sup>31d</sup> sc<sup>8</sup> wa  
sn<sup>X1</sup> v B 1(1)TW-24 (2 strains)  
80 5, 16 Dp(1;1)sc<sup>V1</sup>, y<sup>2</sup> y<sup>+</sup> sc sc<sup>V1</sup> mei-9b  
ct<sup>6</sup> v mei-218 car/FM7c, y<sup>31d</sup>  
sc<sup>8</sup> wa sn<sup>X1</sup> v B 1(1)TW-24 (2  
strains)  
90 FM7a = In(1)FM7, y<sup>31d</sup> sc<sup>8</sup> wa v<sup>Of</sup> B  
100 FM7c, y<sup>31d</sup> sc<sup>8</sup> wa sn<sup>X1</sup> v B  
1(1)TW-24/y mei-218  
110 In(1)dl-49, fa<sup>no</sup>  
120 w  
130 w ct<sup>6</sup> f  
140 w ct<sup>6</sup> m f  
150 wa ct<sup>6</sup>  
160 y  
170 y ac v f su(f)  
180 y cv  
190 y v  
200 y v g f  
210 y v<sup>36f</sup>  
220 y w ct<sup>6</sup> m f  
230 y<sup>2</sup> sc ec cv ct<sup>6</sup> v f<sup>5</sup> car

Chromosome 2 stocks

240 a1 dp b pr c px sp/In(2L)Cy  
In(2R)Cy, a1<sup>2</sup> Cy lt<sup>3</sup> cn<sup>2</sup>  
L<sup>4</sup> sp<sup>2</sup>  
250 bw<sup>D</sup>  
260 C(2L)RM/C(2R)RM  
270 C(2L)RM, j/C(2R)RM, px  
280 cn bw  
290 dp b  
300 In(2L)Cy, a1<sup>2</sup> Cy/In(2LR)bw<sup>V1</sup>,  
ds<sup>33k</sup> dp b bw<sup>V1</sup>  
310 In(2L)Cy, a1<sup>2</sup> ast<sup>3</sup> b pr (Cy not  
present)  
320 In(2L)Cy, a1<sup>2</sup> ast<sup>3</sup> dp b pr (Cy  
not present)

Chromosome 3 stocks

360 In(3L)D, D<sup>3</sup>/In(3L)P In(3R)P  
370 In(3LR)DCxF, ru h D ca/In(3R)C,  
Sb  
380 mei-1  
390 ru h st pP ss e<sup>S</sup>  
400 ry<sup>2</sup>  
410 se  
420 st c(3)G ca/ve h th c(3)G Sb Ubx

Chromosome 4 stocks

430 C(4)RM, ci ey<sup>R</sup>.gvl sv<sup>n</sup> (no free  
4)  
440 ci ey<sup>R</sup>

Chromosome 1-2 stocks

450 su(s)<sup>2</sup> v; bw  
460 v; bw  
470 y/y<sup>+</sup>Y; b cn vg

Chromosome 1-3 stocks

480 +1/BSYy<sup>31d</sup>; In(3LR)TM3, y<sup>+</sup> ri pP  
sep Sb bx<sup>34e</sup> es Ser/mus(3)312  
490 Dp(1;1)sc<sup>V1</sup>, y<sup>2</sup> y<sup>+</sup> sc sc<sup>V1</sup> ec ct<sup>6</sup>  
v mei-218 car/FM6(=In[1]FM6,  
y<sup>31d</sup> sc<sup>8</sup> dm B); mei-1  
500 Dp(1;1)sc<sup>V1</sup>, y<sup>2</sup> y<sup>+</sup> sc sc<sup>V1</sup> mei-9b  
ct<sup>6</sup> v f<sup>5</sup>/FM7c, y<sup>31d</sup> sc<sup>8</sup> wa  
sn<sup>X1</sup> v B 1(1)TW-24; mei-1  
510 FM6(=In[1]FM6, y<sup>31d</sup> sc<sup>8</sup> dm B)/y  
me-218; mei-1  
520 FM7c, y<sup>31d</sup> sc<sup>8</sup> wa sn<sup>X1</sup> v B 1(1)TW-  
24/y mei-9b cv; mei-1  
530 wa ct<sup>6</sup>; mei-1  
540 y; mei-1  
550 y cv; mei-1

Chromosome 1-4 stocks

560 BSY/C(1)DX, y f/y Hw w; C(4)RM,  
spaP<sup>01</sup> (no free 4)  
570 Basc(=In[1]sc<sup>S1</sup>Lsc<sup>8R+S</sup>, sc<sup>8</sup>  
sc<sup>S1</sup> wa B)/y mei-9b cv/y<sup>+</sup>Y;  
spaP<sup>01</sup>  
580 C(1)DX, y f/y mei-218/y<sup>+</sup>Y; spaP<sup>01</sup>

Chromosome 2-3 stocks

590 bw; st  
600 cn bw; e11  
610 In(2L)Cy In(2R)Cy, a1<sup>2</sup> Cy lt<sup>3</sup>  
cn<sup>2</sup> L<sup>4</sup> sp<sup>2</sup>; T(2;3)bw<sup>VDe4</sup>,  
bw<sup>VDe4</sup>

Chromosome 2-3 stocks (cont'd.)

620 In(2L)Cy In(2R)Cy, al<sup>2</sup> Cy lt<sup>3</sup>  
 cn<sup>2</sup> sp<sup>2</sup>; TM2(=In[3LR]Ubx<sup>130</sup>,  
 Ubx<sup>130</sup> es); T(2;3)ap<sup>Xa</sup>, ap<sup>Xa</sup>

Chromosome 1-2-3 stocks

630 Dp(1;1)sc<sup>V1</sup>, y<sup>2</sup> y<sup>+</sup> sc sc<sup>V1</sup> ec  
 ct<sup>6</sup> v f<sup>5</sup>; +2/In(2L)Cy In(2R)  
 Cy, al<sup>2</sup> Cy lt<sup>3</sup> cn<sup>2</sup> sp<sup>2</sup>; mei-1

Chromosome 1-2-3 stocks (cont'd)

640 In(1)sc<sup>8L</sup>sc<sup>S1R</sup> In(1)S, y<sup>S1</sup> y<sup>3P</sup>  
 sc<sup>8</sup>; In(2L)Cy In(2R)Cy, al<sup>2</sup>  
 Cy lt<sup>3</sup> cn<sup>2</sup> sp<sup>2</sup>/In(2LR)bw<sup>V1</sup>,  
 ds<sup>33k</sup> dp b bw<sup>V1</sup>; In(3LR)DCxF,  
 ru h D ca/In(3R)C, Sb

Universität Münster, Dr. H. Traut, Institut für Strahlenbiologie, Hittorfstrasse 17, 4400  
 Münster, West Germany.

- |  |  |
|--|--|
| 1) + (Berlin wild)                                     | 7) y f:=& y sc <sup>S1</sup> B In49 sc <sup>8</sup> ("Binsey") |
| 2) B   | 8) y & y/y <sup>+Y</sup>                                       |
| 3) y   | 9) y f:=/y <sup>+</sup> Y & y/y <sup>+Y</sup>                  |
| 4) w   | 10) y/y/y <sup>+Y</sup> & y/y <sup>+Y</sup> ("Trisom")         |
| 5) e <sup>11</sup>                                     | 11) C(2L)RM, b; C(2R)RM, vg                                    |
| 6) y sc <sup>S1</sup> In49 sc <sup>8</sup> ; bw; st pp |  |

University of Oregon, Dr. E. Novitski, Dept. of Genetics, Eugene, Oregon.

Several distinctly new compound chromosomes have been synthesized over the past several years. They consist of entire chromosomes attached together: C(2)EN consists of two attached second chromosomes with the sequence 2R2L·2L2R; C(3)EN is 3R3L·3L3R; and C(2;3)EN is 2R2L·3L3R. Transmissibility of these chromosomes through the male is variable, ranging from a few percent to the theoretical 50%. Because of the difficulties involved in putting markers on the entire compounds and in adding markers to other chromosomes [C(2)EN and C(3)EN in particular are awkward to mark], we are listing a number of marked lines which should prove useful in certain kinds of experiments. Single arm derivatives of these chromosomes are also available.

C(2)EN,+	C(2)EN,b pr	C(2)EN,+;ru	Basc;C(3)EN,+
C(2)EN,c bw	C(2)EN,cn bw	C(2)EN,+;th st e <sup>S</sup> ca	
C(2)EN,bw			C(2;3)EN/Cy;D
C(2)EN,bw sp	C(1)RM,w;C(2)EN,+	C(3)EN,cu ca	C(2;3)EN,Ki/Cy;D
C(2)EN,sp	C(1)RM,y;C(2)EN,+	C(3)EN,cu sr st ca	C(2;3)EN,dp <sup>ov-1</sup> /Cy;D
C(2)EN,b	Basc;C(2)EN,+	y;C(2)EN,+	C(2)EN;C(3)EN

John Innes Institute, Dept. of Genetics, Colney Lane, Norwich, NR4 7UH, England.

<u>Wild stocks</u>	<u>Chromosome 1</u>	<u>Chromosome 2</u>	<u>Chromosome 3</u>
1. Florida	6. B	11. bw	16. 3
2. Hampton Hill	7. y	12. cn bw	<u>Chromosome 4</u>
3. Poringland	8. w	13. Cy	17. ey <sup>2</sup>
4. Samarkand	9. w <sup>a</sup>	14. vg	<u>Multichromosomal</u>
5. Wellington	10. w m B	15. vg bw	18. bw; e
			19. Cy L4/Pm; H/Sb

University of Swansea, Dept. of Genetics, Swansea, West Glamorgan, U.K.

<u>Wild type stocks</u>	Schio	Est-6 <sup>F</sup>	Basc	H/Sb
Australia (5 strains)	Schio	Est-6 <sup>S</sup>	ec,dx	Sb/Ubx
Canary Islands	Nazzano	Est-6 <sup>O</sup>	g	seEst <sup>F</sup> e
Groningen (Holland)	Nazzano	Est-6 <sup>VS</sup>		seEst <sup>S</sup> e
Marino (Italy)			<u>Chromosome II</u>	ve
New Jersey	<u>ADH stocks</u>		b	e
Padua	ADH <sup>F</sup>		bw75	
Peramola (Spain)	ADH <sup>S</sup>		bw81	<u>Multiples</u>
Schio (Italy)	ADH <sup>O</sup>		CyL4/Pm	bw st
Votanikos (Greece)			c	v bw <sup>D</sup>
	<u>X chromosome</u>		sple	b vg se
<u>Esterase-6 stocks</u>	C1B/fu		tkv	vg se p <sup>P</sup>
Groningen Est-6 <sup>F</sup>	y <sup>2</sup>			vg st
Groningen Est-6 <sup>S</sup>	y59b		<u>Chromosome III</u>	vg est
Schio Est-6 <sup>VF</sup>	V		ca	h <sup>7</sup> BdG/In(3R)C, 1(sA)
			H/LVM	ru, st, c(3) G sr e <sup>S</sup>

Universidad de Santiago, Depto. de Genetica, Santiago de Compostela, Spain.

<u>Mutant stocks</u>	cn	sn <sup>34e</sup>	<u>Wild-type stocks</u>
y	cn <sup>rbr</sup>	sn <sup>36a</sup>	Valencia
w	ft	Cy L4 Pm	Carboneras
b	st	XX dm f	Candás
vg	sn <sup>qr</sup>		

University of New England, Dept. of Animal Science.

<u>Wild stocks</u>	y B	y ec Oce cv ct <sup>6</sup> t <sup>3</sup> dy wy <sup>2</sup> f / FM3	<u>Chromosome 3</u>
4 strains from	B	y cx cv ct <sup>6</sup> t <sup>3</sup> dy wy <sup>2</sup> f / FM3	e11
N.S.W. & Victoria	w ct	y kz cx cv ct <sup>6</sup> t <sup>3</sup> dy wy <sup>2</sup> f / FM3	e se
	ct v f	y ct <sup>6</sup> & y f:=	st
<u>Chromosome 1</u>	y ec	m <sup>d</sup> / FM3	se
w	y cx		
w <sup>b1</sup>	y kz cx cv	<u>Chromosome 2</u>	<u>Multichromosomal</u>
y	y kg cx	vg	w; b
v	y cx cv	cn	vg; e
y w	ec Oce	dp	
y <sup>2</sup> sc1		Cy	

STOCK LISTS - OTHER SPECIESThe College of Wooster, Dept. of Biology, Wooster, Ohio 44691.D. ananassaeWild types

Cristobal: In(2L)A/+; Ins(3L+3R)A/+  
 Majuro (Futch's standard)  
 Texas-3: Ins(3L+3R)A

X chromosome

cop; Ins(3L+3R)A  
 ct<sup>5</sup>; Ins(3L+3R)A  
 ct<sup>5</sup> amb snk; Ins(3L+3R)A  
 dc; Ins(3L+3R)A  
 f<sup>49</sup> Bx2 w<sup>65</sup>; Ins(3L+3R)A  
 fw; In(2L)A/+; Ins(3L+3R)A

X chromosome (cont'd.)

g<sup>3</sup>; Ins(3L+3R)A  
 In(1L)A; Ins(3L+3R)A/+  
 m<sup>2</sup> v<sup>2</sup> g<sup>3</sup>; Ins(3L+3R)A  
 rb; Ins(3L+3R)A  
 rst; Ins(3L+3R)A  
 rst 1b v<sup>2</sup>; Ins(3L+3R)A  
 sc<sup>24</sup>; Ins(3L+3R)A  
 sn<sup>67</sup> rst y<sup>69</sup> rb; Ins(3L+3R)A  
 sn<sup>73</sup> sc<sup>33</sup> m<sup>62</sup> wt/Ins(1L+1R)  
 NG<sup>2</sup>; Ins(3L+3R)A  
 v<sup>2</sup>; Ins(3L+3R)A  
 w<sup>8</sup>; Ins(3L+3R)A  
 y<sup>69</sup>; Ins(3L+3R)A

Chromosome 2

Arc/L, In(2LR)A  
 by<sup>65</sup>  
 ca  
 ca M(2)665/Ins(2L+2R)NG<sup>2</sup>  
 cd; In(3L)A  
 cd cu ca e<sup>65</sup>/D1110, In(2L)A  
 cu ca e<sup>65</sup>  
 cu e<sup>65</sup> se, In(2L)A; In(3R)A  
 D1<sup>2</sup>/eyg, Ins(2L)A + H  
 e<sup>65</sup> pea  
 e<sup>65</sup> pea Pr gv  
 e<sup>76</sup>, In(2L)A  
 eyg, In(2L)A  
 gl, In(2L)A  
 M(2)53/Ins(2L+2R)NG<sup>2</sup>  
 M(2)108/Ins(2L+2R)NG<sup>2</sup>

M(2)127/Ins(2L+2R)NG<sup>2</sup>  
 ma; Ins(3L+3R)A  
 pea uk by<sup>65</sup>  
 Pr; In(3L)A  
 Pu<sup>3</sup> M(2)91 e<sup>65</sup> pea, In(2L)A/  
 Ins(2L+2R)NG<sup>2</sup>  
 se<sup>A</sup>; Ins(3L+3R)A  
 Tp(2L;2R)Sb/M(2)91, In(2L)A

Chromosome 3

Bb<sup>2</sup> stw/bri Rf mot, Ins(3L)  
 A,D + In(3R)A  
 bri  
 bri M(3)172/Tr ri, In(3L)A  
 bri pe stw pc px ru; In(2L)A  
 bri pe stw pc ru; In(2L)A  
 bri pe stw pc ru cy; In(2L)A  
 bri pe stw pc px ru; In(2L)A  
 c<sup>3</sup>, In(3L)A; In(2L)A/+  
 In(3R)B  
 M(3)9/bri Rf mot, Ins(3L)A,D  
 + In(3R)A  
 M(3)281/Tr ri, In(3L)A;  
 In(2L)A/+  
 mot  
 pc; In(2L)A  
 pc, In(3R)E; In(2L)A  
 pe vg<sup>N</sup> stw/Tr ri, In(3L)A;  
 In(2L)A  
 pr (Truk)  
 px; In(2L)A  
 ri; In(3L)A  
 stw

Chromosome 4

bt/M(4)7

Multichromosomal

ca; Ms ru, Ins(3L+3R)A  
 ca; stw  
 rst w<sup>65</sup>; Ins(3L+3R)A; bb<sup>74</sup>  
 T(Y;2)A, ca  
 T(Y;2)B, ca  
 T(Y;2)C, ca  
 T(Y;2;3)A, ca M stw  
 T(Y;3)A, stw  
 T(2;3)A, ca stw/Ins(2L+2R)NG<sup>2</sup>  
 T(2;3)B, ca M stw/Ins(2L+2R)NG<sup>2</sup>  
 T(2;3)E, ca stw/Ins(2L+2R)NG<sup>2</sup>  
 T(2;3)H, ca stw/M(2)91, In(2L)A  
 T(2;3)J, ca Xa stw + In(3LR)A/  
 Ins(2L+2R)NG<sup>2</sup>  
 T(2;3)K, ca stw/M(2)C Pu<sup>3</sup> e<sup>65</sup>  
 pea, In(2L)A  
 T(2;3)L, ca stw/Ins(2L+2R)NG<sup>2</sup>  
 T(2;3)M, ca stw/Pu<sup>3</sup> M(2)91 e<sup>65</sup>  
 Pea, In(2L)A  
 T(2;3)N, ca stw  
 T(2;3)O, ca stw/M(2)C Pu<sup>3</sup> e<sup>65</sup>  
 pea, In(2L)A  
 T(2;3)P, ca stw/Pu<sup>3</sup> M(2)91 e<sup>65</sup>  
 pea, In(2L)A  
 T(2;3)Q, ca stw/M(2)C Pu<sup>3</sup> e<sup>65</sup>  
 pea, In(2L)A

Descriptions and tentative mapping of all mutants and rearrangements in the above stocks can be found in Moriwaki and Tobar (1975, Handbook of Genetics 3:513-535), Hinton (1970, Genetics 66:663-676), Hinton and Downs (1975, J. Hered. 66:353-361) or in the New Mutants section of DIS 55.

University of Swansea, Dept. of Genetics, Swansea, West Glamorgan, U.K.

D. simulans

Wild type stocks

Bebek (Istanbul)  
 Canary Islands  
 Peramola (Spain)

Mutants

w

D. hydei

D. erecta

D. teissieri

D. yakuba

University of New England, Dept. of Animal Science

D. simulans

Mutants

dh b pm  
 jv se  
 st e  
 f<sub>2</sub>

University of Goteborg, Dept. of Genetics, Stigbergsliden 14, S-414 63 Goteborg, Sweden

D. funebris

650 Wild type

Report of M. Ashburner, P. Angel, C. Detwiler, J. Faithfull, D. Gubb, G. Harrington, T. Littlewood, S. Tsubota, V. Velissariou and V. Walker.

In addition to newly reported mutants and aberrations this report includes new information on aberrations induced in other laboratories that we have had occasion to study cytologically and new cytogenetic mapping of some visible and lethal loci.

black<sup>78.1D</sup> (b<sup>78.1D</sup>) [C. Detwiler]. Induced by feeding adult males 20mM diepoxyoctane. Typical black allele.

black<sup>80c2</sup> (b<sup>80c2</sup>) [P. Angel]. Induced by gamma-rays (4000R) in an adult male on a chromosome carrying Sco. Typical black allele. Associated with In(2L)b<sup>80c2</sup> (see below).

cinnabar. Since Df(2R)pk<sup>78k</sup> is cn<sup>+</sup> and this deficiency has its distal limit at 43C3 cn is probably in bands 43C4;43C6.

cinnabar<sup>80c1</sup> (cn<sup>80c1</sup>) [P. Angel]. Typical cn<sup>1</sup> like allele, induced by gamma-rays (4000R) in adult male.

elbow<sup>4</sup> (e<sup>14</sup>) [G. Harrington]. Induced after feeding EMS to adult males. Associated with T(Y;2)e<sup>14</sup> (see below).

frizzled. The cytology of fz<sup>3</sup> and fz<sup>4</sup> suggests that fz is in bands 70D6 or 70D7.

frizzled<sup>3</sup> (fz<sup>3</sup>) [V. Velissariou]. Gamma-ray induced in adult male (3800R). Associated with In(3L)fz (see below). Typical fz.

frizzled<sup>4</sup> (fz<sup>4</sup>) [V. velissariou]. Gamma-ray induced in adult male (3800R). Associated with In(3L)fz<sup>4</sup> (see below). Typical fz allele.

lethal(3)DTS-5 (DTS-5) [Holden and Suzuki 1973, Genetics 73:445]. The cytological location of DTS-5 can be refined to between 73A4 and 73B5.7 on the basis of the limits of two X-ray induced revertants of its dominant temperature sensitive phenotype that are deficiencies (i.e., Df(3L)DTS-5R+3 and Df(3L)DTS-5R+4, see below) and mapping with st- deficiencies. DTS-5 is viable when heterozygous with a deficiency that includes it at 18°C but the flies have thickened L2 wing veins.

M(3)h [see Lindsley and Grell]. This Minute maps within the region 69E2 to 69F based upon the facts that Df(3L)VW1 (see below) is M and that Lindsley et al. (1972, Genetics 71:157) place M(3)h distal to the breakpoint of T(Y;3)R7 (in 69F). M(3)h is not included in any of the vin- deficiencies of Akam et al. (1978, Cell 13:215) indicating that it is to the right of 69B4.5.

M(3)S34 [see Lindsley and Grell]. This Minute maps to bands 76A3 to 76B2 since Df(3L)VW3 (see below) is M and since M(3)S34 is proximal to the breakpoint of T(Y;3)L131 (Lindsley et al. 1972, Genetics 71:157) in 75D4.5 (see Ashburner et al. 1980, DIS 55:196).

M(3)S35 [see Lindsley and Grell]. There is some confusion as to the mapping of M(3)S35. Lindsley et al. (1972, Genetics 71:157) place M(3)S31 between 85E and 86A and M(3)S35 between 86B and 86F. We assume that this is simply a mistake since M(3)S31 is Df(3R)86D1;86D4. The map positions (Lindsley and Grell) for M(3)S35 and M(3)S35<sup>f</sup> (3-64 and 3-62.4 respectively) would suggest a cytological location in region 90, i.e., near that of sr. Yet there is no haplo-insufficient M between 86F (i.e., M(3)S31) and 94E (i.e., M(3)w). We suggest that the M responsible for the haplo-insufficient phenotype found by Lindsley et al. for region 85E-86A is M(3)S35. There is certainly an M in this region since Df(3R)VW4, that lacks 85E11 to 85F11, is M. In summary we suggest that M(3)S35 is located between 85E11 and 85F11.

no ocelli (noc). 2-50. Woodruff and Ashburner (1979, Genetics 92:117) remarked that certain genotypes heterozygous for different Adh- deficiencies were viable and lacked the ocelli and their associated bristles. Study of a much larger series of deficiencies than were then available confirms that there is a region just distal to Adh which, when

homozygously deficient, results in the absence of ocelli, of the ocellar and interocellar bristles and a reduction in the number of anterior postalar bristles. Some interocellar microchaetae may remain but, if so, their pattern is very disturbed. The postvertical bristles are also affected, there often being an adventitious pair of bristles between the normal pair of postverticals. Three alleles of this locus, here called *noc*, are described below. The expressivity of the *noc* phenotype is stronger in the late emerging flies of a culture than in those that emerge first and, moreover, the males are usually more strongly affected than females. All three known *noc* alleles enhance the expression of *Sco*; indeed *Sco* is *noc*<sup>-</sup>. Cytological analysis of *noc*<sup>-</sup> deficiencies place this locus in 35B2.3.

*noc*<sup>2</sup> [S. Tsubota]. Induced in an adult male with EMS. Expressivity much weaker than a *noc*<sup>-</sup> deficiency, three ocelli may be present though usually clearly smaller than normal. The ocelli may be present just as pigmented "ghosts". Anterior postalar bristles reduced in number and arrangement of interocellar microchaetae disturbed. Associated with *In(2L)noc*<sup>2</sup> (see below).

*noc*<sup>3</sup> [S. Tsubota]. Gamma-ray (3800R) induced in an adult male together with *Df(2R)ST1* (see below). Even weaker than *noc*<sup>2</sup>, the ocelli only rarely absent, most often just small. Like *noc*<sup>2</sup>, reduces the mean number of anterior postalar bristles and of the ocellar bristles. Disturbs pattern of interocellar microchaetae. No detectable chromosome aberration other than *Df(2R)ST1*, which is separable.

*noc*<sup>TE146</sup> [G. Ising]. This *noc* allele is associated with the *w<sup>+</sup>rst<sup>+</sup>* transposing element of G. Ising. *TE146* was derived from *TE47*, an insertion of two *w<sup>+</sup>rst<sup>+</sup>* elements into 60AB (Ising and Block, pers. comm.). Cytologically *noc*<sup>TE146</sup> has about five bands inserted into 35B2.3, and we assume that it too is duplicated for the *TE*. Acts as a very strong *noc* allele, homozygotes have no ocelli, few interocellar microchaetae and reduced numbers of ocellar and anterior postalar bristles.

outsread (*osp*). 2-50. This locus was discovered by E.H. Grell who mapped it to *Df(2L)64j*. It appears to be the locus immediately proximal to *Adh*. Weak *osp* alleles have their wings held out from the body at an angle of about 45°. Strong alleles show, in addition, a tenting of the wings, so that the flies resemble homozygotes for *arc*. As with *arc* homozygous *osp* flies may have weakly upturned wings under crowded culture conditions. Maps cytologically to 35B2.3. The following *osp* alleles were induced with EMS by feeding adult males: *osp*<sup>4</sup> [G. Harrington], *osp*<sup>6</sup> [G. Harrington], *osp*<sup>7</sup> [S. Tsubota], *osp*<sup>76e</sup> [T. Littlewood], *osp*<sup>77e</sup> [T. Littlewood]. *osp*<sup>80.1D</sup> [C. Detwiler] was induced by feeding adult males 20mM diepoxyoctane.

*pawn*. On the basis of its inclusion in *Df(2R)pk*<sup>78k</sup> and *Df(2R)pk*<sup>78s</sup> (see below) *pawn* is located in 42E3 to 43C3. Genetically *pawn* maps between *pk* and *cn* at 2-55.4.

pupal (*pu*). The following alleles of *pu* were EMS-induced by feeding adult males. With the exception of *pu*<sup>5</sup>, which shows some wing expansion when heterozygous with *pu*<sup>1</sup>, all are strong alleles at 25°C, the wings remaining as unexpanded pads: *pu*<sup>2</sup> [G. Harrington], *pu*<sup>3</sup> [G. Harrington], *pu*<sup>4</sup> [G. Harrington], *pu*<sup>5</sup> [G. Harrington] and *pu*<sup>76e</sup> [T. Littlewood].

prickle. Cytologically *pk* is in bands 42E3 to 43C3, based upon the limits of *pk*<sup>-</sup> deficiencies (see below). This does not agree with Lindsley and Grell.

reduced<sup>4</sup> (*rd*<sup>4</sup>) [P. Angel]. A gamma-ray (4000R) induced allele similar to *rd*<sup>s</sup> in phenotype, at least when heterozygous with *rd*<sup>s</sup>. As this allele was induced on a chromosome marked with *Sco*, a mutant that strongly suppresses exchange near *rd*, *rd*<sup>4</sup> homozygotes have not been obtained. *rd*<sup>4</sup>/*rd*<sup>s</sup> are female fertile. Not aberrant cytologically other than for *Sco*.

scarlet. New *st*<sup>-</sup> deficiencies allow *st* to be placed in the 73A3.4 doublet.

*st*<sup>5</sup> [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Associated with *In(3L)st*<sup>5</sup> (see below).

- spiny legs. Genetically this is on 2R (and not 2L as in Lindsley and Grell) at approximately 2-56, certainly between pk and cn. Included within both Df(2R)pk<sup>78k</sup> and Df(2R)pk<sup>78s</sup>, i.e., maps to 42E3-43C3.
- thread<sup>3</sup> (th<sup>3</sup>) [V. Velissariou]. Gamma-ray (3800R) induced together with Df(3L)st3 (see below). May be spontaneous existing in the base stock (gl<sup>2</sup> e<sup>4</sup>) prior to mutagenesis.
- transformer. Mapping tra with respect to new st<sup>-</sup> deficiencies places tra just proximal to st in band 73A5.
- vestigial<sup>79f</sup> [M. Ashburner]. Spontaneous strong vg allele on In(2L)C158.1.
- Df(2L)b80e3 [S. Tsubota]. Gamma-ray (6000R) induced, adult male. Df(2L)34C3;35B1. Includes b,j, and rk but not pu,el or Adh.
- Df(2L)b<sup>L</sup> [Bruce Baker]. This Df is Df(2L)34D3;34E3.5 and includes b,j,rk but not pu,el or Adh.
- Df(2L)C75RL<sup>L</sup>C163.41R [M. Ashburner]. Exchange product between In(2L)C163.41 and In(2L)C75RL (see DIS 55:193). New order: 21A-27D1.2/35A1.2-27D1.2/35E1.2-60. Deficient for 35A1.2; 35E1.2. May be aneuploid (either Dp or Df) in 27D since the two 27D breakpoints are derived from different events.
- Df(2L)C158.1LSco<sup>R+11R</sup> [V. Velissariou; see Velissariou and Ashburner 1980, Chromosoma 77:13]. An exchange product between In(2L)C158.1 and In(2L)Sco<sup>R+11</sup> (see DIS 55:193). Is Df(2L)35B3.5;35D1.4, including rd but neither Adh nor osp. See also Dp(2;2)C158.1LSco<sup>R+11R</sup>. New order: 21A-26D1.2/35B3.5-24D1.2/35D1.4-60.
- Df(2L)dol [C. Detwiler]. Induced by feeding adult males 20mM diepoxyoctane. Is Df(2L)35B1.2;35D1.2 including el, noc,Adh,osp and rd, but not pu.
- Df(2L)e1<sup>4</sup>DR15P [G. Harrington and M. Ashburner]. Synthesized from the Y<sup>2</sup> element of T(Y;2)e1<sup>4</sup> and the 2Y element of the "Lindsley-Sandler" T(Y;2)R15. Cytologically is Df for 35A2.4;35B10. Genetically includes pu,el,noc,Adh but not rd. Carries y<sup>+</sup>ac<sup>+</sup> from the R15 chromosome.
- Df(2L)Sco<sup>rev7</sup> [E.H. Grell; see O'Donnell et al. 1977, Genetics 86:553]. This X-ray induced revertant of Sco is cytologically Df(2L)34D5;35D5.7. As O'Donnell et al. showed it is deficient for b to rd.
- Df(2L)Sco<sup>R+23</sup>. Aneuploid segregant from T(2;1)Sco<sup>R+23</sup>.
- Df(2L)TE36-A [D. Gubb]. Induced by gamma-rays (3500R) as a w<sup>-</sup> rst<sup>-</sup> revertant of the w<sup>+</sup> rst<sup>+</sup> TE36 of G. Ising that is inserted in 1(2)br27 (see Woodruff and Ashburner 1979, Genetics 92:133). The deficiency includes 1(2)br27 and two complementation groups immediately distal, i.e., 1(2)br26 and 1(2)br7 [=Su(H)], but not rd (which is proximal to the deficiency). Acts as a dominant suppressor of Hairless.
- Df(2L)VV9 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Df(2L)30B3;30C9.
- Df(2R)pk<sup>78k</sup> [D. Gubb]. X-ray (3000R) induced in adult male. Df(2R)42E3;43C3. Includes pk,pwn,sple but not cn.
- Df(2R)pk<sup>78s</sup> [D. Gubb]. X-ray (3000R) induced in adult male. Is Df(2R)42C1.7;43F5.8 associated with In(2R)42C1.7;59F5.8 (i.e., In(2R)pk<sup>78s</sup>). Includes pk,pwn,sple and cn.
- Df(2R)ST1 [S. Tsubota]. Gamma-ray (3800R) induced in adult male together with noc<sup>3</sup>. Df(2R)43B3.5;43E18. Includes cn.
- Df(3L)DTS-5<sup>R+3</sup> [J. Faithfull]. An X-ray (3500R) induced revertant of the dominant temperature sensitive phenotype of DTS-5. Is Df(3L)72D3.6;73B5.6-C4. Includes DTS-5.st, associated with a T(Y;3) broken at 90BC.



- Df(3L)st2 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Df(3L)73A3;73A5 only. Includes st and tra.
- Df(3L)st3 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Df(3L)72E5-F1;73A4.5. Also carries an independent allele of th (th<sup>3</sup>). Includes st but neither DTS-5 nor tra.
- Df(3L)st4 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Df(3L)72E5-F1;73B5-7. Includes st, tra and DTS-5.
- Df(3L)th1 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Df(3L)71F3.5;72D6.8. Includes th. Lost.
- Df(3L)th2 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Df(3L)70F1.3;72E3.5. Dominant female sterile. Lost.
- Df(3L)VV8 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Df(3L)74B1.2;74F1.2. Lost.
- Df(3L)VW1 [V. Walker]. Gamma-ray (3800R) induced in adult male. Df(3L)69E2-F1;70C1. Minute, presumably due to M(3)h.
- Df(3L)VW3. Gamma-ray (3800R) induced in adult male. Df(3L)76A3;76B2. Minute, presumably due to M(3)S34.
- Df(3R)cu40 [J. Holden]. Cytologically Df(3R)86C1.2;86D8.
- Df(3R)VW4 [V. Walker]. Gamma-ray (3800R) induced in adult male. Df(3R)85E11;85F11. Minute, presumably due to M(3)S35 (see above).
- Dp(2;1)ScoR+23. Aneuploid segregant of T(2;1)ScoR+23.
- Dp(2;2)C158.1<sup>L</sup>ScoR+11R [V. Velissariou, see Velissariou and Ashburner 1980, Chromosoma 77: 13]. See Df(2L)C158.1<sup>L</sup>ScoR+11R. Duplicated for 24D1.2;26D1.2. As expected suppresses M(2)z<sup>B</sup>. Carries two different alleles of Sgs-1 (see Velissariou and Ashburner, loc. cit.).
- Dp(3;3)VV7 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Cytologically a reverse tandem duplication for 66E1 to 67A9. New order 61A-67A9/67A9-66E1/67A9-100.
- In(2L)b80c2 [P. Angel]. Gamma-ray (4000R) induced in adult male. In(2L)34C7;34D6.7. Associated with b80c2. Viable with b<sup>-</sup> deficiency (i.e., Df(2L)b75).
- In(2L)noc2 [S. Tsubota]. EMS induced in adult male. Associated with noc<sup>2</sup>. In(2L)35B1.2;36D3.
- In(2R)pk78s [D. Gubb]. X-ray (3000R) induced in adult male. Associated with Df(2R)pk78s. In(2R)42C1.7;59F5.8.
- In(3L)fz3 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Associated with fz<sup>3</sup>. A complex of two overlapping inversions In(3L)70D6.7;75D3.8 + In(3L)73D3.5;80-81. An In(2L)21D;36F was induced in the same sperm.
- In(3L)fz4 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Associated with fz<sup>4</sup>. A complex of two overlapping inversions In(3L)70D6.7;80-81 + In(3LR)79F;87DE. Also induced in the same sperm was a T(2;3)42F;100F.
- In(3L)st5 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. Associated with st<sup>5</sup>. In(3L)73A2.3;80C.
- In(3L)VV11 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. In(3L)64C4.8;69F3.7.
- In(3LR)P3 [E.B. Lewis]. = In(3LR)75B12.13;85D18.27.

In(3R)cu<sup>5J</sup> [J. Holden]. In(3R)84F11.12;86D1.E2. Associated with cu<sup>5J</sup>.

In(3R)VW10 [V. Velissariou]. Gamma-ray (3800R) induced in adult male. In(3R)94C;99F.

T(Y;2)e1<sup>4</sup> [G. Harrington]. Induced by adult male feeding EMS as an allele of elbow. e1<sup>4</sup>/e1<sup>1</sup> like e1<sup>1</sup> homozygotes and clearly far less extreme in phenotype than e1<sup>1</sup>/e1<sup>-</sup>. We conclude that e1<sup>4</sup> is mutant, but not deficient, for elbow. Cytologically broken at 35A2.4, Y arm not determined.

T(Y;2)TE-60V1 [D. Gubb]. Gamma-ray (3500R) induced as a partial revertant of the w<sup>†</sup>rst<sup>†</sup> TE element TE60. Variagates for white. Broken on 2L at 35D7. Y arm not determined. Male fertile.

T(1;3)N<sup>264-6</sup>. Larry Marsh and Rolf Nothiger have prompted two of us (VW and MA) to restudy the chromosomes of this translocation. Although we can say that the published description (in Lindsley and Grell) is incorrect we are not fully satisfied with all aspects of our interpretation. The "third" chromosome has the order ?/73B1.2-73F1.4/61F5.8-71B7.8/61F5.8-61A. There is clearly, as previously described, a long In(3L) but the third chromosome is also Df(3L)71B;73B. The order of the fragment 73B1.2-73F1.4 cannot be determined with certainty. It will not escape notice that this element appears to be acentric. We suspect that it is capped by the X centromere, i.e., has the order .20/73B1.2-73F1.4/61F etc., though the 73B end is not associated with the chromocenter as often as we would wish to feel confident of this interpretation.

The "X" element consists, as stated in Lindsley and Grell, of an inverted X and inserted third chromosome material. The third chromosome material has the order 75A5.11-71B7.8/73F1.4-80.81, i.e., is both inverted and deficient. This material is normally associated to the chromocenter by its third proximal (i.e., 80-81) end with the distal end free, or it synapses with a normal third. We suggest that the "X" order is ?/73A5.11-71B7.8/73F1.4-81/3C-20/3C-1A, but have no idea what "caps" at 73A5.11.

It is puzzling that this translocation should be said to variegate for pb since this gene is in 84A (Kaufman 1978, Genetics 90:579). We hope that this revised cytology will help those trying to clone tra and urge that further genetic studies of this translocation's nature are needed; these studies we are disinclined to do.

T(2;1)Sco<sup>R+23</sup> [T. Littlewood]. An X-ray (3500R) revertant of Sco. Approximately 35A1.2 to 35C1.2 has been translocated to X-base where it can be seen, in polytene nuclei, as a free fragment usually "floating" within the nucleolus. The Dp(2;1)Sco<sup>R+23</sup> and Df(2)Sco<sup>R+23</sup> segregants can be separately recovered. The duplication is homozygous female viable and fertile and male viable and fertile and covers at least from e1<sup>+</sup> through Adh<sup>+</sup> to rd<sup>+</sup>.

T(2;3)dp [Lindsley and Grell, see Woodruff and Ashburner 1979, Genetics 92:113]. A restudy of this aberration shows that the description by Bridges requires revision. This is a very complex aberration and our best estimate of its new order is: 21-27E1.2/32E2.3-34D7.E1/41-34D7.E1(?)/48A1-60; 61-80/(41-45A/27E2-32E2/45A-48A1)/81-100. Genetically T(2;3)dp is deficient for b and some nearby lethals, but not for j or rk. Our stock (from Bowling Green) is not mutant for dp, and is almost lethal with In(2LR)O,Cy dp1v1 Adh<sup>nB</sup> pr cn<sup>2</sup> and some other Cy balancers (but viable with SMI).

T(2;3)HR30 [Ashburner DIS 49:34]. Revised cytology: T(2;3)34E1.3;70C1.2.

T(2;3)Mpe [Hughes and Shelton DIS 55:204]. Revised cytology: T(2;3)35B2.3;86C1.2. Since ops is very near the 2L breakpoint of this translocation the Mpe phenotype may be due to a dominant osp allele.

T(2;3)pb<sup>3</sup> [Kaufman 1978, Genetics 90:579]. Revised cytology: T(2;3)35B3;83E2.8 + T(2;3)50C14;80 + In(3R)83E2.8;89A9.10. New order: 21-35B3/83E2.8-89A9.10/83E2.8-80/50C14-60; 61-80/50C14-35B3/89A9.10-100F. The 35B breakpoint has produced a viable recessive osp mutant allele.

T(2;3)TE94V1 [D. Gubb]. A gamma-ray (3500R) induced partial revertant of the  $w^{+}rst^{+}$  TE94 that is inserted into 2L at 34D1.2. Variegates for white. Cytologically T(2;3)34D1.2; 80-81.

T(2;3)VW2 [V. Walker]. A gamma-ray (3800R) induced T(2;3)49E-50A4;80C. Phenotypically Minute (?M(3)LS4).

Report of Elisabeth Gateff

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bgn: benign gonial cell neoplasm. On chromosome 2, between dumpy and black. EMS-induced.

Homozygous females as well as males are sterile. Pole cell differentiation is normal. The ovaries of freshly eclosed females appear to consist only of germaria. The vitellaria are present, but are obscure because they are devoid of young follicles. The germaria begin with a terminal filament. The anterior and middle portion of the germarium contains large numbers of oogonia. No clusters of cystocytes are present. Profollicle cells can, in some instances, be observed at the posterior end of the germarium.

As the flies age, oogonia from the germaria enter into the vitellaria, where they continue to divide. In older flies (7 days and above), approximately 0.1% of the cells contain two, rarely three nuclei, which have the appearance of young cystocytes. Each ovariole takes the shape of a sausage in which hundred-thousands of oogonia are tightly packed. The epithelial sheath and the tunica propria appear normal. The muscle sheath is also functional, since the ovarioles perform strong peristaltic movements.

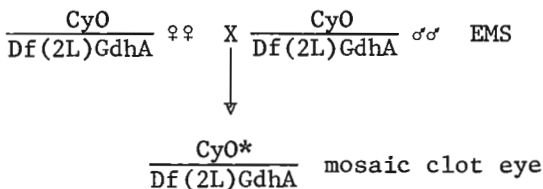
The testes of newly eclosed, as well as of older males, are smaller than wild-type testes and in some cases lack pigmentation. They are filled with spermatogonia, which closely resemble the oogonia in the mutant ovaries. At the anterior tip of the testes, the spermatogonia are in single array, while further down they can be observed sometimes in clusters of several hundreds. There is no trace of primary spermatocyte differentiation. The neoplastic growth of oogonia and spermatogonia in situ is not lethal to the mutant animals.

Young adult ovaries and testes, transplanted into the body cavity of wild-type female flies, grow autonomously in a similar, non-lethal fashion as in situ. Thus, the bgn gene mutation prevents the female and male primordial germ cells from differentiation into cystocytes and spermatocytes respectively, and thus, causes the development of benign gonial cell neoplasms in the ovaries and the testes.

Report of M. Kotarski, S. Pickert and R.J. MacIntyre

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In(2LR)O, Cy dp<sup>lvI</sup> c1<sup>3</sup> pr cn<sup>2</sup> : CyO c1<sup>3</sup>. Two new alleles of clot (cl: 2-16.5) were recovered following EMS mutagenesis (Lewis and Bacher 1968, DIS 43:193) of the CyO balancer chromosome.



The mutagenesis produced seven independently Curly, mosaic clot eyed F<sub>1</sub> flies (n ≈ 13,500), only two of which were fertile and produced F<sub>1</sub>'s that displayed a recessive eye color allelic to clot. Flies carrying c1<sup>3</sup> as CyO c1<sup>3</sup>/Df(2L)GdhA (a deficiency for clot provided by Dr. E.H. Grell) show low viability. The second isolate, In(2LR)O, Cy dp<sup>lvI</sup> c1<sup>4</sup> pr cn<sup>2</sup>, shows

much better viability when heterozygous with this deficiency.

Stocks containing both chromosomes will be sent to the stock centers.

Report of S. Kulkarni and P. Babu

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Sht: Shrunk thorax; 2-54.7. EMS-induced on second chromosome of Canton-S stock. Located  $2.8 \pm 0.4$  map units to the left of cn. The phenotype of this dominant mutation is an indentation across the dorsal mesothorax giving the appearance of shrunk thorax. Typically a groove runs across the thorax in a V shape. There is some variability in the expressivity; a small fraction of flies have only a marginal phenotype. But the penetrance is nearly complete. Newly emerged flies do not often show the phenotype or have only a faint line on the thorax; the groove becomes visible as the cuticle hardens. The mutant flies have good viability and fertility. Sht is homozygous lethal (or is closely linked to a recessive lethal).

Report of D.L. Woods and D.T. Kuhn

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iab-2: infra-abdominal-2 (3-58.8). Spontaneous mutation with bx<sup>9</sup>. Recovered in a single female from a cross between females tuh-1; tuh-3 with males sd<sup>2</sup> bx<sup>3</sup> pbx/TM1. Homoeotic mutation of second abdominal segment towards first abdominal segment. Mutation occurred in the tumorous-head 3B chromosome which carries a recessive lethal presumably associated with In(3L)P, st. Observations made on flies deficient for the iab-2 gene. Cytologically iab-2 is localized to region 89E3-5 by deficiency mapping. It is not uncovered by Df(3R)bx<sup>d100</sup> which suggests a position right of bx<sup>d</sup>, but is uncovered by Df(3R)P10 which indicates that it is to the left of iab-8. Viability good.

bx<sup>9</sup>: bithorax<sup>9</sup> (3-58.8). Spontaneous mutation found with iab-2. Anterior half of metathorax transformed towards mesothorax. A recessive mutant gene with complete penetrance, and somewhat variable expression. It deficiency maps to the left side of the Bithorax complex at 89E1,2 and is uncovered by Df(3R)P9 and Df(3R)bx<sup>d100</sup>. Viability is good.

Report of I.F. Zhimulev, E.S. Belyaeva, G.V. Pokholkova, G.V. Kotchneva, O.V. Fomina, A.V. Bgatov, Ju. Khudyakov, I. Patzevich, V.F. Semeshin, E.M. Baritcheva, M.G. Aizenzon, P. Kraemers\* and J. Eeken\*.

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\*Df(1)ras<sup>P14</sup>. X-rays [Patzevich]. Distal end (D): interband 9E1-2/9E3 - right part of the band 9E1-2. Proximal end (P): 9F4. Includes ras<sup>-</sup> to 1(1)HM5. Induced in MFR31.1 stock.

X-ray induced series of Kotchneva:

\*Df(1)sbr<sup>K1</sup> (4.0kR) D = 9B9-10; P = interband 9F13/10A1-2 - left part of 10A1-2 (mapped with EM), includes ras<sup>-</sup> to 1(1)BP3.

\*Df(1)sbr<sup>K8</sup> (4.5kR) D = 9B1-2; P = right part of 10A1-2, includes ras<sup>-</sup> to 1(1)BP4.

\*have not been mapped to the left of ras.

\*Df(1)sbr<sup>K9</sup> (4.5kR) D = 9A2-4; P = middle of 10A1-2 (mapped with EM), includes ras<sup>-</sup> to 1(1)BP4.

\*Df(1)sbr<sup>K10</sup> (5kR) D = 9A2-4; P = interband 9F13/10A1-2 - left part of the 10A1-2 (mapped with EM), includes ras<sup>-</sup> to 1(1)BP3.

Lefevre's series (Lefevre 1971):

Df(1)v<sup>64f29</sup> D = 9E7-8; P = right part of the 10A1-2 band (mapped with EM), includes 1(1)S12 to 1(1)BP4.

Df(1)v<sup>65b</sup> D = interband 9F12/9F13 - left part of the band 9F13; P = 11A8-9 (mapped with EM), includes 1(1)BP3 to dsh<sup>-</sup> (not mapped further to the right).

Df(1)v<sup>L1</sup> D = right part of the band 9F13 - interband 9F13/10A1-2; P = 10A4-5 (mapped with EM), includes v<sup>-</sup> to 1(1)BP5.

Df(1)v<sup>L2</sup> D = interband 9F12/9F13 - band 9F13; P = middle of the 10A1-2 (mapped with EM), includes 1(1)BP3 to 1(1)BP4.

Df(1)v<sup>L3</sup> D = interband 9F10-11/9F12 - band 9F12; P = band 10A7 - interband 10A6-7/10A8-9 (mapped with EM), includes fliG<sup>-</sup> to 1(1)BP7.

Df(1)v<sup>L4</sup> D = band 9F5-6; P = middle of the 10A1-2 (mapped with EM), includes sbr<sup>-</sup> to 1(1)BP4.

\*Df(1)v<sup>L7</sup> Includes ras<sup>-</sup> to 1(1)BP4.

\*Df(1)v<sup>L11</sup> Includes ras<sup>-</sup> to 1(1)BP4.

\*Df(1)v<sup>L15</sup> Includes ras<sup>-</sup> to 1(1)BP4.

X-ray induced series of Kotchneva:

\*Df(1)v<sup>M1</sup> (3.5kR) D = 9D3; P = middle of the 10A1-2 band, includes ras<sup>-</sup> to 1(1)BP4.

Df(1)v<sup>M5</sup> (3.5kR) D = right part of 9F13 band - interband 9F13/10A1-2; P = middle of 10A1-2 (mapped with EM), includes v<sup>-</sup> and 1(1)BP4.

Df(1)v<sup>M6</sup> (3.5kR) D = interband 9F10-11/9F12 - left part of 9F12; P = middle of the 10A1-2 band (mapped with EM), includes 1(1)BP3 to 1(1)BP4.

\*Df(1)v<sup>M7</sup> (3.5kR) D = 9D3, P = middle of the 10A1-2 band, includes ras<sup>-</sup> to 1(1)BP4.

\*Df(1)v<sup>P5</sup> X-rays (3.5kR) [Patzevich]. D = 9D1-2; P = middle of the 10A1-2 band, includes ras<sup>-</sup> to 1(1)BP4.

Df(1)ras-v<sup>17Cc8</sup> [Lindsley, Grell 1968]. D = 9D1-2; P = right part of the 10A1-2 band - left part of interband 10A1-2/10A3 (mapped with EM), includes ras<sup>-</sup> to sev<sup>-</sup>.

Lefevre's deficiencies (Craymer, Roy 1980):

\*Df(1)HC133 Includes ras<sup>-</sup> to 1(1)HM25.

Df(1)RA37 Includes 1(1)BP8 to dsh<sup>-</sup>.

Df(1)KA7 Includes dsh<sup>-</sup> (not mapped further to the right).

Df(1)N71 Includes dsh<sup>-</sup> (not mapped further to the right).

\*have not been mapped to the left of ras.

Dpv<sup>+</sup>63i [Lefevre 1971]. Cover ras to 1(1)L1, not cover fs(1)M43 and dsh.

Dpv<sup>+</sup>Yy<sup>+</sup> [Lefevre 1971]. Cover 1(1)HM25 to dsh.

T(1;Y)B149 [Stewart, Meriam 1973]. X-chromosome breakpoint in the left part of the 10A1-2 band, genetically to the left of v.

T(1;2)1-v219 [Lindsley, Grell 1968]. X-chromosome breakpoint in the right part of the 10A1-2 band.

T(1;3)v [Lindsley, Grell 1968; Lefevre 1970; Zhimulev et al. 1980]. X-chromosome breakpoint in the middle of the 10A1-2 band to the right of v.

ras 32.35 [Lefevre 1971]. Cytologically - broad (B): right part of 9F1-2 band - 9E7-8, narrow (N): 9E3-4; included in Df(1)v<sup>P14</sup> but not in Df(1)v<sup>64f29</sup>.

1(1)HM25 Hykanthone methan sulfonate (HMS) [Kramers], mapping between 32.53 and 32.67, cytologically - B: 9F4 - 9F5-6, N: 9F5-6; covered by Dpv<sup>+</sup>Yy<sup>+</sup> but not included in Df(1)v<sup>L4</sup>.

sbr Between 32.53 and 32.67. (33.4 according to Lindsley and Grell 1968), cytologically - B: 9F5-6 - 9F10-11, N: 9F7 - 9F10-11 (Zhimulev and Ilyina 1980).

#### Lethal alleles:

sbr<sup>1</sup>ts403 = 1(1)ts403 (Arking 1975), lethal at 29°C, semi-lethal at 25°C, escapers have small body.

1HM424 HMS (Kramers).

124/45A Male recombination factor MR<sup>h12</sup> (Eeken), induced in y mei-9a; mei 41<sup>D5</sup>.

X-ray induced series of Kotchneva:

1K2 (4kR)

1K6 (4.5kR)

1K3 (4kR)

1K7 (4.5kR)

1K4 (4.5kR)

1K11 (5.0kR)

1K5 (4.5kR)

1HM424
124/45A
1K11
1K7
1K6
1K5
1K4
1K3
1K2
1      1ts403

sbr<sup>1</sup>/1 - phenotypically = sbr<sup>1</sup>/Df (see Zhimulev, Ilyina 1980), 1/1 = lethal, 1ts403/sbr (30°C) - viable, sbr<sup>+</sup>. See complementation map above.

fliG 32.67. Cytologically - B: interband 9F10-9F12 - band 9F12, N: interband 9F10-11/9F12; included in Df(1)v<sup>L3</sup> but not in Df(1)v<sup>M6</sup>. Reduced ability to fly (Homyk, Sheppard 1977; Homyk et al. 1980), male fertility 10% of normal, reduced sex combs. Alleles: 1 (Homyk et al. 1980); 2 (Homyk, Sheppard 1977); B186, EMS (Belyaeva) semi-lethal at 18°C; dp224, EMS (Bgatov) induced in Dpv<sup>+</sup>Yy<sup>+</sup>, lethal at 18°C.

1(1)BP1 32.78. Cytologically - B: interband 9F10-11/9F12 - band 9F12, N: interband 9F10-11/9F12; included in Df(1)v<sup>L3</sup> but not in Df(1)v<sup>M6</sup>. Non-lethal allele: bir336, EMS (Fomina);

EA86
dpS42
191
G98
171
G101
bir336 Q54

in homozygotes normal and viable, against exposing deficiencies results in missing about 50% of humeral bristles, other bristles missed with frequency about 1%. The same phenotype against noncomplementing lethals. No crossovers with Q54 in 54,000 males.

Lethal alleles: Q54 = 1(1)Q54 (Lefevre 1971); 191, EMS (Belyaeva); G98, EMS (Pokholkova); 171, EMS (Pokholkova); G101, EMS (Pokholkova); dpS42, EMS (Bgatov) induced in Dpv<sup>+</sup>Yy<sup>+</sup>; EA86.

See complementation map.

1(1)BP3 32.96. Cytologically - B: interband 9F12/9F13 - band 9F13, N: right part of the 9F13 band; included in Df(1)vL<sup>2</sup> but not in Df(1)vM<sup>5</sup>. Lethal alleles: 163, EMS (Pokholkova); 167, EMS (Belyaeva); 183, EMS (Pokholkova); dpS22, EMS (Bgatov) induced in Dp v<sup>+</sup>Yy<sup>+</sup>.

y 33.00 (Lindsley, Grell 1968; Lefevre 1971). Cytologically - left part of the 10A1-2 band between T(1;Y)B149 breakpoint and proximal break of Df(1)vL<sup>4</sup>.

EMS-induced series of Belyaeva: E37, E57, E63, E70, E76, E78, E82, E84, E107, E110, AE111, E118, E119, E124, E129, E146, E154, E158, E160, E184, E195, ESB (induced in FM6).

EMS-induced series of Pokholkova: G57, G64, G73, G90, G100, G117, G121, G126, dpG1 (induced in Dpv<sup>+</sup>Yy<sup>+</sup>).

EMS-induced series of Zhimulev: BN, DK, NK, NN, OS.

EMS-induced series of Khudyakov: J9, J25.

EMS-induced series of Biyasheva (induced in Dpv<sup>+</sup>Yy<sup>+</sup>): dpZ1, dpZ2, dpZ7.

O5, O6, EMS (Fomina).

AM1, EMS (Aizenzon).

1(1)BP4 33.05. Cytologically: left part of the 10A1-2 band between T(1;4)B149 breakpoint and proximal break of Df(1)vL<sup>4</sup>. Probably allele of 1(1)L68 (Lefevre, Wiedenheft 1974).

Semi-lethal alleles: 166 and 162, EMS (Belyaeva), induced in y, viability reduced at 29°C stronger than at 25°C, escapers phenotypically normal.

Lethal alleles: EMS-induced series of Belyaeva: E109, E115, E128, E143, E147. EMS-induced series of Pokholkova: G50, G92, G99, G130, dpG1 (induced in Dpv<sup>+</sup>Yy<sup>+</sup>). J20, EMS (Khudyakov).

sev 33.38 (33.2 according to Harris et al. 1977). Cytologically - B: right edge of the band 10A1-2 - left part of the interband 10A1-2/10A3, N: right part of the 10A1-2 band; included in Df(1)vL<sup>1</sup>, Df(1)ras-v17Cc<sup>8</sup> but not in Df(1)v<sup>64f29</sup> or Df(1)sbr<sup>K8</sup>.

ms(1)BP6 Cytologically: right part of the 10A1-2 band - band 10A4-5; included in Df(1)vL<sup>3</sup>, Df(1)vL<sup>1</sup> but not in Df(1)vM<sup>6</sup>, Df(1)vM<sup>5</sup>, Df(1)vL<sup>2</sup>, Df(1)vL<sup>4</sup> and Df(1)RA37.

Allele: dpS53, EMS (Bgatov) induced in Dpv<sup>+</sup>Yy<sup>+</sup>. Males phenotypically normal, but 100% sterile in heterozygotes with exposing deficiencies.

slm 33.50 (33.7 according to Lindsley, Grell 1968). Cytologically: bands 10A3 - 10A4-5; included in Df(1)vL<sup>1</sup> but not in Df(1)RA37 or Df(1)ras-v17Cc<sup>8</sup>. All alleles including slm<sup>1</sup> (Lindsley, Grell) delay imago eclosion for about 1-2 days.

New alleles: G94, G102, EMS (Pokholkova); E136, E138, E148, E149, EMS (Belyaeva).

1(1)BP5 33.51 (33.49 according to Lefevre 1971). Cytologically: bands 10A3 - 10A4-5, included in Df(1)vL<sup>1</sup> but not in Df(1)RA37 or Df(1)ras-v17Cc<sup>8</sup>.

Lethal alleles: L12 = 1(1)L12 (Lefevre 1971). EMS-induced series of Belyaeva: E54, E112, E114, E120, 164, 169, 187, 193. EMS-induced series of Pokholkova: G62, G67, G76, G93, G95, G96, G105, G139. J21, EMS (Khudyakov). dp025, EMS (Fomina), induced in Dpv<sup>+</sup>Yy<sup>+</sup>. dpZ4, EMS (Biyasheva), induced in Dpv<sup>+</sup>Yy<sup>+</sup>. dpS145, EMS (Bgatov), induced in Dpv<sup>+</sup>Yy<sup>+</sup>. Compounds J21/164, J21/E54, E54/164 are viable both at 29°C and 25°C; J21/G96 viable at 25°C but lethal at 29°C; G76/E54 viable at 29°C and 25°C but lethal at 18°C; viability of compounds J21/G76, E54/G96 and L12/E54 normal at 25°C decreases at 29°C.

Complementation map at 25°C below.

dp025	E112
dpZ4	G105
dpS145	G95
193	G93
187	G67
169	G62
G139	L12      164
E120	J21      G96
E114	G76      E54

1(1)BP8 33.55 (33.57 according to Lefevre 1971). Cytologically: bands 10A6-10A7, included in both Df(1)v<sup>L3</sup> and Df(1)RA37, but not in Df(1)v<sup>L1</sup>.

Lethal alleles: Q66 = 1(1)Q66 (Lindsley, Grell 1968; Lefevre 1971). EMS-induced series of Belyaeva: E62, E72, 153, 174, 175, 194. G97, EMS (Pokholkova). dp05, dp024, EMS (Fomina) both induced in Dpv<sup>+</sup>Yy<sup>+</sup>. dpZ3, EMS (Biyasheva) induced in Dpv<sup>+</sup>Yy<sup>+</sup>. HMS-induced series of Kramers: HM4, HM26, HM445.

1(1)BP7 33.56 (33.55 according to Lefevre 1971). Cytologically: bands 10A6-10A7, included in both Df(1)v<sup>L3</sup> and Df(1)RA37 but not in Df(1)v<sup>L1</sup>.

Lethal alleles: L8 = 1(1)L8 (Lefevre 1971). EMS-induced series of Belyaeva: E66, E67, TE108, E142, 170. G52 and G65, both EMS-induced (Pokholkova).

1(1)L1 33.68 (33.64 according to Lefevre 1971). Cytologically: bands 10A8-9 - 10A10-11, included in Df(1)RA37 but not in Df(1)v<sup>L3</sup> or Df(1)KA7.

New allele: D40, male recombination factor MR<sup>h12</sup> (Eeken).

hfs (haplo female sterile) (See also Lefevre 1969). The locus that, if present in single dose, results in female sterility. Cytologically: bands 10A8-9 - 10A10-11, between proximal end of Df(1)v<sup>L3</sup> and distal Df(1)KA7.

dsh 34.05 (33.7 according to Lindsley, Grell 1968). Cytologically: bands 10B3-10B17, included in Df(1)RA37, Df(1)N71 and covered by Dpv<sup>+</sup>Yy<sup>+</sup>. New information: viability and fertility of males reduced sharply.

fs(1)M43 Cytologically in the region 10B1-2 - 10B17, included in Df(1)RA37 but not covered by Dpv<sup>+</sup>63i.

Allele: 14-31, female sterile (Mohler 1977), fertility of males reduced sharply, lethal against Df(1)RA37.

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#### LINKAGE DATA

Report of C.A. Strommen and R. Falk  
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The following recombination values between the sc<sup>J4</sup> translocated to the tip of chromosome 3L and the genes mwh and ru were determined: y<sup>+</sup> - mwh 1.854% (N=7550), y<sup>+</sup> - ru 2.570% (N=9106). The distance mwh-jv was found to be 16.330% (N=4954). These values are somewhat higher than those obtained by D.B. Roberts and S. Evans-Roberts (1979, Genetics 93:674) but quite lower than Muller's observations (1934, DIS 2:60).



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**ON**

**DROSOPHILA**

**PART SEVEN**

**Irwin H. Herskowitz**

## INTRODUCTION

Bibliography on Drosophila Part VII covers the literature for the period from 1973 through 1978. It contains some titles appearing before 1973 that were not listed in earlier parts of this series. As in the earlier parts, although most of the titles deal with the genetics of Drosophila, all other references to Drosophila are also included. Drosophila continues to increase in usefulness as a research organism. Whereas the average number of references per year was 964 in Part VI, it has grown to 1114 in Part VII.

The 6684 new references included in Part VII are in six sections: D.I.S., Nos. 51: 159-193 (1974); 52: 176-226 (1977); 53:219-244 (1978); 55: 218-237 and 238-262 (1980); and this issue. In each of these sections titles are arranged alphabetically according to author. For the sake of accuracy, references were checked whenever possible with either the original paper, or a copy prepared by its author. This was true for 81 per cent of the titles numbered consecutively.

For indexing, references in the first section (D.I.S., No. 51) are referred to by their page and entry: for example, 163:12 refers to the 12th entry on page 163. References in the remaining sections have been given consecutive numbers, starting with 1 in D.I.S., No. 52, and continuing through 5829 in this issue. The bibliography section in this issue is followed by a Coauthor Index and a Title Index. These indexes cover the references in all of the sections comprising Part VII.

The Title Index is divided into three parts: Part I is a general index, listing various subject headings alphabetically, concluding with headings for the X, Y, II, III, and IV chromosomes. All titles have been indexed under at least one heading. An asterisk preceding a number indicates a reference dealing with a species other than D. melanogaster, as determined from the title. Methods and names of mutants are, in almost all cases, listed alphabetically under the headings "methods" and "mutants"; Part II is a geographical listing; and Part III is a systematic index for Drosophilidae and Drosophila species.

Subscribers may find it helpful to combine the various sections from D.I.S., Nos. 51, 52, 53, and 55 with this section, to make one compact volume of Part VII.

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# TITLE INDEX

## Abbreviations

X	=	X chromosome	iz	=	isozyme
Y	=	Y chromosome	lv	=	larva
II	=	II chromosome	l	=	lethal
III	=	III chromosome	mu	=	mutation
IV	=	IV chromosome	nat	=	natural
beh	=	behavior	plm	=	polymorphism
co	=	crossing over	pop	=	population
dev	=	development	pu	=	pupa
exp	=	experimental	temp	=	temperature
inv	=	inversion	t	=	translocation

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 Ebitani, N. Nurumizu, Japan  
 Eeßen, J.C.J. Leiden, Netherlands  
 Ehrman, L. Purchase, New York  
 Elens, A. Namur, Belgium  
 Ellison, J.R. Pittsburgh, Pennsylvania  
 Elmer, W.A. Atlanta, Georgia  
 Emeny, J. Cambridge, Great Britain  
 Emerson, C.P. Charlottesville, Virginia  
 Endow, S.A. Durham, North Carolina  
 Engels, W.R. Madison, Wisconsin  
 Englert, D.C. Carbondale, Illinois  
 English, D.S. Flagstaff, Arizona  
 Engstrom, L.E. Muncie, Indiana  
 Erbaş, G. Ankara, Turkey  
 Erickson, J. Bellingham, Washington  
 Erk, F. Stony Brook, New York  
 Espinet, S.A. Miami, Florida  
 Espinós, A. Valencia, Spain  
 Fabergé, A.C. Austin, Texas  
 Faccio-Dolfini, S. Milan, Italy  
 Fahmy, M.J. Chalfont St. Giles, Great Britain  
 Fahmy, O.G. Chalfont St. Giles, Great Britain  
 Falk, R. Jerusalem, Israel  
 Farish, D.J. Columbia, Missouri  
 Farmer, J.L. Provo, Utah  
 Farnsworth, M.W. Buffalo, New York  
 Fattig, W.D. Billings, Montana  
 Fausto-Sterling, A. Providence, Rhode Isl.  
 Félix, R. Mexico City, Mexico  
 Felton, A. Cambridge, Massachusetts  
 Fenner, H. Santiago, Chile  
 Ferré, J. Lyon, France  
 Ferro, W. Leiden, Netherlands  
 Ferrus, A. Pasadena, California  
 Feuerbach-Mravlag, H. Vienna, Austria  
 Filgueiras, L. Rio de Janeiro, Brazil  
 Finley, D.W. Tempe, Arizona  
 Fleuriet, A. Clermont-Ferrand, France  
 Fontdevila, A. Santiago, Spain  
 Forbes, C. Moscow, Idaho  
 Fornili, P. Bloomington, Indiana  
 Forrest, H.S. Austin, Texas  
 Fourche, J. Lyon, France  
 Foureman, P.A. Madison, Wisconsin  
 Fowler, G. Ashland, Oregon  
 Fox, A.S. Madison, Wisconsin  
 Fox, D.J. Knoxville, Tennessee  
 Fox, D.P. Aberdeen, Great Britain  
 Frankel, A.W.K. Iowa City, Iowa  
 Frankham, R. Sydney, Australia  
 Franklin, I.R. Sydney, Australia  
 Frei, H.J. Geneva, Switzerland  
 French, W.L. Baton Rouge, Louisiana  
 Frey, F. Gif-sur-Yvette, France  
 Frias, D. Santiago, Chile  
 Friedman, L.D. St. Louis, Missouri  
 Friedman, T.B. Bethesda, Maryland  
 Friedman, T.B. Rochester, Michigan  
 Fritz-Niggli, H. Zürich, Switzerland  
 Frutos, R. de Burjaset, Spain  
 Frydenberg, O. Aarhus, Denmark  
 Fuchs, M.S. Notre Dame, Indiana  
 Fujii, H.M. Fukuoka, Japan  
 Fujii, S. Kobe, Japan  
 Fujita, S.C. Tokyo, Japan  
 Fukatamai, A. Sakado-Machi, Japan  
 Fukunaga, A. Osaka, Japan  
 Fullilove, S.L. Austin, Texas  
 Fuscaldò, K.E. Philadelphia, Pennsylvania  
 Futch, D.C. San Diego, California  
 Fuyama, Y. Tokyo, Japan  
 Fyrberg, E. Pasadena, California  
 Gabay, S.J. Urbana, Illinois  
 Gale, J.S. Birmingham, Great Britain  
 Gall, J.G. New Haven, Connecticut  
 Gallo, A.J. Sao Jose de R.P., Brazil  
 Gamo, S. Sakai, Japan  
 Ganetzky, B. Madison, Wisconsin  
 Garcia, F.A. Bogota, Colombia  
 Garcia, M. Bellaterra, Spain  
 Garcia, P. Barcelona, Spain  
 Gardner, E.J. Logan, Utah  
 Garen, A. New Haven, Connecticut  
 Garen, S. New Haven, Connecticut  
 Gartner, L.P. Baltimore, Maryland  
 Gärtner, S. Basel, Switzerland  
 Gateff, E. Freiburg, W.Germany  
 Gatti, M. Rome, Italy  
 Gay, H. Ann Arbor, Michigan  
 Gay, P. Gif-sur-Yvette, France  
 Gayathri, M.V. Mysore, India  
 Geer, B.W. Galesburg, Illinois  
 Gehring, W. Basel, Switzerland  
 Gelbart, W.M. Cambridge, Massachusetts  
 Gepner, J.I. Cambridge, Massachusetts  
 Gerresheim, F. München, W.Germany  
 Gersh, E.S. Philadelphia, Pennsylvania  
 Gertson, P.N. Salt Lake City, Utah  
 Gethmann, R.C. Catonsville, Maryland  
 Ghosh, M. Calcutta, India  
 Ghosh, R. Calcutta, India  
 Ghosh, S. Calcutta, India  
 Gibson, P.K. Urbana, Illinois  
 Gill, K.S. Ludhiana, India  
 Gill, R.W. Riverside, California  
 Girard, P. Paris, France  
 Glanzman, F. Tempe, Arizona  
 Glätzer, K.H. Düsseldorf, W.Germany

- Gloor, H. Geneva, Switzerland  
 Godbole, N.N. Poona, India  
 Godoy, R. Santiago, Chile  
 Goldstein, E. Tempe, Arizona  
 González, A. Burjaset, Spain  
 González, F.H. Lima, Peru  
 González, F.W. Upton, New York  
 González, R. Barcelona, Spain  
 Gopalan, H.N.B. Nairobi, Kenya  
 Gottlieb, F.J. Pittsburgh, Pennsylvania  
 Gottlieb, J.F. Purchase, New York  
 Götz, K.G. Tübingen, W.Germany  
 Gould, A.B. Newark, Delaware  
 Gouz, J.M. Paris, France  
 Grabiki, E. New Haven, Connecticut  
 Grace, D. Eugene, Oregon  
 Graf, U. Zürich, Switzerland  
 Grainger, R.M. Charlottesville, Virginia  
 Granobles, L.A. Bogota, Colombia  
 Grant, B.S. Williamsburg, Virginia  
 Green, L.H. Cambridge, Massachusetts  
 Green, M.M. Davis, California  
 Greenleaf, A.L. Durham, North Carolina  
 Grell, E.H. Oak Ridge, Tennessee  
 Grell, R.F. Oak Ridge, Tennessee  
 Gromko, M. Bowling Green, Ohio  
 Grossfield, J. New York, New York  
 Grünberg, H. London, Great Britain  
 Gubb, D. Cambridge, Great Britain  
 Guest, W.C. Fayetteville, Arkansas  
 Guevara, P.M. Lima, Peru  
 Guillet, C. Lyon, France  
 Gupta, A.P. Rio de Janeiro, Brazil  
 Gupta, J.P. Varanasi, India  
 Guzmán, J.M.S. Mexico City, Mexico  
 Hackman, W. Helsinki, Finland  
 Hackstein, J. Nijmegen, Netherlands  
 Haendle, J. München, W.Germany  
 Hägele, K. Bochum, W.Germany  
 Hagguist, K. Umea, Sweden  
 Hale, G. New York, New York  
 Halfer, C. Milan, Italy  
 Halfer-Mosna, G. Milan, Italy  
 Hall, J.C. Waltham, Massachusetts  
 Hall, L. Bronx, New York  
 Hames, B.D. Colchester, Great Britain  
 Hanks, G.D. Gary, Indiana  
 Hammerschmidt, H. München, W.Germany  
 Hampel, H. Vienna, Austria  
 Han, J.H. Seoul, Korea  
 Han, S.R. Seoul, Korea  
 Handler, A. Pasadena, California  
 Hanly, E.W. Salt Lake City, Utah  
 Hannah, S.M. York, Great Britain  
 Hannah-Alava, A. Turku, Finland  
 Hansson, L. Umeå, Sweden  
 Hara, K. Fukuoka, Japan  
 Hardy, D.E. Honolulu, Hawaii  
 Hardy, R. La Jolla, California  
 Harford, A.G. Buffalo, New York  
 Harrington, G. Cambridge, Great Britain  
 Harrison, B.J. Norwich, Great Britain  
 Hartl, D.L. West Lafayette, Indiana  
 Hartmann-Goldstein, I.J. Sheffield, Gt. Brit.
- Harvengt, J. Louvain-La-Neuve, Belgium  
 Hauschteck-Jungen, E. Zürich, Switzerland  
 Hay, D.A. Bundoora, Australia  
 Haynie, J.L. Seattle, Washington  
 Hazelrigg, T. Bloomington, Indiana  
 Hedrick, P.W. Lawrence, Kansas  
 Hegde, S.N. Mysore, India  
 Heim, W.G. Colorado Springs, Colorado  
 Heisenberg, M. Würzburg, W.Germany  
 Hengstenberg, R. Tübingen, W.Germany  
 Hennig, W. Nijmegen, Netherlands  
 Herforth, R.S. Minneapolis, Minnesota  
 Herskowitz, I.H. New York, New York  
 Hess, O. Düsseldorf, W.Germany  
 Hexter, W.M. Amherst, Massachusetts  
 Hihara, F. Matsuama, Japan  
 Hildreth, P.E. Charlotte, North Carolina  
 Hill, R. Sydney, Australia  
 Hilliker, A.J. Canberra, Australia  
 Hillman, R. Philadelphia, Pennsylvania  
 Hinton, C.W. Wooster, Ohio  
 Hiraizumi, Y. Austin, Texas  
 Hiroyoshi, T. Osaka, Japan  
 Ho, M.W. Milton-Keynes, Great Britain  
 Hochman, B. Knoxville, Tennessee  
 Hodgetts, R.B. Edmonton, Canada  
 Hoekstra, R.F. Haren, Netherlands  
 Hoenigsberg, H.F. Bogota, Colombia  
 Hoffman, M.F. Bronx, New York  
 Hollingsworth, M.J. London, Great Britain  
 Hollis, R.J. Williamsburg, Virginia  
 Holm, D. Vancouver, Canada  
 Holmgren, P. Umeå, Sweden  
 Homyk, T. Vancouver, Canada  
 Hooper, G.B. Poughkeepsie, New York  
 Hoorn, A.J.W. Utrecht, Netherlands  
 Hotta, Y. Tokyo, Japan  
 Hsieh, T. Durham, North Carolina  
 Hubby, J.L. Chicago, Illinois  
 Hubert, U. Marburg, W.Germany  
 Hughes, M.A. Newcastle, Great Britain  
 Hunt, D.M. London, Great Britain  
 Huth, A.C. Tübingen, W.Germany  
 Ichikawa-Ryo, M. Osaka, Japan  
 Ikeda, H. Matsuyama, Japan  
 Ikeda, K. Duarte, California  
 Ikenaga, M. Osaka, Japan  
 Ilannak, G. St. John's, Canada  
 Imberski, R.B. College Park, Maryland  
 Inagaki, E. Hiroshima, Japan  
 Ingham, P. Brighton, Great Britain  
 Inocencio, B. Purchase, New York  
 Inoue, H. Osaka, Japan  
 Inoue, Y. Misima, Japan  
 Ish-Horowicz, D. London, Great Britain  
 Ishii, Y. Osaka, Japan  
 Israelewski, N. Bochum, W.Germany  
 Iturra, P. Santiago, Chile  
 Ives, P.T. Amherst, Massachusetts  
 Ivy, J. La Jolla, California  
 Iwamoto, R.N. Pullman, Washington  
 Izquierdo, E. Santiago, Spain  
 Izquierdo, J. Oviedo, Spain  
 Jacobs, M.E. Goshen, Indiana

- Jacobson, A.G. Austin, Texas  
Jain, H.K. New Delhi, India  
James, F.W. Sydney, Australia  
Janning, W. Münster, W.Germany  
Jarry, B. Marseille, France  
Jeffery, D.E. Provo, Utah  
Jelisavčić, B. Belgrade, Yugoslavia  
Jenkins, J.B. Swarthmore, Pennsylvania  
Jha, A.P. Bhagalpur, India  
Jinks, J.L. Birmingham, Great Britain  
Johns, M. Eugene, Oregon  
Johnsen, R.C. Garden City, New York  
Johnson, G.B. St. Louis, Missouri  
Johnson, K. London, Great Britain  
Johnson, W.W. Albuquerque, New Mexico  
Johnston, J.S. Austin, Texas  
Jones, G.H. Birmingham, Great Britain  
Jong, G. Utrecht, Netherlands  
Jordan, B. Marseille, France  
Jowett, T. Eugene, Oregon  
Juan, E. Barcelona, Spain  
Judd, B.H. Austin, Texas  
Jungen, H. Zürich, Switzerland  
Kaji, S. Kobe, Japan  
Kalicki, H. Garden City, New York  
Kalisch, W-E. Bochum, W.Germany  
Kambysellis, M.P. New York, New York  
Kamping, A. Haren, Netherlands  
Kaneka, A. Tokyo, Japan  
Kaneshiro, K.Y. Honolulu, Hawaii  
Kang, E. Seoul, Korea  
Kang, Y.S. Seoul, Korea  
Kang-Song, S.J. Seoul, Korea  
Kankel, D. New Haven, Connecticut  
Kaplan, M.L. New York, New York  
Kaplan, W.D. Duarte, California  
Karanja, S.N. Nairobi, Kenya  
Karlik, A. Vienna, Austria  
Karp, R. Cambridge, Great Britain  
Karpin, G. Seattle, Washington  
Kastritsis, C.D. Thessaloniki, Greece  
Kato, T. Osaka, Japan  
Katoh, S. Sakado-Machi, Japan  
Kaufman, T.E. Bloomington, Indiana  
Kaufmann, B.N. Philadelphia, Pennsylvania  
Kauver, L. Pasadena, California  
Kawabe, M. Kobe, Japan  
Kawanishi, M. Misima, Japan  
Kawanishi, M. Misima, Japan  
Kayano, H. Nagasaki, Japan  
Kearsey, M.J. Birmingham, Great Britain  
Keith, T. Cambridge, Massachusetts  
Kekić, V. Belgrade, Yugoslavia  
Keller, E.C.Jr. Morgantown, West Virginia  
Keller, H.E. Morgantown, West Virginia  
Kemphues, K. Bloomington, Indiana  
Kennison, J. La Jolla, California  
Kenny, R. Huntsville, Texas  
Keppy, D.O. Ames, Iowa  
Keränen, L. Oulo, Finland  
Kercher, M.D. Lexington, Kentucky  
Kertesz, J. Dayton, Ohio  
Khan, F. Pakistan  
Khishin, A.F. Assuit, Egypt  
Kidwell, J. Providence, Rhode Island  
Kidwell, M. Providence, Rhode Island  
Kiefer, B.I. Middletown, Connecticut  
Kiger, J.A. Davis, California  
Kijken, F.B. Utrecht, Netherlands  
Kikkawa, H. Osaka, Japan  
Kim, B.Y. Seoul, Korea  
Kim, H.S. Seoul, Korea  
Kim, K.W. Kwangju, Korea  
Kim, S.H. Seoul, Korea  
Kimura, M.T. Sapporo, Japan  
Kindle, K. Pasadena, California  
King, R.C. Evanston, Illinois  
Kirshbaum, W.F. Buenos Aires, Argentina  
Kitagawa, O. Tokyo, Japan  
Klapwijk, P.M. Leiden, Netherlands  
Klug, W.S. Crawfordsville, Indiana  
Knipple, D. Ithaca, New York  
Kobayashi, Y. Hiroshima, Japan  
Kobel, H.R. Geneva, Switzerland  
Koch, P. Marburg, W.Germany  
Koenig, J.E. Duarte, California  
Kohler, N. Valdivia, Chile  
Köhler, W. Berlin, W.Germany  
Kondo, S. Osaka, Japan  
Konopka, R. Pasadena, California  
Koo, D. Vancouver, Canada  
Korge, G. Sakado-Machi, Japan  
Kotarski, M. Ithaca, New York  
Kraakauer, E. Bogota, Colombia  
Kral, L. East Lansing, Michigan  
Kramers, P.G.N. Leiden, Netherlands  
Krause, E. South Orange, New Jersey  
Kreber, R.A. Madison, Wisconsin  
Kreitman, M. Cambridge, Massachusetts  
Kress, H. München, W.Germany  
Kridler, H. Storrs, Connecticut  
Krimbas, C. Athens, Greece  
Krishnamurthy, N.B. Mysore, India  
Krivshenko, J.D. Rochester, New York  
Kroeger, H. Saarbrücken, W.Germany  
Kroman, R.A. Long Beach, California  
Kronic, M. Belgrade, Yugoslavia  
Kubli, E. Zürich, Switzerland  
Kunz, W. Düsseldorf, W.Germany  
Kuo, G. New Haven, Connecticut  
Kurihara, J. Honolulu, Hawaii  
Kuroda, Y. Misima, Japan  
Kurokawa, H. Sakdra-Mura, Japan  
Kusoda, K. Sakado, Japan  
Kwrokawa, Y. Nagasaki, Japan  
Lachaise, D. Gif-sur-Yvette, France  
Laird, C. Seattle, Washington  
Lakhotia, S.C. Varanasi, India  
Lakhotia, S.C. Ahmedabad, India  
Lakovaara, S. Oulu, Finland  
Lamb, M.J. London, Great Britain  
Lambertsson, A. Umeå, Sweden  
Landers, M.H. Burlington, Vermont  
Langley, C. Res. Triangle Pk., N.C.  
Lankinen, P. Oulu, Finland  
Lathe, R. Cambridge, Great Britain  
Latorre, A. Burjasot, Spain  
Laughnan, J.R. Urbana, Illinois

- Laurent, J. Gif-sur-Yvette, France  
 Lavige, J.M. Clermont-Ferrand, France  
 Lawlor, T. La Jolla, California  
 Lawrence, M.J. Birmingham, Great Britain  
 Lechien, J. Namur, Belgium  
 Lechner, J.F. Philadelphia, Pennsylvania  
 Lee, C.C. Seoul, Korea  
 Lee, C.S. Austin, Texas  
 Lee, M.S. Seoul, Korea  
 Lee, T.J. Seoul, Korea  
 Lee, W.R. Baton Rouge, Louisiana  
 Leenders, H.J. Nijmegen, Netherlands  
 Lefevre, G.Jr. Northridge, California  
 Legay, J.M. Lyon, France  
 Leibenguth, F. Saarbrücken, W.Germany  
 Leigh, B. Leiden, Netherlands  
 Leigh-Brown, A.J. London, Great Britain  
 Leister, F. Baltimore, Maryland  
 Lemeunier, F. Gif-sur-Yvette, France  
 Leonard, J.E. Purchase, New York  
 Levan, G. Göteborg, Sweden  
 Levitan, M. New York, New York  
 Lewis, E.B. Pasadena, California  
 Lewis, M. Cambridge, Great Britain  
 Lewis, R. Bloomington, Indiana  
 Lewontin, D. Cambridge, Massachusetts  
 L'Hélias, C. Gif-sur-Yvette, France  
 Libion-Mannaert, M. Namur, Belgium  
 Liebrich, W. Düsseldorf, W.Germany  
 Lindquist, S. Chicago, Illinois  
 Lindsley, D.S. La Jolla, California  
 Lints, C. Louvain-La-Neuve, Belgium  
 Lints, F. Louvain-La-Neuve, Belgium  
 Livak, K. La Jolla, California  
 Ljung, K. Umeå, Sweden  
 Lloyd, L. St. Andrews, Great Britain  
 LoCascio, N. Buffalo, New York  
 Logan, J. Cambridge, Massachusetts  
 Lokki, J. Helsinki, Finland  
 Lokki, M. Helsinki, Finland  
 Louis, C. St.Christol-l-A., France  
 Louis, J. Gif-sur-Yvette, France  
 Louis, M. Gif-sur-Yvette, France  
 Loukas, M. Athens, Greece  
 Loveland, M.J. Sydney, Australia  
 Loverre, A. Rome, Italy  
 Lowy, P.H. Pasadena, California  
 Lubsen, N.H. Nijmegen, Netherlands  
 Lucchesi, J.C. Chapel Hill, N.C.  
 Luce, W.M. Urbana, Illinois  
 Lüers, H. Berlin, W.Germany  
 Lumme, J. Oulu, Finland  
 Lüning, K.G. Stockholm, Sweden  
 Lyttle, T.W. Honolulu, Hawaii  
 MacIntyre, R. Ithaca, New York  
 Magalhaes, L.E. Sao Paulo, Brazil  
 Maher, E.P. Aberdeen, Great Britain  
 Mahowald, A. Bloomington, Indiana  
 Mainx, F. Vienna, Austria  
 Maitra, S.N. Calcutta, India  
 Majumdar, S.K. Easton, Pennsylvania  
 Malogowkin-Cohen, Ch. Haifa, Israel  
 Mandal, S.K. Calcutta, India  
 Maniatis, T. Pasadena, California  
 Manna, G.K. Kalyani, India  
 Manseau, L. Madison, Wisconsin  
 Marcos, R. Bellaterra, Spain  
 Margulies, L. New York, New York  
 Marien, D. New York, New York  
 Marinkovic, D. Belgrade, Yugoslavia  
 Markow, T.A. Tempe, Arizona  
 Maroni, G.P. Chapel Hill, North Carolina  
 Marques, E.J. Mato Grosso, Brazil  
 Marques, E.K. Porto Alegre, Brazil  
 Marsh, L. Basel, Switzerland  
 Martin, A.O. Cleveland, Ohio  
 Martinez, M.J. Burjasot, Spain  
 Martinez, M.N. Porto Alegre, Brazil  
 Martinez, R.M. Hamden, Connecticut  
 Maruyama, T. Misima, Japan  
 Massie, H.R. Utica, New York  
 Mather, K.C.B.E. Birmingham, Great Britain  
 Mather, W.B. Brisbane, Australia  
 Matsuda, T. Asamizodai, Japan  
 Matsumura, T. Nagasaki, Japan  
 Mayeda, K. Detroit, Michigan  
 Mayfield, J.E. Pittsburgh, Pennsylvania  
 Mazar-Barnett, B. Buenos Aires, Argentina  
 McCarron, M. Storrs, Connecticut  
 McCarthy, P.C. New Wilimington, Pennsylvania  
 McCormack, M.K. New Brunswick, New Jersey  
 McCrady, E. Greensboro, North Carolina  
 McCrady, W.B. Arlington, Texas  
 McDonald, J.F. Ames, Iowa  
 Ménsua, J.L. Burjasot, Spain  
 Mercader, J. Mexico City, Mexico  
 Merrell, D.J. Minneapolis, Minnesota  
 Merriam, J. Los Angeles, California  
 Merritt, R. Rochester, New York  
 Merten-Huber, M. München, W.Germany  
 Meyer, G.F. Tübingen, W.Germany  
 Meyer, H.U. Madison, Wisconsin  
 Meyerowitz, E.M. Pasadena, California  
 Michalopoulou, E. Patras, Greece  
 Micheli, A. Rome, Italy  
 Michinomae, M. Kobe, Japan  
 Miglani, G.S. Ludhiana, India  
 Mikasa, K. Sakado-Machi, Japan  
 Miklos, G.L.G. Canberra, Australia  
 Milkman, R.D. Iowa City, Iowa  
 Miller, D.D. Lincoln, Nebraska  
 Miller, O.L.jr. Charlottesville, Virginia  
 Milner, M.J. St. Andrews, Great Britain  
 Minamouri, S. Hiroshima, Japan  
 Minato, K. Misima, Japan  
 Mindek, G. Zürich, Switzerland  
 Miranda, M. Rio de Janeiro, Brazil  
 Mishra, A. Varanasi, India  
 Mitchell, C. Duarte, California  
 Mitchell, H.K. Pasadena, California  
 Mittler, S. DeKalb, Illinois  
 Mohler, J.D. Iowa City, Iowa  
 Mohon-Acharya, P. Calcutta, India  
 Moisand, R. Buffalo, New York  
 Momma, E. Sapporo, Japan  
 Monclus, M. Barcelona, Spain  
 Monks, G. München, W.Germany  
 Montelente, G. Rome, Italy

- Montell, I. Umeå, Sweden  
Montijn, C. Utrecht, Netherlands  
Morea, M. Bari, Italy  
Moree, R. Pullman, Washington  
Mori, S. Nagasaki, Japan  
Moriwaki, D. Tokyo, Japan  
Mortensen, M. Copenhagen, Denmark  
Moskwinski, T. Notre Dame, Indiana  
Mossige, J. Oslo, Norway  
Mourad, A.O. Alexandria, Egypt  
Mourao, C.A. Sao Jose de R.P., Brazil  
Moya, A. Burjasot, Spain  
Muckenthaler, F. Bridgewater, Mass.  
Mukherjee, A.S. Calcutta, India  
Mukherjee, T. Varanasi, India  
Münster, R. Münster, W.Germany  
Muñoz, E.R. Buenos Aires, Argentina  
Muona, O. Helsinki, Finland  
Murakami, A. Misima, Japan  
Murata, M. Chiba, Japan  
Murnik, M.R. Macomb, Illinois  
Myszewski, M.E. Des Moines, Iowa  
Nagaraj, H.J. Mysore, India  
Nagna, F. Naples, Italy  
Najera, C. Burjasot, Spain  
Nakai, S. Osaka, Japan  
Nakamura, Y. Tokyo, Japan  
Nakashima-Tanaka, E. Sakai, Japan  
Nalcaci, O.B. Ankara, Turkey  
Namkoon, Y. Seoul, Korea  
Narise, S. Sakado-Machi, Japan  
Narise, T. Sakado-Machi, Japan  
Nascimento, L. Rio de Janeiro, Brazil  
Nash, D. Edmonton, Canada  
Nash, W.G. Bethesda, Maryland  
Natsubara, K. Sakai, Japan  
Nauaud, D. Paris, France  
Navarro, J. Santiago, Chile  
Nawa, S. Misima, Japan  
Neeley, J.C. Portland, Oregon  
Newman, S. Seattle, Washington  
Nicolosi, R.J. Utica, New York  
Niizeki, S. Tokyo, Japan  
Nilkan, C. Bangkok, Thailand  
Nilsson, J. Umeå, Sweden  
Nishida, Y. Osaka, Japan  
Nissani, M. Madison, Wisconsin  
Nix, C.E. Oak Ridge, Tennessee  
Nokkala, S. Turku, Finland  
Nomura, T. Osaka, Japan  
Nöthel, H. Berlin, W.Germany  
Nöthiger, R. Zürich, Switzerland  
Novitski, E. Eugene, Oregon  
Nuez, F. Valencia, Spain  
Nusslein-Volhard, C. Heidelberg, W.Germany  
Nuviiak, P. St. John's, Canada  
Nygren, J. Umeå, Sweden  
O'Brien, S.J. Bethesda, Maryland  
Oelshlegal, F.J. Ann Arbor, Michigan  
Ofteidal, P. Oslo, Norway  
Ogaki, M. Sakai, Japan  
Ogita, Z. Osaka, Japan  
Oguma, Y. Sakura-Mura, Japan  
Oh, S.K. Seoul, Korea  
Ohanessian, A. Gif-sur-Yvette, France  
Ohba, S. Tokyo, Japan  
Oishi, K. Kobe, Japan  
Okada, M. Sakura-Mura, Japan  
Okada, T. Tokyo, Japan  
Oksala, T.A. Turku, Finland  
Olivieri, G. Rome, Italy  
Oller, R. Tübingen, W.Germany  
Olvera, O.M.S. Mexico City, Mexico  
Ondrej, M. Prague, Czechoslovakia  
Ortiz, E. Madrid, Spain  
Osborn, R. Berkeley, California  
Oshima, C. Misima, Japan  
Oster, I.I. St. John's, Canada  
Oster, P. Bowling Green, Ohio  
Ostrowski, R.S. Charlotte, North Carolina  
Pages, M. Madrid, Spain  
Paik, Y.K. Seoul, Korea  
Pak, W.L. West Lafayette, Indiana  
Pal, T.K. Calcutta, India  
Palabost, L. Paris, France  
Palka, J. Seattle, Washington  
Papaceit, M. Barcelona, Spain  
Paradi, E. Budapest, Hungary  
Parente, A. Detroit, Michigan  
Parisi, G. Naples, Italy  
Park, M.S. Kwangju, Korea  
Parkash, R. Amritsar, India  
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