the recombination frequency in females of *D. melanogaster*[8]. If this supposition is general, we can expect that intercalating agents with clastogenic activity must increase the recombination frequency, as was found for actinomycin D[5].

AF, AO and EB, which significantly increase the crossover frequency in the *ct-f* region in this experiment, act as clastogenic agents in *D. melanogaster*[11,12], while ClQ and Q, which have no effect on recombination frequency, do not seem to exert clastogenic effects either. From our results it appears also that there is a relationship between clastogenic effectiveness and the capacity to induce female recombination. Given the fact that some intercalating agents increase female recombination significantly, and others do not, it is difficult to explain this only on the basis of the induced changes in the DNA conformation. According to Filipski's hypothesis[13], intercalating compounds may competitively inhibit the repair reaction of some nick-closing enzymes and the inhibition of nick repair may be the actual cause for the increase of recombination frequencies.

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Radiation-induced hyperdiploidy in *Hyoscyamus niger* L.[1]

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Summary. A hyperdiploid plant type, approaching the triploid chromosome number, and representing possibly a high level of tetrasomy, was recorded in the progeny of a gamma ray-induced unbranched desynaptic mutant in the M_4 generation. Its meiotic behavior and its possible importance for deriving diverse hyperdiploid lines from desynaptic mutants are outlined.
Key words. Hyperdiploid plant; *Hyoscyamus niger;* radiation-induced mutant.

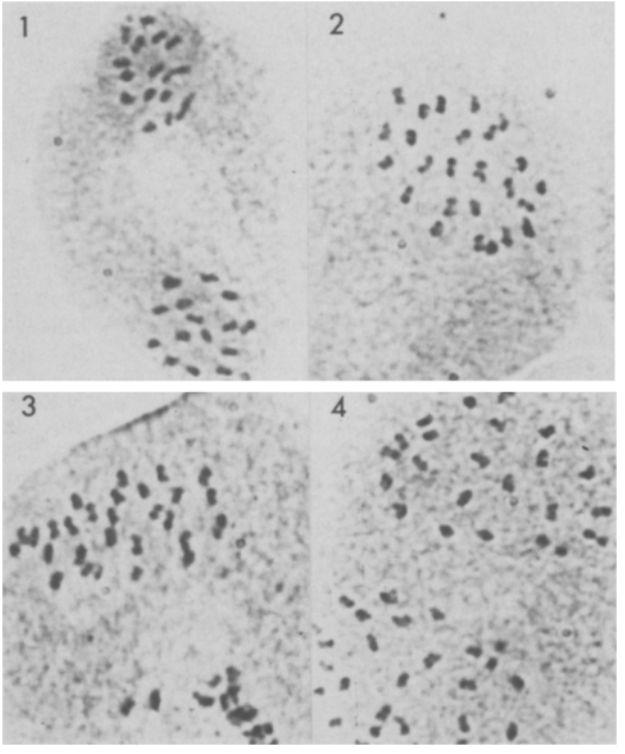
Sharma and Singh[2] reported an unbranched tall mutant in *Hyoscyamus niger*, a solanaceous plant of immense therapeutic value, after 20 kr gamma irradiation of seeds. Its productivity and progeny performance were evaluated. It was found that this mutant which had a high potential for various agronomic characters (plant height, number and size of leaves, etc.) and crude drug content, was a poor seed setter. The analysis of meiotic behavior revealed this mutant to be weakly desynaptic which in turn caused a wide array of symmetric and asymmetric anaphase disjunctional patterns[3]. Incidently, in the M_3 and M_4 populations of this mutant, certain plants did not set seeds either on selfing or in reciprocal crosses with normal control plants. Meiotic analysis was performed on such a plant in M_4, which revealed its hyperdiploid nature, the details of which are given below.

Material and methods. Flower buds of appropriate size were collected between 09.00 and 10.00 h in Carnoy's fixative for meiotic analysis from the sterile mutant plant (MTU-11). This plant resembled the other mutant plants in all characters except fertility. Meiotic and pollen preparations were made following the usual staining in 2% acetocarmine. At least three anthers from each of five flower buds were examined.

Observations. The male meiosis in this plant revealed nearly a triploid chromosome number (diploid 2n = 34) with chromosome numbers varying between 48 and 54, and depicting an array of anaphase I distributional patterns (table, figs 1–4).

At diplotene/diakinesis, metaphase I, the occurrence of a few tetravalents was also noted (i.e. 2–6 tetravalents per cell, the exact frequency distribution of which could not be recorded as there was not sufficient material available from these stages). The pollen grains revealed complete sterility as discerned by nonstainability by acetocarmine.

Discussion. The mutant in question was found to be fully sterile. This sterility is possibly caused by an added dose of chromo-



Figures 1–4. Chromosome separation at anaphase I in *H. niger*. *1* 17:17 separation in control, *2–4* anaphase I in hyperploid plant, *2* one of the anaphase I poles showing 25 chromosomes, *3* 27 chromosomes on one pole and the other pole with chromosomes in two groups, a sign of disturbed polarity, *4* 23:28 separation.

somes which impairs the survival of the gametes and affects the threshold of genes.

It is significant to note that a high level of hyperdiploidy (tetrasomy?) was achieved in the progeny of a desynaptic mutant induced by gamma irradiation. Although the production of trisomics and occasional tetrasomics has been recorded in a variety of plant types from desynaptic lines[4-7], the increase in chromosome number has been limited to the addition of 1–2 chromosomes. Gottschalk and Milutinovic[5], however, recorded a few hyperploid cells reaching near triploidy in the cell population of an otherwise trisomic plant in *Pisum sativum*. The present study records a case going much further. Thus, there is reason to believe that the original mutant might generate progeny of different chromosomal races and various degrees of fertility.

Frequency and pattern of chromosome distribution at anaphase I

	Sum of chromosome Nos at both the poles				
	48	50	52	54	others between 48–54
Frequency of occurrence	22.3%	37.2%	18.1%	16.1%	6.3%

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Fluctuating rates of evolution

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Summary. Constant evolutionary rates are possible only in very large populations, where natural selection does not exhaust variation because mutation supplies fresh variability. In a small population where a small number of genes influence an integrated system like brain and body size which have an allometric relationship, variation is removed rapidly under natural selection, This occurs even when the final fitness of the population is not optimal.
Key words. Evolution; evolutionary rate; stasis; brain; encephalization; body size; fitness.

The concept of 'punctuated equilibria'[1] is a misconception in at least one way. It is based on a rejection of the idea that observed or apparent slow, gradual evolutionary change must be at a constant rate. Given the precision with which evolutionary rates may be measured[2], it would be a rash person who would suggest either that constant rates had been observed or that rates fluctuating about zero had been observed, with large steps at intervals. What does not seem to have been considered in attempting a new 'modern synthesis' is the very straightforward idea that when mutations arise which are favorable, they will be selected steadily until they are fixed, after which stasis may occur, if there is no further genetical variability available, or further change may occur.

This can be the case whether the changes are major or minor. Furthermore, slow change may occur or rapid change may occur without affecting the fossil phenotype, giving rise to the assessment of stasis when changes was the case, or change may occur in a relatively trivial attribute detectable in the fossil record, giving rise to the idea of important change, on account of the inability to assess the importance of the change.

In this note, a model is developed of evolutionary change affecting an integrated system, and it is shown how relatively rapid change may occur within the system, all change occurring by standard Darwinian natural selection, but with breaks in between periods of change, these breaks occasioned by the absence of genetical variability.

The model. Consider the evolution of the human brain. Whatever one's view of man's place in nature, one cannot but agree that man's ability to record his introspection for posterity differs in kind from that of any other living organism. While such records cover no more than perhaps $\frac{1}{10}$ of 1% of man's evolution, man's increasing encephalization is documented imperfectly in the fossil record for perhaps 10 million years. This represents perhaps half a million generations, and there appears to have been no significant change over the last 10% of this time. Given the slowness of even this very rapid change, of course, there may have been undetectable changes during this most recent period. Such changes are not relevant to the present argument.

As has frequently been mentioned by many authors[3], evolutionary change in one organ must be accompanied by accommodation in other organs. Let us therefore set down arbitrarily a simple model for the ontogenetic determination of human brain and body size, and see how this changes under natural selection.

Suppose that there are 15 genes which determine various aspects of size. Three affect the brain only. Three affect brain and body equally. Three affect overall size. Three affect body and pelvis size equally. Three affect pelvis size only.

Now suppose that there is stabilizing selection on overall size. Then if directional selection on brain size occurs, this will interact with the stabilizing selection on overall size.

In the model (table), we shall ignore factors like development instability[4-6] as direct influences but such factors could clearly be of great importance, for example in contributing to selection against extremes.

There have been extensive analyses of the single locus model of the interaction between artificial directional selection and natural selection favoring intermediates, whether through an intermediate optimum or heterozygous advantage; see Nicholas and Robertson[7] for details. These analyses, while generally illuminating, are not directly relevant to the present case where the hypothesized genes have distinctive functions.

Hence, stabilizing selection intensity $= k_1 (1 - \exp(- (n_s - 9)^2))$ where n_s = total number of genes increasing phenotype in categories 2, 3 and 4,