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Heritable Repression due to Paramutation in Maize

In the penetrating analysis and interpretation of paramutation at the *R* locus in maize by Brink, Styles, and Axtell (*1*), information that I have presented on the phenomenon at the *B* locus is briefly considered. Although the *B* data clearly show that paramutation in this system and others might well be interpreted as a meiotic and terminal phenomenon, the interpretation of Brink, Styles, and Axtell is that all paramutation is somatic (or, rather, premeiotic), and that the data for *B* do not raise doubt on this point. Related comments are needed also on their conclusion that paramutation at the *R* locus cannot involve transfer of particles between alleles. Only when these mechanical features of paramutation are defined will it become clear whether paramutation systems involve typical or unique mechanisms of gene regulation, and whether the biological significance of paramutation is ontogenetic or phylogenetic.

Paramutation at the *B* locus occurs late in ontogeny. This conclusion rests on clear evidence, partly phenotypic and partly developmental (*2*). Examples cited by Brink, Styles, and Axtell from several plant species in support of an opposite conclusion all depend on the conventional view that somatic sectoring demonstrates the occurrence of paramutation *in the mitosis* at which the sector was delimited. As discussed elsewhere (*2*), differential mitoses that result in sectors may be differential in the potential for paramutation, rather than in the paramutation event itself. Similar delayed timing in repression-control systems has been found by McClintock (*3*) in the "presetting" phenomenon, in which a gene is programed at one stage of development to function subsequently in patterned concert, even as late as in the next generation. The *B* data show that all or most of a life cycle can intervene between the formation of the paramutational heterozygote and the paramutation event. Consequently, the question of whether paramutation can be generalized as premeiotic (or as meiotic-terminal) is entirely open. Definitive experiments identifying the exact stages of the events have not yet been devised.

The mechanics of paramutation at the *R* locus are discussed by Brink, Styles, and Axtell (*1*). Their data show that increase in functional capacity of *R*, which, they hypothesize, reflects loss of repressor elements, occurs in *Rr* heterozygotes. Since the same change occurs in deficiency heterozygotes (*R*—), loss of repressors, they point out, cannot be occurring by transfer to the absent homologous region. Brink, Styles, and Axtell argue that transfer is thereby excluded as a mechanical process for all *R* paramutation. However, the changes that can be interpreted as due to *gain* of repressors occur only in the presence of R^{st} or alleles with more repressors. Whether paramutation is meiotic or premeiotic, through contact or otherwise, a mechanical process by which gain occurs must be considered, and gain of elements by transfer is a conceptually economical hypothesis for the mechanics of change of *R* to *R′*. According to this view, loss of elements could be permitted by the *Rr* or *R*— condition, since no supply of elements would be provided by the allele. The data do not warrant disposal of the transfer model.

The late timing of paramutation at the *B* locus and the interpretation of particle transfer have led to the suggestion (*2*) that release of a repressor element (from *B′*) is triggered at or near meiosis, and that the element then transfers to the allele (*B*). The mechanical process in terminal pigmenting cells can be viewed as parallel to that in germinal cells but as less efficient, perhaps due to the absence of synapsis. A model of the kind suggested below, even though unduly exact, may express this repressor-transfer view less abstractly. Stent (*4*) has suggested that appended messenger RNA may act as a repressor, and more recently Bonner and Widholm (*5*) have presented evidence for chromosomal RNA that is organ-specific and complementary to nuclear DNA; this chromosomal RNA may be an integral part of gene repression systems. In parallel with repression by end-product feedback in bacteria (*6*), repressor (RNA or otherwise) released from a heritably repressed gene (*B′*, *R′*, R^{st}) could transfer as feedback to the allele (*B*, *R*) and append to the DNA. Since the genetic software (the repressing material) must be able to replicate along with the gene it represses, one would suppose that appended RNA might be capable of replication in place. Transfer of such a repressor, either by contact or by release and migration, would be entirely reasonable and not incompatible with either the *R* or the *B* information.

Exact materials and mechanics for paramutation can be hypothesized, and there will be differences of opinion about the hypotheses. There is full agreement, however, on this important fact: potential for genetic activity can be altered by the history of a gene, and associated software appears to be responsible in both of the cases that have been thoroughly studied.

E. H. Coe, Jr.

U.S. Department of Agriculture and Department of Genetics, University of Missouri, Columbia 65201

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Oceanic Basalt Leads and the Age of the Earth

In a recent report Ulrych (*1*) claims to have derived an "independent age for the earth." He states that the significance of his calculations is that the "age" which he obtains for the earth is independent of the age of the samples used in the calculations. It is true that his method does not require an independent determination of the length of time that a related series of rocks have spent in the crust, as long as their original source was homogeneous from T_0 (the time at which the gross structure of the earth developed) until the time at which the rocks were derived from the source, T_1 (the age of the samples). However, the absence of an independent criterion for determining that this condition is met introduces several problems.

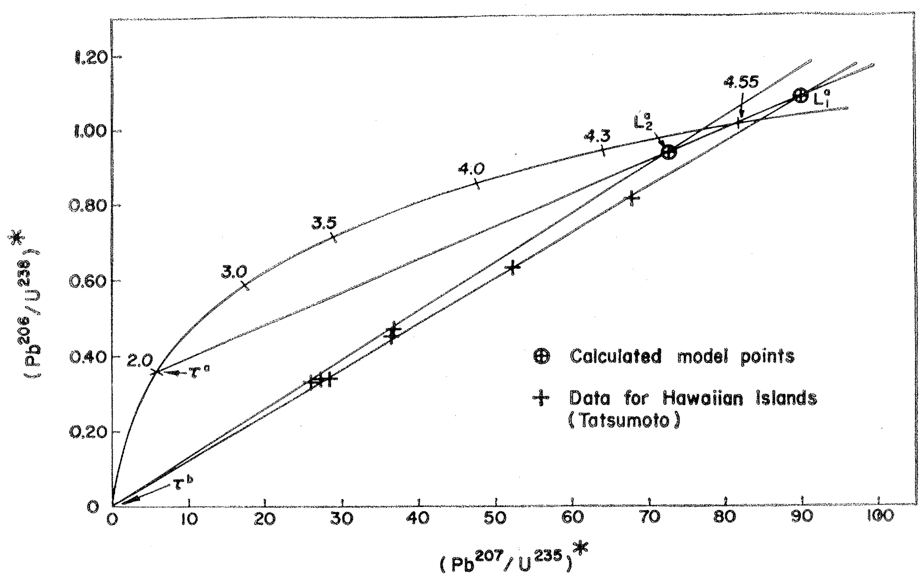

Fig. 1. Concordia plot to illustrate the effect of a change in the U/Pb ratio of the mantle at 2.0 billion years. Points $L_1{}^a$ and $L_2{}^a$ represent present-day mantle systems generated by the 2.0 billion-year event. For a first-stage μ value of 9.0, the second-stage values are 8.0 for $L_1{}^a$ and 10.0 for $L_2{}^a$. The lines passing through these points and the origin give the locus of U-Pb subsystems which could be derived today from these mantle systems (for example, modern basaltic rocks). The unlabeled points are the data of Tatsumoto (*3*) for the Hawaiian Islands.

Ulrych assumes that the U^{238}/Pb^{204} ratio (μ value) observed in a rock at the surface of the earth is representative of its source. This implies fractionation of U and Pb in the mantle by processes unrelated to the formation of the rock. We believe that this is, in general, false, for reasons discussed below. However, we will first show that his method does not improve our knowledge of the age of the earth, even if the U^{238}/Pb^{204} in recent basalts is representative of their source. Using this assumption, Ulrych defines two-stage parent-daughter ratios. The equations which he derived can be reduced to

$$\frac{(Pb^{206})_{\text{radiogenic}}}{(U^{238})_{\text{present}}} = \frac{(Pb^{206})_{\text{total}} - (Pb^{206})_{\text{primordial}}}{(U^{238})_{\text{present}}} \quad (1)$$

$$\frac{(Pb^{207})_{\text{radiogenic}}}{(U^{235})_{\text{present}}} = \frac{(Pb^{207})_{\text{total}} - (Pb^{207})_{\text{primordial}}}{(U^{235})_{\text{present}}} \quad (2)$$

We see immediately that once the initial Pb (primordial Pb) is subtracted from a terrestrial Pb, the Pb^{206}/U^{238} and Pb^{207}/U^{235} ratios may be formally interpreted by the methods outlined by Wetherill (*2*). The gain or loss of U or Pb or both during the short fractionation episode described by Wetherill (*2*) is equivalent to a fractionation in the U/Pb ratio in a given U/Pb system. It is clear from Wetherill's description that the operation that is described in Eq. 1 will produce ratios that plot on the Concordia curve for a system that has not undergone any fractionation of μ (single-stage system). Thus, basaltic liquids derived without fractionation of the U/Pb ratio from a single-stage mantle system must plot on the Concordia curve. This is true for any system, that is, it does not depend on the μ value of the system from which the basalts are derived. For these conditions no linear arrays are possible. Suppose now that we consider a two-stage system, that is, a U/Pb system with a single episode of U/Pb fractionation. Wetherill (*2*) has shown that the present-day Pb^{206}/U^{238} and Pb^{207}/U^{235} ratios for the radiogenic component of a set of systems produced in this way will be a linear array in the coordinates used in plotting the Concordia curve.

This linear array is given by

$$Pb^{206}/U^{238} = K(e^{\lambda T_0} - e^{\lambda T^a}) + (e^{\lambda T^a} - 1) \quad (3)$$

$$PB^{207}/U^{235} = K(e^{\lambda^1 T_0} - e^{\lambda^1 T^a}) + (e^{\lambda^1 T^a} - 1) \quad (4)$$

where

$$K = [(Pb^{206}/U^{238}) \text{ after } T^a / (Pb^{206}/U^{238}) \text{ before } T^a]$$

Such an episode is illustrated in Fig. 1 for a fractionation episode at 2.0 $\times 10^9$ years. For reference, Tatsumoto's (*3*) data for the Hawaiian Islands are also plotted on this figure. The line connecting the 2.0 $\times 10^9$ years point and the age of the earth on the Concordia, and its extension above the Concordia, would be the present-day locus of all systems formed in the 2.0 $\times 10^9$ year event. If one of these systems ($L_1{}^a$) was later fractionated, at time T^b, a new linear array defined by the intercept T^b and the point $L_1{}^a$ would be generated. Fractionation of a different system, which we may designate $L_2{}^a$, will produce a second linear array. Since both subsystems generated by the T^b event have the same lower intercept, but different points of origin on the 2.0 $\times 10^9$ years line, the two subsystem lines must have different slopes. It is important to note that neither the upper intercept with the Concordia curve nor the slope of the second set of linear arrays has any physical meaning, since they will depend on the extent to which the U/Pb ratio was fractionated during the first episode, and the length of time between the first and second episodes. That is, they depend on the parameters K and T^a. It is also important to note that the lower intercept has physical meaning only when the present or observed set of U/Pb systems are derived from a single system, for example, $L_2{}^a$. A limited number of lead systems, say three or four, derived from systems previously fractionated (such as $L_1{}^a$ and $L_2{}^a$) can, when plotted on a Concordia, approximate a straight line in which neither the upper nor lower intercept or slope has any time significance. This situation should be considered if the scatter about a best-fit line on the Concordia diagram is large.

The application of this model to the data discussed by Ulrych (*1*) is now straightforward. For those arrays that pass through T_0 (age of the earth), the lower intercept can have two interpretations. (i) If the U/Pb ratio of a basaltic lava is not fractionated with respect to the source of that liquid when it is formed, that is, if each basalt sample represents one of a family of U/Pb systems that exist in the mantle, the time given by the lower intercept is the time when these mantle systems were created. (ii) If the U/Pb ratio in the basalts was fractionated during the formation of these liquids, the lower intercept represents the time when the basalts were formed. The interpretation of the lower intercept for linear arrays that do not pass through T_0 is the same, but implies the addition of an episode of fractionation of the U/Pb ratios in the mantle, which makes the time inferred from the upper intercept meaningless.

It is clear from the foregoing discussion that in the absence of any criteria for distinguishing whether or not fractionation of mantle systems that make up the source of a given set of basalt samples has taken place, we are unable to select any particular upper intercept with the Concordia curve as T_0, the age of the earth. This is a very serious limitation, since the existence of different upper intercepts indicates that fractionation of mantle systems has taken place. It is of interest to calculate the extent of the fractionation that is required. Consider the case where the mantle differentiation took place 2.0 billion years ago, as a discrete event, that is, the line shown in Fig. 1. Second-stage μ values of 8 and 10 are identified by points L_1^a and L_2^a, respectively. The linear arrays produced by present-day fractionation of these systems have upper intercepts of 4.59 and 4.51, respectively. The upper intercepts for L^a systems with μ values ranging from 12 to 13 range from 4.3 to 4.2 $\times 10^9$ years.

If the time of mantle μ change is more recent than 2.0×10^9 years, then a larger range of second-stage μ values would be required to produce the same range in Concordia intercepts. Conversely, for an earlier μ change, a smaller range of μ_2 values would produce the same range in intercepts. Ulrych (*1*) observes a range in intercepts of 4.46×10^9 to 4.58×10^9 years with one largely divergent intercept of 4.27 $\times 10^9$ years. He concludes that the Guadelupe intercept is indicative of a "three-stage system." We conclude that the spread in his upper Concordia intercepts indicates that a number of the other systems were also "three-stage systems." We differ from Ulrych in the identification of a third stage. We maintain that the third stage begins with a change in μ at the time of formation of the basaltic rocks.

There are several lines of evidence which support the view that the μ values observed in rocks are in general not representative of their source. Alkali basalts have μ values ranging from 9 to 50 [Swainbank (*4*), Tatsumoto (*3*)]. The observed range of μ values for tholeiitic rocks, 2 to 12, is much lower. This systematic difference and the lack of correlation between observed μ values and observed Pb^{206}/Pb^{204} ratios suggest that basaltic liquids, particularly alkaline basalts, differ significantly from their source. The lead isotope data itself argues against Ulrych's position. Several of Tatsumoto's (*3*) Hawaiian samples which presently have high U/Pb but low Pb^{206}/Pb^{204} ratios could not possibly have been formed by the sequence of events suggested by Ulrych (*1*).

For samples representing systems derived by a single fractionation episode from an originally homogeneous source, the age found from the lower Concordia intercept must agree with that calculated from the slope of the linear array. This condition is almost met by the Llano, Texas, data (*5*); however, the scatter is large and several of the samples used by Ulrych are metamorphosed rocks whose primary ages are not established. It is quite possible that the metamorphic rocks are not simply related in their origin, and thus do not fit the conditions of the model. The modern basalts show slope ages which differ from their intercept ages. For these samples, especially those which show negative lower intercepts, Ulrych's model is clearly inadequate. A period of intermediate fractionation is indicated by the disagreement between slope and intercept ages; in the case of negative intercepts, a mixing of two or more separated systems is also indicated. There is an additional problem in Ulrych's interpretation of the Mid-Atlantic Ridge basalts. One of his samples shows evidence for either a three-stage history or a μ value not representative of its source (*6*).

Ulrych (*1*) claims that the Concordia diagram is a valid and sensitive aid in the analysis of lead isotope compositions from modern basalts because he obtains good straight lines. Unfortunately, these lines are controlled largely by the *average* lead composition, and the use of the Concordia diagram buries the small but significant differences in the Hawaiian Island lead compositions found by Tatsumoto (*3*). Random variation in U and Pb contents will cause spreading along the line, but changes in slope can be caused only by variations in the U/Pb ratio which correlate with changes in the lead isotope composition.

To obtain his "independent" age of the earth, Ulrych averages the "ages" determined from the separate systems, excluding the value found from the Guadelupe data. However, since the upper intercept for his plots is determined by the second stage μ value and time of μ change for a two-stage mantle, the direct averaging of a limited amount of data is a very risky way to determine the age of the earth. The claim that the age of the earth can be found independently of the age of the sample is in part a semantic result; in the unfractionated basalt case, as far as the isotope composition and μ values are concerned, the formation of the basalt is not an event. It is thus not surprising that the method is independent of the age of the sample. In cases where fractionation with respect to the source has taken place, the interpretation of the upper intercept is not independent of the time of fractionation, since we have shown that the upper intercept has physical meaning only when the lower intercept represents the time when the fractionation took place, that is, the age of the rock. Therefore, the claim that the age of the earth can be determined independently of the age of the sample is not valid, if it is meant that there need be no knowledge regarding the age of the sample.

The Concordia method is much inferior to the lead evolution diagram, a plot of Pb^{207}/Pb^{204} versus Pb^{206}/Pb^{204}, as a means of analyzing recent basalts, for two reasons. First, it is difficult to distinguish scatter due to variations in lead isotope composition from that due to variations in the U and Pb content. Second, the Concordia method thoroughly masks significant small variations in the lead isotope data from a single region, such as Hawaii. The lead evolution diagram allows very sensitive analysis of small variations in modern lead compositions. We think that the use of the Concordia diagram in the analysis of modern lead data is in general an ill-advised procedure.

V. M. OVERSBY
P. W. GAST

Lamont Geological Observatory,
Columbia University,
Palisades, New York 10964

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13 September 1968

The model on which the Concordia plot (*1*) is based is a two-stage process. It is a simplified form of the lead isotope evolution model for present-day basalts which I presented at the Common Lead and Common Strontium workshop in Denver, Colorado, in August 1967 (*2*). Since the comment by Oversby and Gast deals largely with the assumption which I made in reducing the general model to a two-stage process, I present the general model here.

The lead now observed in a modern oceanic basalt may be a product of three environments: (i) a homogeneous closed system characterized by a U^{238}/Pb^{204} value (at present) of μ_1 and which began t_0 (the age of the earth) years ago; (ii) a second, heterogeneous, stage characterized by μ_2, which differentiated from the homogeneous source at time t_1 and may be related to ocean floor spreading; (iii) finally, the formation of the basalt, essentially at present, with a U^{238}/Pb^{204} ratio μ_3 which is the ratio actually observed.

Following the mathematical representation of Russell *et al.* (*3*), the equations for the ratios Pb^{206}/Pb^{204} (= x) and Pb^{207}/Pb^{204} (= y) are

$$x = a_0 + \mu_1 (e^{\lambda t_0} - e^{\lambda t_1}) + \mu_2 (e^{\lambda t_1} - 1) + \mu_3 (1 - 1)$$
$$y = b_0 + (\mu_1/137.8)(e^{\lambda' t_0} - e^{\lambda' t_1}) + (\mu_2/137.8)(e^{\lambda' t_1} - 1) + (\mu_3/137.8)(1 - 1) \quad (1)$$

where the symbols have their usual meaning. It is clear from Eqs. 1 that from a lead isotope point of view, the samples have seen only two stages.

The diagram which represents the Concordia plot uses the radiogenic ratios α and β (*3*): $\alpha = (x - a_0)/\mu_3$ and $\beta = (y - b_0)\ 137.8/\mu_3$.

The assumption which leads to the two-stage model from the general model is "that the U^{238}/Pb^{204} ratio observed in the rock is representative of its source which was formed t_1 years ago" (*1*), in other words, that $\mu_3 = \mu_2$. This is a two-stage model mathematically. Physically it is still a three-stage process where, with the stated assumption, the third stage has no influence on the observed Pb/Pb or Pb/U ratios.

It is the assumption $\mu_2 = \mu_3$ which is, quite properly, challenged by Oversby and Gast. They examine the effect of this assumption, however, by considering a specific case of mantle fractionation 2000 million years ago which, since the average value of t_1 for the basalts considered (*1*) is 250 million years, is not particularly relevant to my model. Further, I believe that the Concordia plot sheds some light on the possible relationship between μ_3 and μ_2. This may be demonstrated as follows. Let $\mu_3 = k\ \mu_2$, where k is some function. From Eqs. 1 the expressions for α and β become

$$\alpha = \frac{\mu_1}{k\mu_2}(e^{\lambda t_0} - e^{\lambda t_1}) + \frac{1}{k}(e^{\lambda t_1} - 1)$$
$$\beta = \frac{\mu_1}{k\mu_2}(e^{\lambda' t_0} - e^{\lambda' t_1}) + \frac{1}{k}(e^{\lambda' t_1} - 1) \quad (2)$$

Equations 2 may be combined to give

$$\alpha = m\beta + \frac{1}{k}[(e^{\lambda t_1} - 1) - m(e^{\lambda' t_1} - 1)] \quad (3)$$

where

$$m = \frac{e^{\lambda t_0} - e^{\lambda t_1}}{e^{\lambda' t_0} - e^{\lambda' t_1}} \quad (4)$$

Two important conclusions may be drawn from Eqs. 3 and 4. First, Eq. 3 is the equation of a straight line, providing k is a constant. Second, the slope of the line, m, is not affected by the factor k. My assumption that $k = 1$ was based on the fact that the ages t_1 for the mid-Atlantic Ridge and East Pacific Rise samples calculated from Eq. 4 [by using the mean calculated value for $t_0 = 4530$ million years (*1*)] agreed with the corresponding values calculated from the lower intercept (*1*).

The Guadelupe island samples cannot possibly be explained by the mechanism suggested by Oversby and Gast and illustrated in their Fig. 1, owing to the linearity of the Concordia plot for these samples [$m = 0.0153 \pm 0.0003$ (*1*)]. I believe that these basalts, and others, may be interpreted by using a Concordia plot which allows for crustal contamination (*4*), a model which I briefly discussed during the Denver meeting mentioned above.

Oversby and Gast claim that the Concordia method does not lead to a determination of the age of the earth which is independent of the age of the samples. This claim is not correct. The two-stage Concordia plot is an approximation ($k = 1$) for three-stage recent basalts but it is a correct representation for leads which have developed in two closed systems. An example of such leads are the whole rock leads from the Llano Uplift (*5*). The upper intercept in the Concordia plot for such leads gives t_0 [4532 ± 16 million years for the Llano rocks (*1*)] completely independently of the age t_1 of these rocks (*1*, *3*). Another example of leads which apparently conform to the closed two-stage system are the Group I leads discussed by Welke *et al.* (*6*) who obtained a value of $t_0 = 4530 \pm 20$ million years. In this case the μ_3 stage does not exist, since t_1 agrees with the K-Ar ages obtained for these samples (*7*). Since the values of t_0 obtained for the two examples cited above are essentially identical [and agree with other estimates of the age of the earth (*8*)] in spite of the fact that their t_1 ages differ by two orders of magnitude [1000 million years (*1*) and 20 million years (*6*)], the independence of t_0 from a knowledge of t_1 can hardly be called "semantic." For three-stage leads t_0 depends on k as pointed out by Oversby and Gast. For the Hawaiian samples, for example, $t_0 = 4520$ million years if $k = 3$ (say) and $t_0 = 4600$ million years if $k = 0.3$.

I would like, finally, to comment on the concluding remarks of Oversby and Gast. Any method of plotting data acts as a filter on that data. The Concordia filter achieves results which are not readily apparent from the Pb^{207}/Pb^{204} versus Pb^{206}/Pb^{204} plot, but in the filtering process may smooth out certain features. The Concordia plot is not an either-or proposition however. Both methods of data representation may be used. Excellent examples of the importance of the Concordia plot in lead isotope studies have been given by Russell *et al.* (*3*) and Welke *et al* (*6*). The latter paper shows certain advantages of the Concordia plot compared to the lead ratio plot particularly well.

T. J. Ulrych

Department of Geophysics,
University of British Columbia,
Vancouver 8, Canada

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