tooth means of the nonfostered mice for the two teeth in the two strains was high ($r = +0.90$, $p < .05$), indicating that the change is nearly proportional to tooth size. The differences in means between the nonfostered animals of the two strains are assumed to be primarily hereditary in origin and are not unexpected in view of the relatively high heritability of these traits, as previously determined in a randomly bred strain (*3*). Dental regressions of offspring on sire are all nonsignificant ($P > .05$), an indication of no detectable genetic variation within a strain. Dental regressions of nonfostered (and fostered) offspring on dam are similarly nonsignificant, indicating isogenicity and also no detectable intrastrain association of maternal and progeny phenotypes due to the maternal effect. Correlations of tooth size and litter size are generally low, negative, and insignificant.

Within each strain there is a positive correlation of tooth size and body weight, the mean r for the M_2 and body weight being $+0.36$ ($P < .001$) and for the M_3 and body weight being $+0.18$ ($P < .01$). That the difference in tooth size related to the postnatal performance of the two types of females is not due simply to an attendant change in body weight, that is, a general growth phenomenon, can be seen in Table 1. The postnatal effect of strain A mothers was to increase body weight in both strains, whereas tooth size was decreased. Strain B mothers have the opposite effect. Thus, there may be a difference between genotypes with respect to milk and its specific effect on dentition. Alternatively, a given difference in the milk of the two strains may both inhibit body growth and promote dental development and vice versa. A possible cause of the effect may lie in the amino acids which can differ in the milk of different inbred strains of mice (*7*).

The magnitude of the prenatal and postnatal effects relative to one another and to the total intrastrain variance can be estimated from an analysis of variance. The general form of the analysis combines both the cross-classification and hierarchal models (Table 2). The total maternal effect is estimated by the "between-sublitter" component which includes the differences between litters born to different dams within a strain (prenatal litter factor), the difference between sublitters nursed by dams of the two strains (postnatal genotype factor) and the interaction between the two factors, that is, the differential response of the litters to the two postnatal experiences. The interaction also includes any effect of transferring the pups to the foster mother. However, the relative variance contribution of the maternal effect as well as the total variance are very similar in the two sublitter types within each strain, an indication of little, if any, effect of the transference *per se*. The "within-sublitter" component includes differences between individuals and differences between sides within the individual.

The results of the analyses for the two teeth within each strain are presented in Table 3. For the M_2 the relative contribution of each source of variation is quite similar for the two strains. The prenatal effect is relatively large and significant, and the interaction component is essentially absent in this molar. There is a somewhat greater difference between the results for the two strains in the M_3, but a general pattern is discernible. The prenatal factor is present, but insignificant, in strain A and absent in strain B. The interaction component is present in both strains but significant only in strain B. The total relative maternal effect is very similar in three of the analyses, being somewhat lower in the M_3 of strain A.

It appears, then, that the M_2 is influenced by a nongenetic prenatal factor in addition to its strain-specific genetic determination. Evidently development in this molar has proceeded sufficiently far at birth to render it insensitive to the interaction between prenatal-litter factors and postnatal genotype factors, that is, the different prenatal litters tend to respond postnatally in a relatively uniform manner to the genotypic difference between the nursing dams. However, the tooth is clearly not so far along in development that it is unaffected by the postnatal environment, as shown by the presence of a significant postnatal genotypic component. Presumably because it initiates development at a later time, the M_3 is apparently little affected by intrastrain differences in the prenatal environment although it is, of course, strongly influenced by its strain-specific genetic determination. It is, however, more responsive to its postnatal environment than the M_2 since it manifests, at least in strain B, a significant interaction component in addition to the postnatal genotypic effect.

For traits such as general body growth, there may be a postweaning compensation and adjustment to the early influence of the maternal effect (*8*), and a progressive diminution of the relative importance of this effect to the total variance as the animal matures (*9*). In teeth of the type studied here, however, development of the crown has essentially ceased by weaning, so that the effects of the maternal environment are incorporated as a permanent part of the structure.

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References and Notes

1. O. Venge, *Acta Zool.* **31**, 1 (1950); A. G. Searle, *J. Genet.* **52**, 413 (1954); G. L. Hunter, *J. Agr. Sci.* **48**, 36 (1956); D. F. Cox, J. E. Legates, C. C. Cockerham, *J. Animal Sci.* **18**, 519 (1959); J. L. Carmon and F. B. Golley, *Growth* **28**, 105 (1964).
2. A. McLaren and D. Michie, *J. Embryol. Exp. Morphol.* **6**, 645 (1958); H. Grüneberg, *The Pathology of Development* (Blackwell, Oxford, 1963), pp. 262–267.
3. R. S. Bader, *Evolution* **19**, 378 (1965).
4. ———, *J. Mammalogy* **46**, 384 (1965).
5. P. G. Luther, *Proc. Linn. Soc. (London)* **161**, 146 (1949).
6. S. A. Cohn, *Amer. J. Anat.* **101**, 295 (1957).
7. H. Meier, W. G. Hoag, J. J. McBurney, *J. Nutr.* **85**, 305 (1965).
8. C. W. Young and J. E. Legates, *Genetics* **52**, 563 (1965).
9. G. A. Harrison, R. W. Hiorns, J. S. Weiner, *Proc. Roy. Soc. London Ser. B* **160**, 137 (1964).
10. Supported by NSF grant G-19197 and by the Research Board, University of Illinois. We are indebted to Dr. R. W. Touchberry, University of Illinois, for statistical advice.

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Availability of a Cationic Herbicide Adsorbed on Clay Minerals to Cucumber Seedlings

Abstract. *Montmorillonitic and kaolinitic clays are effective in decreasing the toxicity of paraquat, an organic cation, to cucumber plants. The cation was adsorbed on the surface of the kaolinite clay particles and slowly became available to the plants. When it was adsorbed in the interlayer spacings of the montmorillonite clay, however, it was not available to the plants.*

Investigation of the adsorption of several herbicides by various adsorbents have indicated that two organic cationic herbicides, diquat [6,7-dihydrodipyrido-(1,2-*a*:2′,1′-*c*)-pyrazidiinium dibromide] and paraquat (1,1′-dimethyl-4,4-bipyridinium dichloride), are strongly adsorbed on montmorillonite and kaolinite clays (*1*). Both compounds were found to be bound within the interlayer spacings of the montmorillonite clay by coulombic (ion exchange) and van der Waals forces and to the surfaces of particles of kaolinite clay by coulombic ion exchange forces only. Both herbicides were adsorbed by the clays to approximately the cation exchange capacity of the clay minerals. No herbicide was adsorbed by the clays beyond this capacity. Only small amounts (5 percent) of the herbicides could be removed from montmorillonite clay with $1M$ barium chloride solution and this was presumably adsorbed on the exterior surfaces of the clay particles. Approximately 80 percent of the absorbed herbicides was removable from the kaolinite clay however. Because of the strong adsorption of the herbicidal compounds by the two clays, especially montmorillonite, we sought to determine the availability of these tightly bound compounds to plants.

Table 1. Effect of montmorillonite (M) and kaolinite (K) clays on reducing the toxicity of paraquat to cucumber seedlings at two dates.

Sample No.	Paraquat added (μmole)	Clay added		Plant height (cm)		Inhibition (%)*	
		Type	Amt (mg)	7 days	10 days	7 days	10 days
1	0		0	8.0	10.1	0	0
2	0	M	30	8.2	10.0	0	0
3	0	K	600	8.0	10.0	0	0
4	10		0	3.5	1.2†	56	88†
5	10	M	15	4.1	1.7†	49	83†
6	10	M	20	5.7	5.2	29	48
7	10	M	30	8.0	10.0	0	0
8	10	K	215	3.7	2.0†	54	80†
9	10	K	415	3.7	2.2†	54	78†
10	10	K	600	7.1	4.5†	11	55†
S.E.‡				0.3	0.3	4	3
L.S.D. (.05)‡				.9	.9	11	9
H.S.D. (.05)‡				1.1	1.1	14	10

* Percentage inhibition with respect to comparable, untreated plants. † Dead plants. ‡ S.E., standard error; L.S.D., least significant difference; H.S.D., honestly significant difference.

Paraquat (10 μmole) was added to solutions containing clay (*1*) in amounts ranging from 15 to 30 mg of montmorillonite (*2*) and from 215 to 600 mg of kaolinite (*3*). Paraquat was added to the clay in amounts which had previously been found to result in growth inhibition of approximately 90 percent for cucumber plants. Calculations were based on information from previous studies (*1*), so that the 15-mg montmorillonite and 215-mg kaolinite samples would adsorb approximately one-half of the paraquat added and the remaining paraquat in solution would be sufficient to give a plant growth inhibition of 50 percent for the cucumber bioassay. Clay samples of 20 mg of montmorillonite and 415 mg of kaolinite were calculated to adsorb three-fourths of the added paraquat, allowing only one-fourth to remain in solution available for the plants, thereby producing growth inhibition of 25 percent. Samples containing 30 mg of montmorillonite and 600 mg of kaolinite were calculated to adsorb all of the paraquat from the solution. Theoretically the only available paraquat for cucumbers would then be that which was adsorbed on the clays. The larger clay samples were also washed with a 20-ml portion of deionized water to remove loosely adsorbed paraquat.

Chemical analyses of the solutions containing the larger clay samples and the wash solutions showed that no detectable paraquat was present. The clay suspensions were added to 120 g of quartz sand in small glass jars. Four cucumber seedlings, which were later thinned to two, were placed in direct contact with the added clay, and 40 additional grams of quartz sand were added to cover the seedlings. Hoaglands nutrient solution ($0.01M$, *p*H 5.5) was added to the sand each day to provide nutrients and water. A similar set of samples was prepared without clay, to which paraquat was added at various concentrations to yield a standard growth inhibition curve. A set of samples was also prepared without herbicide, to which various additions of the clays were added to determine the effect of the clays alone on plant growth. The small amount of clays used in these studies had no detectable effect on plant growth. There were two replicate samples for each treatment; the same results were obtained when the experiment was repeated. The studies were performed in a growth chamber at 25°C; light intensity was 12,000 lumen/m^2, and day length was 12 hours.

Table 1 illustrates the effect of the montmorillonite and kaolinite clays on the toxicity of paraquat to cucumber seedlings. The 10-μmole rate of paraquat was chosen as the standard rate to demonstrate the effect of the clays on the herbicide. Both of the clay minerals were effective in reducing the toxicity of paraquat at the 7-day period (Table 1). Paraquat, which was adsorbed on the kaolinite clay, was slowly utilized by the cucumber plant, however. Sample 10 shows that plant growth was inhibited by only 11 percent at 7 days, where the only available paraquat was that which was adsorbed on the kaolinite clay. This indicates that only small amounts of the adsorbed paraquat may have been absorbed by the plant roots directly from the clay through cation exchange, or small amounts of the paraquat may have been released into the nutrient solution through exchange equilibria and the free paraquat was then absorbed by the plant roots. The utilization of paraquat by the cucumber seedlings from the kaolinite clay system is illustrated more clearly at 10 days, when growth inhibition was increased to 55 percent.

These plants were completely dead at 10 days. Paraquat which was present in solution in amounts exceeding the adsorption capacity of the montmorillonite clay (that is, in the pots treated with 15 and 20 mg of montmorillonite) was also effective in killing the cucumber plants. In the pots where sufficient montmorillonite clay had been added to adsorb all of the paraquat (that is, the pots treated with 30 mg of montmorillonite), the cucumber plants exhibited no symptoms of phytotoxicity. These plants were allowed to grow for 24 days. New cucumber seedlings were again planted in these pots; after 24 days, these plants also appeared to be normal. Paraquat adsorbed on the montmorillonite clay at below the cation exchange capacity is apparently not available to the cucumber plants, and the small amount which is adsorbed on the surface of montmorillonite clay particles, although it may be available to the plants, is not enough to cause significant inhibition to the plants. This is in agreement with desorption studies which showed that when the herbicides paraquat and diquat were adsorbed on montmorillonite clay, only 5 percent was removed by four extractions with $1M$ $BaCl_2$. When the herbicides were adsorbed on kaolinite clay, however, approximately 80 to 85 percent was removed with the same extraction solutions. This surface-adsorbed paraquat appears to be available to the plant roots. It was also found that one of the organic cations could exchange for the other (*1*), if the clay was first saturated to its cation exchange capacity with one of the cations. Below the cation exchange capacity, however, both of the organic cations were completely adsorbed in exchange for inorganic cations on the clay surfaces. Paraquat, which has been found by x-ray analysis (*1*) to be adsorbed in the interlayer spaces of the montmorillonite clay, is apparently held so tightly or in such a manner that the compound is not available to the cucumber roots. The small amount of paraquat adsorbed on the exterior surfaces of montmorillonite clay is probably available to the plant roots (*4*). The paraquat, which is adsorbed to the exterior surfaces of the kaolinite clay particles, slowly becomes available to the cucumber roots, probably through ion exchange.

The nonavailability, or slow availability, to plants of this cationic herbicide from clay minerals is not of grave concern at present, since this material is applied in amounts from 1 to 2 pounds (2 to 4 kg) per acre. For instance, assuming that none of the paraquat adsorbed on montmorillonite clay is available to plant roots, it would take approximately 2250 pounds of paraquat to saturate the cation exchange capacity of the 6-inch plow layer of a soil which contains 1 percent montmorillonite clay; and this would assume no degradation of the herbicides by microorganisms. It must be determined whether or not this herbicide, when adsorbed in the interlayer spacings of montmorillonite-type clay minerals, is degradable by microorganisms. Preliminary studies utilizing isotope-labeled diquat and paraquat indicate that when these compounds are adsorbed in the interlayer spacings of montmorillonite clay, the amount of degradation by soil microorganisms is very small. These compounds are readily degraded by microorganisms, however, when they are adsorbed on kaolinite clay (*4*).

Another facet of the adsorption of these organic cationic herbicides by soil clays is the effect they have on the water- and nutrient-holding capacity of the clays. Since these compounds are very strongly adsorbed, they no doubt displace water or nutrient elements in the clay minerals. Such displacement could have a beneficial or a deleterious effect on the production potential of a particular soil.

These studies demonstrate the necessity of employing several detection methods when measuring the persistence of herbicides in the soil. Bioassay plants are very useful in detecting the toxicity of herbicides to plants and do indicate the plant-available herbicide present. The amount of paraquat removed from the two clays by extraction with $1M$ $BaCl_2$ has been shown to be related to the amount of the herbicide that was available to cucumber plants, and this may be useful if one is interested in predicting the herbicide in the soil which is available to plant roots. It may be of interest, however, to determine not only the plant-available herbicides in the soil, but also the total amount which is present. Since neither the $1M$ $BaCl_2$ extractions, nor the plant bioassays were able to detect paraquat which was adsorbed in the interlayer spacing of the montmorillonite clay, a stronger extracting solution would be needed to determine the total amount of paraquat in a soil containing this clay mineral.

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References and Notes

1. J. B. Weber, P. W. Perry, R. P. Upchurch, *Soil Sci. Soc. Amer. Proc.* **29**, 678 (1965).
2. Wyoming bentonite with a cation exchange capacity of 0.847 meq/g.
3. Kamel kaolin from North Carolina with a cation exchange capacity of 0.051 meq/g.
4. These studies are under way.
5. Paper No. 2130 of our journal series.

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Tree Shrews: Unique Reproductive Mechanism of Systematic Importance

Abstract. Tupaia *offspring are maintained in a separate nest constructed by the male parent and are suckled by the female only once every 48 hours. The young are nevertheless able to maintain a constant external body temperature of 37°C.*

The tree shrews (family Tupaiidae) are widely regarded as the most primitive members of the order Primates (lemurs, monkeys, apes, and man) and have often been described as a "missing link" relating Primates to Insectivora stock. For this very reason, the tree shrews have been considered as suitable objects for medical research, although hopes in this direction have foundered due to poor breeding successes, the overall laboratory average having been estimated at 20 percent (1).

Opinion is divided over the exact systematic position of the Tupaiidae, although most workers believe that tree shrews are intermediate between the Insectivora and Primates. Primitive features have led some workers (*2*) to place the tree shrews with the Insectivora; some advanced features have led others to include tree shrews with the Primates (*3*). There are also resemblances to Marsupialia and features reminiscent of Rodentia and Lagomorpha. General features of reproduction and the unique breeding mechanism described in this report support much recent evidence that any relationship of the Tupaiidae to the Primates is very tenuous.

Although much work has been carried out on the tree shrew (*4, 5*), a number of important features of the reproductive behavior have remained obscure. Our animals (*Tupaia* sp.) were kept in pairs in cages much larger than has been usual (8 rather than 1 m^3) and were provided with excess food including fresh milk, meat, insects, fresh fruit, and vitamin additives. Suit-