4. Tests for weak alleles at the *Tu-tu* locus.

In earlier tests it was found that when maize varieties of Latin America are crossed on an inbred strain of half-tunicate tu^h tu^h there is marked variation in the development of the glumes on ears of the F_1 plants. Variation ranges from ears in which only the basal kernels are partly covered with glumes, to ears in which all kernels are completely covered. Some of this variation is undoubtedly due to modifying factors and some, perhaps, to environmental influences. There is, for example, some variation in glume development in the same stock from season to season. Much of this variation, however, may be due to differences in alleles at the Tu-tu locus in the Latin American varieties, some of which, although ordinarily regarded as non-tunicate, have glumes appreciably longer than those of most of the commercial varieties of the United States. The Mexican variety Chapalote, for example, has glumes about as long as the kernels.

A rather sensitive test for allelism at this locus has now been developed. Varieties with longer than average glumes, thought to be weak forms of tunicate, are crossed with an inbred strain of sugary, P39 for example, with short glumes. The F_1 hybrid is crossed by a non-sugary inbred strain of half-tunicate tu^h tu^h. If the stock being tested carries an allele somewhat higher (or lower) in the series than that brought into the cross by the sugary parent, there is segregation in the backcross generation, the differences between the two original genes being exaggerated by the presence of the tu^h gene. Thus a cross of non-tunicate, tu tu, by weak tunicate, tu^w tu^w, when backcrossed to half-tunicate, tu^h tu^h, yields two genotypes, tu^w tu^h, tu tu^h, in equal numbers. If the parents differ with respect to sugary endosperm then the backcross also yields two genotypes, Su Su and Su su, in approximately equal numbers. The test for allelism, therefore, usually involves first, the occurrence in the backcross generation of two more or less distinguishable classes with respect to the development of glumes, and secondly, the linkage of these classes with the two genotypes involving sugary. This second test is necessary to exclude the possibility that variation in glume length is the product of major modifying genes on other chromosomes.

The data so far obtained from tests of this kind are summarized in Table 4. In all of the crosses included in this table two classes with respect to glumes have been distinguished, and these classes have shown some degree of association with the two genotypes involving sugary. The average percentage of crossing-over is 37.1. This is within the range of data previously reported fro [sic] crossing over between Su and Tu, but is somewhat higher than the average. This can be attributed to the fact that the classification with respect to glume length is seldom perfect.

Table 4. Tests for allelism and linkage at the Tu-tu locus.

	Longer Glumes		Shorter Glumes			No.
Cross	Su su	su su	Su su	su su	Total	Crossovers
Guatemala 197 x P39	18	19	19	33	84	33
Ecuador 1195 x P39	19	10	13	20	62	23

Chapalote x P39	28	15	22	26	91	37
Pr Tester x P39	31	15	13	29	88	28
Pr Tester x Conn. 75	19	10	17	22	68	27
Conn. 75 x Ecuador 1197	30	59	60	26	175	56
Honduras 1639 x P39	24	49	38	24	135	48
Venezuela 1536 x P39	32	50	53	43	178	75
				Totals	881	327

Average Percent Crossing Over 37.1

Additional tests in which both parents were either Su Su or su su so that linkage relations could not be determined indicate that Conn. 75 and P39 have different alleles and that Chapalote and Pr Tester are also different. In both cases two distinguishable classes for glume length occurred.

The combined data indicate that

1. P39 carries a higher allele than Venezuela 1536 and Honduras 1639.
2. Guatemala 197, Ecuador 1195, Chapalote, Pr Tester, and Conn. 75 all carry higher alleles than P39.
3. Pr Tester has a higher allele than Conn. 75.
4. Chapalote has a higher allele than Pr Tester.

Since all of these stocks have shorter glumes than those conditioned by the allele tu^f, although they have not been tested in crosses with it, it now appears that there are at least seven alleles at this locus, Tu, tu^h, tu^f, tu plus three types of weak tunicate which lie between tu^f and tu and to which symbols have not yet been assigned.

In addition to the crosses listed in Table IV and those mentioned elsehwere we have had one cross, Peru 1715 x P39, in which there was no segregation for glume length. There has also been one cross, Brazil 1691 x P39, in which segregation for glume length occurred but was not associated with segregation for sugary. This cross, however, happened to be segregating for several other characters including cob color, and the longer glumes proved to be linked with the P factor on chromosome 1. The glumes in the Brazilian parent of this cross are not at all like the glumes of weak tunicate, being quite stiff and horny, and resembling the glumes on ears of derivatives from maize-teosinte crosses.

The alleles at the Tu tu locus furnish a substantial sum of variation and, as is shown later, affect other characters of the plant and are undoubtedly a factor in the evolution of maize under domestication. Judged by their appearance and by the glumes produced on F_1 ears when they are crossed with half-tunicate, the majority of inbred strains of field corn in the U.S. are non-tunicate, but some of the sweet corn inbreds including P39 are weak tunicate.