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GENETIC EVIDENCE AND THE ORIGIN OF MAIZE

Jeff Bennetzen, Edward Buckler, Vicki Chandler, John Doebley, Jane Dorweiler, Brandon Gaut,
Michael Freeling, Sarah Hake, Elizabeth Kellogg, R. Scott Poethig, Virginia Walbot,
and Susan Wessler

The origin of maize has been a topic of interest to both biologists and archaeologists. During the twentieth century, the viewpoint that maize is a domesticated form of teosinte received convincing support from biological data and is now broadly accepted among biologists familiar with the issues and data. There is no support of any kind for an alternative view that maize is a hybrid of the grasses Zea diploperennis and Tripsacum.

El origen del maíz ha sido un tema de interés tanto para los biólogos como para los arqueólogos. Durante el siglo veinte, el punto de vista que mantiene que el maíz es una forma de teocinte domesticada ha recibido apoyo convincente de los datos biológicos y hoy día es aceptado ampliamente entre los biólogos quienes conocen bien el tema y los datos. No hay apoyo de cualquier tipo en favor de la proposición que el maíz es un híbrido de Zea diploperennis y Tripsacum.

Over 60 years ago, George Beadle (1939) proposed that teosinte (*Zea* species) was the wild ancestor of maize (the teosinte hypothesis) as an alternative to the “tripartite” hypothesis that maize arose from an extinct wild maize (Mangelsdorf and Reeves 1939). Although a controversy surrounded these competing hypotheses for many years, the 1970s and 1980s witnessed a series of reports supporting the teosinte hypothesis. The teosinte hypothesis subsequently became broadly accepted among biologists, especially maize geneticists and evolutionists who were familiar with the issues, data, and analytical methods (see references below). Nevertheless, a minority viewpoint that teosinte was not ancestral to maize retained some

advocates (Mangelsdorf 1974; Randolph 1975). Recently, the teosinte hypothesis was challenged with the proposal that maize arose from the progeny of a cross between a species of teosinte (*Zea diploperennis*) and another grass (*Tripsacum*) (hereafter the tripsacum-diploperennis hypothesis) (Eubanks 1995). The report of a putative hybrid between *Tripsacum* and *Z. diploperennis* (Eubanks 1995, 1997) was used as evidence in developing the tripsacum-diploperennis hypothesis. MacNeish and Eubanks (2000) have used the tripsacum-diploperennis hypothesis as a platform for reevaluation of the archaeological evidence for the origin of maize.

We write as a group of maize geneticists and evolutionists to make three points that may be of inter-

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est to archaeologists concerned with the origin of maize. First, the biological evidence for Beadle's teosinte hypothesis is overwhelming. Second, the report of a successful tripsacum-diploperennis hybrid upon which the tripsacum-diploperennis hypothesis is based is not credible. Third, there are no data indicating that the maize genome is a mixture of the *Z. diploperennis* and *Tripsacum* genomes as specified by the tripsacum-diploperennis hypothesis.

(1) The support for the teosinte hypothesis is overwhelming. It is beyond our purposes to review this evidence here; however, we note that this evidence comes from a variety of sources including cytology (Kato 1976; McClintock et al. 1981), classical genetics (Beadle 1972; Langham 1940; Szabo and Burr 1996), systematics (DeWet and Harlan 1972; Galinat 1971; Iltis 1971; Kellogg and Birchler 1993), morphology (Galinat 1983; Iltis 1983), biochemical genetics (Doebley et al. 1984), molecular genetics (Dennis and Peacock 1984; Doebley et al. 1987; Fuerstenberg and Johns 1990; Purugganan and Wessler 1994; Walbot 1983), quantitative genetics (Doebley et al. 1990), population genetics (Eyre-Walker et al. 1998; Goloubinoff et al. 1993; Hilton and Gaut 1998; White and Doebley 1999), and phylogenetics (Benz 1999; Buckler and Holtsford 1996; Miranda 1966). More importantly, the evidence comes from a large number of independent researchers, all trained as biologists, and all of whom agree—teosinte is ancestral to maize. Nowhere in this extensive literature has there been evidence for a contribution of *Tripsacum* to maize ancestry.

(2) Although producing a *Tripsacum-Z. diploperennis* hybrid may very well be possible, the reports of Eubanks (1995, 1997) do not demonstrate that *Tripsacum* and *Z. diploperennis* were successfully hybridized. Rather, the statements and figures in these reports suggest that at least some or all of the putative tripsacum-diploperennis hybrids are maize-diploperennis hybrids. First, the chromosome number of the putative tripsacum-diploperennis hybrid is $2n = 20$. This is also the chromosome number of both maize and *Z. diploperennis*, and thus the number one would expect in a maize-diploperennis hybrid. If *Tripsacum* ($2n = 36$ or 72) had been one of the parents, one would have expected the hybrid to have 28 or 46 chromosomes. Second, the high fertility of the putative tripsacum-diploperennis hybrids is typical of maize-teosinte hybrids (Wilkes 1967), while the only known teosinte-tripsacum hybrid (*T. andersonii*) is sterile (Talbert et al. 1990a). Third, the molecular

marker results presented by Eubanks (1995, 1997) do not establish that the putative tripsacum-diploperennis hybrids are real. Specifically, the putative hybrids do not contain the restriction fragments of both of the two putative parents (Eubanks 1995: Figures 8–9). Fourth, the ears of the putative tripsacum-diploperennis hybrids (Eubanks 1995: Figures 5–6; McNeish and Eubanks 2000: Figure 3) look like maize-teosinte (maize-diploperennis) hybrids. The ear structure, chromosome number, fertility and restriction fragment patterns of the putative tripsacum-diploperennis hybrids are all consistent with them being maize-diploperennis hybrids. This possibility must be excluded and positive evidence that they are tripsacum-diploperennis hybrids shown before concluding that they are such. Finally, even if one did successfully hybridize *Tripsacum* and *Z. diploperennis*, such an accomplishment would not discredit the evidence for the teosinte hypothesis.

(3) There is no evidence that the maize genome contains a mixture of *Tripsacum* and *Z. diploperennis* germplasm. In the relevant reports, these taxa are distinct as expected if they are the end-products of divergent evolution (Buckler and Holtsford 1996; Dennis and Peacock 1984; DeWet and Harlan 1972; DeWet et al. 1987; Doebley et al. 1987; Eyre-Walker et al. 1998; Goloubinoff et al. 1993; Hilton and Gaut 1998; Larson and Doebley 1994; White and Doebley 1999). One does not see either *Tripsacum* or *Z. diploperennis* sequences in maize as expected if the tripsacum-diploperennis hypothesis were correct. Most telling are several families of high-copy number sequences for which *Tripsacum* and *Zea* genomes are differentiated, with maize totally lacking any *Tripsacum* sequence (Raz et al. 1991; Talbert et al. 1990a, 1990b; Talbert and Moylan 1991).

The origin of maize has both archaeological and biological components. There are often difficulties for those of us in one of these fields to judge the evidence from the other. We hope our comments as a group of maize geneticists and evolutionists on the biological evidence can contribute in a positive way to the evaluation of the archaeological evidence.

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