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George Beadle's Other Hypothesis: One-Gene, One-Trait

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THREE decades before he was awarded the Nobel prize for his work on the model organism, Neurospora, and the "one-gene, one-enzyme" hypothesis, George Beadle cut his scientific teeth on a distinctly nonmodel organism, teosinte, a wild grass that is closely related to maize. This early work on teosinte began a lifelong fascination with the origin of maize and set Beadle on a mission to confirm a hypothesis that he had settled in his own mind as a graduate student—teosinte is the progenitor of cultivated maize. Although the path of events led him away from this mission during the most productive years of his career, upon retirement from the presidency of the University of Chicago in 1968, Beadle again took up research on teosinte, employing experimental genetics and organizing an expedition to Mexico in search of naturally occurring mutants in teosinte populations that might shed some light on the steps that transformed teosinte into maize. Through these efforts, he played the decisive role in overturning the most advertised theory on maize evolution. But before I tell the tale of our protagonist, I need to make a brief digression on the early history of his on-again, off-again sidekick, teosinte.

From the time of its discovery until 1896, teosinte was known principally to a handful of botanists who had preserved a few dried specimens in European herbaria and bestowed upon it the Latin name, *Euchlaena mexicana*. Teosinte was placed in the genus Euchlaena rather than in Zea with maize (*Z. mays*) because the structure of its ear is so profoundly different from that of maize that 19th century botanists did not appreciate the close relationship between these plants. Indeed, when the first maize-teosinte hybrids were discovered in the late 1800s, they were not recognized as hybrids but considered a new and distinct species—*Zea canina*. It was a Mexican agronomist, José Segura, who made the first experimental maize-teosinte crosses, demonstrating that *Zea canina* was a maize-teosinte hybrid and thereby implying that maize and teosinte were much more closely related than previously thought (Harshberger 1896). But Segura's discovery raised more questions than it answered. Should maize and teosinte be considered the same species? If not, why are two such distinct species able to hybridize? Was teosinte the ancestor of maize? If not, what species was ancestral to maize?

Segura's discovery had fortunate timing, coming as it did shortly before the rediscovery of Mendel's laws of inheritance and the resultant wave of interest in applying the Mendelian approach to all organisms, large and small. G. N. Collins of the USDA's Bureau of Plant Industry was prepared to capitalize on this confluence of events. Collins traveled to Mexico and Guatemala on teosinte hunts, discovered or rediscovered a number of teosinte populations, brought seed back to the United States, and began to study teosinte and its hybrids with maize. He had a central role in raising the interest level in teosinte among maize geneticists in the United States through a series of papers including "Structure of the maize ear as indicated in *Zea-Euchlaena* hybrids" (Collins 1919) and "Teosinte in Mexico" (Collins 1921). His research took the study of maize origins beyond the practice of making inferences from comparative morphology by engaging an experimental approach. He also generously supplied teosinte seed to his colleagues around the country and thus launched a burst of research on teosinte.

Rollins Emerson and teosinte: Now, we pick up Beadle's trail as a graduate student at Cornell University, for among those to take advantage of Collins' teosinte stocks was Beadle's thesis advisor, Rollins A. Emerson (see Nelson 1993). Emerson obtained the seed and took up an interest in teosinte shortly before the Cornell maize group included what was certainly the most eminent cohort of students in the history of plant genetics, Barbara McClintock, Marcus Rhoades, Charles Burnham, and, of course, George Beadle. While the group labored to sort out the relationship between chromosomal behavior and inheritance, Emerson assigned Bea-

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Teosinte ear (left), modern maize ear (right), and their F_1 hybrid (center).

dle the task of working on the cytology and genetics of maize-teosinte hybrids (see Beadle 1972). Together, they published one article on this topic (Emerson and Beadle 1932), and Beadle (1932a,b) published two additional solely authored articles based in part on work he performed at Caltech. The intention of these three articles was not to unravel the origin of maize, and indeed the topic is not mentioned in any of the three. Rather, in keeping with the theme of Emerson's laboratory, the cytological analysis of maize-teosinte hybrids was aimed at sorting out the relationships between the events of meiosis and whether these events would differ in a wide cross. They also sought to determine the degree of homology between maize and teosinte chromosomes.

Despite their silence on the matter of maize evolution, Beadle and Emerson reached some distinct evolutionary conclusions. First, they recognized that teosinte types could be classified into groups on the basis of the chromosomal behavior of their hybrids with maize. Maize hybrids with Mexican annual teosinte (Chalco type) exhibited fully normal meioses, were fully fertile, and showed linkage distances between genes that were the same as those seen in maize-maize crosses. Beadle and Emerson concluded that this form of teosinte was the same species as maize, a fact recognized by taxonomists in 1972 when Mexican annual teosinte was placed in the same species as maize, as *Zea mays* ssp. *mexicana* (Iltis 1972). Maize hybrids with a type of teosinte from Guatemala, known as Florida teosinte, were partially sterile, exhibited incomplete chromosomal homology, produced some univalents, and had reduced linkage distances. From these observations, Beadle and Emerson concluded that Florida teosinte represented a distinct species from maize, a fact recognized more recently by taxonomists when Florida teosinte was granted species status as *Zea luxurians* (Bird 1978). Notably, Beadle and Emerson were applying the biological species concept a decade before Ernst Mayr defined it (Mayr 1942).

Recognizing that some teosintes were of the same species as maize, while others belonged to a distinct species, Beadle (1972) confided to his readers that he and Emerson reached the conclusion that Mexican annual teosinte was the ancestor of maize. Beadle (1980a) attributes to Emerson the idea that a small number of major mutations could have converted teosinte into a useful food plant during the early stages of domestication. These conclusions went against the common view of the day, which considered maize to have been domesticated from a missing or extinct wild maize (Harshberger 1896; Collins 1912; East 1913; Weatherwax 1918). The morphological differences between teosinte and maize were simply too great, it was felt, for maize to have been selected from teosinte by ancient peoples over a few thousand years. Even if not the prevalent view, Beadle and Emerson's ideas that teosinte was the ancestor of maize and that major mutations were involved were not entirely new (Vinson 1877; Schuman 1904; Blaringhem 1906), but they arrived at this opinion on the basis of their own (genetic) evidence. So in 1932, Beadle and Emerson considered the problem of the origin of maize solved and marched off to tackle greater challenges.

What for Beadle and Emerson was a classic no-brainer left many others of their day perplexed, still searching for a Rosetta stone that would unlock the mystery of maize. Why so? Other authors were shackled by two dicta of contemporary thinking among evolutionary biologists, of which Beadle and Emerson were either unaware or unpersuaded. The first was that evolution proceeds from primitive to advanced and can never be reversed. Since teosinte had two advanced traits (single female spikelets and hard glumes covering its kernels) and maize had more primitive traits (paired female spikelets and softer glumes), then maize (a primitive species) could not be derived from teosinte (a more advanced one). For Beadle and Emerson, this was not a consideration; for them, evolution could proceed in whichever direction selection would drive it. The second dictum was that evolution proceeds by accumulating many small changes over very long periods, and thus the dramatic shift from teosinte to maize would simply not be possible in the brief time that humans had been cultivating plants. For Beadle and Emerson, who were intimately familiar with the dramatic morphological mutants of maize, single gene changes of large effect would be sufficient to do the trick.

Competing hypotheses: Beadle's silence on maize origins was to be short lived. In 1938, Paul Mangelsdorf and colleague Robert Reeves (Mangelsdorf and Reeves 1938, 1939) proposed a partially new view on the origin of maize that they christened, with a bit of flair, "the tripartite hypothesis":

Part 1: They proposed that the progenitor of maize was a now-extinct wild maize from South America, an idea borrowed from East (1913) who was Mangelsdorf's thesis advisor at Harvard University.

Part 2: They adopted from Edgar Anderson, another of East's students at Harvard, the suggestion that teosinte was of hybrid origin, the offspring of a cross between another genus of grasses (Tripsacum) and maize.

Part 3: They proposed that a major source of the diversity among modern varieties of maize had been an "infection" of Tripsacum germplasm.

The showpiece of their 1938 paper was their successful cross of maize and Tripsacum. Since Tripsacum has $2n = 36$ and maize $2n = 20$ chromosomes, this was a challenge; however, by trimming the maize silk, making large-scale applications of Tripsacum pollen, surgically rescuing the few resultant embryos, and transferring them to agar plates, they were able to produce a few, largely sterile maize-Tripsacum hybrids. More importantly, however, they had also analyzed backcross populations of maize-teosinte hybrids and identified four factors controlling the morphological differences between maize and teosinte. Mangelsdorf and Reeves interpreted these four factors as four blocks of Tripsacum germplasm that had infected maize, creating teosinte.

In June 1939, less than one year after the publication of the tripartite hypothesis, Beadle made public his opinion on the origin of maize and the tripartite hypothesis. He contended that a cross between maize and Tripsacum, which could be accomplished only by surgical rescue of embryos, was not likely to have ever taken place in nature. He noted that Mangelsdorf and Reeves (1939) had no evidence that the four factors that made maize and teosinte different were four blocks of Tripsacum germplasm and that they might just as well represent four major genes involved in the evolution of maize from teosinte. Finally, he saw no need to propose an imaginary wild maize when the real article, teosinte, was right under our noses. So, he proposed that teosinte was the progenitor of maize and that four (or five) major gene changes (Mangelsdorf and Reeves' four factors) would have been sufficient to convert teosinte into a primitive form of maize. As he had been told by Emerson, one gene would change shattering to solid cobs; another gene would change covered to naked kernels, etc. Thus, in 1939, Beadle laid out a *one-gene, one-trait hypothesis* for the origin of maize or what is known as the "teosinte hypothesis."

Teosinte ear (left) and "reconstructed" small primitive maize ear (right). This small-eared form of maize was bred by George Beadle by crossing teosinte with Argentine popcorn and then selecting the smallest segregants. Beadle's intention was to reconstruct a primitive, small-eared corn that would resemble the earliest archeological corn recovered from the Tehuacán valley in Mexico.

At this point Beadle fell into a three-decade-long silence on the origin of maize while Paul Mangelsdorf rode the wave of his theory to the pinnacle of academic success—a professorship at Harvard and memberships in both the National Academy of Sciences and the American Philosophical Society. The tripartite hypothesis was extolled in the most prestigious of journals (Mangelsdorf 1958; Mangelsdorf and Galinat 1964; Mangelsdorf *et al.* 1964). Mangelsdorf's name became synonymous with the study of maize evolution, and his influence was pervasive, while Beadle's (1939) objection to the tripartite hypothesis was all but ignored. Mangelsdorf was especially influential among archeologists through his collaboration with his Harvard colleague, Richard MacNeish (1964), and in some of the archeological literature the tripartite hypothesis was elevated to fact (*e.g.*, Flannery 1968). From children's books (Aliki 1976) to encyclopedia to the plant breeding literature (Wellhausen *et al.* 1952), the origin of maize was tripartite. Despite his success with the wider audience, Mangelsdorf never succeeded in convincing his colleagues in maize genetics of the tripartite hypothesis. As a graduate student in the late 1970s, I solicited the opinions of a handful of maize geneticists who were active from the 1940s to the 1960s; their private reactions to the tripartite hypothesis were uniform. One put it quite directly: "I never believed a word of it." I should mention that during this period there was some sympathy for the teosinte hypothesis (Langham 1940; Lon-

Some of the participants in George Beadle's teosinte hunt in Mexico City in 1971. Top row: George Beadle, David Galinat, L. R. Randolph, Walton Galinat, H. Garrison Wilkes, H. H. Iltis. Bottom row: Phillip Eugene, Robert I. Brawn, Ted Cochrane, and Robert Gray. Photo by Glenn Price.

GLEY 1941; DARLINGTON 1956; MIRANDA 1966), but the Mangelsdorf school was dominant.

A battle of titans: This was the situation in 1968, when George Beadle "retired" and took up his mission to revive the teosinte hypothesis and banish tripartitism. BEADLE (1972, 1977, 1978, 1980a, 1981) spelled out both his objections to the tripartite hypothesis and his view that the teosinte hypothesis best fits the evidence. To test his view that a few gene changes could account for the transition from teosinte to a primitive form of maize, he grew 50,000 maize-teosinte F_2 plants and observed that 1 in 500 plants was like either the maize or the teosinte parent. This is about the number of parental types one would expect if four or five genes were involved in the evolution of a small-eared primitive maize from teosinte. He supported his genetic arguments with inferences from anthropology, archeology, geography, and linguistics.

Beadle also organized a "teosinte hunt" to Mexico in 1971 to collect seed and search for natural mutants in teosinte populations that might reveal the steps involved in the early evolution of maize. His companions were a *Who's-Who* of maize evolutionists at the time, including Kent Flannery, a University of Michigan archeologist; Walton Galinat, a morphologist and associate of Paul Mangelsdorf; Hugh Iltis, a University of Wisconsin botanist; L. F. Randolph, a Cornell University cytologist; and H. Garrison Wilkes, a student of Paul Mangelsdorf and author of the definitive work on teosinte of the time. Beadle likely hoped to gain a few new converts to the teosinte hypothesis along the way. This group toiled together collecting teosinte on the parched hillsides of the Balsas river valley, where perhaps some 8000 years earlier ancient Mexicans also were searching through the same teosinte fields for a plant with a promising mutation. The expedition yielded no natural mutants of teosinte, but the seed they collected entered germplasm banks and has since been used in many experiments including my own.

Beadle was certainly aware that it was not his colleagues in maize genetics who needed an education on maize evolution, but the broader scientific and lay audiences. [I make this inference in part because Beadle never published a standard peer-reviewed paper on his postretirement work with maize-teosinte hybrids, but rather wrote two popular articles (BEADLE 1972, 1980a) and three reviews (BEADLE 1977, 1978, 1980b).] After all, the origin of maize had been solved in 1939; the word just hadn't gotten out. Beadle also lectured around the country (Caltech, Cornell, Illinois, Wisconsin, and elsewhere) on maize origins, and these lectures are remembered as a "tour de force" by those who heard them (HOROWITZ 1990). As a Madison colleague who works on the maize *r* locus and prefers to remain anonymous put it, "If you walked into the lecture hall with any doubts, you came out a convert to the teosinte hypothesis." I have lectured on maize evolution at dozens of universities during the past two decades, and a good

Some of the participants in the 1972 corn conference at Harvard University. From the left: Ramana Tantravahi, H. Garrison Wilkes, Paul Mangelsdorf, William Davis, George Beadle, Umesh Banerjee, Elso Barghoorn, and Walton Galinat. This is perhaps the only time that these two adversaries shook hands. Photo by Hugh Iltis.

proportion of the time I was approached by people who mentioned to me the "wonderful" lecture they once heard George Beadle give on the topic. Thus, Beadle's strategy was to confront Mangelsdorf, another engaging and convincing man, on his own turf—the public relations arena.

Paul Mangelsdorf, also in retirement during the late 1970s and 1980s, was not mute, but engaged Beadle in the debate. It was a battle of titans between two of the most credentialed biologists of the day. In the face of growing objections to the tripartite hypothesis, Mangelsdorf (1974) abandoned it and offered a revised hypothesis that maize, the domesticated plant, evolved in the wild, and teosinte, the wild plant, was an escaped or feral form of maize. Mangelsdorf (1974) did not acknowledge Beadle as having influenced him, but credited the work of a Harvard student as having upended the tripartite hypothesis. Mangelsdorf's (1974) revised hypothesis was patently indefensible, and Beadle (1972) disputed it even before it appeared in print. To Beadle, it stood logic on its head to propose that maize (the domesticated plant) evolved in the wild without human involvement, was then brought into cultivation, went extinct as a wild plant, and at last escaped back into the wild as teosinte. Beadle (1980a) countered that, if maize could give rise to teosinte as Mangelsdorf proposed, then the reverse should also be possible and far more likely, given that teosinte is a highly successful wild species and maize is not.

The Beadle-Mangelsdorf debate was not carried out just on the dry pages of professional journals, but was played out face-to-face at several small conferences convened to discuss the origin of maize. There was one at the University of Illinois in 1969 and another at Harvard in 1972, and Beadle and Mangelsdorf confronted each other at both. The list of attendees varied from one meeting to the next and included people on both sides of the issue. I am told by Hugh Iltis, who was at both of these meetings, that the discussion was intense and nerves raw, and it is hard to imagine that it could have been otherwise. The outcome was, however, decisive. In part because of Beadle's renewed efforts and in part because there had always been a lingering disbelief in the tripartite hypothesis, the 1970s and early 1980s witnessed a tide of publications from a broad spectrum of plant scientists supporting the teosinte hypothesis (see

Bennetzen *et al.* 2001). Most notably as a direct result of Beadle's influence, the teosinte hypothesis was at last being discussed and the tripartite hypothesis challenged in the archeological literature (Flannery 1973).

I should be quick to mention that, despite what was certainly a fierce debate, both Beadle and Mangelsdorf disposed themselves with civility. I was fortunate to have met both men and found both delightful. Although I was a card-carrying sympathizer of the teosinte hypothesis, I was graciously entertained by Paul Mangelsdorf on several occasions. He was a charming man. He invited me to his retirement home in Chapel Hill on one occasion to show me his small maize and teosinte garden, and he presented me a copy of his and Reeves' 1939 monograph with the inscription "In appreciation of your interest in this subject." On another occasion, we met for dinner, and for several hours he told me captivating stories of his youth and how he went from Kansas farm boy to Harvard scholar. He talked of Collins, Vavilov, and East. I was enchanted and rushed home afterward to write down every word. We did not talk much of the origin of maize, and I think that best.

The aftermath: Has Beadle's teosinte hypothesis prevailed and have the tripartite hypothesis and others like it gone the way of the blending theory of inheritance? The answer is a qualified yes. The era of molecular genetics has provided a wealth of new evidence, all of it consistent with the teosinte hypothesis, and none of it offering any hope to the alternative hypotheses. Thus, among the current generation of maize geneticists familiar with the issues and qualified to evaluate the evidence, I believe there is a unified voice confirming the teosinte hypothesis. Indeed, a group of 12 maize geneticists and evolutionists, myself included, have recently affirmed their support for the teosinte hypothesis (Bennetzen *et al.* 2001). Among archeologists, the tide has turned as well, and I believe it fair to say that those archeologists familiar with the evidence overwhelmingly support the teosinte hypothesis (see Smith 2001). Even the encyclopedias are improving! Nevertheless, as the "scientific" creationists continue to dog Darwin, so the last embers of tripartitism have yet to die and perhaps never will.

There is much still to be learned about the origin of maize, and I do not want to overstate the certainty we can place in a strict one-gene, one-trait model. Indeed, Beadle himself recognized that a wealth of additional genes was required to convert a small-eared primitive maize into the gargantuan ears of modern corn. I also suspect that he would not have been surprised, as a maize geneticist, to learn that some additional "modifier" genes would have been required to provide a background in which his major genes would be stably expressed. What I believe he primarily wished to accomplish was to convince his audience, as he himself was convinced, that the morphological differences between maize and teosinte are not so large that one needs to invoke improbable hypotheses or extraordinary genetic mechanisms. In this regard, he provided commanding leadership and left a lasting legacy of common sense and clear thinking.

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