

# THE MAIZE AND TEOSINTE MALE INFLORESCENCE: A NUMERICAL TAXONOMIC STUDY<sup>1</sup>

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## ABSTRACT

The genus *Zea* consists of the world-wide cultigen, maize, and its wild and weedy relatives, the teosintes, native to Mexico, Guatemala, and Honduras. This study investigates the comparative morphology of the male inflorescence (tassel) from a large sample of teosinte populations and selected maize races. The reason for focusing on the tassel is simply that as an inedible structure it escaped the direct effects of those forces of human selection specifically aimed at its edible female counterpart, the maize ear. Thus, the tassel is the more appropriate morphological structure for comparing maize and teosinte from a taxonomic standpoint. Thirty-six populations of teosinte and four of maize were analyzed. Most of these were either collected from single localities in the field or grown from seed in a common garden near Homestead, Florida. Seventeen morphological traits of the tassel and spikelet were measured on all specimens. The measurements were subjected to canonical variate analysis, a multivariate statistical technique. Consideration of the results obtained in conjunction with cytological, biochemical, and genetic data in the literature led to the circumscription of the following taxa: I section *Luxuriantes*—(1) *Zea diploperennis*; (2) *Zea perennis*; (3) *Zea luxurians*; II section *Zea*—(4a) *Zea mays* ssp. *mays*; (4b) *Zea mays* ssp. *mexicana*; (4c) *Zea mays* ssp. *parviglumis*. The latter taxon contains vars. *parviglumis* and *huehuetenangensis* which, though morphologically similar, differ substantially by some genetic measures. Each taxon is described and illustrated with emphasis on the tassel and spikelet. The morphological data demonstrate that the annual teosintes are not intermediate between maize and *Zea diploperennis*, a fact which casts doubt on the recent hypothesis that these annuals represent the hybrid offspring of *Zea diploperennis* and a "hypothetical wild maize." Furthermore, the morphological-taxonomic evidence lends credence to the hypothesis that annual teosinte is the direct ancestor of maize; either *Zea mays* ssp. *parviglumis* or ssp. *mexicana* gave rise to cultivated maize.

The genus *Zea* consists of a small group of annual and perennial grasses including the economically important cultigen, maize (*Zea mays* ssp. *mays*), and its wild relatives, the teosintes, which are native to Mexico, Guatemala, and Honduras. There are four species included under the popular name teosinte according to the latest taxonomic treatment (Iltis & Doebley, 1980). Thus, *Zea* includes, in addition to the cultigen listed above, the following taxa: (1a) *Zea mays* ssp. *mexicana* from central and northern Mexico, including races Chalco, Central Plateau, and Nobogame of Wilkes (1967); (1b) *Z. mays* ssp. *parviglumis* var. *parviglumis* from southwestern Mexico (= race Balsas of Wilkes); (1c) *Z. mays* ssp. *parviglumis* var. *huehuetenangensis* from western Guatemala (= race Huehuetenango of

Wilkes), the above three all annuals; (2) *Z. luxurians*, an annual from southeastern Guatemala and Honduras; (3) *Z. perennis*, a tetraploid perennial; and (4) *Z. diploperennis*, a diploid perennial teosinte, the latter two both highly local species from southern Jalisco, Mexico (Fig. 1). These four species are separated into sect. *Zea* containing *Z. mays* with its three subspecies, and sect. *Luxuriantes* containing *Z. luxurians*, *Z. perennis*, and *Z. diploperennis* (Doebley & Iltis, 1980).

The genus *Zea*, along with the closely related genus *Tripsacum*, which ranges from South America to temperate North America, belongs to the tribe Andropogoneae of the Panicoid subfamily of the family Gramineae. In addition to similarities in general aspect, these two genera

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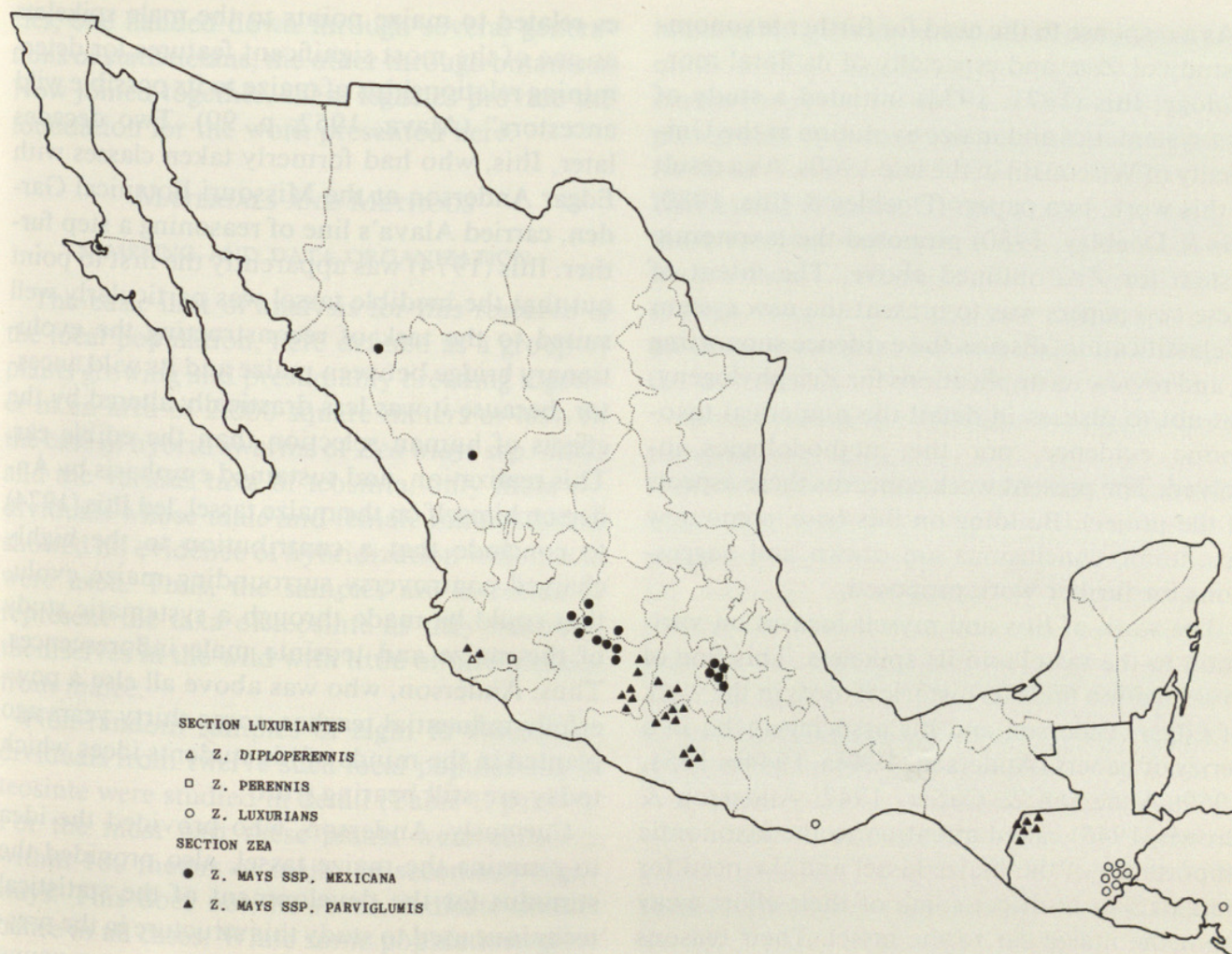


FIGURE 1. Distribution of native populations of the genus *Zea* (Ex Doebley & Iltis, 1980, Fig. 29). In *Zea mays* ssp. *mexicana*, the two northern stations represent the NOBOGAME and DURANGO populations respectively, the two southern clusters CENTRAL PLATEAU (western) and CHALCO (eastern). In *Zea mays* ssp. *parviglumis*, the southern Mexican cluster represents var. *parviglumis*, and the western Guatemalan one var. *huehuetenangensis*.

share in common the highly specialized cupulate fruitcase, but differ from one another in that *Tripsacum* bears its male and female spikelets in the same inflorescence, while *Zea* has separate male and female inflorescences. Additionally, the two genera differ cytologically, *Zea* with a base chromosome number of ten ( $x = 10$ ) and *Tripsacum* with eighteen ( $x = 18$ ).

Some authors segregate *Zea* and *Tripsacum* along with several monoecious Asiatic genera of the Andropogoneae, in the tribe Maydeae (Hackel, 1890). However, this appears to be an unnatural group whose members as a result of convergent evolution all have male and female spikelets in separate inflorescences or separate parts of the same inflorescence (Celarier, 1957; Clayton, 1973; Smith & Lester, 1980). A system that more accurately reflects the phylogeny of these genera by placing *Zea* and *Tripsacum* in one subtribe, the Tripsacinae, and the Old World

genera in another, the Coicinae, has been proposed on the basis of numerical taxonomic evidence by Clayton (1973).

Although *Zea* has long held the interest of botanists, agronomists, geneticists, cytologists, and ethnobotanists, taxonomists have until quite recently ignored *Zea* and especially the teosintes. Indeed, except for an aborted attempt by Gilly in the 1940s (cf. Iltis & Doebley, 1980), it was not until Wilkes (1967), a geneticist and ethnobotanist, undertook a study of racial diversity among the teosintes that the problem was at all addressed in a detailed manner. However, Wilkes, of necessity, largely concerned himself with determining the distribution of the teosintes, relying heavily on geography for the delimitation of his six races of annual teosinte. Although he employed genetics, physiology, and vegetative morphology to a considerable extent, he paid only scant attention to floral morphology.



As a response to the need for further taxonomic study of *Zea*, and especially of its floral morphology, Iltis (1971, 1974) initiated a study of *Zea* systematics and maize evolution at the University of Wisconsin in the late 1960s. As a result of this work, two papers (Doebley & Iltis, 1980; Iltis & Doebley, 1980) proposed the taxonomic system for *Zea* outlined above. The intent of these two papers was to present the new system of classification, discuss the evidence supporting it, and review its implications for *Zea* phylogeny, but not to discuss in detail the numerical taxonomic evidence, nor the methodologies involved. The present work concerns these aspects of the project. Building on this base, some new taxonomic conclusions are drawn and suggestions for further work proposed.

The work of Iltis and myself focuses on variation in the tassel and its spikelets. This line of investigation finds its historical roots in the work of Edgar Anderson and his associates who in a series of papers (Anderson, 1944a, 1944b, 1951, 1969; Anderson & Cutler, 1942; Anderson & Brown, 1948) called attention to the taxonomic importance of the maize tassel and the need for botanists to re-direct some of their effort away from the maize ear to the tassel. Their reasons for arguing in favor of this approach seem quite reasonable, for the tassel and especially its spikelets, are much more easily measured than their highly condensed and morphologically confusing female counterparts (Anderson, 1944b; Anderson & Cutler, 1942).

In the early 1950s, Anderson's student Reino Alava implemented the first and only taxonomic study of cultivated maize based solely on tassel and spikelet characteristics (Alava, 1952). As a result of his research, Alava identified several regional trends in maize male spikelet morphology. His work, however, had little impact on those studying maize race classification, partly because his conclusions were rather limited. What prohibited Alava from generating more far-reaching conclusions was that the only specimens available for his analyses were those preserved in the Missouri Botanical Garden herbarium. Many of these were but single specimens from one locality, and thus they were unable to provide any measure of within-population variability. In addition, these specimens were grown under widely different conditions, giving rise to much environmental variability, which obscures racial boundaries.

Despite these restrictions, Alava drew one important conclusion: "Experience with wild grass-

es related to maize points to the male spikelets as one of the most significant features for determining relationships of maize to its possible wild ancestors" (Alava, 1952, p. 90). Two decades later, Iltis, who had formerly taken classes with Edgar Anderson at the Missouri Botanical Garden, carried Alava's line of reasoning a step further. Iltis (1974) was apparently the first to point out that the inedible tassel was particularly well suited to the task of reconstructing the evolutionary bridge between maize and its wild ancestor, because it was less drastically altered by the effects of human selection than the edible ear. This realization, and sustained emphasis by Anderson himself on the maize tassel, led Iltis (1974) to conclude that a contribution to the highly charged controversy surrounding maize evolution could be made through a systematic study of the maize and teosinte male inflorescences. Thus, Anderson, who was above all else a powerfully influential teacher, some thirty years ago planted in the minds of his students ideas which today are still bearing fruit.

Curiously, Anderson, who provided the idea to examine the maize tassel, also provided the stimulus for the development of the statistical technique used to study this structure in the present report. This came about when, as a young man, he received a scholarship to study in England under the direction of the renowned statistician and evolutionist, Sir Ronald A. Fisher (see Anderson, 1956). At this time Anderson had an active interest in hybridization between species and developed a mathematical means to distinguish the two parental types from their hybrids. He called this technique the hybrid index, a method of great simplicity as well as practicality (Anderson, 1936). Exposed to the hybridization problem by Anderson and using Anderson's data on *Iris*, Fisher (1936) devised a much more sophisticated and at the same time far less biased method of solving this problem. This method is now known as Discriminant Analysis. Other statisticians used Fisher's idea to develop Canonical Variate Analysis, the major statistical technique used in this paper. Curiously enough, these techniques failed to impress Anderson (1944a, 1956) who completely ignored them, believing as he did that disciplined intuition was more important than high-powered mathematics for solving the puzzles of the natural world.

Thus, this imaginative Midwestern botanist, who saw with intuition and who looked to the organ which "graces" the top of the corn plant as a key to the mystery of maize, left two lega-



cies, one handed down through several generations of statisticians, the other through botanists. Now joined together, these legacies provide the foundation for the work presented here.

## MATERIALS AND METHODS

### SAMPLING AND DATA ORGANIZATION

The basic unit of analysis for this research is the local population, here defined as a group of plants growing and presumably breeding together in an area of 2,000 square meters or less. In the case of hybrid swarms of *Zea mays* ssp. *mays* and the various taxa of teosinte, only those individuals whose male and female inflorescences showed no evidence of hybridization with maize were used. Thus, the samples are intended to represent the taxa of teosinte as they maintain themselves in the wild with little or no influence from maize.

Non-random samples of eight to twenty individuals from twelve such local populations of teosinte were studied in detail (Table 1, part A). For the most part these plants were collected within 100 meters of major or secondary highways. This does not, however, indicate disturbance in all cases. While some populations grew as weeds in corn fields, others thrived in quite wild places such as dry open savannas or rocky escarpments.

To supplement the field-collected local populations, this study includes herbarium specimens collected in the wild by various botanists at different times and in different places. These specimens were organized into six groups (Table 1, part B) each of which consists of individuals from a single political state or from the vicinity of a particular city; each such group was treated as a "local population" in the analysis. Together the field-collected local populations and field-collected herbarium specimens cover the entire known geographic range of the teosintes (Fig. 2).

All the preceding field-collected plants, having been grown in their native environments, and thus under conditions to which they are unquestionably adapted, undoubtedly represent morphologically typical specimens of the taxa to which they belong. However, environmental differences among the populations, some growing along streams in the more-or-less mesic montane forest of Jalisco and others on dry rocky escarpments in the seasonally arid Balsas river drainage, modify the phenotypes to an unknown degree. This poses a problem to the interpretation of variability among populations which is best

handled by growing seeds from the populations under similar conditions in a garden. For this reason the present research includes twelve samples grown in a common garden at the Pioneer Hi-Bred International Research Station near Homestead, Florida (Table 1, part C). Each of these samples was derived from seeds collected from a single local population. The morphology of these samples indicates how differences in local environmental conditions may have affected the morphology of the field-collected plants.

Another category of population samples is that composed of specimens cultivated at various times and under various conditions. These specimens were organized into six population samples based on their region of origin (Table 1, part D). Although the environmental component of differences among them is even more complex than for the field-collected population samples, they are included in the analysis because they cover some geographic areas (e.g. Honduras) not represented by the other samples.

In order to have a sample of maize varieties with which to compare the teosintes, three so-called "primitive" maize races were grown at the Purdue University Agricultural Alumni Experimental Station in southern Florida. These include Nal-Tel, Chapalote, and Palomero Toluqueño, the seeds for which were obtained from the International Center for the Improvement of Maize and Wheat (CIMMYT) in Mexico. One other maize population sample collected in the field near Toluca, Mexico, belonging to the "Mexican Pyramidal" or "Conico" race, was studied as well (Table 1, part E).

Local populations were chosen as the basic unit of analysis because individuals within a single local population are probably phylogenetically very closely related and therefore members of the same taxon in the narrowest sense. In most situations, it is not necessary for the taxonomist to attempt to distinguish between members of one local population, but only to distinguish various local populations from one another. Populations which are very similar may be placed together in the same taxon, while those which are distinct, may, depending on the degree of difference, be placed into separate taxa.

### CHARACTERS ANALYZED

To assess the differences and similarities among the 40 populations, 17 quantitative morphological traits (variates) of the tassel and spikelet were measured. Many of these are based on characters



TABLE 1. List of populations.

## A. Populations Collected in the Wild:

1. *Zea diploperennis* (DIPLOPERENNIAL teosinte). Mexico: Jalisco: With tall grass and herbs along small streams in a region of *Pinus-Quercus-Carpinus* forest, LA VENTANA, Cerro San Miguel, Sierra de Manantlan, 7 km ENE of El Durazno, 19°31'45"N, 104°13'W, alt. ca. 2,300 m. Sept. 22, 1978. *Iltis, Guzman, Doebley & Lasseigne* 450. Sample size = 20.
2. *Zea perennis* (PERENNIAL teosinte). Mexico: Jalisco: In and along a small arroyo with *Heteropogon contortus*, *Chaetium bromoides*, and *Leonotis nepetifolia*, in an area of former pine-oak sacaton grassland, 9 km WSW of Ciudad Guzman. 1.5 km ESE of LOS DEPOSITOS, 19°40'N, 103°35'W, alt. ca. 1,650 m. Sept. 24, 1978. *Iltis, Puga, Guzman, Doebley & Lasseigne* 550. Sample size = 20.
3. *Zea perennis* (PERENNIAL teosinte). Mexico: Jalisco: Along dirt roads, on edges of small maize fields, and in orchards on former *Pinus-Quercus* savanna. Ca. 14 km WSW of Ciudad Guzman, 4 km WSW of Los Depositos, 0.2 km due W of PIEDRA ANCHA, alt. 2,100–2,200 m. Oct. 1978. *R. Guzman s.n.* Sample size = 19.
4. *Zea luxurians* (GUATEMALA teosinte). Guatemala: Jutiapa: Weeds in maize field and hedgerow, 2 km N of central park in EL PROGRESO, 14°22'30"N, 89°51'30"W, alt. 1,025 m. Oct. 22, 1978. *K. Lind* 419. Sample size = 20.
5. *Zea luxurians* (GUATEMALA teosinte). Guatemala: Jutiapa: On sides and top of hot dry lava cliff formed by Pan-American Highway road cut. N-side of PAH, 1.6 km E of EL PROGRESO turn-off, 14°21'N, 89°50'W, alt. 925 m. Oct. 22, 1978. *K. Lind* 420. Sample size = 8.
6. *Zea luxurians* (GUATEMALA teosinte). Guatemala: Jutiapa: In rice and maize fields, and along hedgerows, by an old road (Camino Viejo), ca. 2 km NW of EL TABLON, 3 km ENE of Jutiapa, 14°18'15"N, 89°52'45"W, alt. ca. 1,000 m. Oct. 22, 1978. *K. Lind* 421. Sample size = 11.
7. *Zea mays* ssp. *mexicana* (CHALCO teosinte). Mexico: Mexico: Weeds in maize field, Valley of Mexico, ca. 5 km SE of CHALCO at km 46.6 on road to Amecameca, 19°12'N, 98°49'W, alt. ca. 2,300 m. Sept. 11, 1977. *Iltis & Doebley* 4. Sample size = 18.
8. *Zea mays* ssp. *mexicana* (CHALCO teosinte). Mexico: Mexico: On unplowed mound in maize field, Valley of Mexico at km 20.5 on road from LOS REYES to Texcoco. 0.8 km N of Los Reyes, 19°21'N, 98°58'W, alt. ca. 2,150 m. Sept. 12, 1977. *Iltis & Doebley* 8. Sample size = 10.
9. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU teosinte). Mexico: Guanajuato: Weeds in maize field, at km 57 on road from Morelia to Salamanca, 3 km N of URIANGATO, 20°10'N, 101°10'W, alt. ca. 1,900 m. Sept. 17, 1977. *Iltis & Doebley* 96. Sample size = 18.
10. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU teosinte). Mexico: Michoacan: In maize fields, on mostly treeless hillside, lower edge of xerophytic semi-deciduous shrubby savanna, near QUINCEO, 6 km (by air) NW of Morelia, 19°43'N, 101°14'W, alt. ca. 2,000 m. Sept. 18, 1977. *Iltis & Doebley* 161. Sample size = 10.
11. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS teosinte). Mexico: Guerrero: Weeds in maize field in region of semi-deciduous savanna of Leguminosae, *Bursera*, *Pseudomoringium*, and tree *Ipomoea*, at km 103 on road from Iguala to Arcelia, 11 km (by road) W of ACAPETLAHUAYA turn-off, 18°23'N, 100°07'W, alt. ca. 1,050 m. Sept. 22, 1977. *Iltis & Doebley* 361. Sample size = 16.
12. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS teosinte). Mexico: Michoacan: Very steep and ungrazed south facing rocky slope with thorny shrubs, small deciduous trees and grasses, ca. 1 km S of TZITZIO on road to Huetamo, 19°34'N, 100°55'W, alt. ca. 1,500 m. Sept. 15, 1977. *Iltis & Doebley* 87. Sample size = 20.

## B. Populations of Field Collected Herbarium Specimens:

13. *Zea perennis* (PERENNIAL teosinte). Mexico: Jalisco: Among sunflowers, *Bidens* and grasses, 1 mile S of railway station of CIUDAD GUZMAN, 19°41'30"N, 103°28'40"W, alt. 1,520 m. Oct. 28, 1921. *G. N. Collins, s.n.* (US). Sample size = 3.
14. *Zea luxurians* (GUATEMALA teosinte). Guatemala: Jutiapa: Near El Progreso, *Iltis* G-5 (WIS), *Wilkes* 43118 (2 sheets MO, US), 43122 (F); near El Tablon, *Standley* 75842, 75876 (F); near Jutiapa, *Standley* 76058, 76109, 76052 (F); Chiquimula: near Ipala, *Steyermark* 30287 (2 sheets F). Sample size = 11.
15. *Zea luxurians* (GUATEMALA teosinte). Mexico: Oaxaca: Near SAN AUGUSTIN, Oct. 1840. *Liebman* 548 (US). Sample size = 1.
16. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU teosinte). Mexico: Durango: Near DURANGO. *E. Palmer* 743 (4 sheets US, MO, WIS), *G. Collins* 15 (5 sheets US, WIS). Sample size = 9.
17. *Zea mays* ssp. *mexicana* (NOBOGAME teosinte). Mexico: Chihuahua: Near NOBOGAME, *Wilkes s.n.* (2 sheets F, US), *H. S. Gentry* 17973 (US). Sample size = 3.
18. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENAGO teosinte). Guatemala: Huehueten-



TABLE 1. (Continued).

- nango: Near SAN ANTONIO HUISTA, *Iltis & Lind G-120* (7 sheets WIS), *Wilkes s.n.* (2 sheets WIS), 43603 (US), *McBryde 81862* (2 sheets NA, F). Sample size = 12.
- C. *Grown in a Common Garden at Pioneer Hi-Bred International Research Station near Homestead, Florida from October 1978 to February 1979:*
19. *Zea luxurians* (GUATEMALA teosinte). Seeds from Guatemala: Jutiapa: Along hedgerow, small stream and in maize field ca. 5 km W of AGUA BLANCA, 14°29'N, 89°42'W, alt. ca. 920 m. Jan. 1, 1976. *Iltis G-38*. Cult. *Doebley 376*. Sample size = 8.
  20. *Zea luxurians* (GUATEMALA teosinte). Seeds from Guatemala: Jutiapa: Along hedgerow, small stream and in maize fields 1.2 km N of EL PROGRESO on road to Jalapa, alt. 1,040–1,060 m. Dec. 1975. *Iltis G-5*. Cult. *Doebley 377*. Sample size = 8.
  21. *Zea luxurians* (GUATEMALA teosinte). Seeds from Guatemala: Jutiapa: Weeds in maize fields and hedgerows on slopes above laguna, 1 km E of south entrance pass, LAGUNA RETANA, 5–7–9 km N of El Progreso, alt. 1,150 m. Dec. 29, 1975. *Iltis G-20*. Cult. *Doebley 378*. Sample size = 8.
  22. *Zea luxurians* (GUATEMALA teosinte). Seeds from Guatemala: Chiquimula: Maize fields and hedgerows, 2 km N of IPALA on road to Chiquimula, 14°38'N, 89°38'W, alt. ca. 800 m. Jan. 2, 1976. *Iltis G-42*. Cult. *Doebley 379*. Sample size = 10.
  23. *Zea mays* ssp. *mexicana* (CHALCO teosinte). Seeds from Mexico: Mexico: Edges of maize fields 0.5 km SE of LOS REYES on road to Amecameca, 19°20'N, 98°57'W, alt. ca. 2,225 m. Dec. 1, 1971. *Iltis & Cochrane 175*. Cult. *Doebley 374*. Sample size = 10.
  24. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU teosinte). Seeds from Mexico: Michoacan: Weeds in maize field, near QUINCEO, a pueblito on the slope of Pico de Quinceo, 6 km (by air) NW of Morelia, 19°43'N, 101°14'W, alt. ca. 2,000 m. Dec. 4, 1971. *Iltis & Cochrane 276*. Cult. *Doebley 375*. Sample size = 15.
  25. *Zea mays* ssp. *mexicana* (NOBOGAME teosinte). Seeds from Mexico: Chihuahua: Near NOBOGAME, obtained from *G. Beadle s.n.* Cult. *Doebley 370*. Sample size = 8.
  26. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS teosinte). Seeds from Mexico: Guerrero: 4.5 km E of Mazatlan on road to EL SALADO. Nov. 1972. *Wilkes s.n.* (USDA Plant Inventory No. 181, p. 220, Accession No. 384061). Cult. *Doebley 372*. Sample size = 15.
  27. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS teosinte). Seeds from Mexico: Michoacan: Km 127 on road from HUETAMO to Morelia, International Center for the Improvement of Maize and Wheat Accession No. 8761. Cult. *Doebley 373*. Sample size = 18.
  28. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS teosinte). Seeds from Mexico: Michoacan: Roadside cliffs, 1 km S of TZITZIO toward Huetamo, 19°34'N, 100°55'W, alt. ca. 1,500 m. Dec. 6, 1971, *Iltis & Cochrane 308*. Cult. *Doebley 380*. Sample size = 8.
  29. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENANGO teosinte). Seeds from Guatemala: Huehuetenango: Along trail at TZISBAJ, alt. 1,510 m. Feb. 1964. *Wilkes s.n.* (USDA Plant Inventory No. 177, p. 132, Accession No. 343233). Cult. *Doebley 371*. Sample size = 16.
  30. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENANGO teosinte). Seeds from Guatemala: Huehuetenango: Maize fields, ca. 1.5–2.5 km ENE of SAN ANTONIO HUISTA on road to Jacaltenango, 15°40'N, 91°45'W, alt. ca. 1,300–1,400 m. Jan. 1976. *Iltis & Lind G-120*. Cult. *Doebley 381*. Sample size = 8.
- D. *Populations of Herbarium Specimens Cultivated under Dissimilar Conditions:*
31. *Zea perennis* (PERENNIAL teosinte). Seeds or rhizomes from Mexico: Jalisco: 1 mile S of railway station of CIUDAD GUZMAN, Oct. 28, 1921. *Collins s.n.* Cult. *Iltis & Cochrane 26376* (3 sheets WIS), 26372 (2 sheets WIS); *Iltis s.n.* (WIS); *S. Calderon s.n.* (F); *Peebles & Harrison 3527* (US); *Silveus 798* (US). Sample size = 9.
  32. *Zea luxurians* (GUATEMALA teosinte). Origin of seeds uncertain (see Wilkes, 1967: 11): Cultivated at different localities throughout the world. Brazil: *Luederwaldt 22277* (US), *Reits 4744* (US), *Oliva 83* (US). Cuba: *J. G. Jack 6340* (US). Hawaii: *Hitchcock 14889* (US). Phillipines: *E. D. Merrill 11222* (US). USA: Florida: (US sheet 727070). Sample size = 7.
  33. *Zea luxurians* (GUATEMALA teosinte). Honduras: Choluteca: Near SAN ANTONIO DE PADUA (Standley, 1950). *Standley 27317* (2 sheets US), *Freytag s.n.* (2 sheets MO), *Molina 5881, 5882* (US). Sample size = 6.
  34. *Zea mays* ssp. *mexicana* (NOBOGAME teosinte). Seeds from Mexico: Chihuahua: Near NOBOGAME, obtained from *G. Beadle s.n.* grown at Purdue Univ. Agric. Alumni Exp. Stn., Florida City, Fla. Feb.–May 1978. Cult. *Iltis & Doebley s.n.* Sample size = 5.
  35. *Zea mays* ssp. *parviglumis* var. *parviglumis* (JALISCO teosinte). Seeds from Mexico: Jalisco: LA HUER-



TABLE 1. (Continued).

- TITA, Cerro La Petaca, along trail to El Durazno, 8 km (by air) ESE of Casimiro Castillo, 19°33'30"N, 104°22'30"W, Dec. 14, 1977. *Guzman s.n.* Cult. *Doebley 178*. Sample size = 6.
36. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENANGO teosinte). Seeds from Guatemala: Huehuetenango: Near SAN ANTONIO HUISTA. *Anderson s.n.* (MO sheet 1168094), *Weatherwax s.n.* (MO sheet 1213458). Sample size = 2.
- E. Maize Populations:*
37. *Zea mays* ssp. *mays* (Race PALOMERO TOLUQUEÑO). Mexico: Mexico: International Center for the Improvement of Maize and Wheat No. BA 70-539# (Mex 5). Grown at Purdue Univ. Agric. Alumni Exp. Stn., Florida City, Fla. Feb.-May 1978. Sample size = 16.
38. *Zea mays* ssp. *mays* (Race NAL-TEL). Mexico: Campeche: International Center for the Improvement of Maize and Wheat No. tep 62A 906# (Campeche 42c). Grown at Purdue Univ. Agric. Alumni Exp. Stn., Florida City, Fla. Feb.-May 1978. Sample size = 19.
39. *Zea mays* ssp. *mays* (Race CHAPALOTE). Mexico: Sinaloa: International Center for the Improvement of Maize and Wheat No. TL 7B 5# (Sin 2). Grown at Purdue Univ. Agric. Alumni Exp. Stn., Florida City, Fla. Feb.-May 1978. Sample size = 19.
40. *Zea mays* ssp. *mays* (Race Conico). Mexico: Mexico: Depauperate plants 1-1.5 m tall. 2.5 km W of VILLA VICTORIA, 48.5 km W of Toluca on road to Morelia, 19°25'N, 100°02'W, alt. ca. 2,600 m. Sept. 28, 1978. *Ilitis, Doebley & Lasseigne 760*. Sample size = 7.

studied by Alava (1952) and by Wellhausen and his associates (1952). However, since differences exist in how they were applied here and elsewhere, a discussion of each of the 17 traits is necessary.

The traits measured for this study may be divided into three categories: (1) tassel, (2) spikelet, and (3) outer glume. In order to reduce error variability when measuring these characters only pedicellate spikelets from the middle portion of the central spike (see Alava, 1952) and only tassels terminating the main culm (see Wellhausen et al., 1952) were used. However, on some herbarium specimens, one cannot determine if the tassel came from the main culm or from a lateral one, so a few tassels from lateral branches may have been inadvertently included.

A. TASSEL CHARACTERS: [With the exception of branch number these characters were all measured in millimeters (mm) and without magnification.]

1. *Branch Number*. Total number of branches excluding the central spike. Thus, for the tassel in Figure 3 the branch number is fourteen. No attempt was made here to distinguish between primary, secondary, and tertiary branches. Such distinctions, however, are not unimportant taxonomically. In fact, Wilkes (1967, p. 110) has noted differences in degree of tassel branching between his races of teosinte. But, as Wilkes also observed, the distinctions are often obscured by environmental variability.

The terms *primary*, *secondary*, and *tertiary* are used differently by Anderson (1944a, 1951) and

Alava (1952) on the one hand, and Wellhausen and his associates (1952) and the successive authors of the Races of Maize series on the other. What the former authors refer to as the *primary branch* or *central spike*, the latter authors term simply the *central spike* (axis). Then, single branches departing from the central axis are called *secondary branches* by Anderson and Alava, and *primary branches* by Wellhausen. In general, Anderson and Alava always designate branches one order higher than Wellhausen. The Wellhausen system is adopted here (Fig. 3) because most researchers (Wellhausen et al., 1952; Goodman, 1967; Wilkes, 1967; Goodman & Paterniani, 1969) working with maize and teosinte have used it, and because this system has the logical advantage of considering the central spike not as a branch, but as an axis (in the same way that one would not ordinarily refer to the main stem of any plant as a branch).

2. *Central Spike Length*. Distance from the tip of the uppermost spikelet of the central spike to the point of departure of the uppermost primary tassel branch (length A-D on Fig. 3). A few authors (Wilkes, 1967; Mangelsdorf, 1974; Bird, 1978) reported that the southeastern Guatemalan teosinte (*Z. luxurians*) lacks a central spike. However, all teosintes possess a central spike, although it is generally less prominent in tassels of sect. *Luxuriantes*. Photographs of southeastern Guatemalan teosinte tassels often show the central spike, which usually projects beyond the other branches (Wilkes, 1967: plate XVII; Fig. 16, this report). The confusion surrounding this



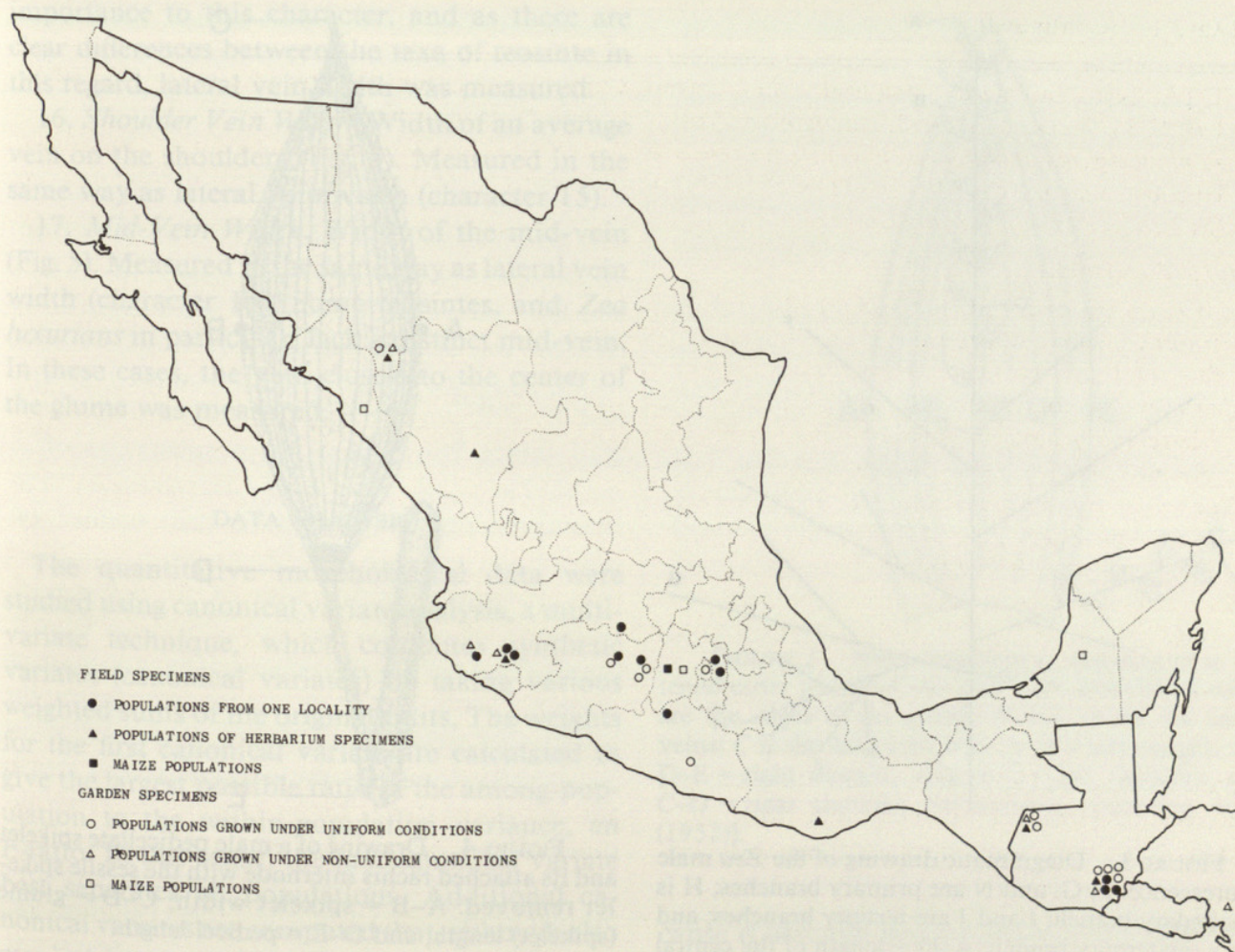


FIGURE 2. Distribution of the populations of *Zea* sampled for this research.

matter has been discussed fully elsewhere (Doebley & Iltis, 1980).

3. *Branching Axis Length* [or *Length of Branching Space* (Wellhausen et al., 1952)]. Distance along the central axis of the inflorescence from the point of departure of the uppermost tassel branch to that of the lowermost (distance D-E on Fig. 3).

4. *Central Spike Internode Length*. Distance between eight spikelet pairs in the middle portion of the central spike (distance B-C on Fig. 3) divided by seven. This average length of the central spike's internodes is a measure of its condensation. A full description of the distribution of spikelet pairs along the central spike in maize requires a measure of how the spikelet pairs are grouped together, such as the Condensation Index applied by Anderson (1944a) to the lowest primary branch. The teosintes, however, nearly always have only one spikelet pair per node (as in branch N of Fig. 3) so Anderson's Condensation Index offers little additional information.

5. *Lateral Branch Internode Length*. Distance between six spikelet pairs in the middle portion of a major lower primary branch (distance M-L on Fig. 3) divided by five. Because the tassel

branches, as opposed to the central spike, do not show the severe effects of domestication, this trait, in contrast to Central Spike Internode Length, should be useful for comparing maize and teosinte.

B. SPIKELET CHARACTERS: [Measured under a binocular dissecting microscope (15×).]

6. *Spikelet Width*. Maximum width of the fully developed spikelet just prior to anthesis, (distance A-B in Fig. 4). Since many herbarium specimens were past anthesis with shriveled spikelets, there exists considerable error variability for this trait.

7. *Pedicle Length*. Pedicle length from the rachis to the base of the spikelet (distance D-E on Fig. 4).

8. *Anther Length*. Length of the longest mature anther in the chosen spikelet. When the central spike of a herbarium specimen had long passed anthesis, an anther from a spikelet of a major lower primary branch was used.

C. OUTER GLUME CHARACTERS:

9. *Glume (Spikelet) Length*. Length from tip to base of spikelet (distance C-D on Fig. 4). Measured under a dissecting microscope (15×).

10. *Glume Width*. Maximum width of glume



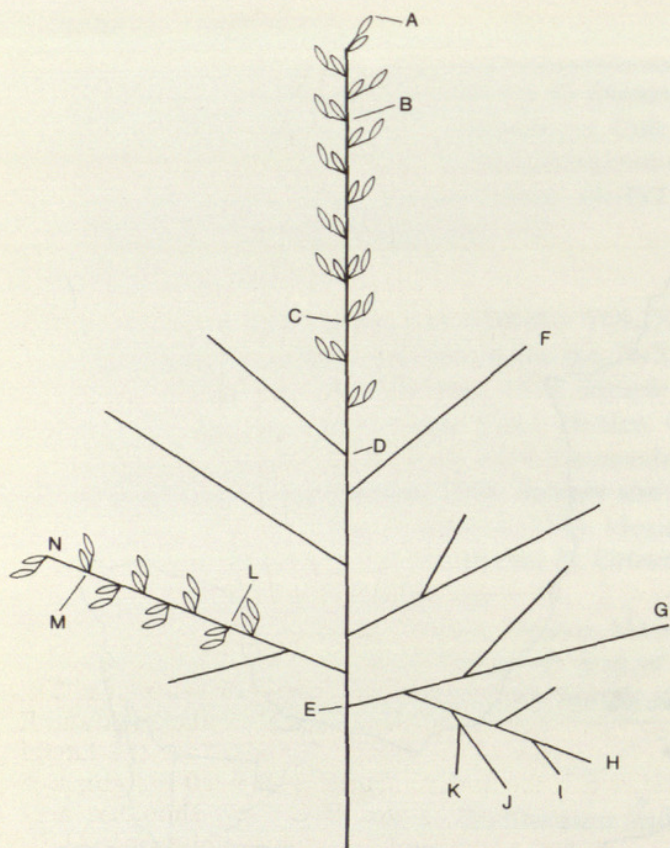


FIGURE 3. Diagrammatic drawing of the *Zea* male inflorescence. F, G, and N are primary branches; H is a secondary branch; I and J are tertiary branches; and K is a quaternary branch; A–D = length of the central spike; D–E = length of the branching axis; B–C = length of seven internodes on the central spike; M–L length of five internodes on a major lower primary branch.

(distance A–E on Fig. 5). The glume was removed from the spikelet, flattened, and mounted on a microscope slide in Permout, a histological mounting medium.

11. *Wing Width*. Width of wing measured where widest, usually 1 or 2 mm below spikelet tip. Wings are projections of the major lateral nerves of the outer glume and are most prominent along the upper one-third of the spikelet. Measured under a dissecting microscope (40 $\times$ ).

Only spikelets of the perennial teosintes possess well-developed, easily measured wings (Hitchcock, 1922; Iltis et al., 1979; Doebley & Iltis, 1980). *Zea luxurians* has much less prominent wings, while all three subspecies of *Z. mays* basically lack this structure or show only traces of it.

12. *Width of the Shoulders*. Distance between the two major lateral nerves (distance B–D on Fig. 5). Measured under a compound microscope (50 $\times$ ) on the same glume that was used for character 10. Although the terminology of Alava (1952) was followed here, the “shoulders” might



FIGURE 4. Drawing of a male pedicellate spikelet and its attached rachis internode with the sessile spikelet removed. A–B = spikelet width; C–D = glume (spikelet) length; and D–E = pedicel length.

also be referred to as the “back” of the glume. Using the term “back” would be especially appropriate for the teosintes of sect. *Luxuriantes* whose glumes are flattened on the “back,” and thus lack shoulders as found in sect. *Zea*.

13. *Shoulder Vein Number*. Number of veins between the two major lateral nerves excluding the mid-vein (e.g., shoulder vein number is four in Fig. 5). Counted under a compound microscope (50 $\times$ ) on glumes mounted on slides.

14. *Total Vein Number*. Total number of veins including the mid-vein, shoulder veins, major lateral veins, and margin veins (e.g., total vein number is ten in Fig. 5). Counted under a compound microscope (50 $\times$ ) on glumes mounted on slides.

15. *Lateral Vein Width*. Width of one of the two major lateral veins. Measured with a compound microscope (50 $\times$ ) on glumes mounted on slides. This measurement probably contains considerable error variability because (1) the margins of the veins are often irregular; (2) many older specimens had indistinct veins; and (3) even at 50 $\times$  magnification the units of measurement were too large to record this trait accurately. Nevertheless, as Alava (1952) attributed some



importance to this character, and as there are clear differences between the taxa of teosinte in this regard, lateral vein width was measured.

16. *Shoulder Vein Width*. Width of an average vein on the shoulders (Fig. 5). Measured in the same way as lateral vein width (character 15).

17. *Mid-Vein Width*. Width of the mid-vein (Fig. 5). Measured in the same way as lateral vein width (character 15). Some teosintes, and *Zea luxurians* in particular, lack a distinct mid-vein. In these cases, the vein closest to the center of the glume was measured.

#### DATA ANALYSIS

The quantitative morphological data were studied using canonical variate analysis, a multivariate technique, which computes synthetic variates (canonical variates) by taking various weighted sums of the original traits. The weights for the first canonical variate are calculated to give the largest possible ratio of the among-population to the within-population variance, an F-ratio. In this sense, the first canonical variate best separates all populations. Additional canonical variates are computed that, although also maximizing the F-ratio, are not correlated with previous ones, and thus contain different information (Seal, 1964; Kowal et al., 1976). One can obtain a picture of how the local populations relate to one another by graphing the first canonical variate against the second for all individuals. Graphs incorporating the third or even further canonical variates may also be useful.

Under some circumstances one wants to look only at a graph of a particular subgroup of local populations included in the overall analysis. To do so one can perform additional canonical variate analyses or close-ups including only the local populations in the subgroup of particular interest. In this way one can get a better picture of the relationships between the local populations within the subgroup. Such close-up analyses can be performed in two ways. (1) One may include all original populations in the close-up analysis but discriminate among and graph only those in the subgroup in question. Here, the pairwise distances between the populations in the full dimensional space will be the same as for the over-all analysis. However a new set of canonical variates will be computed that maximally separates only the graphed populations. This option is best when the variances and covariances of the populations in each subgroup are similar, be-

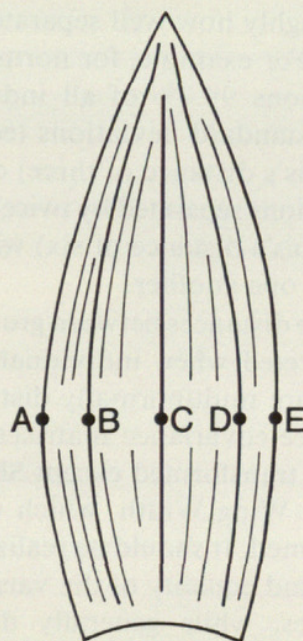


FIGURE 5. Semi-diagrammatic drawing of a flattened outer glume of the *Zea* male spikelet. A and E are the edges of the glume; B and D are the lateral veins; C is the mid-vein; area A-B = left margin; area D-E = right margin; area B-C = left shoulder; area C-D = right shoulder [terminology following Alava (1952)].

cause it uses the best estimate of the error variation. (2) However, if the variances and covariances are not similar, then including all populations would give a biased estimate of the error variation in the smaller group of populations that are being separated by the close-up analysis. Under these conditions one should exclude populations outside the subgroup in question from the close-up analysis. This will result in some changes in the between population distances. The new analysis should more accurately discriminate among the populations as error due to dissimilarity of the variances and covariances has been reduced. For the present data set, dissimilarities in the variances and covariances exist between the populations in different subgroups, so the second option was used.

The canonical variate analysis program used (CANCOV, Kowal, unpublished) standardizes the canonical variates so that the pooled within-population variance of each canonical variate equals one. When this is done each distance between a pair of populations is measured in units of the pooled within-group standard deviation (Kowal et al., 1976). This distance is referred to as Mahalanobis's distance. This is a very useful measure of distance, because if the canonical scores are approximately normally distributed, one can use properties of the normal distribution



to deduce roughly how well separated two populations are. For example, for normally distributed populations 99.7% of all individuals fall within three standard deviations (equivalent to a Mahalanobis's distance of three) of the mean. Local populations separated by twice this amount (a Mahalanobis's distance of six) will be clearly distinct from one another.

Because the distances between groups are more easily interpreted when individuals within the populations are multinormally distributed with equal variance-covariance matrices, all characters were log transformed except Shoulder Vein Number and Wing Width, which were square-root transformed. It should be realized that multinormality and equality of the variance-covariance matrices, while generally desirable, are necessary *only* if one wishes to use the technique to make statements about the probability of correctly classifying individuals. If canonical variate analysis is used solely as a method of projecting points (observations) in a multidimensional space onto a plane (a graph) as done in this paper, then normality and equality of the variance-covariance matrices are irrelevant.

Canonical analysis has three features of importance for taxonomists. First, since taxonomists tend to look for characters which show little variability within taxa and much variability between taxa, they in a sense perform implicitly in their minds what canonical analysis does explicitly, i.e., maximize the ratio of among- to within-population variance. Principal components analysis, which discriminates on the basis of variability among individuals, does not generally work as well with taxonomic problems in which the major goal is seeing how well the taxa are separated (Kowal, pers. comm.; Steudel, 1978). Secondly, canonical analysis does not require the systematist to assign local populations to any taxon, and thus allows all local populations to be judged independently of the researcher's bias as to where they belong in the taxonomic hierarchy. Finally, since canonical analysis provides a graph on which each specimen is represented by a separate point, it allows the taxonomist to keep track of individual plants. For these reasons, canonical analysis is well adapted to systematic endeavors. Indeed, it has been fairly extensively applied by both plant and animal taxonomists (Oxnard, 1969; Robinson & Steudel, 1973; Kallunki, 1976; Riggins et al., 1977; Keller, 1979; Kowal & Ruffin, 1979; Price, 1980;

Doebley & Iltis, 1980; Bell & Lester, 1980; Bowman, 1980; Reynolds & Crawford, 1980).

## RESULTS

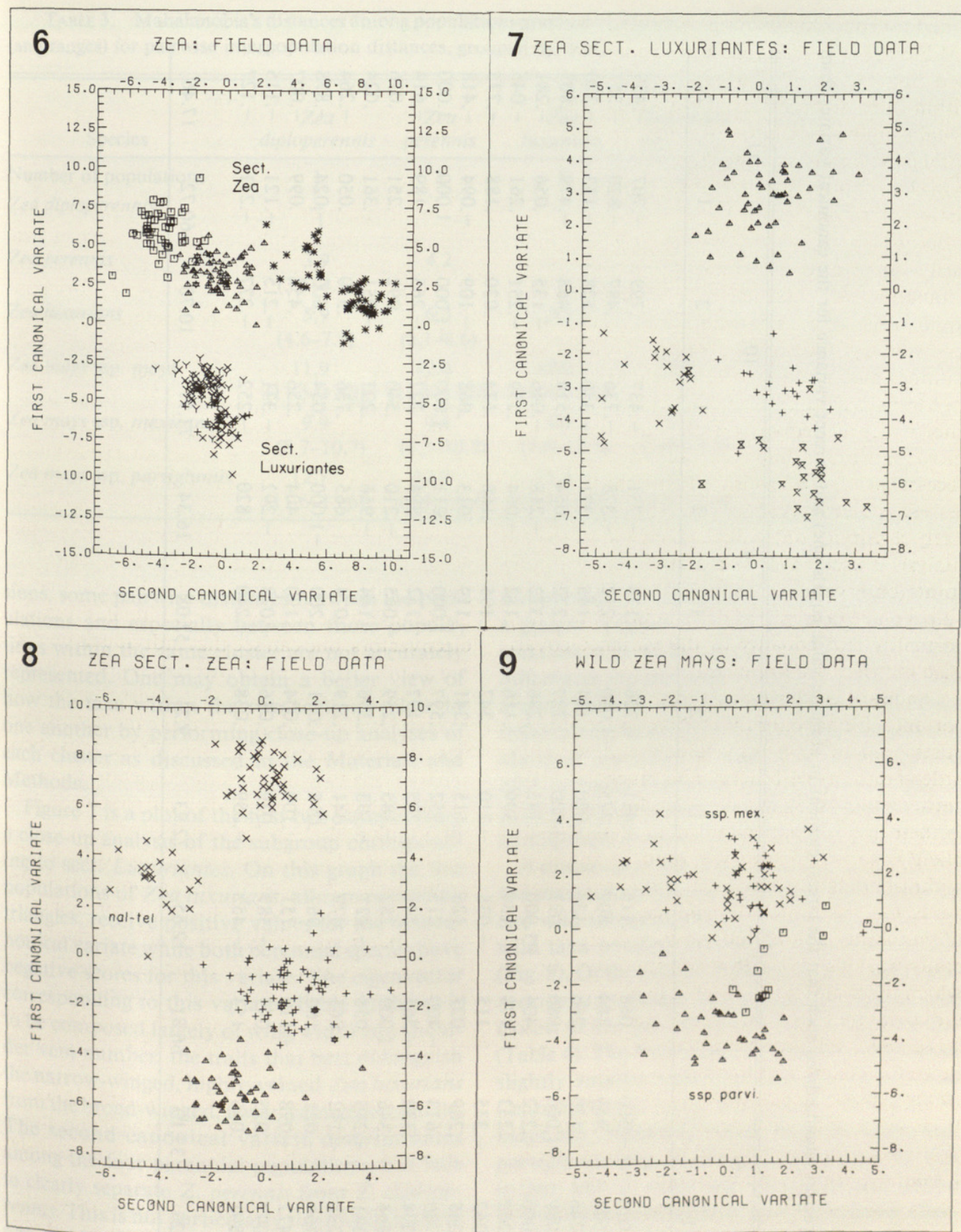
### FIELD DATA

A graph of the first and second variates from an initial canonical variate analysis of the 18 field and four maize populations (Fig. 6) reveals two clusters: one corresponding to sect. *Luxuriantes*, which contains *Zea diploperennis*, *Z. perennis*, and *Z. luxurians*; and one corresponding to sect. *Zea*, which contains all three subspecies of *Z. mays*. The coefficients of the eigenvectors measure the contribution of each trait to each canonical variate, and each eigenvalue, expressed as a percentage of the sum of all eigenvalues, measures the relative amount of the total among-population variance explained by a canonical variate (Table 2). Each eigenvector gives the weights (in standardized form) used to calculate the weighted sum of the original traits, that is the canonical score, for an individual. From the eigenvectors, one can see that individuals on Figure 6 with long lateral branch internodes, narrow glumal wings, wide mid-veins, short glumes, and a small total vein number receive the largest values for canonical variate one. These traits best separate the two sections of the genus. Doebley and Iltis (1980) discuss additional characters useful in differentiating the two sections.

The second canonical variate on Figure 6 separates the three subspecies of *Zea mays* and shows *Z. mays* ssp. *mays* to be closest morphologically to *Z. mays* ssp. *mexicana*. For this canonical variate, the eigenvector (Table 2) indicates that individuals, like those of the maize races involved, with short central branch internodes, long glumes, few tassel branches, and a long central spike receive the largest scores. *Zea mays* ssp. *parviglumis*, on the other hand, with small glumes, long internodes on the central spike, many tassel branches, and a short central spike, receives the smallest values.

The three species that compose the lower cluster of individuals (sect. *Luxuriantes*) do not separate from one another along either axis, although the Mahalanobis's distances between these species are large (Table 3). In fact, *Zea luxurians* is very well separated from the perennial taxa ( $\bar{D} = 6.1$ ). The explanation for this distortion is simply that because Figure 6 is in reality a 17 dimensional figure compressed into two dimen-





FIGURES 6-9. Graphs of the first and second variates from canonical analyses.—6. 18 field populations of teosinte and 4 maize populations including *Zea diploperennis* (+); *Z. perennis* (X); *Z. luxurians* (Y); and *Z. mays* ssp. *mays* (\*), ssp. *parviglumis* (□) and ssp. *mexicana* (Δ).—7. 9 field populations of *Zea* sect. *Luxuriantes* including *Z. diploperennis* (+); *Z. perennis* from CIUDAD GUZMAN (X), LOS DEPOSITOS (X), and PIEDRA ANCHA (X); and *Z. luxurians* (Δ).—8. 13 field populations of *Zea* sect. *Zea* including *Z. mays* ssp. *mays* (X), ssp. *parviglumis* (Δ), and ssp. *mexicana* (+), and race Nobogame (★) of *Z. mays* ssp. *mexicana*.—9. 9 field populations of the wild taxa of *Zea mays* including *Z. mays* ssp. *mexicana* races Chalco (+), Central Plateau (X) and Nobogame (Y); and *Z. mays* ssp. *parviglumis* vars. *parviglumis* (Δ) and *huehuetenangensis* (□).



TABLE 2. Eigenvectors (standardized such that the largest element in absolute value equals one) and percent variance for the canonical variates from Figures 6 to 13.

| Figure<br>Canonical<br>Variate | 6     |        | 7      |        | 8      |        | 9     |        | 10    |        | 11    |       |
|--------------------------------|-------|--------|--------|--------|--------|--------|-------|--------|-------|--------|-------|-------|
|                                | 1     | 2      | 1      | 2      | 1      | 2      | 1     | 2      | 1     | 2      | 1     | 2     |
| Characters                     |       |        |        |        |        |        |       |        |       |        |       |       |
| 1. BRAN-#                      | .015  | -.500  | .068   | .115   | -.411  | -.756  | -.176 | -.751  | -.437 | .799   | -.707 | -.439 |
| 2. CNSP-L                      | .514  | .459   | .184   | .802   | .375   | -1.000 | -.212 | -.378  | -.736 | .487   | -.820 | -.357 |
| 3. BRAX-L                      | .246  | .120   | .266   | .134   | -.020  | -.101  | .145  | .371   | -.350 | .528   | -.133 | -.320 |
| 4. CSIN-L                      | -.089 | -1.000 | .080   | .027   | -1.000 | .727   | -.272 | .054   | -.514 | .468   | -.479 | -.809 |
| 5. LBIN-L                      | 1.000 | .222   | .404   | -1.000 | -.145  | -.286  | -.372 | -.218  | -.046 | -.135  | .056  | -.281 |
| 6. SPIK-W                      | -.262 | .233   | -.178  | .134   | .399   | -.116  | .112  | -.064  | .259  | -.251  | .261  | -.045 |
| 7. PEDI-L                      | -.062 | -.335  | .115   | -.038  | -.210  | .342   | .105  | .168   | .174  | .030   | .188  | -.775 |
| 8. ANTH-L                      | .065  | .209   | .027   | .126   | -.115  | .341   | -.119 | .013   | .068  | -.109  | -.094 | -.418 |
| 9. GLUM-L                      | -.766 | .673   | -.400  | .215   | .952   | .597   | 1.000 | .011   | 1.000 | -1.000 | 1.000 | 1.000 |
| 10. GLUM-W                     | .094  | .332   | -.365  | .241   | .285   | .197   | .132  | .894   | .222  | -.265  | .189  | -.614 |
| 11. WING-W                     | -.964 | -.346  | -1.000 | .282   | -.185  | .259   | -.065 | -.210  | .540  | .092   | .251  | .016  |
| 12. SHLD-W                     | -.341 | -.275  | .058   | -.827  | -.193  | .396   | .144  | -.956  | .207  | -.051  | .361  | .024  |
| 13. SHD-V#                     | -.238 | -.172  | .865   | .079   | .041   | -.219  | .074  | .665   | .736  | .510   | .050  | -.264 |
| 14. TOT-V#                     | -.705 | -.021  | .160   | .962   | .095   | .091   | .200  | -1.000 | .054  | .600   | -.024 | -.878 |
| 15. LATV-W                     | -.422 | -.098  | -.110  | .751   | .109   | .004   | .190  | .404   | .236  | .454   | .099  | -.007 |
| 16. SHVN-W                     | .097  | .025   | .099   | -.587  | .039   | -.086  | -.078 | -.292  | -.331 | -.215  | -.121 | -.115 |
| 17. MIDV-W                     | .801  | .066   | .153   | -.452  | -.259  | .038   | -.240 | .820   | -.252 | -.277  | -.211 | -.127 |
| Percent<br>variance            | 46.26 | 33.10  | 66.81  | 12.65  | 72.93  | 9.21   | 52.08 | 16.34  | 71.97 | 10.70  | 60.72 | 17.46 |



TABLE 3. Mahalanobis's distances among populations graphed on Figure 6. Data given below are the means (and ranges) for pairwise interpopulation distances, grouped by taxa.

| Species                                 | <i>Zea diploperennis</i> | <i>Zea perennis</i> | <i>Zea luxurians</i> | <i>Zea mays</i> ssp. <i>mays</i> | <i>Zea mays</i> ssp. <i>mexicana</i> | <i>Zea mays</i> ssp. <i>parviglumis</i> |
|-----------------------------------------|--------------------------|---------------------|----------------------|----------------------------------|--------------------------------------|-----------------------------------------|
| Number of populations                   | 1                        | 3                   | 5                    | 4                                | 6                                    | 3                                       |
| <i>Zea diploperennis</i>                | —                        |                     |                      |                                  |                                      |                                         |
| <i>Zea perennis</i>                     | 3.9<br>(3.5–4.1)         | 4.2                 |                      |                                  |                                      |                                         |
| <i>Zea luxurians</i>                    | 5.9<br>(4.6–7.9)         | 6.3<br>(5.1–8.6)    | 3.9                  |                                  |                                      |                                         |
| <i>Zea mays</i> ssp. <i>mays</i>        | 11.9<br>(11.5–12.2)      | 12.0<br>(11.1–13.0) | 12.0<br>(9.4–13.9)   | 5.6                              |                                      |                                         |
| <i>Zea mays</i> ssp. <i>mexicana</i>    | 9.9<br>(8.7–10.7)        | 9.4<br>(6.3–10.2)   | 9.0<br>(7.0–12.3)    | 9.3<br>(7.0–11.3)                | 4.1                                  |                                         |
| <i>Zea mays</i> ssp. <i>parviglumis</i> | 12.7<br>(11.6–13.6)      | 12.0<br>(9.4–14.4)  | 11.3<br>(9.4–13.9)   | 12.4<br>(9.6–14.4)               | 6.1<br>(4.5–7.3)                     | 4.1                                     |

sions, some pairwise distances between the populations and especially between those populations within the same cluster are not accurately represented. One may obtain a better view of how the taxa within the two sections relate to one another by performing close-up analyses of each cluster as discussed in the Materials and Methods.

Figure 7 is a plot of the first two variates from a close-up analysis of the subgroup corresponding to sect. *Luxuriantes*. On this graph the five populations of *Zea luxurians*, all represented by triangles, receive positive values for the first canonical variate while both perennial species have negative scores for this variate. The eigenvector corresponding to this variate (Table 2) shows it to be composed largely of wing width and shoulder vein number, the traits that best distinguish the narrow-winged, highly-veined *Zea luxurians* from the broad-winged, fewer-veined perennials. The second canonical variate discriminates among the four perennial populations, but fails to clearly separate *Z. perennis* from *Z. diploperennis*. This is not particularly surprising as these two species are very closely related, *Z. perennis* presumably being the autotetraploid derivative of *Z. diploperennis*. The characters that best distinguish these two taxa are their rhizomes (the diploid having shorter rhizome internodes and tuber-like short shoots) and general robustness of the plants (the diploid having wider leaves and taller stems) (Iltis et al., 1979). In inflorescence

morphology, *Z. diploperennis* has on the average a greater number of tassel branches and wider spikelets with wider shoulders. However, these differences are not large enough to allow its separation from *Z. perennis* on Figure 7. The basic inflorescence structure of the two taxa being nearly identical, one might treat them as two subspecies of *Z. perennis*. However, the great dissimilarities in their rhizomes and general aspect justify maintaining them as separate species (Iltis et al., 1979).

A canonical graph of the taxa of sect. *Zea* shows the maize populations separating well from the two wild subspecies of *Zea mays*, but these two wild taxa overlap somewhat with one another (Fig. 8). Of the two wild subspecies, *Z. mays* ssp. *mexicana* is closest to the cultigen maize, and closest to the Nal-Tel race of maize, in particular (Table 4). The Nobogame specimens, which have slightly smaller spikelets than the Chalco and Central Plateau races, still appear closest to *Z. mays* ssp. *mexicana* rather than *Z. mays* ssp. *parviglumis* (Fig. 8). Part of the reason for this is that, like *Z. mays* ssp. *mexicana* and unlike *Z. mays* ssp. *parviglumis*, race Nobogame characteristically has few tassel branches.

Maize separates from the teosintes along the first canonical variate primarily on the basis of its shorter central spike internodes and longer glumes (Table 2; Fig. 8). These two traits, which are correlated with the number of kernels per ear and kernel size, respectively, probably reflect the indirect effects of domestication. As the pre-Co-



TABLE 4. Mahalanobis's distances among populations graphed on Figure 8. Data given below are the means (and ranges) for pairwise interpopulation distances, grouped by taxa.

| Taxa                                          | <i>Zea mays</i><br>ssp. <i>mays</i> <sup>1</sup> | Race<br>Nal-Tel  | <i>Zea mays</i><br>ssp.<br><i>mexicana</i> | <i>Zea mays</i><br>ssp.<br><i>parviglumis</i> |
|-----------------------------------------------|--------------------------------------------------|------------------|--------------------------------------------|-----------------------------------------------|
| Number of populations                         | 3                                                | 1                | 6                                          | 3                                             |
| <i>Zea mays</i> ssp. <i>mays</i> <sup>1</sup> | 3.88                                             |                  |                                            |                                               |
| Race Nal-Tel                                  | 6.7<br>(6.0–7.3)                                 | —                |                                            |                                               |
| <i>Zea mays</i> ssp. <i>mexicana</i>          | 9.3<br>(8.6–10.9)                                | 7.3<br>(6.4–8.5) | 3.8                                        |                                               |
| <i>Zea mays</i> ssp. <i>parviglumis</i>       | 12.8<br>(11.8–13.9)                              | 9.3<br>(8.9–9.8) | 5.7<br>(4.4–7.0)                           | 4.0                                           |

<sup>1</sup> Excluding race Nal-Tel.

lumbian Mexican Indians selected for larger grains and more grains per ear, they would have inadvertently brought about an increase in male spikelet size and a reduction in the length of internodes on the central spike (Iltis, 1971, 1981; Galinat, 1971; Beadle, 1972; Doebley & Iltis, 1980). Thus, maize differs from the annual teosintes of Mexico and west-central Guatemala mainly in characters that were transformed by human selective pressures, supporting the hypothesis that maize is domesticated teosinte.

Pinpointing the particular taxon of teosinte which was transformed into maize is more difficult. To approach this problem, one may use morphological distance (here measured with Mahalanobis's distance) to measure evolutionary divergence. This procedure is reasonable though certainly not foolproof. On this basis the teosintes of sect. *Luxuriantes*, all of which are morphologically quite distant from maize (Fig. 6; Table 3) cannot be considered likely candidates for the direct ancestor of maize (Doebley & Iltis, 1980). Of the two remaining taxa, *Z. mays* ssp. *mexicana* and ssp. *parviglumis*, the former is morphologically closest to the Mexican maize races studied here (Fig. 6; Table 3). This closeness reflects the facts that *Z. mays* ssp. *mexicana*, like these Mexican races of maize, has larger spikelets, fewer tassel branches, and a longer central spike than *Z. mays* ssp. *parviglumis*.

In Figure 8, race Nal-Tel of maize separates out from the other three maize races (Conico, Palomero Toluqueño, and Chapalote). This is of interest because races Nal-Tel and Chapalote have generally been regarded as closely related (Wellhausen et al., 1952, p. 58; cf. Goodman 1972, p.

179). Yet, the great dissimilarities between these two races in tassel and male spikelet characters mandates that we consider the possibility that their similarity in ear traits results, at least in part, from convergent evolution. The fact that the two races are so widely separated geographically—Nal-Tel from the Yucatan and Chapalote from northwest Mexico—supports this hypothesis.

Results from the study of this small sample of maize races points to the potential of tassel and spikelet traits in helping to understand the taxonomy and evolution of maize races. Such an approach certainly offers an effective and in some ways more objective means of measuring the degree of similarity of maize races to teosinte than is possible with ear characters, given the tremendous differences between the female inflorescences of these two taxa (Anderson, 1944a, 1951).

Figure 9 shows in greater detail the relationship between *Zea mays* ssp. *mexicana* and ssp. *parviglumis*, with each of Wilkes's (1967) races given a separate symbol. Again, the two subspecies separate fairly well with a small area of overlap. Similar results are obtained by graphing these populations using spikelet length versus spikelet width as done by Iltis and Doebley (1980).

Figure 9 also reveals that within *Z. mays* ssp. *mexicana*, races Chalco and Central Plateau do not separate at all, demonstrating that there is no male inflorescence morphological basis for considering them separate taxa. Within *Z. mays* ssp. *parviglumis*, vars. *parviglumis* and *huehuetenangensis* do diverge to some degree along canonical variate two, but with so few specimens



of the latter the case for granting the two races, Balsas and Huehuetenango, even varietal status is weak.

#### GARDEN DATA

To supplement the field data and help elucidate the degree to which environmental differences influence the morphology of the taxa, plants grown in a common garden were studied. Unfortunately, the perennials grew very poorly in the garden and often failed to produce tassels. For this reason only the annual teosintes are included here.

An initial canonical variate analysis of all 12 garden populations (Fig. 10) shows the same basic pattern as the field data. Namely, *Zea luxurians* is very distinct from the other annuals, which in turn separate into *Z. mays* subspecies *mexicana* and *parviglumis*. The major characters involved in separating *Z. luxurians* from *Z. mays* along both the first and second canonical variates are glume length, shoulder vein number, total vein number, wing width, central spike length, branching axis length, lateral vein width, branch number, and length of internodes on the central spike (Table 2). This corresponds well with the field data, which showed *Z. luxurians* to be distinct on the basis of its higher vein number, wider wings, shorter branching axis, and broader lateral nerves.

One difference between the garden and field populations is that the garden populations of the two wild subspecies of *Zea mays* separate much more effectively than the field populations, and without any overlap. The distance between these two subspecies is greater for the garden data (Tables 3 and 5). This sharpening of the differences between the subspecies probably reflects a lessening of environmental variability among local populations. The two subspecies are represented by nearly the same number of samples for the field and garden data, so the sharpening of differences probably does not reflect dissimilar sampling.

Looking more closely at the two wild subspecies of *Zea mays* (Fig. 11), one observes the same basic pattern of variation as seen in the field data except with more effective separation of the two subspecies. One other difference, as compared to the field data, is that race Nobogame appears rather distinct from the other two races of *Z. mays* ssp. *mexicana* and shows a closer association to *Z. mays* ssp. *parviglumis* (Table 5). The

eigenvectors involved in Figure 11 (Table 2) indicate that while races Chalco and Central Plateau differ from *Zea mays* ssp. *parviglumis* by their longer spikelets, shorter branching axes, and fewer branches, race Nobogame is distinguished from *Z. mays* ssp. *parviglumis* by a combination of these characters, as well as fewer nerves on its outer glume and shorter internodes on the central spike.

The distinctiveness of race Nobogame for the garden data does not agree well with the field data, which showed complete overlap of this race with races Chalco and Central Plateau. The probable reason for this is that race Nobogame, being the northernmost teosinte and adapted to flower with longer days, is forced to flower prematurely in Florida before it attains much vegetative development. Thus, the plants are much more depauperate and distinct from specimens of races Chalco and Central Plateau, which flower much later in the garden and obtain a normal amount of vegetative development. For this reason, and because herbarium specimens of races Chalco, Central Plateau, and Nobogame cannot for the most part be told apart, it seems best to include these three races within a single subspecies.

#### MISCELLANEOUS POPULATIONS

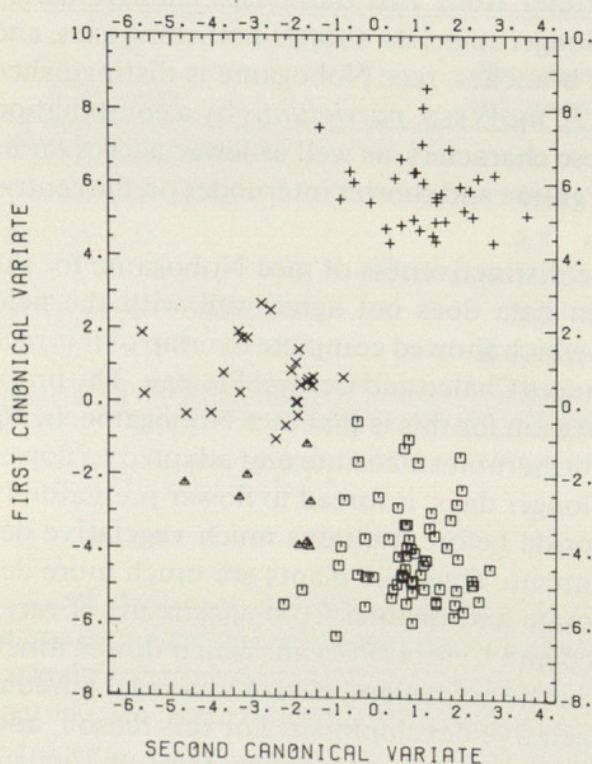
Six populations of plants cultivated under non-uniform (uncontrolled) conditions are of interest as some of them are from areas not otherwise sampled, such as Honduras. Figure 12 includes three such populations, as well as all other populations of sect. *Luxuriantes*. On this graph the Honduras population clusters with the other populations of *Zea luxurians* as does the strictly artificial population composed of Guatemala teosinte plants (diamonds of Fig. 12) cultivated at different localities around the world. Clearly, while the Honduras population does belong in *Zea luxurians* (Guatemala teosinte), where it was placed by Wilkes (1967), more and better material is necessary to determine if it deserves distinction at the subspecific level.

Another pattern of interest revealed in Figure 12 is that the garden populations group together, as do the field populations and the uncontrolled cultivation populations. This demonstrates the extreme effects of the environment on the morphology of the plants, emphasizing the importance of comparing only plants grown under the same conditions, especially when looking at differences at the subspecific level.



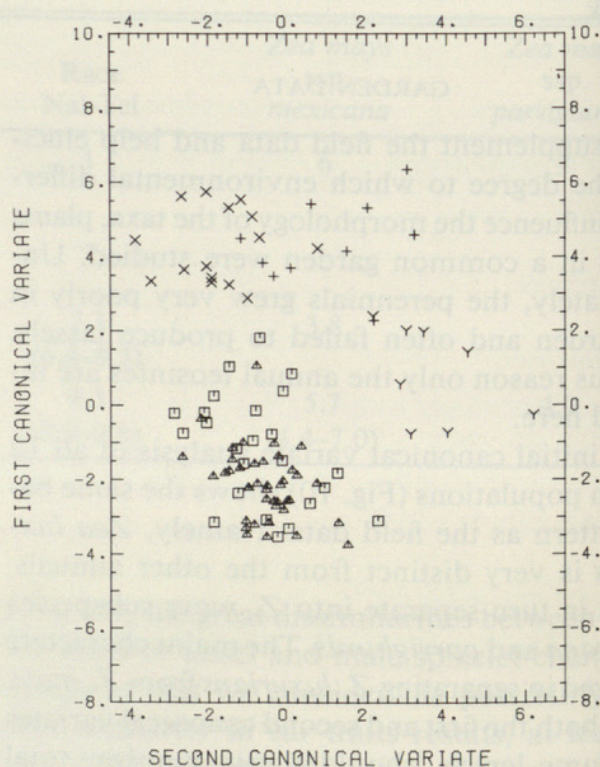
10

ZEA: GARDEN DATA



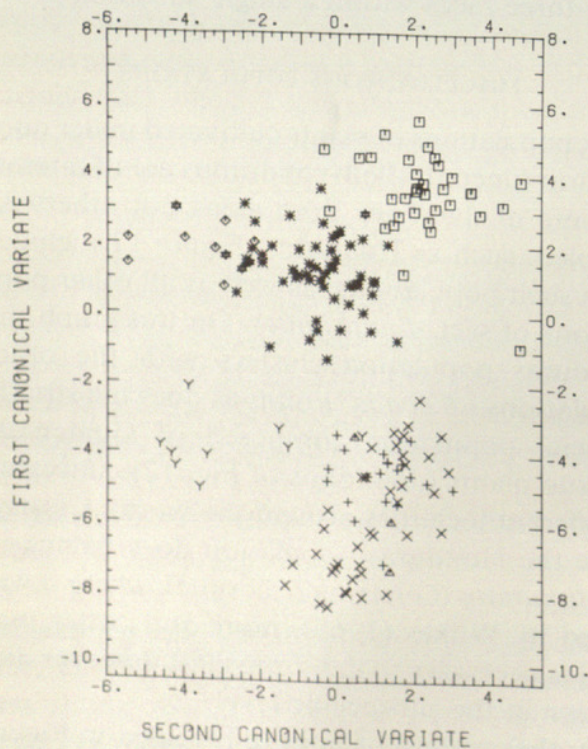
11

WILD ZEA MAYS: GARDEN DATA



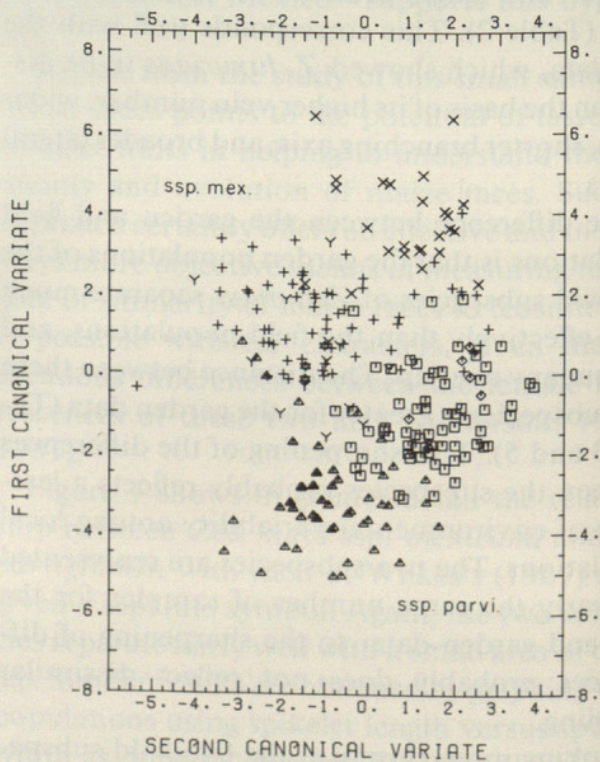
12

ZEA SECT. LUXURIANTES: ALL DATA



13

WILD ZEA MAYS: ALL DATA



FIGURES 10–13. Graphs of the first and second variates from canonical analyses.—10. 12 garden populations of teosinte including *Z. luxurians* (+); *Z. mays* ssp. *mexicana* (X), and ssp. *parviglumis* (□), and race Nobogame (Δ) of *Z. mays* ssp. *mexicana*.—11. 8 garden populations of the wild taxa of *Zea mays* including vars. *parviglumis* (Δ), and *huehuetenangensis* (□).—12. 9 field, 4 controlled garden and 3 uncontrolled garden populations of *Zea* sect. *Luxuriantes* including *Z. diploperennis* (+); *Z. perennis*, 2 field populations (X), uncontrolled garden population derived from Collins's CIUDAD GUZMAN collection (Y) and Collins's CIUDAD GUZMAN field population (Δ); and *Z. luxurians* field populations (\*), Honduras population (★), controlled



TABLE 5. Mahalanobis's distances among populations graphed on Figure 10. Data given below are the means (and ranges) for pairwise interpopulation distances, grouped by taxa.

| Taxa                                              | <i>Zea luxurians</i> | <i>Zea mays</i> ssp. <i>mexicana</i> | Race Nobogame    | <i>Zea mays</i> ssp. <i>parviglumis</i> |
|---------------------------------------------------|----------------------|--------------------------------------|------------------|-----------------------------------------|
| Number of populations                             | 4                    | 2                                    | 1                | 5                                       |
| <i>Zea luxurians</i>                              | 3.1                  |                                      |                  |                                         |
| <i>Zea mays</i> ssp. <i>mexicana</i> <sup>1</sup> | 7.2<br>(6.5–7.9)     | 4.1                                  |                  |                                         |
| Race Nobogame                                     | 10.0<br>(9.7–10.4)   | 6.1<br>(5.4–6.9)                     | —                |                                         |
| <i>Zea mays</i> ssp. <i>parviglumis</i>           | 10.5<br>(8.9–12.0)   | 6.9<br>(5.5–8.1)                     | 5.7<br>(5.3–6.3) | 3.4                                     |

<sup>1</sup> Excluding race Nobogame.

On the lower portion of Figure 12, the *Zea perennis* population composed of plants cultivated from seeds and rhizomes collected by Collins in 1921 shows no closer relationship to Collins's field specimens from the same locality than to the perennial teosinte populations from other stations. In fact, this field collection of *Zea perennis* from Ciudad Guzman is separated by a greater distance from its corresponding cultivated population ( $\bar{D} = 6.0$ ) than from the La Ventana population of *Z. diploperennis* ( $\bar{D} = 5.2$ ). Here then, two samples from the same local population fail to cluster closest to one another due to differences in the environments in which they grew.

Figure 13, which includes the two wild subspecies of *Zea mays*, shows a pattern of variation similar to Figure 12, with the cultivated populations of each subspecies separating slightly from its field populations. On Figure 13 some field populations of *Z. mays* ssp. *mexicana* are closer to garden populations of *Z. mays* ssp. *parviglumis* than they are to garden populations of their own subspecies. Again, this suggests that, at the subspecific level of evolutionary differentiation in *Zea*, genetic differences can be easily obscured by environmental modifications of the phenotypes. The characters which seem to vary most between field and garden populations of both *Z.*

*luxurians* and *Z. mays* are vein number and spikelet width, the ratio of vein number to spikelet width being larger for garden grown plants.

Finally, Figure 13 shows that the annual teosinte population from southwestern Jalisco recently discovered by Guzman (1978) at La Huertita near Casimiro Castillo clusters with *Z. mays* ssp. *parviglumis*. This suggests that this population belongs in *Z. mays* ssp. *parviglumis*, a conclusion supported by their similar vegetative morphologies and the fact that the La Huertita population, like other ssp. *parviglumis* populations, grows in seasonally moist habitats with rainfall in excess of 1,200 mm annually (Doebley, 1984).

SUMMARY OF RESULTS

The preceding analysis of tassel and spikelet morphology shows that the genus can be divided into sections *Luxuriantes* and *Zea*. The former section is characterized by few tassel branches, a short branching axis, short internodes on the tassel branches, and highly nerved outer glumes on which the prominent lateral nerves are developed into wings near the apex of the spikelet. Section *Zea*, on the other hand, is characterized by a larger number of tassel branches, a longer branching axis, longer internodes on the tassel

garden populations (□) and uncontrolled garden population (◇).—13. 9 field, 8 controlled garden and 3 uncontrolled garden populations of the wild taxa of *Zea mays* including *Z. mays* ssp. *mexicana*, 5 field populations (+) and 2 garden populations (X); *Z. mays* ssp. *mexicana* race Nobogame, field population (★) and 2 garden populations (Y); and *Z. mays* ssp. *parviglumis*, 4 field populations (△), 5 garden populations (□) and the LA HUERTITA, Jalisco population (◇).



branches, and fewer-nerved outer glumes that lack wings. Within sect. *Luxuriantes*, *Zea luxurians* is completely distinguished from the perennials on the basis of its much more numerous nerved outer glumes with smaller apical wings and slightly greater number of tassel branches. *Zea diploperennis* and *Z. perennis* could not be distinguished on the basis of tassel morphology. Within sect. *Zea*, the wild populations (teosintes) can be divided into two groups corresponding to *Z. mays* ssp. *mexicana* and ssp. *parviglumis*. On the canonical variate analysis graphs, these two subspecies showed a small area of overlap for field data but no overlap for plants grown in a uniform garden. For both the field and garden data, the two subspecies were distinguished in that *Z. mays* ssp. *mexicana* has fewer branches, a shorter branching axis, and larger spikelets and anthers than *Z. mays* ssp. *parviglumis*. Within *Z. mays* ssp. *mexicana*, races Central Plateau, Chalco, and Nobogame were completely indistinguishable for field data; however, for the garden data, race Nobogame separates from the other two. Garden specimens of race Nobogame tend to have fewer tassel branches and smaller spikelets than typical *Z. mays* ssp. *mexicana*. This seems to be an artifact of its adaptation to the long days of northern Mexico, which forces it to flower prematurely in Florida. Within *Z. mays* ssp. *parviglumis*, no consistent differences were found between vars. *parviglumis* and *huehuetenangensis*. Finally, *Z. mays* ssp. *mays* was shown to differ from its two conspecific wild subspecies only on the basis of characters that could have been altered during the domestication process. These characters include the length of internodes on the central spike, which are shorter in maize, and the length of the spikelets, which are longer in maize. Internode length would have decreased as man selected for a condensed ear with a large number of grains. Male spikelet size would have increased as man selected for larger female spikelets (kernels). In both cases, the parallel variation in the tassel and ear results because these structures are homologous (Anderson, 1944a).

#### ILLUSTRATION OF TAXA

Iltis and Doebley (1980) provided a taxonomic synopsis of *Zea*, while Doebley and Iltis (1980) illustrated the male spikelets of *Zea* to some extent, providing a dichotomous key to the group. The goal here is to describe and illustrate further the taxa, with special reference to male floral

morphology. Those aspects of vegetative and female inflorescence morphology that are essential to the circumscription of the taxa are also described. However, the female inflorescence, and especially its immensely complex branching patterns in the teosintes are slighted here, and are in need of a separate detailed study. Similarly, hybrids of the various teosintes and maize, although common in the field, are not described below.

***Zea*** Linnaeus, Species Plantarum 971. 1753; Genera Plantarum, ed. 5, 419. 1754.

**I. Section *Luxuriantes*** Doebley and Iltis, Amer. J. Bot. 67: 982. 1980.

**1. *Zea diploperennis*** Iltis, Doebley, and Guzman, Science 203: 186. 1979.

*Male inflorescences* with (0–)3–13 ± divergent to nodding branches, these 6–15 cm long, 12–20 mm wide, the central spike barely exceeding the tassel branches in length (Fig. 14); *branching axis* 1–4 cm long; *spikelets* 8.5–11.5 mm long, in sessile-pedicellate pairs, these distichously arranged on the branches; *branch internodes* scaberulous with prominent abscission layers between them, broad (1 mm wide), in cross-section triangular with ciliate edges, and short (2–6 mm), the spikelets therefore crowded and overlapping (e.g. 14 spikelet pairs in 4 cm), with the tip of the sessile spikelet of each pair reaching the base of the next higher pair above on the same side (Figs. 22–23); *pedicels* scabrous, enlarged below the spikelet, 1.5–3.5 mm long; *glumes* of the spikelet glabrous (rarely scaberulous), sublustrous, often purple tinged, stiff and firm and somewhat brittle when old; outer glume flat on back and tightly enclosing the inner, strongly green-nerved, the nerves often clustered marginally near the apically ciliate prominent lateral wings (Fig. 37); inner glume keeled along the mid-nerve, scaberulous where it contacts the rachis.

*Female inflorescences* consisting of slender distichous spikes, each with 5–10 cupulate fruitcases, these trapezoidal-cylindric, 6–9 mm on the long side, 2.5–4.5 mm on the short side, 4–5 mm in diameter, when mature light sepia to grayish brown, and speckled with dark brown or nearly black; weight of 100 mature fruitcases 6.8–7.5 g.

Loosely clump-forming perennial, with both cord-like and tuber-like rhizomes, both of these with short (2–6 mm) internodes. Rare, endemic to Sierra de Manantlan, Jalisco, Mexico, alt. 1,400–2,400 m.





FIGURES 14-17. Pressed male inflorescences.—14. *Zea diploperennis*, Iltis, Guzman, Doebley and Las-seigne 450 (plant GG).—15. *Zea perennis*, Guzman s.n. (plant I).—16. *Zea luxurians*, K. Lind 421 (plant T).—17. *Zea mays* ssp. *mays* (Mexican Pyramidal), Iltis and Doebley 405 (plant B). (Scale in cm.)



2. *Zea perennis* (Hitchcock) Reeves and Mangelsdorf, Amer. J. Bot. 29: 817. 1942.

*Euchlaena perennis* Hitchcock.

*Male inflorescences* similar to those of *Zea diploperennis*, except with fewer, (0-)3-8, erect or rarely somewhat nodding branches (Fig. 15), these 6-12 cm long, 10-20 mm wide; *branching axis* 1-2.5 cm long (see also Figs. 24, 25, 38).

*Female inflorescences* similar to those of *Zea diploperennis*, except with the fruitcases commonly gray or sepia, speckled with dark brown; weight of 100 mature fruitcases 8.3 g.

Densely sod-forming perennial, with cord-like rhizomes, these with long (1-6 cm) internodes. Rare, endemic to the vicinity of Ciudad Guzman, Jalisco, Mexico, alt. 1,520-2,200 m.

3. *Zea luxurians* (Durieu and Ascherson) Bird, Taxon 27: 363. 1978.

*Euchlaena luxurians* Durieu and Ascherson.

*Male inflorescences* with (0-)4-25 erect branches, these 7-20 cm long, 8-15 mm wide, the central spike often exceeding the branches in length (Fig. 16); *branching axis* 1-9 cm long; *spikelets* 8.5-12.5 mm long, in sessile-pedicellate pairs, these distichously arranged on the branches (Figs. 26-27); *branch internodes* densely scaberulous or strigose with prominent abscission layers between them, broad (1 mm wide), triangular in cross-section with ciliate edges,  $\pm$  short (3-6 mm), spikelets therefore  $\pm$  crowded and overlapping (e.g. 10 pairs in 4 cm) with the tip of the sessile spikelet of each pair reaching the base of the next higher pair above on the same side (Figs. 26-27); *pedicels* scaberulous or strigose, enlarged below spikelet, 1.5-3.8 mm long; *glumes* of the spikelet scaberulous, rough, stiff and somewhat brittle when old; outer glume flat on back, tightly enclosing inner glume, and having numerous (10-28) indistinct nerves between its two prominent ciliate lateral nerves, the latter produced into narrow wings apically (Fig. 39); inner glume with 5-12 nerves, keeled along mid-nerve.

*Female inflorescences* consisting of slender distichous spikes, each with 5-9 light brownish gray trapezoidal cupulate fruitcases, these 7-11.5 mm on long side, 3.7-6.5 mm on short side and 3-5 mm in diameter; weight of 100 mature fruitcases 7.6-9.9 g.

Robust annual, main culm usually highly branched and without any or only few tillers in

the wild. Honduras, southeastern Guatemala (Provinces of Jutiapa, Chiquimula, and Jalapa), and southeastern Mexico (Oaxaca, San Augustin only), alt. 410-1,100 m.

## II. Section *Zea*.

4. *Zea mays* Linnaeus, Species Plantarum 971. 1753.

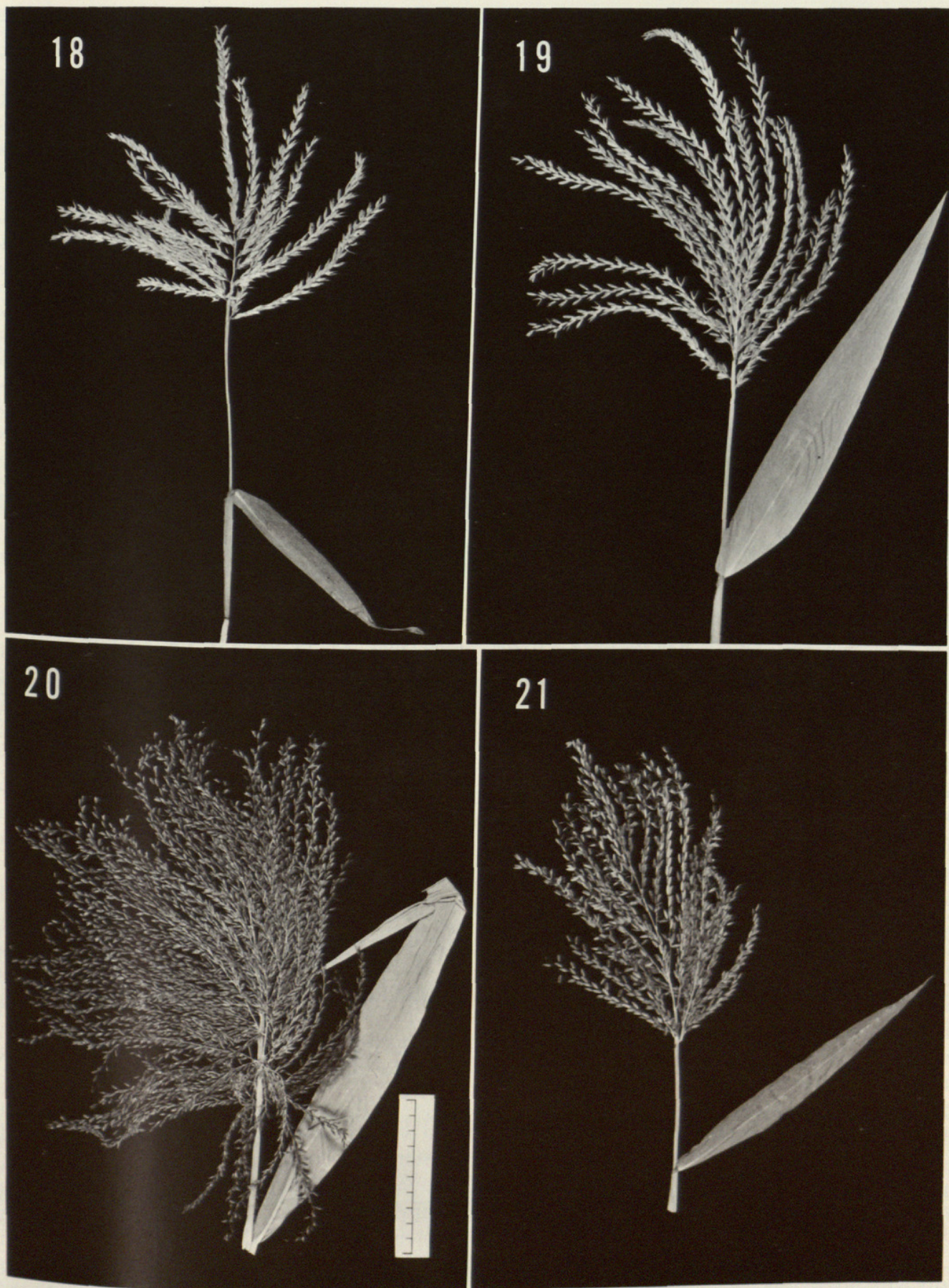
*Male inflorescences* with numerous branches (in well grown plants many more than 12, except in certain races of cultivated *Z. mays*), these lax (stiff in some races of maize), the central spike occasionally somewhat stiffer, stronger, and more densely beset with spikelets than the tassel branches (this highly exaggerated in cultivated *Z. mays*) (Figs. 17-21); *branching axis* usually (1-)3-18 cm long; *spikelets* 4.6-13.0 mm long, usually in sessile-pedicellate pairs; *branch internodes* variously scabrous-pubescent, slender (less than 1 mm wide), rounded on the back, not strongly flattened, elongated (3.5-8.2 mm or more) (except in central spike of maize), spikelet arrangement therefore loose and open and with the tip of the sessile spikelet of each pair not reaching the base of the next higher pair above on the same side (Figs. 28-35); abscission layers between the internodes strongly to weakly developed (totally absent in *Z. mays* ssp. *mays*), the tassel branches therefore often tardily disintegrating (or not at all in maize); *pedicels* slender, 1-7 mm long; *glumes* of the male spikelet variously scabrous-pubescent, rounded on back, the outer glume only loosely embracing the inner one, both flexible and  $\pm$  papery in texture; outer glume with few (6-15) veins, the two major lateral veins only slightly stronger than the secondaries between them and not winged; cilia along the keels hair-like and soft, and not scaberulous and tooth-like (Figs. 40-45); inner glume 3-8 nerved.

*Female inflorescences* either (in maize) a single massive polystichous spike (with occasional smaller subsidiary spikes), terminal on a lateral branch, or (in teosinte) consisting of slender distichous spikes, these composed of 5-12 or more  $\pm$  triangular cupulate fruitcases.

4a. *Zea mays* L. ssp. *mays*.

*Male inflorescences* highly variable, with (0-) 3-30 or more branches, these 5-30 cm long, the central spike almost always strongly distinguished from the tassel branches (Fig. 17); *spikelets* 6-13 mm or more long, in sessile-pedicellate





FIGURES 18–21. Pressed male inflorescences. — 18. *Zea mays* ssp. *mexicana* race Chalco, *Iltis and Doebley* 9 (plant U). — 19. *Zea mays* ssp. *mexicana* race Central Plateau, *Palmer* 743. — 20. *Zea mays* ssp. *parviglumis* var. *parviglumis* (race Balsas), *Iltis and Doebley* 362 (plant A). — 21. *Zea mays* ssp. *parviglumis* var. *huehuetenangoensis* (race Huehuetenango), *Doebley* 371 (cultivated in Homestead, Fla.). (Scale in cm.)



pairs, these distichously arranged on the lateral branches (Figs. 28–29) and polystichously arranged on the central spike (here single spikelets or groups of three spikelets are not uncommon, the pedicellate spikelet sometimes essentially sessile), the spikelets on the latter extremely crowded and overlapping (up to 26 or more spikelet pairs in 4 cm); *glumes* of the spikelet glabrous, scabrous, lanate, sericeous or villous (Fig. 40).

*Female inflorescences* consisting of a single terminal spike ("ear"), this polystichous (8–20 or more rows of grain), gigantic with 100–2,000 naked caryopses ("grains"), these, attached to a massive central axis ("cob"), laterally displaced from their reduced, collapsed, empty, and hidden cupules, the entire spike tightly enclosed in a series of 8–12 or more leaf sheaths ("husks"), all borne on a thick peduncle ("shank").

Monopodial or sparsely tillered annuals. World-wide cultigen.

**4b. *Zea mays* L. ssp. *mexicana* (Schrader) Iltis** in Annual Rev. Genet. 4: 450. 1971; *Phytologia* 23: 249. 1972; emended circumscription Amer. J. Bot. 67: 1001.

*Male inflorescences* with 0–20(–35) nodding branches, these 5–25 cm long, the central spike identical with to slightly larger than the tassel branches (Figs. 18–19); *spikelets* (6.6–)7.5–10.5 mm long, in sessile-pedicellate pairs, these distichously arranged on all branches (Figs. 30–31); *glumes* sparsely to densely scabrous (Figs. 41–43).

*Female inflorescences* consisting of slender distichous spikes; each spike consisting of 9–12 or more triangular cupulate fruitcases, the former enclosed in a single sheath and borne on a short to elongate slender peduncle; fruitcases 6–10 mm long, 4–6 mm wide, often pointed or "pinched" on the axial side, variable in color, gray, tan, or dark brown, and mottled or speckled with dark brown; weight of 100 mature fruitcases 5.6–10.4 g.

**4b-I. Race Chalco of Wilkes.**

Plants vegetatively robust, maize-like, generally with no or only few (1–6) tillers; leaf sheaths densely pilose and often dark red in color; leaves sparsely pilose; Valley of Mexico and its slopes, Mexico (cf. Wilkes, 1967), alt. 2,150–2,500 m.

**4b-II. Race Central Plateau of Wilkes.**

Essentially identical to race Chalco except leaf

sheaths less densely pilose and not as deep red in color. Some populations are vegetatively somewhat depauperate and resemble race Nobogame. Michoacan, Guanajuato, and eastern Jalisco (cf. Wilkes, 1967), alt. 1,750–2,100 m.

**4b-III. Race Nobogame of Wilkes.**

Similar to race Chalco and especially race Central Plateau except the plants vegetatively less robust with fewer tassel branches, narrower and shorter leaves, and slightly smaller male and female spikelets, the male spikelets having a fewer-nerved outer glume. Nobogame, Chihuahua (cf. Wilkes, 1967), alt. ca. 1,900 m.

**4c. *Zea mays* L. ssp. *parviglumis* Iltis and Doebley, Amer. J. Bot. 67: 1001. 1980.**

*Male inflorescences* similar to those of ssp. *mexicana* except more delicately and often much more densely branched (up to 100 or more branches) with tertiary branching much more frequent (Figs. 20–21); *spikelets* markedly smaller than those of ssp. *mexicana* 4.6–7.2(–7.9) mm long (Figs. 32–35, 44–45), 1.6–2.8 mm wide.

*Female inflorescences* similar to those of ssp. *mexicana* except with fewer (5–10) triangular cupulate fruitcases per spike; fruitcases smaller (5.0–8.0 mm long, 3.0–5.0 mm wide) and blunt on the axial side; weight of 100 fruitcases 3.1–5.6 (–7.9) g.

**4c-I. *Zea mays* L. ssp. *parviglumis* Iltis and Doebley var. *parviglumis*. Race Balsas of Wilkes.**

*Leaves* commonly at least sparsely pilose to velvety pubescent, plants up to 3.5 m tall. Plants of thorn scrub and open summer-green tropical deciduous forest, as well as maize fields and their edges, on well-drained slopes of mountains and hills in the Rio Balsas valley of Guerrero, Michoacan, and Mexico at 600–1,600 m alt. (–1,950 m? cf. Wilkes, 1967, p. 119), these in huge dense and clearly wild stands, and rarely in southwestern Jalisco at 400–1,200 m, this a distinct population with a moister ecology and later flowering date (Guzman, 1978, 1982); flowering from September through October, with ripe fruit by December.

**4c-II. *Zea mays* L. ssp. *parviglumis* Iltis and Doebley var. *huehuetenangensis* Iltis and Doebley, Amer. J. Bot. 67: 1002. 1980. Race Huehuetenango of Wilkes.**

*Leaves* essentially glabrous, plants up to 5 m tall, the tallest of all teosintes. Plants of old maize





FIGURES 22–23. Lateral branch segment of a male inflorescence of *Zea diploperennis*, *Iltis, Guzman, Doebley and Lasseigne 450* (plant GG).—22. Abaxial view.—23. Adaxial view. (Scale in mm.)

fields, edges of fields and oak forest, Province of Huehuetenango, Guatemala, from 900–1,650 m alt. (fide Wilkes, 1967, p. 56); flowering from late November to January and fruiting from January through February, depending on the onset of the rainy season, which here, as in the habitat of the typical variety, is tremendously variable from year to year.

Since the time of its original description, it has been learned that *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* can be distinguished from the typical variety by its essentially glabrous leaves (see above). It has also been learned that, although the habitat of *Zea mays* ssp. *parviglumis* in the Balsas river valley is highly seasonal and extremely dry during the winter months, this region receives 120–160 cm of rainfall annually making it seasonally, at least, quite moist (Doebley, 1984). In this sense then, *Zea mays* ssp. *parviglumis* var. *parviglumis* (Balsas teosinte) occupies a habitat (seasonally mesic) similar to the mesic habitat of var. *huehuetenangensis*. This is not surprising, considering their similar morphologies.

#### THE PHYLOGENY OF *ZEA*

Little attention has been devoted to discussion the phylogeny of the teosintes, ostensibly because so few have regarded them as anything more than sporadic hybrids of maize and either *Tripsacum*

or some hypothetical, primeval teosinte. The first of these ideas, the theory of Mangelsdorf and Reeves (1939), that teosinte is a maize-*Tripsacum* hybrid, has now been dismissed as untenable even by its author (Mangelsdorf, 1974). The various other proposals that racial diversity in teosinte represents nothing more than the incorporation of varying amounts of maize germplasm into some primitive teosinte still have their supporters. In this section I will examine the morphological and other evidence in relation to one of these theories, namely Wilkes (1979) and Mangelsdorf's (Wilkes & Mangelsdorf, 1979; Mangelsdorf et al., 1981) most recent hypothesis that all the races of annual teosinte are the products of the hybridization of *Zea diploperennis* and maize. Further, I will articulate my own view that all the teosinte taxa represent the products of adaptive radiation and geographic speciation with only minor if any maize introgression.

If one believes with Wilkes and Mangelsdorf that the annual teosintes were conceived through the miscegenation of maize and diploperennial teosinte, then they should exhibit intermediacy between these two taxa for at least some traits. Intermediacy may result from processes other than hybridization, and therefore cannot on its own establish the occurrence of hybridization. Nevertheless, intermediacy for at least some traits is a common outcome of hybridization. Thus,





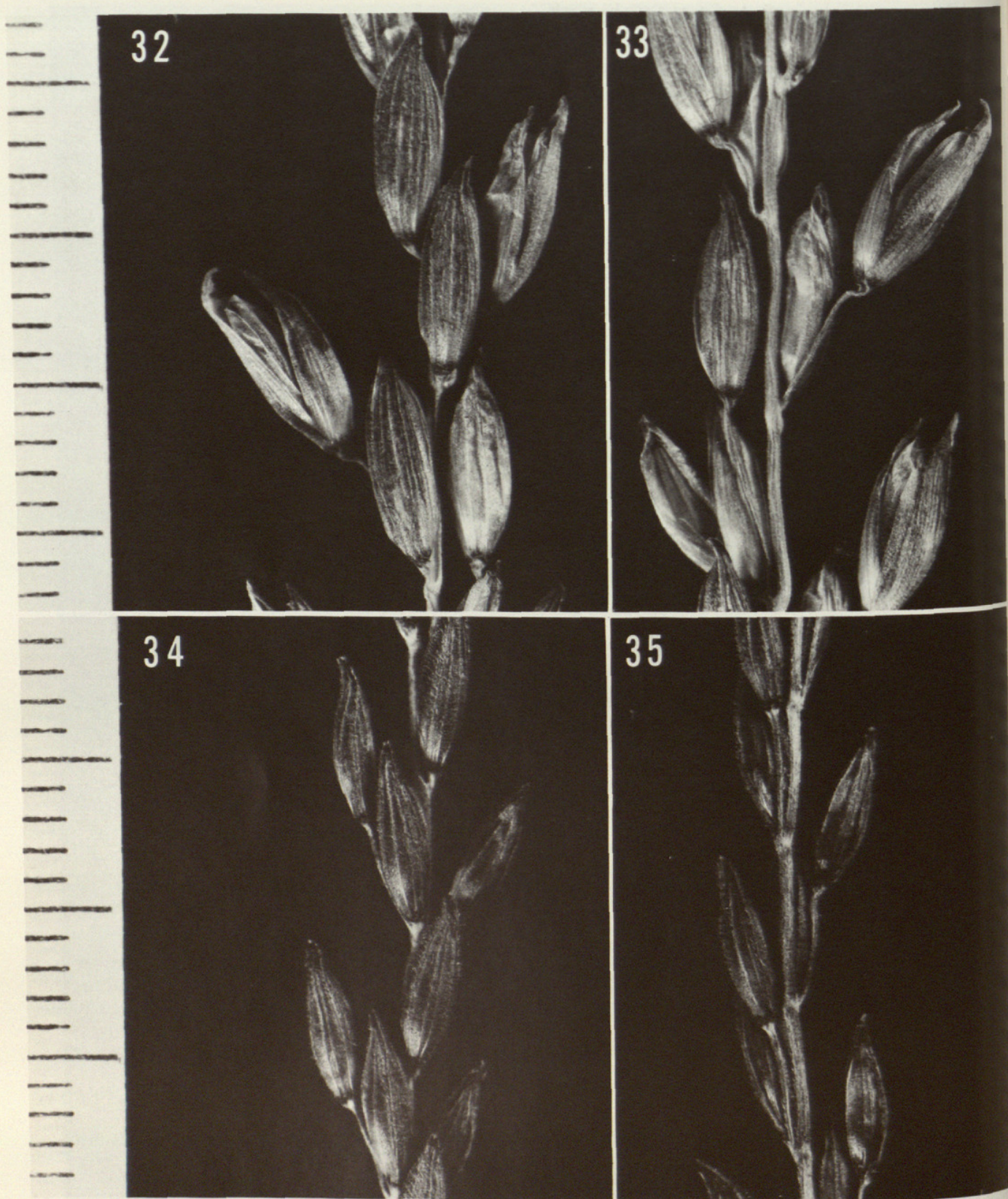
FIGURES 24-27. Lateral branch segment of a male inflorescence.—24-25. *Zea perennis*, Iltis, Puga, Guzman, Doebley and Lasseigne 550 (plant C).—24. Abaxial view.—25. Adaxial view.—26-27. *Zea luxurians*, K. Lind 419.—26. Abaxial view.—27. Adaxial view. (Scale in mm.)





FIGURES 28-31. Lateral branch segment of a male inflorescence.—28-29. *Zea mays* ssp. *mays* race Nal-Tel (cultivated in Homestead, Fla.).—28. Abaxial view.—29. Adaxial view.—30-31. *Zea mays* ssp. *mexicana* race Central Plateau, *Iltis and Doebley* 96.—30. Abaxial view.—31. Adaxial view. (Scale in mm.)





FIGURES 32-35. Lateral branch segment of a male inflorescence.—32-33. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (race Huehuetenango), Doebley 417 (cultivated in Homestead, Fla.).—32. Abaxial view.—33. Adaxial view.—34-35. *Zea mays* ssp. *parviglumis* var. *parviglumis* (race Balsas), Iltis and Doebley 362 (plant A).—34. Abaxial view.—35. Adaxial view. (Scale in mm.)

one can check Wilkes and Mangelsdorf's hypothesis by inspecting the mean values for some important taxonomic traits of the taxa presumably involved in this event (Table 6). In order

to give this hypothesis the best possible chance of validation, I have listed on this table two rather extreme forms of so-called "primitive" maize. Mangelsdorf, himself, has used one of these maize



rices (Palomero Toluqueño) to test this hypothesis (Camara H. & Mangelsdorf, 1981).

In Table 6, there is scarcely any evidence to bolster the theory of Wilkes and Mangelsdorf. For glume length, spikelet width, and vein number, all of the Mexican annual teosintes have small values outside of the range between *Zea diploperennis* and maize. For pedicel length and length of internodes on both the central spike and the lateral branches, all of the Mexican annuals have values larger than either maize or diploperennial teosinte. For caryopsis weight and central spike length, *Z. mays* ssp. *parviglumis* has values smaller than either of the two hypothetical "parental" species. For pedicel length, vein number, and length of internodes on the central branch, *Z. luxurians* has values outside of the range between diploperennial teosinte and maize. Clearly then these data in no way verify the hypothesis that the annual teosintes sprang forth from the hybridization of maize and *Z. diploperennis*.

On the other hand, if one cares to hypothesize that *Zea luxurians* and not *Z. diploperennis* fulfilled the role of the primeval pure teosinte involved in the hybridization with maize, the same difficulties arise. As can be seen from Table 6, the Mexican annual teosintes are no more intermediate between *Z. luxurians* and maize than they are between maize and *Z. diploperennis*. This conclusion is further supported by Figure 6 which demonstrates that the Mexican annual teosintes are in no way morphologically intermediate between maize and the teosintes of sect. *Luxuriantes*.

Other independent evidence also reflects disparagingly on Wilkes's hypothesis. First, analysis of isoenzymatic variation in *Zea* shows a large number of alleles restricted to sect. *Luxuriantes* and absent from all taxa of sect. *Zea*, as well as a close association between maize and Mexican annual teosinte, and thus, no evidence for the intermediacy of the annual teosintes (Doebley et al., 1984). Similarly, the seed proteins of the taxa of sect. *Zea* are electrophoretically identical to one another and different from those of *Z. luxurians* (Smith & Lester, 1980). Further, the electrophoresis of DNA from chloroplasts and mitochondria reveals substantial variation in banding patterns with most species and subspecies having their own distinctive pattern (Timothy et al., 1979; Timothy et al., 1982). The tremendous diversity of cytoplasm DNAs is especially damaging to Wilkes and Mangelsdorf's

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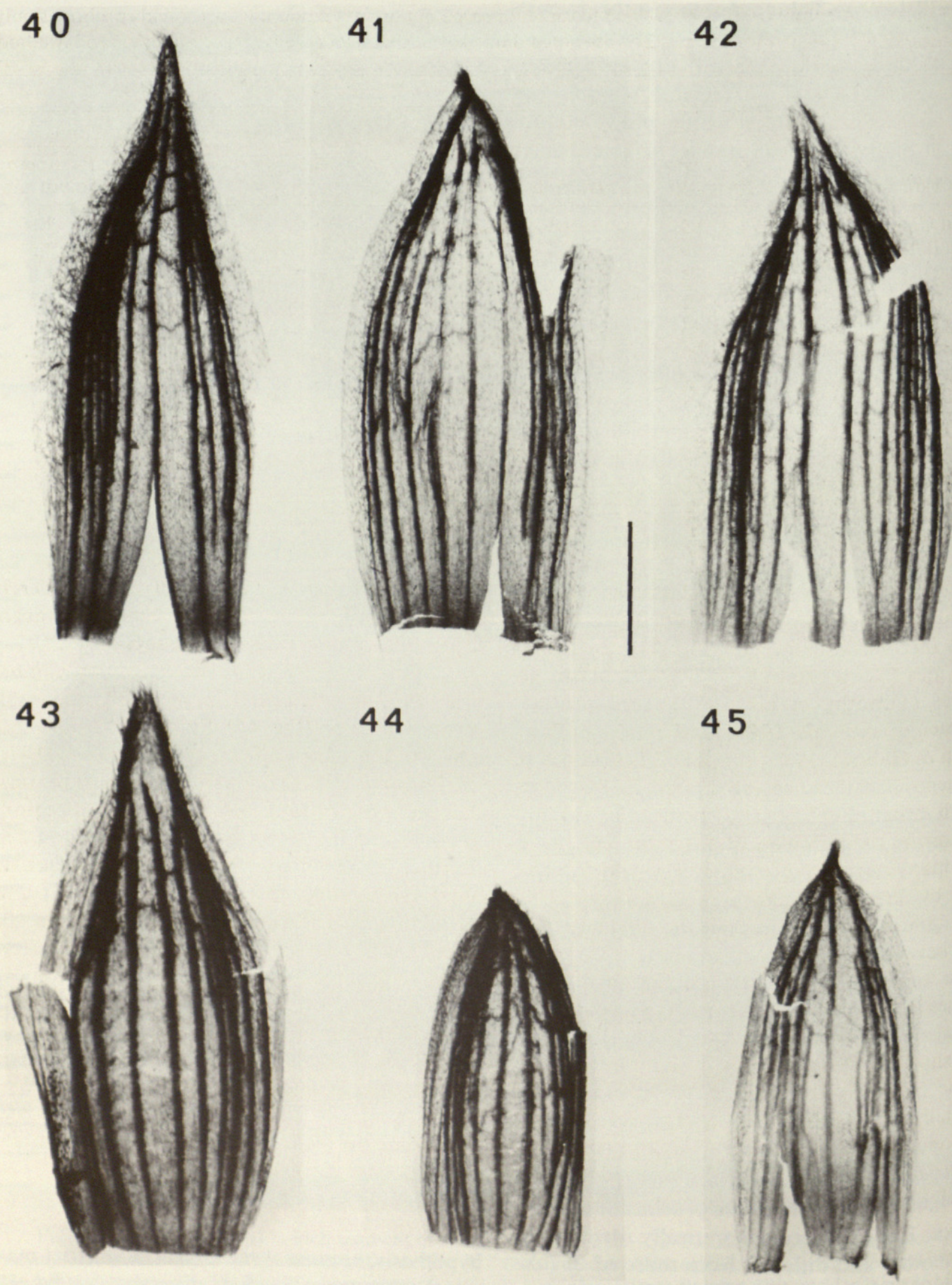


FIGURES 36–39. Outer glumes of *Tripsacum* and teosinte.—36. *Tripsacum australe* from Peru (cultivated at Fairchild Tropical Garden Redlands Nursery, Row 44 Space 2, FG67-257).—37. *Zea diploperennis*, Iltis, Guzman, Doebley and Lasseigne 450 (plant O).—38. *Zea perennis*, Iltis, Puga, Guzman, Doebley and Lasseigne 550 (plant V).—39. *Zea luxurians*, Doebley 376 (cultivated in Homestead, Fla.). (Bar = 2 mm.)

hypothesis, because these DNAs have strict maternal inheritance, so their diversity can be explained only by gradual evolution. Hybridization could not have been involved.

Much more sense can be made of the available information on variability in *Zea* if we simply treat the various taxa of this genus as the products of allopatric, geographic speciation and adaptive radiation. First, morphological evi-





FIGURES 40–45. Outer glumes of *Zea mays* sensu lato.—40. *Zea mays* ssp. *mays* race Chapalote (cultivated in Homestead, Fla.).—41. *Zea mays* ssp. *mexicana* race Chalco, Doebley 374 (cultivated in Homestead, Fla.).—42. *Zea mays* ssp. *mexicana* race Central Plateau, Doebley 375 (cultivated in Homestead, Fla.).—43. *Zea mays* ssp. *mexicana* race Nobogame, Doebley 370 (cultivated in Homestead, Fla.).—44. *Zea mays* ssp. *parviglumis* var. *parviglumis*, Doebley 372 (cultivated in Homestead, Fla.).—45. *Zea mays* ssp. *parviglumis* var. *huehuetenangoensis*, Doebley 371 (cultivated in Homestead, Fla.). (Bar = 2 mm.)



TABLE 6. A comparison of maize and teosinte for some important taxonomic traits (field specimens only). All measurements are in mm unless otherwise noted. For a key to character acronyms see Materials and Methods.

| Characters         | Taxa                                 |                                |                                               |                                            |                 |                       |
|--------------------|--------------------------------------|--------------------------------|-----------------------------------------------|--------------------------------------------|-----------------|-----------------------|
|                    | <i>Zea diplo-</i><br><i>perennis</i> | <i>Zea</i><br><i>luxurians</i> | <i>Zea mays</i><br>ssp.<br><i>parviglumis</i> | <i>Zea mays</i><br>ssp.<br><i>mexicana</i> | <i>Zea mays</i> |                       |
|                    |                                      |                                |                                               |                                            | Nal-tel         | Palomero<br>Toluqueño |
| 9 GLUM-L           | 9.3                                  | 9.8                            | 6.1                                           | 9.0                                        | 9.0             | 11.9                  |
| 6 SPIK-W           | 2.7                                  | 2.5                            | 1.8                                           | 2.5                                        | 2.6             | 3.5                   |
| 7 PEDI-L           | 2.2                                  | 2.7                            | 4.3                                           | 4.2                                        | 1.9             | 1.8                   |
| 13 SHD-V#          | 7.2                                  | 12.7                           | 2.5                                           | 3.4                                        | 3.2             | 3.3                   |
| 14 TOT-V#          | 16.3                                 | 21.2                           | 8.1                                           | 10.6                                       | 11.1            | 10.9                  |
| Caryopsis wt. (mg) | 27.0                                 | 36.0                           | 23.0                                          | 42.0                                       | 70.0            | 145.0                 |
| 1 BRAN-#           | 6.5                                  | 13.3                           | 22.1                                          | 19.7                                       | 42.2            | 2.8                   |
| 4 CSIN-L           | 3.2                                  | 4.4                            | 5.1                                           | 5.2                                        | 1.9             | 1.6                   |
| 5 LBIN-L           | 3.1                                  | 4.5                            | 5.8                                           | 6.0                                        | 5.2             | 4.8                   |
| 2 CNSP-L           | 114.6                                | 136.4                          | 99.5                                          | 136.3                                      | 221.6           | 261.7                 |
| 3 BRAX-L           | 23.8                                 | 45.3                           | 73.5                                          | 86.5                                       | 166.5           | 15.2                  |

dence presented in this paper demonstrates that *Zea* divides into two clearly defined groups, sections *Luxuriantes* and *Zea* (Fig. 46). Data from isozymes (Doebley et al., 1984), cytoplasm genomes (Timothy et al., 1979), seed proteins (Mastenbroek et al., 1981), and cytology (Pasupuleti & Galinat, 1982) support this division of the genus. Of these sections, sect. *Luxuriantes*, which rather closely resembles the related genus *Tripsacum*, is undoubtedly the more primitive. The many morphological features held in common by *Tripsacum* and sect. *Luxuriantes*, but lacking in sect. *Zea*, bespeak the phyletic affinities between these two taxa. These features include typically many-nerved, flattened outer glumes of the male spikelets with two prominent lateral nerves developed into wings (Figs. 36–39), short, thick internodes in the male portion of the inflorescence, trapezoidal fruitcases, perennial rhizomatous root system, and weakly monopodial habit. Further, *Tripsacum* and sect. *Luxuriantes* characteristically have many terminal heterochromatic regions on their chromosomes (Doebley & Iltis, 1980; Pasupuleti & Galinat, 1982).

After this initial and probably quite ancient divergence of sections *Luxuriantes* and *Zea*, diversification continued within each of these two taxa. Within sect. *Luxuriantes*, *Zea luxurians* probably separated quite early from the perennials. It might have abandoned the perennial habit as an adaptation to the dry and highly seasonal environment in southeastern Guatemala. The di-

vergence between *Z. diploperennis* and *Z. perennis* apparently came somewhat later by means of autopolyploidy (Shaver, 1962; Galinat, 1971).

Within section *Zea*, *Z. mays* ssp. *parviglumis* var. *huehuetenangensis* is probably the most primitive taxon (Fig. 46). Evidence for this conclusion comes in part from cytology. Kato (1976; cf. Longley, 1941b) has shown that this teosinte has many terminal heterochromatic regions (knobs) like the teosintes of sect. *Luxuriantes*. Further, isoenzymatic data show this teosinte to have substantially diverged from the other taxa of section *Zea* (Doebley et al., 1984). On the other hand, tassel morphology (this paper), cytoplasm genomes studies (Timothy et al., 1979), and seed protein work (Smith & Lester, 1980; Mastenbroek et al., 1981), all show the clear relationship of this teosinte to the other teosintes of sect. *Zea* and to maize. Thus, it seems that *Z. mays* ssp. *parviglumis* var. *huehuetenangensis* is to some degree intermediate between the two sections though clearly belonging to section *Zea* (Fig. 46). Given the extent of the genetic distinctiveness of this variety, it might best be elevated to a subspecies.

*Zea mays* ssp. *parviglumis* var. *huehuetenangensis* shows its closest relationship to *Z. mays* ssp. *parviglumis* var. *parviglumis*, although these two teosintes are distinct both in terms of their genetics and their vegetative morphology. They are in part distinguished by the many internal heterochromatic regions (knobs) found on the chromosomes of the typical variety but lacking



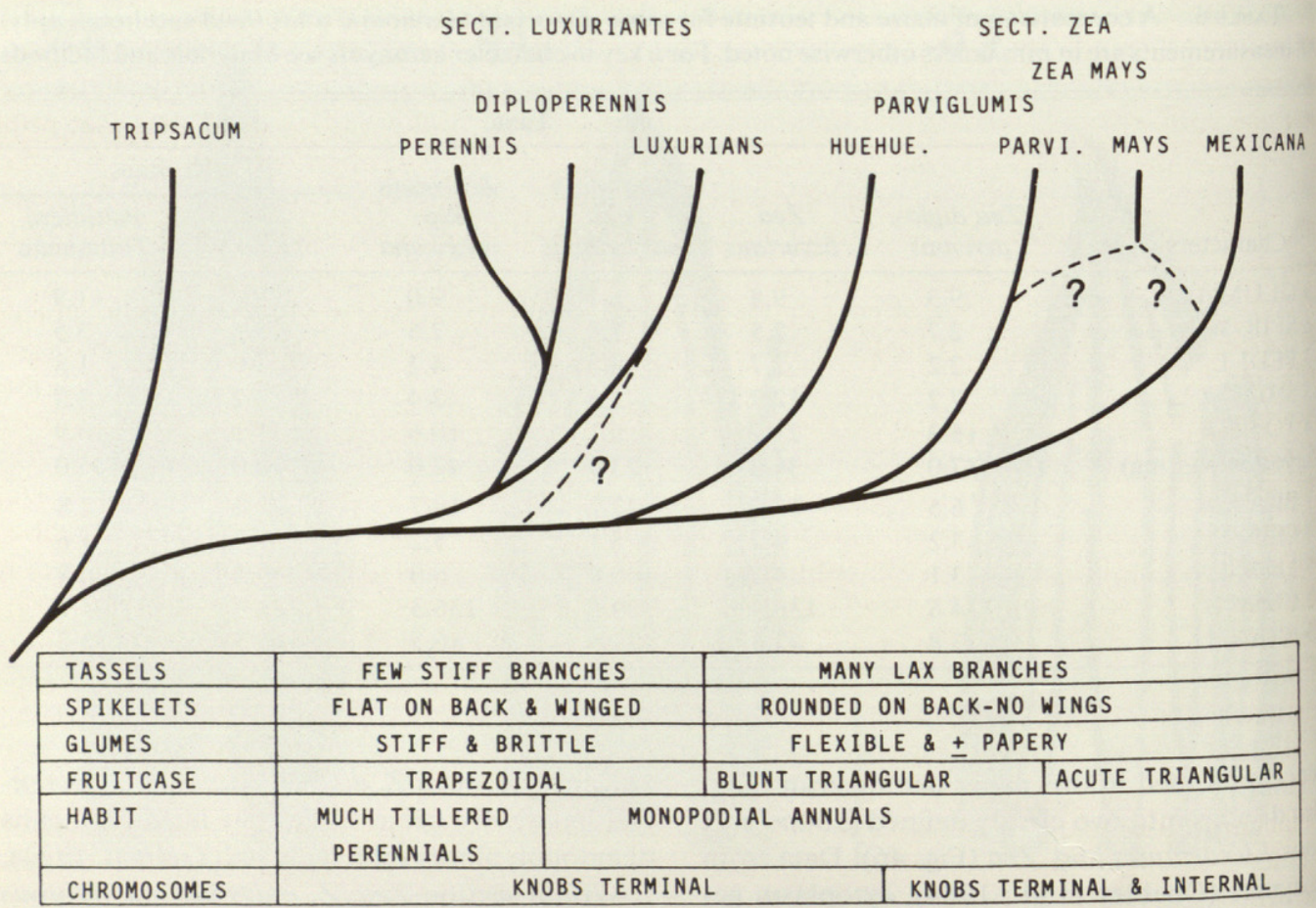


FIGURE 46. A phylogeny for *Zea* that is supported by much of the available data. Dashed lines indicate possible alternative pathways. While the figure seems to indicate *Z. mays* ssp. *mays* has acutely triangular fruitcase, the fruitcase is essentially absent from maize, being represented only by the cupules which are hidden within the ear.

on those of Huehuetenango teosinte (Fig. 46). They are similar in tassel morphology (this paper), seed proteins (Mastenbroek et al., 1981), and cytoplasm genomes (Timothy et al., 1979). These two varieties also share an adaption to a somewhat similar environment and this may partially account for their similar inflorescences. Both grow in low altitude (400–1,600 m), warm, seasonally moist sites with a long growing season. As discussed by Doebley (1984), the small seeds, glabrous, green or dilute red sheaths, small male spikelets, and many tassel branches characteristic of these two varieties may be adaptations to warm, moist environments. The typical variety is most common in the Balsas river valley; however, subpopulations of it inhabit similar environments in the lower, tropical deciduous forest of southwestern Jalisco, Mexico. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* is disjuncted from the Mexican population, occurring in the moist, warm montane oak forest of western Guatemala—the wettest of all teosinte stations.

The next group to diverge in Fig. 46 is *Z. mays* ssp. *mexicana*. This subspecies shows a much different adaptation than *Z. mays* ssp. *parviglumis*. It has colonized the higher, colder, drier sites with a shorter growing season, and is characterized by large seeds, red hairy sheaths, large male spikelets, and fewer tassel branches as an adaptation to this environment (Doebley, 1984). This subspecies includes three extant populations defined by Wilkes (1967): (1) race Chalco, the most extreme form adapted to the highest, coldest habitat of any teosinte, (2) race Central Plateau, adapted to the slightly lower, dry Meseta Central and (3) race Nobogame, a highly local population of the high, arid, short-seasoned Tarahumare Valley.

Despite the diametrical ecologies of the two subspecies, *Z. mays* ssp. *mexicana* and ssp. *parviglumis* var. *parviglumis* show some genetic similarities as compared to Huehuetenango teosinte. Both have internal chromosome knobs (Kato, 1976) and they are similar though distinct



isoenzymatically (Doebley et al., 1984). Figure 46 indicates this affinity in that *ssp. mexicana* and *ssp. parviglumis* var. *parviglumis* are placed near one another.

Although the evolutionary scheme just outlined best accommodates the morphological and other information, other possibilities cannot be entirely dismissed. For example, *Zea luxurians*, while being related to the perennials, may also be the ancestor of the other annual teosintes. As indicated by the dashed line on Figure 46, *Zea luxurians* may have emerged from the mainstock of *Zea* after the perennials and then the other annuals may have evolved from it. Although this scheme requires the annual habit to be derived only once, one would expect a closer relationship between *Z. luxurians* and *Z. mays* sensu lato were this system correct. In fact, its annual habit notwithstanding, *Z. luxurians* shows no closer relationship to *Z. mays* than does *Z. diploperennis*. Indeed, the many-nerved outer glumes, highly elongate trapezoidal fruitcases, and large terminal chromosome knobs of *Z. luxurians* show it to have diverged further from sect. *Zea* than the perennials.

#### WHENCE CAME MAIZE?

The origin of maize has puzzled botanists, archaeologists, and others for over a hundred years. During this time many authors have supported either the view that maize evolved from a polystichous wild maize (Mangelsdorf, 1974; Randolph, 1976; Wilkes, 1979; Bird, 1980) or that teosinte is the ancestor of maize (Beadle, 1939, 1972, 1980; Langham, 1940; Longley, 1941a; Darlington, 1956; Miranda Colin, 1966; Iltis, 1971, 1972, 1983; Galinat, 1971, 1975; DeWet & Harlan, 1972; Harlan et al., 1973; Kato, 1976; Senadhira, 1976; Doebley & Iltis, 1980). Although in recent years the tide of opinion has moved in favor of the latter theory, the opponents of the teosinte theory have not regarded this trend with equanimity and the subject remains controversial. In the following discussion I will review the implications of the present study to this debate.

As mentioned above, any explanation of the origin of maize must of necessity provide an understanding of diversity among the teosintes. So, if the teosintes are nothing more than fortuitous hybrids of some ancient polystichous wild maize and *Tripsacum*, it would be quite reasonable to conclude that maize evolved from maize and not teosinte. Yet, the existence of such a wild maize

has never been documented, and more importantly, the teosintes are quite clearly not hybrids of maize and *Tripsacum*. Similarly, if we hypothesize as Wilkes (1979, p. 12) has that prior to man's meddling there were only two forms within the genus *Zea*, (1) *Z. diploperennis*, the primitive *Tripsacum*-like perennial, and (2) *Z. mays*, the polystichous wild maize, and that these two forms hybridized to produce the annual teosintes, we will find ourselves equally besieged with difficulties. First, it seems unlikely that polystichy, a trait of obvious utility to man, arose in the wild among this group of grasses, the Andropogoneae, in which distichy is the universal rule, while the distichous wild relatives of maize, the annual teosintes, arose under domestication when maize crossed with *Zea diploperennis*. In this sense Wilkes's theory turns the most probable explanation inside-out by having the domesticated species emerge in the wild and the highly successful wild taxa emerge under domestication.

A much more parsimonious interpretation of the facts is to view the distichous taxa, the teosintes, as the products of natural selection within the purely distichous Andropogoneae, and the anomalous polystichy of maize that is found only in the cultigen as the utilitarian artifact of domestication (Doebley & Iltis, 1980). The present study supports this view by revealing teosinte (*Zea*) to be a genus with a relatively complex internal structure, as foreshadowed by Wilkes (1967), and one in which each population is genetically and morphologically sculptured to meet the demands of its particular environment.

In addition to implicating teosinte as the direct ancestor of maize, the biosystematic data aid in pinpointing the exact locality in which the cultivation of maize began. If one considers the morphological evidence, the teosintes of sect. *Luxuriantes* must be immediately dismissed as potential progenitors of maize, because their characteristic many-nerved, winged outer glumes and flattened male spikelets are unknown in this cultigen. The genetic evidence discussed in the previous section also enables us to rule out *Z. mays* ssp. *parviglumis* var. *huehuetenangensis* as a possible ancestor of maize. Of the remaining taxa, *Z. mays* ssp. *mexicana* and *ssp. parviglumis* var. *parviglumis*, the former shows the closest morphological relationship to maize (see Results). Certain populations of race Central Plateau in particular display the smallest Mahalanobis's distances from race Nal-Tel of *Z. mays* ssp. *mays*.



Although this suggests that maize could be domesticated *Z. mays* ssp. *mexicana* race Central Plateau, the nature of the resemblance cautions us to look more closely. *Zea mays* ssp. *mexicana* displays greater affinity to maize than does *Z. mays* ssp. *parviglumis* primarily because of its larger spikelets and fewer tassel branches. As these two traits have themselves undergone considerable transformation during the domestication process, they can provide only flaccid evidence on which to pinpoint either *Z. mays* ssp. *mexicana* or ssp. *parviglumis* as the ancestor of maize.

Other available data augment the morphological evidence. First, the isoenzymatic work of Senadhira (1976, Fig. 12) showed that some populations of Balsas teosinte (*Zea mays* ssp. *parviglumis*) cluster closest to the maize races Chapalote and Arrocillo Amarillo. Another isoenzymatic study involving a broader sample of teosintes also suggested maize to be closest to Balsas teosinte (Doebley et al., 1984). Kato's (1976) cytological studies revealed that both B chromosomes and abnormal chromosome 10 (type I), which are relatively common in Mexican maize races, co-occur only in teosinte from the Balsas region and are unknown in the Chalco area. This again points to the Balsas river drainage as the cradle of maize domestication.

Thus, most genetic data are consistent with the theory that maize arose from Balsas teosinte, while morphology would suggest that *Z. mays* ssp. *mexicana* is closest to maize. Prudence would advise that further information be gathered before rendering a final verdict.

While it has long been recognized that the biosystematic evidence points to teosinte as the ancestor of maize, the archaeological evidence available apparently does not. The earliest archaeological maize specimens recovered from Tehuacan possess long soft glumes, a narrow flexible rachis, and shallow non-indurate cupules (Mangelsdorf, 1974), traits which would be difficult to derive from the female teosinte spike. It is for this reason, among others, that Mangelsdorf and his supporters have remained adamant in their belief that maize evolved not from teosinte, but from a "wild maize." Recently, Iltis (1981, 1983) has proposed a new theory, his Catastrophic Sexual Transmutation Theory, which attempts to explain both the biosystematic and archaeological evidence. Quite simply, he suggests that the teosinte female spike is *not* the ancestor of the maize ear, as has long been thought, but rather that the *central spike of the*

*teosinte tassel*, which normally terminates a lateral branch, gave rise to the familiar maize ear. This new theory draws in part from older theories on the origin of the maize ear (Kellerman, 1895; Montgomery, 1906; Iltis, 1911; Weatherwax, 1918).

This theory has an initial appeal to the morphologist because the maize ear is terminal on a lateral branch, a position which in teosinte is usually occupied by a tassel. Thus, the early domestication of maize would have involved a sex change of the central spike of the terminal tassel on the lateral branches from male to female. Iltis believes this change and the subsequent (or concurrent) condensation of the central spike into the maize ear happened rapidly; thus we have the *Catastrophic Sexual Transmutation Theory*.

The aspect of this theory that most stirred my imagination was its implications for the archaeological specimens from Tehuacan. As described above, they do not fall neatly into a sequence between the teosinte female spike and the maize ear. However, under Iltis's theory, they are exactly the intermediates one would predict. The central spike of the teosinte tassel has a flexible rachis, shallow non-indurate cupules, and spikelets with long soft glumes [much like Mangelsdorf's (1974) ancestral pod-corn!], all characters of the Tehuacan specimens. Further, the central tassel spike of teosinte has two functional spikelets per node (cupule) as does the maize ear but unlike the teosinte ear, so that by applying Iltis's theory the reactivation of a suppressed spikelet is not necessary (cf. Beadle, 1972).

While the *Catastrophic Sexual Transmutation Theory* has some attractive features, it needs experimental verification. The developmental morphology of the male and female inflorescences of *Zea* should be studied with this theory in mind. Such work might not only resolve the origin of the maize ear, but may also provide a yardstick for the assessment of primitive versus advanced traits of the ear. Such a yardstick has been sadly lacking in all studies of racial variation in maize to date.

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APPENDIX A. Means (and standard deviations) for all characters and all populations. For key to population and character numbers see Materials and Methods. All measurements are in millimeters except characters 15, 16 and 17 which are in microns.

| Character | Population      |                 |                 |                 |                 |                 |                 |                 |
|-----------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|           | 1               | 2               | 3               | 4               | 5               | 6               | 7               | 8               |
| 1         | 6.5<br>(2.7)    | 3.8<br>(1.2)    | 4.5<br>(1.1)    | 11.8<br>(6.1)   | 13.6<br>(7.2)   | 14.5<br>(5.2)   | 10.6<br>(6.7)   | 15.9<br>(8.1)   |
| 2         | 114.6<br>(15.5) | 98.8<br>(8.1)   | 84.7<br>(9.4)   | 113.3<br>(25.0) | 138.5<br>(29.5) | 137.5<br>(19.2) | 120.0<br>(42.0) | 112.3<br>(29.0) |
| 3         | 23.8<br>(11.7)  | 12.2<br>(5.6)   | 13.6<br>(5.7)   | 45.6<br>(25.1)  | 43.6<br>(13.4)  | 46.8<br>(16.3)  | 47.5<br>(25.0)  | 71.8<br>(26.6)  |
| 4         | 3.2<br>(.55)    | 3.1<br>(.43)    | 3.8<br>(.51)    | 4.7<br>(.67)    | 4.0<br>(.80)    | 4.5<br>(.49)    | 5.5<br>(1.22)   | 4.8<br>(1.83)   |
| 5         | 3.1<br>(.44)    | 2.9<br>(.32)    | 3.9<br>(.61)    | 4.6<br>(.83)    | 4.3<br>(.77)    | 4.5<br>(.60)    | 5.8<br>(.92)    | 5.9<br>(1.22)   |
| 6         | 2.7<br>(.18)    | 2.5<br>(.17)    | 2.4<br>(.23)    | 2.6<br>(.17)    | 2.5<br>(.09)    | 2.4<br>(.27)    | 2.5<br>(.31)    | 2.4<br>(.27)    |
| 7         | 2.2<br>(.57)    | 2.4<br>(.56)    | 2.7<br>(.60)    | 2.9<br>(.65)    | 2.6<br>(.45)    | 2.7<br>(.51)    | 4.1<br>(1.27)   | 4.1<br>(.63)    |
| 8         | 5.2<br>(.28)    | 4.9<br>(.21)    | 4.8<br>(.28)    | 5.2<br>(.42)    | 5.2<br>(.60)    | 4.8<br>(.29)    | 5.0<br>(.65)    | 4.8<br>(.49)    |
| 9         | 9.3<br>(.90)    | 9.9<br>(.48)    | 9.1<br>(.68)    | 10.2<br>(1.00)  | 9.5<br>(1.14)   | 9.7<br>(.69)    | 8.7<br>(.83)    | 8.6<br>(.75)    |
| 10        | 3.6<br>(.31)    | 3.4<br>(.16)    | 3.3<br>(.29)    | 3.7<br>(.23)    | 3.4<br>(.22)    | 3.4<br>(.22)    | 3.9<br>(.30)    | 3.2<br>(.27)    |
| 11        | .312<br>(.038)  | .390<br>(.056)  | .299<br>(.046)  | .188<br>(.039)  | .200<br>(.052)  | .196<br>(.028)  | .024<br>(.028)  | .024<br>(.034)  |
| 12        | 2.3<br>(.34)    | 1.6<br>(.26)    | 2.0<br>(.31)    | 2.3<br>(.22)    | 2.0<br>(.28)    | 2.0<br>(.30)    | 1.9<br>(.22)    | 1.9<br>(.32)    |
| 13        | 7.2<br>(1.01)   | 5.8<br>(1.15)   | 5.6<br>(1.42)   | 12.7<br>(1.56)  | 11.9<br>(2.30)  | 13.5<br>(1.43)  | 2.7<br>(.84)    | 3.2<br>(.92)    |
| 14        | 16.3<br>(1.33)  | 15.0<br>(1.07)  | 13.5<br>(1.42)  | 19.9<br>(1.59)  | 21.9<br>(1.89)  | 21.8<br>(1.94)  | 9.5<br>(1.58)   | 9.8<br>(1.13)   |
| 15        | 128.<br>(14.6)  | 128.<br>(16.6)  | 109.<br>(12.2)  | 114.<br>(15.3)  | 101.<br>(9.2)   | 91.<br>(16.2)   | 109.<br>(13.3)  | 108.<br>(15.2)  |
| 16        | 55.<br>(11.6)   | 46.<br>(8.4)    | 66.<br>(12.9)   | 61.<br>(8.2)    | 71.<br>(6.9)    | 62.<br>(12.7)   | 85.<br>(18.0)   | 92.<br>(27.7)   |
| 17        | 57.<br>(15.9)   | 50.<br>(12.3)   | 72.<br>(11.1)   | 63.<br>(7.9)    | 69.<br>(4.9)    | 63.<br>(12.3)   | 100.<br>(17.6)  | 96.<br>(14.0)   |
| Character | Population      |                 |                 |                 |                 |                 |                 |                 |
|           | 9               | 10              | 11              | 12              | 13              | 14              | 15              | 16              |
| 1         | 28.4<br>(12.7)  | 24.0<br>(6.7)   | 35.0<br>(21.5)  | 10.2<br>(5.5)   | 3.3<br>(1.5)    | 7.4<br>(3.7)    | 22.0<br>—       | 10.7<br>(7.7)   |
| 2         | 141.1<br>(27.8) | 172.5<br>(28.2) | 118.4<br>(29.2) | 100.1<br>(23.1) | 105.7<br>(20.0) | 109.5<br>(26.5) | 97.0<br>—       | 119.1<br>(48.6) |
| 3         | 106.4<br>(42.8) | 120.0<br>(21.6) | 105.5<br>(36.4) | 45.5<br>(26.7)  | 9.3<br>(8.0)    | 33.5<br>(23.0)  | 49.0<br>—       | 48.9<br>(37.0)  |
| 4         | 4.8<br>(.99)    | 5.6<br>(1.26)   | 5.3<br>(1.18)   | 5.2<br>(1.22)   | 4.3<br>(.44)    | 4.8<br>(.76)    | 4.9<br>—        | 4.4<br>(.63)    |
| 5         | 5.4<br>(.87)    | 6.8<br>(.97)    | 6.0<br>(.74)    | 6.5<br>(.81)    | 4.3<br>(.12)    | 4.4<br>(1.05)   | 4.6<br>—        | 4.8<br>(.71)    |



APPENDIX A. (Continued).

| Character | Population     |                |                |                |                |                |           |                |
|-----------|----------------|----------------|----------------|----------------|----------------|----------------|-----------|----------------|
|           | 9              | 10             | 11             | 12             | 13             | 14             | 15        | 16             |
| 6         | 2.4<br>(.34)   | 2.5<br>(.21)   | 1.8<br>(.21)   | 1.8<br>(.12)   | 2.5<br>(.07)   | 2.6<br>(.25)   | 2.4<br>—  | 2.3<br>(.22)   |
| 7         | 4.5<br>(.99)   | 4.2<br>(1.08)  | 4.4<br>(.87)   | 4.4<br>(.77)   | 3.0<br>(.88)   | 2.9<br>(.74)   | 2.8<br>—  | 2.9<br>(.86)   |
| 8         | 5.3<br>(.72)   | 5.5<br>(.60)   | 3.7<br>(.44)   | 3.9<br>(.29)   | 5.1<br>(.55)   | 4.7<br>(.45)   | 4.8<br>—  | 4.7<br>(.98)   |
| 9         | 9.1<br>(.75)   | 9.6<br>(1.29)  | 6.0<br>(.55)   | 5.8<br>(.53)   | 9.5<br>(.29)   | 9.5<br>(.62)   | 9.8<br>—  | 8.1<br>(1.00)  |
| 10        | 3.7<br>(.34)   | 3.3<br>(.33)   | 2.9<br>(.34)   | 2.6<br>(.34)   | 3.4<br>(.32)   | 3.6<br>(.27)   | 3.4<br>—  | 3.4<br>(.27)   |
| 11        | .024<br>(.028) | .040<br>(.033) | .020<br>(.020) | .026<br>(.027) | .413<br>(.101) | .156<br>(.033) | .12<br>—  | .049<br>(.017) |
| 12        | 1.7<br>(.21)   | 1.8<br>(.26)   | 1.5<br>(.21)   | 1.3<br>(.12)   | 2.1<br>(.25)   | 2.0<br>(.28)   | 1.7<br>—  | 1.7<br>(.27)   |
| 13        | 2.9<br>(1.02)  | 4.8<br>(1.32)  | 2.1<br>(1.00)  | 2.2<br>(1.01)  | 6.7<br>(2.08)  | 11.3<br>(2.83) | 14.0<br>— | 2.9<br>(1.27)  |
| 14        | 9.0<br>(1.64)  | 13.9<br>(2.08) | 8.3<br>(1.89)  | 7.8<br>(1.77)  | 14.7<br>(1.53) | 19.1<br>(2.88) | 22.0<br>— | 10.6<br>(1.13) |
| 15        | 112.<br>(14.9) | 83.<br>(9.2)   | 87.<br>(16.6)  | 90.<br>(8.7)   | 121.<br>(9.3)  | 127.<br>(15.0) | 110.<br>— | 88.<br>(12.4)  |
| 16        | 91.<br>(20.6)  | 73.<br>(9.6)   | 81.1<br>(18.2) | 80.<br>(10.6)  | 68.<br>(10.7)  | 61.<br>(7.6)   | 40.<br>—  | 72.<br>(10.2)  |
| 17        | 112.<br>(17.1) | 79.<br>(4.9)   | 78.<br>(13.9)  | 91.<br>(11.1)  | 59.<br>(19.3)  | 66.<br>(14.0)  | 40.<br>—  | 84.<br>(15.4)  |

| Character | Population     |                |                 |                |                 |                |                 |                 |
|-----------|----------------|----------------|-----------------|----------------|-----------------|----------------|-----------------|-----------------|
|           | 17             | 18             | 19              | 20             | 21              | 22             | 23              | 24              |
| 1         | 5.7<br>(1.5)   | 16.6<br>(7.5)  | 16.6<br>(5.3)   | 12.0<br>(4.3)  | 16.0<br>(3.6)   | 15.5<br>(6.4)  | 13.5<br>(9.0)   | 8.3<br>(2.5)    |
| 2         | 92.0<br>(22.5) | 79.8<br>(22.0) | 105.6<br>(20.2) | 88.0<br>(15.7) | 106.4<br>(13.6) | 94.3<br>(13.8) | 139.3<br>(75.8) | 173.9<br>(41.5) |
| 3         | 36.0<br>(7.0)  | 69.4<br>(31.3) | 62.6<br>(14.3)  | 56.0<br>(15.2) | 59.5<br>(10.8)  | 66.5<br>(23.4) | 61.7<br>(27.4)  | 57.5<br>(22.6)  |
| 4         | 5.7<br>(.93)   | 4.9<br>(.82)   | 5.6<br>(.82)    | 5.3<br>(.45)   | 4.9<br>(.82)    | 5.6<br>(.39)   | 5.7<br>(1.48)   | 7.9<br>(1.51)   |
| 5         | 5.3<br>(.42)   | 4.8<br>(1.00)  | 6.2<br>(.85)    | 5.7<br>(.99)   | 5.5<br>(.30)    | 6.4<br>(.71)   | 6.7<br>(1.08)   | 7.8<br>(1.56)   |
| 6         | 2.4<br>(.22)   | 1.9<br>(.29)   | 2.9<br>(.30)    | 3.1<br>(.16)   | 2.9<br>(.18)    | 2.8<br>(.24)   | 3.0<br>(.32)    | 3.1<br>(.39)    |
| 7         | 3.2<br>(1.09)  | 4.1<br>(.96)   | 3.9<br>(.76)    | 4.3<br>(.82)   | 2.9<br>(.85)    | 4.4<br>(.78)   | 4.1<br>(2.34)   | 4.9<br>(.84)    |
| 8         | 4.7<br>(.59)   | 3.9<br>(.57)   | 5.1<br>(.45)    | 5.1<br>(.49)   | 5.2<br>(.17)    | 5.3<br>(.29)   | 5.9<br>(.89)    | 5.8<br>(.71)    |
| 9         | 7.5<br>(.57)   | 6.5<br>(.83)   | 10.0<br>(.50)   | 10.9<br>(.54)  | 10.2<br>(.58)   | 10.7<br>(1.08) | 10.6<br>(1.43)  | 11.1<br>(1.69)  |
| 10        | 3.0<br>(.26)   | 2.8<br>(.33)   | 4.3<br>(.38)    | 4.1<br>(.51)   | 4.1<br>(.29)    | 3.4<br>(.28)   | 3.9<br>(.72)    | 4.1<br>(.48)    |
| 11        | .013<br>(.023) | .020<br>(.020) | .175<br>(.020)  | .185<br>(.056) | .160<br>(.043)  | .160<br>(.042) | .024<br>(.027)  | .064<br>(.042)  |



APPENDIX A. (Continued).

| Character | Population    |                |                |                |                |                |                |                |
|-----------|---------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
|           | 17            | 18             | 19             | 20             | 21             | 22             | 23             | 24             |
| 12        | 1.5<br>(.23)  | 1.4<br>(.25)   | 2.7<br>(.32)   | 2.4<br>(.53)   | 2.8<br>(.34)   | 2.2<br>(.20)   | 2.2<br>(.52)   | 2.4<br>(.40)   |
| 13        | 2.3<br>(1.15) | 3.3<br>(.98)   | 15.6<br>(2.07) | 14.3<br>(3.56) | 15.8<br>(2.31) | 14.2<br>(1.40) | 3.7<br>(1.25)  | 5.9<br>(.80)   |
| 14        | 8.7<br>(1.15) | 8.3<br>(1.42)  | 25.1<br>(2.53) | 24.9<br>(3.56) | 26.5<br>(1.69) | 24.4<br>(2.07) | 11.0<br>(3.09) | 14.3<br>(1.45) |
| 15        | 102.<br>(9.3) | 101.<br>(19.0) | 114.<br>(11.9) | 102.<br>(9.9)  | 113.<br>(9.2)  | 117.<br>(13.3) | 98.<br>(9.0)   | 103.<br>(15.5) |
| 16        | 96.<br>(19.4) | 74.<br>(12.5)  | 72.<br>(9.6)   | 79.<br>(11.0)  | 80.<br>(8.5)   | 74.<br>(8.8)   | 85.<br>(13.5)  | 93.<br>(15.7)  |
| 17        | 87.<br>(10.7) | 98.<br>(22.9)  | 72.<br>(13.8)  | 78.<br>(8.5)   | 8.3<br>(11.6)  | 7.7<br>(7.7)   | 8.6<br>(15.7)  | 9.8<br>(14.8)  |

| Character | Population     |                |                |                 |                |                 |                |                 |
|-----------|----------------|----------------|----------------|-----------------|----------------|-----------------|----------------|-----------------|
|           | 25             | 26             | 27             | 28              | 29             | 30              | 31             | 32              |
| 1         | 9.8<br>(4.0)   | 31.3<br>(12.2) | 28.9<br>(9.9)  | 16.3<br>(7.5)   | 23.8<br>(7.2)  | 37.4<br>(12.1)  | 5.3<br>(3.9)   | 11.4<br>(5.5)   |
| 2         | 83.8<br>(19.0) | 81.2<br>(18.5) | 83.6<br>(19.1) | 118.9<br>(44.6) | 80.2<br>(18.8) | 85.9<br>(40.6)  | 97.4<br>(17.4) | 116.6<br>(37.5) |
| 3         | 39.3<br>(11.7) | 92.9<br>(22.8) | 90.4<br>(22.7) | 64.4<br>(25.2)  | 94.6<br>(15.4) | 132.3<br>(16.4) | 24.0<br>(24.6) | 36.6<br>(15.1)  |
| 4         | 4.6<br>(.80)   | 5.4<br>(.49)   | 5.9<br>(.77)   | 6.6<br>(1.29)   | 5.7<br>(.43)   | 4.9<br>(.87)    | 3.5<br>(.68)   | 3.8<br>(.41)    |
| 5         | 5.2<br>(.63)   | 6.2<br>(.92)   | 6.8<br>(1.19)  | 7.0<br>(1.36)   | 6.0<br>(.67)   | 5.7<br>(1.05)   | 3.7<br>(.43)   | 4.0<br>(.55)    |
| 6         | 2.2<br>(.20)   | 2.1<br>(.25)   | 2.3<br>(.22)   | 2.0<br>(.13)    | 2.3<br>(.22)   | 2.2<br>(.33)    | 2.1<br>(.34)   | 2.2<br>(.12)    |
| 7         | 2.3<br>(.61)   | 4.4<br>(.82)   | 4.6<br>(.92)   | 5.3<br>(1.17)   | 5.4<br>(1.14)  | 4.0<br>(1.11)   | 2.2<br>(.60)   | 2.4<br>(.31)    |
| 8         | 4.1<br>(.65)   | 4.0<br>(.37)   | 4.0<br>(.43)   | 4.3<br>(.49)    | 4.7<br>(.42)   | 4.0<br>(.66)    | 4.0<br>(.60)   | 5.0<br>(.40)    |
| 9         | 7.4<br>(.59)   | 6.9<br>(.60)   | 7.2<br>(.34)   | 5.9<br>(.92)    | 7.7<br>(.74)   | 6.8<br>(.94)    | 8.4<br>(.48)   | 8.2<br>(.68)    |
| 10        | 2.7<br>(.42)   | 2.7<br>(.33)   | 2.9<br>(.28)   | 3.0<br>(.53)    | 3.2<br>(.29)   | 2.6<br>(.22)    | 2.8<br>(.30)   | 2.7<br>(.26)    |
| 11        | .025<br>(.030) | .016<br>(.020) | .024<br>(.024) | .020<br>(.021)  | .022<br>(.021) | .030<br>(.028)  | .340<br>(.021) | .154<br>(.015)  |
| 12        | 1.4<br>(.30)   | 1.3<br>(.24)   | 1.5<br>(.18)   | 1.5<br>(.32)    | 1.5<br>(.15)   | 1.5<br>(.19)    | 1.4<br>(.27)   | 1.7<br>(.20)    |
| 13        | 2.6<br>(.74)   | 3.1<br>(1.09)  | 3.4<br>(1.28)  | 3.6<br>(1.41)   | 4.0<br>(1.26)  | 3.0<br>(.93)    | 8.6<br>(1.67)  | 12.3<br>(1.98)  |
| 14        | 8.1<br>(.83)   | 10.5<br>(1.88) | 11.3<br>(2.34) | 11.1<br>(1.64)  | 12.7<br>(1.70) | 9.0<br>(2.20)   | 15.4<br>(1.23) | 18.9<br>(2.67)  |
| 15        | 82.<br>(6.9)   | 86.<br>(12.4)  | 85.<br>(9.0)   | 93.<br>(11.1)   | 87.<br>(10.1)  | 95.<br>(12.9)   | 133.<br>(25.0) | 99.<br>(27.8)   |
| 16        | 73.<br>(10.5)  | 79.<br>(11.0)  | 74.<br>(7.1)   | 84.<br>(13.1)   | 80.<br>(9.5)   | 77.<br>(12.9)   | 58.<br>(18.0)  | 41.<br>(10.5)   |
| 17        | 8.4<br>(15.3)  | 86.<br>(10.2)  | 82.<br>(11.3)  | 93.<br>(7.0)    | 85.<br>(11.7)  | 89.<br>(18.6)   | 56.<br>(15.4)  | 44.<br>(8.8)    |



APPENDIX A. (Continued).

| Character | Population      |                |                |                |                 |                 |                 |                 |
|-----------|-----------------|----------------|----------------|----------------|-----------------|-----------------|-----------------|-----------------|
|           | 33              | 34             | 35             | 36             | 37              | 38              | 39              | 40              |
| 1         | 10.3<br>(4.3)   | 11.0<br>(9.8)  | 35.2<br>(11.1) | 15.5<br>(3.5)  | 2.8<br>(.86)    | 42.2<br>(11.9)  | 7.4<br>(4.0)    | 4.9<br>(3.0)    |
| 2         | 121.7<br>(26.8) | 97.4<br>(8.3)  | 67.7<br>(17.7) | 85.5<br>(10.6) | 261.7<br>(23.1) | 221.6<br>(37.9) | 311.1<br>(50.8) | 258.4<br>(29.4) |
| 3         | 48.3<br>(24.9)  | 37.6<br>(23.9) | 98.8<br>(13.9) | 91.5<br>(23.3) | 15.2<br>(13.6)  | 166.5<br>(19.5) | 52.6<br>(26.0)  | 26.4<br>(19.7)  |
| 4         | 5.6<br>(.81)    | 4.2<br>(.71)   | 4.7<br>(.47)   | 5.0<br>(.61)   | 1.6<br>(.35)    | 1.9<br>(.51)    | 2.6<br>(.82)    | 2.1<br>(.25)    |
| 5         | 5.1<br>(.56)    | 4.6<br>(.86)   | 6.3<br>(.61)   | 5.2<br>(.28)   | 4.8<br>(.82)    | 5.2<br>(.68)    | 5.0<br>(.49)    | 5.3<br>(.77)    |
| 6         | 2.6<br>(.42)    | 2.5<br>(.33)   | 2.1<br>(.15)   | 1.9<br>(0.0)   | 3.5<br>(.27)    | 2.6<br>(.23)    | 3.2<br>(.36)    | 3.0<br>(.17)    |
| 7         | 3.5<br>(1.09)   | 2.1<br>(1.21)  | 3.3<br>(.31)   | 6.0<br>(.18)   | 1.8<br>(.87)    | 1.9<br>(1.04)   | 2.8<br>(1.3)    | 2.9<br>(1.7)    |
| 8         | 5.3<br>(.62)    | 4.9<br>(.77)   | 4.1<br>(.51)   | 3.4<br>(.18)   | 6.8<br>(.48)    | 5.5<br>(.51)    | 7.1<br>(.49)    | 7.6<br>(.48)    |
| 9         | 10.9<br>(.97)   | 8.4<br>(1.16)  | 7.5<br>(.39)   | 6.8<br>(.35)   | 11.9<br>(.72)   | 9.0<br>(.71)    | 12.9<br>(1.30)  | 12.8<br>(1.19)  |
| 10        | 3.0<br>(.53)    | 3.3<br>(.37)   | 2.8<br>(.19)   | 2.7<br>(.09)   | 3.9<br>(.40)    | 3.8<br>(.31)    | 4.5<br>(.59)    | 4.0<br>(.61)    |
| 11        | .173<br>(.033)  | .008<br>(.017) | .033<br>(.030) | .020<br>(.028) | .028<br>(.024)  | 1.07<br>(.020)  | .023<br>(.020)  | .023<br>(.021)  |
| 12        | 1.8<br>(.27)    | 1.6<br>(.32)   | 1.5<br>(.15)   | 1.4<br>(.20)   | 2.0<br>(.32)    | 1.6<br>(.31)    | 1.8<br>(.32)    | 2.1<br>(.35)    |
| 13        | 13.0<br>(2.83)  | 2.8<br>(1.30)  | 3.8<br>(1.60)  | 3.5<br>(.70)   | 3.3<br>(1.13)   | 3.2<br>(1.11)   | 4.1<br>(1.55)   | 3.7<br>(1.60)   |
| 14        | 22.5<br>(3.56)  | 9.0<br>(2.12)  | 11.3<br>(1.75) | 8.5<br>(2.12)  | 10.9<br>(1.88)  | 11.1<br>(2.06)  | 13.5<br>(2.25)  | 10.6<br>(1.62)  |
| 15        | 102.<br>(11.7)  | 106.<br>(24.3) | 88.<br>(7.8)   | 74.<br>(13.1)  | 92.<br>(8.6)    | 97.<br>(11.3)   | 103.<br>(16.0)  | 81.<br>(12.8)   |
| 16        | 42.<br>(15.2)   | 93.<br>(16.1)  | 84.<br>(19.5)  | 70.<br>(6.6)   | 84.<br>(10.2)   | 81.<br>(12.0)   | 91.<br>(9.6)    | 73.<br>(11.3)   |
| 17        | 50.<br>(12.7)   | 106.<br>(22.4) | 85.<br>(18.1)  | 65.<br>(0.0)   | 90.<br>(12.7)   | 95.<br>(13.6)   | 94.<br>(14.0)   | 82.<br>(13.6)   |





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