

TAXONOMY OF ZEA (GRAMINEAE). I. A SUBGENERIC CLASSIFICATION WITH KEY TO TAXA¹

JOHN F. DOEBLEY AND HUGH H. ILTIS

Department of Botany, University of Wisconsin, Madison, Wisconsin 53706

ABSTRACT

The genus *Zea* is here divided into the Sect. LUXURIANTES Doebley & Iltis sect. n., including the perennials *Z. diploperennis* ($2n = 20$) and *Z. perennis* ($2n = 40$) and the annual *Z. luxurians* ($2n = 20$); and Sect. ZEA, including the wild *Z. mays* ssp. *parviglumis* and *Z. mays* ssp. *mexicana* (both $2n = 20$), and *Z. mays* ssp. *mays* ($2n = 20$), the highly domesticated and tremendously variable derivative of the latter. This division is verified by a multivariate analysis of a large number of morphological characters of the male inflorescence. Cytogenetic and chemotaxonomic evidence supports the morphological conclusions. A consideration of the phylogeny of *Zea* within the conceptual framework offered by this new sectioning of the genus points convincingly to annual teosinte (*Z. mays* ssp. *mexicana*) as the ancestor of cultivated maize.

THE GENUS *Zea* contains, according to its latest taxonomic treatment (Iltis & Doebley, 1980), six distinct taxa classified into four species: 1) *Z. mays* L., *sensu lato*, including *Z. mays* ssp. *mays*, the cultivated maize; *Z. mays* ssp. *mexicana* (Schradler) Iltis, and *Z. mays* ssp. *parviglumis* Iltis and Doebley, the latter two the widespread annual teosintes from Mexico and west central Guatemala; 2) *Z. luxurians* (Durieu and Ascherson) Bird, the annual teosinte from southeastern Guatemala and Honduras; 3) *Z. perennis* (Hitchc.) Reeves and Mangelsdorf, the tetraploid perennial teosinte; and, finally, 4) *Z. diploperennis* Iltis, Doebley and Guzmán, the recently discovered diploid perennial teosinte, the latter two both highly local species from southern Jalisco, Mexico.

These taxa could be arranged subgenerically in several ways, depending on one's criteria. Thus, if one follows the only taxonomic system so far published (Post and Kuntze 1903; cf. Wilkes, 1967), the genus would be divided into Sect. ZEA, containing only the cultigen *Z. mays* *sensu stricto*, and Sect. EUCHLAENA (Schradler) Kuntze, containing all five remaining taxa, the teosintes. The reasons the genus was thus

divided are obvious enough. First, not only are the gigantic, *polystichous*, many-seeded, non-disarticulating female ears of maize *totally unique* in the Andropogoneae (or, for that matter, in the Gramineae), but the slender, *distichous*, few-seeded, disarticulating female spikes of all teosinte species are so similar to each other as to nearly defy taxonomic discrimination. Similarly with the tassel, the male inflorescence. Maize tassels are always easily recognized by their thick and highly condensed central (terminal) spike (i.e., with many spikelets per unit length), the lateral branches in contrast being always slender and uncondensed. Teosinte tassels, on the other hand, have uniformly slender and uncondensed branches, with the central (terminal) spike scarcely if at all differentiated from the lateral branches. As a matter of fact, experienced "teosinte hunters" can soon learn to distinguish teosinte and maize from a car window at quite some distance by scanning the cornfield "skyline" with binoculars and looking for the central branch of the tassel. If uncondensed and slender, it's teosinte; if stiff and thick, it's maize! Thus, simply on the basis of spikelet arrangement in both male and female inflorescences, Kuntze's taxonomic division would seem, on the face of it, to be correct and unassailable.

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The uniqueness of the maize ear notwithstanding, any classification of an economic genus which places the object of human desire into one subgeneric category and all its wild relatives in another is, *a priori*, open to suspicion. In other words, we may state as a general principle that the fundamental systematic classification of economic genera should never be based primarily on those morphological features deliberately selected for by man. To do so leads to a taxonomy where the generally large- and many-seeded cultivars are placed in

one subgeneric division and their close, and presumably ancestral, small- and few-seeded relatives in another. One can hardly think of a better way to misrepresent true phylogenetic relationships.

Now, if cultivated maize *did* evolve from a polystichous species of *Zea*, the hypothetical "wild maize" (Mangelsdorf and Reeves, 1939; Weatherwax, 1955; Mangelsdorf, 1974; Randolph, 1977; Wilkes, 1977b; Wilkes and Mangelsdorf, 1979), then formal segregation of maize into its own section, subgenus, or even genus, would be not only justified but mandatory, for then maize would represent the sole surviving member of an anomalously polystichous, hence morphologically unique and probably ancient, line. But, and this is the crux of the issue, *except for maize, and maize alone*, in the whole of the giant tribe *Andropogoneae* polystichy of any sort is *totally unknown*, and distichy the universal rule! Whence then did this unique polystichy arise? And why is it found only in a cultivar and nowhere else?

We may hypothesize the following sequence of events. When the aboriginal domesticators of maize selected for higher crop yield and easier harvestability, they brought about a dramatic transformation of the slender terminal male spike of the terminal inflorescence of each primary (*lateral*) teosinte branch into a thick maize ear. Indirectly, and concurrently, there was a homologous transformation of the terminal tassel branch of the terminal (male) inflorescence of the main stem into a greatly thickened central spike (Kellerman, 1895; Montgomery, 1906; Anderson, 1944; Iltis, 1971, 1979; Allen and Iltis, 1980). Support for this position has come from the many authors who since the 1870's and 1880's (Wilkes, 1967) considered maize simply domesticated teosinte on morphologic, genetic and geographic grounds (Ascherson, 1879; Harshberger, 1896; Beadle, 1939, 1972; Langham, 1940; Longley, 1941; Darlington, 1956; Miranda Colin, 1966; Iltis, 1971, 1972, 1979; Galinat, 1971, 1975; Harlan, DeWet, and Price, 1973; Smith and Lester, 1979b). Polystichy of maize may then be viewed simply as a highly utilitarian anthropogenic artifact closely related to selection for apical dominance, its giant ear analogous to the giant head of the domesticated monocephalic sunflower, *Helianthus annuus* var. *macrocarpus* (Iltis, 1971). Because the unique morphology of the female maize inflorescence is the direct result of domestication, its structure (including its polystichy) cannot be used to delimit the fundamental taxonomic divisions within *Zea*. A re-examination of intrageneric relationships within *Zea*, employing a different

set of morphological features than those traditionally utilized, seems now doubly justified.

We have chosen to study the male inflorescence of *Zea* for the very good reason that, as an inedible structure, it was of no great primary interest to aboriginal man, hence was not directly subject to deliberate selection.

Morphological data obtained so far have now given us an ample base for a reclassification on new and quite different lines. If, for a moment, we ignore the unique features of the female maize ear and the thick central spike of the male tassel, its morphological homologue (Anderson, 1944), and consider polystichy, large seed size, great seed number, and the solid crowded inflorescence rachis, all simply as anomalies due to human selection for increasing yield and improving harvestability; and if we concentrate instead on the basic morphology of structures *neutral* to the preferences of pre-Columbian man (e.g., male glume nervation, tassel branching), a taxonomy of the genus drastically different from that proposed by Kuntze (Post and Kuntze, 1903) becomes immediately apparent.

In re-assessing the relationships within *Zea*, we have aimed at constructing a phylogenetically valid classification, one that, because it shows natural relationship, will not only be useful to agronomists, evolutionists, and anthropologists, but will help clear away the misunderstanding which for too long now has shrouded the origins of this most important cultivar in a veritable "maize mystique."

MATERIALS AND METHODS—Previous to the early 1960's and Wilkes' (1967) pioneering field work, very little herbarium material or seeds of teosinte were available for study. It would seem that taxonomists in general have always had a great aversion to the collection and preservation of maize specimens and an equal aversion to collecting maize's weedy "double," teosinte. Except for special collections at Harvard, Indiana University and the Missouri Botanical Garden, there are next to no specimens of these in U.S. herbaria, certainly hardly any "ears" whatever. Such "a policy of avoidance," to quote a sarcastic Edgar Anderson (1952), propagated for decades what we might call the "Great Ethnobotanical Paradox," namely that often the plants most useful to man are the ones least understood taxonomically. Certainly, until recently, far too few teosinte specimens were preserved to carry out meaningful biometrical analyses. Since that time, however, much material has accumulated, not only herbarium specimens collected by Wilkes as vouchers for his work, but also pop-

TABLE 1. *List of populations*

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 Manantlán, 7 km ENE of El Durazno, 19°31'45"N, 104°13'W, alt. ca. 2,300 m. Sept. 22, 1978. *Itlis, Guzmán, Doebley and Lasseigne 450.*
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 sacatonal grassland, 9 km WSW of Ciudad Guzmán, 1.5 km ESE of LOS DEPOSITOS, 19°40'N, 103°35'W, alt. ca. 1,650 m. Sept. 24, 1978. *Itlis, Guzmán, Puga, Doebley and Lasseigne 550.*
3. *Zea perennis* (PERENNIAL Teosinte). Mexico, Jalisco: Among sunflowers and *Bidens* and grasses (Collins, 1921), 1 mile S of the railway station of CIUDAD GUZMÁN, 19°41'30"N, 103°28'40"W, alt. 1,520 m. Oct. 28, 1921. *G. Collins and J. Kempton s. n.* This population consists of several cultivated specimens derived from live rhizomes collected at this locality in 1921, plus two original field specimens.
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.*
5. *Zea luxurians* (GUATEMALA Teosinte). Guatemala, Jutiapa: Near JUTIAPA, field and cultivated herbarium specimens.
6. *Zea luxurians* (GUATEMALA Teosinte). Honduras, Morazon: MORAZON population, field-collected herbarium specimens. (Grown from seed collected in Dept. Choluteca.)
7. *Zea luxurians* (GUATEMALA Teosinte). Mexico, Oaxaca: Near SAN AUGUSTIN, Oct., 1840. *Liebman 548* (US Natl. Herbarium).
8. *Z. mays* ssp. *mexicana* (NOBOGAME Teosinte). Mexico: Chihuahua: vicinity of NOBOGAME, field and cultivated herbarium specimens.
9. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU Teosinte). Mexico, Durango: Vicinity of DURANGO, field-collected herbarium specimens (*E. Palmer 743; G. N. Collins 15*).
10. *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. *Itlis and Doebley 96.*
11. *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. *Itlis and Doebley 8.*
12. *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. *Itlis and Doebley 4.*
13. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENANGO Teosinte). Guatemala: Huehuetenango: HUEHUETENANGO population, vicinity of San Antonio Huista, field and cultivated herbarium specimens.
14. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS Teosinte). Mexico, Guerrero: Weeds in maize field in regions of semi-deciduous savannah of Leguminosae, *Bursera*, *Pseudomdingium* 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. *Itlis and Doebley 361.*
15. *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. *Itlis and Doebley 87.*
16. *Zea mays* ssp. *mays* (NAL-TEL race). Mexico: Campeche: International Center for the Improvement of Maize and Wheat No. tep 62A 906# (Campeche 42c). Grown at Purdue Univ. Agric. Exp. Stn., Florida City, Fla. Feb. through May, 1978.
17. *Zea mays* ssp. *mays* (CHAPALOTE race). Mexico: Sinaloa: International Center for the Improvement of Maize and Wheat No. TL 7B 5# (Sin 2). Grown at Purdue Univ. Agric. Exp. Stn., Florida City, Fla. Feb. through May, 1978.

ulation samples of the authors (Table 1), some including as many as 100 individuals from one site. These workers, as well as George W. Beadle, T. Angel Kato, and collectors from the *Centro Internacional de Mejoramiento de Maíz y Trigo* (CIMMYT) near Mexico City, have in addition gathered large seed samples now available for distribution through "germplasm banks," such as those at CIMMYT and several USDA Plant Introduction Stations (Wilkes, 1972).

In the present study three types of population samples were used: 1) grab samples of 20 to 30 individual plants from local populations (made largely by the authors, and deposited in the University of Wisconsin Herbarium); 2)

samples, each of 20 to 30 individual plants, grown in Florida from seeds collected by Wilkes, Beadle, CIMMYT, and the authors; 3) samples, composed of many individual herbarium specimens, collected by various botanists at different times but in the same general region such as the vicinity of a particular city. These specimens were lent to us by the U.S. National Herbarium, the U.S. National Arboretum, the Missouri Botanical Garden and the Chicago Natural History Museum (Table 1).

By utilizing all three types of population samples (a total of 17 populations), the entire known geographic range of *Zea* was repre-

sented. However, few collections were available of DURANGO teosinte, which appears to be extinct both in nature and cultivation, and NOBOGAME. These two presumably are northern extremes of *Z. mays* ssp. *mexicana* Race CENTRAL PLATEAU.

Building upon methodologies originally developed by Edgar Anderson (Anderson and Cutler, 1942; Anderson, 1944) and his student Alava (1952), we based our study primarily on characters of the male spikelets and tassel. To assess differences and similarities among the 17 populations, ten quantitative morphological traits (variates) were measured as follows:

1. TASSEL BRANCHING TRAITS:

- a) *Tassel branch number*, ranging from 0 to 63.
- b) *Tassel branching axis length*, ranging from short (1 cm) and thus generally with few branches, to long (11 cm) and with many branches.
- c) *Lateral tassel branch internode length*, ranging from short, with spikelets densely overlapping (imbricate), to long, with little overlap.

2. MALE SPIKELET OUTER GLUME TRAITS:

- a) *Wing width*, ranging from narrow and scarcely, if at all developed, to wide and greatly differentiated from the lateral nerve from which it arises (cf. Fig. 1-9).
- b) *Pedicle length*.
- c) *Primary lateral vein width*, ranging from narrow, and scarcely if at all more prominent than the secondary veins, to wide and much more prominent than the other veins (cf. Fig. 10-27).
- d) *Median vein width*.
- e) *Distance between the two primary lateral veins*.
- f) *Number of veins between primary lateral veins*, from 1 to 17.
- g) *Total vein number*, from 5 to 24.

These data then were subjected to canonical analysis, a multivariate technique that computes synthetic variates (canonical variates) by taking various weighted sums of the ten original variates.

The first canonical variate is computed so that it gives the largest possible ratio of the among-population to the within-population variance. Thus, it best separates all populations. Then, additional canonical variates are computed, which (though less effective at separating the populations) are uncorrelated with previous ones (Kowal, Lechowicz, and Adams, 1976).

Use of the first two canonical variates to graph all individuals provides a two-dimen-

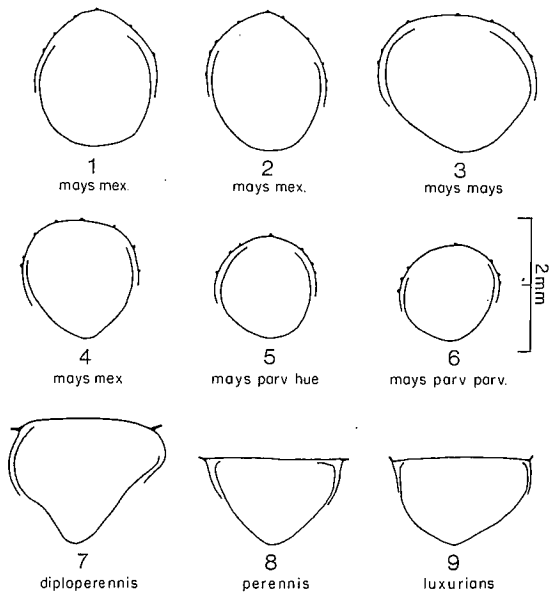


Fig. 1-9. Spikelet cross-sections showing shape and relative size of the glumes. 1. *Z. mays* ssp. *mexicana*, CHALCO Teosinte (Iltis & Doebley 404). 2. *Z. mays* ssp. *mexicana*, CENTRAL PLATEAU Teosinte (Iltis & Doebley 96). 3. *Z. mays* ssp. *mays*, Chapalote race of maize. 4. *Z. mays* ssp. *mexicana*, NOBOGAME Teosinte, cultivated in Madison, Wisconsin (Doebley 175). 5. *Z. mays* ssp. *parviglumis* var. *huehuetenangensis*, Huehuetenango Teosinte (Wilkes 43603). 6. *Z. mays* ssp. *parviglumis* var. *parviglumis*, Balsas Teosinte (Iltis & Doebley 361). 7. *Z. diploperennis* (Iltis, Guzman, Doebley & Lasseigne 450). 8. *Z. perennis* (Iltis, Guzman, Puga, Doebley & Lasseigne 550). 9. *Z. luxurians* (K. Lind 419).

sional picture that shows the relationship of the various populations to one another.

In addition, each individual specimen studied was assessed in regard to the following nine qualitative morphological traits:

1. TASSEL BRANCHING TRAITS:

- a) *Tassel branch stiffness*, whether lax or erect.
- b) *Prominence of central tassel branch (spike)*, whether identical to the lateral branches, or much thicker and stiffer (as in maize).
- c) *Abscission layer*, whether developed strongly, weakly, or absent.
- d) *Rachis shape* in cross section, whether round or flattened.

2. MALE SPIKELET OUTER GLUME TRAITS:

- a) *Texture*, whether thin and flexible or stiff and brittle.
- b) *Curvature*, whether rounded or flattened.
- c) *Hair type on lateral vein margins*, whether stiff and tooth-like (scaberulous) or flexible and hairlike (pilose).

3. FEMALE SPIKELET TRAITS:

- a) *Cupulate fruitcase shape*, whether triangular or trapezoidal.

The results of both the quantitative and the qualitative analyses were used in determining how the species of *Zea* would best be arranged into subgeneric divisions.

THE SUBGENERIC DIVISION OF ZEA—When the measurements made on each of the ten quantitative morphological traits are subjected to canonical analysis the species of *Zea* segregate into two clearly defined natural subgroups as represented by the two clusters in Fig. 28. The cluster in the upper portion of the figure includes the two perennials, *Z. perennis* and *Z. diploperennis* as well as the Guatemalan annual, *Z. luxurians*. This subgroup of three species we shall call LUXURIANTES. The cluster in the lower portion of Fig. 28 includes not only the cultivated *Z. mays* ssp. *mays* but also *Z. mays* ssp. *mexicana* and ssp. *parviglumis*. Since it includes the type species of the genus this subgroup must be called ZEA. In this figure, individuals with wide glume wings, short internodes on the lateral tassel-branches, high total vein number, and narrow midveins on the outer glumes, receive the largest values for canonical variate one.

These subgeneric divisions, which we have chosen to recognize as sections, have radically different circumscriptions than the sections used by previous workers. Between our classification and that of previous workers, two key differences need to be stressed. First of all, despite its astoundingly massive female inflorescence, maize is here not segregated into a section all its own; rather, it is closely and properly aligned with those wild teosinte populations from which, presumably, it evolved into cultivation some 8,000 years ago. Secondly, despite its annual habit, the eastern Guatemalan *Z. luxurians* does not remain

aligned with the other annuals, from which it differs in many important characters of the tassel; instead it is placed with the two perennial species of western Mexico, its morphologically close though geographically distant relatives. This new classification finally allows botanists and anthropologists to place the domestication of *Zea mays* and its anthropogenic antecedents in a morphologically realistic, phylogenetically coherent, and geographically localized conceptual framework.

I. Section LUXURIANTES Doebley et Iltis, sect. nov.

Spicae inflorescentiae masculine spiculibus densibus imbricatis; glumae exteriores nervibus principalibus alatis; plantae perenne vel annuae.

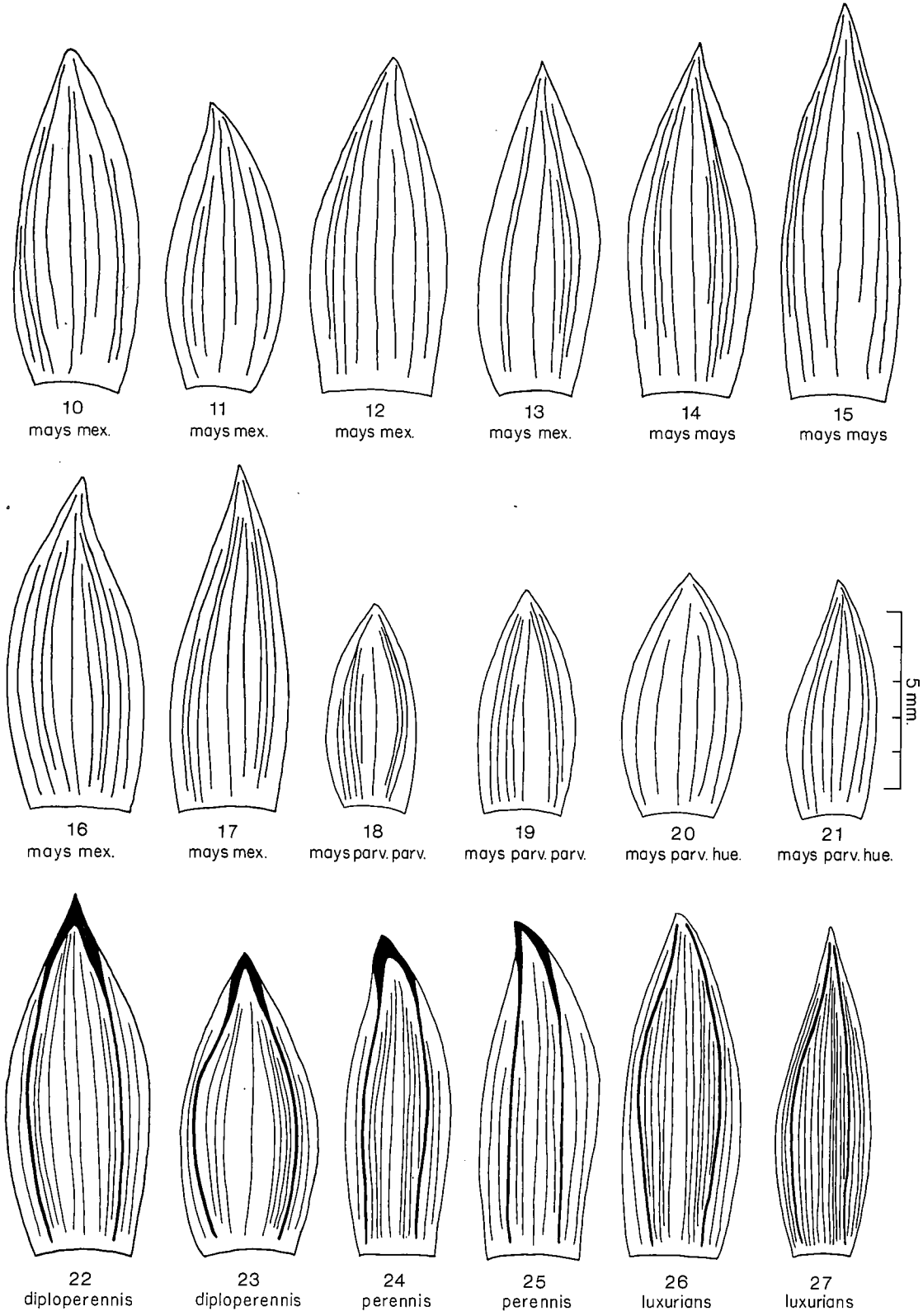
Typus: *Zea luxurians* (Durieu et Ascherson) Bird, Taxon 27: 361–363, 1978.

Male tassel branches few, 1–10(–25) from the short central branching axis, stiff and straight, erect or ascending, sometimes divergent and weakly arched, the central (terminal) spike² slender, scarcely if at all distinct from the lateral branches; branch internodes short, 2.4–6.2 mm long, the spikelets therefore densely imbricate, with the tip of the sessile spikelet of each pair reaching to or overlapping the base of the next-higher pair above it on the same side; abscission layers strongly developed, the

² Despite various views to the contrary (Wilkes, 1967, p. 103; Bird, 1978), a central spike (or terminal branch), i.e., the continuation of the central inflorescence axis, is here present as in all taxa of *Zea*. The prevalent confusion may be traced to (a) the speed and ease with which the tassel branches of sect. LUXURIANTES soon tend to disarticulate, especially the terminal spike, which as the first to flower, hence the first to mature, is therefore often "missing" in older tassels; and (b) the remarkably short inflorescence branching axis in all taxa of sect. LUXURIANTES, the relatively few branches seemingly originating all from the "same" point, hence the terminal spike not particularly differentiated.

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Fig. 10–27. Flattened outer glumes showing relative size and venation. 10. *Z. mays* ssp. *mexicana*, CHALCO Teosinte (Iltis & Doebley 4). 11. *Z. mays* ssp. *mexicana*, CHALCO Teosinte (Iltis & Doebley 8). 12. *Z. mays* ssp. *mexicana*, DURANGO (CENTRAL PLATEAU) Teosinte (E. Palmer 743, MO). 13. *Z. mays* ssp. *mexicana*, CENTRAL PLATEAU Teosinte (Iltis & Doebley 96). 14. *Z. mays* ssp. *mays*, Nal-Tel race of maize. 15. *Z. mays* ssp. *mays*, Chapalote race of maize. 16. *Z. mays* ssp. *mexicana*, NOBOGAME Teosinte (grown in Florida). 17. *Z. mays* ssp. *mexicana*, NOBOGAME Teosinte (grown in Florida). 18. *Z. mays* ssp. *parviglumis* var. *parviglumis*, BALSAS Teosinte (Iltis & Doebley 87). 19. *Z. mays* ssp. *parviglumis* var. *parviglumis*, BALSAS Teosinte (Iltis & Doebley 361). 20. *Z. mays* ssp. *parviglumis* var. *huehuetenangensis*, HUEHUETENANGO Teosinte (Iltis & Lind G-120). 21. *Z. mays* ssp. *parviglumis* var. *huehuetenangensis*, HUEHUETENANGO Teosinte (O'Hara s. n., MO 1168094). 22. *Z. diploperennis* (Iltis, Guzman, Doebley & Lasseigne 450). 23. *Z. diploperennis* (Guzman 777). 24. *Z. perennis* (Peebles & Harrison 3527, US). 25. *Z. perennis* (Iltis, Guzman, Puga, Doebley & Lasseigne 550). 26. *Z. luxurians*, GUATEMALA Teosinte (Wilkes 43122, F). 27. *Z. luxurians*, GUATEMALA Teosinte (Merrill 11222, US).



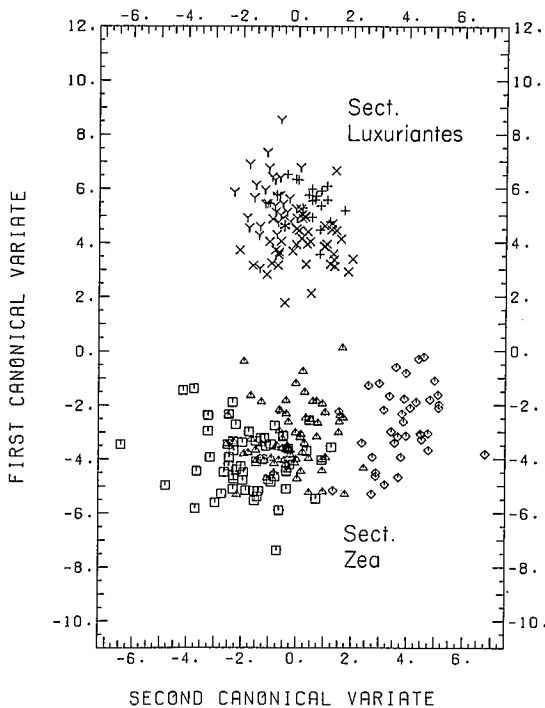


Fig. 28. Graph of the first and second variates from a canonical analysis of 17 populations of the genus *Zea*, showing a) Sect. LUXURIANTES, including *Z. perennis* = + (2 populations); *Z. diploperennis* = x (1 population); *Z. luxurians* = Y (3 populations); *Z. luxurians* = * (1 individual specimen from San Augustin, Oaxaca, Mexico); and b) Sect. ZEA, including *Z. mays* ssp. *mays* = ◇ (2 populations); *Z. mays* ssp. *mexicana* = △ (4 populations); *Z. mays* ssp. *parviglumis* = □ (3 populations). For detailed information about each population see Table 1.

tassels readily disarticulating shortly after anthesis on drying; branch rachis strongly flattened on the back.

Glumes of male spikelet stiff and firm, somewhat brittle when old, the outer flattened on the back, tightly enclosing the inner (Fig. 7-9); veins (nerves) of outer glumes usually numerous (9-12-20(-24), the two primary lateral veins much wider than the slender inconspicuous secondary ones between them, prominent, keeled, becoming winged towards apex, the wings projecting outward (Fig. 22-27), bearing stiff, broad-based, toothlike, scaberulous cilia. Female cupulate fruit cases trap-ezoidal.

Geography, taxonomy and cytology: Three taxa, one peripheral to the generic center (*Z. luxurians*, $2n = 20$) and two relictual, in minute, locally endemic populations (*Z. diploperennis*, $2n = 20$; *Z. perennis*, $2n = 40$), all of these mapped in Fig. 29. Chromosome knobs all terminal (Longley, 1941; Galinat, 1973; Kato, 1975; W. Galinat, letter to H. H. I., April 6, 1979).

II. Section ZEA.

Type Species: *Zea mays* L. Species Plantarum 971: 1753.

Male inflorescences (tassels) with numerous branches (in well grown plants usually many more than 12, except in certain races of cultivated *Z. mays*), these lax (stiff in some races of maize), the central (terminal) occasionally somewhat stiffer and stronger, and more densely-beset with spikelets than the lateral ones (this highly exaggerated in cultivated *Z. mays*); branch internodes slender and long (except in the central spike of maize), 3.5-8.2 mm or more long, the spikelet arrangement therefore loose and open, with the tip of the sessile spikelet of each pair not reaching the base of the next higher pair above it on the same side; abscission layers between internodes strongly to weakly developed (totally absent in *Z. mays* ssp. *mays*), the tassel branches therefore often tardily disintegrating (or not at all in *Z. mays* ssp. *mays*); branch rachises rounded on the back, not strongly flattened.

Outer glumes of male spikelet rounded on back, only loosely embracing the inner (Fig. 1-6), both flexible and \pm papery (except in some races of *Z. mays*); veins of outer glume few (6-15), the two major laterals scarcely or only slightly stronger than the secondaries between them and not winged, the cilia along the keel hairlike and soft and not scaberulous and toothlike. Female cupulate fruit cases usually triangular (in maize, compressed horizontally and fused to become part of the "cob," the cupules there empty, very narrow and shallow and sometimes totally collapsed).

Geography, taxonomy and cytology: One species, *Zea mays* ($2n = 20$), with three subspecies, one a world-wide cultivar (ssp. *mays*), the other two wild: ssp. *mexicana* with three allopatric races endemic to central upland Mexico, and ssp. *parviglumis* with two allopatric varieties at lower elevations on the Pacific slope of Southern Mexico and Guatemala (all these taxa mapped in Fig. 29). Chromosome knobs both terminal and internal.

DISCUSSION—Supporting evidence—This taxonomic realignment of the genus *Zea* into the sections LUXURIANTES and ZEA receives support by way of morphological, chemical, cytological and genetic information, much of which, in fact, has been available in the literature for quite some time. Beadle (1932) reported experimental hybrids between *Z. luxurians* and *Z. mays* ssp. *mexicana* race DURANGO to show irregular meiosis and a high percentage of aborted pollen grains, while hybrids between *Z. mays* ssp. *mays* and *Z. mays*



Fig. 29. Distribution of native populations of the genus *Zea*. 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 Guatemalan one var. *huehuetenangensis*.

ssp. *mexicana* (including races CHALCO and DURANGO) were essentially normal in both respects. Similarly, Beadle (1932) found that cultivated maize formed cytologically normal hybrids with *Z. mays* ssp. *mexicana* but abnormal ones with *Z. luxurians*.

Cytogenetically, *Z. luxurians*, *Z. perennis* and *Z. diploperennis* are similar, all having terminal chromosome knobs or telomeres, while lacking internal ones. These knobs are most pronounced in *Z. luxurians* (Longley, 1941; Kato, 1975; W. Galinat, letter to H.H.I., April 6, 1979). On the other hand, all the subspecies of *Z. mays* have, in general, many internal knobs and few or no terminal ones (Kato, 1975).

Genetically, Levings, Timothy and associates (Levings et al., 1978; Timothy et al., 1979) have found electrophoretic banding patterns of chloroplast DNA (using two different restriction enzymes) of *Z. perennis* and *Z. luxurians* (both Sect. LUXURIANTES) to be identical to one another, and different from those of *Z. mays* ssp. *mays* and ssp. *mexicana*, the

two latter (both Sect. ZEA) in turn similar to each other. Gray and Perkins (1973) found that leaf flavonoids of ssp. *mays* and *mexicana* are very similar but entirely different from those of *Z. perennis*. Similarly, studying proteins of *Zea* by gel electrophoresis, Smith and Lester (1979a) found *Z. mays* ssp. *mays* and *mexicana* to have banding patterns identical to each other but different from that of *Z. luxurians*.

Is Zea luxurians perennial?—Our conclusion, namely that *Z. luxurians* and the two perennial species are so closely related to each other that they must be placed into one and the same section of the genus, opens up the old question of the perennial propensities of *Z. luxurians*. Some authors (cf. Wilkes, 1967: 6–13) have reported GUATEMALA teosinte grown in Florida (hence the misleading name “Florida Teosinte”) to be somewhat perennial in habit, and many earlier as well as several recent authors have repeatedly mentioned either this condition (Wilkes, 1967: pl. XXV; Galinat, 1973; Bird, 1978), or at least a “pro-

fuse tillering" (cf. Hooker, 1876; Wilkes, 1977b). Now, it would strongly support our classification if *Z. luxurians* were in fact a perennial, even a short-lived one, that characteristically would tiller profusely! Yet, not only is much of the evidence at hand ambivalent, but our own field experience clearly suggests it to be an annual in its native habitat. Certainly, in Guatemala *Z. luxurians* has exactly the same root system as *Z. mays* ssp. *mexicana*, ssp. *parviglumis*, and ssp. *mays*, without any rhizomes or caudices and, in fact, with hardly any lower branches and certainly no rooting ones. This is true of the most robust, 4-m tall specimens, as well as depauperate ones, and of those growing by themselves out in the open, as well as those subject to dense competition. In a week of field work in south-eastern Guatemala during January, 1976, and thus very late in its growing season, the second author found no indication in literally hundreds of plants dug out or pulled up that *Z. luxurians* is anything but a typical annual, all its parts dying at the end of the growing season. The root habit differed in no significant way from well-developed maize or annual teosinte. Only on rare occasions were basal branches produced and then no more than 3 or 4, and these several centimeters above the ground and not rooting at the lower nodes.

Why do other reports then persistently state that it is a "perennial"? Photographs of plants cultivated in El Salvador (Central America), and drawings of plants grown in Cairo, Egypt, show huge many-stemmed, semi-perennial plants (Hooker, 1876). Even if grown in more northern latitudes it forms immense and highly tillered clumps (cf. Wilkes, 1967: 100–103). Is it because teosinte in general has the propensity to form huge clumps if placed into highly fertilized cultivation, free of competition and well-watered for a long time?

Reports of the "perennialness" of *Z. luxurians* may be due in part to an initial mistake by the first collector of the original GUATEMALA seeds, a mistake which has been discussed by Wilkes (1967) and Kempton and Popenoe (1937). The collector, a horticulturalist, was the victim of an understandable confusion, for he evidently sent to Europe, together with seeds of *Z. luxurians*, a description of a common rhizomatous Guatemalan *Trip-sacum* (sic!), which somewhat resembles teosinte.

To us, reports of the perennialness of Guatemala teosinte thus continue to remain an enigma. We do not know if it is simply a reflection of continued watering during critical times of cultivation, or a unique response to longer days.

Evolutionary implications—The origin of *Z. mays* ssp. *mays* has been a subject of great dispute for over 100 years, one in which often the promise of evolutionary enlightenment was hardly commensurate with the heat of the argument. The main positions of the various schools of thought in this frequently violently emotional polemic have been summarized repeatedly, alas often uncritically, in the last 15 years (Goodman, 1965; Mangelsdorf, 1974; Kato, 1975; Randolph, 1977). Recently, while an ever-growing number of authors have argued for annual teosinte as maize's ancestor (Langham, 1940; Darlington, 1956; Miranda Colin, 1966; Iltis, 1971, 1972, 1979; Galinat, 1971, 1975; Harlan et al., 1973; Beadle, 1939, 1972, 1978, 1980), the view that maize evolved from a "wild maize" continues to have its supporters. Suffice it to say that the critical dogma of "The Maize Mystique" has been the pre-Columbian extinction of a hypothetical species, the *polystichous* "wild maize" (Weatherwax, 1955; Mangelsdorf, 1974; Randolph, 1977; Wilkes, 1977b).

Unfortunately for all, the taxonomic-morphological evidence was never rigorously applied to the "wild maize" by its proponents. Yet, in any dispute concerning the origins of a taxon, be it cultivated or not, *it is always essential to argue from a sound taxonomic base*. The presentation of our classification in this and our companion paper (Iltis and Doebley, 1980), based as it is on anthropogenically "neutral" characters, adds to the growing body of data which inescapably points to *Zea mays* ssp. *mexicana*, the annual teosintes still locally so prevalent in the great valleys of Central Mexico, as the progenitor of maize. These data, along with other published evidence, show the genus *Zea* to have a complex internal structure in which the cultivated maize is closely aligned to its ancestor *Z. mays* ssp. *mexicana* in all genetic, cytological, biochemical and anthropogenically neutral morphological traits, differing from it only in characters changed to suit the needs of its hungry pre-Columbian cultivators.

As a consequence of our new taxonomic classification, various theories regarding a putative geographic evolutionary series from Guatemala northwestward to Mexico, produced with or without the help of pre-Columbian man, proposed by Longley (1937, 1941) and others, are shown to be based more on imaginative interpretations of cytology than on taxonomic facts. Similarly, the recent suggestion that cultivated maize evolved from *Z. luxurians* (GUATEMALA teosinte), (Galinat, 1973), can now be rejected, since the species of Sect. *ZEA* (including the cultivar) and Sect.

LUXURIANTES are quite distinct morphologically and genetically, with *no trace* of spontaneous LUXURIANTES germ plasm ever having been found in cultivated maize as far as we know at present (or for that matter, the reverse introgression, of cultivated *Z. mays* into *Z. luxurians*!).

Our new classification also sheds light on the relationship of *Zea* to its ancestral genus *Tripsacum*. Clearly, on the basis of both male spikelet morphology and female spikelet (cupule) shape, Sect. LUXURIANTES is the more primitive of the two sections, approaching in its characters certain species of *Tripsacum* and other Andropogoneae. Indeed, various authors have recognized this by regarding both the perennial species and *Z. luxurians* as the most primitive members of *Zea* (Wilkes, 1967; Galinat, 1973; Iltis et al., 1979). This relationship is further supported by: a) the perennialness of two of its three species, with rhizome systems not unlike those of *Tripsacum* and b) the fact that all species of Sect. LUXURIANTES as well as of *Tripsacum* have terminal chromosome knobs unlike those of Sect. ZEA (Long-

ley, 1941; Kato, 1975; W. Galinat, letter to H.H.I., April 6, 1979). Conversely, Sect. ZEA is more highly specialized, not only in the acute-angled abscission layers of the female inflorescence, resulting in triangular cupulate fruit cases, and in the loosely imbricated and distantly spaced spikelets on the tassels, especially in the most highly derived wild taxon, *Z. mays* ssp. *parviglumis*, but also in its uniformly annual habit.

In summary, the large number of morphological, genetic and biochemical traits held in common by the taxa of each of the two sections into which the genus has here been divided suggests them to be natural evolutionary units, the species of each being much more closely related to one another than to those of the other section. Of the two sections, LUXURIANTES is clearly the more primitive as its species more closely resemble the ancestral genus *Tripsacum* in spikelet structure and general morphology. Section ZEA is the more derived, with *Zea mays* ssp. *mays* being merely a highly domesticated, yet certainly a quite remarkable form of *Z. mays* ssp. *mexicana*.

KEY TO THE TAXA OF ZEA
(Use well-grown specimens if possible)

1. Cupulate fruit cases trapezoidal; outer glume of male spikelet \pm flat on back, stiff, and brittle (when old), its two lateral (primary) nerves very prominent and each produced into winged keels near the apex, the intermediate nerves much thinner; outer glume strongly enclosing the inner before anthesis; male rachis internodes 2.4–6.2 mm long
Sect. LUXURIANTES
2. Perennials with scaly rhizomes, forming many-stemmed clumps; outer glumes of male spikelets with strong apical wing.
 3. Plants robust; rhizomes with internodes 0.2–0.6 cm long and often forming tuberlike short shoots. Sierra de Manantlán, Jalisco, Mexico; $2n = 20$
Z. diploperennis
 3. Plants more slender; rhizomes with internodes 1–6 cm long and lacking tuberlike short shoots; lower north slopes of the Volcán de Colima, Jalisco, Mexico; $2n = 40$
Z. perennis
2. Plants annual, the culms solitary or with few tillers (in the wild); outer glume of male spikelet many-nerved, with a weak apical wing. Honduras, southeastern Guatemala (Provinces of Jutiapa, Chiquimula and Jalapa), and southeastern Mexico (Oaxaca, San Augustin only³); $2n = 20$
Z. luxurians
1. Cupulate fruit case triangular (or horizontally squashed, empty, and hidden in *Z. mays* ssp. *mays*); outer glume of male spikelets round on back, papery in texture, its two lateral nerves barely or not at all stronger than those in between and never forming winged keels; outer glume only loosely enclosing the inner before anthesis; male rachis internodes 3.5–8.2 mm long (much shorter in the central spike of maize)
Sect. ZEA
4. Female spikes on lateral inflorescence few to many, each a slender distichous spike with caryopses ("seeds") hidden inside the glume-covered cupulate fruitcases, each enclosed in a single sheath or husk, and borne on a slender peduncle. Male tassel disarticulating by \pm prominent abscission layers, the central branch (spike) with only 2–4 spikelet-pairs/cm, and as slender as the lateral branches. Plants wild or weedy. "Annual Teosinte."
5. Male spikelets small, 4.6–7.2(–7.9) mm long, female fruitcases small, 5–8 mm long, 3–5 mm wide, their axial side blunt; tassel delicate and densely branched with 1–65 or more tassel branches; southwestern Mexico to Guatemala
Zea mays ssp. *parviglumis*
6. Plants of the southern escarpment of Mexico, the Río Balsas drainage and westward (Mexico, Guerrero, Michoacán and Jalisco), rarely crossing with maize, flowering in September and October *Zea mays* ssp. *parviglumis* var. *parviglumis*
6. Plants of west central Guatemala (Huehuetenango), commonly crossing with maize, flowering in December and January
Zea mays ssp. *parviglumis* var. *huehuetenangensis*

³ In October of 1842, Liebmann collected a teosinte at San Augustin in Oaxaca, which was illustrated by Wilkes (1967, Plate IV, p. 10) as a specimen of BALSAS Teosinte, and later discussed by him (1977a) as having characteristics of both BALSAS and GUATEMALA (*Zea luxurians*). However, this is clearly a specimen of *Z. luxurians* and not the much smaller-spikeleted (with a fewer-nerved outer glume) *Z. mays* ssp. *parviglumis* (BALSAS race) as shown by its position on Fig. 28. This is the earliest surviving specimen of Teosinte collected in the wild. The species has never been recollected in Mexico.

5. Male spikelets robust (6.6–7.5–10.5 mm long; female fruitcases 6–10 mm long, 4–6 mm wide, their axial side pointed (“pinched”); tassel rather robust and open with 1–20(–35) tassel branches; Central Plateau of Mexico (Pueblo to Eastern Jalisco and Chihuahua) *Zea mays* ssp. *mexicana*
4. Female spikes (“ears”) gigantic, polystichous, solitary and terminal on primary lateral branches of stems and tillers, with all lateral female spikes suppressed, the caryopses (“seeds”) naked, these, attached to a massive central axis (“cob”), laterally displaced from their reduced, collapsed, empty and hidden cupules, tightly enclosed in a series (8–12 or more) sheaths (“husks”) borne on a telescoped axis (“shank”). Male tassel lacking abscission layers on rachis, hence not disarticulating, the strongly differentiated, erect central spike densely crowded with 5–6 or more spikelet pairs/cm, and much thicker than the lateral branches. World-wide obligatory cultivar. “Maize” or “Indian Corn” *Zea mays* ssp. *mays*

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