

## TAXONOMY OF ZEA (GRAMINEAE). II. SUBSPECIFIC CATEGORIES IN THE ZEA MAYS COMPLEX AND A GENERIC SYNOPSIS<sup>1</sup>

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### ABSTRACT

A compromise classification of the genus *Zea*, reflecting both phylogeny and practical needs, recognizes six taxa, as follows: Section LUXURIANTES: *Zea perennis*, *Zea diploperennis*, *Zea luxurians*. Section ZEA: *Zea mays* ssp. *mexicana* (Neo-volcanic Plateau), *Zea mays* ssp. *parviglumis* Iltis & Doebley ssp. n. var. *parviglumis* (Rio Balsas drainage, Pacific slope from Guerrero to Jalisco), *Zea mexicana* ssp. *parviglumis* var. *huehuetenangensis* Iltis & Doebley var. n. (Pacific slope, western Guatemala, Prov. Huehuetenango), *Zea mays* ssp. *mays*. The new subspecies is distinguished by smaller spikelets and rachis joints, the varieties by different habitats, blooming dates and their genetic behavior in relation to cultivated *Zea mays*. *Zea mays* ssp. *mexicana* is the ancestor of corn.

THE CULTIVATED "CORN" OR "MAIZE" of the American Indians and world commerce, *Zea mays* ssp. *mays*, is a species whose taxonomic circumscription has never been questioned. Its wild relatives, the "teosintes," however, have for quite some time now been considered by many workers to present a number of taxonomic problems. This study attempts to resolve some of these.

Most modern but orthodox systems of classification included in the genus *Zea* not only cultivated maize but also one to five annual, and now two perennial, taxa of teosinte (Reeves and Mangelsdorf, 1942; Wilkes, 1967; Iltis et al., 1979). All annual forms of teosinte have generally been included within *Zea mexicana* (Schrader) Kuntze (= *Euchlaena mexicana* Schrader). Native to Mexico Guatemala and Honduras, these are often as robust and tall as maize and many workers, noting this and other similarities, consider them to be the ancestors, or at least the closest relatives, of this important crop. In fact, certain teosinte populations are genetically so close to maize and so easily crossed with it that they were recently reduced to a subspecies of *Z. mays* as ssp. *mexicana* (Iltis, 1972).

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Since the beginning of this century, it has gradually become apparent that several elements were included within wild "*Zea mexicana*," each with its own biological-morphological features, geographic distribution, and ecology. Not surprisingly, therefore, agronomists and geneticists, who from the start published extensively on the various types of annual teosintes and their maize hybrids, conveniently named their experimental teosinte materials after the regions of origin (e.g., DURANGO teosinte, CHALCO teosinte, etc.), or, in the case of GUATEMALA, after its initial center of cultivation for silage and fodder (e.g., "FLORIDA" teosinte).

During the first four decades of this century, the genetics and cytology of various populations of annual teosinte were examined by many investigators, including Harshberger, Collins, Kempton, Popenoe, Mangelsdorf, Longley, Randolph, McClintock, Reeves, Langham, and Beadle (cf. Wilkes, 1967). These researchers, however, paid only the scantest attention to teosinte taxonomy or phylogeny. Not until the mid-1940s was a formal taxonomic study of teosinte attempted, this by the late Charles Gilly, then a student of I. E. Melhus at Iowa State University in Ames. Gilly identified seven geographic "phases" of teosinte by informal geographic names, such as GUERRERO or CHALCO teosinte (see Table 1). These names, however, were never formally published and we know of their existence solely from annotations on teosinte specimens in some of the major U.S. herbaria and from Gilly's unpublished notes and proposed thesis outline (Gilly, 1948) which, fortuitously preserved in the files of the Michigan State University Herbarium at East Lansing, were

TABLE 1. *Comparative taxonomy of teosinte and maize*

Gilly (Unpublished thesis proposal and specimen annotations, 1948)	Wilkes (Teosinte, the closest relative of maize, 1967)	Ilits & Doebley (1980) and Doebley & Ilits (1980)
ZEA <i>Zea mays</i>	Section ZEA <i>Zea mays</i>	Section ZEA <i>Zea mays</i> ssp. <i>mays</i>
EUCHLAENA <i>Euchlaena mexicana</i>	Section EUCHLAENA <i>Zea mexicana</i>	ssp. <i>mexicana</i>
(Incl. in DURANGO PHASE?) DURANGO PHASE	NOBOGAME RACE (Incl. in CENTRAL PLATEAU RACE)	NOBOGAME RACE (Incl. in CENTRAL PLATEAU RACE)
BAJIO PHASE	CENTRAL PLATEAU RACE	CENTRAL PLATEAU RACE
BARRANCA PHASE (Guadalajara)	?	?
CHALCO PHASE	CHALCO RACE	CHALCO RACE ssp. <i>parviglumis</i> var. <i>parviglumis</i> var. <i>huehuetenangensis</i>
GUERRERO PHASE	BALSAS RACE	
HUEHUETENANGO PHASE	HUEHUETENANGO RACE	Section LUXURIANTES
JUTIAPA PHASE <i>Euchlaena perennis</i>	GUATEMALA RACE <i>Zea perennis</i>	<i>Zea luxurians</i> <i>Zea perennis</i> <i>Zea diploperennis</i>

unearthed by the senior author a few years ago.

In Gilly's only *published* work on teosinte (Gilly and Melhus, 1946: 235), the teosinte variants are simply dismissed with the pregnant but cryptic comment that the "... geographic distribution and range of variability within this group of plants are considerably greater than is indicated in the existing literature." Unfortunately, Gilly's annotations had little if any direct effect on the evolutionary thinking of his time. Thus, the book-length *Races of maize in Mexico* (Wellhausen, Roberts and Hernandez, 1952) and *Races of maize in Central America* (Wellhausen, Fuentes and Hernandez, 1957) discuss annual teosinte and its relationship to maize without *any* mention of subspecific variability whatsoever. Wellhausen even presents a distribution map of teosinte, the first ever published, with all the then-known geographic locations indicated by identical symbols. This map, based on an unpublished manuscript map of Hernandez and Gilly (cf. Wilkes, 1967, p. 18), does not indicate any geographic differentiation.

A landmark in our understanding of the botany and geography of *Zea mexicana* is Wilkes' (1967) splendidly illustrated book-length monograph, *Teosinte: The closest relative of maize*. As Paul Mangelsdorf's doctoral student at Harvard University, Wilkes was the first, not only to bring together all available literature on teosinte, indeed a prodigious feat, but also to describe the various races of annual teosinte. Unlike Gilly, who did relatively little field work on teosinte in Mexico, Wilkes carried out thorough and long-lasting field explorations of practically all teosinte stations then

known in Mexico, Guatemala and Honduras, and discovered many new stations as well. Within an all-inclusive *Zea mexicana*, Wilkes delimited six allopatric teosinte races on morphological genetic physiological and geographic grounds. These races agreed in most essentials with those previously proposed by Gilly (Table 1). Unlike Gilly, however, Wilkes was able to document this in print and show to anyone willing to study his evidence that the "species" *Zea mexicana* (teosinte) comprises, in effect, a complex of many taxa endemic to Mexico and Central America and with a complicated internal taxonomic-geographic structure.

Wilkes, however, neither stated this fact explicitly nor, seemingly, appreciated its devastating implication to Mangelsdorf's theories (Mangelsdorf and Reeves, 1939). Although he stressed that teosinte must have had an ancient history, he equivocated on the putative hybrid origin of teosinte, believing as he did that previous to maize domestication only one type of teosinte was in existence—all other races or species being the result of subsequent post-agricultural introgressions of maize into this one original type. His own evidence, however, showing distinct taxonomic differentiations, makes unlikely any such recent origin of these taxa. In fact, the morphological pattern of variation in *Zea* is typical of a genus whose species evolved by allopatric speciation and, in one instance, by polyploidy. Nevertheless, the clear demonstration of the existence of these races alone marks Wilkes' work as one of the major turning points in the "origin of maize" controversy.

Although Wilkes' abundant documentation,

as well as our own field and laboratory work of the past 20 years, showed that these various geographic races differ from each other in the relative *degree* of morphological, physiological and genetic distinctiveness, these *differences in degree of differentiation* were in no way reflected in their taxonomic rankings. Wilkes himself was aware that some of his races were more distinct than others. Nevertheless, he chose to designate all simply as "races" of the "annual teosinte," *Zea mexicana*. Southeastern GUATEMALA (*Florida* or *Jutiapa*) teosinte, which Wilkes knew to be quite distinct, thus was recognized as a race equivalent to any other, even though previous authors treated it as a distinct species or variety (*Euchlaena luxurians* Durieu and Ascherson; *Euchlaena mexicana* Schrad. var. *luxurians* [Durieu & Ascherson] Haines; cf. Collins, 1931). In any case, Wilkes did not *formally* recognize any of these races taxonomically, being schooled in genetics and ethnobotany rather than systematics, and having other than taxonomic aims.

For some time now a need for a formal yet practical teosinte taxonomy has been evident, one which will recognize these differing degrees or levels of distinctiveness, both within more narrowly defined *Zea mexicana* and the genus *Zea* as a whole. Now that the annual GUATEMALA race has been properly re-elevated to full species status under *Zea* as *Z. luxurians* (Bird, 1978), and the two perennial taxa are recognized as species as well, we are left with at least five macropopulations of annual teosinte which, though more closely related to each other than to GUATEMALA, nevertheless show among themselves sufficient morphological diversity to merit taxonomic attention.

To begin with, as was implied by Wilkes (1967), these races are divisible into two major groups: 1) *The Chalco-Central Plateau* (including *Nobogame*) *Complex*, native from the Valley of Mexico and adjoining Puebla across the central Neo-volcanic Plateau west to Michoacán and north to Chihuahua (NOBOGAME). 2) *The Balsas (Guerrero)-Huehuetenango Complex*, native to the somewhat drier and lower elevations of the Pacific slopes of southwestern Mexico, namely in the Río Balsas drainage of Guerrero and Michoacán and, rarely, to southwestern Jalisco, and in a highly disjunct area in the highlands of west-central Guatemala in the Province of Huehuetenango. (The latter has often, and confusingly, been referred to as *northern* Guatemala teosinte, this quite distinct from southern GUATEMALA (*Jutiapa*) teosinte of southeastern Guatemala.)

The purpose of this paper is, therefore, to describe the morphological differences between these two annual teosinte complexes,

and to provide them as well as all other taxa of *Zea* with appropriate scientific names (cf. Iltis, 1972).

MORPHOLOGICAL DIFFERENTIATION WITHIN *ZEA MAYS* ssp. *MEXICANA* and ssp. *PARVIGLUMIS*—Excluding GUATEMALA teosinte, the wild annual teosinte species may be readily divided, even on visual inspection, into two rather well-defined complexes: 1) *The Chalco-Central Plateau Complex*, which we shall call *Zea mays* ssp. *mexicana*, characterized in well-grown plants by rather robust open tassels, by large spikelets, and by relatively large fruitcases, which are pointed or often "pinched" (abruptly contracted) on the axial side; and 2) *The Balsas-Huehuetenango Complex*, which we shall call *Zea mays* ssp. *parviglumis*, characterized by more delicate, frequently more densely and more abundantly branched tassels, by smaller spikelets, and by smaller fruitcases which, more blunt on the axial side, are never pinched.

This major division of the annual *Zea mexicana* type of teosinte (i.e., exclusive of *Z. luxurians*) into two groups is graphically confirmed in scatter diagrams of population samples (mass collections). Using male spikelet length/spikelet width (Fig. 1, 2), these diagrams demonstrate a clear division of *Z. mexicana* into two morphological groupings with only a minor amount of overlap. Similar but less effective results would have been obtained with the use of other characteristics, such as numbers of tassel-branches/glume length, weight/length of "seeds" (i.e., fruitcases), and probably others. One may note that Fig. 1 shows that measurements of individuals of HUEHUETENANGO from the wild show in general a relatively much greater overlap with the CHALCO-CENTRAL PLATEAU complex than do those from the BALSAS region. The somewhat larger average size of HUEHUETENANGO spikelets from the wild, however, might be interpreted as reflecting the relative ease of hybridization with the larger-spikeleted cultivated maize, as any mass collection from San Antonio Huista, Guatemala, demonstrates, where up to 8% or more of the teosinte plants in some weedy maize fields may be first generation hybrids (Wilkes, 1977 and pers. commun.; see observations under *Iltis & Lind G-120*, below). Nevertheless, *clear* proof of any such introgression of maize into teosinte is yet forthcoming. The reverse introgression, of course, has often been documented (e.g., Wilkes, 1968, 1970; Mangelsdorf, 1952; Galinat, 1977). Further, plants of the two varieties of *Z. mays* ssp. *parviglumis* grown in uniform conditions in Homestead, Florida at the Pioneer Hi-Bred

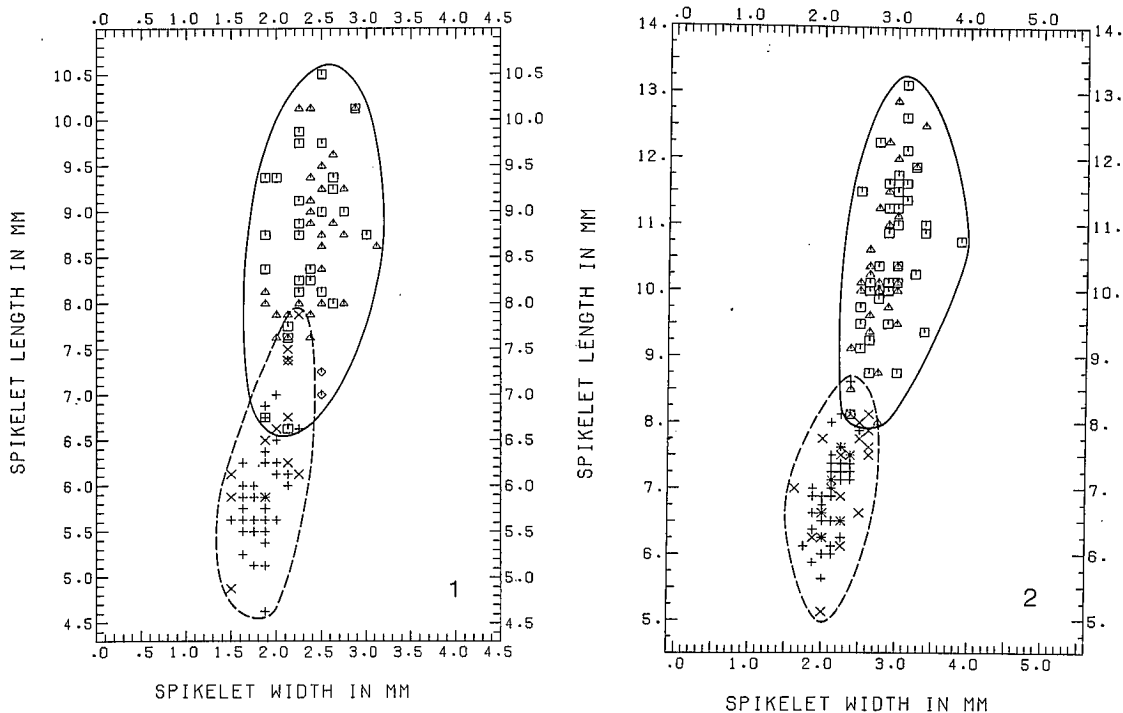


Fig. 1-2. Scatter diagrams of spikelet length versus width of annual teosinte specimens with individuals of *Zea mays* ssp. *mexicana* and ssp. *parviglumis* encircled: + = BALSAS race, x = HUEHUETENANGO race, □ = CENTRAL PLATEAU race, Δ = CHALCO race, ◇ = NOBOGAME race. 1. Field collected specimens: BALSAS populations from TZITZIO and ACAPETLAHUAYA; HUEHUETENANGO population from HUEHUETENANGO; CENTRAL PLATEAU populations from DURANGO and URIANGATO; CHALCO populations from CHALCO and LOS REYES; NOBOGAME specimens from NOBOGAME. 2. Specimens grown in controlled environment in Florida: BALSAS populations from EL SALADO, HUETAMO and TZITZIO; HUEHUETENANGO populations from SAN ANTONIO HUISTA and TZISBAJ; CENTRAL PLATEAU populations from COPANDIRO and QUINCEO; CHALCO populations from LOS REYES and CHALCO. For exact location data on each population, see Table 2. For drawings of spikelets, see Doebley and Iltis 1980, Figs. 1-27.

International Company experimental station had spikelets whose range of variability not only overlapped each other nearly completely but, in fact, separated rather neatly from those of *Z. mays* ssp. *mexicana* (Fig. 2). This suggests that perhaps a moister environment, rather than only introgression, may play an important part in producing the larger spikelet size in wild HUEHUETENANGO.

In addition to these morphological criteria, supporting evidence for this classification of annual teosinte comes from recent biochemical and cytological work: First, Levings, Timothy and associates (Levings et al., 1978; Timothy et al., 1979) have shown that the cytoplasmic (mitochondria, chloroplast) genomes of BALSAS and HUEHUETENANGO are similar to one another and distinct from those of CHALCO and CENTRAL PLATEAU, the latter in turn being similar to each other. Second, Kato (1975) reports on an experimental hybrid between BALSAS and HUEHUETENANGO in which 261 meiotic cells showed 100% normal bivalent formation, with not a single univalent seen, suggesting very

close genetic affinity between these races. On the other hand, hybrid plants between BALSAS and GUATEMALA (*Zea luxurians*) show 2-14 univalents in 30-70% of all cells counted. This indicates relatively much greater genetic distance and reflects their rather distinct morphologies, belonging as they do to different sections of *Zea* (Beadle, 1932; Rogers, 1950; O'Mara, 1942; Bird, 1978).

Some evidence which does not seem to support the taxonomic division suggested here is Kato's (1975) observation that the chromosome knob configurations of HUEHUETENANGO seem to resemble more closely those of GUATEMALA (having only terminal knobs) than those of any of the Mexican types (these having both internal and terminal knobs). In contrast to Kato, however, Ting (1958) found six internal knobs and only two terminal ones in HUEHUETENANGO from San Antonia Huista, demonstrating its affinities to the Mexican forms (cf. Longley, 1937). These cytological differences may simply be a matter of interpretation and may revolve around the some-

TABLE 2. *List of populations*

## A. Populations collected in the wild:

1. *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 and Doebley 4*.
2. *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 and Doebley 8*.
3. *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 and Doebley 36*.
4. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU Teosinte). Mexico: Durango: vicinity of DURANGO, collected by various botanists.
5. *Zea mays* ssp. *mexicana* (NOBOGAME Teosinte). Mexico: Chihuahua: vicinity of NOBOGAME, collected by various botanists.
6. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS Teosinte). Mexico: Guerrero: Weeds in maize field in regions of semi-deciduous savannah of Leguminosae, *Bursera*, *Pseudomodinium* 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 and Doebley 361*.
7. *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 and Doebley 87*.
8. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENANGO Teosinte). Guatemala: Huehuetenango: HUEHUETENANGO population, vicinity of San Antonio Huista, collected by various botanists.

## B. Grown under controlled conditions in Homestead, Florida.

9. *Zea mays* ssp. *mexicana* (CHALCO Teosinte). Mexico: Mexico: Edges of maize fields ½ km SE of LOS REYES on road to Amecameca, 19°20'N, 98°57'W, alt. ca. 2,225 m. Dec. 1, 1971. *Iltis and Cochrane 175*, cult.
10. *Zea mays* ssp. *mexicana* (CHALCO Teosinte). Mexico: Mexico: Maize field, 14 km SE of CHALCO at km 43 on road to Amecameca, 19°12'N, 98°50'W, alt. ca. 2,300 m. Nov. 30, 1971. *Iltis and Cochrane 178*, cult.
11. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU Teosinte). Mexico: Michoacan: Edge of field, near COPANDIRO, alt. 1,850 m. Dec., 1963. *Wilkes 48703* (USDA Plant Inventory No. 177, p. 132, Accession No. 343244), cult.
12. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU Teosinte). 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 and Cochrane 276*, cult.
13. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS Teosinte). Mexico: Guerrero: 4.5 km E of Mazatlán on road to EL SALADO. Nov., 1972. *Wilkes s. n.* (USDA Plant Inventory No. 181, p. 220, Accession No. 384061), cult.
14. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS Teosinte). Mexico: Michoacan: km 127 on the road from HUETAMO to Morelia, International Center for the Improvement of Maize and Wheat Accession No. 8761, cult.
15. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS Teosinte) 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 and Cochrane 308*, cult.
16. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENANGO Teosinte). 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.
17. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENANGO Teosinte). 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 and Lind G-120*, cult.

what subjective distinction between larger more visible chromosome knobs and the smaller "chromomeres," Kato (1975) perhaps dismissing as chromomeres what Ting records as knobs. For example, Kato (1975) reports that *Z. perennis* has knobless chromosomes even though both W. Galinat (letter to H. H. I., April 6, 1979) and Longley (1941) have noted that this species has small terminal knobs (cf. Doebley and Iltis, 1980).

In addition to the major dichotomy proposed here between CHALCO-CENTRAL PLATEAU and BALSAS-HUEHUETENANGO, it is apparent from

the literature and our own field observations that several important differences exist between the geographically isolated BALSAS and HUEHUETENANGO populations, in spite of the fact that these are not as yet distinguishable on the basis of their reproductive morphology or cytoplasmic genomes.

These differences include: 1) ecology, and hence vegetative morphology, the plants of the much moister Huehuetenango region being somewhat taller and having a higher average sheath length (cf. Wilkes, 1967); 2) ethology (specifically, the time of flowering), plants of

BALSAS usually flowering from September through November, this being on the average some two months earlier than those of HUEHUETENANGO, which may not be in full bloom until late December or early January, and 3) crossability with maize, plants of HUEHUETENANGO on occasion crossing freely with maize in nature and producing many hybrids (see above) while those of BALSAS tend to cross with maize only rarely.

Considering these differences as well as their allopatric geographic areas, these two populations also deserve some sort of nomenclatorial recognition, especially since they have and are being used in genetic research.

**SPECIES, SUBSPECIES OR VARIETY?—A PERENNIAL PROBLEM IN SEARCH OF SOLUTION**—Anyone working with recently evolved, especially actively speciating groups is often faced with the two most persistent questions of taxonomic categorization: 1) into how many taxa is a group to be divided, and 2), at what level are these to be placed in relation to each other? The questions are paradoxical because the need for a practical taxonomy is complicated by other, non-taxonomic considerations; namely, that the greater the importance of the organism to science or agriculture and the more detailed or at least voluminous the systematic and genetic literature, the greater will be the need for a realistic hierarchy of subspecific categories. And so certainly with *Zea*, a scientifically much-studied, economically supremely important genus!

The hierarchical problem in *Zea* has been particularly vexing to us because there are several equally useful and equally valid ways in which one may arrange the "races" of teosinte. Thus, for example, in this group of closely related annual teosintes one might recognize either: a) three full species, namely, the small-flowered and large-flowered wild groups discussed above, as well as cultivated maize, or b) only two species, namely the wild groups as one and the cultivar as another (this would find its analogue in the treatment of the giant-fruited *Solanum muricatum* Ait., the "pepino" of the Andes, whose wild ancestor is deemed distinct enough to bear a different name, *S. caripense* H. & B. [Heiser, 1964]) or c) two species, one of these combining the cultivar *Zea mays* and the races CHALCO-CENTRAL PLATEAU-NOBOGAME and having two subspecies and the other composed of the races BALSAS-HUEHUETENANGO being a parallel but distinct species (This course, while perhaps the one most reflective of true phylogeny, presents nevertheless practical and logical problems too

difficult to dismiss.) or d) only one super-species, with several subspecies.

The last alternative, the ultimate in "lumping," leads to an all-inclusive *Zea mays*. Considering that HUEHUETENANGO and (even if to a lesser extent) BALSAS, not to speak of the utterly promiscuous CHALCO-CENTRAL PLATEAU-NOBOGAME complex, spontaneously cross with cultivated maize to produce hybrids and hybrid swarms, resulting in effective introgression of teosinte germ plasm into cultivated maize (Wilkes, 1968, 1970; Mangelsdorf, 1952), one can well justify the recognition of all of these races as subspecies of a polymorphic super-species. Recognizing the cultivated maize as the nomenclatorially typical subspecies, one could then attach the wild forms to it as two or three subspecies. The taxonomic recognition of cultivars as conspecific with their wild ancestors *does* have its practical uses; it emphasizes their profound genetic similarity and close phyletic position, both reason enough for recognizing the cultivar as *Zea mays* ssp. *mays*, and the wild taxa as *Zea mays* ssp. *mexicana* (East, 1913; Darlington, 1956; Miranda-Colín, 1966; Iltis, 1972). As Mangelsdorf (1961, p. 162) astutely stated in discussing the abundant hybrids of CHALCO with maize: "A more realistic classification would say that here maize and teosinte represent a single dimorphic species in which one component is preserved by man and the other by nature."

In the present paper, we too have struggled long and hard with the dilemma of choosing appropriate nomenclatorial categories<sup>2</sup>—and have opted for the latter course, as suggested by one of us previously (Iltis, 1972), for such a course would do the least damage to evolutionary concepts, yet would well reflect the biological differentiations that have taken place. We have chosen then the following taxonomic system for *Zea*: a) Cultivated maize is maintained as a subspecies because of its complete interfertility with its ancestral teosinte populations, remembering that during its evolution from the wild to the cultivated state, despite undergoing both the most drastic and most rapid *morphological* transformation of any vascular plant known to us, the maize phy-

<sup>2</sup> Shortly before the first attempt ever to deal with the taxonomy of *Zea* and *Euchlaena* by Gilly (remarkably successfully, considering the totally inadequate herbarium materials available to him for study), he and W. H. Camp struggled long and hard with the "species problem" in their notorious, pathbreaking and still valuable treatise on biosystematics (Camp & Gilly, 1943). Their frustrations are irreverently reflected in a charming cartoon which these authors included with complimentary copies sent to fellow taxonomists, and which herewith is reproduced for the first time (see p. 1004).

letic line still retains near total genetic identity with its ancestor. This situation and its taxonomic treatment is somewhat analogous to that found in *Helianthus annuus* var. *macrocarpus* (DC.) Ckll., the monocephalic sunflower (Heiser, 1976). b) The wild forms of this annual relationship, easily separated from the cultivated *Zea mays* by the female inflorescence, are here divided into two morphologically rather distinct geographically allopatric subspecies as outlined above, namely, the large-spikeleted, robustly paniced *Zea mays* ssp. *mexicana* and the small-spikeleted, delicately paniced *Z. mays* ssp. *parviglumis* (cf. Doebley & Iltis, 1980: Fig. 29). c) The morphologically nearly identical, but geographically isolated and ethologically differentiated populations of *Z. mays* ssp. *parviglumis* are recognized as two geographic varieties, namely, var. *parviglumis* of Pacific Mexico (=BALSAS) and var. *huehuetenangensis* of west central Guatemala (=HUEHUETENANGO). d) With Wilkes (1967), we recognize the three central and northern Mexican teosintes simply as three very poorly differentiated geographic races (i.e., CHALCO, CENTRAL PLATEAU and NOBOGAME) of *Z. mays* ssp. *mexicana*, since outside of geographic allopatry no consistent, even minor taxonomically useable characteristics have yet been found to distinguish them. All evidence seems to suggest (Iltis, 1979) that CHALCO OF CENTRAL PLATEAU, or both, are the ancestors of cultivated maize.

A synopsis of the nomenclatorial history and descriptions of the new taxa and new combinations are given below, while illustrations of spikelets and a dichotomous taxonomic key to the sections and species of *Zea* was presented by us in the preceding companion paper (Doebley & Iltis, 1980).

#### TAXONOMIC SYNOPSIS OF ZEA

*Zea* Linnaeus, Species Plantarum 971. 1753; Genera Plantarum ed. 5, 419. 1754. Type species: *Zea mays* L.

I. Section LUXURIANTES Doebley and Iltis, Amer. J. Bot. 67: 986-987. 1980. Type species: *Zea luxurians* (Durieu & Ascherson) Bird.

Section EUCHLAENA (Schrader) Kuntze pro parte, not including type.

1. *Zea perennis* (Hitchc.) Reeves & Mangelsdorf, Amer. J. Bot. 29: 817. 1942.

*Euchlaena perennis* Hitchc., Jour. Wash. (D.C.) Acad. Sci. 12: 207. 1922. Type: MEXICO, JALISCO: Zapotlan (Ciudad Guzmán), Hitchcock 7146 (Holotype US!)

"PERENNIAL Teosinte" of authors.

2. *Zea diploperennis*, Iltis, Doebley & Guzmán, Science 203: 186. 1979. Type: MEXICO, JALISCO: La Ventana, Sierra de Manantlán, Iltis, Doebley, Guzmán & Lasseigne 450 (Holotype IBUG! [Univ. of Guadalajara], Isotypes WIS! and 20 additional herbaria, cf. orig. descr.) "DIPLOPERENNIAL Teosinte"

3. *Zea luxurians* (Durieu & Ascherson) Bird, Taxon 27(4): 363. 1978.

*Reana luxurians* Durieu, Extraits des Proces-Verbaux, Bull. Soc. d'Acclimate. 19: 581. 1872, nomen nudum (cf. Hitchcock 1922. 206; Chase & Niles 1962, 2:89).

*Euchlaena luxurians* Durieu & Ascherson, Sitz. Ber. Ges. Nat. Freunde Berlin 1876: 164. 1876, descr.; reprinted Bull. Mens. Linn. Soc. Paris 1(14):107. 1877. (cf. Wilkes, 1967; Bird, 1978) Type: GUATEMALA, JUTIAPA?: Exact location unknown. "Ex cultiv. ex Seminibus Guatemalens." Cairo, Aegypt. 1877-1878, G. Schweinfurth s.n. (Lectotype K, photo Wilkes, 1967, Plate II, p. 8! Curtis Bot. Mag. XXXV: Tab. 6414! [J. D. Hooker, 1879]; Isotype: P, photo Wilkes, 1967, Plate III, p. 9!)

*Euchlaena mexicana* Schrader var. *luxurians* (Durieu & Ascherson) Haines, The Botany of Bihar and Orissa (India) pt. 6: 1065. 1924.

*Euchlaena floridana* Randolph, Indian J. Genet. Plant Breed. 12: 2. 1959, nomen nudum (based on "Florida Teosinte"?).

*Zea mays* L. ssp. *luxurians* (Durieu & Ascherson) Iltis, Phytologia 23: 249. 1972.

"Race GUATEMALA" of Wilkes (1967). "JUTIAPA Phase" of Gilly (1948) and others.

"SOUTHERN GUATEMALA" or "FLORIDA" Teosinte of authors, especially of agriculturalists.

"New Teosinte" of Rogers (1950).

II. Section ZEA.

*Euchlaena* Schrader, Index Sem. Hort. Goettingen, 1832; reprinted Linnaea 8: Litt. 25. 1833. Type species: *Euchlaena mexicana* Schrader.

*Reana* Brignolia, Index Sem. Hort. Mutin., 1849; reprinted Flora (n. s.) 8: 400. 1850; Jour. Wash. (D.C.) Acad. Sci. 12: 206. 1922. Type

species: *Reana giovannini* Brign. Section EUCHLAENA (Schrader) Kuntze, in Post & Kuntze, *Lexicon* 599. 1904.

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

Type: Linn. Herb. No. 1096-1; Savage Catalogue 1945, p. 167.

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

"Maize, Corn, Indian Corn"

The specific and subspecific nomenclature for this obligatory cultivar is hopelessly confused and complex, and beyond the scope of this synopsis; for a complete synonymy, fully 105 names (see Chase and Niles 1962, 3: 527-532).

4b. *Zea mays* L. ssp. *mexicana* (Schrader) Iltis, in *Ann. Rev. Genet.* 4: 450. 1971; *Phytologia* 23: 249. 1972, emended circumscription.

*Euchlaena mexicana* Schrader, *Index Sem. Hort. Goettingen*, 1832; reprinted in *Linnaea* 8: Litt. 25. 1833. Type: MEXICO. State and locality unknown, "e. hort. Goett." Grown from seeds collected in Mexico by Dr. Muhlenfordt, ex Herb Trinius, Schrader s.n. (Holotype, sheet No. 1 of 4, LE!, fragment and photo US! WIS!, authentic material ex Bernhardt Herbarium, MO!)

*Reana giovannini* Brign. Brunhoff, *Index Sem. Hort. Multinensis (Modena)* 1849; reprinted *Ann. Sci. Nat. Bot.* III 12: 365, 1849; *Flora* (n. s.) 8: 400, 1850; *J. Wash. D.C. Acad. Sci.* 12: 206. 1922. Type: MEXICO, location unknown, *Melchoir Giovannini s.n.* (Holotype unknown).

*Euchlaena giovannini* (Brign.) Fournier, *Bull. Soc. Bot. Belg.* 15: 468. 1876.

*Euchaena Bourgaei* Fournier, *Bull. Soc. Bot. Belg.* 15: 468. 1876. Type: MEXICO: Collines des roches au Chiquihuite, Valle de Mexico, Oct. 10, 1865. *Bourgeau s.n.* (Holotype P, photo and fragment US!).

*Zea mexicana* (Schrader) Kuntze, in Post & Kuntze, *Lexicon* 599. 1904.

4b- $\alpha$ . "Race CHALCO" of Wilkes (1967) (all of the above synonyms probably go with this race).

4b- $\beta$ . "Race CENTRAL PLATEAU" of Wilkes (1967). "BAJIO Phase" of Gilly. "DURANGO Teosinte" of authors.

4b- $\gamma$ . "Race NOBOGAME" of Wilkes (1967).

4c. *Zea mays* ssp. *parviglumis*, Iltis & Doebley, ssp. nov.

Subspecies *mexicana* similis, sed inflorescentibus gracilioribus, spiculis masculinis parvioribus (4.6-7.2 mm longis, 1.6-2.8 mm latis), ramis paniculae densioribus subtilibus, segmentis spicae feminae paucioribus (5-9). Typus: *Iltis & Doebley* 379.

Similar to ssp. *mexicana* but male and female spikelets smaller, the male inflorescence (tassel) more delicate and often much more densely branched with tertiary branching more frequent (with up to 65 or more branches), because of the small size of the spikelet the branches appearing more delicate and open. Male spikelets 4.6-7.2(-7.9) mm long, 1.6-2.8 mm wide; mature female fruitcases on average ca. 5-9(10)/spike, 5.0-8.0 mm long, 3.0-5.0 mm wide, the axial side blunt.

South and Southwest Mexico (Jalisco to Guerrero) and western Guatemala (Huehuetenango), at alt. of 600-1,900 m (Doebley & Iltis, 1980; Fig. 29).

Type: MEXICO, GUERRERO: Large populations in grassy thickets along road, and in arroyos and open woods on rocky slopes of mountains of the Rio Balsas drainage (region of semi-deciduous tropical savanna of Leguminosae, *Bursera* sp., *Pseudomodogium pernicosum* and tree *Ipomoea*), on road from Iguala to Arcelia near km 100, 7-8 km W of *Acapetlahuaya* turn-off, ca. 24 km (by air) W of *Teloloapan* 18°20'N, 100°05'W, alt. ca. 1,100 m, Sept. 22, 1977, *Iltis and Doebley* 379. Holotype WIS; Isotypes ARIZ, B, BH, BM, CHAPA, COL, ENCB, F, GH, GUAD, IBUG, ILL, K, LE, MEXU, MICH, MO, P, TAES, TEX, TNS, UC, US, VEN, XAL.

Selected collections: MEXICO, GUERRERO: Km 328.5 of Chilpancingo-Arcelia highway near Palo Blanco, *Lundell* 12602 (UC, US). *Acahuizola*, *Randolph & Randolph* 63-10-12-3 (BH, Photo WIS). Mazatlan, 1,350-1,400 m, *Wilkes* 25150, 32474 (WIS, US). Teloloapan, 1,400 m, *Wilkes* 4455 (WIS). Cerro Ranchos Nuevos, on road from Teloloapan to Arcelia, 1,510 m, *Wilkes* 47711B (WIS). Cerro de los Chivos, Teloloapan-Arcelia, 814 m, *Wilkes* 85, 92, 93 (all WIS). 10 km N de Agua de Obispo, Municipio de Chilpancingo, 1,100 m, *Rzedowski* 26890 (WIS). 10 km WNW of Teloloapan, on highway 51 to Arcelia, 1,600 m, *Iltis & Cochrane* 3, 4, 5, 6, 7, 8, 9, 10 (all WIS). 17 km W of Teloloapan, on highway 51, 1,750 m, *Iltis & Cochrane* 11, 12, 13, 14, 15, 16, 17, 18, 19, 20 (all WIS). 5 km E of Teloloapan, *Iltis & Cochrane* 151 (WIS). 10 km E of Teloloapan, 1,490 m, *Iltis & Doebley* 243, 277 (WIS). 24 km (by air) W of Teloloapan, at Km 100 on



highway 51 to Arcelia, 1,100 m, *Iltis & Doebley 379* (WIS-type). 20 km WNW (by road) of Telo-oapan, Km 83 on highway 51, 1,750 m, *Iltis & Doebley 386* (WIS). 10 km (by road) WNW of Telo-oapan near El Pochote, 1,600 m, *Iltis & Doebley 301* (WIS). ESTADO DE MEXICO: San Nicolas-Sta. Barbara, 1,300 m, *Matuda 29544* (US). Valle de Bravo, 1,500 m, *Matuda 26965* (US). Cerro de la Culebra, Luvianos, Progreso, 1,300 m, *Matuda 31453* (US). La Junta, Santo Tomas, 750 m, *Matuda 29366* (US). Temascaltepec, Plaza de Gallos, 950 m, *Hinton 1,750* (MO, US, K). MICHOACAN: Along road from Tzitzio-Huetamo-Altamirano, *Sohns 941* (USNH). Rock ledges and steep rocky slopes and canyon, 1 km S of Tzitzio, 1,600 m, *Iltis & Cochrane 308, 309, 310, 311* (all WIS), *Iltis & Doebley 62, 63, 64, 74, 87* (all WIS).

In ssp. *mexicana*, the male spikelets average (6.6–)7.6–10.5 mm long and 2.3–3.8 mm wide, with the shorter measurements found only in the extreme northwest end of its range (DURANGO and NOBOGAME) or in depauperate plants, these of course common in both subspecies, depending on competition and the aridity, rockiness and drainage of the habitat. The tassels in well grown plants of ssp. *mexicana* tend to be larger, with more robust, stiffer, but generally fewer branches. The dense tangles of slender secondary and tertiary branches, such as in *Randolph & Randolph 63-10-12-3* (BH, photo WIS!) from Guerrero, are common in robust, gigantic extremes of ssp. *parviglumis*, but do not occur in similarly large plants of ssp. *mexicana*!

The fruitcases of ssp. *mexicana* average 9–12 per spike rather than 5–9(10) in ssp. *parviglumis*, and tend to be larger (6–10 mm long, 4–6 mm wide) and heavier, with the axial side (the side opposite the glume) pointed or “pinched” at its apex.

Subspecies *mexicana* occurs allopatrically to the north of ssp. *parviglumis*, from Puebla and the Valley of Mexico through Michoacán north to Durango and Nobogame, almost always in the basins and slopes of the Neo-volcanic Plateau usually above 2,000 m, and mostly associated with *Zea mays* ssp. *mays* cultivation (see Doebley & Iltis, 1980: Fig. 29).

Subspecies *parviglumis*, on the other hand, occurs in Guerrero and Michoacán (Wilkes 1967, 1972) and very rarely in Jalisco, always on the Pacific slope of the southwestern escarpment, especially in the drainage of the Río Balsas, at elevations of 600–1,400(–1,900) m, (var. *parviglumis*), as well as in an extensive population isolated from the previous population on the Atlantic slope of western Guate-

mala (var. *huehuetenangensis*). A map showing the geographic distribution of these taxa is provided by Doebley and Iltis (1980: Fig. 29).

4c- $\alpha$ . *Zea mays* ssp. *parviglumis* var. *parviglumis*. “Race BALSAS” of Wilkes (1967). “GUERRERO phase” of Gilly and others.

Plants of thorn scrub and open summer-green tropical deciduous forest (*Selva baja caducifolia* of Flores-Mata et al., 1971) as well as maize fields and their edges, on well-drained slopes of mountains and hills in the Río Balsas drainage of Guerrero, Michoacán, and Mexico at 600–1,400 m (–1,950 m ? cf. Wilkes, 1967: 119) these in huge, dense and clearly wild stands, and rarely in Southwestern Jalisco at 1,200 m, this possibly a distinct population with a moister ecology and later flowering date (Guzmán, Doebley and Iltis, unpubl.). Flowering from September through October, with ripe fruit by December.

4c- $\beta$ . *Zea mays* ssp. *parviglumis* var. *huehuetenangensis*, Iltis & Doebley, var. nov.

Varietatis *parviglumis* similis, sed anthesis seratina, habitatione humidior, hybridatione cum *Z. m. mays* commune, et endemica Provincia Huehuetenanga, Guatemala. Typus: *Iltis & Lind G-120*.

“HUEHUETENANGO phase” of Gilly. “Race HUEHUETENANGO” of Wilkes (1967). “SAN ANTONIO HUISTA teosinte” of authors (cf. Kempton and Popenoe, 1937, p. 210–215).

Plants of old maize fields, edge of fields and oak forests, Province of Huehuetenango, Guatemala, from 900–1,650 m (fide Wilkes, 1967, p. 56), flowering from late November to January (and later than var. *parviglumis*), with ripe fruit from late 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.

Type: GUATEMALA: HUEHUETENANGO: Abandoned old maize fields with large populations of *Zea mays* ssp. *parviglumis* and many (ca. 7% or more) F<sub>1</sub> hybrids, on steep slopes along road to Jacaltenango, ca. 1.5–2.5 km ENE of San Antonio Huista (in general region of subtropical dry forest), (15°40'N; 91°45'W), alt. 1,300–1,400 m, January 9, 1976, *H. Iltis & K. Lind, G-120*. Holotype WIS; Isotypes ARIZ, B, BM, CHAPA, ENCB, F, GH, GUAD, IBUG, K, LE, MEXU, MICH, MO, P, TAES, TEX, US, XAL.

Selected Collections: GUATEMALA. HUEHUETENANGO: Petatán, 1,700 m, *Standley 81862* (F, NA). San Antonio Huista, 1,600 m,

*Standley 81680* (F, USNA), 1,242 m, *Wilkes 43,603*, 1,250 m, *Ilitis & Lind G-119* (WIS), *G-120* (WIS, see above). Many other collections cited by Wilkes (1967).

CULTIVATED: Seed from Nojoya, Huehuetenango, Guatemala, *O'Hara* s.n. (MO). Seed from Tzibaj, Huehuetenango, Guatemala, collected by *H. G. Wilkes*, USDA Plant Inventory #177, page 132 (1969) accession 343233 (WIS). Seed from Jutiapa, Guatemala (sic!) collected by *P. Weatherwax* (MO) (collection locality without doubt in error, this clearly var. *huehuetenangensis*).

While ssp. *mexicana* and ssp. *parviglumis* are clearly distinct, var. *parviglumis* is only statistically differentiated in some of its characters from var. *huehuetenangensis*. Nevertheless, the following reasons seem to justify this division: 1) sharp geographic allopatry (Mexico vs. Guatemala); 2) differences in ecology (thorn scrub and open tropical deciduous forests with a short wet season of summer rains, the most xeric of all teosinte populations vs. open oak forests with 8 month long moist seasons of much fog and rain, the most mesophytic of all teosinte populations (cf. Wilkes, 1967: 55–56); 3) differences in flowering dates (var. *parviglumis* blooming and fruiting about six to eight weeks earlier); 4) genetic behavior vis-a-vis cultivated maize (var. *parviglumis* quite rarely hybridizing and most plants clearly "wild" vs. var. *huehuetenangensis* extremely promiscuous, with up to 8% F<sub>1</sub> hybrids and most plants in weedy populations in or near maize fields); 5) various minor though possibly significant cytological differences (Kato, 1975).

#### 5. HYBRIDS OF ZEA MAYS with other ZEA species.

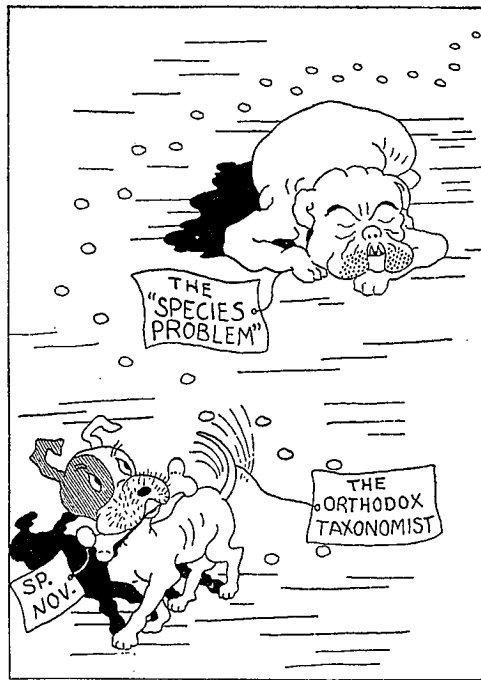
- a. ZEA MAYS L. ssp. MAYS × ZEA MAYS ssp. MEXICANA (Schrader) Ilitis *Zea × canina* S. Watson, Proc. Amer. Acad. Arts Sci. 26: 158. 1891.
- b. ZEA MAYS L. ssp. MAYS<sup>♂</sup> × ZEA PERENNIS (Hitchc.) Reeves & Mangelsdorf<sup>♀</sup>.

*Euchlaeza mertonensis* Janaki Ammal, in Bor, Grasses of Burma, India, and Pakistan 266. 1960. Published without a Latin diagnosis.

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with the  
 COMPLIMENTS OF THE AUTHORS  
 of  
 THE STRUCTURE AND ORIGIN OF SPECIES  
 — W.H.C & C.L.G.

This book plate accompanied W. H. Camp and C. L. Gilly's "The Structure and Origin of Species" (Brittonia vol. 4, 1943) and, except for expressing our taxonomic problems with *Zea*, needs no further comment (see p. 999).