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## Forum

This section of the Annals of the Entomological Society of America is reserved for interpretive articles dealing with the broader manifestations of entomological activities, and the basic scientific approach to these activities. Dissenting viewpoints may be published subsequently if they meet the editorial criteria of the Annals.

### Evidence for Co-evolution of Leafhoppers in the Genus *Dalbulus* (Cicadellidae: Homoptera) with Maize and Its Ancestors<sup>1</sup>

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#### ABSTRACT

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The corn leafhopper, *Dalbulus maidis* (DeLong & Wolcott) and the "Mexican corn leafhopper", *D. elimatus* (Ball) were collected from the perennials *Zea diploperennis* Iltis, Doebley & Guzmán, *Z. perennis* (Hitchc.) and *Tripsacum lanceolatum* Rupr. ex Fourc. in Jalisco, Mexico. These maize relatives represent new host records for these leafhoppers as well as potential overwintering sites. A new species, *Dalbulus tripsacoides* DeLong and Nault n. sp., was collected from *Tripsacum dactyloides* (L.) L. on the southwestern side of the Sierra de Autlán. *Dalbulus tripsacoides* is morphologically the most primitive member of the genus, supporting our hypothesis that leafhoppers of the genus *Dalbulus* coevolved with maize from its *Tripsacum* ancestors. We also speculate that the *Dalbulus* species and the corn stunt spiroplasma, maize bushy stunt mycoplasma and maize rayado fino virus, pathogens vectored by these leafhoppers, have influenced the speciation and distribution of maize and its predecessors.

Deltocephaline leafhoppers of the genus *Dalbulus* DeLong (1950) are small (4 mm), pale yellow or cream colored and inconspicuous. These leafhoppers would go largely unnoticed and unstudied except that several species have been reported as vectors of three maize stunting pathogens endemic to the neotropics (Nault 1980, Nault and Bradfute 1979, Nault et al. 1980). *Dalbulus* species reported as vectors of these pathogens are *D. maidis* (DeLong & Wolcott), *D. elimatus* (Ball) and *D. guevarai* DeLong. Other species in the genus, none of which have been tested as vectors, are *D. acus* DeLong, *D. gelbus* DeLong, *D. longulus* DeLong and *D. distans* Linnovuari.

Southern Mexico appears to be a center for speciation of *Dalbulus* and the closely related *Balduvus* Oman (Fig. 1). This region is also the center of evolution for maize, *Zea mays* L. (Mangelsdorf 1974, Galinat 1977, Wilkes plant species most often recorded as a host for maize). Recently, a distant maize relative, *Zea diploperennis* Iltis, Doebley and Guzmán was discovered in Jalisco, Mexico (Iltis et al. 1979). The existent diploid, perennial teosinte was predicted earlier (1977) and others. The species is morphologically primitive and more than any other *Zea* spp. its presumed *Tripsacum* ancestors (Doebley 1980).

We have considered the possibility that *Dalbulus* and *Balduvus* leafhoppers have coevolved

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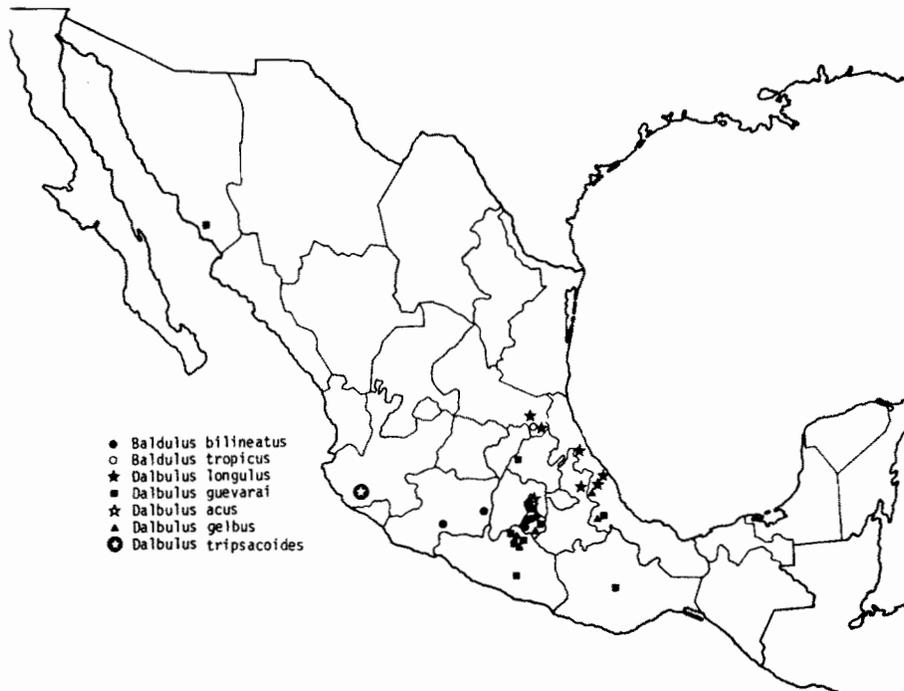


FIG. 1.—Distribution of Mexican *Baldulus* and *Dalbulus* spp. Locations are from Barnes (1954), DeLong (1950) and the DeLong collection, Ohio State University. Distributions of the two most abundant species, *D. maidis* and *D. elimatus* are given by Barnes (1954).

and its progenitors. Southern Jalisco could harbor unknown *Dalbulus* or *Baldulus* species which might offer clues to evolution of these genera. This region is not only the habitat for *Z. diploperennis* but its probable ascendent, the tetraploid, perennial teosinte, *Z. perennis* (Hitchc.) Reeves and Mangelsdorf (Galinat 1977, Iltis et al. 1979). Populations of Balsas teosinte (*Z. mays* ssp. *parviglumis* Iltis and Doebley), considered the most specialized of the annual teosintes (Doebley and Iltis 1980 and Iltis and Doebley 1980), also occur in Jalisco as well as several *Tripsacum* species.

The first author joined an expedition comprised of taxonomists, agronomists and plant pathologists (see Acknowledgment) to visit *Zea* and *Tripsacum* populations as well as cultivated maize in Jalisco. Since the male inflorescence is necessary for species identification of these grasses, the time of the trip (10–30–79 to 11–3–79) coincided with maturation of these species. Here we report the results of this survey for *Dalbulus* leafhoppers including the description of a new species. Based on these findings as well as previous work, we speculate on the putative co-evolution of these leafhoppers with maize and its ancestors.

### Results

At the time of collection, most maize in Jalisco was dry with few plants still green. A notable exception was

maize at breeding plots of the Instituto de Agronomico, Universidad de Guadalajara, Zapopán. Both *D. maidis* and *D. elimatus* were collected with a sweep net from maize foilage (Table 1). A small planting of *Z. diploperennis* (established by R. Guzmán M.) and a population of *T. lanceolatum* Rupr. ex Fourn. were infested with *D. maidis* and *D. elimatus*. At a commercial corn field near Santa Ana Acatlán, several plants at the field edge were still green. *Dalbulus maidis* as well as *D. elimatus* were collected. *Dalbulus maidis* were collected from *Z. diploperennis* at Zarza Mara, located just E. of Las Joyas high in the Sierra de Manantlán Occidental, ca. 22 km SSE of Autlán, 15 km SSW of El Chante, and both *D. maidis* and *D. elimatus* were collected from *Z. perennis* at Piedra Ancha near Ciudad Guzmán. A population of Balsas teosinte (*Z. m.* ssp. *parviglumis*) and an unidentified *Tripsacum* sp. near El Palmar were examined for leafhoppers, but due to lateness of season and previous drought, plants were dry and no leafhoppers were collected.

In addition to the collection of *D. maidis* and *D. elimatus* the following new *Dalbulus* species was collected.

*Dalbulus tripsacoides* DeLong & Nault n. sp. (Fig. 2)

Length of male 4 mm, female 4.3 mm. Crown rounded, typical of other species of *Dalbulus* (DeLong

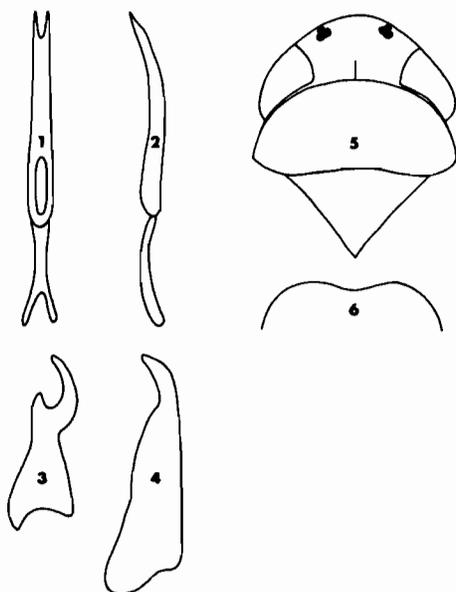


FIG. 2.—*Dalbulus tripsacoides* n. sp. 1. aedeagus (0.33 mm in length) ventrally, 2. aedeagus laterally, 3. style laterally, 4. plate ventrally, 5. head (1 mm in width), 6. posterior margin of seventh sternum of female.

1950). Color similar to *D. maidis*. Crown golden yellow with a round black spot just above margin, each side, closer to eyes than to median line. Yellowish coloration usually paler around each black spot. Pronotum yellow, disc usually darker golden brown. Scutellus yellow. Forewings yellowish, subhyaline, veins concolorous.

Female seventh sternum typically produced, spatulate-like, broadened apically, posterior margin broadly rounded.

Male genital plates four times as long as median width, narrowed on apical fourth and curved outwardly, apices blunt. Style with apophysis curved outwardly and narrowed to slender apex. Aedeagus elongate, slender, curved slightly dorsally, apex divided dorsoventrally, forming two parallel apical lateral processes. Pygofer rounded apically. Female genitalia with posterior margin of seventh sternum slightly roundly produced, broadly, slightly notched at middle.

Holotype male, 5–6 km S. of Puerto Los Mazos, 19°

42'N, 104° 26'W, Jalisco, Mexico X-30- '79, L. Nault coll. Collected by aspirator from *Tripsacum dactyloides* (L.) L. Paratypes 5 females, 8 males, same as holotype. Types in DeLong collection, Ohio State University.

*Dalbulus tripsacoides* has similar coloration to *maidis* but is easily separated by the distinct aede structures.

No nymphs of *D. tripsacoides* were collected from *T. dactyloides*, no doubt due to lateness of the season. Despite this we consider this *Tripsacum* sp. as the leafhopper's host plant. While collecting specimens with an aspirator, the first author frequently noted disturbed individuals to fly from their resting sites on *T. dactyloides* leaves and always return to alight on this plant despite the nearby presence of several other monocotyledonous and dicotyledonous plants.

The leaves of the *Tripsacum* host extended to 2–3 m high. Specimens were collected (R. Guzmán and L. Nault, voucher no. 1505) and deposited in herbarium, Instituto de Botanica, Universidad de Guadalajara. The type-locality is at 840 m above sea level on the north facing slope of a steep mountainside on SW side of Sierra de Autlán, part of Sierra Madre Occidental, halfway between Autlán de Navarro and Jimiro Castillo on Rt. 80. Other plants in the area include leguminous shrubs, composites and *Muhlenbergia* grasses.

#### Discussion

The corn leafhopper, *D. maidis*, is aptly named, though restricted to the New World, the species is found abundantly on maize in all tropical regions from southern USA (Nault and Knoke 1980) to Argentina and South America (Oman 1948). The species was recorded from the annual teosintes in Mexico by Barnes (1919). From our collections we can add *Z. diploperennis*, *T. lanceolatum* to the list of hosts. The first author has confirmed the status of the perennial spp. as hosts for *D. maidis* in laboratory and greenhouse studies (Nault, unpublished). Pitre (1966, 1970a, 1970b) earlier demonstrated *T. dactyloides* as an experimental host for *D. maidis*; nevertheless, leafhoppers reared on this grass took longer to develop, their survival was poorer and resultant adults weighed less than those reared on maize.

The second species, *D. elimatus*, also a maize specialist, has tentatively been designated as the "Mexican corn leafhopper" by Nielsen (1968). In his compre-

Table 1.—Collection of *Dalbulus maidis*, *D. elimatus* and *D. tripsacoides* from Jalisco, Mexico, 10–30–79 to 11–3–79.

Locality	Altitude (m)	Host	<i>D. maidis</i>		<i>D. elimatus</i>		<i>D. tripsacoides</i>
			♂	♀	♂	♀	
Las Joyas	1900	<i>Zea diploperennis</i>	4	3	0	0	0
Santa Ana Acatlán	1600	<i>Zea mays</i>	5	1	2	0	0
Ciudad Guzmán	2000	<i>Zea perennis</i>	3	19	8	7	0
Zapopán	1640	<i>Zea diploperennis</i>	31	13	0	1	0
		<i>Zea mays</i>	29	10	5	3	0
		<i>Tripsacum lanceolatum</i>	17	10	4	0	0
Los Mazos	1840	<i>Tripsacum dactyloides</i>	0	0	0	0	9

study of *Dalbulus* in Mexico, Barnes (1954) provided ample evidence for this name. Moreover, he noted that while both *D. elimatus* and *D. maidis* coexist on the former species was the most frequent above 1600 m while the latter dominated below this altitude in other regions. This is in contrast to our data. From collection sites in Jalisco at 1600 m or above, *D. maidis* was always more abundant than *D. elimatus* (see Table 1). Barnes concluded from his field and laboratory data that *D. maidis* utilizes only maize and teosinte as host. However, *D. elimatus* is less fastidious. Following maize harvest, the species disperses to wild and cultivated plants which serve as food plants during the cool, winter period. Moreover, some leafhoppers lay eggs in wheat and barley where resultant nymphs develop and mature to adults. Of 15 wild and introduced species tested, two *Bromus* species were hosts. Despite the fact that maize was still the host preferred by *D. elimatus*, unfortunately, Barnes failed to test or collect from *Tripsacum* species. Although few in number, we took *D. elimatus* from the two perennial *Zea* spp. and *T. lanatum*. It is possible that both *D. maidis* and *D. elimatus* use the perennial *Zea* and *Tripsacum* species as wintering hosts in Jalisco. However, the potential range of these grasses in this capacity may be limited to their infrequent occurrence.

Barnes (1954) also reported collecting low numbers of *gelbus* and *D. longulus* from maize. In referring to studies of Ramirez et al. (1975), De Leon (pers. comm.) reported that these workers also collected these species as well as a third, *D. guevarai*, from maize at the Morelos research station of Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT) at Tlaxcala. However, the ratio of these three species was low when compared to *D. maidis*. We do not consider maize as a principal host for *D. guevarai*. On 9–10–1979, the second author collected 954 *D. guevarai* by sweeping native grasses near Iguala, Guerrero. None of the leafhoppers in this large series was collected on maize.

Leafhoppers in the genus *Baldulus* are morphologically similar to *Dalbulus*. At one time *D. maidis* was placed in the genus *Baldulus* until DeLong (1950) separated the two based on differences of shapes of the female and male genitalia. The similarity between the genera may be more than morphological. An eastern species, *B. tripsaci* Kramer and Whitcomb, was recorded for its host, *T. dactyloides* (Kramer and Whitcomb 1968). Although *B. tripsaci* was never collected on maize, Granados and Whitcomb (1971) reared it on weetcorn for 8 months under laboratory conditions used it as a corn stunt vector. Unfortunately, plants are not known for two Mexican species, *B. bilineatus* DeLong and *B. tropicus* DeLong, or a Southern USA species, *B. montanus* Oman.

We propose that *Dalbulus* and *Baldulus* leafhoppers trace their origins back to *Tripsacum* and perhaps to its *isuris*-like, andropogonoid predecessors (Weatherwax 1935, Wilkes 1977, Galinat 1977). Furthermore we assume that the *Tripsacum* lineage which led to perennial *Zea* (Doebley and Iltis 1980) carried with it the *ulul* but not *Baldulus* leafhoppers. No *Baldulus* species has been collected from maize and we predict

that like *B. tripsaci*, hosts for other *Baldulus* species will be *Tripsacum* or perhaps *Manisuris* species. As the annual teosintes evolved from the perennials (Iltis and Doebley 1980), further speciation among the *Dalbulus* occurred. These species are represented today by *maidis*, *elimatus*, *gelbus*, *longulus*, and *guevarai*. When pre-Columbian man began to interfere with the evolution of *Zea* some 9,000 years ago, "creating" and then dispersing Indian corn throughout the Americas, one leafhopper from among those which co-evolved with the teosintes readily adapted to maize and outcompeted all others. The species is *D. maidis* which now has achieved the status of a maize pest. *Dalbulus tripsacoides*, the first *Dalbulus* species described from a *Tripsacum* host, assumes a central role in our argument. Its long, slender aedeagus is simpler and less elaborated than other members of the genus, suggesting its primitive status. This is precisely where we would anticipate an ancestral form to occur if Weatherwax (1935), Iltis (1972) and Doebley and Iltis (1980) are correct in assuming that *Tripsacum* is the forebearer of *Zea*.

Moreover, we consider it likely that the *Dalbulus* leafhoppers and the pathogens they transmit have had an influence on the speciation and distribution of maize and its ancestors. These vectors and pathogens would select against those genotypes not well adapted to their presence. Although the leafhopper transmitted corn stunt spiroplasma (CSS), maize bushy stunt mycoplasma (MBSM) and maize rayado fino virus (MRFV) have restricted host ranges, these hosts include several of the teosinte species and at least one *Tripsacum* sp. (Nault 1980, Nault et al. 1980). The distribution of extant Balsas teosinte populations at elevations above 800 m in Mexico (Wilkes 1972) may be due to *Dalbulus* and these pathogens. Corn stunt spiroplasma predominates at the low and middle elevations in Mexico (Davis 1974, Davis 1977, Maramorosch 1955), thus the Balsas teosintes may escape the damaging effects of this pathogen. Although MBSM (=Mesa Central corn stunt, Nault and Bradfute 1979) is found at high elevations in Mexico (Davis 1974, Davis 1977, Maramorosch 1955), susceptible teosinte species may tolerate presence of this mycoplasma under the cooler climatic conditions which prevail there. Experiments conducted in controlled environments revealed that MBSM causes a lethal maize disease at a high "tropical" temperature but not at a lower one (Nault 1980). Although these experiments were conducted only with maize, the response of susceptible annual teosinte species may be quite similar. The perennial teosintes, *Z. diploperennis* and *Z. perennis*, are either immune to or tolerant of MRFV and MBSM, but both are highly susceptible to CSS (Nault 1980, Nault et al. 1980). Both perennials are known only from high altitudes in Jalisco, a distribution which may be enforced by CSS. Maize rayado fino virus does not show a preference for either the warm low tropics or the cool highlands of Latin America (Gamez et al. 1979) nor does temperature affect symptom severity in maize (Martinez-Lopez 1977) as it does for CSS and MBSM, thus MRFV may not have influenced the geographical distribution of the *Zea* species. However, the high degree of susceptibility and lethal effects of MRFV to certain maize genotypes (Gamez 1980) does suggest

that this virus may have been a strong force in the evolution of maize ancestors. Lastly, we must not exclude the possibility that the *Dalbulus* leafhoppers alone, may have been a potent selective factor in maize evolution. Evidence for this comes from southern California where silage corn sustains severe damage due to the feeding of *D. maidis* (Bushing and Burton 1974) even in the absence of corn stunting pathogens.

We speculate that continued study of *Dalbulus* spp. in Meso America will provide further validation of hypotheses concerning maize evolution, provide an understanding of key factors influencing the distribution of extant *Tripsacum* and teosinte species, as well as primitive maize races, and reveal important sources of leafhopper and disease resistant germ plasm.

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