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GRASSHOPPERS OF THE MEXICANUS GROUP, GENUS MELANOPLUS (ORTHOPTERA: ACRIDIDAE)

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Introduction

Since the historic outbreaks of the Rocky Mountain grasshopper (*Melanoplus spretus* (Walsh)) in the 1870's, the close relatives of that species, especially the one recently called *M. mexicanus* (Saussure), have been of great economic importance in the United States and Canada. The present study was undertaken to clarify the status of the various taxonomic entities in this complex, and we hope it will stimulate further clarifying studies. We have also attempted to summarize briefly the more important information on the biology of each species.

For many years the status of *spretus* has been a puzzle to entomologists because no specimens have been collected since the early 1900's. Gradually the opinion developed that *spretus* disappeared because it was the migratory phase of a normally solitary grasshopper, and it was supposed that *mexicanus* was that species. Our study of

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the aedeagus indicates that *spretus* is a distinct species. Any further evidence bearing on this opinion naturally is very desirable.

It is chiefly on the basis of the differences in the aedeagus that *mexicanus* has been found to be distinct from the species commonly misidentified as *M. mexicanus* by American entomologists. The species most frequently misidentified as *mexicanus* is *M. bilituratus* (Walker), and the structure of the aedeagus further suggests that three subspecies merit recognition.

Limits of Group

The *mexicanus* group consists of *Melanoplus mexicanus* and five closely related species. There are five subspecies in addition to the typical ones. Distribution is limited to North America, from southern Mexico to the Arctic. At this stage in our knowledge of the species groups of *Melanoplus*, the best that can be offered as a definition of the *mexicanus* group is a somewhat loose combination of the following characters:

1. Pronotum with hind margin of the dorsal surface produced posteriorly, either broadly angulate or rounded (fig. 15).

2. Tegmina usually covering most or all of abdomen, often extending beyond it, sometimes covering only about a third of the abdomen (pl. 5), but always elongate, never lobate.

3. Male cercus (figs. 7, 8) varying from slender and somewhat rectangular to broadly and irregularly oval.

4. Male subgenital plate tending to develop a dorsal lip at the apex, sometimes posteriorly produced, frequently with twin apical knobs (figs. 11, 16).

5. Dorsal valve of aedeagus anterior to the apical portion of the main stem, usually well sclerotized, more or less concave laterally (figs. 1, 2, 3). Ventral valve of aedeagus relatively short, straplike, its apex usually visible in lateral view near the base of the dorsal valve, dorsad of the accessory lobe. Accessory lobe of aedeagus moderate to large, weakly sclerotized.

The name of the *mexicanus* group is taken from the specific name that has been used most often in the literature in recent years, though, as now restricted, *mexicanus* is neither the most widely distributed nor the most important species. *M. bilituratus* is the most widely distributed, and since the outbreak of *spretus* ended it has been the most important. Hebard (1935a, p. 57) recognized a *borealis* group; earlier (1928) he briefly discussed some members of the *mexicanus* group as he conceived it. It seems to us that the *mexicanus* group is sufficiently cohesive to be recognized as we are treating it, with *borealis* included, at least until the group relationships within *Melanoplus* are better understood. *M. femur-rubrum* (De Geer), genotype of *Melanoplus*, has not been included in this group, though the male cercus is very much like that of *borealis borealis*. The subgenital plate of *femur-rubrum* is not produced apically as in the members of this group. A distinctive character of *femur-rubrum* is a small

spinelike structure (x of fig. 1,*i*) borne near the base of the accessory lobe of the aedeagus; it does not seem homologous with the lateral projection from the dorsal valve in *mexicanus*.

TABLE 1.—*Checklist and index to specific and infraspecific names in the* mexicanus *group of* Melanoplus

(Page numbers refer to the present work; synonyms are shown in italics)

Name	*Author and year*	*Original genus*	*Present status*
affinis (p. 14)	Scudder, 1897 (Proposed as distinct species.)	Melanoplus	Syn. of bilituratus bilituratus
affinis (p. 42)	Scudder, 1897 (Proposed as form of M. devastator.)	Melanoplus	Syn. of devastator
alaskanus (p. 45)	Scudder, 1897	Melanoplus	Syn. of bruneri
angelicus (p. 14)	Scudder, 1897	Melanoplus	Syn. of bilituratus bilituratus
arcticus (p. 14)	Walker, 1870	Caloptenus	Syn. of bilituratus bilituratus
ater (p. 41)	Scudder, 1897	Melanoplus	Syn. of devastator
atlanis (p. 14)	Riley, 1875	Caloptenus	Syn. of bilituratus bilituratus
bilituratus (p. 12)	Walker, 1870	Caloptenus	Valid species
borealis (p. 67)	Fieber, 1853	Caloptenus	Valid species
bruneri (p. 45)	Scudder, 1897	Melanoplus	Valid species
caeruleipes (p. 52)	Cockerell, 1889 (Proposed as var. of spretus.)	Caloptenus	Syn. of spretus
coeruleipes (p. 14)	Cockerell, 1888 (Proposed as var. of atlanis.)	Melanoplus	Syn. of bilituratus bilituratus
cockerelli (p. 75)	Scudder, 1900	Melanoplus	Syn. of borealis stupefactus
consanguineus (p. 41)	Scudder, 1897	Melanoplus	Syn. of devastator
conspicuus (p. 42)	Scudder, 1897 (Proposed as form of devastator.)	Melanoplus	Syn. of devastator
defectus (p. 38)	Scudder, 1897	Melanoplus	Valid subspecies of bilituratus
devastator (p. 41)	Scudder, 1878	Melanoplus	Valid species
diminutus (p. 41)	Scudder, 1897	Melanoplus	Syn. of devastator
dimidipennis (p. 15)	Bruner, 1904	Melanoplus	Syn. of bilituratus
excelsus (p. 45)	Scudder, 1897	Melanoplus	Syn. of bruneri
extremus (p. 67)	Walker, 1870	Caloptenus	Syn. of borealis borealis
intermedius (p. 14)	Scudder, 1897	Melanoplus	Syn. of bilituratus bilituratus
junius (p. 68)	Dodge, 1876	Pezotettix	Syn. of borealis borealis
latifercula (p. 75)	Caudell, 1903	Melanoplus	Syn. of borealis stupefactus
mexicanus (p. 8)	Saussure, 1861	Pezotettix	Valid species

TABLE 1.—*Checklist and index to specific and infraspecific names in the* mexicanus *group of* Melanoplus—Continued

Name	*Author and year*	*Original genus*	*Present status*
monticola (p. 68)	Scudder, 1897	Melanoplus	Syn. of borealis borealis
obscurus (p. 42)	Scudder, 1897 (Proposed as form of devastator.)	Melanoplus	Syn. of devastator
palaceus (p. 78)	Fulton, 1930	Melanoplus	Valid subspecies of borealis
parvus (p. 68)	Provancher, 1876	Caloptenus	Syn. of borealis borealis
sapellanus (p. 75)	Scudder, 1900	Melanoplus	Syn. of borealis stupefactus
scandens (p. 68)	Scudder, 1897	Melanoplus	Syn. of borealis borealis
scriptus (p. 14)	Walker, 1870	Caloptenus	Syn. of bilituratus bilituratus
selectus (p. 8)	Walker, 1870	Caloptenus	Syn. of mexicanus
septentrionalis (p. 67)	Saussure, 1861	Pezotettix	Syn. of borealis borealis
sierranus (p. 15)	Scudder, 1897	Melanoplus	Syn. of bilituratus bilituratus
spretis (p. 55)	Thomas, 1865	Acridium	Unrecognizable; see p. 55
spretus (p. 52)	Walsh, 1866	Caloptenus	Valid species
stupefactus (p. 75)	Scudder, 1876	Pezotettix	Valid subspecies of borealis
typicalis (p. 42)	Scudder, 1897 (Proposed as form of devastator.)	Melanoplus	Syn. of devastator
uniformis (p. 41)	Scudder, 1897	Melanoplus	Syn. of devastator
utahensis (p. 81)	Scudder, 1897	Melanoplus	Valid subspecies of borealis
virgatus (p. 42)	Scudder, 1897	Melanoplus	Syn. of devastator
vulturnus (p. 25)			New subspecies of bilituratus

The species here treated in the *mexicanus* group were distributed by Scudder (1897b) in five different "series" of *Melanoplus*, and *M. borealis stupefactus* (Scudder) was in the genus *Podisma*. Those "series" of Scudder are not comparable to the groups of Hebard and other modern workers.

ANATOMY OF THE MALE GENITALIA

Since the appearance of Hubbell's (1932) important study, the concealed male genitalia of Acrididae have been utilized for distinguishing species and subspecies to a considerable extent. Roberts (1941) coordinated the terms for the structures useful to taxonomists with those studied by morphologists, and proposed several new single-word terms. Dirsh (1956) carried the study further, comparing nearly 800 genera and modifying previous terminology by several changes and a number of new terms.

The male genital mass or assemblage, preferably known as the phallic complex, including the aedeagus and its supporting apodemes, as well as the epiphallus—located anterior to the aedeagus (fig. 2,*b*)—is situated at the end of the abdomen beneath the supra-anal plate and the pallium (membranous covering usually dorsad of the subgenital plate). Taxonomically, the aedeagus and epiphallus are the most important organs of the phallic complex, and the critical parts of each are illustrated by *M. femur-rubrum* (fig. 1,*h*,*i*).

Methods and Technics

A brief outline of the technic employed in examining the male phallic complex may be helpful.

With freshly collected specimens it is a simple matter to slip back the pallium with a dissecting needle, thus exposing the aedeagus. The attaching muscles are easily disrupted sufficiently to permit the phallic complex to be lifted and pulled posteriorly. It is then exposed, attached to the subgenital plate, and is readily visible in the pinned specimen. However, for the most detailed study, removal of the phallic complex and its examination in alcohol are recommended. It may be preserved in a micro-vial, *partly filled* with glycerine, set at an angle beneath the grasshopper, with the pin passing through the cork of the micro-vial. The dry preparations still attached to specimens are adequate for sorting and for moderately critical study. In the case of dry grasshoppers, sufficient relaxation to permit exposure or removal of the phallic complex may be effected either by placing the specimens in a moist relaxing chamber for one or two days, or by dipping the end of the abdomen for a minute or two in water that is coming to a boil. Although very quick, the latter method frequently destroys the natural colors of the hind legs and results in crumpled tegminal apices; so the relaxing chamber is recommended if the future appearance of specimens is important.

Because of the difficulty of identifying females to species in some cases, our maps and distribution records, except as noted, are based on males. This practice has eliminated many uncertainties which otherwise would have entered into the distribution plotting for subspecies and for species of similar appearance which occupy the same areas. Lists of localities from which specimens have been examined, or full data on specimens, have been given only where they appear to be of considerable value. Localities are listed roughly in the order that they appear on the map, taken in rows from north to south, beginning in the east. For two or more localities very close together, only one spot is shown on the map. The intensive field work of the junior author in Manitoba, Saskatchewan, and Alberta would, for some species, have permitted the inclusion of an almost solid mass of dots on the map,

so in those cases only limital and representative localities are shown.

Tegmen (front wing or elytron) length is subject to inconsistencies unless a standard measurement is taken. Thus, it is measured "from the distal extremity of the tubercle formed by the junction of the subcostal and radial veins" (Proc. 4th Internat. Locust Conference, Cairo, p. 97, 1937) (also see Dirsh, 1953, for a treatment of standard measurements). We have tried to select specimens with tegminal apices intact, thus avoiding difficulties encountered when the tip of the tegmen is frayed (see Ramchandra Rao, Bull. Ent. Res., vol. 33, pp. 247–249, 1942).

Acknowledgments

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Several other entomologists have cooperated in supplying information or other help, and acknowledgment of their assistance appears in our discussion of the various species.

Figures 1,*a*,*d*,*e*; 2 (all except *f*); 9,*f*,*g*,*h*-2; and 15 were made by Arthur D. Cushman, Entomology Research Division, U. S. Department of Agriculture. All other drawings and the maps were made by the senior author.

Systematic Treatment

Key to species and subspecies of the *mexicanus* group of *Melanoplus*

(Based on males)

1. A distinct mesosternal swelling or "hump" present (fig. 1,*d*,*f*,*g*) 2
   Without a mesosternal "hump," or with a weakly developed one (fig. 1,*e*) . 7
2. Dorsal valve of aedeagus (fig. 3,*k*) of a general circular shape, appearing thin and parchment-like, and with a triangular projection (x of fig. 3,*k*) on the dorsal rim; subgenital plate usually without twin apices well developed (fig. 11,*a*-1,2,4,5), occasionally with them distinct (fig. 11,*a*-3). (Distribution: figs. 12, 13) . . . . . **bruneri** Scudder
   Dorsal valve variously formed (fig. 3,*a*–*h*) but not with a generally circular shape as in fig. 3,*k*; subgenital plate normally with well-developed twin apices (fig. 9,*f*,*h*-2), best seen in posterior view (fig. 10,*u*–*x*) 3
3. Dorsal valve of aedeagus strongly recurved laterally and posteriorly (fig. 3,*a*), the hornlike structure heavily sclerotized (pl. 2,D). (Distribution: fig. 14). **spretus** (Walsh)
   Dorsal valve (fig. 3,*b*–*f*) variously shaped, but not as in opposite category . 4
4. Dorsal valve of aedeagus with a lateral projection (p) from its ventrobasal region (fig. 3,*b*-1, lateral view; fig. 3,*b*-2, lateroventral view). (Distribution: figs. 4, 6) . . . . . **mexicanus** (Saussure)
   Dorsal valve without a lateral projection from its ventrobasal region . . 5
5. Dorsal valve of aedeagus (fig. 3,*c*) typically produced into a blunt hook or knob at lateroanterior angle (y), especially by a carina (x) which separates main lateral surface from a concave, heavily sclerotized ventroanterior marginal area (z). (Distribution: fig. 6). **bilituratus vulturnus,** new subspecies
   Dorsal valve (fig. 3,*d*–*f*) without a hook or knob at lateroanterior angle, and without a carina on main lateral surface, though the ventroanterior margin usually recurves as a lip (z of fig. 3,*d*) 6
6. Dorsal valve of aedeagus appearing inflated, typically with a concave anterior margin (x of fig. 3,*d*) and with a sinuate margin (z) of the recurved anterior flap (y), the latter wide. (Distribution: fig. 6). **bilituratus defectus** Scudder
   Dorsal valve with little appearance of inflation, without a concave anterior margin, and with a relatively straight margin of the recurved anterior flap, the latter of variable width, often narrow (fig. 3,*e*). (Distribution: figs. 5, 6) . . . . . **bilituratus bilituratus** (Walker)
7. Cercus (fig.7,*h*) narrow; subgenital plate usually with twin apices (fig. 9,*h*-2), though variable and occasionally poorly developed (fig. 10,*x*); aedeagus with apex produced dorsally beyond the base of dorsal valve (figs. 2,*k*; 3,*i*); dorsal valve extending primarily dorsoanteriorly. (Distribution: fig. 14) . . . . . **devastator** Scudder

Cercus (figs. 7,*j;* 8,*a–e*) usually less slender than above; subgenital plate most often without twin apices (fig. 11, *b–f*); apex of aedeagus scarcely extending dorsally beyond base of dorsal valve (fig. 3,*j*); dorsal valve extending primarily anteriorly, with a lateral twist. (Distribution: figs. 17, 18) . . 8

8. Tegmina covering about one-half of abdomen (pl. 5,E,F). (Occurs at very high altitudes; distribution: fig. 18). . . **borealis stupefactus** (Scudder)

Tegmina covering more than one-half of abdomen. 9

9. Subgenital plate with scarcely any or comparatively little dorsal or posterior development of the apex (fig. 16,*d*). (Distribution: figs. 17, 18).
borealis borealis (Fieber)

Subgenital plate with considerable dorsal or posterior development of the apex (fig. 16,*e–g*) 10

10. Subgenital plate (fig. 16,*f;* pl. 4,B) with apex conspicuously produced posteriorly. (Distribution: fig. 18) . . . . . **borealis utahensis** Scudder

Subgenital plate (fig. 16,*e*) produced dorsally more than posteriorly. (Abdomen often conspicuously recurved as in pl. 4,D.) (Distribution: fig. 18.)
borealis palaceus Fulton

Melanoplus mexicanus (Saussure)

FIGURES 2,*c;* 3,*b;* 4; 6; 7,*a;* 10,*f,g;* PLATE 1,A

Pezotettix mexicana Saussure, Rev. Mag. Zool., ser. 2, vol. 13, p. 160, 1861 (male, female, Temperate Mexico). Lectotype, here designated: Male labeled "Cordova, t. c." (printed), a separate green label "Melanoplus mexicanus Sauss." (apparently in Saussure's longhand). (Museum d'Histoire Naturelle, Geneva, Switzerland.)

Caloptenus selectus Walker, Catalogue of the specimens of Dermaptera Saltatoria in the collection of the British Museum, pt. 4, p. 682, 1879 (female, Oajaca (sic), Mexico). Lectotype, one of two females, selected by Uvarov (1925, p. 298).

The condition of the lectotype of *mexicanus* is good, with all appendages except antennae, right middle leg, and left hind tibia present. It is not an alcoholic specimen, and color is well preserved. Dark dorsal bands on hind femora are well developed, also the pale area of the lower third of the outer paginal area and the pink ventral surface. The hind tibia is deep pink. The aedeagus (dry on specimen) is typical of the species as shown by the series examined. The cercus is somewhat less robust than the one from Bledos, Mexico, illustrated (fig. 7,*a*-1). The mesosternal hump is well developed.

Charles Ferriere, curator of entomology at the Museum of Natural History in Geneva, has located 16 specimens (6 males, 10 females) of the original series of *mexicanus*. He kindly loaned 8 specimens, all bearing green name labels like that above. One female has the same locality label as the lectotype. Two females bear "Orizaba, Sumichrast," and one female "Orizaba, M. H. de Saussure." Two males without locality labels and one female "Orizaba, reg. temp. Sumichrast" prove to be *M. femur-rubrum* (De Geer), showing that the original series was a mixed one.

It is probable that the green labels are not original ones, but later ones written by Saussure, since the generic name *Pezotettix* is not used. The history of Saussure's travels suggests that the specimens seen are part of the original series studied by Saussure. Burr's obituary of Saussure (Ent. Record, vol. 17, pp. 167–170, 1905) records Saussure's visit to the New World, and mentions an article published by him about the volcano of Orizaba in 1858. This volcano is adjacent to Córdoba (spelling now usually followed). Saussure (1870, p. 2) referred to Fr. Sumichrast (one of the collectors of *mexicanus* types) as his old aide and travel companion. The abbreviation "t. c." is Spanish for "tierra caliente" (warm region), as indicated by Hebard (1932a, p. 281). However, the specimens may have been taken under temperate conditions, as Córdoba, about 50 to 60 miles west of Veracruz, in the State of Veracruz, is at the base of Mount Orizaba. The wide variety of zonal conditions encountered when one descends from Mount Orizaba to Córdoba is mentioned by Goldman (1951, p. 279). Also, Sumichrast, and apparently Saussure too, collected extensively at nearby Mirador (see Goldman, p. 276), and, depending on the detail with which specimens were labeled, some of the original *mexicanus* series may have originated there. Five males taken at La Cumbre, near Córdoba, at an elevation of 6,000 feet, by Dr. H. R. Roberts in 1936, agree perfectly with the lectotype.

Uvarov (1925, p. 298) placed *selectus* in synonymy. A male from Ocotlán, Oaxaca, which is near the type locality of *selectus*, has been examined by us and is considered typical of *mexicanus*.

Two specimens, male and female (ANSP), from "littoral du Mexique," labeled as "*Platyph. mexicanus* Sauss.," apparently by Saussure, and as paratypes of *Platyphymus mexicana* Saussure by Hebard, are really *Melanoplus mexicanus*. The incorrect name labels may have been prepared accidentally by Saussure; at any rate *Platyphyma mexicanum*, described by Brunner in 1861, is a very different insect with short elliptical tegmina. Hebard (1932a, p. 281) treated *mexicanum* Brunner as a synonym of *Pedies virescens* Saussure. The two specimens noted probably are the "paratypes" mentioned under *Melanoplus mexicanus* by Hebard (1928, p. 279), since they are standing under *M. mexicanus* in the Philadelphia collection. Walker's *Caloptenus mexicanus* (1870, p. 682) was placed in the synonymy of *Platyphyma mexicanum* Brunner (there called *Paradichroplus mexicanus*) by Scudder (1897b, p. 19).

The early literature dealing with *Melanoplus mexicanus* is scanty. Thomas (1873, p. 222) merely listed it (as *Pezotettix mexicana*) from Mexico, and he paraphrased Saussure's description. Bruner (1908, p. 301) stated that he saw specimens of *M. devastator* which were labeled, probably by Saussure, as *Pezotettix mexicana* with a query.

Bruner further inferred that Saussure's type series may have been mixed, and that another included species may have caused Brunner von Wattenwyl (1900, p. 257) to transfer *mexicana* to *Dichroplus*. Bruner felt that Brunner must have examined Saussure's types. We have not seen the material which Brunner recorded from Colombia as *Dichroplus mexicanus*, but an error probably occurred. Scudder (1897b, p. 404) listed *Pezotettix mexicana* as undetermined, but (p. 405) he suggested that it might be the same as *Melanoplus atlanis*. Kirby (1910, p. 513) correctly placed *mexicana* near *atlanis* Riley and *spretus* Thomas (true *spretus*, though incorrectly credited to Thomas), but elsewhere (p. 487) placed it in *Trigonophymus*. The latter placement apparently refers only to the portion of Saussure's type series which Brunner associated with Colombian specimens. Hebard (1917, p. 271) first brought the name *mexicanus* into general use when he applied it to the widespread grasshoppers which we now recognize as a complex, and he placed *atlanis* of authors in synonymy, though retaining *atlanis* Riley for a population of eastern United States and vicinity.

Descriptive notes: A small to medium-sized member of the *mexicanus* group. Head with dorsal carinae of vertex more prominent and conspicuous, and closer together at anterior margins of eyes than in *bilituratus*, especially in male; antenna about one-third longer than head and pronotum combined (male), about equal to combined length (female); a small to medium-sized mesosternal hump present in male.

Male genitalia: Cercus with extremes as illustrated (fig. 7,*a*), usually approximating that of figure 7,*a*-2; furculae slender, tapering, usually divergent, about one-third as long as supra-anal plate; subgenital plate moderately upturned in lateral view, twin apices (posterior view) prominent, the intervening depression rather deep and well rounded; dorsal valve of aedeagus not extending dorsad nearly so far as apex of aedeagus, the anterior and dorsal margin covered by a light membrane, a pronounced lateral process (P of fig. 3,*b*) borne on ventral margin, near tip of ventral valve; accessory lobe large for group, larger than in *bilituratus*.

Female genitalia: As illustrated (fig. 10,*f*,*g*); cercus triangular, apex well rounded.

Coloration: General color not distinctive, medium to dark for group, no rich yellow specimens seen. Hind femur with four dark transverse dorsal bands (including knee), inner paginal area irregularly tinged with pinkish, followed by solid pink below, outer paginal area dull brownish, paler along ventral margin and at base, ventral surface deep pink; hind tibia variable, either dark pink or ashy greenish gray.

VARIATION: Seven representative males, measured in millimeters, vary in pronotal length from 3.3 to 4.5 (average, 4.0), in length of hind femur from 9.5 to 13.0 (av. 11.3), and in length of tegmen from 13.2 to 19.0 (av. 16.0). The smallest male is from Atoyac, Mexico, the largest ones from Mt. Alvarez, Mexico, and 18 miles north of Alpine, Tex. Three measured females vary in pronotal length from 4.3 to 5.1 (av. 4.7), in length of hind femur from 12.4 to 13.5 (av. 12.8), and in length of tegmen from 17.0 to 21.0 (av. 18.7). The tegmina of most specimens exceed the hind femur by about the maximum width of hind femur, by somewhat more than that in a few specimens, while in one specimen (north of Tehuacán) the tegmina reach only to the femoral apices. Most, but not all, specimens collected within the past 20 years have pink hind tibiae, but in most old specimens and a few recent ones the hind tibiae are ash or greenish gray. Apparently some variation occurs in nature, though killing agents and the conditions of preservation may be responsibile for some loss of color.

The shape of the dorsal valve of aedeagus is variable in dry preparations, due to shriveling. The membrane along the anterior margin then often becomes indistinct and the margin becomes irregular, sometimes indented. The lateral process is of uniform length, for the most part, but is below average length in the male from Alpine, Tex. The dorsal shoulder at the base of the apical "scoop" of the dorsal ovipositor valve is somewhat variable, occasionally more angular than in fig. 10,*q*.

DISTRIBUTION: The map (fig. 4) shows the distribution of *mexicanus*, based on specimens examined. Two lots of Texas specimens have been examined: 4 miles west of Ft. Stockton, Pecos Co., Aug. 8, 1955, J. R. Hilliard (2 ♂, 3 ♀); in Jeff Davis Co. 18 miles north of Alpine, June 19, 1939, F. B. Isely (1 ♂). Hebard (1917; 1932a) listed other Mexican localities, but only one Mexican State, Querétaro, additional to those on the map, is represented by those records. It is probable that all or most localities represented by Bruner's specimens (1908) were reported by Hebard because he acquired Bruner's collection of North American Orthoptera. Hebard (1925b) did not report *mexicanus* from Sinaloa, but collections from northwestern Mexico, in general, have not been extensive. More collecting is needed to determine the distribution of *mexicanus* in Texas, but the paucity of records suggests scarcity or localized occurrence. Tinkham (1948, p. 619) had no records other than to repeat the El Paso record of *atlanis* by Rehn and Hebard (1909). El Paso specimens have not been examined, but they probably represent *M. bilituratus defectus*.

BIOLOGY: No detailed information on the biology of *mexicanus* is available. The data on the specimens examined show occurrence in central Nuevo León at altitudes of both 2,200 and 7,000–8,000 feet,

in Guerrero at altitudes ranging from 5,000 to 8,000 feet, and in Michoacán from 6,000 to 8,000 feet. The series of about 35 Mexican specimens examined includes captures made in all months except January and April, and it is evident that there is more than one generation, perhaps continuous breeding, slowed down by unfavorable local conditions.

Melanoplus bilituratus (Walker)

This widespread, variable species is represented by most of the material which, in recent years, has been referred to *Melanoplus mexicanus mexicanus*. Exceptions are specimens now recognized as true *M. mexicanus*, and *M. spretus*. Specimens of *M. bilituratus* from the Far West occasionally have been confused with *M. devastator*, sometimes referred to as *M. mexicanus devastator*. As mapped by Newton and Gurney (1956–57) (as *mexicanus complex*), *bilituratus* occurs almost throughout the United States, except for peninsular Florida. Our present maps (figs. 5, 6) are based on males the aedeagi of which have been examined to determine the subspecies concerned.

While more detailed research may warrant the recognition of a larger number, the material now examined, which is representative of most areas, seems to justify only three subspecies. There is some indication that ecological subspecies, recognized by color and size, do occur, especially in Canada and Alaska (see p. 20). Brooks (1958, p. 20) has recognized these differences by treating *atlanis* (Riley) as a valid subspecies; however, the senior author doubts the value of applying names to these questionable ecological subspecies at this stage in the study, and *atlanis* is regarded as a synonym.

The reason that the three populations concerned are recognized as subspecies, and not species, is that in each case intergradation in structural characters of the aedeagus occurs. Except for material from Texas, intergrading specimens are here discussed under the appropriate subspecies. Those from Texas are of sufficiently uncertain relationship that it seems best to discuss them in one place. Males from Gainesville and several other Texas localities as listed below are typical or essentially typical of *bilituratus vulturnus*. Some divergence, in that the carina of the dorsal valve of aedeagus is not well developed, is shown by some specimens from Austin and Wichita Falls. The male from Phantom Lake, Davis Mountains, appears typical of *bilituratus defectus*, but one from nearby Marfa and those from Blanco County, Plainview, Lubbock, and Sweetwater are not typical *bilituratus defectus* and are best considered intermediates of uncertain relationship. The specimen from Kokernot Mountain, Alpine, Tex., is unusual in that the anterior margin of the dorsal

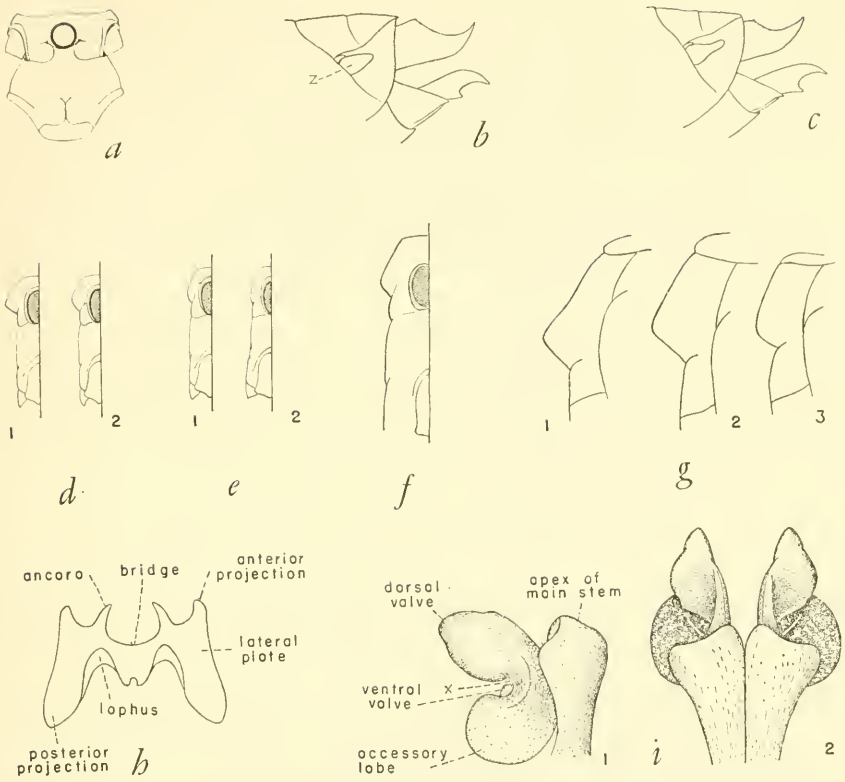

FIGURE 1.—*a*, Sketch showing location (circle) of mesosternal hump in ventral view of thorax of certain species of *Melanoplus*. *b*, *Melanoplus bilituratus bilituratus*, female, Medicine Lake, Mont., apical portion of abdomen (z, cercus). *c*, *M. femur-rubrum*, female, Poplar, Mont., same view as *b*. *d–g*, Males, showing lateral view of mesosternal area in lateral profile: *d*, *M. bilituratus:* 1, *M. b. vulturnus*, Marshall, Mo.; 2, *M. b. bilituratus*, Pullman, Wash. *e*, *M. devastator:* 1, 2, two specimens from Tulare, Calif. *f*, *M. spretus*, Minnesota, Oct. 6, 1876. *g*, *M. bruneri:* 1, East Spanish Peak, Colo.; 2, Fishers Peak, Colo.; 3, Mt. Moriah, Nev. *h–i: M. femur-rubrum*, male, Euclid, Minn.: *h*, dorsal view of epiphallus; *i*, aedeagus: 1, lateral view; 2, dorsoposterior view.

valve is irregular (fig. 3,*g*); the specimen is not typical of any one of the subspecies, nor is it like the Marfa specimen. Additional material from western Texas is required to determine the relationship of the one or more populations present.

Texas males of *bilituratus* examined are as follows:

M. bilituratus vulturnus: Gainesville, Wichita Falls, Quanah, Dallas, College Station, Austin, Wimberley, 2 miles east of Cedar Creek, Bastrop Co.

M. bilituratus defectus: Phantom Lake (Davis Mountains).

Intermediates of uncertain relationship (*M. bilituratus* in a broad sense): Blanco Co., Plainview, Lubbock, Sweetwater, Marfa.

As mentioned under the respective subspecies, the occurrence of two annual generations has been reported for *bilituratus defectus*, and evidence suggesting two generations or a partial second generation has been presented for *bilituratus vulturnus* and typical *bilituratus*. In some cases the evidence consists of a second peak of adult abundance during a year. In recent years several important discoveries have been made concerning diapause in the eggs of grasshoppers, as reviewed by Lees (1955, pp. 7, 46, 68, 127). Further studies may disclose that the subspecies of *bilituratus* differ with respect to diapause.

Entomologists frequently have had difficulty distinguishing between the females of *bilituratus* (in the past usually called *mexicanus* or *atlanis*) and *femur-rubrum*. With a little practice it usually is a simple matter to separate them by the cerci (fig. 1,*b*,*c*), which are much more slender and apically acute in *femur-rubrum*.

Melanoplus bilituratus bilituratus (Walker)

FIGURES 1,*b*,*d*-2; 2,*e*,*f*; 3,*e*,*m*; 5; 6; 7,*f*,*g*,*l*; 8,*j*,*m*; 9,*g*; 10,*g*,*n*; PLATE 1,B,C.

Caloptenus bilituratus Walker, Cat. Derm. Salt. B. M., pt. 4, p. 679, 1870 (male, female, Vancouver Island, Canada; not 2 females, see Uvarov, 1925, p. 298). Lectotype, designated by Uvarov (1925, p. 298): Male from Vancouver Island (BM).

Caloptenus scriptus Walker, Cat. Derm. Salt. B. M., pt. 4, p. 680, 1870 (females, Vancouver Island, Canada). Lectotype, designated by Uvarov (1925, p. 298): Female from Vancouver Island (BM).

Caloptenus arcticus Walker, Cat. Derm. Salt. B. M., pt. 4, p. 681, 1870 (one female, "Arctic America. Presented by Dr. Rae"). New synonymy.

Caloptenus atlanis Riley, Seventh Ann. Rep. Nox. Benef. Ins. Missouri, p. 169, 1875 (males, females, Boscawen, Merrimack Co., N. H.). New synonymy. Lectotype, here designated: Male labeled "N. H., type no. 1153, U. S. N. M., Type, Caloptenus Atlanis Riley" (USNM).

Melanoplus atlanis, var. *coeruleipes* Cockerell, Entomologist, vol. 21, p. 301, 1888 (near Templar Rock, Custer Co., Colo.). New synonymy.

Melanoplus affinis Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 20, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 132, 171–172, pl. 12, fig. 2, 1897. (See Hebard, 1917, footnote, p. 251.) (Males, females, 8 localities in Utah, Wyoming, Washington, and British Columbia.) New synonymy. Lectotype, designated by Rehn and Hebard (1912, p. 79): Male from Salt Lake Valley, Utah (ANSP).

Melanoplus angelicus Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 22, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 133, 202–203, pl. 13, fig. 10, 1897 (2 males, Los Angeles, Calif.). New synonymy. Lectotype, designated by Rehn and Hebard (1912, p. 80): Male from Los Angeles, Calif. (USNM).

Melanoplus intermedius Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 20, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 132, 172–174, pl. 12, figs. 3, 4, 1897 (males, females, 5 localities in Colorado, Montana, Wyoming, Idaho, and Washington). New synonymy. Lectotype, designated by Rehn and Hebard (1912, p. 79): Male from Yellowstone, Mont. (ANSP).

Melanoplus sierranus Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 21, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 133, 193–194, pl. 13, fig. 1, 1897 (males, females, Lake Tahoe, Placer Co., Calif.; Placer Co., Calif.; Truckee, Nevada Co., Calif.). New synonymy. Lectotype, designated by Rehn and Hebard (1912, p. 80): Male from Truckee, Nevada Co., Calif. (MCZ).

Melanoplus dimidipennis Bruner, Colorado Agr. Exp. Sta. Bull. 94, pp. 66–67, 1904 (one male, Fort Collins, Colo.). New synonymy.

The unique type of *dimidipennis* and all lectotypes except those of *bilituratus* and *scriptus* have been examined. Uvarov (1925) synonymized *scriptus* and also suggested (p. 299) that *arcticus* may represent *M. femur-rubrum* (De Geer), but Dr. David R. Ragge (in litt., Feb. 22, 1957) has reported that the cercus of the unique female type of *arcticus* is much blunter than that of *femur-rubrum*, and he states definitely that the two names are not synonymous. He has found that except for pale color *arcticus* agrees very well with an Alaskan specimen of *bilituratus* which was sent for comparison; the wing lengths of the two specimens are almost identical. Since the Rae specimen described by Walker apparently came from the region of the Mackenzie and Slave Rivers (see Richardson, 1852, p. 476), and specimens of *bilituratus* from that region agree essentially with the Alaskan ones, we regard *arcticus* as a synonym. Hebard (1928, pp. 279–280) placed *affinis*, *atlanis*, and *intermedius* as synonyms of *M. mexicanus mexicanus;* this was done without reference to the aedeagus. Hebard (1929, p. 391) placed *dimidipennis* as a synonym of *bruneri;* however, the aedeagus of the type shows that it is *bilituratus*. The type of *dimidipennis* is small and unusually short-winged, with the external genitalia including features like both *bruneri* and *bilituratus*, but not fully typical of either. It probably is an abnormal individual, as Hebard suggested. Scudder (1879b, p. 179) placed *coeruleipes* as a synonym of *atlanis*. No type specimens of *coeruleipes* are known, and since Cockerell (1888) simply applied the name without a formal description to individuals of *atlanis* (as then so-called) with bluish hind tibiae, and only one nominal form of *bilituratus* occurs in the area concerned, *coeruleipes* is relegated to the synonymy. The spelling was given as "*caeruleipes*" by Cockerell (1889).

Descriptive notes: A usually medium-sized, fully winged member of the *mexicanus* group. Head with dorsal carinae of vertex moderately prominent; mesosternal hump strongly developed in male, absent in female.

Male genitalia: Cercus variable (fig. 7,*f*), over most of eastern half of range about as in figure 7,*f*-1; in Utah, California, Idaho, Oregon, Washington, and coastal British Columbia averaging narrower (fig. 7,*f*-2–4); in Nevada often decidedly slender, especially from near Reno (fig. 7,*f*-5–6); furculae about one-third to nearly one-half as long as supra-anal plate, straight or divergent; subgenital

plate (fig. 10,*w*) with twin apices usually conspicuous, rarely poorly differentiated. Aedeagus with dorsal valve well sclerotized and with a narrow to rather wide marginal fold, anterior margin usually broadly rounded, rarely with traces of sinuation such as in *bilituratus defectus*; accessory lobe of medium size for group; epiphallus with lophus rarely showing anterior angulation in lateral view, and then poorly developed, usually erect, in dorsal view the apex of lophus broad and semitruncate (figs. 2,*e,f;* 3,*e;* 8,*j,m*).

Female genitalia: Cercus (fig. 10,*g*) subtriangular, relatively blunt; dorsal valve of ovipositor with "scoop" (fig. 10,*n*) moderately rounded, the shoulder obtusely angular.

Variation: The size of 11 representative males, measured in millimeters, varies in pronotal length from 3.4 to 5.1 (av. 4.3), in length of hind femur from 9.8 to 13.7 (av. 11.6), and in length of tegmen from 15.0 to 25.0 (av. 21.1). Eight measured females vary in pronotal length from 3.7 to 5.5 (av. 4.7), in length of hind femur from 12.0 to 14.0 (av. 12.8), and in length of tegmen from 17.0 to 21.0 (av. 18.0). Eastern specimens average smaller than those from the West.

Tegminal length is decidedly variable. Unusually long-winged specimens are occasionally encountered. Among them are a female from Doniphan Co., Kans., Sept. 9, 1940, with tegmina reaching 9 mm. posterior to the hind femora, and two females taken in Fergus Co., Mont., Aug. 16, 1940, with comparable measurements of 6.5 and 7.5 mm. A series of six females and two males was found dead in a recently baited field at Fort Benton, Mont., July 14, 1940, by Parker and Butcher. The average length of the tegmina extending beyond the hind femora in the females of that series is 5.1 mm., with

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Explanation of Figure 2

Lateral views of aedeagus, and (*b* only) dorsal view of aedeagus and epiphallus in natural position within phallic complex.

a, b: *Melanoplus bruneri*, Ft. McLeod, Alberta, Canada.
c: *M. mexicanus*, Mt. Alvarez, Mexico.
d: *M. mexicanus*, Guerrero, Mexico.
e: *M. bilituratus bilituratus*, Placer Co., Calif.
f: *M. bilituratus bilituratus*, Victoria, Vancouver Island, British Columbia, Canada.
g: *M. bilituratus*, uncertain subspecific position, Guymon, Okla.
h: *M. bilituratus*, uncertain subspecific position, 18 miles north of Alpine, Tex.
i: *M. bilituratus defectus*, Mesilla Park, N. Mex.
j: *M. bilituratus vulturnus*, Stone Mountain, Ga.
k: *M. devastator*, lectotype.
l: *M. bilituratus defectus*, Casa Grande, Ariz.
m: *Melanoplus* sp., probably abnormal *bilituratus vulturnus*, Muscatine Co., Iowa.
n: *M. spretus*, Nebraska.

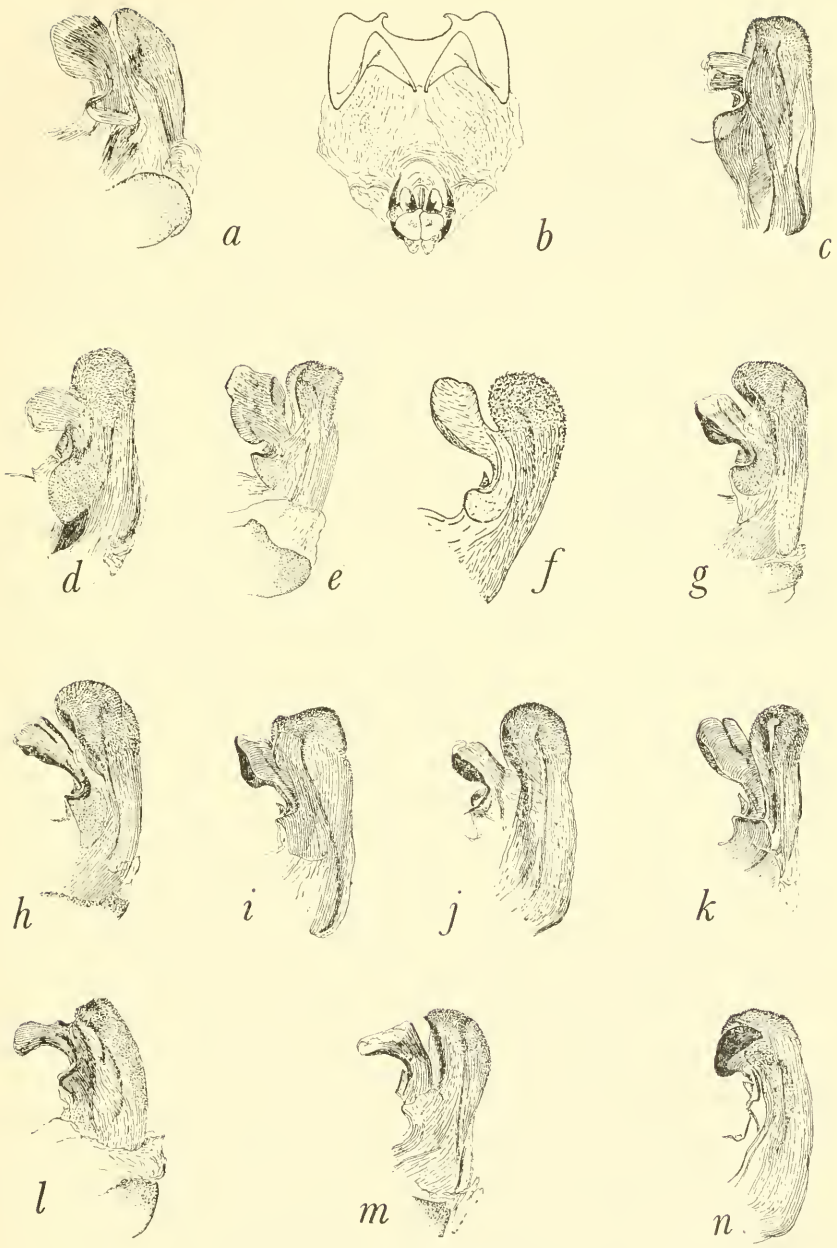

FIGURE 2.—Explanation on facing page.

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a maximum of 8.5; for the males the average is 8.3, the maximum 11.0 mm. The aedeagus of the shorter-winged of the two males is normal for *bilituratus bilituratus,* and the cercus is comparatively narrow. The other male, with a wider cercus (fig. 7,*g*), has the dorsal valve of the aedeagus rather irregular along the lateroanterior margin, but without any indication of *spretus.* A male with a similarly abnormal dorsal valve was taken in Flathead Co., Mont., July 8, 1917, and its tegmina exceed the hind femora by 5.5 mm. Rehn (1952) noted the considerable variation shown by Alaskan specimens. The folded tegmina of some individuals examined by him scarcely surpassed the apices of hind femora, while those of other individuals exceeded the femora by a distance about equal to pronotal length.

Rehn and Hebard (1906), under the names *intermedius, atlanis,* and *bilituratus,* discussed the variation observed in the cerci and other organs of specimens from various Western States. When recording this grasshopper from Oregon, Fulton (1930) used the name *M. mexicanus bilituratus,* and he observed that cerci of males vary from a little less than twice as long as middle width to nearly three times as long as broad. He noted that a series from Malin had consistently narrower cerci than those from other Oregon localities.

It is evident from rearing experiments under different conditions of temperature, relative humidity, and food (Parker, 1930) for *bilituratus bilituratus* (called *mexicanus mexicanus*), that size, color, spotting of tegmen, length of tegmen, and color of hind tibia vary in

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Explanation of Figure 3

Except as noted, lateral views of aedeagus drawn from preparations in glycerine.

a: *Melanoplus spretus:* 1, Arapahoe Peak, Colo.; 2, 3, neotype, posterior and lateral views of aedeagus, dry preparation.

b: *M. mexicanus:* 1, 18 miles north of Alpine, Tex.; 2, Durango, Mex., lateroventral view of aedeagus (p, lateral projection).

c: *M. bilituratus vulturnus:* 1, holotype, dry; 2, Priest Bridge, Md. (m, membranous fold; x, carina; y, hooklike apex; z, concave area).

d: *M. bilituratus defectus,* Tempe, Ariz., reared (x, anterior margin; y, flaplike area of dorsal valve; z, sinuate margin of flap).

e: *M. bilituratus bilituratus,* Wasaga Beach, Ontario, Canada.

f: Intermediate between *M. bilituratus bilituratus* and *M. bilituratus defectus,* Baker, Nev., dorsal valve only.

g: *M. bilituratus,* uncertain subspecific position, Kokernot Mt., Alpine, Tex., dorsal valve only.

h: *M. bilituratus defectus,* Chandler, Ariz.

i: *M. devastator,* Roseville, Calif.

j: *M. borealis borealis,* Nachvak Bay, Labrador, Canada.

k: *M. bruneri,* Mt. Moriah, Nev. (x, triangular projection of dorsal rim of dorsal valve).

l: Same specimen as *k*, right half of aedeagus in dorsal view.

m: *M. bilituratus bilituratus,* Vancouver Island, British Columbia, Canada, same view as *l.*

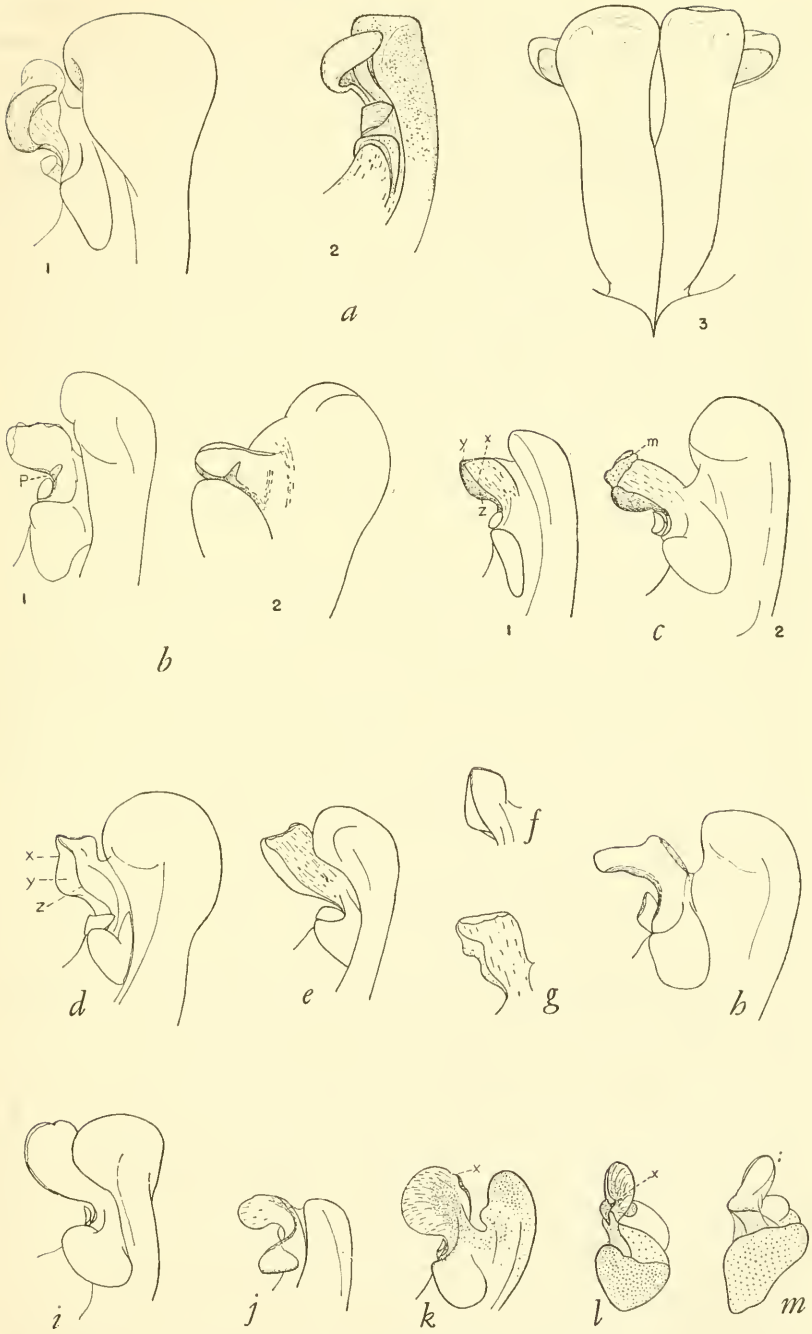

FIGURE 3.—Explanation on facing page.

response to ecological conditions. For these reasons, and perhaps because of genetic factors as well, *bilituratus bilituratus* shows much diversity in superficial appearance. This is especially evident in regions where a number of comparatively distinct, large, and relatively stable ecological associations occur; such large and diverse areas occur across southern Canada and in the mountains. The junior author has attempted to segregate Canadian specimens on the basis of the above and other external characters. In the southern coastal areas of British Columbia and from Vancouver Island there are small to medium-sized, moderately dark, often more hairy specimens, the tegmina frequently barely covering the abdomen. In most of the interior of southern British Columbia (range lands) specimens of moderate size, more brownish, and with red hind tibiae occur. A single series taken at Westbank, British Columbia, in 1923 includes rather large, predominantly yellowish specimens with the tegmina only about long enough to cover the abdomen. In northern British Columbia, Northwest Territories, and in Alaska the type usually developed is very large, blackish, with reddish hind tibiae, and very long tegmina; obviously of the same type but somewhat smaller are specimens from the foothills of Alberta and from the forested regions of Alberta, Saskatchewan, and Manitoba. In the grasslands of southern Alberta, Saskatchewan, and Manitoba the predominant type is of moderate size and grayish, with the tegmina extending scarcely beyond the abdomen, and usually with bluish or buff hind tibiae; in the eastern, more humid part of this area (parklands) the form is similar but more brownish and more often with reddish hind tibiae, very like specimens from interior British Columbia. In Ontario and Quebec specimens are nearly intermediate between those from the forested area of the prairie provinces and from the eastern grasslands, usually have red hind tibiae, and are comparatively stable in appearance. In dry years, during periods of grasshopper abundance, and when there is a trend toward swarming, the grassland types of central Canada develop longer tegmina, are of increased size and paler color, and usually have bluish hind tibiae. By and large, in Canada, observations suggest that most if not all major ecological areas have a smaller, grayer, shorter-winged type during "poor grasshopper years" and a larger, more yellow, and longer-winged type during "good grasshopper years." These differences seem more noticeable in areas which generally are dry than in those where moisture is abundant.

Genitalic characters of the populations in different parts of Canada do not differ significantly or consistently enough to warrant, at this stage of our knowledge, the recognition of separate subspecies. It would appear that the superficial appearance of the populations in

different areas is largely the result of surrounding conditions. Eventually, studies may show that the recognition of additional named segregates is desirable.

The dorsal valve of the aedeagus may have a narrow anterior flap and a rather shallow lateral concavity (figs. 2,*f;* 3,*e*), or approach the more swollen type found in intergrades with *defectus* (fig. 3,*f*), with wide anterior margin and deep lateral concavity. Practice is required to become familiar with the variation, which apparently is partly individual and partly geographic. A very small male with abortive wings, collected at Clark, Wyo., Aug. 7, 1937, has the dorsal valve rather stubby, without the usual details, and apparently imperfect because of the failure of the individual to develop normally.

FIGURE 4.—Distribution of male specimens of *Melanoplus mexicanus* examined.

The distribution of males of *bilituratus bilituratus* examined is shown in figures 5 and 6.

BIOLOGY AND ECONOMIC IMPORTANCE: The great importance of *M. bilituratus bilituratus*, which represents the northern subspecies of what usually has been called *M. mexicanus* or *M. atlanis*, is well known. Important bulletins dealing with this grasshopper are by Herrick and Hadley (1916) and by Shotwell (1930, 1941). Although crop and range damage occur most often west of the Mississippi River, injury on a smaller scale occurs in the Eastern States. Washburn (1953) described a severe outbreak on two farms near Palmer, Alaska, in late July 1951, in which populations up to 300 per square yard were

recorded, and vegetables, oats and raspberries were seriously injured. Early July in that locality was the warmest in 35 years, and that condition may have brought about the early maturity and great abundance of this grasshopper.

M. bilituratus bilituratus is decidedly migratory at times, and in areas of abundance is usually much more inclined to loose group movements than are most grasshopper species. Parker, Newton, and Shotwell (1955) have described the spectacular flights which in 1938–1940 occurred in North Dakota, South Dakota, Montana, and portions of nearby States and Canada. These flights occurred during an outbreak cycle, and a general population increase had preceded the flights. Drake and Tauber (1946) discussed flights which entered Iowa from the west in 1941 and earlier years.

Corkins (1922) reported on extensive flights in 1920, mainly in Bottineau and Renville Counties, N. Dak., and he noted their resemblance to the historic flights of *spretus*. By the use of an airplane one heavy swarm was examined and found to be most dense at an altitude of 500–800 feet, with a few individuals at 1,650 feet.

Nymphs as well as adults occasionally migrate (Parker, et al., 1955, p. 16; Shotwell, 1930, p. 24).

Early papers (Herrick and Hadley, 1916; Shotwell, 1930) gave the impression that *bilituratus bilituratus* is almost omnivorous in its food habits. In recent years, however, entomologists have become keenly aware that many grasshoppers are far from being the general feeders which they were once thought to be, and several investigations

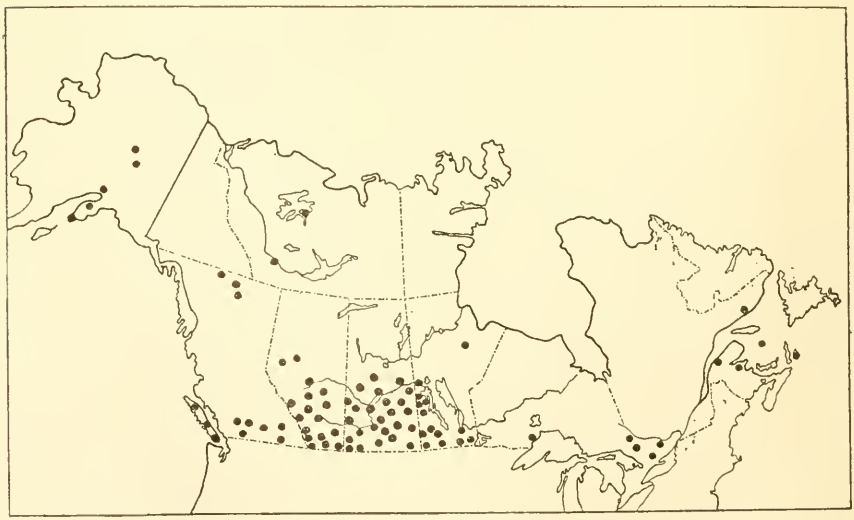

Figure 5.—Distribution of male specimens of *Melanoplus bilituratus bilituratus* examined from Alaska and Canada.

suggest that *bilituratus bilituratus* has definite responses and preferences concerning food plants. In cage studies conducted in eastern Wyoming, Pfadt (1949) found that adults preferred dandelion and wheat to all other plants which he tested, that tansymustard and dandelion gave the most nymphal growth, and that dandelion, wheat, and tansymustard were most favorable to egg production. In Manitoba, Smith, Hanford, and Chefurka (1952) fed certain plants through three successive generations (in cages) and recorded survival, rate of development, and the number of eggs laid. They found that wheat, barley, and dandelion were the most favorable food plants, and that Russian thistle and alfalfa were the least favorable. However, Anderson and Wright (1952) found during Montana field studies that feeding occurred on a wide variety of plants, representing a wider host range than suggested by Pfadt's cage studies. Hebard (1929, p. 391) recorded a pair of *Melanoplus* (probably *bilituratus bilituratus*) from Perth, Nev., which were very small, with malformed, reduced wings. They occurred in alfalfa and, although normal specimens were abundant, perhaps the pair in question fed entirely or mainly on alfalfa. Scharff (1954) reviewed the effects of food plants and weather.

Environments occupied by *bilituratus bilituratus* are extremely variable, Hebard (1925a, p. 112) stating that it (*atlanis*) "is equally at home in weedy waste land or on the sage-brush plains, its environment having a very decided effect on its general appearance." The general preference for light, sandy soils has been mentioned by Morse (1920). In the grain belt (Shotwell, 1930) it frequents fence row areas and wheat-stubble fields, especially where Russian thistle grows. In southern Michigan, Cantrall (1943) concluded that this grasshopper is characteristic of, and prefers, a mixed grass-herbaceous habitat, and that in many other environments where the grasshopper appears it probably is a sporadic member of the fauna, since it wanders a great deal.

Altitudinally, the range of *bilituratus bilituratus* captures extends from sea level in many places to the Alpine Zone (see Alexander, 1951, pp. 107–108, for critical comments on occurrence in the Alpine Zone of Colorado, also notes by Gurney, 1953, p. 317). Through the courtesy of Dr. George E. Wallace, Carnegie Museum, we have examined a rather long-winged male of *bilituratus bilituratus* taken by the late Dr. Walter Sweadner, Aug. 9, 1932, at an altitude of 7,200 feet, imbedded in the Sperry Glacier, Glacier National Park, Mont. No further details are available.

In New England *bilituratus bilituratus* occurs from the seashore to the summits of the highest mountains (Morse, 1920). Some altitudes on the labels of specimens examined are as follows: Junction of Moose

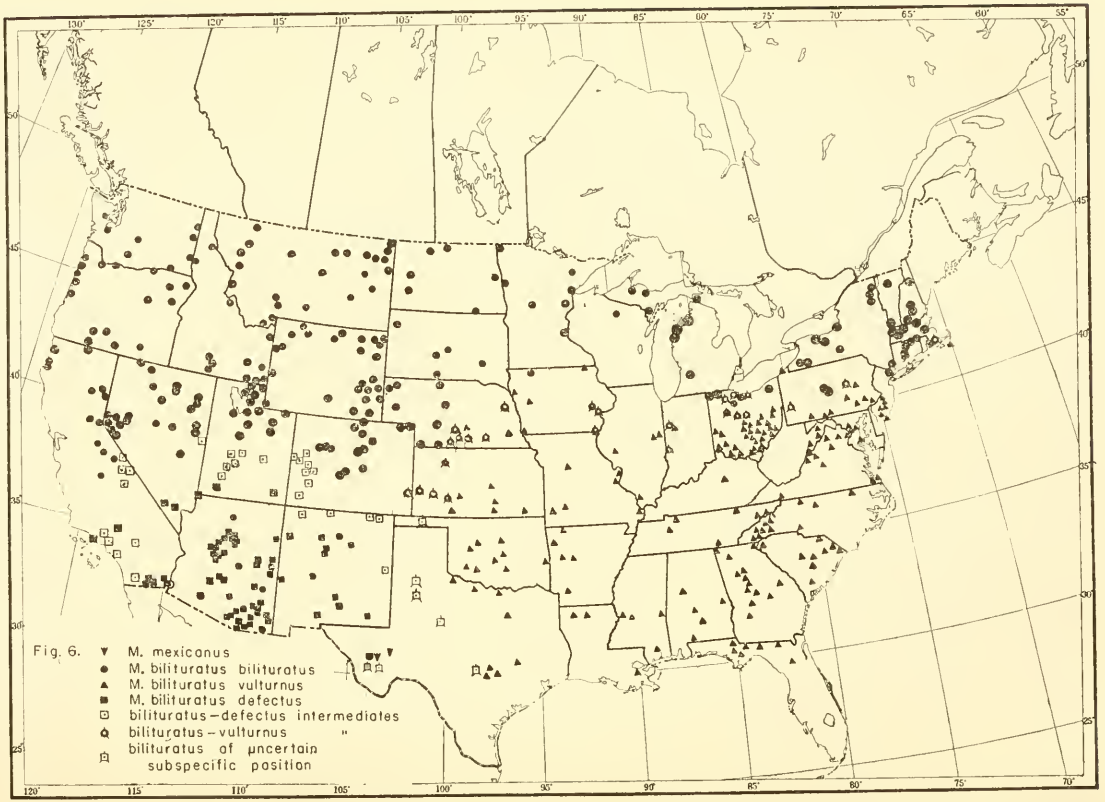

FIGURE 6.—Distribution of male specimens of *Melanoplus mexicanus* and *M. bilituratus* examined from United States localities.

Pass-Hope Highway and Moose Pass-Kenai Highway, Alaska, 1,800 ft.; Signal Peak, Wash., 5,000 ft.; Wasatch Mts., Utah, 7,400 ft.; Chaffee Co., Colo., 8,000–8,500 ft.

The classic report on the effects of temperature and moisture on this grasshopper is by Parker (1930). MacCarthy (1956) dealt with the correlation between adult populations and weather factors in Saskatchewan.

Criddle (1918, 1924) and Shotwell (1930) are among those who have described the egg pods of *bilituratus bilituratus*, and Cantrall (1943) gave a detailed account of the way the ovipositing female prepares the hole in the soil. Parker (1930) recorded one caged female which laid 15 egg pods, and the average for 30 females observed by him was 8.8 pods. Other data on egg production were presented by Pfadt (1949) and Smith, Handford, and Chefurka (1952). In laboratory cages, using material from central Saskatchewan, Pickford (personal communication to A. R. B.) has obtained an average of 30 pods for each of 9 females with a calculated maximum of 43 pods (872 eggs) for one female of the lot.

A description by Handford (1946) compared nymphs of *bilituratus bilituratus* with those of other species of *Melanoplus*. The seasonal history varies a great deal, depending on the weather (Shotwell, 1930, p. 23) and the location. The majority of adults studied by us were collected in July or August, but those collections undoubtedly reflect the habits of collectors almost as much as those of the grasshopper. Shotwell has noted oviposition as late as November. Cantrall (1943) found adults from early July until late October in Michigan, and he suspected that there were two generations. It is suspected that two years are required for the completion of the life cycle in parts of British Columbia (Canad. Insect Pest Rev., vol. 34, p. 273, 1956).

***Melanoplus bilituratus vulturnus*, new subspecies**

FIGURES 1,*d*-1; 2,*j*,*m*; 3,*c*; 6; 7,*d*; 8,*k*; 9,*f*; 10,*o*; 15,*b*,*c*; PLATE 1,D,E.

MALE (holotype): Size medium for group; fully winged; general appearance as in *M. bilituratus bilituratus*. Pronotum not strangulate in dorsal view, the posterior margin with the sides forming an angle of about 120°, apex well rounded; median carina of prozona and metazona proportioned as to length as 21 : 24, in lateral view only slightly depressed at the principal sulcus; tegmen with portion extending posterior to the apex of the hind femur in proportion to tegminal length as 3.5:17.5; hind femur moderately swollen for group. Furculae slender, sharply tapered, scarcely divergent, extending one-third the length of supra-anal plate; cercus as in figure 7,*d*-1; subgenital plate moderately upturned, with twin apices closely associated, evident but poorly separated.

Aedeagus (dry) as in figure 3,*c*-1, the apex of the dorsal valve strongly curved laterally with anterior margin very heavily sclerotized and excavate along entire length, main portion of dorsal valve less heavily but well sclerotized, decidedly concave, dorsal marginal membrane inconspicuous. Epiphallus with apex of each lophus (fig. 8,*k*) broad in dorsal view, in lateral view with lophus erect, much elevated, the apical margin barely angulate anteriorly.

Coloration: General coloration pale brown, with the customary markings of blackish, mottled with undertones of brown; head with fairly wide blackish brown postocular bar; pronotum mottled with brown above, laterally with irregular blackish longitudinal bar; tegmen lightly speckled with brown, markings very inconspicuous on apical half; hind femur with three fairly noticeable dorsal dark bars, these weakly suggested on external paginal area, ventral portion of paginal area yellowish, section between paginal area and ventral keel pink, ventral and mesal surfaces yellowish, with traces of pinkish, knee crescents black; hind tibiae pale, greenish gray mesally and yellowish brown externally, spines and apical half of spurs blackish brown.

Measurements in millimeters: Body, 22.0; pronotum, 4.5; front femur, 3.5; hind femur, 12.0; tegmen, 17.5. Greatest width of pronotum (posterior, including lateral lobes in perspective from above), 3.8; of hind femur, 2.9.

Explanation of Figure 7

a–j: Lateral view of left cercus of male.

a: *Melanoplus mexicanus:* 1, from Bledos, Mexico; 2, from Teotihuacan, Mexico.

b: *M. spretus:* 1, neotype; 2, from Kansas, 1874.

c: *M. bilituratus defectus*, Casa Grande, Ariz.

d: *M. bilituratus vulturnus:* 1, holotype; 2, from Quincy, Fla.; 3, from Independence, Kans.; 4, from Nantucket, Mass.

e: *M. bilituratus defectus:* 1, from Tempe, Ariz.; 2, from Camarillo, Calif.; 3, from Mount Charleston, Nev.

f: *M. bilituratus bilituratus:* 1, from Gun Lake, Mich.; 2, from Washington Territory; 3, from Spokane, Wash.; 4, from Eureka, Calif.; 5, from Placer Co., Calif.; 6, from Doyle, Calif.

g: *M. bilituratus bilituratus*, with abnormal dorsal valve, Fort Benton, Mont.

h: *M. devastator:* 1, from Clarkson, Calif.; 2, from Roseburg, Calif.; 3, from Sisson, Calif.; 4, from Grant's Pass, Oreg.; 5, from Alpine, Calif.

i: *M. bruneri:* 1, 2, from Ft. McLeod, Alberta, Canada (2 specimens); 3, from Chilcotin, British Columbia, Canada; 4, from Mt. Moriah, Nev.

j: *M. borealis borealis:* 1, from Churchill, Manitoba, Canada; 2, from Laggan, Alberta, Canada; 3, from Matanuska, Alaska; 4, from Cummington, Mass.; 5, from Grant, Colo.

k, l: Ventral view of right cercus of male (basal end at bottom of page):

k: *M. devastator*, Tacoma, Wash.

l: *M. bilituratus bilituratus*, Dorris, Calif.

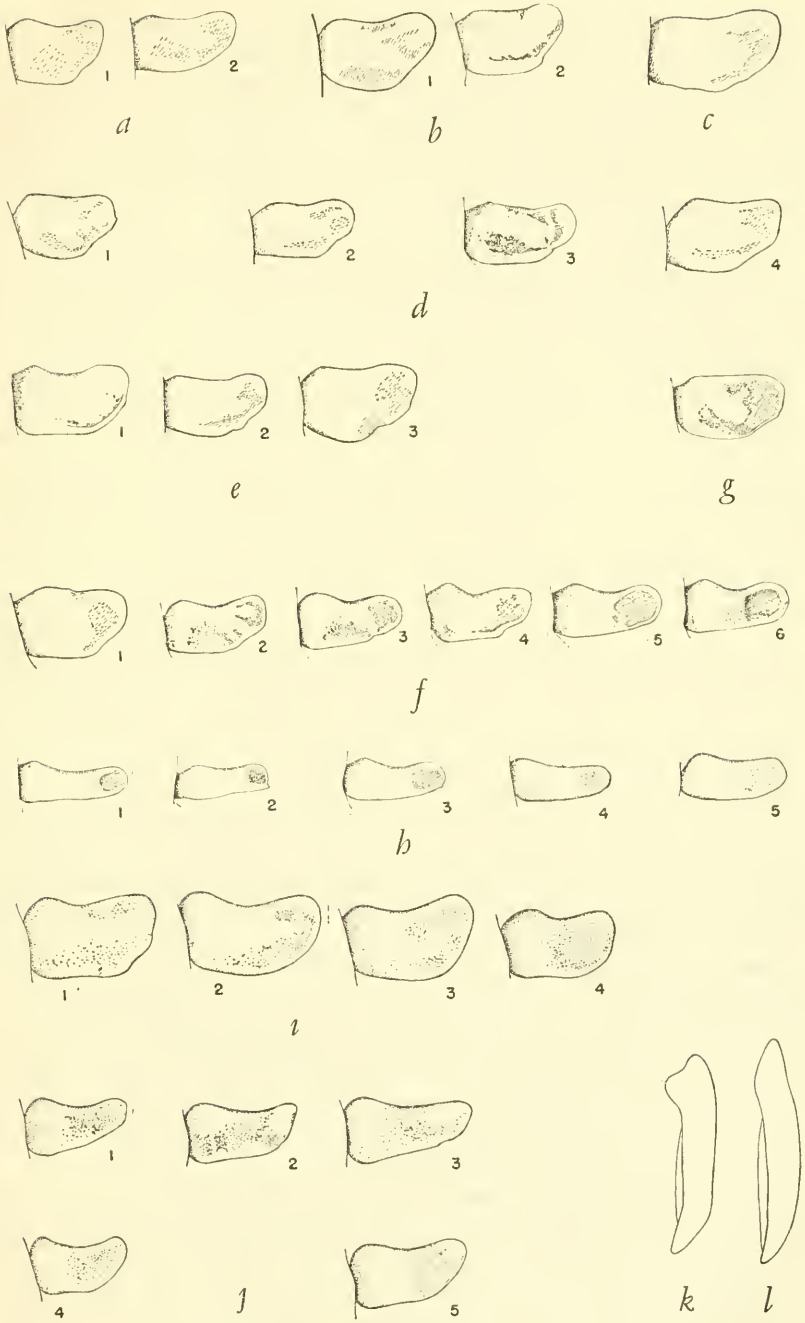

FIGURE 7.—Explanation on facing page.

FEMALE (allotype): General form as in male, slightly more robust; differing as follows: Compound eyes less globose; longitudinal carinae of vertex more widely separated and less prominent; median carina of prozona and metazona proportioned as 21:26, in lateral view somewhat more angulate at principal sulcus; mesosternal hump lacking; cercus as in *bilituratus defectus* (fig. 10,*h*); dorsal valve of ovipositor as in figure 10,*o*.

Coloration: Somewhat darker than in holotype; hind tibia red.

Measurements in millimeters: Body, 23.0; pronotum, 4.7; front femur, 3.2; hind femur, 13.0; tegmen, 18.0. Greatest width of pronotum, 4.2; of hind femur, 3.2.

VARIATION: The size of 10 representative males measured (in millimeters) varies in pronotal length from 3.5 to 5.0 (av. 4.4), in length of hind femur from 10.0 to 14.0 (av. 12.0), and in length of tegmen from 15.5 to 21.8 (av. 18.3). Six measured females vary in pronotal length from 4.2 to 5.3 (av. 4.7), in length of hind femur from 11.5 to 14.0 (av. 12.8), and in length of tegmen from 16.5 to 23.5 (av. 18.5). Western specimens average larger than eastern ones. In most specimens the tegmen extends about 2 to 3 mm. beyond the apex of the hind femur, but in some it scarcely exceeds it by as much as 5 mm. The male cercus usually is essentially like that of the holotype, but the tiny apicoventral "tooth" frequently is absent, and general shape is somewhat variable (fig. 7,*d*-2,*d*-4). Very little variation in the shape of the epiphallus has been noted.

Intergradation is shown by the shape of the dorsal valve of the aedeagus; in intermediate specimens the ventroanterior margin of the dorsal valve varies between the clearly excavate one of *bilituratus vulturnus* and the simply recurved margin of *bilituratus bilituratus*. Wet preparations often show membranous folds apically ("m" of fig. 3,*c*). Some intergrading specimens represent one of the two subspecies more strongly; others represent the other one, and some are fully intermediate. In some cases, as is true of material from Erie and Wood Counties, Ohio, and from Lafayette, Ind., fairly large series of males taken at the same time and place vary. This situation suggests that a mingling of genes of the two subspecies is occurring and that the populations are intergrading, though certain individuals appear nearly typical of one subspecies.

A specimen collected at Muscatine, Iowa, Sept. 12, 1935, by R. L. King probably is *bilituratus vulturnus*, but the dorsal valve (fig. 2,*m*) is very unusual, recalling certain very long-winged Arizona specimens of *bilituratus defectus*. The specimen is very long-winged, the tegmen 27 mm. long and extending 11.5 mm. posterior to the hind femur. In 1935 Iowa was experiencing a buildup of grasshoppers, but there is no record of extensive flights into the State then, though at other

times "light swarms of what appeared to be nearly typical *spretus* entered Iowa from the northwest and settled down in the western and southwestern parts of the state" (Drake and Tauber, 1946). The aedeagus of this specimen appears to be abnormal, but an explanation of this condition merits future attention.

Special interest is attached to the material reared by Brett (1947) which he ascribed to *M. mexicanus* and the most long-winged specimens of which he believed comparable to *spretus*, the latter considered by him a synonym. Specimens were deposited in the U. S. National Museum by Dr. Brett, and additional ones have been loaned by F. A. Fenton of Oklahoma A. & M. College, where Brett's main reared series are preserved. He reared specimens in cages, mainly feeding head lettuce, alfalfa, corn, and sorghum. The largest individuals reared were fed head lettuce at 100° F. and 35 percent and 50 percent relative humidity. Some of them resembled *spretus* in body size and tegminal length, though none of them examined by us has the *spretus*-type of aedeagus. At the other extreme, individuals reared on alfalfa were comparatively small, and in many of those reared under cool, humid conditions the tegmina were poorly developed as well as short.

The aedeagus of a total of 65 males from the Brett material has been examined, these specimens representing the extremes of temperature and relative humidity under which rearing occurred, as well as tegminal lengths varying from abortive to extending as much as 6 mm. posterior to the hind femoral apices. Dr. Brett has informed us (in litt., Dec. 17, 1956) that his stock used at temperatures of 75° and 80° F. was collected at Bennet, Nebr. (about 11 miles southeast of Lincoln), that stock for rearings at temperatures above 80° was collected near Stillwater, Okla., and that no Kansas stock was used. Reared material from both the Nebraska and Oklahoma stocks is variable in the structure of the dorsal value of the aedeagus, and there are indications that both stocks are from tension areas where *bilituratus bilituratus* and *bilituratus vulturnus* influence occurs, but the great majority of males may readily be recognized as *bilituratus vulturnus* and we have not considered them intergrades. Males collected at Lincoln, Nebr., and Stillwater, Okla., are comparable to the reared series in aedeagal structures and variation. No reared specimen has an aedeagus like that of *spretus*, but several reared specimens have the dorsal valve well sclerotized and with little of the shape characteristic of adults of *bilituratus vulturnus*. It seems most likely that the aedeagus of these specimens failed to mature completely, though the cerci, supra-anal plate, and subgenital plate are, with few exceptions, the type normal for adult *bilituratus vulturnus*. The tegmina of these particular specimens are mostly abortive or mal-

formed, suggesting that the individuals had difficulty developing normally.

Twelve males from Pittsburgh, Pa., have been examined, including four from a single area within the city, Forbes Field. As a whole, the aedeagus indicates an intergrading population, with no specimens fully typical of either *bilituratus bilituratus* or *bilituratus vulturnus*. There is variation, even within the series from Forbes Field, but most of the specimens are nearer *bilituratus vulturnus*. Although Presque Isle, Pa., is considerably north of Pittsburgh, the two males from there both are typical of *bilituratus vulturnus*. Perhaps a series would show intergradation. Jennings (1909) reported that though the flora of Presque Isle is more northern than southern in its affinities, some of the plants are typical of those centering in the lower Ohio basin and on the Piedmont Plateau. Possibly this grasshopper represents such a relationship. Jennings illustrated the many ecological habitats which occur on Presque Isle.

The single male from Nantucket examined is typical *bilituratus vulturnus*, though a male from Marion, in the nearby Fall River area of Massachusetts, is intermediate. Other Massachusetts specimens

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EXPLANATION OF FIGURE 8

a–e: Left cercus of male, lateral view:
- *a:* *Melanoplus borealis palaceus:* 1, holotype; 2, topotype; 3, 4, from Lakeview area, Mont. (2 specimens).
- *b:* *M. borealis utahensis:* 1, holotype; 2, from Ogden, Utah; 3, from Big Cottonwood Canyon, Utah.
- *c:* Intermediate between *M. borealis utahensis* and *M. b. palaceus*, 3 miles north of Mantua, Utah.
- *d:* *M. borealis stupefactus:* 1, lectotype; 2, from Los Pinos, Colo.; 3, from Mineral Co., Colo.
- *e:* Intermediate between *M. borealis stupefactus*, *M. b. palaceus*, and *M. b. borealis*, Tomboy, Colo.

f–i: Outline of epiphallus in dorsal view:
- *f:* *M. borealis borealis*, Nachvak Bay, Labrador, Canada.
- *g:* *M. b. utahensis*, holotype.
- *h:* *M. b. stupefactus*, holotype of *latifercula*.
- *i:* *M. bilituratus defectus*, Casa Grande, Ariz.

j–l (2): Outline of epiphallus of male in dorsal view, lophi only:
- *j:* *M. bilituratus bilituratus*, Tuttle, Idaho.
- *k:* *M. bilituratus vulturnus*, holotype, dry preparation.
- *l:* *M. devastator:* 1, from Davis, Calif.; 2, from Sacramento Co., Calif.

l (3)–*m:* Epiphallus in lateral view [*l* (5)–*m* showing lateral outline of lophus only]:
- *l:* *M. devastator:* 3, lectotype; 4, from Roseville, Calif.; 5, from Tacoma, Wash., dry preparation; 6, from Tulare, Calif., dry preparation; 7, from Gibson, Calif.; 8, same specimen as 7, in lateroposterior view; 9, from Lower Lake, Calif.
- *m:* *M. bilituratus bilituratus*, Milford, Calif.

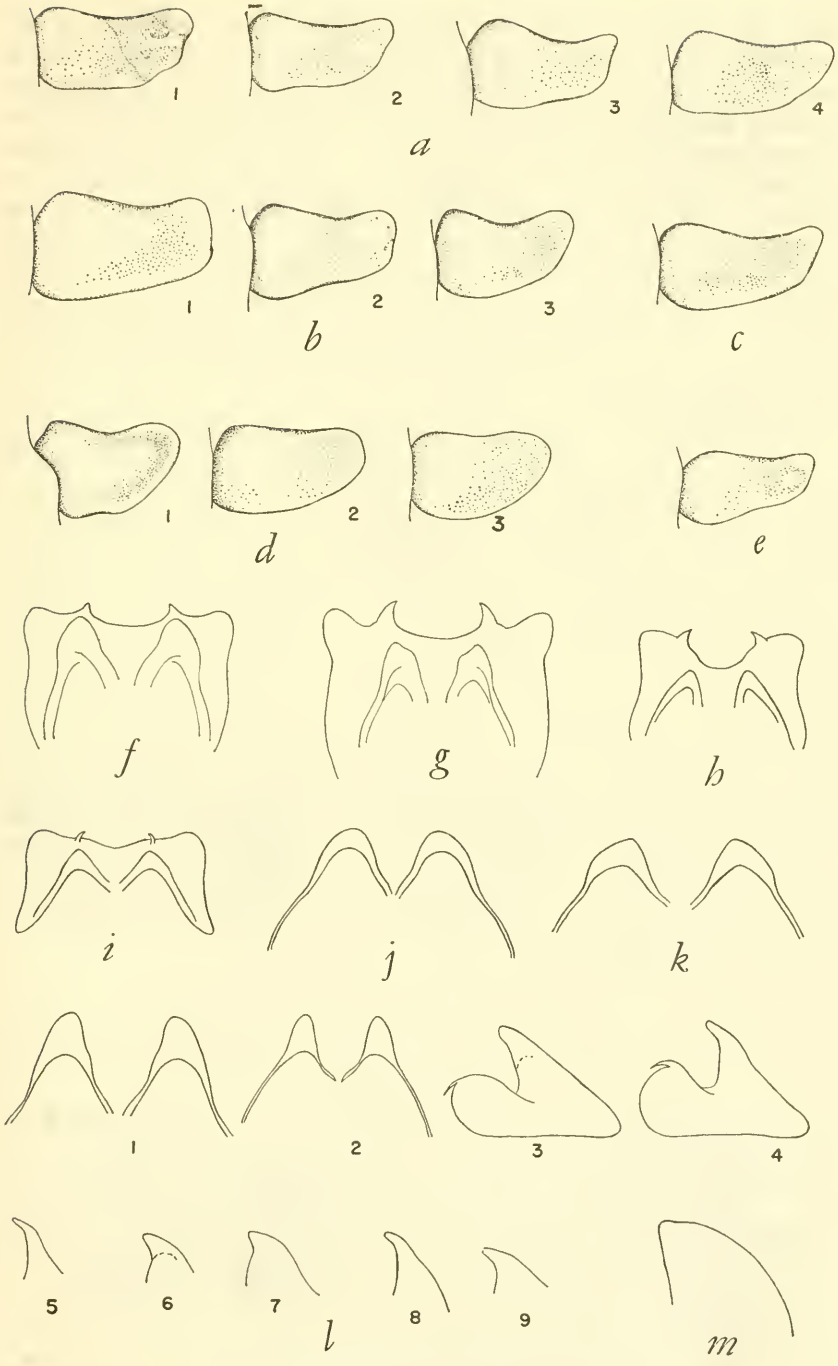

FIGURE 8.—Explanation on facing page.

are typical *bilituratus bilituratus*. Detailed field work in southeastern Massachusetts might be very informative. Scudder (1878a) noted that Nantucket specimens (reported as *atlanis*) have a peculiar coloring and nearly all specimens have pale glaucous hind tibiae. Griscom and Folger (1948) reported that the limited flora and fauna of Nantucket include "many southern and relict species," and the climate averages milder than that of Boston. A comparable situation probably occurs in the relation of Long Island to upstate New York. It is surprising that intermediate specimens or typical *bilituratus* have not been found in the Appalachian Mountains south of Pennsylvania. Specimens from Spruce Knob, W. Va., and Mt. Davis, Pa., show a slight trend toward *bilituratus bilituratus*, though they are not recognized as intermediates.

Color variation in *bilituratus vulturnus* runs through the usual range common to this group. About 18 percent of the specimens examined have pale or glaucous hind tibiae, the remainder red. Brett (1947, pp. 32–33) felt that food, temperature, and humidity are closely related to the color of the hind tibiae. Specimens reared by him on corn and head lettuce had a higher percentage of red hind tibiae than those reared on alfalfa. High temperature and humidity tended to produce red tibiae. On the other hand, King and Slifer (1955), after rearings from stock collected at Iowa City, Iowa, concluded that red hind tibiae "are dependent on the presence of a dominant, autosomal gene and that blue tibiae are produced when its recessive allele is present in the homozygous condition." Nymphs which Brett reared under crowded conditions tended to develop dark patterns characteristic of the gregarious phase of migratory grasshoppers, but adults resulting from such rearings were not distinctively colored, and they tended to have shorter wings than those reared under solitary conditions (Brett, 1947, p. 37).

EXPLANATION OF FIGURE 9

Dorsal view of supra-anal plate and furculae of males; *f* and *h*(2) show full view of apical portion of abdomen.

a: *M. bruneri:* 1, from Ft. McLeod, Alberta, Canada; 2, from Mt. Moriah, Nev.; 3, from Crook Co., Wyo.

b: Intermediate between *M. borealis utahensis* and *M. b. palaceus*, 3 miles north of Mantua, Utah.

c: *M. borealis borealis:* 1, from Matanuska, Alaska; 2, from Chelsea, Iowa; 3, from Churchill, Manitoba, Canada.

d: *M. borealis stupefactus:* 1, from Los Pinos, Colo.; 2, from Mineral Co., Colo.

e: *M. borealis utahensis:* 1, from Big Cottonwood Canyon, Utah; 2, from Ogden, Utah.

f: *M. bilituratus vulturnus*, Stokes, S. C.

g: *M. bilituratus bilituratus*, Pompey's Pillar, Mont.

h: *M. devastator*, 1, from San Bernardino, Calif.; 2, from Chico, Calif.

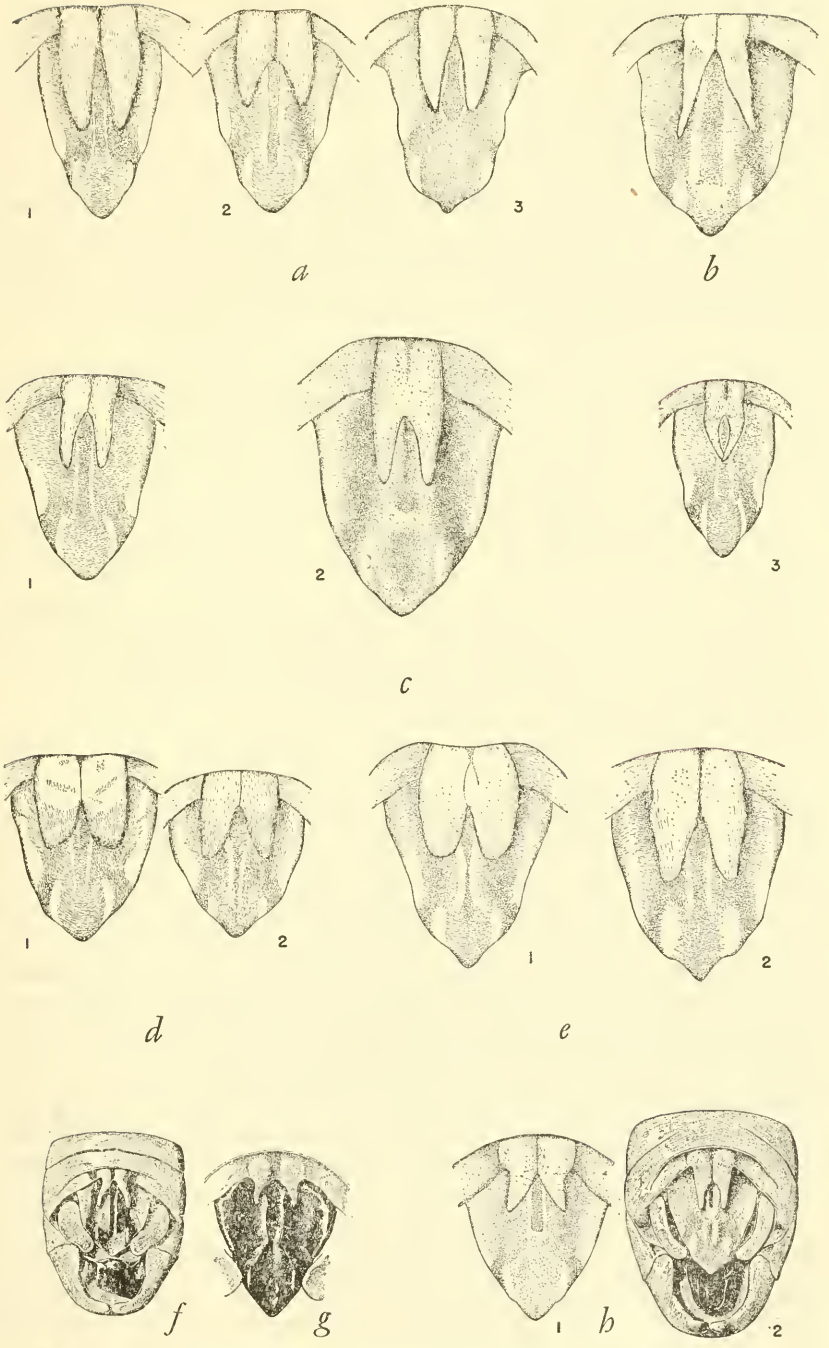

FIGURE 9.—Explanation on facing page.

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TYPE: USNM 63543.

TYPE LOCALITY: Stokes, Colleton Co., S. C.

The holotype male was collected by Miss Lotta Bootle in September 1924. The allotype (USNM) was taken at Columbia, S. C., Sept. 22, 1923, by Philip Luginbill.

There are 99 male and 36 female paratypes deposited in the U. S. National Museum, Canadian National Museum, Academy of Natural Sciences of Philadelphia, Museum of Comparative Zoology, University of Michigan, University of Arizona, Clemson Agricultural College, Florida Plant Board, and the collection of John R. Hilliard. The paratypes are from the following localities:

NORTH CAROLINA: Weldon, Greensboro, Pilot Mt., Charlotte, Roan Valley, Mt. Mitchell, Asheville, Hendersonville, Black Mts., Valley of Black Mts., Balsam, Sunburst, Highlands.

SOUTH CAROLINA: Green Sea, Mullins, Cheraw, Florence, Manning, Columbia, St. Paul, Eutawville, Stokes, Clemson, Madison.

GEORGIA: Rabun Bald, Black Rock Mountain, Tallulah Falls, Louisville, Dublin, Stone Mountain, Atlanta, Locust Grove, Cedar Rocks (5 miles north of Jackson), Barnesville, Macon, Montezuma, Smithville, Calhoun, Sand Mountain (near Trenton).

FLORIDA: Gainesville, Alachua Co., Hamilton Co., Houston, Lake Miccosuke (Jefferson Co.), Quincy, Gadsden Co., Rock Bluff Landing (Liberty Co.), "Camp Torreya" (Liberty Co.), Jackson Co., Marianna, Chipola.

ALABAMA: Auburn, Stokes, Selma, Greenville, Flomaton, Canebreak.

MISSISSIPPI: Meridian, Perkinston, Jackson, Vicksburg.

LOUISIANA: Harahan, Ruston, Sibley.

Most of the specimens from additional localities shown on the map (fig. 6) for *bilituratus vulturnus* are typical, but some vary toward *bilituratus bilituratus*, though not sufficiently to be considered intermediates, and so are not designated as paratypes. However, males from other localities, as mapped, are considered intermediates between *bilituratus bilituratus* and *bilituratus vulturnus*.

BIOLOGY AND ECONOMIC IMPORTANCE: In many localities *bilituratus vulturnus* becomes extremely abundant, and it is highly important economically, especially in the western part of its range. Kansas, Oklahoma, and Missouri are the chief States where it is very injurious. Wilbur and Fritz (1940) stated that during the 1933–39 outbreak in the bluestem region of eastern Kansas it was the most injurious crop infesting grasshopper, and they briefly described the buildup of its population during several drought years.

Morse (1904, p. 42) referred to this grasshopper as "probably the most widely and generally distributed" of those found in the Southeastern States, but this opinion differs from that of Rehn and Hebard (1916, p. 237), who found *bilituratus vulturnus* (reported as *atlanis*)

"relatively infrequent in the Coastal Plain south of North Carolina and the lower Gulf drainage of southern Georgia, in addition to having never been definitely recorded from peninsular Florida." Material examined suggests that in northern Florida *bilituratus vulturnus* is fairly widely distributed, though it is not generally abundant. Friauf (1953) examined a wide variety of grassland and other habitats on an area of about 2,180 acres in Putnam County, Fla., collecting an estimated 24,000 specimens of Orthoptera and Dermaptera during a period of more than 15 months in the field, yet he did not find *bilituratus vulturnus*. There is a paucity of records from the lower coastal plain of South Carolina and Georgia. The pertinent physiographic regions are shown on a map by Rehn and Hebard (1916, p. 95), and a comparison of their collecting stations (map, p. 91) with those indicated by Morse (1904, p. 10) suggests that the latter did relatively less sampling of the coastal plain fauna in Georgia and South Carolina, while his collecting trip (made in 1903) did not include peninsular Florida at all.

This grasshopper occurs most frequently in fields and uncultivated, open areas. Fox (1917) mentioned its tendency to congregate in Virginia in farm lands on sandy soils, and Isley (1938), in eastern Texas, classified it as a species of shallow soil. Like the northern subspecies, *bilituratus vulturnus* is found in many less typical environments, such, for example, as the shale barrens of Virginia which Gurney (1941) described as the habitat of *M. impudicus* Scudder. Fox reported it quite scarce in the higher Appalachians, but our records and those of Hebard (1945) show that it is frequent in clearings at higher elevations. The following are among the altitudes cited on labels of specimens examined: White Top Mountain, Va., 5,500 ft.; Little Bald, Great Smoky National Park, Tenn., 4,800 ft.; Unaka Mountains, Tenn., 3,500 ft.

As to food, Isley (1938) found that *bilituratus vulturnus* (reported as *mexicanus*) "selected rather widely among monocotyledons and dicotyledons showing a definite preference for crop plants."

In a report on the sculpturing and other detailed features of grasshopper eggs by Tuck and Smith (1939), descriptions of *mexicanus* eggs probably are attributable to *bilituratus vulturnus* because the work was conducted mainly in eastern Kansas.

Regarding the seasonal occurrence of adults, the following early and late dates from labels of specimens examined may be cited; Jackson Co., Ohio, June 12, 1932; Vinton Co., Ohio, Nov. 24, 1936; McNeill, Miss., May 8, 1925; Austin, Tex., April 15, 1956; College Station, Tex., June 17, 1920, Nov. 20, 1924; Weatherford, Okla.,

June 6–7, 1938; Ft. Sill, Okla., Nov. 10, 1918; House Springs, Mo., Nov. 11, 1925; Clarksville, Tenn., Oct. 14, 1916. In Virginia, Fox (1917) concluded from observations of adult prevalence that there are two generations per year. He found that adults appear about June 1, reach a peak of abundance, and then in late July decline in numbers; about the middle of August he noted the appearance of a new group of adults. In Kansas, Wilbur and Fritz (1940) recorded a peak of abundance from the middle of June until late July; in 1934 there was a fall peak of adults between October 6 and November 9.

REMARKS: The name of this subspecies is from "vulturnus ventus," a Roman term for a south-southeast wind, chosen in allusion to the distribution of this subspecies.

EXPLANATION OF FIGURE 10

a–e: Epiphallus in lateral view, males:
- *a:* *Melanoplus spretus*, Neotype.
- *b:* *M. bruneri:* 1, from Ft. McLeod, Alberta, Canada; 2, from Mt. Moriah, Nev.
- *c:* *M. borealis borealis*, Nachvak Bay, Labrador, Canada.
- *d:* *M. borealis stupefactus*, holotype of *latifercula*.
- *e:* *M. borealis utahensis*, holotype.

f–m: Left cercus of females:
- *f:* *M. mexicanus*, Cuernavaca, Mex.
- *g:* *M. bilituratus bilaturatus*, Hogeland, Mont.
- *h:* *M. bilituratus defectus*, San Carlos Indian Reservation, Ariz.
- *i:* *M. devastator*, Gazelle, Calif.
- *j:* *M. bilituratus defectus*, Chandler, Ariz.
- *k:* *M. bruneri*, Isle Royale, Mich.
- *l:* *M. borealis borealis*, lectotype of *septentrionalis*.
- *m:* *M. borealis stupefactus*, Mineral Co., Colo.

n–p: Left dorsal valve of ovipositor:
- *n:* *M. bilituratus bilituratus*, Hogeland, Mont.
- *o:* *M. bilituratus vulturnus*, allotype.
- *p:* *M. devastator*, Gazelle, Calif.

q: Female apical abdominal structures of *M. mexicanus*, Cuernavaca, Mexico.

r–t: Left dorsal valve of ovipositor:
- *r:* *M. bruneri*, Isle Royale, Mich.
- *s:* *M. borealis borealis*, lectotype of *septentrionalis*.
- *t:* *M. borealis palaceus*, allotype.

u–x: Apex of male subgenital plate in posterior view:
- *u:* *M. bilituratus defectus*, Chandler, Ariz.
- *v:* *M. spretus:* 1, from Pueblo, Colo., July 8–9, 1877; 2, from Argentine Pass, Colo., July 16, 1877.
- *w:* *M. bilituratus bilituratus*, Poplar, Mont.
- *x:* *M. devastator:* 1, from Merced River, Yosemite National Park, Calif.; 2, from Tehachapi, Calif.; 3, from Alpine, Calif.; 4, from Grant's Pass, Oreg.

FIGURE 10.—Explanation on facing page.

***Melanoplus bilituratus defectus* Scudder, new combination**

FIGURES 2,*i*,*l*; 3,*d*,*h*; 6; 7,*c*,*e*; 8,*i*; 10,*h*,*j*,*u*; 16,*b*; PLATES 2,A,B,C; 4,A.

Melanoplus defectus Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 20, 32, 1897; Proc. U. S. Nat. Museum, vol. 20, pp. 132, 177–178, pl. 12, fig. 6, 1897. (One male, one female, Grand Junction, Mesa Co., Colo.) Lectotype, designated by Rehn and Hebard (1912, p. 80): Male from Grand Junction, Colo. (ANSP).

Hebard (1929, p. 390) placed *defectus* as a synonym of *bruneri*, but the aedeagus of the lectotype shows that it belongs to the Grand Junction population of *bilituratus*, here considered to be encompassed within the limits of the southwestern subspecies. The lectotype is small, with a body length of 19.5 mm. The tegmina fail by about 2 mm. to reach the tips of the hind femora. The dorsal valve of the aedeagus is poorly sclerotized and pale, but is comparable in shape to other specimens of this subspecies from southwestern Colorado. The optimum development of *bilituratus defectus* occurs in the central and southern portions of Arizona and New Mexico, and it is unfortunate that the type locality is not within that area. The lectotype shows closer relationship to the optimum development of *bilituratus defectus* than it does to *bilituratus bilituratus*. The term "intermediate" as used for this subspecies (including the explanation of fig. 6), connotes specimens showing intergradation between the optimum population of *bilituratus defectus* and *bilituratus bilituratus*. From a nomenclatural point of view those specimens are not intermediates comparable to those discussed elsewhere in this paper because the type locality of *bilituratus defectus* is outside the area of optimum development.

The most distinctive character of *bilituratus defectus* is the dorsal valve of the aedeagus, which in specimens of optimum development has the anterior margin (x of fig. 3,*d*) concave and the lateral flap-like area (y) wide and with a sinuate margin (z). In some specimens, mainly those intermediate with *bilituratus bilituratus* (fig. 3,*f*), the lateral portion is not typically developed. (Also see second paragraph below.) The male cercus usually is about as in figure 7,*e*-2), though occasionally it is much broader (fig. 7,*e*-3). Especially in intermediate specimens from Baker, Nev., the cercus is narrower.

VARIATION: The size of 13 representative males, measured in millimeters, varies in pronotal length from 3.5 to 5.7 (av. 4.3), in length of hind femur from 9.8 to 14.5 (av. 12.4), and for length of tegmen from 11.5 to 22.5 (av. 17.8). Eight measured females vary in pronotal length from 4.5 to 6.0 (av. 5.4), for length of hind femur from 13.0 to 16.0 (av. 14.5), and for length of tegmen from 17.5 to 23.4 (av. 21.0). Specimens from Ft. Wingate, N. Mex., and Kaibab,

Ariz., are small and dark, in marked contrast to the richly colored, more yellowish specimens reared on winter mustard at Tempe, Ariz. In average specimens of *bilituratus defectus* the tegmen extends about 4 mm. beyond the hind femur. With the exception of material noted in the next paragraph, extremes among specimens examined are a male from Kaibab, Ariz., and one from Phoenix, Ariz., in which the tegmen extends 1.5 and 7 mm., respectively.

Six males and 11 females from several Arizona localities are so long-winged and, in the case of males, have so unusual an aedeagus that they are discussed separately in order that all the data will be assembled for future reference if importance should become attached to them as a distinct population. The aedeagus in lateral view (figs. 2,*l*; 3,*h*) has the dorsal valve extending anteriorly and with little development of a concave lateral surface; however, the dorsal valve differs slightly in length and shape, and in one specimen the anterior apical margin is very weakly recurved in a suggestion of *bilituratus defectus*; another specimen (from Tumacacori National Monument) has a second right dorsal valve present, which approaches that of *bilituratus defectus*, although the left one and the other right one are essentially as figured. It appears that the aedeagus in this series is abnormal or not fully developed, and that the specimens are *bilituratus defectus*. Fred Skoog, collector of the Chandler specimens, has informed us that they were taken among *bilituratus defectus* where the population was 50 to 75 per square yard in an alfalfa field, and 500 to 1000 along the margins of the field. The few unusually long-winged specimens found by him had only recently become adult, and their somewhat teneral condition may have had a bearing on the shape of the aedeagus. Other genitalic characters of these specimens fall within the normal variation of *bilituratus defectus*; the following figures illustrate them: 7,*c*; 8,*i*,; 10,*j*,*u*; 16,*b*.

The general appearance of the above specimens is as shown (plates 2,C; 4,A). Gurney (1953, pl. 7, fig. c) previously illustrated one of the females from Chandler, and Barnes (1956) referred to long-winged Arizona specimens; both authors applied the name *M. mexicanus mexicanus*. The lengths of the tegmen and hind femur of these specimens are, respectively, as follows: Males, 26.0–31.0 (av. 27.90), 13.3–14.8 (av. 14.02); females, 27.0–33.5 (av. 29.67), 15.0–17.2 (av. 15.93). The extremes and averages of the distance from apex of hind femur to apex of tegmen are as follows: Male, 9.0–14.0 (av. 11.28); female, 8.0–13.5 (av. 10.04).

The following label data accompany this long-winged material (all from Arizona): Casa Grande, swept from alfalfa, July 20, 1951, N. J. Nerney (1♂); Chandler, lush irrigated alfalfa, May 1945, F. Skoog (2♂, 8♀); Tempe, alfalfa, Aug. 31, 1938, O. L. Barnes

(1♂); Tempe, swept from alfalfa, June 8, 1950, N. J. Nerney (1♀); Theba, on alfalfa, Oct. 26, 1939, O. L. Barnes (1♂); Tumacacori National Monument (Pendleton Ranch), Sept. 9, 1939, E. R. Tinkham (1♂); Yuma, alfalfa, Aug. 2, 1938, O. L. Barnes (1♀); Yuma, alfalfa, Nov. 11, 1936, O. L. Barnes (1♀).

Of 311 specimens of *bilituratus defectus* examined, only two (one each from Las Vegas, N. Mex., and Lupton, Ariz.) have glaucous hind tibiae; the others are red. However, 13 of 57 specimens which are intermediate with *bilituratus bilituratus* have glaucous hind tibiae. None of these intermediate specimens is as long-winged and large as the most optimum specimens of *bilituratus defectus*. Several of the intermediates from southern Colorado and northern New Mexico are noticeably small and dark.

The distribution of males of *bilituratus defectus* examined is shown in figure 6. The single Texas locality is Phantom Lake, Davis Mountains.

Biology and economic importance: This grasshopper is important economically and is most injurious in irrigated areas (Ball, Tinkham, et al., 1942; Harper, 1952). It is said by Harper not to have become a pest in the Imperial Valley of California until 1915 when farming there became extensive. Cultivated crops are injured more severely than grazing areas.

Barnes (1955) compared five plants as food for *bilituratus defectus* in cage studies in Arizona, and his paper should be consulted for observations on mating, egg development, adult body dimensions, and weights of adults, as influenced by diet. Two annual generations usually are reported, and Barnes feels that a considerable difference in average size of individuals representing the two generations probably is due to the plants available as food. For instance, in 1944 the second generation in the Yuma, Ariz., area developed almost exclusively on dry alfalfa and Bermuda grass, and resulting adults were much smaller than first generation adults. A comparable difference in adult size at the San Carlos Indian Reservation, Ariz., was noted in the two generations in 1953. First generation nymphal diet consisted mainly of forbs, while the second generation had to develop mostly on grasses. It may be significant that all of the especially long-winged specimens discussed in detail, which bear habitat data, were associated with alfalfa.

In southern California (Harper, 1952), *bilituratus defectus* first hatches by March or early April; then the second generation occurs in September and October. Some early and late dates on labels of adults examined are as follows: Yuma, Ariz., Jan. 5, 1937; Bard, Calif., Jan. 19, 1937; Yuma, Calif., Apr. 17, 1942; Saugus, Calif., Oct. 19, 1950; Zion National Park, Utah, June 18, 1953; same, Sept.

5, 1926; Peeples Valley, Ariz., Oct. 2, 1936; Chino Valley, Ariz., Nov. 23, 1936; Roll, Ariz., Nov. 12, 1943; same, Dec. 1, 1936.

Altitudinally, *bilituratus defectus* ranges in distribution from about sea level in Imperial Co., Calif., to 11,800 feet on Mt. Charleston, Nev. Other high altitudes indicated on labels of specimens examined are the following: Magdalena Mts., N. Mex., 7,100 ft.; Lee Canyon, Spring Mountains, Nev., 8,600 ft.; Rim Rock Peak, Sandia Mts., N. Mex., 9,500–10,000 ft. The specimens from high elevations average somewhat smaller than specimens of optimum development from low elevations, and they are relatively dark in color, but in general they are not distinctive.

Melanoplus devastator Scudder

FIGURES 1,*e*; 2,*k*; 3,*i*; 7,*h*,*k*; 8,*l*; 9,*h*; 10,*i*,*p*,*x*; 14; PLATE 3,B,C.

Melanoplus devastator Scudder, Proc. Boston Soc. Nat. Hist., vol. 19, pp. 287, 288, 1878. (Males, females, Shasta Valley, Sissons, Sausalito, Calif.; Lake Tahoe, Reno, Glen Brook, Nev.; Beaver Brook, Morrison, Colo.) Lectotype, here designated: Male labeled "Sept. 1, 1874, Sauzalito, Cal.," "Scudder's Type," "Mel. devastator typicalis Scudder's Type, 1895,"[3] "Sc. reference Rev. Melanopli 1897, p. 198," "M. devastator Scudd. Cab. S. H. Scudder." (ANSP). Sausalito is one of the original localities mentioned by Scudder (1878b), who said that the form named *M. d. typicalis* "best represents the original types of the species when first described," and this specimen is one so identified by him.

Melanoplus ater Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 22, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 133, 194–195, pl. 13, fig. 2, 1897 (two males, 3 females, San Francisco, Calif.). Lectotype, designated by Rehn and Hebard (1912, p. 80): Male (ANSP).

Melanoplus consanguineus Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 21, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 133, 192–193, pl. 12, fig. 10, 1897 (male, female, Sacramento Co., Calif., Sonora Co. in plate explanation, p. 409, error for Sonoma Co.; see Rehn and Hebard, 1912, p. 80). New synonymy. Lectotype, designated by Rehn and Hebard (1912): Male (USNM).

Melanoplus diminutus Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 21, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 133, 190–191, pl. 12, fig. 9, 1897 (males, females, San Francisco, Calif.; Monterey, Calif.). New synonymy. Lectotype, designated by Rehn and Hebard (1912, p. 80): Male from Monterey, Calif. (MCZ).

Melanoplus uniformis Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 22, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 133, 201–202, pl. 13, fig. 9, 1897 (males, females, five California localities). New synonymy. Lectotype, designated by Rehn and Hebard (1912, p. 80): Male from Sacramento, Calif. (USNM).

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[3] Labels such as this one, with "Scudder's Type, 1895" printed, were affixed to many of the specimens studied by Scudder in connection with his revision (1897b). Species described by other authors, as well as those by Scudder, and, where series were available, more than one specimen of the same species, were so treated. The principal function of this label today is to indicate a specimen studied by Scudder himself, and one presumably considered by him to be typical of the species named.

Melanoplus virgatus Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 22, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 133, 199–201, pl. 13, fig. 8, 1897 (males, females, six California localities). Lectotype, designated by Rehn and Hebard (1912, p. 80): Male from Siskiyou Co., Calif. (MCZ).

Melanoplus devastator affinis Scudder, Proc. U. S. Nat. Mus., vol. 20, p. 199, pl. 13, fig. 6, 1897 (males, Sierra, Sacramento, and Los Angeles Counties, Calif., also "California, S. Henshaw."). Lectotype, here designated: Male labeled "Cal. (Ricksecker) S. Henshaw," "Mel. devastator affinis Scudder's Type 1895," and figured by Scudder, 1897b (MCZ).

Melanoplus devastator conspicuus Scudder, Proc. U. S. Nat. Mus., vol. 20, p. 199, pl. 13, fig. 7, 1897 (males, Sacramento, El Dorado, Amador, and Merced Counties, Calif.). Lectotype, here designated: Male labeled "Clarkson, Eldorado Co. Cal. 14/8, 85, Type No. 1160, U. S. N. M., Mel. devastator conspicuus Scudder's Type, 1895" (USNM). (We have been unable to locate a Clarkson in El Dorado County, and the label may have been in error for Clarksona, Amador County, which is nearby. The male from Sacramento, Calif., figured by Scudder has not been found. El Dorado County is the second locality mentioned.)

Melanoplus devastator obscurus Scudder, Proc. U. S. Nat. Mus., vol. 20, pp. 198–199, pl. 13, figs. 3, 4, 1897 (males, San Francisco, Calif.; Sierra, Placer, Marin, Sacramento, El Dorado, Alameda, Siskiyou, and Los Angeles Counties, Calif.). Lectotype, here designated: Male labeled "Sissons Cal., Drawn, S. H. Scudder Coll, Type 15439, Mel. devastator obscurus Scudder's Type, 1895" and figured by Scudder, 1897b (MCZ).

Melanoplus devastator typicalis Scudder, Proc. U. S. Nat. Mus., vol. 20, p. 199, pl. 13, fig. 5, 1897 (males, "nearly every county . . . from Shasta to San Diego and from Marin to Sierra," Calif.). (The sexes and number of specimens of this and the previous three entities were not given by Scudder, but male specimens were figured. In each case both sexes were before him, as shown by preserved specimens.) Lectotype, here designated: Male labeled "Tighe Calif., Drawn, S. H. Scudder Coll, Type 15441, Mel. devastator typicalis Scudder's Type, 1895" and figured by Scudder (1897b) (MCZ).

Scudder listed Dr. Edward Palmer as the collector of the Tighe specimen. We have been unable to find Tighe on available maps, and for the information that Tighe was about 8 miles east of Ramona, Calif., are indebted to Rogers McVaugh, a botanist who has made a study of Palmer collecting localities. This location, about 45 miles northeast of San Diego, apparently was a ranch. Palmer's unpublished notes indicate that he was there July 5–6, 1875. For a biography and sketch of Palmer's travels, see Safford (Pop. Sci. Monthly, vol. 78, pp. 341–354, 1911) and McVaugh's (1956) recent book, wherein (p. 333) the locality is listed as Tigh(e)'s (Ranch or Station).

All the lectotypes mentioned have been examined, in each case including the aedeagus and epiphallus, and they are considered to represent a single species, *M. devastator* Scudder. Kirby (1910) placed *d. affinis*, *d. conspicuus*, *d. obscurus*, and *d. typicalis* as synonyms of *devastator*, and Caudell (1915) did likewise for *virgatus* and affirmed the synonymy of *d. affinis* and *d. typicalis*. He also considered

consanguineus a synonym of *diminutus*. *M. d. affinis* should not be confused with *M. affinis*, described by Scudder (1897b, p. 171), which preoccupies it. The types of *ater*, *diminutus*, and *d. obscurus* are small, very dark individuals; those of *uniformis*, *virgatus*, and *d. conspicuus* are noticeably large and yellowish; *consanguineus* is relatively small and moderately dark; *d. affinis* is medium-sized and yellowish; *devastator* and *d. typicalis* are medium-sized and moderately dark.

DESCRIPTIVE NOTES: A medium-sized, usually fully winged member of the *mexicanus* group. Head with dorsal carinae of vertex about as in *bilituratus bilituratus*; mesosternal hump absent or weakly developed in male, absent in female.

MALE GENITALIA: Cercus elongate and slender for group, with a characteristic preapical knob extending ventrally and mesally on the mesal surface (fig. 7,*k*), typically as in figure 7,*h*-1, sometimes proportionally shorter, often with a small tooth near the ventroposterior angle (fig. 7,*h*-2,3); furculae sometimes more divergent than illustrated (fig. 9,*h*-2); subgenital plate weakly to moderately upturned (pl. 3,B), in posterior view (fig. 10,*x*) with twin apices usually distinct, rarely (fig. 10,*x*-4) scarcely developed; aedeagus (figs. 2,*k*; 3,*i*) with dorsal valve lightly sclerotized, rather thin and parchment-like, the anterior margin with narrow fold, in dry specimens a basal lobe along ventroanterior margin usually evident; when dry the dorsal valve often is more concave and the margin is more recurved than when preserved wet; accessory lobe medium-sized to large for group; epiphallus (fig. 8,*l*-3,9) distinctive in that lophus is angulate in lateral view near apex, the angulation correlated with more or less acute apex in dorsal view (fig. 8,*l*-1,2).

FEMALE GENITALIA: Cercus (fig. 10,*i*) relatively acute for group, not so robust and blunt as in *bilituratus bilituratus*; dorsal valve of ovipositor with "scoop" well developed.

VARIATION: The size of 10 representative males, measured in millimeters, varies in pronotal length from 3.7 to 5.3 (av. 4.3), in length of hind femur from 9.7 to 15.2 (av. 11.4), and in length of tegmen from 12.0 to 21.8 (av. 14.8). Seven measured females vary in pronotal length from 3.6 to 5.9 (av. 4.8), in length of hind femur from 10.0 to 15.5 (av. 12.8), and in length of tegmen from 10.6 to 23.1 (av. 17.5). There is great variation in size, and small specimens are frequently encountered in the San Francisco, Calif., area, and in Oregon and Washington. The tegmina of the smaller specimens usually do not surpass the apex of the hind femur, and in some specimens they are as much as 2 mm. short of the femoral apex. In larger specimens with optimum development the tegmina frequently exceed the hind femora by about 3 mm.

DISTRIBUTION: Figure 14 shows the distribution of *devastator* as known to the authors. However, uncertainty concerning identifications in the group during the past has been responsible for early published records which pointed to a much wider distribution. Both Essig (1926, p. 81) and Harper (1952) include Arizona in the distribution, but Hebard (1935b, p. 304) stated that *devastator* does not occur there. Buckell (1922, p. 31) included *devastator* in his British Columbia list, based on a Vancouver Island record by Caudell. Caudell (1908, p. 77) recorded *devastator conspicuus* from Wellington, British Columbia, and a manuscript note written by him in 1926 indicated that the record was based on a female specimen. The specimen, a female with red hind tibiae, is in the U. S. National Museum, and is *bilituratus bilituratus*.

Male specimens of *Melanoplus devastator* have been examined from the localities shown in figure 14.

BIOLOGY AND ECONOMIC IMPORTANCE: When Scudder (1878b) originally described *devastator*, he stated that it probably "is the source of most of the damage to crops in California," and it frequently has been of much importance there. The fullest early account is Coquillett's (1892) report on the 1891 infestation, which includes biological notes. Woodworth (1902) stated that *devastator* was one of the two most destructive California grasshoppers in 1901. Brief later accounts are by Essig (1926) and Harper (1952). Fulton (1930, p. 634) referred to *devastator* as one of the "more strictly prairie species" of the Willamette Valley of western Oregon and universally present there during the proper season.

A concise summary of the biology and economic importance of *devastator* by Wilson (1947) points out that it is the dominant species on much of the semiarid range in California, and that preventing mass migrations from natural habitats to cultivated crops is one of the critical control measures, in addition to preventing serious damage to range forage. Nymphs inhabit much of the range and feed on legumes, alfilarias, bromes, and hordeums, in the order named, as long as they remain succulent. Wilson, to whose excellent summary the reader is referred for more detailed information on habits and seasonal occurrence, commented as follows on the physiological distinctness of *devastator:*

> By the second week of July the species has largely reached the adult stage. To the casual observer the adults resemble the lesser migratory grasshopper (*M. mexicanus* Sauss.). However, field and microscopic observations show that these two species differ in external anatomy, habitat, and seasonal history. *M. devastator* is naturally found on the range, whereas *M. mexicanus* is found in California and Nevada, largely, if not entirely, in irrigated alfalfa fields. Dissections have shown that, unlike *M. mexicanus* and many of the other economic species that begin oviposition within 10 days after reaching the adult stage, *M. devastator* has a

preoviposition period ranging from 90 to 176 days, during which no ovarian development or copulation takes place. The breaking of this diapause, or period of arrested development, apparently depends on temperature and food. Cool fall weather, with rains sufficient to germinate the seed of annual plants, appears to be the determining factor in breaking the diapause.

Middlekauff (1958) more recently summarized observations on the bionomics of *devastator*.

The following are some early and late capture dates noted on specimens examined: California: San Bernardino, May 14; Kern Lake, Kern Co., May 22; San Luis Obispo, June 14; Monterey Co., Oct. 31; Roseville, Nov. 26; Red Bluff, Dec. 2. Washington: Tacoma, Sept. 25.

Melanoplus bruneri Scudder

Figures 1,*g*; 2,*a*,*b*; 3,*k*,*l*; 7,*i*; 9,*a*; 10,*b*,*k*,*r*; 11,*a*; 12; 13; 16,*h*; Plate 3,a.

Melanoplus bruneri Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 19, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 132, 164–166, pl. 11, fig. 7, 1897 (males, females, 12 localities in Alberta, Montana, Nebraska, Colorado, and Washington). Lectotype designated by Rehn and Hebard (1912, p. 79): Male labeled "Ft. McLeod, B. A. Aug. 82" (near southwest corner of Alberta; itinerary described by Bruner, 1883, who was given as collector by Scudder, 1897b, p. 166) (ANSP).

Melanoplus excelsus Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 19, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 132, 166–167, pl. 11, fig. 9, 1897 (males, females, above timber, 11,000 to 13,000 ft., Mt. Lincoln, Park Co., Colo.). Lectotype designated by Rehn and Hebard (1912, p. 79): Male (MCZ).

Melanoplus alaskanus Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 20, 32, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 132, 169–170, pl. 12, fig. 1, 1897 (2♂, 1♀, Alaska; Spilmacheen, British Columbia). Lectotype designated by Rehn and Hebard (1912, p. 79): Male from Alaska (USNM).

Hebard (1929, p. 390) considered *M. defectus* Scudder and *M. dimidipennis* Bruner synonyms of *M. bruneri*, but the types indicate that *defectus* is a subspecies of *bilituratus*, and *dimidipennis* a synonym of *bilituratus bilituratus*.

Hebard (1928, p. 284; 1929, p. 390) indicated the synonymy of *excelsus*, which is borne out by the lectotype. The posterior surface of the subgenital plate is dimpled, but not vertically grooved nor incised at the apex, a condition included in the variation of *bruneri*, and the aedeagus is typical of *bruneri*.

Walker (1910, 1920) indicated the synonymy of *alaskanus*, and the lectotypes of *alaskanus* and *bruneri* demonstrate that synonymy. Earlier, Walker (1906) had recorded *alaskanus* from Vernon, British Columbia, with the identity questioned. In 1909 Walker discussed the variation shown by an Ontario series, as correlated with the differences in Scudder's descriptions of the two supposed species (*alaskanus* and *bruneri*) and he then reduced *alaskanus* to a variety of

bruneri. Pettit and McDaniel (1918) treated the Michigan population as *alaskanus*. Essig (1926, p. 81) listed *alaskanus* as a synonym of *bruneri*. Hebard (1925a, p. 114) questioned the synonymy indicated by Walker, and later said (1928, pp. 281–282) he believed *alaskanus* to be a geographic race of *mexicanus* if nominal recognition is warranted. Rehn (1952) agreed with Hebard's opinion.

Because of the difference of opinion concerning *alaskanus*, it may be helpful to discuss the type in more detail. It is the specimen selected by Rehn and Hebard, and was received at the U. S. National Museum on Feb. 29, 1892, from T. C. Mendenhall of the U. S. Coast and Geodetic Survey. Accession records show that the material was collected by J. E. McGrath during an expedition which was active along the Alaskan Boundary during September 1890–May 1891. McGrath (1893) has described the general experiences of the party which he led up the Yukon River, and (p. 185) has commented about the plentiful insects found near the river in summer. It appears that the type specimen was collected along the Yukon River somewhere between Ft. Yukon and the 141st Meridian.

A male of *bruneri*, collected in 1948 near Fairbanks, Alaska, a locality at about the same latitude as the intersection of the Yukon River and 141st Meridian, confirms the presence of this species in Alaska, so there is no reason to doubt the source of the *alaskanus* lectotype. Hebard did not examine the aedeagus of the lectotype and so did not have this evidence which shows agreement with *bruneri*.

Although *bruneri*, *excelsus*, and *alaskanus* were all described in the same publication, the action of the first revisers (Hebard, 1928, for *excelsus;* Walker, 1910, for *alaskanus*) establishes the precedent of using *bruneri* as the valid name of this species. It is much the best known of the three names, and has page priority in Scudder (1897b). Though not required, page priority was recommended in the 1953 Copenhagen Decisions of Zoological Nomenclature when other conditions are equal.

Descriptive notes: A usually medium-sized, fully winged member of the *mexicanus* group, most closely related to *bilituratus*, from which it differs mainly in male genitalia. Mesosternal hump variable (fig. 1,*g*), averaging fully as prominent in male as in *bilituratus*, absent in female; tegmina usually reaching slightly beyond tip of abdomen, sometimes short of it. Females not always separable from *bilituratus*, but in any given locality where both species occur *bruneri* females usually more robust and often shorter-winged; males usually recognizable by cercus and subgenital plate, but in doubtful cases the dorsal valve of aedeagus of *bruneri* is highly distinctive in its much more expansive and thin, striated, conformation.

Male genitalia: Cercus (fig. 7,*i*) variable, usually about as in

figure 7,*i*-2 more incurved along dorsal margin and more evenly rounded along ventroposterior margin than frequent in *bilituratus*; supra-anal plate (fig. 9,*a*) elongate, lateral elevations prominent; furculae usually reaching to middle of supra-anal plate or approximately so; subgenital plate in lateral view with apical portion strongly upturned, sometimes rather abruptly so (fig. 16,*h*), often superficially accentuated by upward curvature of abdomen; posterior view of subgenital plate usually as in figures 11,*a*-1 or 11,*a*-4, with apical margin entire and posterior surface grooved, frequently apical margin is dimpled (fig. 11,*a*-2), or there are well formed twin apices (fig. 11,*a*-3), and rarely margin is squarish and irregular (fig. 11,*a*-5). Aedeagus with main stem relatively short; dorsal valve moderately sclerotized, thin, often appearing almost parchment-like, large and marked with striations; in dorsal view a triangular projection (x in fig. 3,*k*) of the well-sclerotized dorsal rim of the dorsal valve is distinctive; accessory lobe large for group; epiphallus as in figure 10,*b*.

Female genitalia: Cercus (fig. 10,*k*) relatively short and blunt, the dorsal margin often somewhat irregular; ovipositor with "scoop" of dorsal valve (fig. 10,*r*) strongly concave.

Variation: The size of nine representative males, measured in millimeters, varies in pronotal length from 3.6 to 5.1 (av. 4.6), in length of hind femur from 9.0 to 13.0 (av. 11.9), and in length of tegmen from 12.0 to 19.5 (av. 16.6). Seven measured females vary in pronotal length from 3.6 to 6.0 (av. 4.8), in length of hind femur from 9.6 to 16.0 (av. 13.1), and in length of tegmen from 11.5 to 20.7 (av. 17.1). The smallest specimens seen are from Mt. Moriah, Nev., the largest from Michigan.

Coloration: General coloration about as in *bilituratus*, varying from pale brown to blackish; hind femur usually with three external and dorsal dark bands, poorly developed in pale individuals; hind tibia varying from pale greenish yellow to red, usually pinkish to red.

Distribution: Several records of *bruneri* add significantly to the distribution based on male specimens examined (figs. 12, 13). Fulton (1930) reported it from Grant's Pass, Oreg.; Hebard (1925a) listed Nipigon and Dwight (Ontario), Norrie and Oregon (Wisconsin), Gordon (Nebraska), and Englewood (South Dakota); Hebard (1932b) reported a specimen from Onawa, Iowa; and Hebard (1935a, p. 68) said that Beulah and Agua Fria Park are eastern limits in New Mexico. Stehr (1936) gave several Minnesota records which supplemented those of Hebard (1932b; 1934a).

Biology and economic importance: On the high montane ranges of the Northwestern States and western Canada, *bruneri* is injurious to grazing areas. There have been fairly frequent references to the importance of *bruneri* in western Canada (Canad. Insect Pest Rev.,

vol. 23, p. 2, 1945; vol. 24, p. 348, 1946; vol. 28, p. 255, 1950; vol. 33, pp. 10, 341, 1955). Treherne and Buckell (1924, p. 26) described it and *Bradynotes chilcotinae* Hebard (now *Buckellacris chilcotinae chilcotinae*) as the most common and injurious grasshoppers "in the lightly timbered areas of the summer range in the Chilcotin section (of B. C.) during 1920 and 1921." In 1921 A. G. Ruggles reported to the Insect Pest Survey, U. S. Department of Agriculture, that damage by *bruneri* was occurring at Grand Rapids, Minn. The frequency of its capture on upland ranges in Montana suggests its importance there, as do comments on its abundance by Pepper, et al. (1953).

An unusual infestation of *bruneri* occurred on Mt. Moriah, Nev., in the 1930's. Material collected Sept. 2, 1937, and Aug. 16, 1939, is in the U. S. National Museum, and data on the infestation have been obtained from Lee M. Burge, Division of Plant Industry, Nevada Department of Agriculture. Mt. Moriah is located about 35 miles east of Ely, Nev., just north of Baker. The infested range is a large table area at an elevation of about 11,000 feet, bearing a valuable stand of bunch grasses and grazed over by sheep. Injurious populations of *bruneri* existed there in 1936–1938. During the first 5 days of September 1937, poison bait was carried up to the sheep range by pack mules and spread by hand. Later in 1937 a survey indicated that approximately 2,000 acres carried a population of 20 adults per square yard. A visit made by Nevada entomologists during 1938 coincided with a hail storm, and it was estimated that half of the large population then existing was killed by the hail and cold.

No detailed food-plant studies of *bruneri* have been reported, but the general ecology is rather well known. Morse (1908) described the species (as *alaskanus*) as the dominant *Melanoplus* on Isle Royale, Mich., and recorded it from clearings, along trails, rock ridges, the

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EXPLANATION OF FIGURE 11

Posterior view of male subgenital plate (except *e*(4), which is ventroposterior view).

a: *Melanoplus bruneri:* 1, 2 from Ft. McLeod, Alberta, Canada (2 specimens); 3, 4 from Mt. Moriah, Nev. (2 specimens); 5, from Crook Co., Wyo.

b: *M. borealis stupefactus:* 1, lectotype; 2, 4, 5, 6, from Mineral Co., Colo. (4 specimens); 3, from Los Pinos, Colo.; 7, from Silverton, Colo.

c: *M. borealis borealis:* 1, from Nain, Labrador, Canada; 2, 3, from Cummington, Mass. (2 specimens).

d: *M. borealis palaceus:* 1, 2, 4, from Lakeview area, Mont. (3 specimens); 3, topotype; 5, holotype (*x*, rectangular vertical area).

e: *M. borealis utahensis:* 1, holotype; 2, from Big Cottonwood Canyon, Utah; 3, from Ogden, Utah; 4, ventroposterior view of same specimen as 3.

f: Intermediate between *M. borealis utahensis* and *M. borealis palaceus*, 3 miles north of Mantua, Utah.

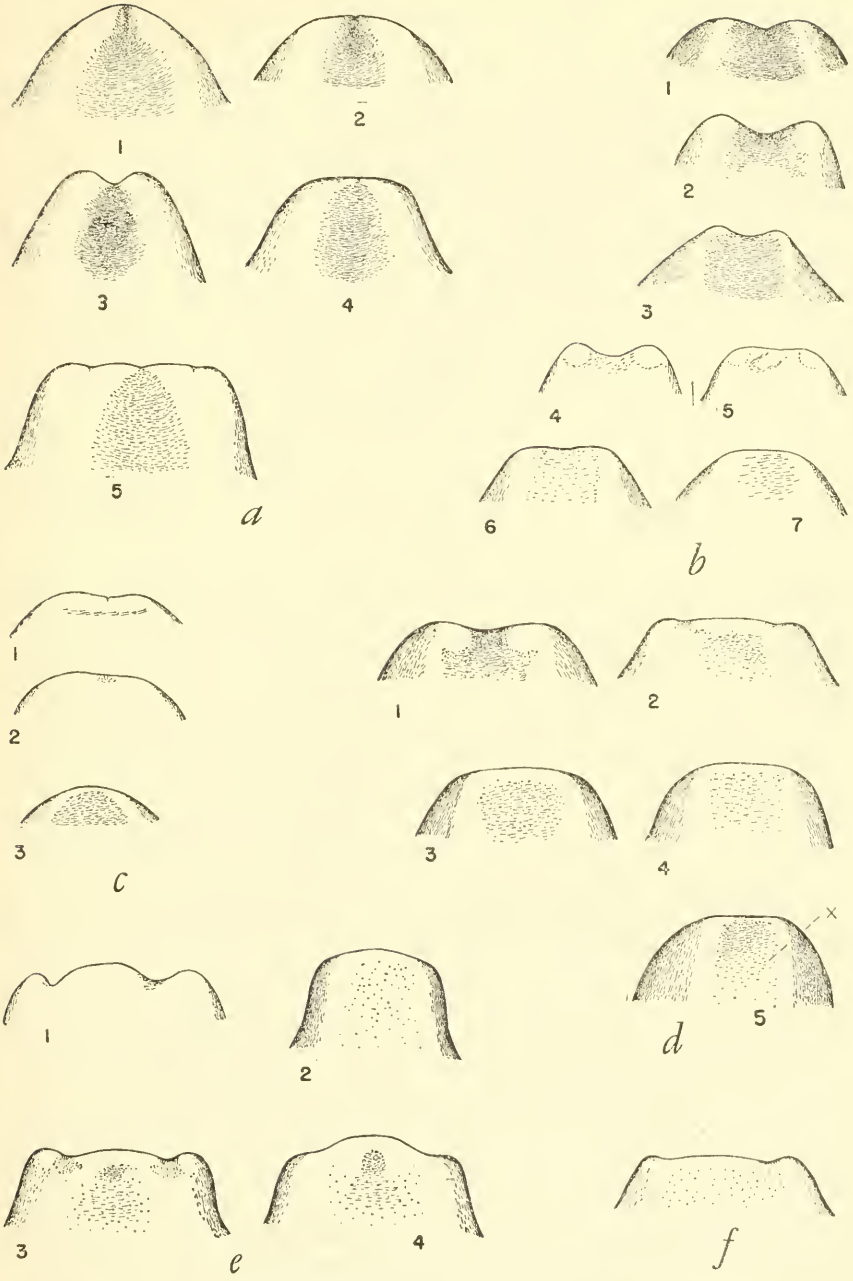

FIGURE 11.—Explanation on facing page.

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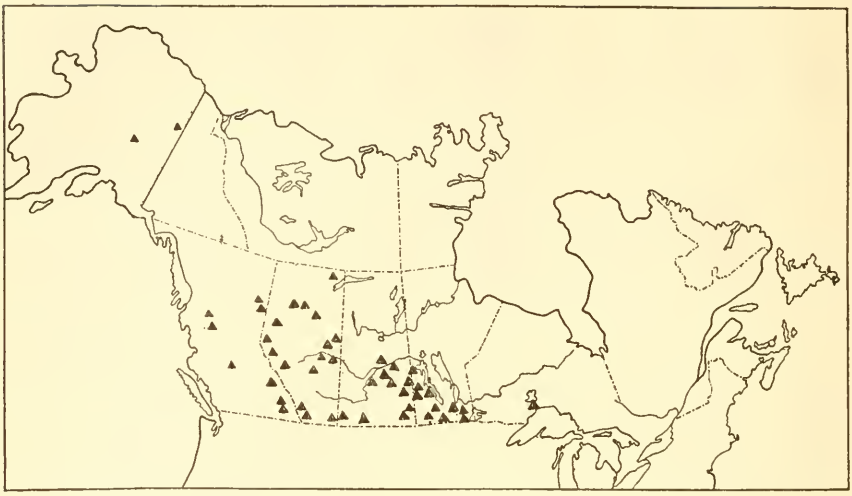

FIGURE 12.—Distribution of male specimens of *Melanoplus bruneri* examined from Alaska and Canada.

beach heath zone, and other environments. Hebard (1925a, p. 114) stated that in the United States *bruneri* is strictly sylvan, living in brushy forest undergrowth, and that this contrasts with the preferred habitat in the Chilcotin District, British Columbia. In the latter area Treherne and Buckell reported that *bruneri* normally lives "among rank-growing grasses and plants growing under the aspen poplar groves which often form belts separating the open range from the timbered hills," also that it sometimes advances into open glades and small mountain meadows where vegetation is thick and green. Probably on the basis of these observations, Buckell (1921), in a summary of ecological preferences of Chilcotin Orthoptera, classified *bruneri* as a semi-sylvan species which extends into the geophilous campestrian area where the open range adjoins the forest. The described Chilcotin habitat seems comparable to the Lake Upsilon, N. Dak., habitat where Hubbell (1922) found *bruneri* "quite common in a dry clearing covered with low bushes and shrubs of various kinds (*Corylus rostrata*, young aspens, willows, birches, etc.) and tall herbaceous plants such as fireweed and goldenrod, interspersed with small, grassy areas." In the prairie provinces of Canada the habits of *bruneri* are similar to those reported by Buckell (1921). In the Cypress Hills plateau of southeastern Alberta, as well as in the foothills of western Alberta, where the open grasslands are replaced rather suddenly by coarse plants, low shrubs, and aspen poplar leading to the evergreen forest, *bruneri* just as suddenly replaces *bilituratus* as the dominant species. Similarly, grassy clearings within the forest margin in the Prince Albert-Whitefox area of Saskatchewan are

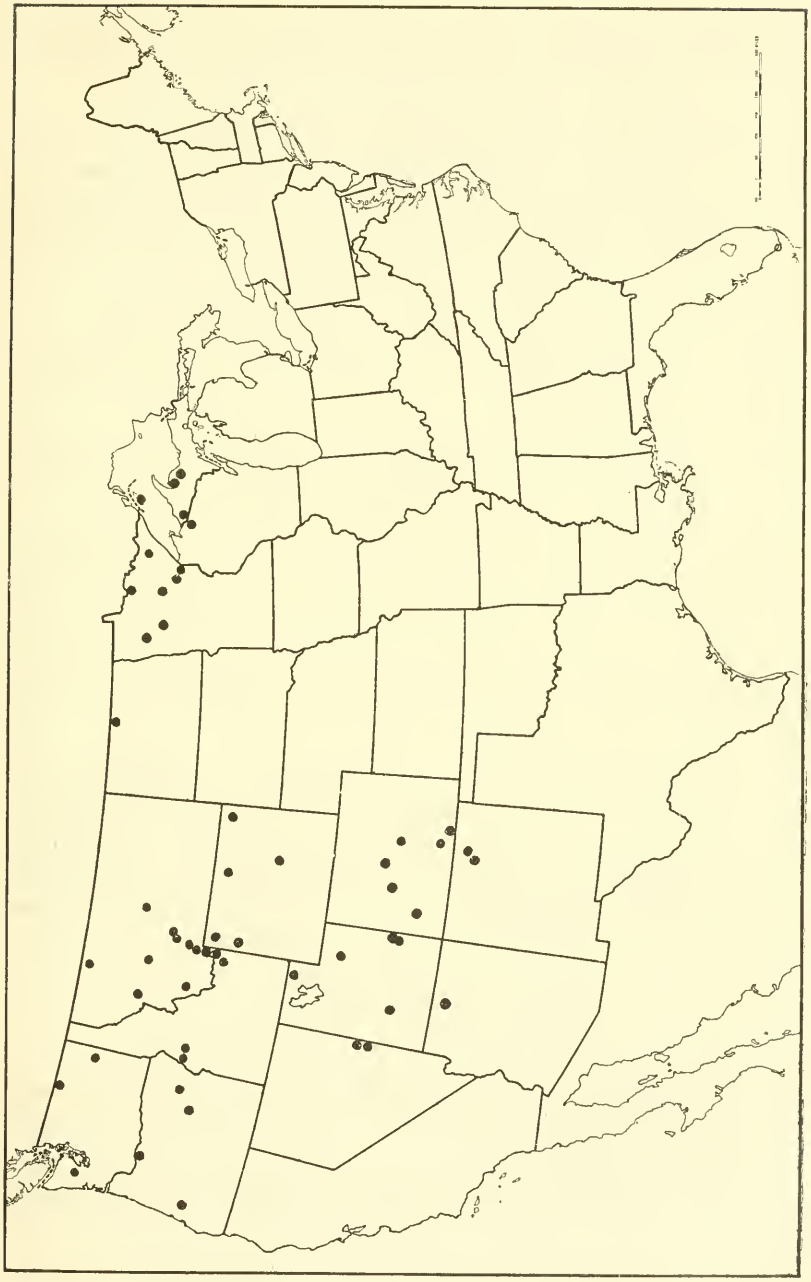

FIGURE 13.—Distribution of male specimens of *Melanoplus bruneri* examined from United States localities.

populated mostly by *bilituratus* while the margins of those clearings support *bruneri*. Hebard (1930) remarked on the very different habitat preferences of *bruneri* and *bilituratus* (*mexicanus*), and this distinction was also brought out by Handford (1946, p. 172). The "rather hot and dry valley fields" where Fulton (1930) found *bruneri* in Oregon probably were adjacent to sylvan conditions. Specimens of *bruneri* (10 ♂, 9 ♀) in the Philadelphia collections, from Red Banks in Logan Canyon, Utah, apparently are those referred to by Hebard (1936b, p. 173) as *M. utahensis*, said to be abundant in areas of "cow cabbage" (*Wyethia amplexicaulis* Nutt.)

Nymphs of *bruneri* have been illustrated by Handford (1946), who found that they resembled darker nymphs, at least, of *bilituratus bilituratus* (=*mexicanus*) in every respect.

In northern Michigan adults of *bruneri* are not abundant until the beginning of August (Hebard, 1909). It has been suggested (Canad. Insect Pest Rev., vol. 33, p. 10, 1955) that since the 1954 outbreak in parts of British Columbia seemed related to one in 1952, while the 1953 infestation was light, the life cycle there may occupy two years. Collection dates on the great majority of specimens examined are in August and late July. Some of the more limital dates are as follows: Francis Lake, British Columbia, July 5; Castleton, Utah, July 5; Chilcotin, British Columbia, Aug .1; 37 miles southeast of Fairbanks, Alaska, Sept. 1; Drain, Oreg., Sept. 11; Therma, N. Mex., Sept. 12; Gallatin Canyon, Mont., Oct. 3.

Some of the altitudes (in feet) on labels of specimens examined are as follows: Evergreen, Idaho, 3,600; Strawberry Mts., Oreg., 4,450; McCall, Idaho, 5,000–5,050; Jackson Hole, Wyo., 6,500; Fishers Peak, Colo., 7,000–8,000; Cascade Canyon, Teton National Park, Wyo., 9,000; southwest base of Delano Peak, Utah, 10,000; Mt. Wheeler, Nev., 10,000–10,600; Mt. Lincoln, Colo., 11,000–13,000.

Melanoplus spretus (Walsh)

FIGURES 1,*f*; 2,*n*; 3,*a*; 7,*b*; 10,*a*,*v*; 14; 15,*a*,*d*; 16,*a*; Plate 2,D

Caloptenus spretus Walsh, Pract. Ent., vol. 2, p. 1, 1866 (Highland, Kansas). Neotype here designated: Male labeled "Lawrence, Kans. June 18, 1877, Geo. F. Gaumer" (USNM).

Caloptenus spretus caeruleipes Cockerell, Entomologist, vol. 22, p. 127, 1889 (probably Glencoe, Nebr., where observations by Dodge (1878) presumably were made).

The condition of the neotype is excellent, with colors well preserved and all appendages present. The aedeagus and epiphallus have been exposed as dry preparations still attached to the body (see figs. 3,*a*-2,3; 10,*a*). The subgenital plate and cercus are shown in figures 16,*a*-2 and 7,*b*-1. Measurements (in millimeters) are as follows:

Length of body, 26.5; tegmen, 23.0; hind femur, 12.5; extent of tegmen posterior to apex of hind femur, 9.0; pronotum, 4.6. The E/F ratio (length of tegmen divided by length of hind femur; see comments on p. 6) is 1.840. The general coloration is light brown, the head with gena rather pale and postocular dark bar distinct; antenna reddish brown; dorsum of occiput with broken, indistinct longitudinal dark streaks; tegmen with dark flecks in basal half only; hind femur with three transverse blackish bars (exclusive of knees) primarily on mesal half of dorsal surface; hind tibia and tarsus pale red, spines, claws, and apical half of spurs black.

Five additional males and one female examined bear the same data as the neotype. The locality where the neotype was collected, Lawrence (Douglas Co.), Kans., is about 65 miles south of the type locality, Highland (Doniphan Co.), Kans. George F. Gaumer, the collector of the neotype, was a special assistant to the U. S. Entomological Commission who worked in Kansas in 1877. He has reported (Gaumer, 1878) that on June 16, 1877, he observed locusts flying over the Wakarusa River (which is about 3 miles south of Lawrence). He observed them on June 18 also, and, though a precise locality is not described, it can be inferred that the same general locality was involved. The locusts were seen flying in a north-northeast direction, and at 5 p. m. many specimens dropped to the ground. This information published by Gaumer explains the probable background of the historic specimen chosen as neotype.

Walsh (1866) did not give a formal description of *spretus*, though he gave various characters and compared it to *M. femur-rubrum*, and he attributed the specific name to Uhler, who Walsh said had given the locust the name *Caloptenus spretus* without describing it. Since no published proposal of the name by Uhler was made, the name dates from Walsh. Walsh had specimens which were sent to him by Prof. W. S. Robertson of the Indian Orphan Institute, Highland, Kans. Since he did not consider that he was describing *spretus* as new, possibly specimens were not preserved, at any rate no such specimens nor further references to them have been found, in spite of an examination of the principal historic collections of *Melanoplus*. In case specimens were preserved in the Walsh collection, they probably were destroyed in 1871, when the Walsh material was burned in the great Chicago fire (Burks, 1953, p. 16). Since no type is known to exist, in spite of efforts to locate one, selection of a neotype is advisable. This is especially true because *spretus* is of great historic importance. It has not been collected recently, and old specimens are scattered in many collections, and eventually the number of good examples may become scarce.

The name *caeruleipes* was proposed by Cockerell (1889) for the

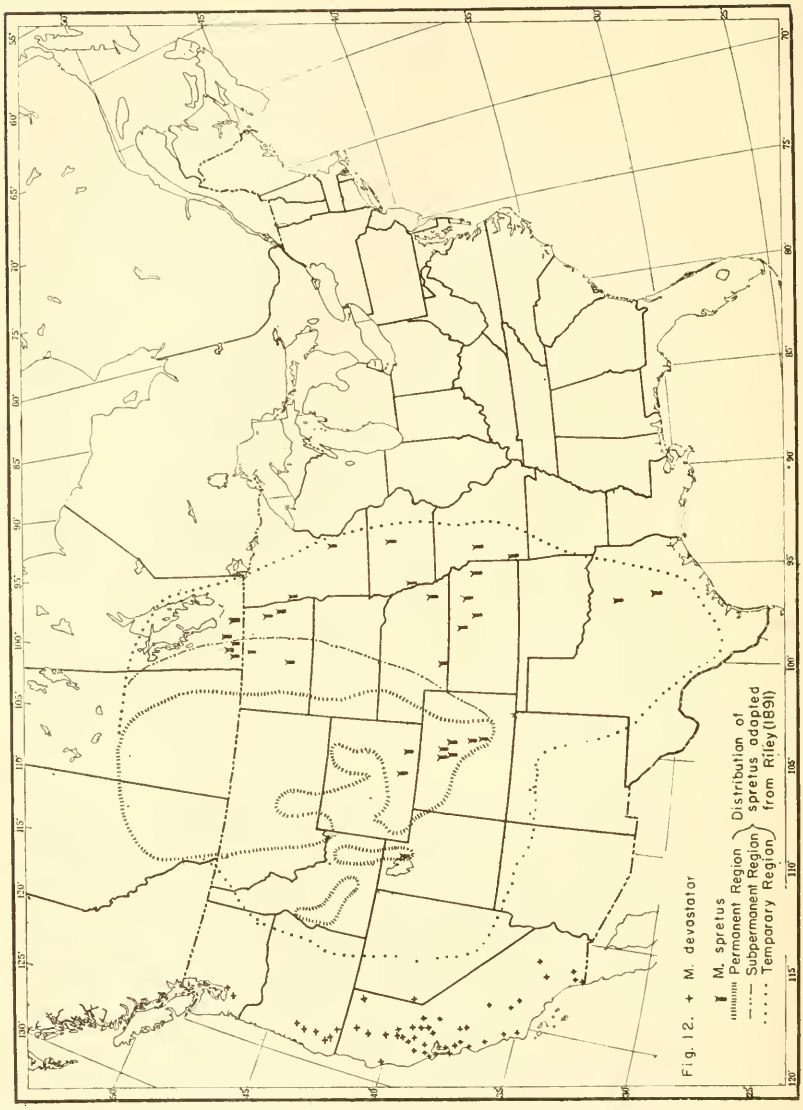

FIGURE 14.—Distribution of male specimens of *Melanoplus devastator* and *M. spretus* examined.

variety "of *spretus* with blue hind tibiae." He referred to material reported by Dodge (1878), but no types are known to exist, and probably none was set aside. It was previously reported (Riley, et al., 1878, p. 47) that some specimens of *spretus* had blue hind tibiae, and it appears clear that no nominal significance should be attached to such individuals. Scudder (1897b, p. 185) placed *caeruleipes* Cockerell in the synonymy of *spretus*, and Hebard (1925a, p. 113) referred to the synonymy.

Melanoplus spretis—originally described in *Acridium* and credited to Uhler by Thomas (1865) but in reality described by Thomas himself because Uhler had published no description—is of uncertain identity and the source of some confusion in the literature. No type specimens of *spretis* were mentioned by Frison (1927) or Hebard (1927). Riley, et al. (1878, pp. 43–44), stated that there must have been some mistake in the description, and that the original specimens of *spretis* were destroyed soon after the paper was written. The name *spretis* occasionally has been used in the sense of the Rocky Mountain grasshopper, as when Rehn (1900) recorded it from Mexico, following which Hebard (1917; 1932a, p. 289) pointed out the misidentification of *mexicanus*. Scudder (1897b, p. 185) treated *spretis* Thomas as a synonym of *spretus* Walsh, and Hebard (1934b, p. 197) did likewise. Earlier, however, Hebard (1925a, p. 113) considered *spretis* a synonym of *atlanis* Riley. He appears to have overlooked the fact that *spretis* antedated *atlanis* by 11 years! Thomas (1865) stated that *spretis* was quite common in Illinois, which we believe was untrue of *spretus*, and it would seem that *Melanoplus bilituratus* was involved. The measurements given by Thomas apply fully as well to *spretus* as to Illinois specimens of *bilituratus*, however. Thomas (1878) credited *spretus* (sic!) to himself and referred to the Illinois State Agricultural Report. Because of uncertainties over the identity of *spretis*, and the confusion with *spretus* if both names were to be retained for distinct populations, it is best to treat *Acridium spretis* Thomas 1865 as unrecognizable.

Scudder (1878b) was the first to assign *spretus* to the genus *Melanoplus*.

Descriptive notes: A large, long-winged member of the *mexicanus* group (pl. 2,d). Head with fastigium comparatively far in advance of compound eyes; the dorsal carinae of vertex less prominent and farther apart than in *mexicanus;* eyes less rounded and bulging than in *mexicanus;* especially in male; pronotum (fig. 15,*a*) with strangulate narrowing of sides in front of principal transverse sulcus, this conspicuous on lower portions of lateral lobes; in lateral view the principal sulcus lower than remainder of median carina; mesosternal hump well developed in male, absent in female.

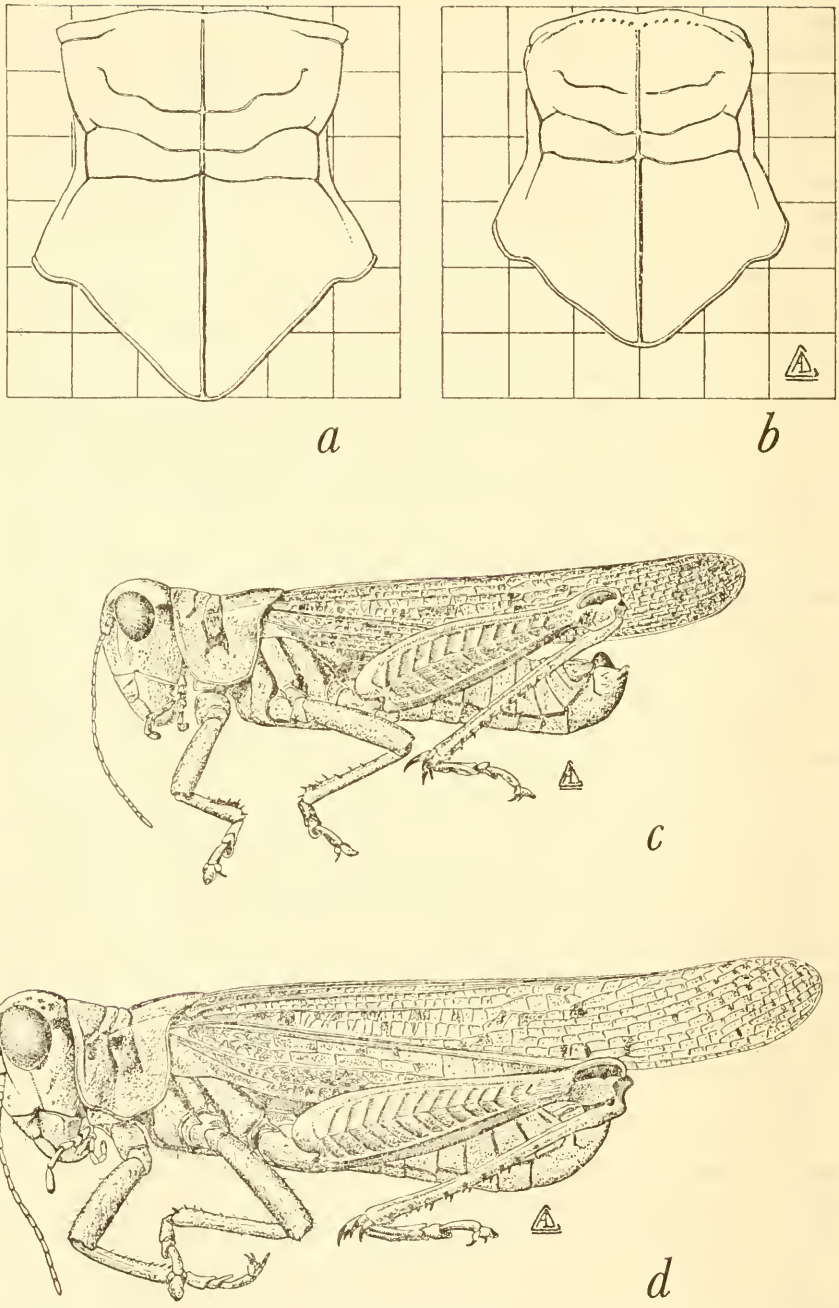

FIGURE 15.—*a*, *b*, Dorsal view of pronotum, with grid to show extent of constriction: *a*, *M. spretus*, male, Pueblo, Colo.; *b*, *M. bilituratus vulturnus*, Wellington, Kans. *c*, *d*, Lateral view of: *c*, *M. bilituratus vulturnus*, Wellington, Kans.; *d*, *M. spretus*, male, Pueblo, Colo.

MALE GENITALIA: Cercus (fig. 7,*b*) broad for group, the apex oblique at ventral side; subgenital plate (fig. 16,*a*) strongly upturned, twin apices (posterior view) well developed; aedeagus (figs. 2,*n;* 3,*a*) with dorsal valve extending laterally more than anteriorly, and recurved dorsally and posteriorly, conspicuously concave on posterior surface, the apex of valve (dorsally) membranous; accessory lobe comparatively elongate; apex of aedeagus dorsally produced beyond dorsal valve.

FEMALE genitalia: Cercus slightly more robust and blunt than in *mexicanus;* dorsal valve of ovipositor with "scoop" well developed, the dorsal shoulder at base angular.

COLORATION: General coloration relatively dark for group. Hind femur with four dark transverse dorsal bands (including knee), inner paginal area rich yellowish, occasionally tinged with pinkish, outer paginal area yellowish to light brown, paler along ventral margin, ventral surface yellowish, the outerhalf tinged with pink; hind tibia usually red; tegmen with conspicuous blackish flecks; wing transparent, with faint tinges of yellowish near base. (Brett, 1947, p. 33, reported that of 100 specimens of *spretus* he examined in the Bruner Collection, University of Nebraska, 85 percent had red hind tibiae and 15 percent glaucous or pale hind tibiae.)

VARIATION: The size of 14 representative males, measured in millimeters, varies in pronotal length from 4.2 to 5.5 (av. 4.8), in hind femur from 11.5 to 14.2 (av. 13.0), and in tegmen from 19.0 to 26.0 (av. 22.8). Seven measured females vary in pronotal length from 4.8 to 5.4 (av. 5.1), in hind femur from 13.2 to 15.2 (av. 14.2), and in tegmen from 23.0 to 25.5 (av. 24.6). No correlation between size differences and geographic distribution has been recognized.

The extent to which the tegmen extends posteriorly beyond the apex of hind femur varies from 4.5 to 10 mm., with an average of about 7 mm. for males examined. For females, extremes of 5, and 10, and an average of about 8 mm. occur.

Measurements by Riley, et al. (1878, pp. 47–49), are not comparable to the present ones because the former concern the distances that various body structures exceed others. Faure's (1933) measurements are expressed in averages only. His averages for length of tegmen are higher than ours, perhaps because more distance at the very base of the tegmen was included through not using the method later recommended by the International Locust Conference (see p. 6 of the present paper).

Of the males seen, there is none with pale hind tibiae which may not owe the lack of pigmentation to immersion in fluid. The hind tibiae of two or three of the females seem to be pale from original coloration, though fading is suggested by some of the oldest specimens.

Furculae vary from straight to markedly divergent. Very little variation in the male cercus has been seen. The aedeagus seldom varies much, except in appearance due to shriveling from drying. The apical portion of the main stem shrivels considerably and often is smaller and somewhat distorted when dry. The apical valve usually is heavily and darkly sclerotized, extending decidedly more laterally and posteriorly, like "horns," in dry than wet preparations. In wet preparations the apical membrane of the dorsal valve is much more noticeable, decreasing the hornlike appearance. The dorsal valve occasionally is well anterior of the apex of the main stem, but frequently, especially in dry preparations, extends laterad of the apex. The apex of the ventral valve sometimes extends out from the main stem, but usually is tightly appressed to the anteriobasal portion of the aedeagus. The accessory lobe usually shrivels and has little distinctive shape following drying.

Distribution: The map (fig. 14) shows the distribution of males examined which have precise locality data. Males with only State labels are from Montana and New Mexico, as well as from eight other States and Provinces from which there are precise data. Females examined which add significantly to the distribution shown by males are from Taos Peak, N. Mex., only. The Permanent, Subpermanent, and Temporary Regions (fig. 14) in the sense of the U. S. Entomological Commission, are adapted from Riley (1891). Riley (1877) and Riley, et al. (1880), also mapped the distribution of *spretus*. It was frankly stated by Riley and his associates that various details as presented on their maps were based on fragmentary data and so should be taken as tentative only. Many early records of *spretus* are unsupported by specimens, so there is no way of checking identifications. It seems possible that some early Nevada records may be attributable

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Explanation of Figure 16

Subgenital plate of male, in lateral view.

a: *Melanoplus spretus:* 1, from Argentine Pass, Colo., July 16, 1877; 2, neotype.

b: *M. bilituratus defectus*, Casa Grande, Ariz.

c: *M. borealis stupefactus*, Los Pinos, Colo.

d: *M. borealis borealis:* 1, from Cummington, Mass.; 2, from Churchill, Manitoba, Canada; 3, from Pikes Peak, Colo.

e: *M. borealis palaceous:* 1, holotype; 2, topotype; 3, from Lakeview area, Mont.; 4, from Cedar Breaks, Utah.

f: *M. borealis utahensis:* 1, holotype; 2, from Ogden, Utah; 3, from Big Cottonwood Canyon, Utah.

g: Intermediate between *M. borealis utahensis* and *M. b. palaceus:* 1, 2, from 3 miles north of Mantua, Utah (2 specimens).

h: *M. bruneri:* 1, from Ft. McLeod, Alberta, Canada; 2, from Chilcotin, British Columbia, Canada; 3, from Drain, Oregon; 4, from Mt. Moriah, Nev.

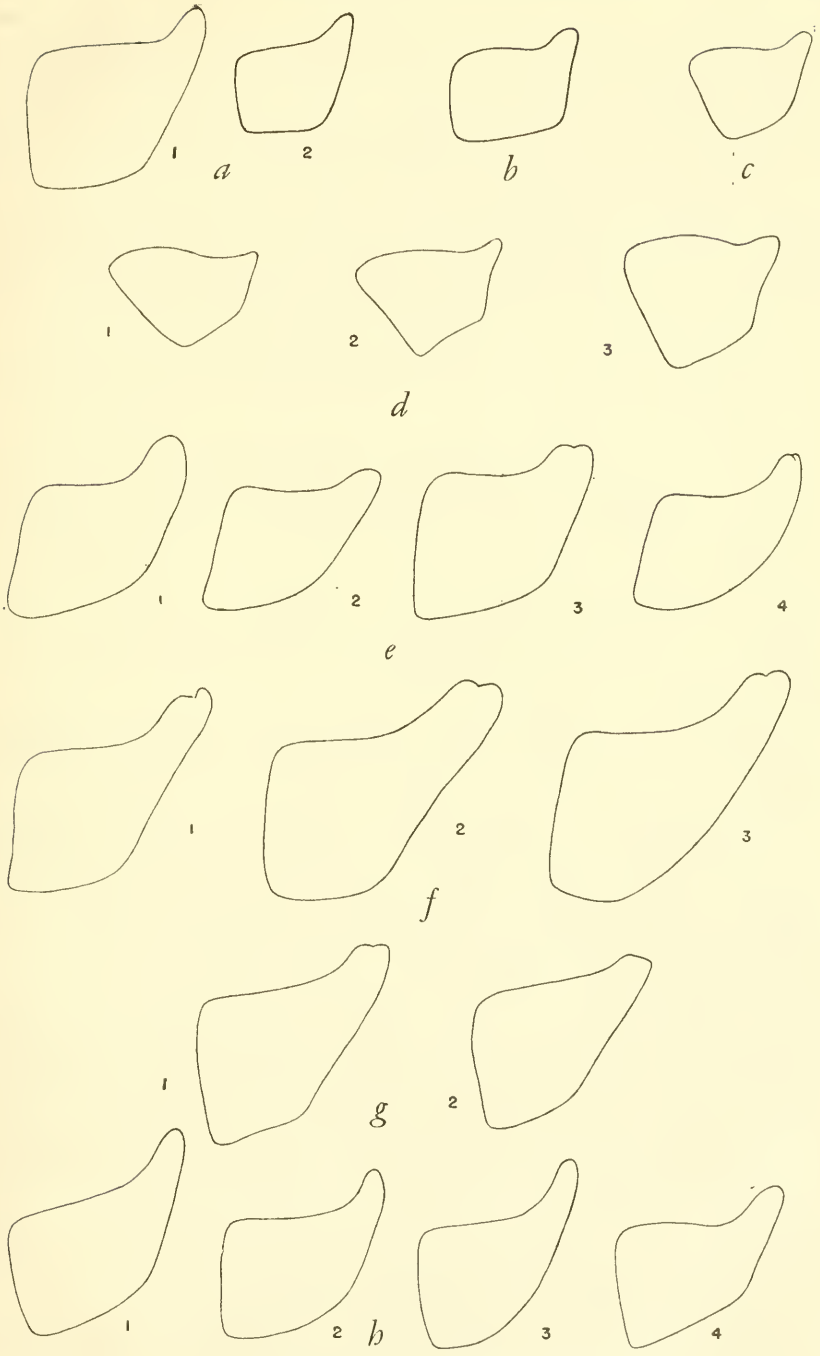

FIGURE 16.—Explanation on facing page.

to the Nevada sage grasshopper, *Melanoplus rugglesi* Gurney. For instance, Riley, et al. (1880, p. 7), included the following paragraph:

> This year [1878], as well as 1877, was a locust year in this sparsely settled territory. July 11 great numbers appeared at Winnemucca, and disappeared the 13th; on the 18th and 19th swarms again appeared. (United States Weather Report).

Since the season of the year noted above is normal for *rugglesi*, and Winnemucca is in the same area through which swarms of *rugglesi* passed in the late 1940's, also since *rugglesi* could have been mistaken for *spretus* by local observers, it seems quite possible that *rugglesi* is the species responsible for the report quoted.

Specimens of *Melanoplus spretus* examined, with full locality label data except State names:

CANADA: Rosebank, Manitoba, (1 ♂, 1 ♀);[3] Aweme, Manitoba, July 19, 1902, N. Criddle (1 ♂, 1 ♀); Fairfax, July, J. Fletcher (1 ♂, 1 ♀);[4] Boissevain, Manitoba, Aug. 26, 1879 (1 ♂); Delorain (Manitoba), July 8, 1898 (1 ♂, 1 ♀); Manitoba, Aug. 28, 1877 (1 ♂); Arctic America, R. Kennicott, S. H. Scudder (1 ♂).[5]

MINNESOTA: Glyndon, Aug. 1877 (1 ♀); Glyndon, Clay Co., July 1, 1875 (1 ♀); Minneapolis, Aug. 16, 1877 (2 ♂); "Minnesota," Oct. 6, 1876 (3 ♂, 6 ♀).

NORTH DAKOTA: Bismark, July 23, 1877, Geo. W. Sweet (4 ♂, 1 ♀); Clifford, Traill Co., July 25, 1891 (2 ♂); Larimore, July 29, 1901 (1 ♂); Turtle Mts.[6] (1 ♂, 2 ♀); "N. Dakota," July, 1900 (1 ♂).

MONTANA: "Mont" (1 ♂, 1 ♀).

IOWA: Ackley, Sept. 1, 1877 (2 ♂); Dallas Co., Aug., Allen (1 ♀); Harrison Co., Aug. 4, 1873 (1 ♂); Monona Co., Aug. 1873 (1 ♀); "Iowa," June 1877 (1 ♂).

NEBRASKA: Lincoln, June 28, 1893, 1,150 ft., Bruner (1 ♂); Red Willow Post Office, Aug. 1874, John Byfield (1 ♂); "Nebr." 1868 (3 ♂, 1 ♀); "Nebr." 1874 (3 ♂, 2 ♀).

WYOMING: Alkali St(ation), 6,000 ft., July 27, 1877 (1 ♂, 1 ♀); Steele, "flying from S. & S. W.," July 1879, C. A. H. McCauley (1 ♂); Steele, July 1878 (1 ♂); Steele, July 1879 (1 ♀); "Wyo. Terr." (1 ♂).

UTAH: Salt Lake Valley, 4,300 ft., Aug. 1–4, 1877 (3 ♂); Salt Lake, Aug. 16 (1 ♀); Salt Lake (1 ♀).

COLORADO: Argentine Pass, 13,000 ft., July 16, 1877 (2 ♂); Arapahoe Peak, 11–12,000 ft., Packard (2 ♂); Boulder, July 19, 1877 (2 ♂); Colorado Springs, July 1878 (1 ♂), July 26, 1877 (2 ♂, 2 ♀), July 21, 1877 (1 ♀), Aug. 1, 1877 (1 ♀), July 1877 (2 ♀); near Denver, L. Agassiz (1 ♂); Georgetown, 85–9,500 ft., July 12–13, 1877 (1 ♂, 2 ♀); Mt. Lincoln, above timber, 11–13,000 ft., Aug. 13, 1877 (2 ♀); Pueblo, July 8–9, 1877 (1 ♂); White River, Aug. 6, 1877, Mrs. E. H. Danforth (1 ♀); "Colorado," July 1877 (1 ♀); "Colorado," H. V. Morrison (1 ♂).

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[3] These specimens probably are part of the "enormous numbers" of *spretus* reported by Mitchener (1954, p. 50) to have been found at Fairfax, Manitoba, July 4, 1901, by James Fletcher.

[5] Probably collected by Kennicott in the Winnipeg area of Manitoba, as discussed by Scudder (1897b, p. 187), the Scudder name on the label probably referring only to the Scudder collection.

[6] These Turtle Mt. specimens probably are from the same source as a large collection preserved at the University of Nebraska and reported by Brett (1947, p. 14) as collected by Lawrence Bruner in the early 1880's. O. S. Bare (in litt., Dec. 19, 1946) has informed us that M. S. Swenk once told him that the Turtle Mt. series was collected about 1890.

New Mexico: Taos Pk., 13,000 ft. (1 ♀); "N. Mexico," July 21, 1877 (1 ♂), July 21, 1877 (1 ♀).

Missouri: Sarcoxie, July 10, 1877 (2 ♀); Jackson Co., 1874 (2 ♀); Jasper Co., Nov. 12, 1876 (1 ♂, 1 ♀); Johnson Co., 1874 (1 ♂, 1 ♀); "N. Mo.," 1868 (1 ♂); "Central Mo.," 1874 (1 ♀); Holt Co., 1868 (2 ♀).

Kansas: Cawker City, 1874, N. B. Freeland (1 ♂, 1 ♀); Lawrence, June 18, 1877, Geo. F. Gaumer (6 ♂, one the neotype, 1 ♀); Manhattan, Nov, 1876 (3 ♀), 1874, W. C. Howard (2 ♂); Salina, Oct. 1877 (1 ♂, 1 ♀); Douglas Co., Oct. 1877, G. F. Gaumer (1 ♂, 1 ♀); "Kans.," 1874 (2 ♂, 2 ♀), 1876 (1 ♀), Nov. 1876 (1 ♂, 2 ♀).

Texas: Near Brenham, 1868, Thos. Affleck (1 ♀); Calvert, devouring kernels of corn, J. F. Moulton, Jr. (1 ♂); Dallas, Boll[7] (1 ♂); Salado, May 1877, J. H. Myers (1 ♀); "Texas," Belfrage[7] (1 ♂, 1 ♀); "Texas, common everywhere, has been very destructive in this and adjoining counties, the past few years," Belfrage (1 ♀); "Texas," Pope, May 15 (1 ♀); "Texas" 1868 (1 ♀).

Locality uncertain: An original Uhler specimen, probably sent to Scudder by Uhler, belonging to the Museum of Comparative Zoology, with a round pink disk, also the labels, "Collection of P. R. Uhler"; "S. H. Scudder Coll"; "Melanoplus spretus Scudder's Type, 1895"; "Caloptenus spretus Uhler NRR migratory" (1 ♂) (manuscript notes from the late H. S. Barber include a list of abbreviations given him by Uhler; NRR meant "North Red River"; also see Scudder (1897b, p. 187)).

Biology and economic importance: Prior to 1885 the literature dealing with the Rocky Mountain grasshopper probably was more extensive than that then available concerning any other single native American insect. Since there is no recently gathered information and it is impossible to sift facts from opinions in much of the voluminous early record, the biology of *spretus* will be reviewed briefly. The most important references on biology are those of Packard (1877), Riley (1876, 1877a, 1877b, 1891), and Riley, et al. (1878, 1880, 1883). There is a great deal of repetition in those reports, and Riley's summary (1891, pp. 9–26) is recommended. When Cyrus Thomas began the field study of *spretus* in 1869 (Riley, et al., 1880, p. 73), he believed from the first year's observations that the species was essentially sedentary, but later he and the other commissioners decided that it was predominantly migratory. Areas inhabited were defined as follows (Riley, 1891, map; and elsewhere): Permanent Region, or native breeding grounds, where the species is always found in greater or less abundance; Subpermanent Region, which the species frequently invades, in which it can perpetuate itself for several years, but from which in time it disappears; Temporary Region, or that only periodically visited, and from which the species disappears within a year (see map, fig. 14).

Riley, et al. (1878, 1880), supposed portions of Canada (then customarily referred to as Arctic America, or British America) to be an

[7] G. W. Belfrage (1834–1882) and Jacob Boll (1823–1880), both well-known early collectors in Texas. Belfrage collected most in Bosque and McLennan Counties.

important part of the Permanent Region, but it is not clear how important a part. Walker (1910, p. 336) summarized distributional findings of the U. S. Entomological Commission for Canada, so far as the "Regions" were concerned, but he added little new information. Criddle (1917), perhaps basing an opinion on observations during years long after the main outbreak period, said that "invasions of Canada" occurred only during dry seasons, the swarms arriving in July and August. Roe (1951), in his discussion of the buffalo, said that in the 1870's and 1880's there was quite common ignorance of western Canada. It may have been easy to ascribe the source of something poorly understood (i. e., swarms of *spretus*) to a vast, distant region that was little known entomologically.

Within the Permanent Region, *spretus* did not breed everywhere, but instead it did so in favorable spots. River bottoms, sunny slopes of uplands, and subalpine grassy areas among the mountains were considered to be favored egg-laying sites. After maturity was reached, flights within the Permanent Region were common. More devastating and consequently much more widely publicized, however, were the "invading swarms" which went primarily in a southerly or southeasterly direction (except when west of the Rocky Mountains). A day's flight was estimated to be from 20 to 150 miles. Stops were usually made at night, but not always. During brief stops, or when settled in an area for egg-laying, the swarms ate nearly all crops and wild plants. Swarms might stop anywhere in the Temporary Region. Riley (1877b, p. 95) stated that in 1876 swarms left Montana about the middle of July and reached Texas by the end of September, thus covering 1,500 miles in 75 days, an average of 20 miles per day.

Swarms developing from eggs laid in the Temporary Region usually migrated northward or northwestward. In the southern part of the infested area a partial second generation sometimes occurred, but *spretus* had essentially a single generation per year. The time of hatching, as a general rule, varied from the middle to end of March in Texas, to the middle of May or beginning of June in Montana. The young grasshoppers typically displayed gregarious habits soon after hatching and initial feeding near the hatching site. The nymphs were described as moving in "schools or armies," generally "marching in a given direction until toward evening" (Riley, 1891, p. 21). Sometimes the nymphs migrated in a band a mile wide across the front (Riley, 1877b, p. 233). Usually, marching occurred only during the warm hours of the day.

Melanoplus spretus was considered to be nearly omnivorous on both native and cultivated plants, with vegetables and cereals a "mainstay," though at least in some instances sorghum and broom corn

were left untouched (Riley, et al. 1878, p. 251). No thorough analysis of preferences among the native food plants of the Permanent Region seems to have been made, leading Pfadt (1949, p. 39) to conclude that there is no information concerning the food-plants on which *spretus* originally developed.

During the years when it was more or less prevalent, *spretus* varied considerably in its abundance and destructiveness. Riley (1891, p. 10) gave a résumé of the relative abundance between 1818 and 1888. Bethune (1875) briefly described the early destructive outbreaks in Manitoba, and a recent summary is by Mitchener (1954). Some of the summaries of experience with grasshoppers in various States, such as that of Smith (1954) for Kansas and of Munro (1949) for North Dakota, have not always differentiated between various species, as of course it is impossible to do for many of the early years. Schlebecker (1953) has given perspective to the general subject of grasshopper outbreaks, and has reviewed the period of great damage by *spretus*. The year 1866, when the Rocky Mountain grasshopper did great damage in Kansas, Nebraska, northwestern Texas, and also invaded western Missouri, is described as one of the first years in which it attracted national attention. The years of greatest abundance were 1873–1876, with 1874 the high point in destructiveness. In 1874, Colorado, Nebraska, and Kansas were overrun, and parts of Wyoming, the Dakotas, Minnesota, Iowa, Missouri, New Mexico, Oklahoma, and Texas were ravaged by swarms from Montana and Canada where they were abundant (Riley, 1891). As recorded by Riley, et al. (1880), and recalled by Bruner (1883), infestations dwindled in 1877. Widespread abundance of *spretus* never occurred again, though some injury in various years of the 1880's is attributed to it, including an important local outbreak in Otter Tail Co., Minn., in 1888. None of the 1888 specimens is preserved, so far as known (Hebard, 1932b, p. 37). Riley, et al. (1883), mapped the reported hatching and flights of 1880 and 1881. Bruner (1893) reported *spretus* present in many parts of middle and eastern Nebraska in 1892, and quite common at Lincoln, Nebr.

It is probable that the layers of *spretus* in Grasshopper Glacier, Park Co., Mont., were deposited during the major recorded swarming years for *spretus*, or in earlier years that were comparable, though not recorded. This glacier, located near the northeastern corner of Yellowstone National Park, has been discussed in detail by Gurney (1953). Flights of grasshoppers, probably aided by favorable air currents, occasionally pass over the glacier, even at its altitude of nearly 11,000 feet, and specimens landing on the snow are preserved when the necessary subsequent conditions of freezing and snowfall occur. Several species have been collected alive on the snow of the

glacier in recent years, but *spretus* is the only species identified from the remains imbedded in layers here and there in the glacier, and sometimes conspicuous on the vertical face at the foot. Preserved samples have long been supposed to be *spretus*, but during the period when *spretus* was considered a migratory phase of *mexicanus*, and before the critical features of the aedeagus were known, the samples were not identifiable other than as *mexicanus* (as then called). Study of the aedeagus of specimens now shows the samples in the U. S. National Museum to be *spretus*; unfortunately, this had not been done when the 1953 glacier paper was published. Prior to 1898, grasshoppers were known to be preserved in the glacier, and they were first examined and identified as *spretus* in 1914. The rather fragmentary samples now at the U. S. National Museum represent 13 specimens, from which two males taken in 1949 by Dr. J. R. Parker and one taken in 1952 by Dr. Irving Friedman have been dissected and found to be *spretus*. The dorsal valve of those males is well preserved and typical. Fragments of grasshoppers collected from the central and bottom portions of the glacier in 1952 by Dr. Friedman, of the U. S. Geological Survey, were sent by him to W. F. Libby, then of the Institute for Nuclear Studies and Department of Chemistry, University of Chicago, for age determination by the carbon–14 method. Dr. Libby reported (in litt., Apr. 15, 1953) that the results indicated an age of 45 ± 300 years and that the limits of error were 45 ± 600 years. He has since reported (Libby, 1954) the age as 45 ± 150 years. The specimens are thus indicated as quite modern, and the likelihood is that the layers of preserved *spretus* are not more than 200 years old, perhaps much younger.

Various writers at about the turn of the century remarked on the strange disappearance of *spretus*. Cooley's (1904a) experience of not capturing a specimen during five years of collecting in all parts of Montana was typical. Except for the Grasshopper Glacier material, the only specimens collected since 1890 that we have examined are from Clifford, N. Dak., 1891; Lincoln, Nebr., 1893; Delorain, Manitoba, 1898; "North Dakota," 1900; Larimore, N. Dak., 1901; Fairfax, Manitoba, apparently 1901; Aweme, Manitoba, 1902.[8] Rehn and Hebard (1906, p. 408) and Hebard (1928, p. 283; 1929, p. 390) recorded three specimens (as *spretus*) which Hebard collected at Pike's Peak and near Manitou, Colo., in 1904. The single male, from Pike's Peak, on examination of the aedeagus, proves to be *M. bilituratus bilituratus*. Thus, *spretus* is not known to have existed since 1902.

Why *spretus* disappeared and whether it is extinct are unknown. Riley, et al. (1883), included a long discussion by Lawrence Bruner,

[8] All these latest records are represented by males. Aweme, where Norman Criddle lived and worked for many years, is near Treesbank, and about 15 to 20 miles southwest of Carberry, Manitoba.

the foremost American field student of grasshoppers of his time, of factors of weather, natural enemies, and other influences thought to be related to *spretus* abundance, but the enigma remains. Cantrall and Young (1954) hinted at an influence by the American buffalo: "It is obvious that any disturbance in a habitat is accompanied by population fluctuations with the increase of some species and the decrease of others. The appearance of the migratory locust, *Melanoplus mexicanus* migratory phase *spretus*, following reduction of the great buffalo herds may be a classical example of the phenomenon." We have examined the well-documented reports of Hornaday (1889) and Roe (1951) in an effort to determine whether there is a chronological correlation between the disappearance of the buffalo and the abundance or disappearance of *spretus*. So far as the southern herd, centered in Kansas and adjacent States, is concerned, the last hunting on a large scale occurred during the winter of 1875–1876. In 1871, by which time much attention already had been attracted to the migration of *spretus*, millions of buffalo remained in Kansas, Oklahoma, and the Texas Panhandle. The northern herd, located mainly in Wyoming, Montana, and the Dakotas, was slaughtered later than the southern one. The years 1878–1883 were the biggest hunting years, with the last major hunt in the season (about October–February) of 1882–1883. Therefore, in Montana, which was the heart of the Permanent Region for *spretus*, the peak of grasshopper outbreaks had passed (1877) before the buffalo herd was removed. After considering possible effects of the buffalo in feeding and trampling on the range, and the feeding by young nymphs on dry buffalo manure, it is difficult to see any relation other than near chronological coincidence between grasshopper and buffalo.

Uvarov (1921) advanced the "phase theory" of locusts, which later became generally accepted as a fact, and Hebard (1925a, pp. 112, 113; 1928, pp. 281–284) suggested that *spretus* might be the migratory phase of *mexicanus*. Faure (1933) concluded, following rearing experiments, that he had demonstrated that nymphs of *bilituratus* [*mexicanus*] could change into *spretus*, thus establishing the phase explanation. However, the measurements of his laboratory-reared "*spretus*" are not fully typical of the historical specimens of *spretus*, and his demonstration was not conclusive (Hebard, 1936c, p. 48). Brett (1947) also believed that by regulating the food and laboratory environment of growing nymphs he had produced "*spretus*." His material, samples of which have been deposited in the U. S. National Museum, shows considerable variation in wing length, but the aedeagi of all the males seen are ascribable to *M. bilituratus vulturnus*, and no approach to the aedeagus of *spretus* is shown. If *spretus* were a

phase of *bilituratus*, it might be supposed that during the fairly extensive flights of the 1930's, as reported by Parker, et al. (1955), there would have been signs of *spretus* development. But such was not the case, and now, in the light of aedeagal characters here discussed, it seems that *bilituratus* and *spretus* are distinct species. Nevertheless, for 25 years the view that *spretus* is the migratory phase of *bilituratus* [*mexicanus*] had considerable acceptance (Hebard, 1929, 1931, 1936c; Gurney, 1953, p. 314, pl. 7, fig. D; Parker, et al., 1955).

Brett (1947) felt that settlement of *spretus* breeding grounds for farming and grazing was responsible in some way for the disappearance of the grasshoppers. Impressed by short-winged specimens reared on alfalfa, he also stressed a possible correlation between the increase in alfalfa acreage and *spretus* decline. Pfadt (1949, p. 39) expressed doubt that alfalfa was a major factor and implied that the little available information concerning preferred native food plants of *spretus* is an inadequate basis for any general conclusions explaining the disappearance. We have failed to learn of any pronounced range-plant changes in Montana during the 1860's, 1870's, or 1880's, so far as the general disappearance or replacement of plant species is concerned. (See Andrewartha and Birch (1954, esp. pp. 594–600) for a discussion of conditions related to population fluctuations.)

The irregular periodicity of historic *spretus* swarms, the apparently nearly omnivorous appetite and very long-winged condition of swarming adults, and the marching behavior of nymphal bands suggest the occurrence of a migratory phase. If this view is correct, *spretus* probably had a solitary phase which occurred in relatively localized colonies, possibly adapted to a specialized environment. There is the example of *Melanoplus rugglesi*, which in the Great Basin attracted widespread attention for about 13 years (1939–1952) as a migratory phase. Previously, *rugglesi* had been virtually unknown, and at present the solitary phase is scarcely found except by entomologists acquainted with the specialized habitat of the small localized colonies. A handicap in studying the possible correlation of weather conditions and *spretus* abundance is a shortage of reliable weather records, prior to 1886, for such Western States as Montana.

Criddle (1917) discussed the former prevalence of *spretus*, and added: "At present, however, the insect seems to have vanished completely. Indeed, there are some who would place it with the Passenger Pigeon as an object of the past. It seems almost incomprehensible, however, that such can be the case. More probably the real permanent breeding grounds are more restricted than was supposed, and the locust will yet be located either by the discovery of its real haunts or by a new invasion following favorable weather conditions for breeding purposes." One immediately wonders whether a solitary

phase of *spretus* still exists, and if so what are the most likely breeding places. Montana, east of the Continental Divide, and North Dakota would seem likely possibilities. A solitary phase of *spretus*, if it exists, probably is smaller and shorter-winged than the historic specimens, and the aedeagus may be the only reliable distinguishing character. It is possible that specimens of a solitary phase now exist in collections, but if so they have not been recognized. Populations of the *mexicanus* group, both preserved specimens and field samples, should have the aedeagus examined critically on the chance that new evidence bearing on the *spretus* problem will be disclosed.

Melanoplus borealis (Fieber)

The distribution of this species is indicated by the two maps of its subspecies (figs. 17, 18) and, for the United States, by Newton and Gurney (1956, map 56). As the specific name suggests, this is a boreal insect, which in the United States is primarily northern or occurs in mountainous areas.

Mostly on the basis of tegminal length and the shape of the male subgenital plate, four subspecies are here recognized. Our study of the aedeagus has failed thus far to show differences in the aedeagus among the subspecies. However, Hebard (1935a, p. 67), in writing of what he called the *borealis* group, stated: "Examination of the penis now shows that this organ is of the same general type in all of the recognized races but shows distinct proportionate differences in some." Some differences in the epiphallus are here reported, but the examination of more material is required before their significance can be fully evaluated.

Melanoplus borealis borealis (Fieber)

FIGURES 3,*j*; 7,*j*; 8,*f*; 9,*c*; 10,*c*,*l*,*s*; 11,*c*; 16,*d*; 17; 18; PLATE 5,A,B,D.

Caloptenus borealis Fieber, Lotus, vol. 3, p. 120, 1853 (unstated number of specimens from "(Grönland) Nord. Cap. (Labrador) M. Hal. Fieb."). Lectotype here designated: Male from original Fieber series (according to Dr. Max Beier, in litt., Jan. 17, 1957) with the following labels: "*Podisma borealis* Fieb. Gronl."; "Mus. Caes. Vindebon."; "det. Holdhaus *Melanoplus borealis* Fieb."; "Par."; "23" (Naturhistorisches Museum, Vienna).

Pezotettix septentrionalis Saussure, Rev. Mag. Zool., p. 159, 1861 (unstated number of specimens from Labrador). Lectotype here designated: Female labeled "*P. septentrionalis* Sss. Type"; "Labrador"; and with a lectotype label attached by Gurney (Museum d'Histoire Naturelle, Geneva). (The Saussure collection contains two series of *septentrionalis*, one consisting of lectotype, a second containing 17 specimens (15 from Labrador and 2 from "Hudson") (C. Ferriere, in litt., Jan. 23, 1957).)

Caloptenus extremus Walker, Cat. Derm. Salt. B. M., Pt. 4, p. 681, 1870 (two females from "Arctic America"). Lectotype here designated: Female labeled *Caloptenus extremus* and as type, and with both hind legs present (British Museum). (The second original female lacks both hind legs. The lectotype

also bears an accessions registration label, "51/49," which is associated with the following notebook data: "District watered by Mackenzie and Slave R. Presented by Sir John Richardson." (D. R. Ragge, in litt., Jan. 10, 25, 1957).)

Pezotettix junius Dodge, Canad. Ent., vol. 8, pp. 9–10, 1876 (males, females, from Glencoe, Dodge Co., Nebr.). New synonymy. Lectotype here designated: Male labeled "Pez. Junius ♂G. M. Dodge Type; Collection C. V. Riley" (USNM). (A similarly labeled female is associated with the lectotype. Though no original locality label exists, Dodge stated that the species occurred at Glencoe, Nebr.)

Caloptenus parvus Provancher, Nat. Canad., vol. 8, p. 110, 1876 (one male from Cap Rouge, Quebec [southern outskirts of Quebec City]). Lectotype here designated: The first of two males pinned in Provancher's first collection (Musée de la Province, Quebec). (N.–M. Comeau has reported (in litt., Jan. 8, 1957) that although a single specimen was originally mentioned, an 1877 catalog mentioned two, and that both are now in very good condition.)

Melanoplus extremus scandens Scudder, Proc. U. S. Nat. Mus., vol. 20, p. 289, pl. 1, fig. f, 1897 (unstated number of specimens from Big Horn Mountains, Wyo., and several localities in New England, as well as unstated localities "in the high north"). Lectotype here designated: Male labeled "White Mts. Alpine. Scudder, Drawn, Mel. extremus Scudder's Type, 1895, Drawn for Appalachia, S. H. Scudder Coll., Type 15466" (MCZ). (Tegmina of lectotype extend 5 mm. behind the apex of abdomen. A female with similarly long tegmina bears the same data.)

Melanoplus monticola Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 24, 34, 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 135, 290–291, pl. 19, fig. 5, 1897 (two males, two females from "above timber line on Sierra Blanca, Colorado"). New synonymy. Lectotype designated by Rehn and Hebard (1912, p. 84): The figured male (MCZ). (Only fragments of the lectotype remain. The second original male is at Philadelphia (ANSP); its subgenital plate is about as in fig. 16,*d*-2, in lateral view, and in posterior view two prominences are developed, much as in fig. 11,*b*-4.)

The following four specimens of *borealis* were loaned from Vienna by Dr. Beier in addition to the lectotype: One nymph labeled as from Greenland; a female labeled Labrador, 1870; a female from Okak Islands, Labrador, 1838; a female from Nain, Labrador, 1832. The last two specimens bear labels reading "Coll. Br. v. W. Labrador, Coll. Sommer." M. C. Sommer was a Danish handler and collector of insects who died in 1868, from whom Brunner is recorded as obtaining Orthoptera, and it seems probable that these are the female specimens from Labrador recorded by Brunner (1861, p. 223) as *Caloptenus borealis*. At the same time he recorded material from Valdivia [Chile], the latter doubtless being a misidentification. Brunner's specimens may not have been available to Fieber in 1853, hence the lectotypic selection of the male which does not provide a clear type locality, though it unmistakably is the species currently called *Melanoplus borealis* (aedeagus exposed, preserved in dry condition).

There is no record of *borealis* from Greenland since Fieber. Henriksen and Lundbeck (1917) and Henriksen (1939) did not report it, and S. L. Tuxen of Copenhagen, who is familiar with current work on Greenland, has assured us (in litt., Jan. 26, 1957) that the Fieber record must be incorrect. No Acrididae have been taken on Greenland by Danish entomologists who in summer collect there regularly.

Likewise there is no subsequent record of *borealis* from North Cape or elsewhere in Norway (Ander, 1949a, 1949b; Knaben, 1943), although Scudder (1897b, p. 272) assumed that Fieber's locality "Nord. Cap." is the one in Norway. Since Fieber included *borealis* in a treatment of European Orthoptera, and did not enclose the locality in parentheses, as he did the two non-European localities, it is fair to assume that he regarded North Cape, Norway, as one of his localities. On the other hand, there is North Cape, Prince Edward Island, and Cape North, Nova Scotia, which may have been unknown to him though ports of call for North Atlantic shipping. There is a strong probability that none of Fieber's specimens originated in either Norway or Greenland. Therefore, no definite type locality can be recognized; the lectotype probably came from Labrador or nearby. No information is available about any Fieber material of *borealis* which may have been deposited at Halle, Germany; the main Fieber collection is in Vienna.

The synonymy of *septentrionalis* was indicated by Scudder (1897b, p. 270) and later by Blatchley (1920, p. 424). Blatchley also treated *extremus* and *parvus* as synonyms of *borealis*. Essig (1926, p. 81) incorrectly listed *extremus* as a synonym of *bruneri*. Hebard (1925a, p. 111) treated *extremus* as a synonym of *borealis borealis*, and he also placed *scandens* as a synonym of *borealis junius*. Scudder (1897b, p. 287) synonymized *parvus* under *extremus*. His interpretation recognized *parvus* as the northern form with red color prominent on the hind legs rather than the pale type as represented by the synonymous *junius*. It is in agreement with Provancher's description of *parvus*, which refers to the red color on both hind femur and hind tibia. Hebard (1925a, p. 111) may have overlooked this feature of *parvus*, and thus was incorrect in regarding *parvus* as identical with *junius*. Both *junius* and *parvus* were described in 1876, in journal issues of January and April, respectively, though actual dates of mailing have not been ascertained by us. The dates and the identity of *parvus* are important if in the future the southeastern population should be restored to subspecific rank.

Scudder utilized what he believed to be differences in the shape of the apical part of the male subgenital plate to separate *borealis*, *extremus* and *monticola*, but his differences are not constant in series of specimens. His *scandens* consisted of individuals mainly from

high altitudes and was characterized by tegmina reaching somewhat beyond the apices of the hind femora, while in *junius* the tegmina usually did not quite reach those apices. Hebard (1930, p. 397) noted that *monticola* is separated from typical *borealis* largely by shorter wings and tegmina, but he indicated that some far northern specimens would be assigned to *borealis monticola* if that character was followed, and he clearly was impressed by the local variation occurring in the Northwest. For the most part, specimens from the northeastern United States and southeastern Canada have the lower surfaces of the hind femora yellowish, and the hind tibiae are yellowish or dirty pale brown, while specimens from further north and the Rocky Mountains usually have the lower femoral surfaces and the hind tibiae reddish. Series from Ontario and Manitoba show intermediate conditions, and as a whole the populations represented by *junius* and *monticola* do not seem sufficiently defined for their recognition to serve a useful purpose. Hebard (1929, p. 387) said that *borealis monticola* was the least well defined of four races of *borealis* which he recognized, and (1932b, p. 37) he stated that *junius* is a "very weakly defined race." Later (Hebard 1934a, p. 105), he noted the difficulty of separating *borealis junius* and *borealis borealis* in northern Minnesota and suggested that *junius* might be merely a pallid color phase developed in response to a more temperate environment. White and Rock (1941) recorded both *borealis borealis* and *borealis junius* from Alberta, and later (1945) recorded *borealis monticola* also. In 1945 they discussed variation and the problem of trying to justify the recognition of these subspecies. Blatchley (1920) and Morse (1920) have discussed the variation shown by *borealis*. Scudder (1897b, pp. 270, 272) placed *Caloptenus arcticus* Walker in the synonymy of *borealis*, with some uncertainty, and Blatchley (1920) did so definitely. This is now considered untrue, as here discussed under *M. bilituratus bilituratus* (p. 15).

In Canada the junior author has recognized two races or ecological forms within *borealis borealis*. Specimens from Labrador, James Bay, Northwest Territories, northern Quebec and Ontario, northern Manitoba, Saskatchewan and Alberta, and from British Columbia are heavier, darker, more discolored, with more evident spotting on the tegmina, and consistently higher tegmina/femur ratios in both long- and short-winged forms than the more southern counterparts. The form from the southern or grassland portion of the prairie provinces is smaller, generally pale brownish yellow, with tegminal spotting much reduced, and frequently with the hind femur entirely pale.

A broad zone of transition between the two forms is evident in eastern Saskatchewan and in Manitoba, the smaller, paler form

occurring in southern (aspen-willow association) localities, the larger, darker form in the north (aspen-spruce association). Both forms contain long-winged and short-winged individuals, often together in one population; the short-winged type usually predominates but occasionally (as in the Cypress Hills in 1952) the long-winged type appears more numerous.

DESCRIPTIVE NOTES: A small to medium-sized, fully winged member of the *mexicanus* group; closely related to *borealis stupefactus*, from which it differs primarily in wing length, and to *borealis palaceus*, from which it differs mainly in the less strongly upturned male subgenital plate. Males with tegmina usually varying from slightly short of the apex of the abdomen to slightly beyond the abdomen, occasionally a little short of reaching supra-anal plate or at the other extreme with as much as one-fourth of the tegmen reaching beyond the abdomen. Females with tegmina varying from a condition in which about two-thirds of the abdomen is covered to one in which the tegmina extend beyond the abdomen by nearly one-fourth of their length. Posterior third of male abdomen occasionally strongly recurved dorsally, especially in specimens from northern Rocky Mountains, but usually abdomen is horizontal or only moderately recurved.

VARIATION: The size of 12 representative males measured (in millimeters) varies in pronotal length from 3.7 to 4.7 (av. 4.2), in length of hind femur from 9.7 to 12.2 (av. 10.8), and in length of tegmen from 8.4 to 16.4 (av. 12.6). Eight females vary in pronotal length from 4.1 to 5.5 (av. 4.8), in length of hind femur from 10.2 to 12.7 (av. 11.4), and in length of tegmen from 11.0 to 16.6 (av. 13.0). The largest specimens are from the northwest, particularly the Northwest Territories and Alaska.

MALE GENITALIA: Cercus (fig. 7, *j*) variable, usually about as in figure 7,*j*-1; supra-anal plate with lateral elevations strongly raised; furculae usually strongly tapered, separation evident to base, and scarcely reaching middle of supra-anal plate (fig. 9,*c*-1), sometimes variable (fig. 9,*c*-2, *c*-3); subgenital plate in lateral view with dorsal margin varying from essentially straight or slightly upturned apically (fig. 16,*d*-1) to moderately upturned, in posterior view with margin usually entire, rarely with an indication of twin apices (fig. 11,*c*-1); posterior surface of subgenital plate rather evenly rounded, without development of the rectangular-shaped disk usually characteristic of *borealis palaceus*, as in fig. 11,*d*-5. Aedeagus with main stem relatively short; dorsal valve moderately sclerotized but not parchment-like as in *bruneri*, in dorsal view lacking the triangular projection shown for *bruneri* (fig. 3,*k*,*l*); accessory lobe relatively large and frequently directed somewhat laterally; epiphallus as drawn (fig. 8,*f*).

FEMALE GENITALIA: Cercus (fig. 10,*l*) averaging more slender, the dorsal "scoop" of the dorsal ovipositor valve less excavate than in *bruneri*, but females of the two species not always separable.

COLORATION: General coloration about as in *bilituratus;* hind femur usually unbanded except dorsally on mesal side where three dark transverse bands usually occur, external bands sometimes present, as in specimens from Hudson Bay area which have the pale areas along the dorsal surface of the hind femur noticeably yellowish in fresh specimens; ventral surface of hind femur and lateral surface ventrad of paginal area usually reddish except in specimens from the Plains States eastward and in southern Ontario and Quebec, reddish area of femur normally correlated with red hind tibia.

Males of *borealis borealis* from the Big Horn Mountains, Wyo., and Fremont Co., Idaho, show a trend toward *borealis palaceus*, and they suggest intergradation although they are not fully intermediate. Males from Smithers, British Columbia, show a noticeable development of the dorsal lip at the apex of the subgenital plate.

DISTRIBUTION: The principal recorded distribution of *M. borealis borealis*, additional to what is shown on our maps (figs. 17, 18), is that noted by Morse (1920) for Maine, and Hebard's statement (1931, p. 184) that *borealis junius* is known from Mountain Grove in the Ozark Mountains of south-central Missouri. J. W. H. Rehn (1939) recorded *borealis* from Grande Miquelon and St. Pierre, near Newfoundland.

Male specimens of *Melanoplus borealis borealis* have been examined from the localities shown in figures 17 and 18.

BIOLOGY AND ECONOMIC IMPORTANCE: This subspecies is significant as a rangeland pest, and occasionally it attacks crops, but it is not of major importance. Information from the Bozeman, Mont., laboratory of the Entomology Research Division, U. S. Department of Agriculture, indicates that this is one of the important grasshoppers in the Targhee National Forest, Fremont Co., Idaho, and the Bridger National Forest, Wyo. It is reported to have been the dominant grasshopper in 1952 in the northern Cariboo and the Prince George Districts of British Columbia (Canad. Insect Pest Rev., vol. 30, p. 307, 1952; Neilson, 1953), as well as injuring alfalfa, grain, and vegetable gardens in northern Saskatchewan (Canad. Insect Pest Rev., vol. 30, p. 150, 1952).

Buckell (1921) characterized *borealis* in the Chilcotin District of British Columbia as an *humicolous hygrophile*, an "inhabitant of the tall rank vegetation beneath birch and willow on the borders of streams." He found it a sluggish, richly colored insect. Tolerance for a variety of habitats is shown by W. J. Brown's experience (in litt., Mar. 1, 1949) of collecting it at Churchill, Manitoba, in areas supporting trees, though at Reindeer Depot he collected it on gently

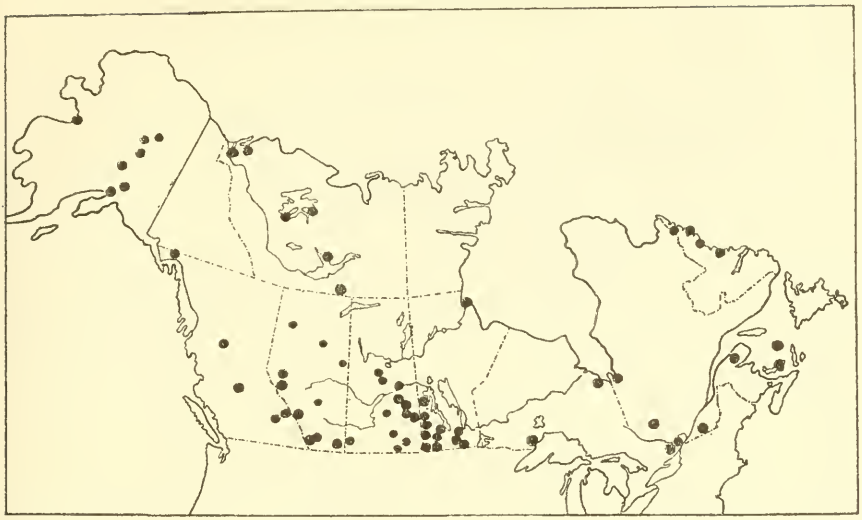

FIGURE 17.—Distribution of male specimans of *Melanoplus borealis borealis* examined from Alaska and Canada.

rolling, treeless, Arctic tundra that consisted of damp, cold sphagnum which thawed only from 11 to 19 inches during summer. Plants present there included Labrador tea, blueberry, grasses, sedges, and others. Readers interested in the limits of the true Arctic Zone are referred to Kimble and Good (1955) and Munroe (1956).

Caudell (1900) suspected *borealis* of being localized in Alaska, after the collector of the specimens he reported, T. Kincaid, found it in a sphagnum swamp at Kukak Bay, but nowhere else in the surrounding countryside. The only habitat notes from Labrador which have been seen are those of Scudder (1897b, p. 272), who reported that a collector described finding *borealis* abundant in luxuriant plants beside a mountain brook.

In the United States and southern Canada *borealis* has been found most often in cool, damp situations, as discussed by Blatchley (1920) and Morse (1920), but, while it appears to enjoy bogs and areas of sedges and other plants found in mountain meadows, it also occurs in moist open pastures and mowed fields in New England (Gurney 1935). Cantrall (1943) considered it a characteristic inhabitant of "the leatherleaf stratum of the bog habitat" in southern Michigan. In the prairie provinces of Canada the subspecies inhabits tall rank vegetation on the borders of streams and ponds within a forested area. Similar situations in the open grasslands are not occupied. The distribution is therefore local in grassland areas.

The biology of *borealis borealis* has not been studied fully. Nymphs are described by Handford (1946). It has been suggested that in

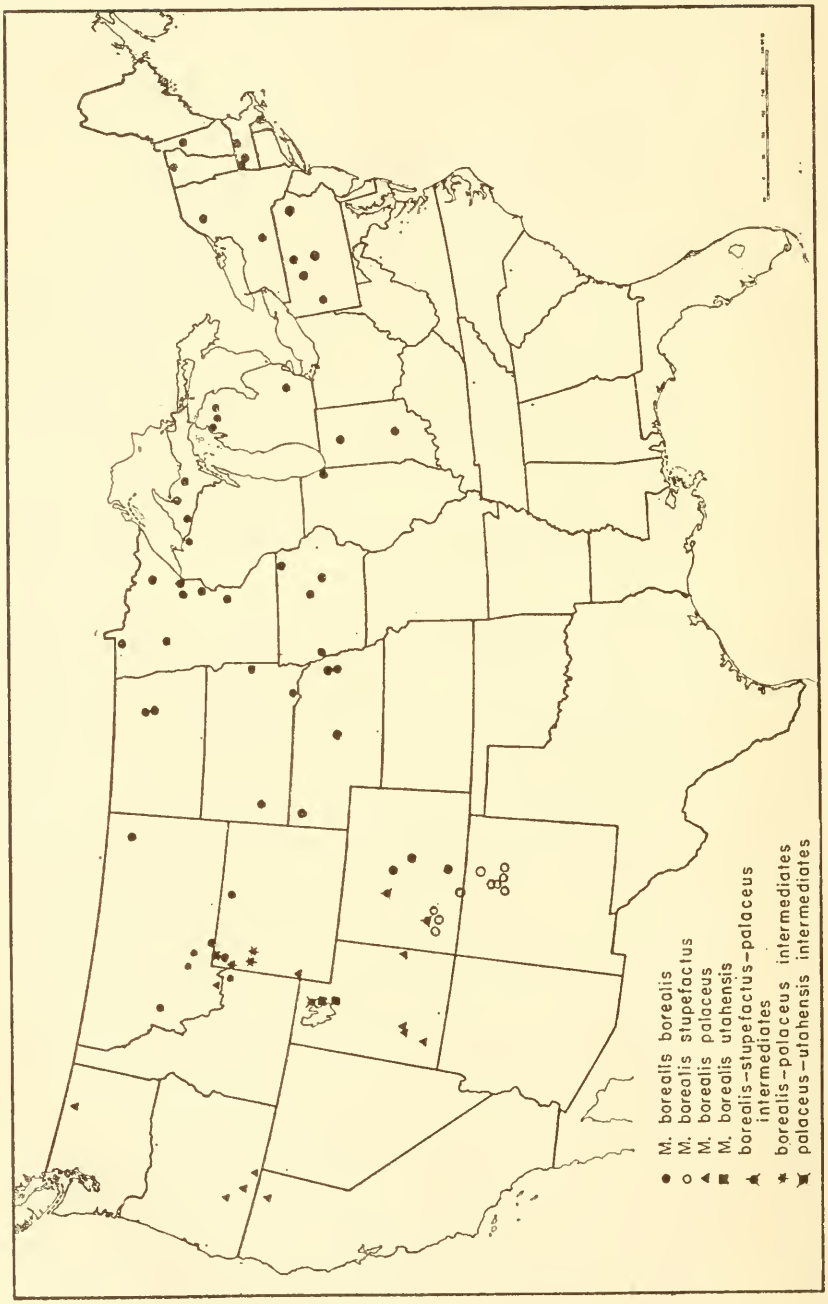

FIGURE 18.—Distribution of male specimens of *Melanoplus borealis* examined from United States localities.

parts of British Columbia two years are required for a complete life cycle (Canad. Insect Pest Rev., vol. 34, p. 273, 1956). Seasonally, it has been considered an early form by Morse (1920) and Cantrall (1943). The following are extreme dates on the labels of specimens examined: Warren Woods, S. Dak., May 28; Cummington, Mass., June 12–Aug. 16; Mt. Greylock, Mass., July 3, Aug. 17; Bloomington, Ind., June 16; Sawmill Bay, Northwest Territories, July 14; Chilkat Pass, British Columbia, July 13; Reindeer Depot, Northwest Territories, Aug. 3, Aug. 16; Fairbanks, Alaska, July 4, Sept. 2; Nain, Labrador, Aug. 4; Hopedale, Labrador, Sept. 6; Big Horn Mts., Wyo., Aug. 15. Morse (1921) reported collections in Maine from June 6 to Aug. 25, and Alexander (1951, p. 109) reported that both nymphs and adults (as *M. b. monticola*) were taken in August from several high Colorado peaks.

This subspecies is known from many mountainous areas in the southern part of its range, but it is not confined to high altitudes. Localities near sea level in Labrador, in the bogs at Mer Bleue,[9] Ontario, at about 1,400 feet in Cummington, Mass., and at various localities in Michigan, Minnesota, and Iowa show that fact. The following are some of the altitudes, shown on labels, at which it has been collected: Chilkat Pass, British Columbia, 3,500 ft.; Yoho Valley, British Columbia, 5,000 ft.; Yellowstone National Park, 6,800 ft.; Pikes Peak, Colo., 12,000 ft.

***Melanoplus borealis stupefactus* (Scudder)**

FIGURES 8,*d,h;* 9,*d;* 10,*d,m;* 11,*b;* 16,*c;* 18; PLATE 5,E,F.

Pezotettix stupefactus Scudder, Rep. Surv. W. of 100th Mer., App. JJ, p. 283, 1876 (1 male, 3 females, nymphs, Taos Peak, Sangre de Cristo Mountains, N. Mex.). Lectotype designated by Hebard (1929, p. 387): Male (USNM).

Melanoplus cockerelli Scudder, Psyche, vol. 9, pp. 124–125, 1900 (1 male, 1 female, summit of range between Pecos and Sapello Rivers, N. Mex., near headwaters of Pecos). Lectotype designated by Hebard (1929, p. 388): Male labeled "Top of range betw. Sapello and Pecos Rivers. Alt. 11,000 ft. Aug." (MCZ).

Melanoplus sapellanus Scudder, Psyche, vol. 9, p. 125, 1900 (1 male, 3 females, same locality as *cockerelli*). Lectotype designated by Hebard (1929, p. 388): Male (MCZ).

Melanoplus latifercula Caudell, Proc. U. S. Nat. Mus., vol. 26, pp. 803–804, pl. 55, fig. 4, 4a, 1903 (1 male, Cumbres, Colo.) (USNM).

Hebard (1929) indicated the synonymy here shown, which is supported by our study of the four types. Scudder (1897b) placed *stupefactus* in the genus *Podisma*, and then when he described *cockerelli* he failed to recognize *stupefactus* and considered it a relative of

[9] A large area containing many sphagnum bogs, near the southeastern city limits of Ottawa. F. A. Urquhart and E. G. Munroe have informed us that Carlsbad Springs is near the eastern extremity of the bog area, and that Hawthorne is at the northwest corner. Auer (1930, fig. 1) shows Mer Bleue as some 10 to 15 miles east of Ottawa.

Melanoplus dawsoni (Scudder). His *sapellanus*, with data identical to those of *cockerelli*, was based largely on a male with imperfectly developed genitalia.

DESCRIPTIVE NOTES: A short-winged, flightless subspecies averaging smaller than *borealis borealis* and with the furculae usually wider than in the latter. Tegmina broadly lanceolate, usually overlapping narrowly but sometimes not quite attingent, covering from scarcely more than one-third to slightly more than one-half of abdomen (about 1⅓ to 1½ times length of pronotum); wings vestigial. Posterior third of abdomen moderately to considerably recurved dorsally.

MALE GENITALIA: Cercus (fig. 8,*d*) proportionately broader than in the other subspecies (distorted by drying in lectotype of *stupefactus*, fig. 8,*d*-1); furculae usually as in figure 9,*d*-2, seldom a little more tapering, and sometimes broader (fig. 9,*d*-1); subgenital plate in lateral view with posterior portion of dorsal margin upturned as a lip about to the extent in figure 16,*c*, not sinuate, posterior margin sometimes more nearly vertical and less oblique than in the figured specimen, in posterior view the dorsal margin variable (fig. 11,*b*) but usually with at least weakly indicated twin apices. Aedeagus as in *borealis borealis;* epiphallus with rather deep emargination of anterior margin between ancorae, lophi lanceolate in dorsal view, rather highly elevated and with profile of posterior portions evenly rounded in lateral view (fig. 10,*d*).

FEMALE GENITALIA: About as in *borealis borealis*, the cercus averaging more robust (fig. 10,*m*).

COLORATION: Typically dark for the species; hind tibia and ventral surface of hind femur, reaching slightly onto external paginal area, dark red; dark transverse bands of hind femur visible dorsally, variable on external surface.

VARIATION: The size of eight representative males, measured in millimeters, varies in pronotal length from 3.6 to 4.5 (av. 4.0), in length of hind femur from 9.0 to 10.8 (av. 9.7), and in length of tegmen from 4.7 to 7.0 (av. 5.9). Three measured females vary in pronotal length from 4.4 to 4.7 (av. 4.5), in length of hind femur from 11.2 to 11.3 (av. 11.3), and in length of tegmen from 6.5 to 7.4 (av. 6.9).

Hebard (1929, p. 389) reported 29 males, 27 females, and 2 nymphs from Tomboy, Colo., also a nymph from Trout Lake, San Miguel Co., Colo., which he regarded as intermediate between *borealis monticola* and *borealis stupefactus*. Specimens from the Tomboy series and a male from White River Forest, Colo., have the tegmina covering about three-fourths of the abdomen, the furculae averaging narrower than in typical *borealis stupefactus*, the dorsal lip of the apex of the male subgenital plate higher and without twin apices developed. These specimens average larger than *borealis stupefactus*, and have an average

tegminal length of 9.5 mm. in males, 10.8 mm. in females. We regard them as intermediate between *b. borealis*, *b. stupefactus*, and *b. palaceus*.

Distribution: Hebard's record from Gothic, Colo. (1929), is a northern extension of the distribution (fig. 18) based on specimens examined.

Specimens of *Melanoplus borealis stupefactus* have been examined from the following localities:

Colorado: Mineral Co.; Silverton, San Juan Co.; Lizard Head; peak north of Cumbres, Cumbres Range, Conejos Co.; Los Pinos, Conejos Co.; Cumbres.

New Mexico: Taos Peak; Truchas Peak; Beulah; top of range between Sapello and Pecos Rivers; Santa Fe Baldy; head of Nambe Creek, Sangre de Cristo Range.

The following material is intermediate between *Melanoplus borealis stupefactus*, *M. b. borealis*, and *M. b. palaceus:*

Colorado: Tomboy, Marshall Basin, San Juan Range (about 2 to 3 miles northeast of Telluride; A. B. G.), 11,400 ft., Sept. 2, 1921, Rehn and Hebard (12 ♂, 15 ♀); White River Forest, Aug. 1933 (1 ♂).

The male from Trout Lake, San Miguel Co., Colo., collected by Hebard Sept. 4, 1921, at 9,700 feet, and reported by him (1929, p. 389) as intermediate between *borealis monticola* and *b. stupefactus* has tegmina covering slightly more than one-half of the abdomen. We regard it as *b. stupefactus*.

Biology and economic importance: Most of the known biological data on this grasshopper have been summarized by Hebard (1929, pp. 388–389; 1935a, p. 67). It is of no recognized economic importance, and there have been no detailed studies of its bionomics. Distribution is mainly if not entirely in the Arctic Alpine and Hudsonian zones in northern New Mexico and southwestern Colorado. The lowest altitude at which it has been recorded is 8,500 feet at the head of Chupidero Creek, N. Mex., and the highest 12,629 feet at the summit of Santa Fe Baldy, N. Mex.

Small numbers of specimens have been recorded well above timber line, there occurring in patches of green vegetation, but it has been found abundant on mountain slopes and in mountain meadows of lush grasses and other plants such as marsh marigold (*Caltha leptosepala* Hooker). At each of two localities (Los Pinos, Colo.; head of Chupidero Creek, Sangre de Cristo Range, N. Mex.), Hebard reported more than 50 adult specimens take by himself and Rehn, while on Neff Mountain, Cumbres Range, Colo., he reported their collecting more than 100 adults. Collection dates range from July 24 to September 11, and nymphs have been observed throughout July and August. Hebard found about two-thirds of the specimens at the summit of Santa Fe Baldy still immature on August 1. Many nymphs of the intermediate population at Tomboy, Colo., were taken on Sept. 2, 1921, by Rehn and Hebard.

Melanoplus borealis palaceus Fulton

FIGURES 8,*a*; 10,*t*; 11,*d*; 16,*e*; 18; PLATE 4,D.

Melanoplus borealis palaceus Fulton, Ann. Ent. Soc. Amer., vol. 23, pp. 619–620, fig. 1,F–H, 1930 (5 males, 8 females, Upper Klamath Marsh, Oreg.). The holotype male and allotype female were designated by Fulton (USNM).

DESCRIPTIVE NOTES: A usually fully winged subspecies, averaging slightly larger than *borealis borealis*, moderately larger than *b. stupefactus*, and slightly smaller than *b. utahensis*. Characterized especially in the male by the strongly upturned and recurved apical third of the abdomen, and by the subgenital plate which apically is considerably produced dorsally though only moderately produced posteriorly. Male tegmina usually reaching about to apex of abdomen and apices of hind femora, sometimes a little shorter; female tegmina averaging a little shorter, rarely slightly exceeding hind femora.

MALE GENITALIA: Cercus usually as in figure 8,*a*-2, somewhat variable (fig. 8,*a*-3,4), and in holotype (fig. 8,*a*-1) its lateroposterior margin rather irregular; supra-anal plate and furculae of holotype and of most specimens much as in figure 9,*d*, in a few specimens the furculae somewhat shorter and less widely separated at their apices; subgenital plate in lateral view (fig. 16,*e*) somewhat variable, the apical portion of dorsal margin much elevated, in posterior view the dorsal margin (fig. 11,*d*) usually entire, sometimes with traces of emargination, rarely with a median depression creating twin knobs, the posterior surface of subgenital plate usually with a roughly rectangular vertical area which is sometimes weakly excavate (x of fig. 11,*d*-5); one paratype (Univ. Michigan) with subgenital plate less elevated and with rectangular area of posterior surface less well defined than in holotype. Aedeagus essentially as in *borealis borealis*; epiphallus in dorsal view usually about as in figure 8,*f*, in holotype the apices of lophi somewhat more lanceolate, in lateral view lophus usually noticeably flattened at top near apex, much as in figure 10,*e*.

FEMALE GENITALIA: About as in *borealis borealis*; cercus of allotype essentially like figure 10,*l*, in some specimens slightly more acute; dorsal ovipositor valve with "scoop" of allotype (fig. 10,*t*) and several other specimens more deeply excavate than usual in *b. borealis*, but in other females not clearly different, margins of "scoop" slightly irregular, seldom with a deep notch as in allotype.

VARIATION: The size of seven representative males, measured in millimeters, varies in pronotal length from 4.2 to 4.8 (av. 4.5), in length of hind femur from 10.8 to 11.7 (av. 11.2), and in length of tegmen from 11.0 to 14.5 (av. 12.6). Seven measured females vary in pronotal length from 4.9 to 5.9 (av. 5.3), in length of hind femur

from 12.3 to 14.8 (av. 13.4), and in length of tegmen from 11.7 to 15.3 (av. 14.3).

Coloration: Averaging rather dark for group; hind femur usually with transverse bands evident only dorsally, ventral surface, part of mesal surface and external surface ventrad of paginae usually reddish, rarely yellowish; hind tibia reddish.

Specimens intermediate between *borealis palaceus* and *b. utahensis* are discussed under the latter. Three males and one female from Teton Co., Wyo., 5 males from Togwatee Pass (about 30 mi. east of Jackson Hole), Wyo., and 2 males from Yellowstone National Park, Wyo. (south side of Mt. Washburn, 8,600 ft.; Camp Cowan, Fireside River, 7,100 ft.), are considered intermediate between *b. palaceus* and *b. borealis* because of the shape of the male subgenital plate. Males typical of *b. borealis* also have been seen from Yellowstone National Park, and it is evident that the latter is a tension area. Males from southern Utah are not fully typical of *b. palaceus*, and they seem to vary toward *b. borealis*. Three males from Hackamore, Calif., also are atypical. The apex of the subgenital plate of those males is dorsally produced less than in typical *palaceus*, and there is scarcely any development of a rectangular area on the posterior surface of the subgenital plate. The number of localities from which *b. palaceus* is known are too few and too scattered to permit a complete understanding of the relationships of this subspecies.

Distribution: Male specimens of *Melanoplus borealis palaceus* have been examined from the following localities:

Montana: Lakeview area.
Wyoming: Cokeville.
Utah: La Sal Mts., Grand Co.; Puffer Lake, Tushar Mts.; East Fork of Merchant Valley, Tushar Mts.; Beaver; Cedar Breaks.
Washington: Bonaparte Lake, Okanogan Co.
Oregon: Upper Klamath Marsh; Bly; Bulls Prairie, Warner Mts.
California: Hackamore, Modoc Co.

Biology and economic importance: The types of *M. borealis palaceus* were "found near the pine woods on the border of a large meadow land known as Upper Klamath Marsh, situated on the plateau" east of Crater Lake, Oreg. (Fulton, 1930). A male and female from Bly, in Klamath Co., Oreg., about 50 miles southeast of the type locality, are labeled "Swp. mdw.," presumed to mean swampy meadow. There is little information about altitudinal preferences of this grasshopper beyond the general upland character of all the areas where collections have occurred. In the La Sal Mountains, the most easterly locality where *palaceus* has been taken, various habitats are available, as discussed by Tanner and Hayward (1934). At Upper Klamath Marsh, Oreg., adults have been taken on June 23 and August

11, and in the Lakeview area, Mont., from July 4 to August 24. The Bonaparte Lake, Wash., record is based on a male taken on July 14 at an altitude of 4,000 feet. Three males and one female from Hackamore, Calif., were taken July 17. The Hackamore area is characterized by swampy places in which wildlife refuges have been established, but there is no record of the habitat from which the specimens were taken. Specimens taken by Rehn and Hebard in the Tushar Mountains, Utah, were at altitudes varying from 8,200 to 9,000 feet, while on the Markagunt Plateau at Cedar Breaks, Utah, captures occurred at 10,400 feet. Dates of these Utah captures by Rehn and Hebard ranged from August 20 to August 31.

Because of the scanty information about the environment in most of the localities where *palaceus* has been collected, a brief description of the Lakeview area, Mont., is appropriate. For these notes we are indebted primarily to Frank T. Cowan, who loaned an unpublished manuscript prepared by the late H. M. Jennison, when, as a member of a research team under the direction of J. R. Parker in the early 1930's, he studied the vegetation of the Centennial Valley. Lakeview is a small village in the Centennial Valley, in extreme southeastern Beaverhead County. This high mountain valley is 40 to 45 miles long and 3 to 8 miles wide, and is bounded on the south by the Centennial Mountains. The lowest level of the valley floor, through which the Red Rock River flows westward, is about 6,400 feet, and Red Rock Pass, at the east end of the valley, is about 7,000 feet. In the spring, run-off from melting snow in the mountains provides many wet areas in the meadows of wild hay, and it also supports several shallow lakes. Specimens of *palaceus* are noted in the Bozeman laboratory records as having been taken in two environments, one dominated by wiregrass and the other by bluegrass.

Wiregrass (*Juncus balticus*) is dominant in extensive swales, or areas of low marshy ground. In an average year the swales are wet with slowly moving water until July, and some arms remain wet until late July or early August. The bluegrass areas include two or more species of *Poa*, as well as species of *Hordeum* and *Puccinella*. Greasewood (*Scarcobatus*) also occurs. These bluegrass areas are much drier than the wiregrass swales, but often are adjacent to the latter or appear as islands in their midst. They are green and succulent in spring and early summer, but by mid-July the grasses usually have matured and are light straw-colored or almost white. Both these environments are considered steps in the development of the grassland climax, as contrasted with the sagebrush climax in other parts of the valley.

***Melanoplus borealis utahensis* Scudder, new combination**

FIGURES 8,*b,g;* 9,*e;* 10,*e;* 11,*e;* 16,*f;* 18; PLATE 4,B

Melanoplus utahensis Scudder, Proc. Amer. Philos. Soc., vol. 36 (154), pp. 19, 32' 1897; Proc. U. S. Nat. Mus., vol. 20, pp. 132, 167–168, pl. 11, fig. 10, 1897 (1 male, Salt Lake Valley, Utah).

The unique male type, cited by Rehn and Hebard (1912, p. 79), is labeled "S. L. Val. Utah 8–30"; "L. Bruner Collector"; "Drawn"; "Mel. utahensis Scudder's Type, 1895." Also, the specimen bears a Bruner manuscript label and more recently attached type labels and comments on type locality (USNM).

Neither precise type locality nor the year of the type's capture is definitely known. When Hebard examined the type, probably in the late 1920's, he attached a label reading "From a western canyon of the Wasatch Mts., back from Ogden." A male and female from a series of four specimens from Ogden in the Philadelphia (ANSP) collection were labeled by Hebard as topotypes. Each of these bears a printed label "Ogden, Utah," and one male is labeled "*Melanoplus utahensis* Bruner, Type spec.," apparently in Bruner's handwriting. The pair labeled as topotypes by Hebard bear the further notation "Taken w. type," added by Hebard. Neither in Scudder's revision nor elsewhere have we found any information relating to these four specimens. It may be that Bruner did not send them to Scudder for inclusion in the revision and that, although Bruner gave them a manuscript name, they were not studied again until his North American collection became available to Hebard. Scudder referred to the Bruner manuscript name when *utahensis* was described, and the unique type has a Bruner name label like the one on the Ogden male. These labels may have led Hebard to assume that the whole series was taken together.

Unless more information supporting Hebard's opinion becomes available, it seems logical to conclude from the itinerary discussed by Bruner (1890) that the type was collected near Salt Lake City in 1890, and that the Ogden specimens are not topotypes. In a report to C. V. Riley dated Sept. 1, 1890, Bruner described a trip made in August, primarily to Idaho. Near the end of the trip he went to Ogden and Salt Lake City, "at both of which points collections were made." Thence, he went directly home to Lincoln, Nebr., by train. Because of the date on the specimen, August 30, it is probable that the specimen was collected during Bruner's last day in the field. Since Big Cottonwood Canyon, where *utahensis* has been collected, is within a few miles of Salt Lake City, that or a nearby area may well have been the locality which Bruner visited. The 1890 trip is the only one for which a record apparently satisfying the known data has been found. The fact that the specimen was deposited in

the Riley collection, as recorded by Scudder, suggests that it was taken while on a Federal assignment such as the one in 1890.

M. borealis utahensis, considered by Hebard (1928, p. 281) probably to be a distinct species closely related to *M. bruneri*, is shown by the aedeagus to belong instead to the *borealis* line of development.

Descriptive notes: A nearly fully winged subspecies of medium to large size in relation to other subspecies. Characterized especially in the male by the posteriorly prolonged (as well as elevated) subgenital plate. Tegmina failing by about 2 to 3 mm. to reach the tips of hind femora and the end of the abdomen. Posterior third of abdomen strongly upturned.

Male genitalia: Cercus typically as in figure 8,*b*-1–2, sometimes with the apex more obliquely rounded (fig. 8,*b*-3); furculae broad, in holotype about as in figure 9,*e*-1, sometimes more tapering; subgenital plate in lateral view extremely prolonged, somewhat variable in shape (fig. 16,*f*), in posterior view with dorsal margin varying from twice emarginate (fig. 11,*e*-1–3) to entire. Aedeagus as in *borealis borealis;* epiphallus (fig. 8,*g*) with lophi somewhat oblique anteriorly in dorsal view, in lateral view (fig. 10,*e*) rather flattened anteriorly.

Female genitalia: Cercus about as in *borealis borealis* (fig. 10,*l*); ovipositor essentially as in *b. borealis* except that "scoop" of dorsal valve averages slightly more excavate, with apex more upturned.

Coloration: Type with narrow yellowish green longitudinal stripes on lateral carinae of pronotum, lower half of lateral lobe of pronotum and lower part of head similar; metepisternal stripe conspicuously yellowish; tegmen brown, unmarked; hind femur with external paginal area light brown, paler toward base, dorsal surface with three distinct dark bars, in addition to dark brown knee, external surface ventrad of paginae pink, mesal surface tinged with pink; hind tibia pink. Specimens from Big Cottonwood Canyon lighter-colored than type, tegmina and dorsum of pronotum light brown, most of remainder of body yellowish brown, hind tibia weak pinkish.

Variation: Measurements (in millimeters) of the holotype are: Body, 27.0 (Scudder's measurement); pronotum, 6.1; hind femur, 14.3; and tegmen, 17.0 Specimens from Ogden average larger than those from Big Cottonwood Canyon. Measurements of the Ogden specimens are: Males (2), pronotum, 5.3, 5.5 (av. 5.4), hind femur, 12.0, 12.0 (av. 12.0), tegmen, 15.3, 18.8 (av. 17.1); females (2), pronotum, 5.7, 6.0 (av. 5.9), hind femur, 13.7, 14.7 (av. 14.2), tegmen, 12.5, 15.5 (av. 14.0). Measurements of representative Cottonwood Canyon specimens are: Males (3), pronotum, 4.6 to 5.0 (av. 4.8), hind femur, 11.4 to 11.6 (av. 11.5), tegmen, 11.3 to 11.8 (av. 11.5); females (2), pronotum, 5.1, 5.3 (av. 5.2), hind femur, 12.4, 12.5 (av. 12.5), tegmen, 12.3, 12.5 (av. 12.4).

The series from 3 miles north of Mantua, Utah, which was labeled in the Philadelphia (ANSP) collection by Morgan Hebard as atypical *Melanoplus utahensis,* is here considered intermediate between *borealis utahensis* and *b. palaceus.* External male genitalia are as illustrated (figs. 8,*c;* 9,*b;* 11,*f;* 16,*g*), and the subgenital plate suggests the intermediate relationship of the population. The lophi of the epiphallus are apically lanceolate in dorsal view, well flattened at the top in lateral view. The general color of these specimens is dull yellowish brown; hind tibiae are tinged with pink. The general color suggests that of the Red Banks series of *bruneri* and may reflect comparable ecological conditions.

Measurements (in millimeters) of representative Mantua specimens are: Males (5), length of pronotum, 5.9 to 6.4 (av. 6.2), hind femur, 12.4 to 14.2 (av. 13.5), tegmen, 12.5 to 15.5 (av. 14.3); females (2), length of pronotum, 6.5, 7.0 (av. 6.8), hind femur, 14.8, 15.5 (av. 15.2), tegmen, 15.0, 16.0 (av. 15.5).

Distribution: This grasshopper appears to be a relatively localized subspecies of the northern Wasatch Mountains, and to be more or less surrounded by *M. borealis palaceus* rather than being distributed linearly adjacent to *M. b. palaceus.* There may be altitudinal differences also, so that material from additional localities is likely to clarify the situation. Full data on all specimens examined are as follows: Salt Lake Valley, Utah, Aug. 30, L. Bruner (1♂, holotype); Big Cottonwood Canyon, Wasatch Mts., Utah, 7,400 ft., Canadian zone, Aug. 19, 1924, Rehn and Hebard (8♂, 8♀); Ogden, Utah (2♂, 2♀).

Intermediate between *Melanoplus borealis utahensis* and *M. b. palaceus:* 3 miles north of Mantua, Box Elder Co., Utah, Wasatch Mts., 5,800 ft., Aug. 9, 1928, Rehn & Hebard. (18♂, 17♀, 1 juv. ♂, apparently 5th instar).

Biology and economic importance: We are indebted to Rehn and Hebard for the only notes on the biology of this poorly known grasshopper. In Big Cottonwood Canyon, Utah, on Aug. 18, 1924, they found it in the Canadian zone at 7,400 feet, present "in moderate numbers in lush herbage near stream on flat with much aspen and spruce" (Hebard, 1936b, p. 173). Hebard also gave notes on a grasshopper taken at Red Banks in Logan Canyon, and ascribed to *utahensis,* but, as previously mentioned under *M. bruneri,* the only specimens we have seen with corresponding data prove to be *bruneri.*

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Plates 1–5

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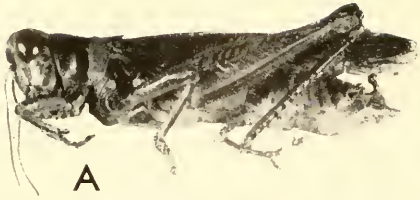
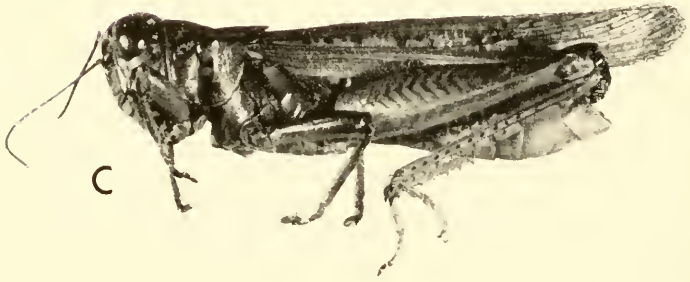
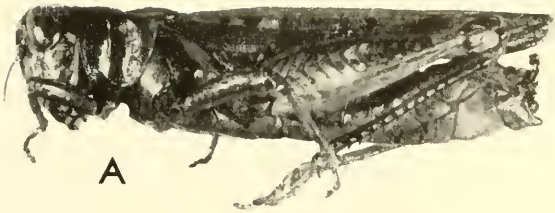
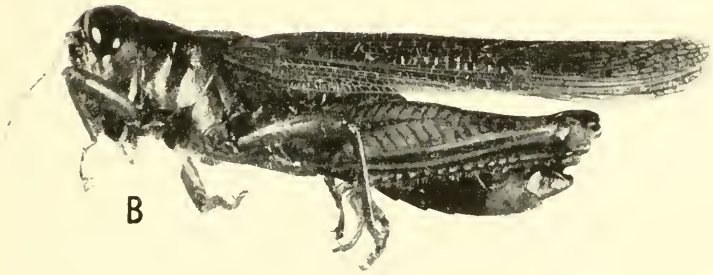
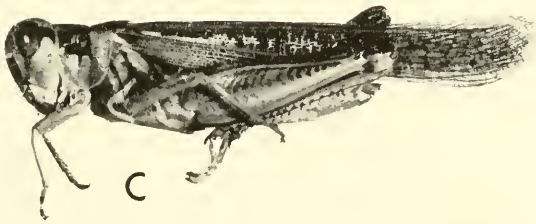




A, *Melanoplus mexicanus*, male, La Cumbre, Mexico. B, C, *M. bilituratus bilituratus*, males: B, from Vancouver Island, British Columbia, Canada; C, from Claydon, Saskatchewan, Canada. D, E, *M. bilituratus vulturnus*, females: D, from Stony Man Mountain, Shenandoah National Park, Va.; E, from Independence, Kans.







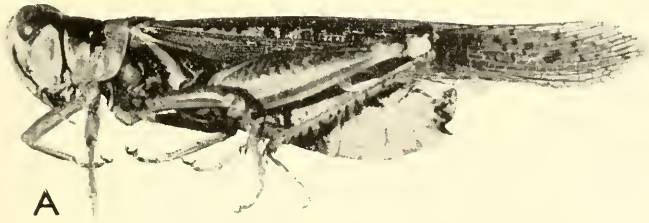
A-C, *Melanoplus bilituratus defectus*: A, male from Pendleton's Ranch, 4 miles south of Tumacacori, Ariz.; B, male from Tempe, Ariz., reared; C, female from Chandler, Ariz. D, *M. spretus*, female from Iowa, 1873.

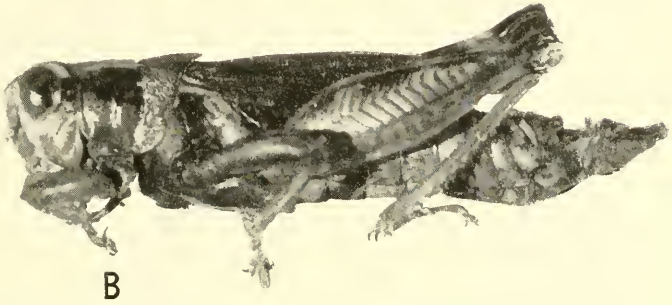
A

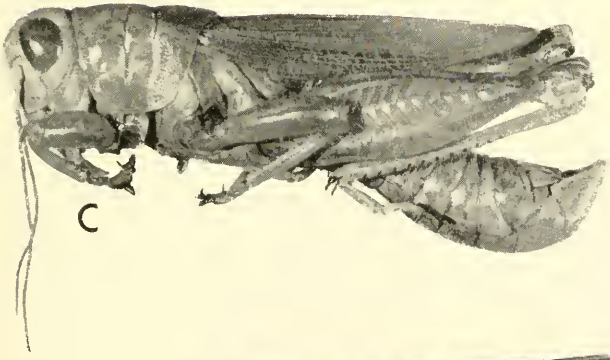
B

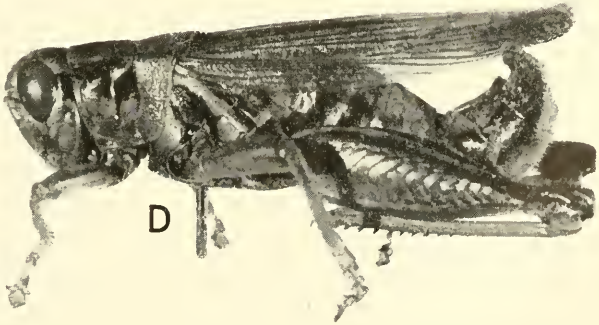
C

A, *Melanoplus bruneri*, male, from Sheridan County, Wyo. B, C, *M. devastator:* B, male, from Folsom, Calif.; C, female from El Dorado County., Calif.

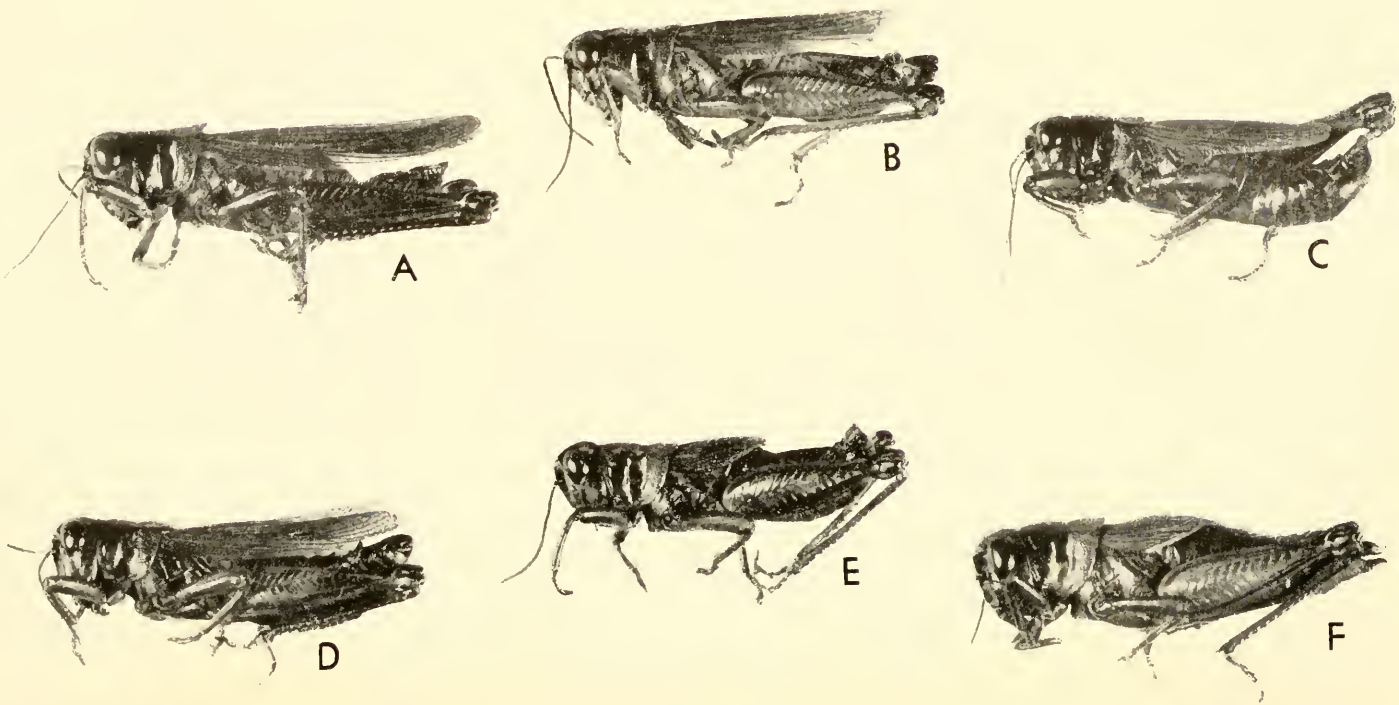








A, *Melanoplus bilituratus defectus*, male, from Chandler, Ariz. B, *M. borealis utahensis*, male, from Ogden, Utah. C, male, intermediate between *M. borealis utahensis* and *M. borealis palaceus*, from 3 miles north of Mantua, Utah. D, *M. borealis palaceus*, male, holotype.



A, B, D, *Melanoplus borealis borealis*, males: A, from Reindeer Depot, Northwest Territories; B, from Boissevain, Manitoba; D, from Nain, Labrador, Canada. C, Intermediate between *M. borealis borealis*, *M. b. stupefactus*, and *M. b. palaceus*, male, from Tomboy, Colo. E, F, *M. borealis stupefactus*: E, male, from Mineral County, Colo.; F, female, from peak north of Cumbres, Colo.