

Homoptera (Insecta) in Pacific Northwest grasslands. Part 2 – Pleistocene refugia and postglacial dispersal of Cicadellidae, Delphacidae and Caliscelidae

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ABSTRACT

Biogeographic analysis suggests that 241 Cicadellidae, 33 Delphacidae and 1 Caliscelid are restricted to grasslands in the Pacific Northwest. Nearly half of these (120 or 44%) are endemics. This grassland endemic fauna is third only to those of the prairies and desert grasslands. Of these, only six taxa probably postdate retreat of continental glaciers. The present distribution of the older taxa indicates that this fauna are descended from nine main glacial-era refugia (in descending order of importance): (1) east slopes of the Cascade Range, from Washington state to southern Oregon; (2) Columbia basin including Palouse hills of Washington and canyons of western Idaho; (3) south-facing slopes on the Rocky Mountains of Montana and western Wyoming; (4) the headwaters of the Snake River and south-facing slopes north of the Snake River in southern Idaho; (5) east of the Coast Range of Oregon; (6) edges of glacial Lake Missoula in western Montana; (7) a periglacial grassland near the ice front in Alberta; (8) the mountains of south-central Oregon; and (9) the coast of the Queen Charlotte Islands. Additional refugia might have been in the mountains of Colorado, Utah, eastern Arizona, and eastern Wyoming, where there are an additional 22 endemics. Postglacial warming brought grasslands and their endemic insects to British Columbia on the islands of the Strait of Georgia, to the East Kootenay valley and to the upper Fraser River of BC. Faunal exchanges have occurred across at least nine mountain passes on the continental divide. Three of these passes still provide continuous grassland connections between the prairies and the intermontane grasslands, yet not more than 14 slow-moving prairie species have surmounted any one pass.

INTRODUCTION

Pacific Northwest grasslands, characterized in Part 1 of this study, are widely scattered across a largely mountainous landscape extending across six states and two provinces (Fig. 1). Specifically to the context of grasslands, Pacific Northwest (PNW) refers to the Great Basin and adjacent deserts, grasslands and open forests west of the continental divide extending from latitude 42°N both northwards and up slopes in mountainous areas to coniferous forests. This area encompasses all but the mountains of the states of Idaho (ID), Oregon (OR) and Washington (WA), plus the western parts of Montana (MT) and Wyoming (WY). Grassy intermontane valleys of southern and central British Columbia (BC) and on its coastal islands, plus foothills prairie of Alberta (AB) are also included in this faunal region. Similar grasslands extend southeast (Fig. 2) into the mountains of eastern Arizona (AZ), Colorado (CO) and Utah (UT). Low elevation grasslands of AZ, California (CA), western CO, Nevada (NV) New Mexico (NM) and UT are considered to be desert grasslands of the Great Basin and Sonoran subregions, or Mediterranean-zone shrublands.

PNW grasslands have undergone many vicissitudes during the last million years. Glaciers carved out most of the valleys in BC down into northern WA, ID and MT; other valleys in western MT have been inundated by glacial Lake Missoula as recently as 12,000 years ago;

and the Columbia Basin of WA has been repeatedly scoured by catastrophic floods emanating from glacial Lake Missoula (Waite and Swanson 1987). It has been thought that, during the height of glaciation, tundra extended as far south on lowlands as WY and the Palouse hills of eastern WA, and in the mountains, as far south as southern CO and UT (Brunnschweiler 1962). Increased rainfall and colder temperatures also would have resulted in continuous spruce forest throughout the rest of the PNW. Such enormous changes in the PNW should have resulted in decimation of PNW grasslands by a combination of cool, wet weather and localized catastrophic events. That any fauna could survive appears almost incredible. Wholesale replacement of any grassland and its endemic insect fauna with widespread grassland species from southern refugia is the expected outcome. During the warmest postglacial period (the Hypsithermal) grasslands could have invaded the mountains from the prairies; but if so, grasslands must have been more extensive and less discontinuous in the PNW than at present.

It would seem unlikely therefore that PNW grasslands could ever have constituted a continuous, discrete ecozone. Yet many Homoptera are unique to these grasslands (for examples of new taxa, see Part 1 of this study). Furthermore, some are distributed relatively uniformly throughout the extent of the PNW. For example, *Texanus extremus* (Ball) not only ranges throughout the Cordilleran region, but is also found on the foothills prairie of southwestern AB. The purpose of this paper is to explore this paradox on the basis of evidence of recent insect distributions, and to deduce the factors responsible for this distinctive faunal assemblage. This study is the second detailed project emanating from a larger effort to study the leafhoppers endemic to North American grasslands, initiated by H.H. Ross in 1952. An overall summary was presented orally (Hamilton 1993) and a detailed study of the leafhopper fauna of the Yukon has been completed (Hamilton 1997).

Leafhoppers (Cicadellidae) are particularly important in characterizing native grasslands. They include the largest number of insect species endemic to the Great Plains (Ross 1970). There are more than 200 species endemic to prairies, and another 136 known only from desert grasslands, part of a total of some 800 grassland species in more than 80 genera (Hamilton and Whitcomb 1993). These insects contrast with other grassland arthropods such as spiders and ground beetles in being comparatively inefficient dispersers little influenced by microhabitat. Their dispersal rates are usually slower than 1 km/yr (Hamilton 1999a). Smaller numbers of Fulgoroidea (planthoppers) belonging to the families Delphacidae and Caliscelidae show similar endemism although (on limited data available) their dispersal appears to be more rapid than that of leafhoppers. Data are also available on grassland Delphacidae from the Yukon (Wilson 1997).

METHODS

Materials. Ranges and host associations of Homoptera are based mainly upon surveys of PNW grasslands carried out by the author in July-August 1976, August 1978, June 1984, August 1985, May-June 1987, May-June 1992 and May 1995, which yielded samples of more than 57,000 specimens. Particular attention was focussed on 15 of the lowest Rocky Mountain passes between British Columbia and Wyoming (Table 1), plus adjacent grasslands at lower elevations. These records were supplemented by collections made by R.F. Whitcomb of USDA from 1977-1997 in most western states including MT, UT and WY, plus incidental records from the H.H. Ross "GL" (grassland) survey and other material in the Canadian National Collection of Insects (CNCI). Data from revisionary works (Lindsay 1940; Kramer 1971a; Johnson and Blocker 1979; Blocker and Johnson 1988, 1990; Hamilton and Zack 1999; Bartlett and Deitz 2000), and the only regional faunas, for WA (Wolfe 1955) and BC (Maw et al., 2000) are also cited; these represent thousands of additional specimens. Host records are those confirmed by my collecting, unless otherwise noted. For other recent revisions and

taxonomic methodology, see Part 1.

Table 1.

Rocky Mountain passes sampled for Homoptera, BC to WY, lettered as in Figure 3. Omitted because not sampled: Deer Lodge Pass (1900 m), Elk Park, Flesher, Homestead and Stemple passes in MT (2000 m), and on the ID/MT border, Reynolds and Red Rock passes (2100 m) and Bannack Pass (2300 m). Species numbered as in faunal list; hybrids (e.g., 14×87) are recorded for both parental populations.

| Pass | locale | elevation | direction | species in pass | species near pass | through pass? | total |
|------------------------|--------|-----------|------------|---------------------------------------|----------------------------------|---------------------------|-------|
| "Crooked River" (A) | BC | 700 m | N/S | | 27, 30 | 1, 8, 10, 14, 21, 50 | 8 |
| Yellowhead | BC/AB | 1200 m | E/W | | 30 | | 1 |
| Kicking Horse | BC | 1700 m | E/W | | 13 | | 1 |
| Crowsnest (B) | BC/AB | 1400 m | E/W | | 9, 19, 26, 28, 51, 68 | 1, 2, 7, 10, 24 | 11 |
| Rogers (C) | MT | 1800 m | N/S | 1, 11, 16, 57, 50, 72 | 13, 20, 22, 31 | 28 | 11 |
| Lolo | MT/ID | 1800 m | N/S | 57, 67 | 74 | | 3 |
| MacDonald (D) | MT | 2000 m | E/W | 13, 30, 57, 68 | 7, 17, 72 | 51 | 8 |
| Pipestone | MT | 2000 m | N/S | 11, 67 | | 24 | 4 |
| "Grassy" (E) | MT | 2100 m | N/S (open) | 28, 43, 73 | 3, 7, 13, 21, 22, 33, 38, 51, 53 | 4, 5 | 14 |
| Lost Trail (F) | ID/MT | 2100 m | N/S | | 22, 43, 68, 72 | 5, 32, 41, 57, 61, 69 | 10 |
| Chief Joseph | MT | 2200 m | E/W | | | 2, 12 | 2 |
| Lemhi (G) | ID/MT | 2200 m | E/W (open) | 3, 17×91, 36, 43, 72, 73 | 19, 31, 51, 83 | 32 | 12 |
| Bannock (H) | ID/MT | 2200 m | N/S (open) | 3, 22, 29, 36, 41, 43, 51, 53, 72, 73 | 87 | 4, 5, 22 | 14 |
| Monida (J) | ID/M | 2100 m | N/S (open) | 33, 34, 43, 57, 61 | 24, 51 | 6, 20 | 9 |
| Great Divide Basin (K) | WY | 2000 m | all (open) | 18 | 3, 17, 20, 23, 25 | 9, 15, 19, 21, 29, 31, 50 | 14 |

Biogeography of Homoptera. The PNW grassland fauna includes three introduced Eurasian species, the beet leafhopper *Nealiturus (Circulifer) tenellus* (Zetterstedt), a sedge-feeding leafhopper *Euscelis obsoleta* (Kirschbaum), and the planthopper *Toya propinqua* (Fieber). They are excluded from this analysis because they were not part of the prehistorical fauna of the region.

As a first step in this biogeographic analysis, prehistorical patterns of endemism must be distinguished from stochastic patterns derived from rapid, opportunistic dispersal. For this reason, wind-dispersed "microleafhoppers" (Cicadellidae of the subfamily Typhlocybinæ) are excluded from this biogeographic analysis. Other leafhoppers ("macroleafhoppers") include a few migratory species, of which only *Exitianus exitiosus* (Uhler) is a grassland species.

Planthoppers of the families Delphacidae and Caliscelidae also are used to determine whether the PNW fauna is essentially a prairie fauna, or an endemic intermontane fauna that survived glaciation. Slowest of all are "flightless" species of the genus *Errhonus* (although males can fly, their wingless females cannot have dispersed long distances: Hamilton and Zack 1999). Such insects are important in elucidating where glacial refugia could have been located.

Second, native grassland species must be distinguished from those with wider ranges. The former either feed exclusively on grasses, or are always associated with grassland sites provided that they do not feed on trees. In cases where their hosts are unknown, they are presumed to be similar to those of the most closely related species. This latter criterion is usually sufficient to distinguish tree-feeding species which are almost always in separate genera from those feeding on forbs and grasses. Many genera of leafhoppers and planthoppers feed exclusively on grasses, but this is a less reliable criterion since such genera often include sedge feeders of fens and bogs.

Almost all planthoppers of the families Delphacidae and Caliscelidae in the PNW are restricted to grasslands, with the exception of the rush and sedge-feeding Delphacid genera *Achorotile* Fieber, *Kelisia* Fieber, *Megamelus* Fieber, *Pentagramma* Van Duzee and *Stenocranus* Fieber, plus eleven common and widely dispersing species: one sedge-feeding Caliscelid, *Peltonotellus histrionicus* Stål; and ten Delphacids, *Delphacodes campestris* (Van Duzee), *D. consimilis* (Van Duzee), *D. lutulenta* (Van Duzee), *D. magna* (Crawford), *D. puella* (Van Duzee), *Javesella pellucida* (Fabricius), *Liburniella ornata* (Stål), *Phyllodinus nervatus* Van Duzee, *Pissonotus delicatus* Van Duzee and *Stobaera tricarinata* (Say).

The 38 leafhopper target genera are discussed in the first part of this project. Three genera are reported but not analysed here. *Ballana* (over 100 described species: DeLong 1964) needs revision. Preliminary analysis of this genus suggests that most of the species are confined to California and the Sonoran subregion, but that distribution patterns similar to those discussed below will be found in the PNW. The leafhopper genera *Deltocephalus* Burmeister (13 described species: Kramer 1971b) and *Draeculacephala* Ball (7 species complexes in northern North America: Hamilton 1985) present unresolved taxonomic and biological problems, with many (but not all) species restricted to sedge fens rather than to grasslands.

With these exceptions, the complete PNW fauna of "macro-leafhoppers" and planthoppers was examined to determine quantitative degrees of endemism, and to deduce dispersal rates. First, all native species of leafhoppers and planthoppers known from PNW grasslands were sorted according to their overall distribution patterns and known biology. Species that range into northern grasslands, prairies, or southern ("Great Basin" and "Sonoran subregion") grasslands are distinguished from those that appear to be truly endemic. Next, species that occur along the continental divide are individually analysed to determine whether dispersal patterns are discernible from present distributions. Finally, centres of endemism are compared for evidence of glacial-age refugia.

Grassland characterization. PNW grasslands are diverse, both geographically and botanically. The following is a synopsis drawn from many sources, including my own observations of areas sampled from surveys extending over seven years. For example, good collecting areas are usually found on south-facing slopes in Canada (Ross 1970) but farther south these become too arid. West-facing slopes are preferred by leafhoppers in the PNW.

For this analysis, PNW grasslands are assumed to be biologically similar to small (possibly relict) grasslands in areas outside the PNW, such as south-facing hillsides of the Yukon (Hamilton 1997). This study identifies such grasslands in the drier valleys of western and central British Columbia, and west-facing hillsides in the Rocky Mountains as far south as CO. These grasslands are subdivided into nine disjunct areas (Fig. 2 A-J), from west to east:

(A) coastal areas of Pacific islands from the Queen Charlotte Islands (Fig. 2, star) of

- northwestern BC, south to small islands in Puget Sound of northwestern WA;
- (B) Pacific coastal grasslands, grassy "balds" on hills of the Coast Range, and valleys between the Coast and Cascade ranges of OR;
 - (C) the eastern slopes of the Cascade Range, from WA to the California border;
 - (D) the mountains of south-central OR;
 - (E) the Columbia basin including Palouse hills of WA-OR, adjacent canyons of western ID, and intermontane valley systems of central BC as far north as the Fraser River;
 - (F) the Snake River valley in southern ID and south-facing slopes north of the Snake River;
 - (G) the Upper Clark Fork valley system in western MT [for detailed analysis of dispersal patterns, subdivided into the smaller Blackfoot (Fig. 3, GA), Bitterroot (GB), and Rock Creek (GC) valleys];
 - (H) prairies east of the Continental Divide, from AB south to the Bighorn Mountains of northern WY; and
 - (J) a southward chain of high altitude grasslands in the mountains of eastern ID, western and southern WY, north-central CO, northern and central UT and eastern AZ.

Botanically, PNW grasslands form a complex of habitats (Munroe 1956; Küchler 1985; Ricketts et al. 1999) that are of four main types (Fig. 4):

- (1) the largest area, extending from isolated valleys in BC south into WA and ID was originally Palouse prairie, dominated by mixed grasses generically similar to those on the prairies (Ecoregion 53 = Küchler zone 43);
- (2) extensive sagebrush steppe (Ecoregion 75 = Küchler zone 49) has an ecotonal fringe of Palouse grasslands dominated in less arid areas by drought-hardy wheat grass (*Agropyron* spp.) and rice grass (*Oryzopsis* spp.);
- (3) foothills prairie dominated with fescues (*Festuca* spp.) form a narrow altitudinal grassland on the eastern slopes of the Rocky Mountains (Ecoregion 57 = Küchler zone 56); and
- (4) a limited area of oak savannah once occupied the Willamette Valley between the Coast Range and the Cascades (Ecoregion 6 = Küchler zone 24).

RESULTS

Using admittedly subjective criteria, the Homopteroous fauna of PNW grasslands, including adjacent montane grasslands, is calculated to consist of 215 species and 26 subspecies of "macro-leafhoppers" plus 34 species of planthoppers. This totals 275 taxa with a wide variety of dispersal characteristics (Faunal Synopsis and Index).

Species characteristic of boreal grasslands spread readily across mountain divides. There are 36 such leafhoppers that range as far north as the Yukon (Hamilton 1997) but only 17 leafhoppers and 4 planthoppers range from boreal grasslands into the PNW (Faunal Synopsis and Index). Their dispersal is stochastic; patterns are not discernible. They can be expected to occur wherever cool-season grasses are found.

Eight Delphacids and 50 leafhoppers are found in PNW grasslands southwards into CA and low elevations of AZ (Faunal Synopsis and Index). Some of these, notably *Orocastus tener* (Beamer & Tuthill) and *Psammotettix latipex* (DeLong & Davidson), range far into northern Canada (Hamilton 1997). These species most likely found a refugium in the southwest because north-south geographic barriers are minimal and summer winds bring flying insects such as migratory leafhoppers northwards from the Great Basin into western MT and southern BC (Carter 1927). All such planthoppers and all but 16 (65%) such leafhoppers have been found in Canada (Maw et al., 2000). By contrast, only one of four flightless southern leafhoppers migrated north to Canada. One of these, *Lystridea uhleri* (Baker), was able to cross the Columbia River only recently, almost certainly by human assistance (Hamilton and

Zack 1999).

More than 50 prairie species are widespread across the continental divide. There is no clear evidence for the direction of this spread, either onto the prairies from a montane refugium, or into intermontane grasslands from a prairie refuge. This fauna includes the only grassland Caliscelid in the PNW, *Bruchomorpha beameri* Doering, seven Delphacids, and 46 leafhoppers. Of these, 31 taxa range only a short distance into PNW grasslands. A comparison of their distributions may serve to indicate where the continental divide has been crossed recently and whether the territory available for colonization has been filled. Their dispersal routes are inferred on the assumption that the most direct routes are the ones that were actually taken.

This leaves 120 species and subspecies that are endemic to PNW grasslands plus 22 species which are endemic to montane grasslands adjacent to the PNW and are included for comparison. These together constitute 142 taxa endemic to grasslands of the PNW and adjacent mountains. Only six of these (Table 1, designated "?") are not known in sufficient detail to permit analysis.

The 136 well studied endemic taxa (114 from the PNW plus 22 from adjacent mountains) are compared to 25 prairie leafhoppers and six planthoppers that have limited distribution in the PNW. Their probable refugia and dispersal routes are discussed in three main faunistic sections.

First, the endemic taxa are divided into 130 ancient taxa and six subspecies which appear to be of postglacial origin. All six, belonging to the genus *Errhonus* (Hamilton and Zack 1999), either form local "swarms" of intermediate forms between adjacent, closely related species, or (in *E. truncus* Oman and *E. similis medialis* Oman) have unusual genitalic characters that appear to serve as distinguishing specific markers enhancing species barriers ("character displacement") where their ranges came in contact.

Next, 20 of the 130 taxa are considered to be glacial in origin since they have sibling taxa in adjacent areas, either separated by the continental divide, or occurring in isolated areas of the PNW. Taxa without close relatives, or ones whose ranges overlap, are considered to be preglacial in origin.

Finally, data from these 130 endemic taxa are synthesized for probable ecological distributions during the glacial period. They may or may not cross the continental divide, but have not invaded the prairies to any noticeable extent. Some are merely montane segregates of species that once were transcontinental; they now appear as pairs of sister taxa across the continental divide. Such species may have weathered Pleistocene glaciation in southerly locations, in which case their present distribution may show how they arrived where they now live. Other endemics represent pairs of sister taxa within the PNW, or as isolated species in small areas of the PNW that have no close relatives elsewhere. It seems reasonable to assume that these represent a fauna that survived the Pleistocene in intermontane valley refugia within, or close to, PNW grasslands. The location of these refugia may be traced most easily where modern distribution patterns are circular or elliptical, centred around a particular valley. Where this is not the case, it is assumed that the species has migrated northwards and/or to higher elevations in postglacial times, retreating from desertification to which it is not adapted.

DISCUSSION

Three species that are characteristic of true prairies are aggressive dispersers, occurring in most suitable habitats: *Auridius auratus* (Gillette & Baker) (Hamilton 1999b, map 1), *Paraphlepsius lascivius* (Ball) (Hamilton 1975, map 9), and the planthopper *Laccocera lineata* Scudder (from the Fraser River of central BC southeast in PNW grasslands to the mountains of central UT, eastward to Saskatchewan, and found on the MT/ID border near

Rogers and "Grassy" passes, and in Bannock and Monida passes). Three species of *Hebecephalus* are also widespread (Hamilton 1998a), but their distribution in PNW grasslands is more erratic. All these species seem to be generalists on grasses. One other species, *Hardya dentata* (Osborn & Ball) from the prairies west to UT (being found just north of "Grassy Pass" and in Lemhi and Bannock passes but not in the Snake River valley of ID), also has a "spotty" distribution in south-central BC and adjacent WA, and in OR east of the Cascade mountains. Still more disjunct are the known sites for two grass-feeding specialists of the leafhopper genus *Flexamia* DeLong (Whitcomb and Hicks 1988, figs. 30, 41). Since two-thirds of these species show disjunct distributions, the probability is great that some or all of these may represent the descendants of PNW relict populations of pre-glacial widespread ranges which have spread by opportunistic dispersal to other favourable sites.

Numerous species of the PNW appear to be endemic to the region. For example, of the 27 nearctic species of leafhoppers belonging to the genus *Hebecephalus*, 21 are endemic to the PNW and adjacent areas (Hamilton 1998a); and of the 47 taxa of the flightless leafhopper genus *Errhomus*, all but two are found exclusively in the PNW (Hamilton and Zack 1999). Only a few leafhoppers are widely dispersed throughout the PNW (Fig. 5).

The 140 PNW-endemic taxa analysed below show two major influences: (1) mountain chains, particularly the continental divide, which separate prairie-inhabiting species from those in PNW grasslands, and (2) glacial-era grassland refugia, which predetermined the subsequent dispersal and modern range of many PNW-endemic leafhoppers and planthoppers. The latter can be subdivided into refugia within the PNW, and those to the south of the PNW which may have contributed to the modern PNW fauna.

The most significant barrier between the eastern and western grasslands is the continental divide, which permits only limited faunal exchanges (Fig. 6, stars). A second barrier is formed by the Bitterroot Mountains along the northern half of the boundary between ID and MT. Although the latter is pierced by the Clark Fork River, this valley lies deep in the coniferous forest and is impassable to grassland flora and fauna. The only significant passes along this ridge north of the continental divide are at Lookout Pass (1400 m elevation), also deep in coniferous forest near Wallace, ID, and Lost Trail Pass (Fig. 6, F). An additional 21 main passes penetrate the continental divide between northern BC and the mountains of CO (Fig. 6, circles). Two of these passes do not have any official name. The one near Summit Lake on the Crooked River north of Prince George, BC is here referred to as "Crooked River Pass" to distinguish it from the better-known Summit Lake Pass in northern BC. The second, between Mt. Haggin and Grassy Mt. just south of Anaconda, MT is here called "Grassy Pass." The following faunal analysis details the evidence for 21 northern prairie leafhoppers and 3 planthoppers crossing the continental divide by way of these passes.

Species that penetrate the continental divide in CO or further southward, such as *Sorhoanus orientalis* (DeLong & Davidson), do not occur in PNW grasslands and are not included in this analysis.

Of the many species that are endemic to PNW grasslands, 14 pairs of sister taxa (16 leafhoppers, 10 planthoppers) occur on opposite sides of the continental divide. These sister-taxa appear to be of most recent origin, and might possibly be kept geographically separate by interspecific competition. Six taxa appear to be subspecies of postglacial origin. Another 28 species are widespread in the PNW but lack close relatives and are probably derived from preglacial stock; six of these occur as three pairs of sister-taxa in disjunct areas of the PNW. These PNW endemic faunas tend to have range extensions southeast into the mountains of CO, UT and WY. In addition, there are 22 endemic species that only occur in these areas marginal to the PNW: 12 in the mountains of CO and adjacent eastern WY (with two ranging north to southern MT), eight in the mountains of UT and adjacent western WY, and one (*Latalus histrionicus* Beirne) in the highest plateau of eastern AZ and also on Vancouver Island in BC.

The remaining 56 endemic species are limited to isolated parts of the PNW: 15 each in inland OR and in inland WA, 10 along the ID/MT border, six along the west coast of OR and WA, six in BC, and four in western MT, restricted to the upper reaches of the Clark Fork River and its tributaries (the basin of glacial Lake Missoula).

Species crossing the continental divide.

(A) CALISCELIDAE

1. *Bruchomorpha beameri* Doering is a planthopper of the northern prairies (records from southern Arizona and the Sacramento Valley of California [Doering 1940] must surely refer to other species) that is also found in many of the intermontane valleys of BC (Fraser, Okanagan and Kootenay rivers), northeastern WA (on the Pend Oreille River), and the Lake Missoula basin of MT. It seems to have been able to surmount both "Crooked River" and Crowsnest passes on the Alberta border, and has been taken in Rogers Pass, MT.

(B) CICADELLIDAE

2. *Amblysellus wyomus* Kramer is a leafhopper of the western prairies, a specialist on June grass, *Koeleria macrantha* (Ledeb.) Schultes [= *K. cristata* (L.) Pers.], that has been taken in the East Kootenay of southeastern BC and (Kramer 1971a) in the Bitterroot Valley of western MT. It has probably reached these sites across the continental divide by way of Crowsnest and Chief Joseph passes.

3. *Athysanella attenuata* Baker is a prairie leafhopper that feeds on wheatgrasses, *Agropyron* spp. It has been taken in both Lemhi and Bannock passes as well just north of "Grassy Pass" in MT (Fig. 7) and west of the Great Divide Basin in WY (Fig. 6 E, G, H, K). From these locations it has spread further west along both sides of the Snake River valley of ID.

4. *Athysanella obesa* Ball & Beamer is a grass-feeding prairie leafhopper that specializes on June grass. It is found east of the continental divide at Badger Pass (2000m elevation) west of Dillon, MT, and on the other side of the divide in the upper Snake River valley of eastern ID, on the Lost River Range due south of Bannock Pass (Fig. 6, H), and also in MT due west of "Grassy Pass" (Fig. 6, E) in Rock Creek valley.

5. *Athysanella robusta* Baker has the same range and grass host as *A. obesa*, but has not been taken in the upper Snake River valley. Its migration route was probably the same as that of *A. obesa*; neither is likely to have migrated from ID back into MT by way of Lost Trail Pass as neither species has been found in the Bitterroot valley.

6. *Athysanella terebrans* (Gillette & Baker) is a leafhopper of the prairies, a specialist on sand grass, *Calamovilfa longifolia* (Hook.) Schribn. which may have come to the upper Snake River drainage basin in eastern ID by way of Monida Pass. Four females have been taken at two sites.

7. *Auridius helvus* (DeLong), a June grass-feeding leafhopper of the western prairies and eastern "prairie peninsula" from Minnesota to Michigan, has invaded southeastern BC (probably through Crowsnest Pass) and the valleys of western MT (Hamilton 1999b, map 2) where it occurs in the headwaters of the Clark Fork River system. Populations have been found on either side of "Grassy" and MacDonald passes, suggesting multiple invasions across the continental divide. One population is found in Arizona near the Colorado River, and has probably come there in the same way as *Unoka gillettei* Metcalf (#25).

8. *Auridius ordinatus* (Ball), a grass-feeding leafhopper of the northern prairies ranging from the mountains of CO to isolated grasslands of Alaska (Hamilton 1999b, map 4) has invaded the upper Fraser valley of central BC by way of "Crooked River Pass."

9. *Ceratagallia arida* (Oman) is a polyphagous prairie leafhopper that crosses the

continental divide in southeastern BC near Crowsnest Pass (Fig. 6, B) and in southern ID, probably by way of the Great Divide Basin of WY (Hamilton 1998b, map 3).

10. *Ceratagallia viator* Hamilton is a northern prairie species with remote populations in the northwest and southwest (Hamilton 1998b, map 2). It has entered PNW grasslands only along the upper Fraser River and southeastern BC, probably by way of "Crooked River" and Crowsnest passes.

11. *Ceratagallia vulgaris* (Oman) is a polyphagous leafhopper that is widespread in eastern North America and also has populations on the far western plains including Rogers and Pipestone passes on the continental divide in MT (Hamilton 1998b, map 4).

12. *Flexamia decora* Beamer & Tuthill is a specialist on mat muhly, *Muhlenbergia richardsonis* (Trin.) Rydb. It is widespread on the prairies and has penetrated the continental divide at several places (Whitcomb and Hicks 1988, fig. 39). One population found in the Clark Fork valley, MT, probably came by way of Chief Joseph Pass, since other MT populations occur southeast of this pass. One population in Sublette Co., western WY, suggests that other populations in UT came there by surmounting the Great Basin divide.

13. *Diplocolenus c. configuratus* (Uhler) is the typical subspecies of a grass-feeding leafhopper of eastern North America that has crossed the continental divide on the ID/MT border at MacDonald Pass, probably also at Rogers and "Grassy" passes, and also at Bannock Pass (Fig. 8, open circles). Its tolerance of boreal conditions makes it the only prairie-inhabiting leafhopper that is known to have crossed Kicking Horse Pass between Banff and Yoho National Parks, having been found only 35 km west of the pass in BC. In more southerly passes it hybridizes with other subspecies (see # 83, 139 and Fig. 8, bull's-eyes).

14. *Elymana circius* Hamilton is a grass-feeding leafhopper of the Canadian prairies that also occurs in the Peace River district of AB and the upper Fraser River of central BC (Chiykowski and Hamilton 1985, fig. 8), probably by way of "Crooked River Pass," BC (Fig. 6, A).

15. *Idiodonus heidemanni* (Ball) is a leafhopper of the western plains as far north as MT that is also known from the upper Snake River in WY. It probably came there by way of the Great Divide Basin of WY. It is not the species recorded as "*Idiodonus heidemanni*" from CA (DeLong and Severin 1948) which is actually *Bonneyana schwartzi* (Ball).

16. *Mesamia ludoviciana* Ball is a specialist on prairie sage, *Artemisia gnaphalodes* Nutt. (= *A. ludoviciana* Nutt.) that has been taken at Rogers Pass, MT.

17. *Mocuellus caprillus* Ross & Hamilton is a specialist on western wheatgrass, *Agropyron smithii* Rydb., that occurs throughout the grasslands of MT and WY, and southeast of the mountains of UT (Fig. 9). It has crossed the continental divide at least twice, probably at MacDonald Pass and Great Divide Basin, judging by the proximity to known sites for this species. It is also found at Lemhi Pass on the ID/MT border, where it hybridizes with *Mocuellus caprillus anfractus* (#88).

18. *Norvellina clarivida* (Van Duzee) is a specialist of *Atriplex* spp. in southern AB and SK, south in the mountains of CO and NM, and also occurs in UT (Lindsay 1940), having crossed Great Divide Basin at Creston, WY.

19. *Orocastus labeculus* (DeLong) is a northern prairie leafhopper feeding on spear grasses (*Stipa* spp.) It also has been found in southeastern BC (Cranbrook, Skookumchuck), eastern ID (Carmen) and the Unitas of northern UT (Duchesne) and therefore must have penetrated the continental divide in at least three places: Crowsnest, Lemhi and Great Divide Basin passes seem indicated. A short series containing only females and nymphs from south-central BC (Hedley) may prove to be an undescribed sister-species when males are found.

20. *Orocastus perpusillus* (Ball & DeLong) is an abundant northern prairie leafhopper feeding on spear grasses. It has penetrated the continental divide at two locations (Fig. 10): in the Lake Missoula valley and in the upper reaches of the Snake River. The most likely passes

it could have come through, considering its known range, are Rogers and Monida passes (Fig. 6, C, J). Its presence in western WY suggests that it has also crossed the Great Divide Basin.

21. *Pinumius sexmaculatus* (Gillette & Baker) is a grass-feeding leafhopper of the northwestern plains that also occurs along the Fraser River of central BC, just north of "Grassy Pass," MT, and on the foothills of the Unita Mountains of UT. The northern and southernmost populations west of the continental divide probably came there by way of "Crooked River Pass," BC and the Great Divide Basin of WY.

22. *Prairiana kansana* (Ball) is a prairie leafhopper that probably feeds on some woody plant. It has been found just west of Rogers Pass and just north of "Grassy Pass" in MT, in Bannock Pass and south of Lost Trail Pass in ID. As this species is not known from the Bitterroot valley of MT, it probably has approached Lost Trail Pass from the south, via Bannock Pass.

23. *Psammotettix totalis* (DeLong & Davidson) is a grass-feeding leafhopper of the northwestern plains from northern MT to WY that also occurs in the Snake River valley of south-central ID (DeLong and Davidson 1935), probably by way of the Great Divide Basin of WY (DeLong and Davidson 1935: "Cane Tree" and "Cattail Spring," WY are unknown localities).

24. *Rosenus cruciatus* (Osborn & Ball) is a leafhopper specialist on June grass that is widespread on the northern prairies including western MT. Populations throughout the Lake Missoula Basin and south of Monida Pass in ID probably are derived from the only one found to the east, on the upper reaches of the Missouri River. This would imply that the Lake Missoula Basin populations came through one or more of the many passes near Butte. From the dispersal patterns of other species, Pipestone Pass seems the most likely route. This leafhopper also occurs on the foothills of the Unita Mountains of UT, and in southern BC. Whether the southern populations arrived in UT from the Snake River plain of ID, or across the Great Divide Basin of WY, cannot be ascertained at present. The population in the East Kootenay of eastern BC must have come there through Crowsnest Pass. A female (incorrectly recorded as *Rosenus obliquus* by Maw et al. [2000]) taken at Kelowna, BC and a male from Myncaster (near the WA border) show that an isolated population also inhabits the Okanagan Valley. The source for this population is unknown; possibly it is a Hysithermal relict.

25. *Unoka gillettei* Metcalf is a leafhopper specializing on sand dropseed, *Sporobolus cryptandrus* (Torr.) A. Gray, and ranging from southern Alberta and southwestern MT east to Minnesota and south to Colorado. It is also found on the same host in southwestern WY, UT and adjacent AZ and NV, and thus appears to have crossed the Great Divide Basin of WY (Fig. 6, K) and travelled down the Green River to the Grand Canyon (Fig. 6, stars). Populations in southern AZ are probably derived from a more southerly pass, as this species specializes on gyp dropseed, *Sporobolus nealeyii* Vasey from TX to AZ.

(C) DELPHACIDAE

26. *Elachodelphax pedaforma* (Beamer) is a planthopper of the northern plains that also occurs just beyond Crowsnest Pass at Fernie, BC.

27. *Eurybregma magnifrons* (Crawford) is a prairie planthopper that has invaded the upper reaches of the Fraser River in central BC via "Crooked River Pass," and migrated as far north as Alaska, but has not crossed more southerly passes (Fig. 11).

28. *Laccocera canadensis* Beirne is a planthopper of the northern plains that also occurs in the East Kootenay valley, BC, and in MT along Rock Creek and the Blackfoot River in Lake Missoula Basin, and on "Grassy Pass." The population in eastern BC must have come there through Crowsnest Pass, while that on Rock Creek came by way of "Grassy Pass" and the lower pass at Silver Lake just to the west. The population on the Blackfoot River probably came there by way of Rogers Pass.

29. *Laccocera flava* Crawford is a northern prairie planthopper that has entered the headwaters of the Snake River of ID (Fig. 12, filled circles) by way of UT, probably traversing the Great Divide Basin of WY, and is also in the Lake Missoula valley of MT. Whether it came to the latter by way of MacDonald or by "Grassy Pass" cannot be determined. Its presence in both Bitterroot and Rock Creek valleys suggests that it was once widespread in the headwaters of the Clark Fork River. Its range may have become fragmented during the formation of glacial Lake Missoula. It also reaches the continental divide at Bannock Pass.

30. *Laccocera vittipennis* Van Duzee is a common polyphagous planthopper of northern prairies and Peace River grasslands on the western half of the continent, although not confined to grasslands in eastern North America. It has been found in BC just beyond "Crooked River" and Yellowhead passes, in MacDonald Pass and west of the pass in the upper reaches of the Lake Missoula valley (Fig. 13).

31. *Nothodelphax foveatus* (Van Duzee) is a common planthopper of northern prairie including the Peace River district. It also has been found in ID (the Lemhi Valley and in the upper Snake River plain), MT (Blackfoot River Valley), OR (shore of the Columbia River) and UT (foothills of Unita Mountains). Possibly it crossed the continental divide by way of Rogers, Lemhi and Great Divide Basin passes; from the Snake River plain it has invaded the Columbia River near its junction with the Snake.

Pairs of sister taxa separated by the continental divide.

(A) CICADELLIDAE

32. *Athysanella occidentalis megacauda* Hamilton (see Part 1) is a grass-feeding prairie leafhopper known only from southern interior of BC and northern WA, south along the Columbia as far as Vantage, WA. It was probably restricted to the Columbia canyon during the Pleistocene. Typical *occidentalis* occurs only east of the continental divide. A short distance to the west of the continental divide from the Bitterroot Valley of MT, south through the headwaters of the Salmon River and the Camas valley in ID occur a hybrid swarm between these two subspecies. To attain this distribution these hybrids must have crossed Lost Trail Pass and the still higher Galena Summit (2700m elevation) between the headwaters of the Salmon and Camas rivers. How typical *occidentalis* came across the continental divide is not known, but the most likely route is through Lemhi Pass (Fig. 6, G) which lies halfway between the extremes of its distribution to the west of the divide.

33. *Attenuipyga (Dorycara) minor* subspecies *setosa* Oman is a grass-feeding leafhopper known from widely scattered PNW grasslands of central OR and adjacent WA, southern BC, and the upper Snake River plain in ID. Its related subspecies, typical *A. minor* (Osborn), is entirely east of the continental divide. Individuals that appear to be hybrids between these subspecies have been taken just north of "Grassy Pass" in MT, and (Oman 1985) on the upper Snake River plain not far from Monida Pass, in the mountains of CO and northern UT, and central NV.

34. *Auridius ordinatus* subspecies *crocutus* Hamilton, a grass-feeding leafhopper, occurs throughout PNW grasslands and as far south as northern NV (Hamilton 1999b, map 4). It was probably widespread in PNW grasslands during the Pleistocene. It has two related geographical subspecies: typical *A. ordinatus* Ball (#8), a northern prairie subspecies, and subspecies *amarillo* Hamilton in the mountains of NM. Hybrids between the typical subspecies and *crocutus* are found at Monida Pass and adjacent areas of the upper Snake River valley.

35. *Ceratagallia nanella* subspecies *zacki* Hamilton, a polyphagous leafhopper in WA and southernmost BC (Hamilton 1998b, map 9), is related to two widely disjunct geographical subspecies: typical *C. nanella* Oman of the prairies and southwestern grasslands from Canada to AZ, and subspecies *australis* Hamilton in the mountains of Mexico. Subspecies *zacki* was probably widespread on the Columbia basin during the Pleistocene.

36. *Ceratagallia siccifolia* subspecies *compressa* Hamilton, a polyphagous leafhopper widespread in PNW grasslands, is related to two geographical subspecies: the widely disjunct subspecies *alaskana* Hamilton in the far northwest, and typical *C. siccifolia* (Uhler) which is mainly a prairie subspecies. Because the typical subspecies is widespread and aggressive, having been taken at Bannock and Lemhi passes, and up to 3300 m elevation in CO, it is assumed here to have been able to traverse all the mountain passes. It appears to have invaded the PNW before postglacial times. Its populations have completely swamped the PNW subspecies at higher elevations. Subspecies *compressa* is now confined mostly to valley bottoms (Hamilton 1998b, map 10).

37. *Psammotettix beirnei* Greene is a grass-feeding leafhopper known only from 7600' [2500 m elevation] on Mt. Harry in the Selkirk Mountains near Revelstoke, BC, erroneously recorded from Northwest Territories (Greene 1971). Its sister-species, *P. alexanderi* Greene is known only from the White Mountains of New Hampshire (Greene 1971).

38. *Stenometopiellus vader* Hamilton (see Part 1) has a sister species *S. cookei* (Gillette) on the northern prairies and mountains of CO. Both are sedge-feeding leafhoppers, the former at present known only from the Lost River Range of eastern ID and just north of "Grassy Pass" in MT. Its glacial-age refugium was probably the upper Snake River valley. Whether it spread to southern MT by way of Lemhi or Bannock pass and later entered the Lake Missoula basin by way of "Grassy Pass", or whether it invaded the Lake Missoula basin directly by way of Lost Trail Pass, cannot be determined at present.

39. *Unoka dramatica* Hamilton (see Part 1) is known only from southern BC (Fig. 6, filled circle) widely disjunct from its sister species *U. gillettei* (#25). This PNW endemic of sandy areas probably survived the Pleistocene in the upper reaches of the Columbia basin on sandy outwashes from terminal moraines.

(B) DELPHACIDAE

40. *Elachodelphax mazama* Hamilton (see Part 1) is known only from the Methow Valley in northwestern WA. Its presence near the arid inland valleys of southern BC suggest that its parent species was once widespread throughout central BC. Its sister species is *E. borealis* Hamilton (see Part 1), a planthopper widespread from coastal Labrador and high mountains of New Hampshire west to the Peace River district of Alberta that is not known to have penetrated the Rocky Mountains.

41. *Eurybregma eurytion* Hamilton (see Part 1) includes in its extensive PNW range the Lake Missoula valley in MT, indicating that it must have surmounted Lost Trail Pass, as it has Bannock Pass (Fig. 11). It was probably widespread in PNW grasslands during the Pleistocene. Its sister-species, the prairie-inhabiting *E. magnifrons* (#27) is found north of the range of *E. eurytion*, except where they co-occur at Princeton, BC.

42. *Laccocera oregonensis* Penner has a disjunct distribution, in eastern ID and around the Columbia basin from southern BC to OR (Fig. 12, open circles). This suggests that it was probably widespread in PNW grasslands during the Pleistocene. Its sister species, *L. flava* (#29), may be inhibited in its westward spread by *L. oregonensis* just west of Lemhi Pass.

43. *Laccocera vanduzeei* Penner, sister species to *Laccocera vittipennis* (#30), is widespread from central BC to ID, and has many populations in the mountains of AZ, CO and UT (Fig. 13, open circles) where it probably found glacial refugia. It occupies the southern part of the Lake Missoula valley as well as the headwaters of the Missouri River in MT. It has been found in "Grassy", Lemhi, Bannock and Monida passes and adjacent to Lost Trail Pass. Multiple crossings of the continental divide seem indicated.

44. *Nothodelphax venustus* (Beamer), sister species to *N. foveatus* (#31), is confined to the mountains of southern BC and adjacent WA, southern WY and adjacent CO, and northern AZ.

Endemic pairs of sister taxa in PNW (CICADELLIDAE only).

45. *Athysanella expulsa* Blocker is a grass-feeding leafhopper known only from central OR east of the Cascade Mts. (Blocker and Johnson 1990).

46. *Athysanella repulsa* Hamilton (see Part 1), sister-species to *A. expulsa*, is known only from Flint Creek on the upper reaches of the Clark Fork valley of MT.

47. *Auridius cosmeticus* Hamilton (Hamilton 1999b, map 3) is a sedge-feeding leafhopper found only in the upper reaches of the Blackfoot and Bitterroot valleys of MT, where it seems to have found a refugium from the waters of glacial Lake Missoula.

48. *Auridius vitellinus* Hamilton, sister species to *A. cosmeticus* (Hamilton 1999b), is known only from southernmost OR east of the Cascade Mts.

49. *Latalus histrionicus* Beirne is known only from Vancouver Island, BC, and the high plateau of eastern AZ. Its range appears to reflect two isolated glacial-age refugia rather than competition with its sister-species (see #50), because both species can be found near Alpine, AZ.

50. *Latalus intermedius* Ross & Hamilton is a common grass-feeding leafhopper of mountains in eastern AZ, CO, UT and western WY (which were probably its glacial-age refugia). It has also established colonies in southeastern ID near the UT border, and at Rogers Pass, MT, and three sites in the north: Peace River district of AB and BC, on the upper Fraser River of central BC, and at Norman Wells on the Mackenzie River, Northwest Territories. It must have spread from central BC through "Crooked River Pass" to reach the Peace and Mackenzie rivers, and across the Great Divide Basin to reach UT and ID.

51. *Sorhoanus debilis* (Uhler) is a grass-feeding leafhopper from the eastern foothills of the Cascade Mountains from northern OR to intermontane valleys of southern BC and ID, and the mountains of central UT, eastern WY and CO (Fig. 14), all of which may have provided glacial refugia. It has crossed the Crownsnest Pass to Watertown, AB, and has invaded the headwaters of the Missouri River in MT by way of Bannock Pass and possibly also Lemhi and Monida passes. From the vicinity of Helena it may have crossed MacDonald Pass to establish a colony on the headwaters of the Clark Fork River; possibly it also crossed "Grassy Pass".

52. *Sorhoanus virilis* Hamilton (see Part 1), sister species to *S. debilis*, is known only from the Cascade Mountains of southernmost OR.

Endemics without close relatives, widespread in PNW.**(A) CICADELLIDAE**

53. *Attenuipyga (Dorycara) omanae* (Beamer) is a leafhopper specialist on bluebunch fescue, *Festuca idahoensis* Elmer in widely scattered PNW grasslands from southern BC south to the highlands of central OR, east to Bannock Pass (Fig. 6, H) and just north of "Grassy Pass." A nymph, possibly belonging to this species, has also been taken at Missoula, MT. It was probably widespread in WA-ID grasslands during the Pleistocene.

54. *Auridius safra* Hamilton is a grass-feeding leafhopper endemic to the hill country of central and eastern OR and central ID. Its single site in the mountains of northeastern CA (Hamilton 1999b, map 1) probably represents the area of its glacial refugium.

55. *Ceratagallia gallus* Hamilton is a polyphagous leafhopper endemic to sagebrush-grassland ecotone in southeastern ID and central UT. It probably survived the glacial period and accompanying inundation of central UT on arid hillsides of the Wasatch Plateau, as has the flightless, endemic sagebrush-feeding leafhopper *Errhomus naomi* (#155).

56. *Chlorotettix similis* DeLong is a grass-feeding leafhopper of the oak savannah of BC and OR, and of Palouse grasslands from southern BC to western ID. It was probably widespread in WA grasslands during the Pleistocene.

57. *Endria montana* (DeLong & Slesman) is a leafhopper of the Columbia basin (Wolfe 1955) and high elevation grasslands and also occurs on oak savannah in Vancouver Island, yet

it has penetrated only a short distance into Canada (Fig. 15), probably by way of the Columbia-Kootenay valley system. It apparently feeds on Letterman needlegrass, *Stipa lettermanii* Vasey, and has been taken at Rogers, MacDonald and Monida passes, from whence it has been able to invade the upper reaches of the Missouri and Yellowstone rivers. Presumably it came to the Lake Missoula valley by way of Lost Trail Pass. It has also been taken at Lolo Pass (1800 m elevation) in the Bitterroot Range and just beyond this pass on the upper reaches of the Lochsa River, a tributary of the Clearwater. Oddly, it is not known from mountains south of ID. Its glacial refugium was probably the Snake River valley of ID and MT, from whence it retreated as postglacial temperatures rose.

58. *Errhonus lineatus* (Baker) is a flightless leafhopper specialist on balsamroot, *Balsamorhiza* spp., endemic to Palouse grasslands of eastern WA, northeastern OR and western ID (Hamilton and Zack 1999, map 6). Its typical subspecies is a hybrid of 3 peripheral subspecies (see #100-102), suggesting that there were at least 3 glacial refugia. Since the parental morphs are no longer adjacent, it is impossible to tell whether this hybrid swarm originated before the latest glacial period and survived on the Palouse hills of WA, or whether it represents a highly successful postglacial hybrid that has completely swamped the intervening parental populations.

59. *Errhonus similis kahlotus* Oman is a subspecies of a widespread but flightless balsamroot-feeding leafhopper species endemic to the Columbia basin in both WA and OR. Populations of subspecies *kahlotus* Oman and its probable hybrid *dubiosus* Oman are widespread but sparse on the Columbia basin of WA. They must have survived the glacial period across most of the Columbia basin, except where intermittent Pleistocene inundations swept away populations in low-lying areas. They represent 2 of 12 subspecies of *E. similis* (see also # 106, 123-126) that reflect subdivision of the basin and eastern foothills of the Cascade Mountains of WA and OR due to canyons formed by the glacial-age rerouted Columbia River (Hamilton and Zack 1999, map 7).

60. *Hebecephalus caecus* Beamer is a grass-feeding leafhopper known only from the eastern foothills of the Cascade Range in OR (Beamer 1936) and from the mountains of southern ID just northeast of Boise. It was probably once widespread in OR-ID grasslands, but during the Pleistocene found separate refugia on the eastern slopes of the Cascades in OR and on the Snake River plains of ID.

61. *Hebecephalus callidus* (Ball) is a grass-feeding leafhopper known from the Palouse hills of WA (Ball 1899a), the East Kootenay valley of BC, the mountains of southern ID north of the Snake River plains, and the Bitterroot River valley of MT. It probably weathered the Pleistocene in the mountains of northern WY, and must have come to the Bitterroot valley of MT by way of Lost Trail Pass.

62. *Hebecephalus crassus* (DeLong) is a grass-feeding leafhopper known from Yellowstone Park, WY (DeLong 1926), from the Lost River Range in southeastern ID, and from Mt. Baldy (2000m elevation) in south-central BC. Its glacial-age refugium was probably in the mountains of northern WY.

63. *Hebecephalus firmus* Beamer has been taken in WA (Beamer 1936) and I have taken it near Yellowstone Park on both sides of the MT-WY border. Its glacial-age refugium was probably in the mountains of WY.

64. *Hebecephalus hilaris* Beamer is a grass-feeding leafhopper known only from the mountains of southeastern WY (Beamer 1936), and at Stevens Pass (1200m elevation) in the Cascade Range of WA on redtop (*Agrostis gigantea* Roth.), an introduced grass.

65. *Hebecephalus sagittatus* Beamer & Tuthill has been found in small numbers in scattered localities throughout the grasslands of the PNW, from the Blue Mountains of OR (Beamer and Tuthill 1935) east to the Lost River Range of eastern ID, and from the foothills of the Unita Mountains of UT north to the Okanagan Valley of BC. The Unita Mountains may

have been its glacial-age refugium. Specimens have also been taken on south-facing slopes of the Aishihik Canyon in southwestern Yukon, showing the close relationship between the grasslands of these very widely separated areas. Its spread to the Yukon may well have been accomplished before the present interglacial era (Hamilton 1997).

66. *Laevicephalus salarius* Knull is a specialist on alkali grass, *Distichlis stricta* (Torr.) Rydb. It has been found most commonly in UT on the Wasatch Plateau and in the north, but has also been taken at Kamloops in southern BC, and just north of Denver, CO. Its distribution probably reflects lack of collecting on this grass at intervening localities.

67. *Latalus curtus* Beamer & Tuthill is a grass-feeding leafhopper widespread in PNW grasslands that also has been taken at Pipestone Pass, at Lolo Pass on the MT/ID border west of Missoula, and on the upper Fraser River in central BC.

68. *Latalus mundus* Beamer & Tuthill is a grass-feeding leafhopper of PNW grasslands from the Okanagan Valley of southern BC to the Grand Teton Mountains of WY (which may have been its glacial-age refugium). It is also found in southeastern BC not far from Crowstest Pass (probably by way of the Columbia-Kootenay valley system), at MacDonald Pass, MT, and in the Bitterroot Valley, MT, below Lost Trail Pass.

69. *Mocuellus larrimeri* (DeLong) is a grass-feeding leafhopper of PNW grasslands from scattered localities in south-central BC to western ID, and is also known from the East Kootenay of BC (probably by way of the Columbia-Kootenay valley system), Missoula, MT (DeLong 1926), and Rattlesnake Ridge in southern WA. It was probably widespread in WA-ID grasslands during the Pleistocene but has moved northwards since then. Presumably it came to MT by way of Lost Trail Pass.

70. *Norvellina rubida* (Ball) is a leafhopper that feeds on fleabane, *Eriogonum* spp. (Asteraceae), which can grow at high elevation on south-facing mountain slopes. Nevertheless, it is confined to the zone of PNW grasslands (Fig. 5, filled circles) and may have been widespread in WA-ID grasslands during the Pleistocene.

71. *Norvellina vermiculata* Lindsay is found on the Snake River plain, ID and northern UT to northwestern CO. It has also been taken just over the continental divide at White Sulphur Springs in western MT.

72. *Orocatus pinnipenis* Ross & Hamilton is a leafhopper feeding on Sandberg's blue grass, *Poa secunda* Presl. that occurs on west-facing slopes at about the 2000m level throughout most of ID and western MT (Fig. 16); elsewhere it is a valley or plateau species. It was probably widespread in ID grasslands during the Pleistocene. It has been taken in Rogers, Lemhi, Bannock and Monida passes and also close to Lost Trail and MacDonald passes, but has invaded only the fringe of the prairies, preferring the higher elevation of the Little Belt mountains of MT and the Bighorns of WY.

73. *Psammotettix attenuens* (DeLong & Davidson) is a grass-feeding leafhopper ranging from the mountains of CO to coastal BC (Fig. 17). It was probably widespread in the CO mountains and WA-ID grasslands during the Pleistocene. It has been taken in "Grassy", Lemhi and Bannock passes but has not penetrated the continental divide

74. *Sorhoanus xiphosura* Hamilton (see Part 1) is a grass-feeding leafhopper widespread through the PNW. It is tolerant of high altitudes (e.g., it is found just beyond Lolo Pass on the ID side of the border). Evidently it crosses passes readily.

(B) DELPHACIDAE

75. *Caenodelphax atridorsum* (Beamer) was described from the eastern slopes of the Cascade Range in OR and has subsequently been discovered at two locations west of the continental divide in MT (west side of Clark Fork Valley at Missoula, and in the Blackfoot Valley).

76. *Pissonotus rubrilatus* Morgan & Beamer was described from Colorado and has

subsequently been found in widely scattered localities in WY, ID, and central BC (Bartlett and Deitz 2000).

Taxa endemic to AB and inland BC.

(A) CICADELLIDAE

77. *Ceratagallia okanagana* Hamilton is known only from southernmost Okanagan Valley in BC (Hamilton 1998b). It may have been limited to the northern part of the Columbia basin during the Pleistocene.

78. *Cuerna cuesta* Hamilton. Although not strictly confined to grasslands (Fig. 18), this forb-feeding leafhopper of BC is most often associated with grassy areas including lodgepole pine stands. Its range extends into eastern WA and northern MT. It may have been limited to the northern part of the Columbia basin during the Pleistocene. Its sister species *C. septentrionalis*, which also ranges northwards into coniferous forest glades, is entirely on other side of divide from BC to CO, crossing into the Pacific watershed only in the Yukon (Hamilton 1997).

79. *Hebecephalus planaria* Hamilton (1998a) is a grass-feeding leafhopper known only from southern interior of BC. It may have been limited to the northern part of the Columbia basin during the Pleistocene.

80. *Rosenus decurvatus* Hamilton & Ross is a grass-feeding leafhopper known only from south-facing bluffs above the Peace River near the BC/AB border. It probably found a glacial-age refugium on south-facing hillsides in MT and followed the retreating ice front northwards during deglaciation.

(B) DELPHACIDAE

81. *Paraliburnia furcata* Hamilton (see Part 1) is a planthopper known only from the upper Fraser River of central BC.

82. *Paraliburnia lecartus* Hamilton (see Part 1) is a planthopper known only from the Peace River district of BC. Like the preceding species (#80, 81), it probably found a glacial-age refugium on south-facing hillsides in MT.

Taxa endemic to ID/MT border (CICADELLIDAE only).

83. *Athysanella castor* Hamilton (see Part 1) is a leafhopper found on both sides of the ID/MT border and also across the continental divide in the Rock Creek valley of MT. It has been found just west of the divide at Lemhi Pass. It may have found a glacial-age refugium on the MT foothills to the east of the pass.

84. *Athysanella nielsoni* Blocker is a leafhopper known only from the upper Snake River valley of ID about 5 km north of Idaho Falls. A short series was taken on "sage" (Blocker and Johnson 1990), but all other species in this genus are grass feeders, and this one probably is also. It may never have moved from its glacial-age refugium, although a female that may belong to this species has been found in western ID near the junction of the Salmon and Snake rivers.

85. *Diplocolenus configuratus bicolor* Hamilton (see Part 1) has quite a restricted range although technically this leafhopper occurs in three states (Fig. 8, stars). It is confined to the continental divide and adjacent mountain ridges extending along only 400 km. During the Pleistocene it may have been restricted to the upper end of the Snake River valley. Its range now abuts that of the common eastern *D. configuratus* s.s. (#13) where they hybridize (Fig. 8, bull's-eyes).

86. *Hebecephalus crenulatus* Hamilton (1998a) is a grass-feeding leafhopper that has been taken from the upper Snake River plain. It may never have moved from its glacial-age refugium. Unassociated females from near the Utah border may be conspecific with this

species.

87. *Hebecephalus ferrumequinum* Hamilton (1998a) is a grass-feeding leafhopper that is known only from just west of Bannock Pass. It may never have moved from its glacial-age refugium.

88. *Hebecephalus picea* Hamilton (1998a) is a grass-feeding leafhopper that is known only from a stony plain in the Lost River valley 30 km north of the Snake River plain. It may never have moved from its glacial-age refugium.

89. *Hebecephalus pugnus* Hamilton (1998a) is a grass-feeding leafhopper that is known from several sites in the upper Snake River valley of ID, and near the headwaters of Lost River which flows into the Snake River plain. It probably found a glacial-age refugium on the upper Snake River valley.

90. *Hebecephalus veretillum* Hamilton (1998a) is a grass-feeding leafhopper that is known only from a west-facing hillside at Ketcham, ID on the north side of the Snake River plains. It may never have moved from its glacial-age refugium.

91. *Mocuellus caprillus anfractus* Hamilton (see Part 1) is a grass-feeding leafhopper with a nearly circular distribution centred around the upper Snake River valley of ID (Fig. 9, filled circles) which is probably its glacial-age refugium. It has spread to hills within 200 km N or S, and 150 km E or W. The typical subspecies (see #17) inhabits the prairies and hybridizes with this subspecies at Lemhi Pass on the ID border.

92. *Rosenus obliquus* (DeLong & Davidson) is a grass-feeding leafhopper known only from two valley sites in the mountains of south-central ID. It probably found a glacial-age refugium on the upper Snake River valley.

Taxa endemic to Lake Missoula basin, MT (CICADELLIDAE only).

93. *Errhomus braccatus* Hamilton & Zack is a flightless balsamroot-feeding leafhopper found only in the upper reaches of the Bitterroot valley of MT, where it seems to have found a refugium from the waters of glacial Lake Missoula (Hamilton and Zack 1999, map 9).

94. *Errhomus camensis* Hamilton & Zack is a flightless balsamroot-feeding leafhopper found only in the south of the Blackfoot valley of MT, where it seems to have found a refugium from the waters of glacial Lake Missoula (Hamilton and Zack 1999, map 10).

95. *Errhomus rivalis* Hamilton & Zack is a flightless, polyphagous leafhopper found only on the west bank of the Bitterroot River of MT, where it joins the Clark Fork River to the west of Missoula, MT. (Hamilton and Zack 1999, map 9). Since this site was under 300m of water only 12,000 years ago, it must have survived on nearby Black Mountain.

96. *Errhomus solus* Oman is a flightless, polyphagous leafhopper found on hillsides around Missoula and in the Blackfoot valley of MT (Hamilton and Zack 1999, map 9). As these sites are separated by the Clark Fork River, it must have found refugia from the waters of glacial Lake Missoula in at least two localities.

Taxa endemic to inland OR and western ID (CICADELLIDAE only).

97. *Ceratagallia acerata* Hamilton is known only from southernmost OR east of the Cascade Mts. (Hamilton 1998b).

98. *Ceratagallia clino* Hamilton is known only from the eastern slopes of the Cascade range in OR (Hamilton 1998b).

99. *Ceratagallia lophia* Hamilton is known only from the 1500m high summit of the Jackass Mts. in southeastern OR (Hamilton 1998b).

100-101. *Errhomus affinis* Oman is a flightless balsamroot-feeding leafhopper known only from the high elevations on either side of Hells Canyon on the OR-ID border (Hamilton and Zack 1999, map 9). The populations divided by this canyon on the ID side (typical subspecies, #100) and on the OR side (subspecies *attenuatus* Hamilton & Zack, #101) must predate the

formation of the canyon at least 1.5 million years ago.

102. *Errhomus josephi* Oman is a flightless balsamroot-feeding leafhopper known only from high elevations in the Grande Ronde canyon of northwestern OR and adjacent WA (Hamilton and Zack 1999, map 8).

103. *Errhomus lineatus cordatus* Hamilton is now confined to the north shore of Coeur d'Alene Lake in ID, and may have survived the glacial period along the adjacent Spokane River of eastern WA where hybrids with the typical subspecies are now found.

104. *Errhomus lineatus idahoensis* Oman is now found east of the Snake River in ID and probably was confined to canyons there during the glacial maximum.

105. *Errhomus lineatus umatilla* Oman occurs in scattered localities of northeastern OR and may have been confined to the south banks of the lower Columbia canyon during the Wisconsinian.

106. *Errhomus ochoco* Oman is a flightless balsamroot-feeding leafhopper known only from the 1500m high summit of the Ochoco Mts. in central OR (Hamilton and Zack 1999, map 7).

107. *Errhomus pallidus* Oman is a flightless potentilla-feeding leafhopper known only from the foothills of the Wallowa Mts. in northwestern OR (Hamilton and Zack 1999, map 10).

108. *Errhomus serratus* Oman is a flightless balsamroot-feeding leafhopper endemic to widely separated PNW grasslands of northeastern OR and the eastern foothills of the Cascade Mountains of WA (Hamilton and Zack 1999, map 9). It must have ranged around the entire periphery of the Columbia basin before Pleistocene temperatures eliminated its northernmost populations, leaving 3 subspecies in areas which might have provided glacial refugia (see also #116, 117). The typical subspecies is found only on the southern flanks of the Blue Mts. of OR.

109. *Errhomus similis medialis* Oman, together with possible hybrids (*E. similis minutus* Oman, *E. similis nanus* Oman) and populations showing character displacement (*E. similis truncus* Oman) occurs south of the lower Columbia canyon. All may be postglacial taxa derived from a single glacial refugium.

110. *Errhomus variabilis erratus* Hamilton & Zack, is restricted to the Salmon River on the west (OR) side of the canyon.

111. *Errhomus variabilis gracilis* Hamilton & Zack is restricted to the Salmon River on the east (ID) side of the canyon.

112. *Errhomus variabilis mimicus* Hamilton & Zack is found on the southern flanks of the Blue Mts. of OR.

113. *Errhomus winquatt* Oman is a flightless balsamroot-feeding leafhopper known only from the south bank of the lower Columbia canyon where it penetrates the Cascade Mts. in southern OR (Hamilton and Zack 1999, map 8).

114. *Psammotettix greenei* Hamilton (see Part 1) is a grass-feeding leafhopper known only from southernmost OR east of the Cascade Mts. (Greene 1971).

Taxa endemic to inland WA (CICADELLIDAE only).

115. *Ceratagallia vipera* Hamilton is known only from the 1000m high summit of Rattlesnake Ridge, an eastern outlier of the Cascade Mts. in southern WA (Hamilton 1998b).

116-117. *Errhomus brevis* Oman is a flightless balsamroot-feeding leafhopper known only from the north bank of the lower Columbia canyon and inland regions of southern WA adjacent to the Cascade Mts. (Hamilton and Zack 1999, map 6). The canyon populations (typical subspecies, #116) and inland ones (subspecies *simcoe* Oman, #117) form hybrid swarms where they meet at the mouth of the Klickitat River (*idem*, map 11).

118. *Errhomus calvus* Oman is a flightless polyphagous leafhopper known only from the

Okanogan highlands of northern WA and adjacent BC (Hamilton and Zack 1999, map 2).

119. *Errhomus paradoxus* Oman is a flightless balsamroot-feeding leafhopper known only from the northern bank of the lower Columbia canyon in southern WA just to the east of the range of *Errhomus brevis* (Hamilton and Zack 1999, map 8).

120. *Errhomus picturatus* Hamilton & Zack is a flightless balsamroot-feeding leafhopper known only from a single site near Wenatchee Lake in northwestern WA adjacent to the Cascade Mts. just to the east of the range of *Errhomus wolfei* (Hamilton and Zack 1999, map 8).

121. *Errhomus praedictus* Hamilton & Zack is a flightless balsamroot-feeding leafhopper known only from a single site on the south slopes of the Simcoe Mts. in southern WA just to the east of the range of *Errhomus brevis* (Hamilton and Zack 1999, map 8, as *inconspicuous* [sic]).

122. *Errhomus reflexus* Oman is a flightless balsamroot-feeding leafhopper known only from two populations on either side of the Kittitas Valley in central WA east of the Cascade Mts. (Hamilton and Zack 1999, map 8).

123. *Errhomus satus* Oman is a flightless balsamroot-feeding leafhopper known only from just north of Satus Pass in the Simcoe Mts. in southern WA just to the east of the range of *Errhomus brevis* (Hamilton and Zack 1999, map 8).

124. *Errhomus serratus instabilis* Oman is found only in the Naches valley of WA.

125. *Errhomus serratus obliteratedus* Hamilton occurs on the arid eastern slopes of the Wenatchee Mts. of WA.

126. *Errhomus similis* Oman, typical subspecies, and its probable hybrids *E. similis confinis* Oman and *Errhomus similis relativus* Oman, occur on the eastern foothills of the Cascade Mountains on WA.

127. *Errhomus similis sobrinus* Oman is confined to the angular bend made by the Columbia in the Pascoe Basin, WA. This appears to be an area that was east of the Columbia until the river shifted to its present location at least 5 million years ago.

128. *E. similis socius* Oman is confined to an area to the west of the Columbia canyon in WA south of Lake Chelan and north of the Wenatchee River canyon.

129. *Errhomus similis zonarius* Oman is found north of the Columbia canyon and east of the Okanogan valley in WA.

130. *Errhomus variabilis* Oman is a flightless balsamroot-feeding leafhopper endemic to the northern edge of the Columbia basin of WA, and the Snake River valley on the ID-OR boundary (Hamilton and Zack 1999, map 10). Its various subspecies reflect at least 4 glacial-age refugia, the typical subspecies being found on the Columbia basin and the others (#107-109) in peripheral areas.

131. *Errhomus wolfei* Oman is a flightless balsamroot-feeding leafhopper known only from the Wenatchee River canyon of northwestern WA (Hamilton and Zack 1999, map 8).

132. *Limotettix zacki* Hamilton is known only from the 300m high summit of Badger Mt. just west of the Columbia River in WA (Hamilton 1994a).

Taxa endemic to Pacific coast north of CA (CICADELLIDAE only).

133. *Athysanella valla* Blocker and Johnson is a grass-feeding leafhopper known only from southernmost OR west of the Cascade Mts. (Blocker and Johnson 1990).

134. *Ceratagallia omani* Hamilton is known from Saturna I. off Vancouver Island, BC, along the entire OR coast, and inland on the Coast Range as high as 1000m (Hamilton 1998b).

135. *Evacanthus lacunar* Hamilton is a *Scrophularia*-feeding leafhopper known only from Marys Peak (1100m) in the Coast Range of OR (Hamilton 1983).

136. *Latalus occidentalis* (DeLong) is known from Marys Peak and adjacent coast of OR, and possibly also from Vancouver Island in BC (based on an unassociated female). This

species appears to be a closely related to an undescribed species from 1100m elevation in the Cuyamaca Mts. of southernmost CA.

137. *Limotettix beameri* (Medler) is found along the coast of OR including the Coast Range, and near Puget Sound in WA.

138. *Psammotettix diademata* Hamilton (see Part 1) is known only from the shore of the Queen Charlotte Islands in BC (Fig. 2, star).

139. *Psammotettix nesiotus* Hamilton (see Part 1) is known only from both sides of the Strait of Georgia that separates Vancouver Island from mainland BC.

Taxa endemic to mountains of CO and adjacent WY.

(A) CICADELLIDAE

140. *Athysanella gardenia* Osborn was described from the mountains of CO and has subsequently been recorded from both CO and WY (Blocker and Johnson 1988) without any more specific information. Its circumscribed distribution seems to indicate montane endemism.

141. *Athysanella hyperoche* Hamilton (see Part 1) is known only from a pass in the Laramie Mountains of WY (see Part 1).

142. *Diplocolenus configuratus nigrrior* Ross & Hamilton is a rather rare grass-feeding leafhopper known only from mountains in AZ and CO (where it probably found glacial-age refugia), and across about 200 km of the foothills of the Unita Mts. on the borders of ID, UT and WY (Fig. 8, filled circles) to the west of *D. configuratus*. It appears to hybridize (Fig. 8, bull's-eyes) with both *D. configuratus* s.s. and *D. configuratus bicolor*.

143. *Errhomus montanus* (Baker) is a flightless potentilla-feeding leafhopper found on high mountains from CO and western WY to southern MT (Hamilton and Zack 1999, map 1). It was probably more widely distributed during the Pleistocene, and has since retreated into its montane fastness as temperatures increased 10,000 years ago.

144. *Hebecephalus chandleri* Hamilton is a grass-feeding leafhopper known only from the Bighorn Mountains of northern WY (Hamilton 1998a). It is a sister-species of *H. atralbis* Emeljanov from Siberia.

145. *Hebecephalus vinculatus* Ball is a grass-feeding leafhopper found in the mountains of CO (Ball 1899b). It was incorrectly recorded from WY and Labrador (see Hamilton 1998a)

146. *Idiodonus josea* (Ball) is a leafhopper of the mountains of CO and southern MT (near Yellowstone N.Pk.) Nymphs that are also reddish, but evenly coloured instead of maculate, perhaps may be conspecific; these are known from southern BC and adjacent ID.

147. *Norvellina saucia* (Ball) is known only from the mountains of CO (Lindsay 1940).

148. *Orocastus hyalinus* (Beamer) is a grass-feeding leafhopper known only from the mountains of CO (Beamer 1938).

149. *Psammotettix viridinervis* Ross & Hamilton is a grass-feeding leafhopper known only from the mountains of southeastern WY (Ross and Hamilton 1972).

150. *Sorhoanus involutus* Hamilton (see Part 1) is known only from the mountains of CO.

(B) DELPHACIDAE

151. *Kosswigianella irruutilo* Hamilton (see Part 1) is known only from the mountains of CO. It has no known relatives.

Taxa endemic to northern UT and adjacent WY

(A) CICADELLIDAE

152. *Athysanella obscura* Johnson is known from "Antelope, UT" (Johnson and Blocker 1979) and an unspecified locality in WY (Blocker and Johnson 1990).

153. *Hebecephalus abies* is a grass-feeding leafhopper that is only known from the foothills of the Unita Mountains and the West Tavaputs Plateau of UT (Hamilton 1998a).

154. *Hebecephalus filamentus* Hamilton & Ross is a grass-feeding leafhopper that occurs in northeastern UT and also on the mountains of southeastern WY (Hamilton 1998a).

155. *Mocuellus quinquespinus* Hamilton (see Part 1) is a grass-feeding leafhopper that is only known from a single locality in the foothills of the Unita Mountains of UT (Fig. 9, star), an area particularly rich in PNW grassland leafhoppers, including *Hebecephalus abies* (# 149).

156. *Norvellina curvata* Lindsay is known only from the Grand Teton Mountains of WY (Lindsay 1940).

(B) DELPHACIDAE

157. *Achorotile apicata* Hamilton (see Part 1) is a planthopper known only from the Unita Mountains of northeastern UT. It is related to a transboreal species.

158. *Elachodelphax unita* Hamilton (see Part 1) is a planthopper known only from the Unita Mountains of northeastern UT. It is related to *E. mazama* (#40) from the Cascade Mountains of WA.

Taxa endemic to mountains of central UT

(A) CICADELLIDAE

159. *Errhomus naomi* Hamilton & Zack is known only from an isolated location in the Fish Lake mountains of the Wasatch Plateau, UT. Its relatives inhabit western MT. It feeds on the common species of the Great Plains, hoary sagebrush (*Artemisia cana* Pursh) rather than on the common Rocky Mountain species (*A. tridentata* Nutt.)

(B) DELPHACIDAE

160. *Kosswigianella wasatchi* Hamilton (see Part 1) is a planthopper known only from the Wasatch Plateau of central UT. It is related to a transcontinental species.

CONCLUSIONS

Endemism. Endemics account for approximately half (44%) of the entire PNW grassland fauna of 275 taxa. If one adds the 22 taxa that are endemic to the mountains of CO, UT and WY the total endemic fauna rises to 142 taxa (52% of the PNW fauna). This is one of the highest percentages of regional endemism in North America. The total number of endemics is third only to those of the prairies and desert grasslands. Clearly this represents an unique fauna of great age that has managed to survive Pleistocene climate change in some refugium. But where? This can be determined only after deducing how much the fauna moved in response to postglacial (Hypsithermal) warming, and to what degree mountain passes proved to be a barrier to dispersal.

Hypsithermal change. The only valleys in the PNW with few endemics and limited southern faunal elements are the isolated glaciated valleys of central and eastern BC. These valleys must have been repopulated largely by prairie insects coming over "Crooked River" and Crowsnest passes, for they are essentially an Alberta fauna found mainly along the upper Fraser River (#1, 8, 14, 21, 27, 31) and in the East Kootenay valley (#1, 2, 9, 19, 24, 26, 28). This faunal invasion probably occurred during the Hypsithermal as these passes are now completely forested for many kilometres. Hypsithermal grasslands probably extended as far north as the Mackenzie River but not into the Yukon (Hamilton 1997; see also #50). Faunal exchange this far north was probably at a still warmer time, possibly during the height of the Sangamon interglacial 124,000 years ago (Matthews 1979).

It is unlikely that Hypsithermal warming ever brought together ranges of PNW grasslands sufficiently to permit free faunal interchange. Widely dispersing leafhoppers seldom are found

throughout PNW grasslands. For example, the endemic leafhoppers *Norvellina rubida* (#70) and *Sorhoanus xiphosura* (#74) range throughout much of the PNW grasslands from Wyoming to southern British Columbia, but, even more than the grasslands themselves, they have fragmented ranges (Fig. 5, filled circles and stars).

PNW-prairie passes. In the U.S.A. there is a sharp division between faunas of the PNW grasslands and those of the prairies. As the two are connected across a number of grassy passes (Fig. 6) and are botanically identical on both sides, this becomes hard to understand with our present knowledge. Yet there are at least 59 prairie taxa that range up to the continental divide; at least six do not cross it at all (the typical subspecies of #32-35, plus *Stenometopiellus cookei*, sister-species of #38, and *Elachodelphax borealis*, sister-species of #40), while 31 penetrate only a short way into the PNW (#1-31). Five taxa that inhabit the PNW do not cross these passes although they range up to them (#53, 67, 68, 73, 91). Four PNW endemics have crossed the divide to invade adjacent foothills prairie (#51, 62, 72, 83). Another 18 PNW taxa which range up to the continental divide appear to be confined to mountains or high latitudes (#62-64, 74, 76, 85, 87, 140-151) and are therefore unlikely to invade the prairies.

Yet despite the few cases of faunal exchange between these grasslands, there are many passes in MT, ID and WY which show numerous cases of insect migrations (Table 1). Three components seem to govern whether passes are suitable for leafhopper dispersal.

Predictably, "open" (grassland) passes have the largest number of grassland leafhopper taxa. The wide pass at Great Divide Basin, WY was probably a conduit for 14 species, but only a single grassland species has been taken actually in the pass which is now very arid. A similar number probably crossed Bannock Pass, and 10 are still found there. Less certain evidence has been found that "Grassy Pass" also has been the conduit for 14 species, of which only three have been found in the pass. Ten to 12 taxa can be inferred to have crossed through Lemhi, Monida and Lost Trail passes. Possibly "Grassy," Lemi and Monida Trail passes have been open grasslands only recently, having been forested during the Pleistocene, and then arid during the Hypsithermal. Lost Trail Pass is currently forested on its southern flank, but might have been open during the Hypsithermal.

Elevation is the second most important component governing whether leafhoppers can use passes. Crowsnest Pass in southern BC (1400 m) and Rogers Pass, one of the lowest passes in MT (1800 m), are both good leafhopper conduits (for 11 taxa each). MacDonald Pass (2000 m) has a substantially smaller number of taxa associated with it (eight taxa, four in the pass). Increasing elevation of passes south of this is offset by the increasing elevation of the montane grassland at this latitude, so that Lemhi and Bannock on the ID/MT border (both at 2200 m) are "open" passes through which at least 12 taxa have passed.

Direction of the pass also seems to play an important role in dispersal of leafhoppers. The passes most used by leafhoppers tend to have a north-south extent. East-west passes such as MacDonald Pass (2000 m) and Chief Joseph, MT (2200 m) show much less influence in leafhopper spread than one would expect. The direction of transfer has been mainly north to south at "Crooked River," Rogers and Monida passes, and south to north at "Grassy Pass". In each case the dominant direction is from the prairies into the intermontane grasslands, and not *vice versa*. Probably the winds that aid most in leafhopper dispersal are the strong prairie southerlies of summer. The prevailing northwesterlies of spring and fall appear to occur too early and late to transfer gravid females. Such winds would carry Homoptera over local barriers formed by north and east-facing slopes, which are cooler and not as suitable for grassland insects.

Refugia. There are 32 widespread PNW grassland Homoptera (#34, 36, 41-43, 51, 52-76) that may be either widely dispersing or merely disjunct relicts of a formerly widespread

distribution. These include 20 taxa (#34, 36, 41-43, 51, 53, 54, 63, 65-76) which fail to match each other in distribution (e.g., Fig. 5) so no conclusions can be reached about their Pleistocene distribution. The probability is greatest that these have each survived the Pleistocene in more than one refugium, from whence they have spread to outlying areas in a discordant manner. Three other such species are *Endria montana* (#57) whose range is divided between grasslands on southern Vancouver Island, BC and those of the Rocky Mountains, centred around the upper end of the Snake River Valley; *Hebecephalus caecus* (#60) whose range is divided even today between the eastern slopes of the Cascades in OR and upper end of the Snake River Valley; and *Hebecephalus hilaris* (#64) which is known only from the Cascade Range of WA and the mountains of southeastern WY.

By contrast, there are 80 taxa endemic to just a part of the PNW (#45-52, 77-151). The most strikingly different PNW grassland fauna is that of oak savannah and other Coast Range grasslands such as the grassy "bald" above 1200 m elevation on Marys Peak, OR (Fig. 5, filled triangle), the latter with two endemic species (#135, 136). This coastal grassland shares with inland sites only three PNW leafhoppers (#56, 57, 73; see Figs. 15, 17). Seven grassland taxa (#133-139) are restricted to the Pacific coast side of the Cascade range. One of these, *Psammotettix diademata* (#138) is known only from the shores of the Queen Charlotte Islands far to the north of other PNW grasslands. These islands also have one other endemic leafhopper, *Evacanthus grandipes* Hamilton (1983) and an endemic spittlebug, *Aphrophora regina* Hamilton (1982), both of which are forest insects, so the weather on the seaward side of the islands was probably mild enough for all three of them to weather Pleistocene glaciation there. Further evidence that the Queen Charlotte Islands were not glaciated during the last ice advance is provided by Nearctic earthworms, that exist here and on Vancouver Island although eradicated from the rest of Canada by glaciation (Hendrix and Bohlen 2001, fig. 1).

Other geographic areas with distinctive faunas, from north to south, are inland BC plus AB with six taxa (#77-82), eastern ID plus adjacent MT with 10 taxa (#83-92), inland WA with 18 taxa (#115-132), and inland OR plus western ID with 18 taxa (#97-114). Do these four geographic areas represent four additional Pleistocene refuges? Concurrence between individual distribution patterns should resolve this question.

In addition to these 54 localized taxa endemic to inland PNW grasslands, there are six leafhoppers that represent three pairs of sister taxa with widely disjunct ranges (#45-52). Three of these, one from each pair, are associated either with the eastern slopes of the Cascade Mountains in OR (#45, 48), or with the Cascades themselves in the south of OR (#52). Their sister-taxa are found either on the upper reaches of the Clark Fork river in MT (#46, 47) or are widely dispersed around the drainage basin of the Columbia River and the Clark Fork river (#51). This suggests a PNW-wide dispersal pattern that became fragmented into an OR component associated with the southern Cascades, a Columbia basin component, and a Clark Fork component; subsequent catastrophic flooding of the Columbia basin in the late Pleistocene may have wiped out intervening populations of all but the species most adapted to high elevations, *Sorhoanus debilis* (#51). This disjunct distribution pattern is similar to that of *Hebecephalus caecus* (#60), discussed above. Confirmation of a fragmented grassland habitat is found in the several groups of local endemics that mirror this pattern, as well as some widespread prairie species whose PNW range is separated by hundreds of kilometres, e.g., *Flexamia inflata* (Osborn & Ball) (Whitcomb and Hicks 1988, Fig. 41).

The easternmost of these disjunct grasslands occurs along the upper reaches of the Clark Fork River from St. Regis, MT to the continental divide. This area has seven of the eight endemic leafhoppers of MT (#46, 47, 93-96, plus *Macrosteles skalkahiensis* Beirne from 2200 m elevation in Skalkaho Pass, east of the Bitterroot Valley: Beirne 1952). Most of these endemics are members of the flightless genus *Errhonus*. Three (#93, 94, 96) inhabit two of the four main tributaries of the valley that was once Lake Missoula: the Bitterroot and

Blackfoot rivers. A fourth (#95) is found on the west bank of the Clark Fork river where these rivers converge at Missoula. This flightless species must have survived inundation of the valley on south-facing mountain slopes at least 300 m higher than its present locality. Another genus is represented along the third tributary, Rock Creek: *Athysanella repulsa* (#46).

A much larger number of local endemic taxa are associated with the land to the east of the Cascade Range in WA and OR (#45, 48, 52, 60, 97, 98, 106, 109, 113, 114, 116-129, 131, 132), a total of 27 endemics in this area. Sixteen of these species are highly localized, flightless leafhoppers of WA and adjacent OR (#107, 108, 116-129, 131), and two of these each have two subspecies (#116, 117; 124, 125) in adjacent areas, suggesting occupancy of this area for a considerable time. Three others appear to have had another refugium in southwestern OR (#52, 97, 114). Two became stranded on isolated mountain crests east of the Cascades in WA (#115, 132). Two species are known from single hills in south-central OR (#99, 106). It appears clear that at least patches of grassland survived along with their leafhopper faunas in numerous isolated situations, probably south-facing hillsides and canyon slopes. The only species of *Errhonus* that inhabits the most arid parts of the Columbia plateau, *E. similis*, now favours north and east-facing slopes of coulees that are not so subject to drought as level ground or south and west-facing slopes (Hamilton and Zack, 1999). This suggests that they found glacial-age refugia on south-facing slopes. The grasslands of WA were probably more severely modified than those of OR, resulting in a much more fragmented WA fauna.

The intervening area between these eastern and western grasslands is largely Columbia basin. There, 13 endemic taxa are members of the flightless leafhopper genus *Errhonus* which feed on arid-adapted perennial composites: four in WA and adjacent ID (#58, 59, 103, 130) and nine along Hell's Canyon on the ID/OR border, and up into the Blue Mountains of OR (#100-102, 104, 105, 107, 108, 110-112). All other, more mobile endemic leafhoppers have migrated northwards from the Columbia basin, usually into many adjacent areas (#32, 33, 35, 56, 78 and probably many of the widely dispersing species). Four (#39, 40, 77, 79) are known only from glaciated valleys in southern BC and northern WA and must have come from refugia further south.

Nine species belonging to five genera (#38, 61, 84, 86, 88-92) are associated with the headwaters of the Snake River and one (#60) has a disjunct population associated with a tributary river northeast of Boise in the western part of the state. Curiously, none are members of *Errhonus* although the genus is speciose both east and west of this valley. Pleistocene volcanism that flooded much of the Snake River valley in ID may have decimated populations of this arid-adapted genus. Other leafhoppers may have survived in this region through their greater powers of dispersal. For example, *Mocuellus caprillus anfractus* (#91) has a nearly circular range strongly suggestive of dispersal from a single valley bottom refuge. The other species are scattered in various valleys along the south-facing slopes of the ranges crossing central ID or the upper Snake canyon where it penetrates the WY border. This pattern is highly suggestive of a Pleistocene rain-shadow grassland in the upper Snake River plains, together with isolated grassland patches on south-facing slopes from the Lost River Range westward to the present site of Boise.

Other leafhoppers may have adapted to cooler conditions during the Pleistocene, and subsequently sought refuge after glaciers melted by migrating to higher elevation grasslands. Some PNW endemics (e.g., #55) are now limited to a few valley bottom sites in a linear pattern suggesting migration north from a glacial refugium. At least four widespread species (#20, 27, 43, 73) have migrated far northwards into glaciated areas. Four others (#29, 51, 62, 72) are now found in mountains or grasslands at lower elevation less far north. One (#37) is known only from a glaciated mountain. Fifteen other endemic taxa are characteristic of limited areas of the Rockies of southern MT/ID (Bitterroot Range) south to CO (#83, 85, 87, 140-151). These may have shifted their ranges vertically rather than longitudinally, in the same

manner that nine endemics in UT and adjacent WY (#152-160) almost certainly have done. One flightless species (#143) and two others (#142, 146) are presently found in isolated mountains in three states, so the refugium may have extended a considerable distance along the mountain range. One species (#144) is presently confined to the Bighorn Mountains of north-central WY, which may represent an isolated grassland refugium.

Three species are presently known only from the "Crooked River" Pass vicinity, on the upper Fraser River of BC (#81) and south-facing bluffs along the Peace River in Alberta (#80, 82). These may once have been inhabitants of the eastern slopes of the Rockies; but this would require a very extensive displacement northwards during the Hypsithermal not evident among other Homoptera.

Pleistocene climate. There is ample evidence that PNW grasslands and their fauna are endemic phenomena. Indeed, there is only evidence for a Hypsithermal invasion of prairie grasslands into two northern, deglaciated mountain valleys. How, then, can one reconcile the biological evidence for extensive endemism with the geological evidence for extensive permafrost patterns across the breadth of the PNW?

First, glacial-age circular features known as "stone rings" may not be indicative of permafrost at all. That they have been cited as evidence of permafrost (Brunnschweiler 1962) may be due to superficial similarities to ice mounds in modern tundra. This view has not found favour among modern geologists (Matthews 1979). Stone rings are found only on tablelands in the PNW (Fig. 19). These structures may point towards yearly alternations of extremes of heat and cold. They were probably formed of rock fragments forced outwards around the edges of ponds that froze solid each winter, then completely melted again each summer, leaving a depression to collect yet more water and thus grow to a larger size each successive year.

Second, land slope and direction are obvious components of microclimate. South-facing slopes are particularly subject to aridity and high summer temperatures; west-facing slopes show similar but less severe conditions and are the modern preferred habitat of PNW grassland leafhoppers. A number of endemic grassland leafhoppers in the Yukon are associated with south-facing slopes (Hamilton 1997). That such a phenomenon was very much a part of glacial-age ecology is shown by pollen and subfossil assemblages in the Saint Lawrence valley of Québec (Mott et al. 1981). At a time when the whole valley was extensive "spruce-aspen forest" following the retreat of "tundra" conditions 10,000 years ago, Mont St. Hilaire had high levels of oak pollen and even an oak-feeding treehopper (Membracidae), presumably from the sun-warmed slopes.

Thirdly, timing is probably a factor. Permafrost soil structures indicate the overall coldness of a site, but not the duration of that cold. Thus, a long and severe winter could well be succeeded by a mild (perhaps even hot) but short summer. This is probably the explanation of why the majority of endemic flightless leafhoppers in *Errhonus* have survived the Pleistocene on the Columbia Basin by feeding on a spring-flowering host, balsamroot.

In total, 38 PNW-endemic taxa belong to *Errhonus* (#58, 59, 93-96, 98-105, 109-114, 116-131, plus six subspecies of postglacial origin). These often occupy adjacent territories that follow geological features erased long before the Pleistocene (Hamilton and Zack 1999). The evidence is thus strong that these regions suffered little climate change during the Pleistocene, although the extent of the arid areas of the Columbia basin were probably more limited than at present. *Errhonus* are mostly insects that emerge early in spring to take advantage of perennials that dry up in summer. During the Pleistocene their hosts may have grown in mid-summer instead of springtime. If these leafhoppers are active during cool weather, they would have been able to adjust their seasonality so that their ranges were little affected by Pleistocene conditions.

Nine of the 12 balsamroot-feeding species of *Errhonus* in WA and OR are found very

close to (but not on) ring-patterned ground (Fig. 19, # 1-9). Six exceptions to this lifestyle are only found in the most northerly or montane species: *E. calvus* (Fig. 19, # 10) north of the Columbia, *E. pallidus* in the Blue Mountains of OR (Fig. 19, # 12), *E. solus* and *E. rivalis* (Fig. 19, # 14-15) near the deepest part of the Lake Missoula valley, *E. montanus* in the highest mountains of CO and WY, and *E. naomi* above 3000 m in the Wasatch Plateau of UT. All have shifted to other hosts, probably when balsamroot became scarce under Pleistocene conditions. In all of the glaciated area east of OR, only the highly localized *E. camensis* (#94) still feeds on balsamroot.

Additional evidence for short but warm Pleistocene summers close to ice margins comes from eastern Canada. There, the endemic Gulf of St. Lawrence aster, *Aster lautentianus* Fernald is presumed to have weathered the Pleistocene on the ice-free Magdalen Is and subsequently spread to adjacent deglaciated coasts of New Brunswick and Prince Edward I (Hamilton 2002, fig. 2). This aster flowers after two to three months, as contrasted to its continental relatives *A. brachyactis* Blake and *A. frondosus* (Nutt.) T. & G. at six to eight months each (Houle and Haber 1990).

How hot was the PNW glacial age summer? East of the Rockies and south of the ice sheet, summer was much cooler than at present except in the far south (Brunnschweiler 1962). This was probably due to extensive cloud cover associated with increased precipitation. Prairie-like conditions ("periglacial grassland") existed only close to the ice front (Hamilton 1994b) where a permanent high pressure system over the glacier field suppressed summer rainfall. South of the PNW there is also evidence of reduced evaporation and increased precipitation: glacial-age Lake Bonneville completely filled the northwestern valley of UT to overflowing (it is now shrunk to Salt Lake). But, as in eastern North America, summer temperatures near the ice front may well have been close to spring temperatures today. Evidence for this in western North America comes from four endemic species (#80-82, 138) associated with the northern grasslands of the Peace River in AB, the upper Fraser River and on the Queen Charlotte Islands of BC. Such a suppression of rainfall is indicated by the distribution of loess in the PNW, which would have been driven from glacial moraines southward with strong winds off the ice sheet across treeless areas, and deposited where open vegetation (grasslands or open woodlands) broke the force of the wind. Major loess deposits on the Columbia basin as far south as the Blue Mountains of OR, and on the Snake River plains of ID, suggest the presence of open forests or grasslands there (Fig. 20).

Conversely, the numerous glacial-age lakes across UT, NV and southern OR show that these areas were cooler and wetter than at present. This belt must have been a zone of constant frontal activity between a stationary high-pressure system over the ice sheet, and a stationary low-pressure system over the semideserts of Arizona and New Mexico (Fig. 20). Between these two pressure systems the prevailing winds would have been driven from east to west, drawing moisture from the Gulf of Mexico northwestward towards UT. This would have constituted a real monsoon system, reversing the usual air flow patterns of the winter season.

Summary. At least nine PNW Pleistocene grasslands can be deduced. These are listed in descending importance as refuges for leafhoppers and planthoppers:

- (1) east slopes of the Cascade Range (Fig. 2C), from Washington state to northern California, with 27 endemics, two of which are sister species of Montana endemics;
- (2) Columbia basin (Fig. 2E) including Palouse hills of Washington and canyons of western Idaho, with 22 endemics, mostly with flightless females incapable of traversing deep canyons;
- (3) Rocky Mountains of Montana south to Colorado (Fig. 2J) where 19 endemics must have persisted on grassy south-facing slopes close to their present highly restricted ranges;
- (4) the Snake River and south-facing slopes north of the Snake River in southern Idaho (Fig.

- 2F) must have been grassland near the headwaters, as all 12 endemics are found in that end of the valley;
- (5) the Pacific coast, Mary's Peak (Fig. 5, triangle) and the Willamette Valley (Fig. 2B) west of the Cascade Range of Oregon have nine endemics;
 - (6) the Upper Clark Fork valley in western Montana (Fig. 2G) has six grassland endemics (including ones with flightless females) which must have survived the Pleistocene on the edges of glacial Lake Missoula;
 - (7) grassland patches along the upper Fraser and Peace rivers of BC have three endemics which are deep in glaciated areas and must have come from grasslands east of the Continental Divide (Fig. 2H, northern end); these and possibly a single widespread PNW species (#50) with a similar distribution along the Fraser and Peace rivers to the Mackenzie River are probably remnants of a periglacial grassland near the ice front in Alberta;
 - (8) the mountains of south-central OR (Fig. 2D) have two endemics; and
 - (9) the coast of the Queen Charlotte Islands (Fig. 2, star) has a single endemic grassland leafhopper. Other grasslands on islands further south (Fig. 2A) were repopulated by hypsithermal invasion.

Additional refugia might have been in the mountains of Utah and adjacent Wyoming, but these may have been further southwards.

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FAUNAL SYNOPSIS AND INDEX

to species numbered in text

(*) indicates taxa of probable post-glacial origin

CALISCELIDAE

Bruchomorpha beameri Doer. #1 (prairie)

CICADELLIDAE

Acinopterus viridis Van Duz. prairie

Amblysellus grex (Oman) southern

A. wyomus Kramer #2 (prairie)

Athysanella acuticauda (Bak.) **northern**

A. attenuata Baker #3 (prairie)

A. castor Hamilton #83 (MT)

A. expulsa Blocker #45 (OR)

A. gardenia Osborn #140 (CO-WY)

A. hyperoche Hamilton #141 (WY)

A. nielsoni Blocker #84 (ID)

A. obesa Ball & Beamer #4 (prairie)

A. obscura Johnson #152 (UT-WY)

A. occidentalis megacauda H. #32 (PNW)

A. repulsa Hamilton #46 (MT)

A. robusta Baker #5 (prairie)

A. terebrans (Gillette & Bak.) #6 (prairie)

A. strobila Blocker southern

A. utahna Osborn prairie

A. valla Blocker and Johnson #133 (OR)

Attenuipyga omanae (Beamer) #53 (PNW)

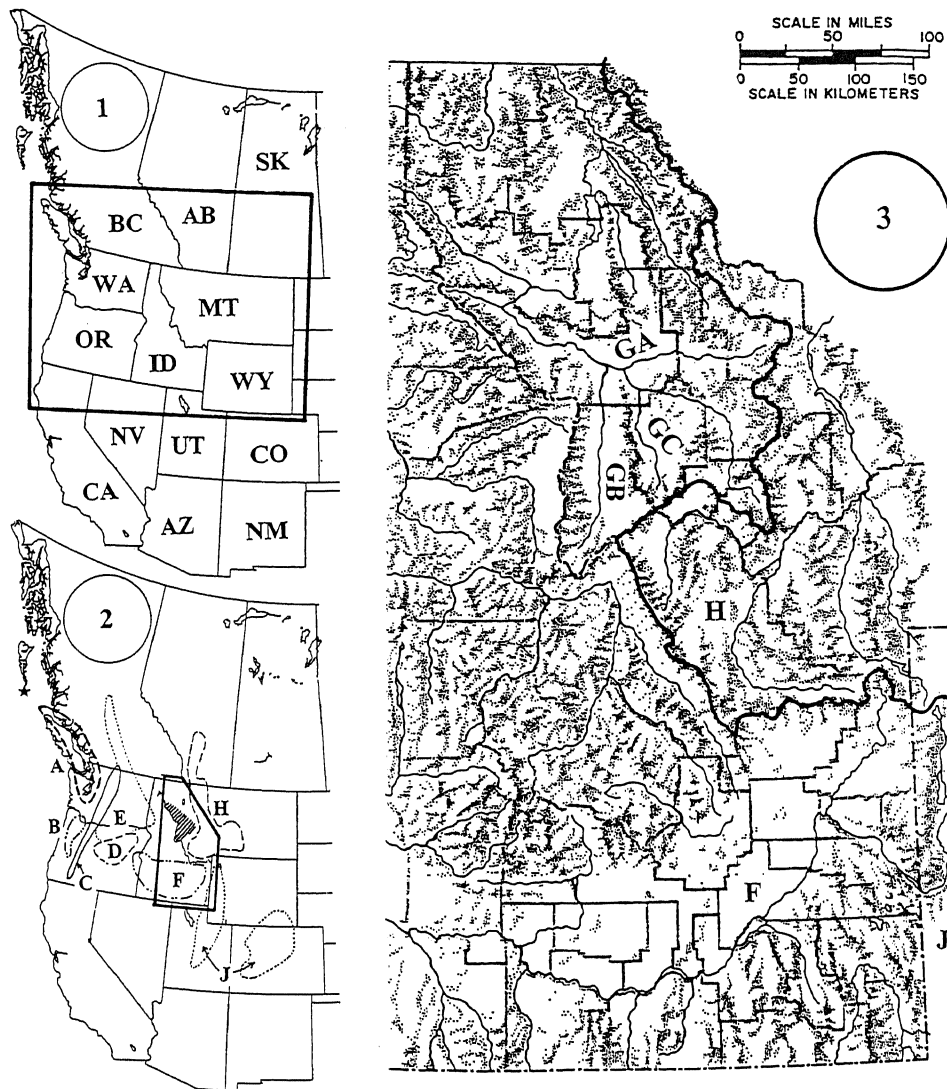
A. platyrhynchus setosa Om. #33 (PNW)

Auridius auratus (Gill. & Bak.) prairie

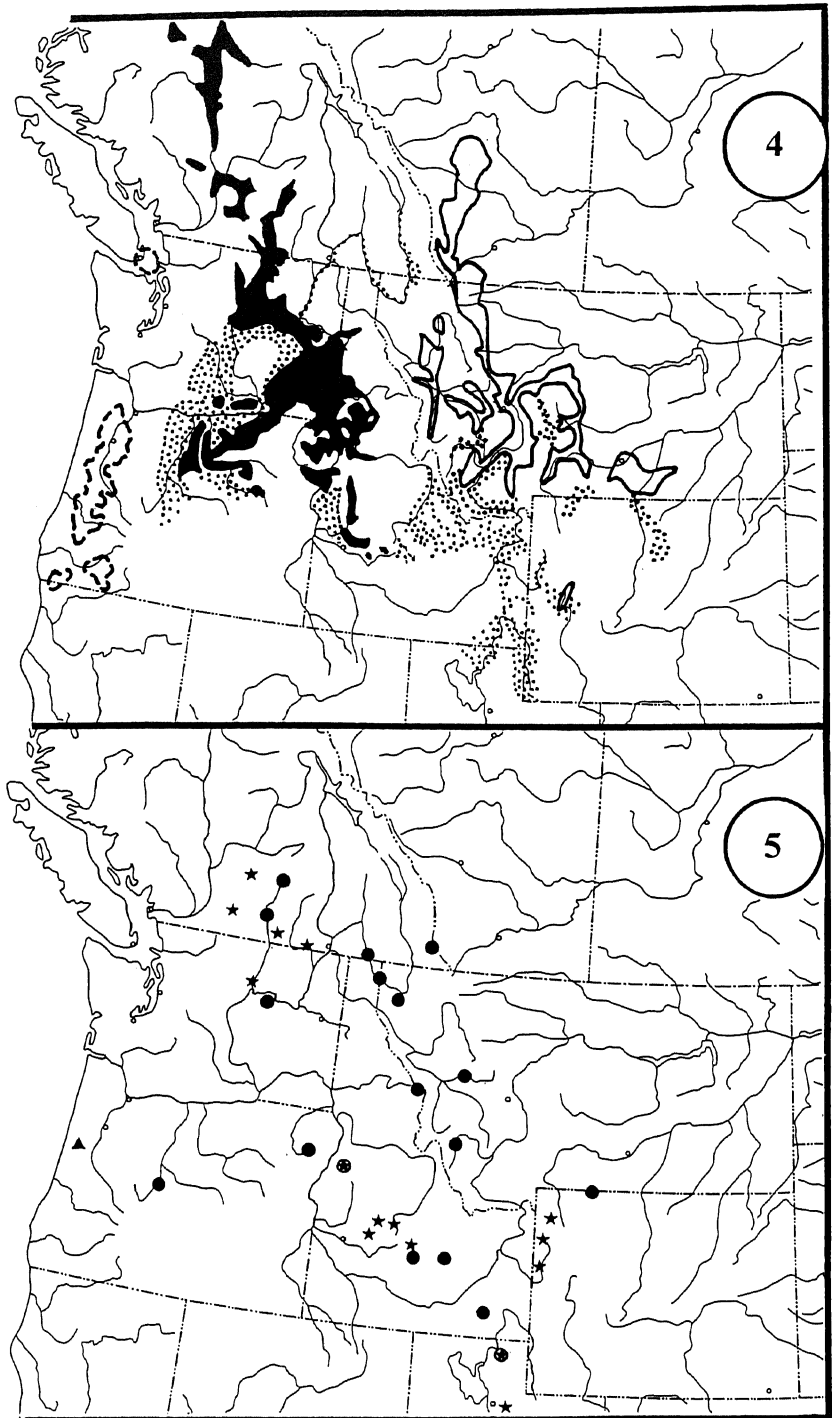
- A. cosmeticus* Hamilton #47 (MT)
A. helvus (DeLong) #7 (prairie)
A. ordinatus (Ball) #8 (prairie)
A. o. crocatus Hamilton #34 (PNW)
A. safra Hamilton #54 (PNW)
A. vitellinus Hamilton #48 (OR)
Balclutha confluens (Rey) **northern**
B. manitou (Gillette & Baker) **northern**
B. neglecta DeLong & Dav.) prairie
B. punctata (Fabricius) **northern**
Ballana spp. (11) southern
B. atridorsum (Van Duzee) prairie
B. chrysothamna DeLong ? (ID)
B. curvidens DeLong ? (ID)
B. ortha DeLong prairie
B. spinosa DeLong ? (ID-OR)
Carsonus aridus (Ball) southern
C. furcatus (Oman) southern
C. irroratus (Ball) southern
Ceratagallia acerata Ham. #97 (OR)
C. arida (Oman) #9 (prairie)
C. artemisia Oman southern
C. californica (Baker) southern
C. clino Hamilton #98 (OR)
C. gallus Hamilton #55 (ID-UT)
C. lophia Hamilton #99 (OR)
C. nanella zacki Hamilton #35 (BC-WA)
C. okanagana Hamilton #77 (BC)
C. robusta poudris (Oman) southern
C. omani Hamilton #134 BC/OR)
C. siccifolia (Uhler) **northern**
C. siccifolia compressa H. #36 (PNW)
C. vipera Hamilton #115 (WA)
C. viator Hamilton #10 (prairie)
C. vulgaris (Oman) #11 (prairie)
Chlorotettix similis DeLong #56 (BC/ID/
OR)
Colladonus aureolus (Van D.) southern
Commellus sexvittatus (V. D.) prairie
Cuerna cuesta Hamilton #78 (BC-MT-
WA)
Deltocephalus artemisiae
Gillette & Baker prairie
D. fuscineruosus Van Duzee southern
D. minutus Van Duzee southern
D. vanduzeei Gillette & Baker ? (PNW)
D. vanfus Kramer southern
Diplocolenus brevior R. & H. **northern**
D. configuratus (Uhler) #13 (prairie)
D. c. bicolor Hamilton #85 (ID-MT-
WY)
D. c. nigrior Ross & Hamilton #142 (AZ-ID)
D. evansi (Ashmead) **northern**
Draeculacephala bivoltina H. southern
D. borealis orea Hamilton ? (PNW)
D. crassicornis Van Duzee ? (PNW)
- D. robinsoni* Hamilton **northern**
Elymana circius Hamilton #14 (prairie)
Endria inimica (Say) prairie
E. montana (DeLong & Sl.) #57 (PNW)
Errhomus affinis Oman #100 (ID)
E. affinis attenuatus Hamilton #101 (OR)
E. braccatus Hamilton #93 (MT)
E. brevis Oman #116 (WA)
E. brevis simcoe Oman #117 (WA)
E. calvus Oman #118 (BC-
WA)
E. camensis Hamilton #94 (MT)
E. josephi Oman #102 (OR-
WA)
E. lineatus (Baker) #58 (WA)
E. lineatus cordatus Hamilton #103 (ID)
E. lineatus idahoensis Oman #104 (ID)
E. lineatus umatilla Oman #105 (OR)
E. montanus (Baker) #143 (CO/
MT-WY)
E. naomi Hamilton #159 (UT)
E. ochoco Oman #106 (OR)
E. pallidus Oman #107 (OR)
E. paradoxus Oman #119 (WA)
E. picturatus Hamilton #120 (WA)
E. praedictus Hamilton #121 (WA)
E. reflexus Oman #122 (WA)
E. rivalis Hamilton #95 (MT)
E. satus Oman #123 (WA)
E. serratus Oman #108 (OR)
E. s. instabilis Oman #124 (WA)
E. s. obliteratedus Hamilton #125 (WA)
E. similis Oman #126 (WA)
E. s. confinis Oman* #126 (WA)
E. s. dubiosus Oman* #59 (WA)
E. s. kahlotus Oman #59 (WA)
E. s. medialis Oman #109 (OR)
E. s. minutus Oman* #109 (OR)
E. s. nanus Oman* #109 (OR)
E. s. relativus Oman* #126 (WA)
E. s. sobrinus Oman #127 (WA)
E. s. socius Oman #128 (WA)
E. s. truncus Oman* #109 (OR)
E. s. zonarius Oman #129 (WA)
E. solus Oman #96 (MT)
E. variabilis Oman #130 (WA)
E. v. erratus Hamilton #110 (OR)
E. v. gracilis Hamilton #111 (ID)
E. v. mimicus Hamilton #112 (OR)
E. wolfei Oman #131 (WA)
E. winquatt Oman #113 (OR)
Euscelis relativa (Gill. & B.) **northern**
Evacanthus lacunar Hamilton #135 (OR)
Flexamia decora Beam. & T. #12 (prairie)
F. inflata (Osborn & Ball) prairie
F. serrata Beamer & Tuthill prairie

| | | | |
|---------------------------------------|--------------------|--|--------------------|
| <i>Frigartus frigidus</i> (Ball) | prairie | <i>N. curvata</i> Lindsay | #156 (WY) |
| <i>Gyponana hasta</i> DeLong | southern | <i>N. perelegantis</i> (Ball) | southern |
| <i>Hardya dentata</i> (Osborn & B.) | prairie | <i>N. rubida</i> (Ball) | #70 (PNW) |
| <i>Hebecephalus abies</i> Hamilton | #153 (UT) | <i>N. saucia</i> (Ball) | #147 (CO) |
| <i>H. caecus</i> Beamer | #60 (ID/OR) | <i>N. vermiculata</i> Lindsay | #71 (ID/CO) |
| <i>H. callidus</i> (Ball) | #61 (PNW) | <i>Orocistus hyalinus</i> (Beamer) | #148 (CO) |
| <i>H. chandleri</i> Hamilton | #144 (WY) | <i>O. labeculus</i> (DeLong) | #19 (prairie) |
| <i>H. crassus</i> (DeLong) | #62 (BC/ ID-WY) | <i>O. pinnipenis</i> Ross & H. | #72 (ID-MT) |
| <i>H. crenulatus</i> Hamilton | #86 (ID) | <i>O. perpussillus</i> (Ball & DeL.) | #20 (prairie) |
| <i>H. ferrumequinum</i> Hamilton | #87 (ID) | <i>O. tener</i> (Beamer & Tuthill) | southern |
| <i>H. filamentus</i> Hamilton & R. | #154 (ID) | <i>Paluda gladiola</i> (Ball) | northern |
| <i>H. firmus</i> Beamer | #63 (WA/ MT-WY) | <i>Paraphlepsius lascivius</i> (Ball) | prairie |
| <i>H. hilaris</i> Beamer | #64 (WA/WY) | <i>P. occidentalis</i> (Baker) | southern |
| <i>H. occidentalis</i> Beamer & T. | prairie | <i>Pinumius sexmaculatus</i> (Gillette & Baker) | #21 (prairie) |
| <i>H. planaria</i> Hamilton | #79 (BC) | <i>Prairiana kansana</i> (Ball) | #22 (prairie) |
| <i>H. picea</i> Hamilton | #88 (ID) | <i>Psammotettix amplus</i> (D. & D.) | southern |
| <i>H. pugnus</i> Hamilton | #89 (ID) | <i>P. attenuens</i> (DeLong & D.) | #73 (PNW) |
| <i>H. rostratus</i> Beamer & Tut. | prairie | <i>P. beirnei</i> Greene | #37 (BC) |
| <i>H. sagittatus</i> Beamer & Tut. | #65 (PNW) | <i>P. dentatus</i> Knull | southern |
| <i>H. truncatus</i> Beamer & Tut. | prairie | <i>P. diademata</i> Hamilton | #138 (BC) |
| <i>H. veretillum</i> Hamilton | #90 (ID) | <i>P. greenei</i> Hamilton | #114 (OR) |
| <i>H. vinculatus</i> Ball | #145 (CO) | <i>P. lividellus</i> (Zetterstedt) | northern |
| <i>Hecalus montanus</i> (Ball) | northern | <i>P. nesiotus</i> Hamilton | #139 (BC) |
| <i>H. viridis</i> (Uhler) | prairie | <i>P. obesus</i> Knull | southern |
| <i>Idiodonus heidemanni</i> (Ball) | #15 (southern) | <i>P. shoshone</i> (DeLong & Dav.) | southern |
| <i>I. josea</i> (Ball) | #146 (CO/MT) | <i>P. totalis</i> (DeLong & Dav.) | #23 (ID- MT-WY) |
| <i>Laevicephalus salarius</i> Knull | ? (BC/UT) | <i>P. viridinervis</i> Ross & H. | #149 (WY) |
| <i>Latalus curtus</i> Beamer & Tut. | #67 (PNW) | <i>Rosenus cruciatus</i> (Osborn & Ball) | #24 (prairie) |
| <i>L. histrionicus</i> Beirne | #49 (BC/AZ) | <i>R. decurvatus</i> Hamilton & R. | #80 (BC) |
| <i>L. intermedius</i> Ross & H. | #50 (PNW) | <i>R. obliquus</i> (DeLong & Dav.) | #92 (ID) |
| <i>L. missellus</i> (Ball) | northern | <i>Scaphytopius diabolus</i> (Van Duzee) | southern |
| <i>L. mundus</i> Beamer & Tuthill | #68 (PNW) | <i>S. oregonensis</i> (Baker) | southern |
| <i>L. occidentalis</i> (DeLong) | #136 (OR) | <i>Sorhoanus bimaculatus</i> (Gillette & Baker) | northern |
| <i>Lebradea flavovirens</i> (G. & B.) | northern | <i>S. debilis</i> (Uhler) | #51 (PNW) |
| <i>Limotettix beameri</i> (Medler) | #137 (OR/WA) | <i>S. involutus</i> Hamilton | #150 (CO) |
| <i>Limotettix bullatus</i> (Ball) | southern | <i>S. uhleri</i> (Oman) | northern |
| <i>L. finitimus</i> (Van Duzee) | southern | <i>S. virilis</i> Hamilton | #52 (OR) |
| <i>L. glomerosus</i> (Ball) | southern | <i>S. xiphosura</i> Hamilton | #74 (PNW) |
| <i>L. symphoricarpae</i> (Ball) | prairie | <i>Stenometopiellus vader</i> Ham. | #37 (ID-MT) |
| <i>L. zacki</i> Hamilton | #132 (WA) | <i>Stragania atra</i> (Baker) | prairie |
| <i>Lonatura salsura</i> (Ball) | prairie | <i>S. rufoscutellata</i> (Baker) | prairie |
| <i>Lystridea uhleri</i> Baker | southern | <i>Texananus cumulatus</i> (Ball) | southern |
| <i>Mesamia frigida</i> (DeL. & H.) | southern | <i>T. dolus</i> DeLong | prairie |
| <i>M. ludovicica</i> Ball | #16 (prairie) | <i>T. extremus</i> (Ball) | southern |
| <i>Mocuellus caprillus</i> Ross & H. | #17 (prairie) | <i>T. lathropi</i> (Baker) | southern |
| <i>M. c. anfractus</i> Hamilton | #91 (ID) | <i>T. latipex</i> (DeLong) | southern |
| <i>M. c. strictus</i> Ross & H. | northern | <i>T. oregonus</i> (Ball) | southern |
| <i>M. larrimeri</i> (DeLong) | #69 (PNW) | <i>T. proximus</i> Crowder | southern |
| <i>M. quinquespinus</i> Hamilton | #155 (UT) | <i>Twiningia fasciatus</i> (Beamer) | southern |
| <i>Norvellina clarivida</i> (Van D.) | #18 (prairie) | <i>T. pellucidus</i> (Ball) | southern |
| <i>N. columbiana</i> (Ball) | prairie | <i>T. scrupulosus</i> (Ball) | southern |
| | | <i>Unoka dramatica</i> Hamilton | #39 (BC) |

| | | | |
|---|-----------------|---|-----------------|
| <i>U. gillettei</i> Metcalf | #25 (prairie) | <i>Laccocera canadensis</i> Beirne | #26 (prairie) |
| <i>Xerophloea zionis</i> Lawson | southern | <i>L. flava</i> Crawford | #29 (prairie) |
| DELPHACIDAE | | | |
| <i>Achorotile apicata</i> Hamilton | #157 (UT) | <i>Laccocera lineata</i> Scudder | prairie |
| <i>Caenodelphax atridorsum</i> (Beamer) | #75 (MT/OR) | <i>L. oregonensis</i> Penner | #42 (PNW) |
| <i>Delphacodes anufrievi</i> Wils. | northern | <i>L. vanduzeei</i> Penner | #43 (PNW) |
| <i>D. gillettei</i> (Van Duzee) | southern | <i>L. vittipennis</i> Van Duzee | #30 (prairie) |
| <i>D. lineatipes</i> (Van Duzee) | northern | <i>Megamelanus bicolor</i> Ball | southern |
| <i>D. neoclusa</i> Muir & Gifford | southern | <i>Nothodelphax foveatus</i> (Van Duzee) | #31 (prairie) |
| <i>D. occlusa</i> (Van Duzee) | southern | <i>N. glacia</i> Wilson | northern |
| <i>Elachodelphax mazama</i> Ham. | #40 (WA) | <i>N. venustus</i> (Beamer) | #44 (PNW) |
| <i>E. pediformis</i> (Beamer) | #27 (prairie) | <i>Parkana alata</i> Beamer | southern |
| <i>E. unita</i> Hamilton | #158 (UT) | <i>Paraliburnia furcata</i> Hamilton | #81 (BC) |
| <i>Eurybregma eurytion</i> Ham. | #41 (PNW) | <i>P. kilmani</i> (Van Duzee) | northern |
| <i>E. magnifrons</i> (Crawford) | #27 (PNW) | <i>P. lecartus</i> Hamilton | #82 (BC) |
| <i>Javesella lutulentella</i> (Muir & Gifford) | southern | <i>Pissonotus frontalis</i> (Crawford) | southern |
| <i>Kosswigianella irrutilo</i> Ham. | #151 (CO) | <i>P. rubrilatus</i> Morgan & B. | #76 (PNW) |
| <i>K. wasatchi</i> Hamilton | #160 (UT) | <i>Prokelisia carolae</i> Wilson | southern |
| | | <i>P. salina</i> (Ball) | prairie |



Figures 1-3. Distribution of Pacific Northwest grasslands and widespread endemic leafhoppers. 1, provinces and states of the Pacific Northwest (boxed area); 2-3, geographical areas of PNW grasslands, with ID/MT border (box) enlarged to show Clark Fork valley system (shaded in Fig. 2, GA-GC in Fig. 3). Bold line: continental divide indicated by dividing area H (prairies) from areas F (Snake River plains) and G (Clark Fork valley); grey lines: county boundaries. For abbreviations, see text.



Figures 4-5. Distribution of types of PNW grasslands (4) and leafhoppers (5). Black, Palouse grasslands; stippled, grassland-sagebrush ecotone; outline, fescue grasslands; dashed outline, oak savannah; filled triangle, *Evacanthus lacunar* on Mary's Peak; filled circle, *Norvellina rubida*; star, *Sorhoanus xiphosura*.

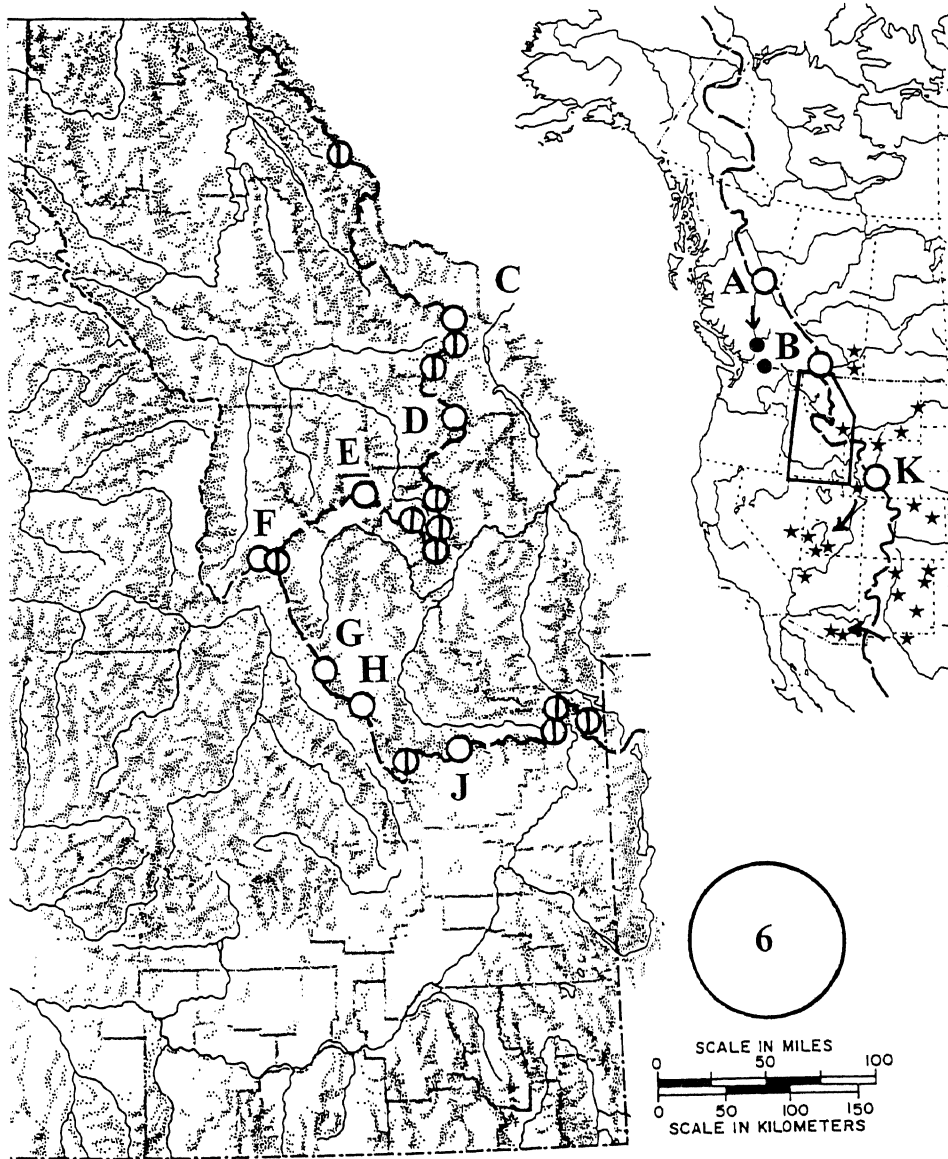


Figure 6. Distribution of *Unoka gillettei* (stars) and *U. dramatica* (filled circles) west of 101°W, showing invasion of montane area across Pacific continental divide (dashed line). Major passes from British Columbia to Wyoming (circles), from N to S: A, "Crooked River Pass," BC; B, Crowsnest Pass, BC/AB; (continued in detail) C, Rogers, MT (1800 m); D, MacDonald Pass; E, "Grassy Pass", MT; F, Lost Trail Pass, ID/MT; G-H, Lemhi and Bannock passes, ID/MT; J, Monida Pass, ID/MT; K, Great Basin Divide, WY. Open circles represent most important passes for leafhopper dispersal; split circles, other passes.

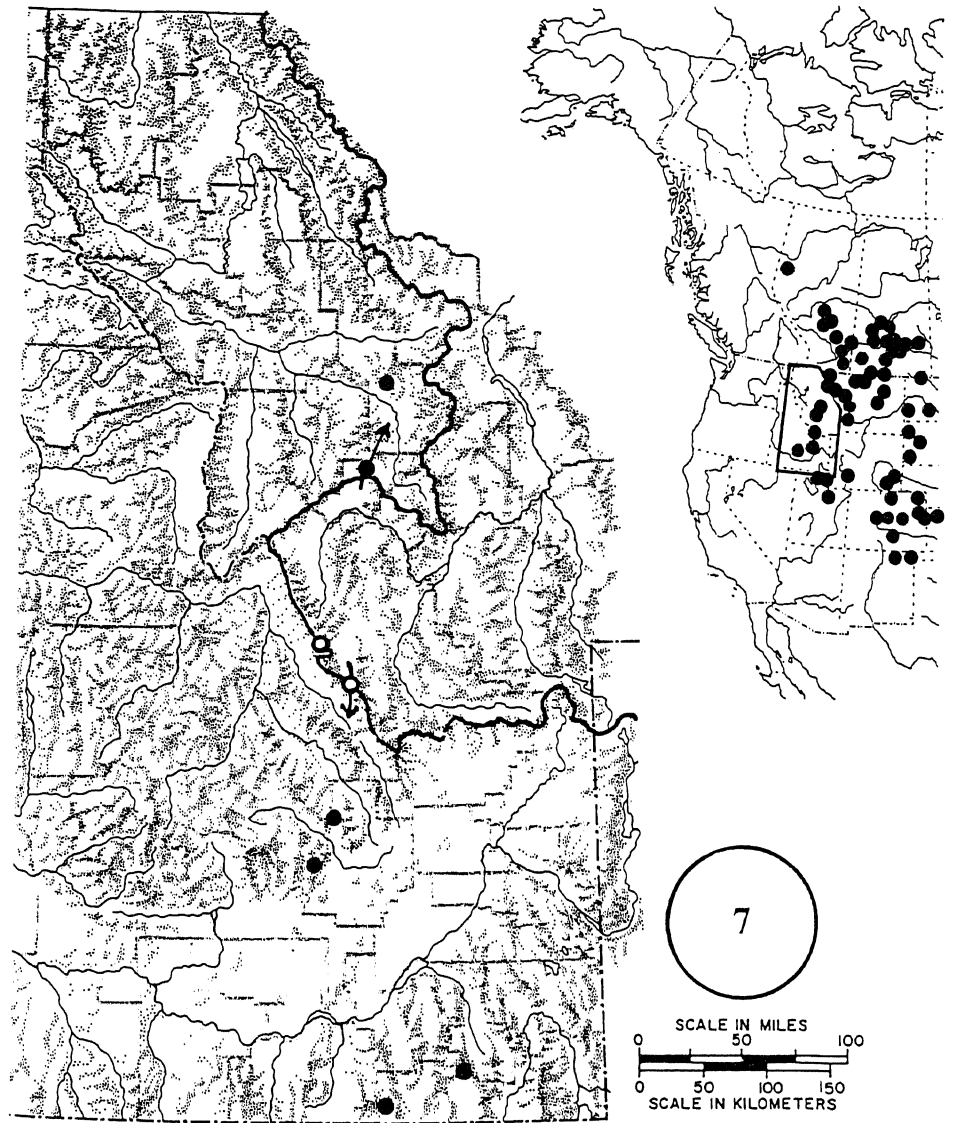


Figure 7. Distribution of the leafhopper *Athysanella attenuata* west of 101°W . Box, area of detail; solid line, continental divide; open circles, dispersal routes across Lemhi and Bannoch passes.

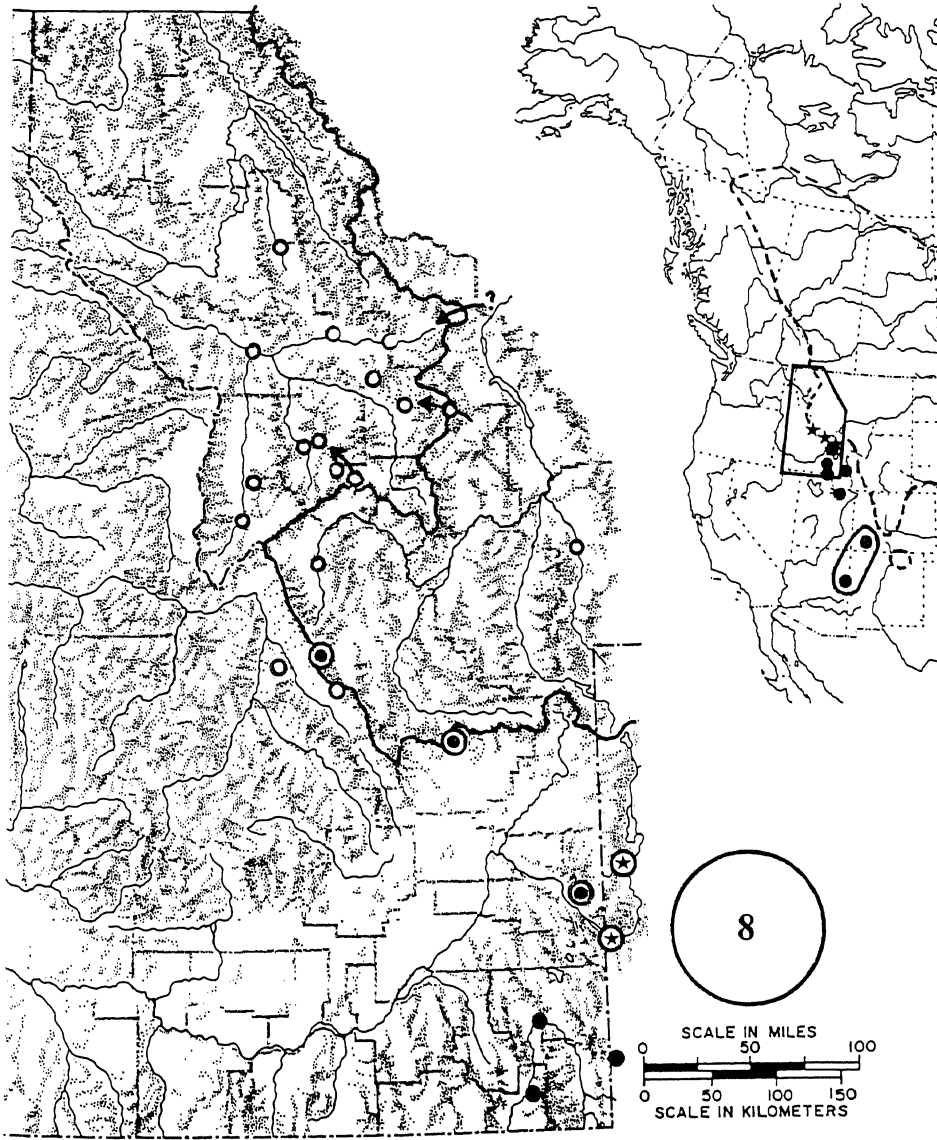


Figure 8. Distribution of the leafhoppers *Diplocolenus configuratus* (dashed line and open circle), *D. configuratus bicolor* (star) and *D. configuratus nigrrior* (filled circle) west of 101°W. Box, area of detail; oval, populations confined to mountains; bull's eye, hybrid populations.

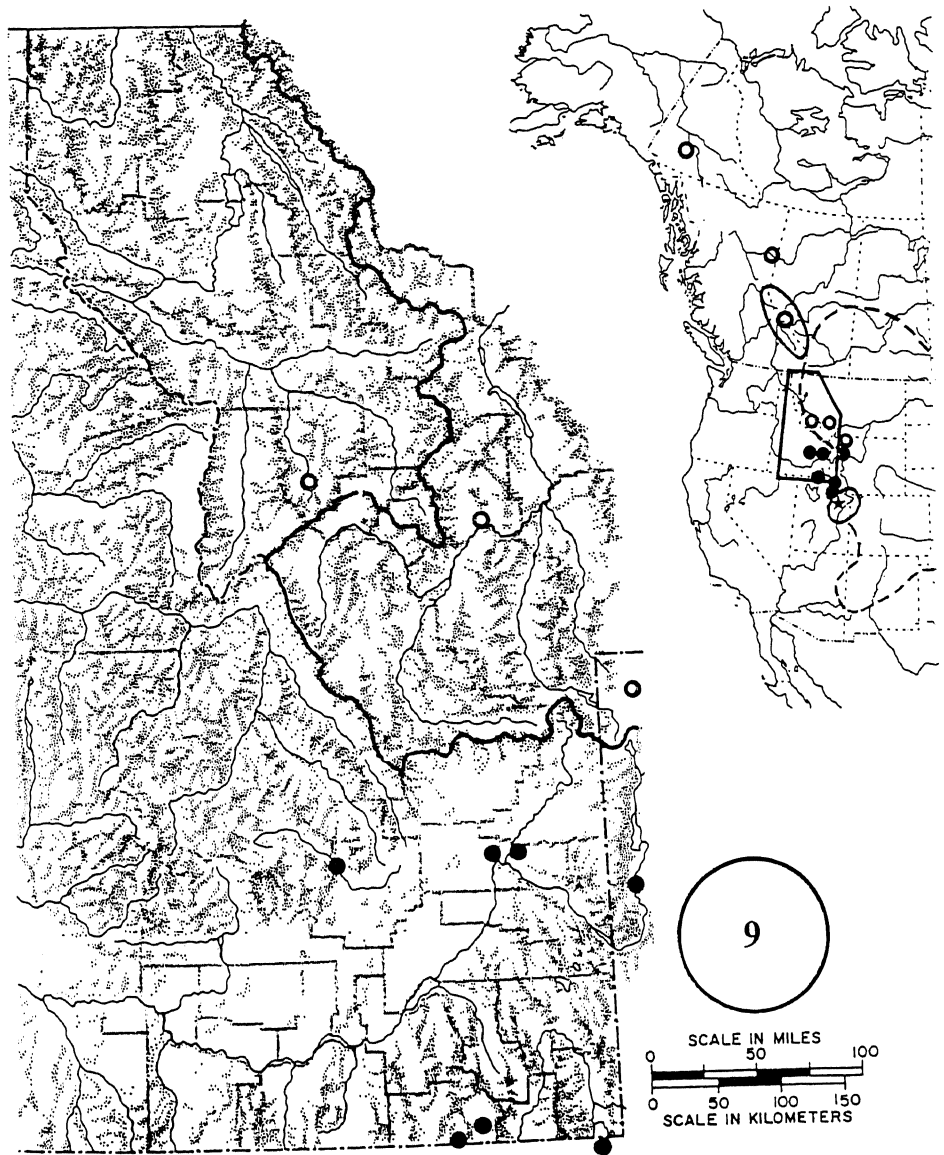


Figure 9. Distribution of the leafhoppers *Mocuellus quinquespinus* (star), *M. caprillus* (dashed line), *M. caprillus anfractus* (filled circles) and *M. caprillus strictus* (open circles). Box, area of detail; ovals, populations confined to mountains; arrows, inferred dispersal route across Lemhi and "Grassy Pass."

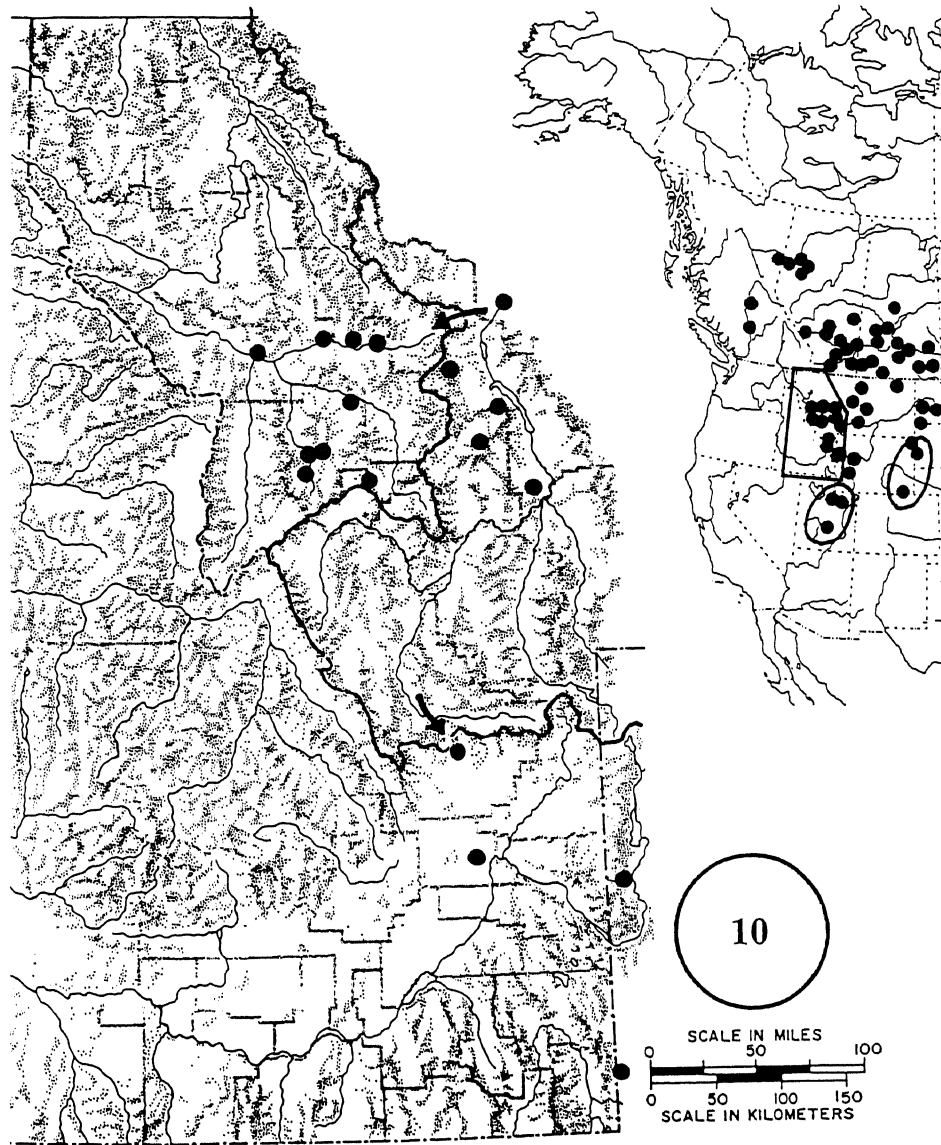


Figure 10. Distribution of the leafhopper *Orocastus perpusillus* west of 101°W. Box, area of detail; ovals: southern populations confined to mountains; arrows, inferred dispersal route across Rogers and Monida passes.

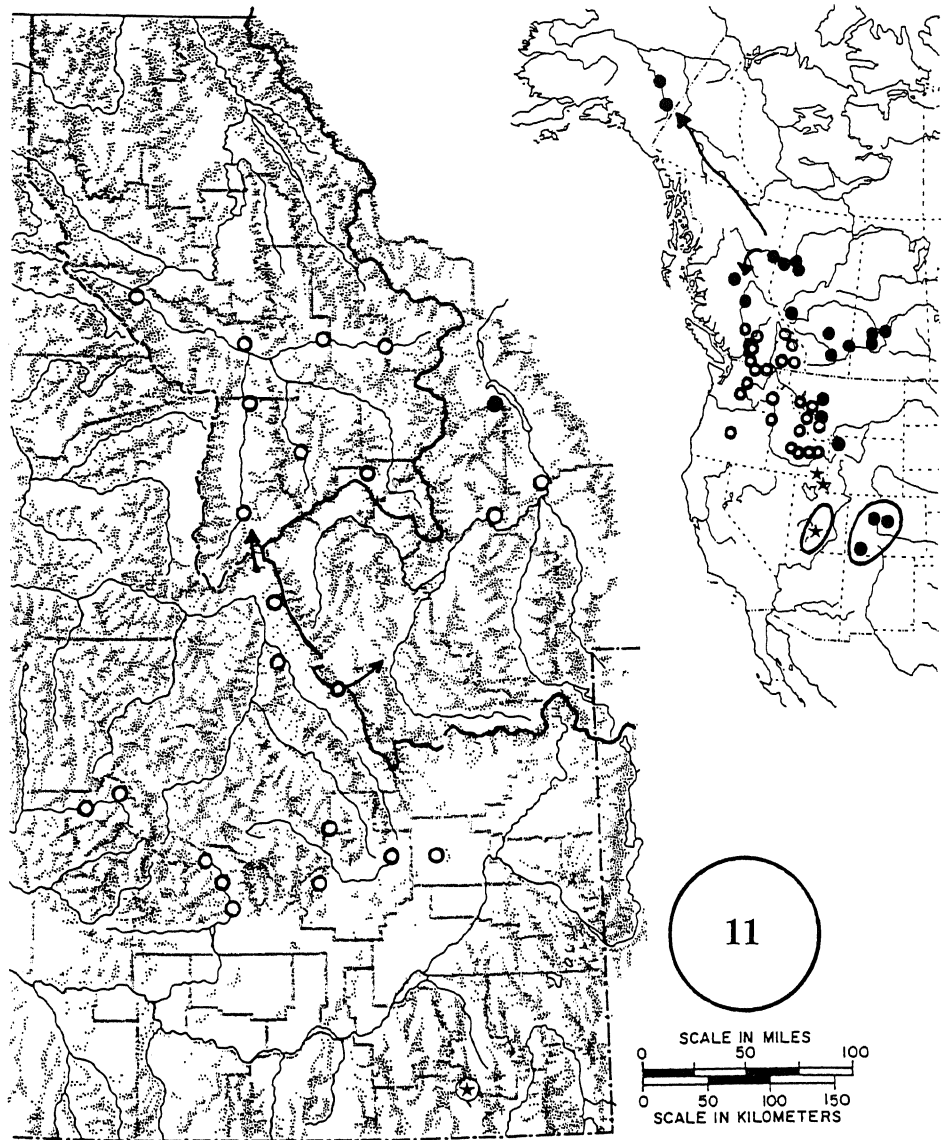


Figure 11. Distribution of the planthoppers *Eurybregma eurytion* (open circles) and *Eurybregma magnifrons* (filled circles). Ovals, populations confined to mountains; arrows, inferred dispersal routes.

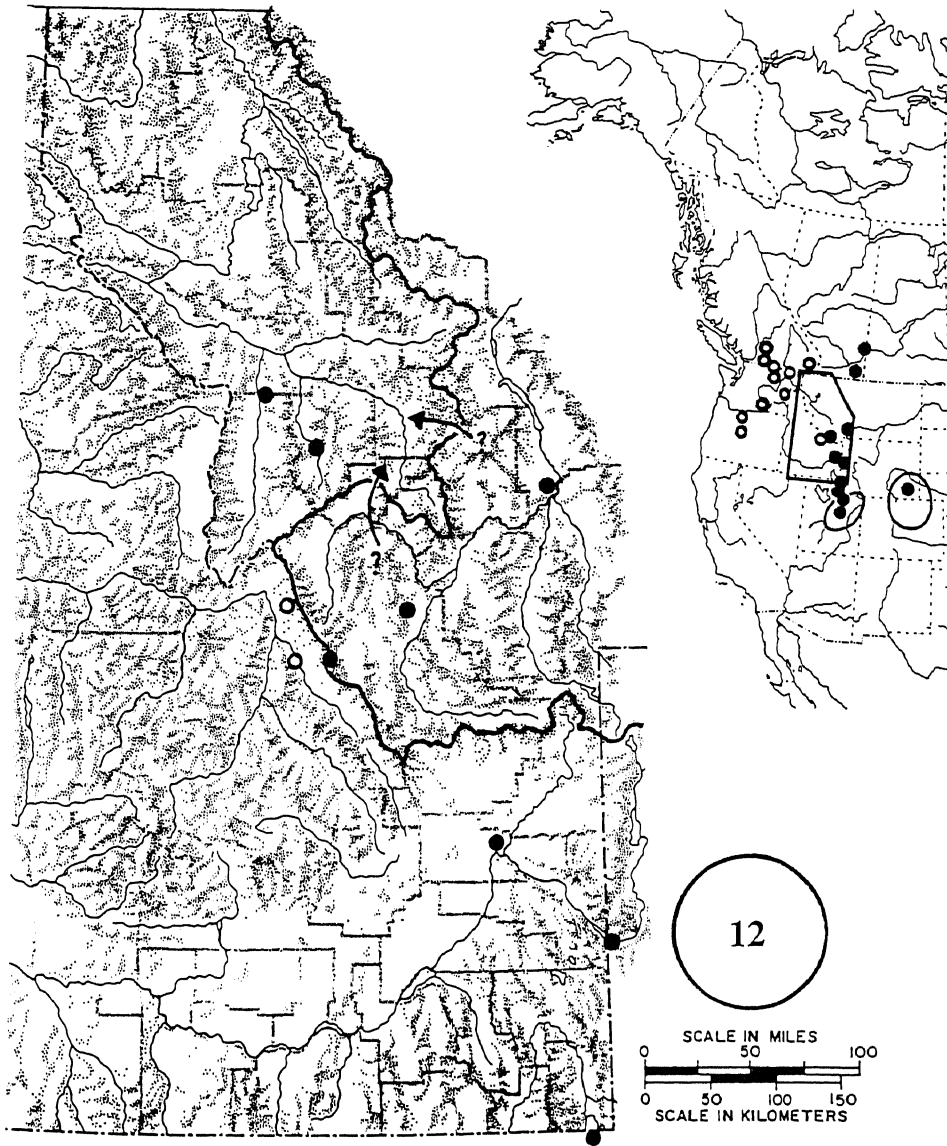


Figure 12. Distribution of the planthoppers *Laccocera oregonensis* (open circles) and *Laccocera flava* (filled circles). Box, area of detail; ovals, populations confined to mountains; arrows, inferred dispersal route across MacDonald or "Grassy Pass."

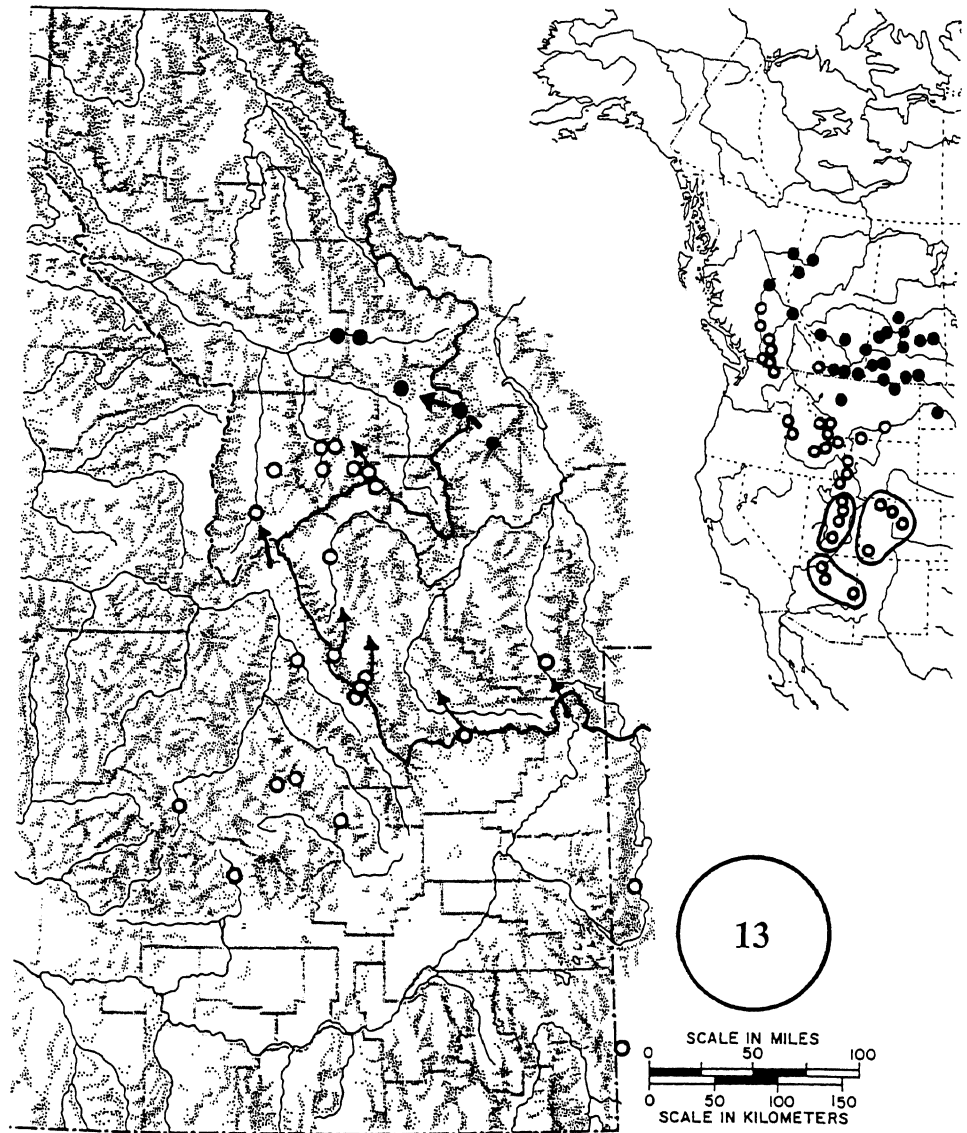


Figure 13. Distribution of the planthoppers *Laccocera* spp. (*vittipennis* group) west of 101°W. Open circles, *L. vanduzeei*; filled circles, *Laccocera vittipennis*; outlines, populations confined to mountains; arrows, inferred dispersal route across MacDonal, "Grassy Pass", Lost Trail, Lemhi, Bannock, Monida and Reynolds passes.

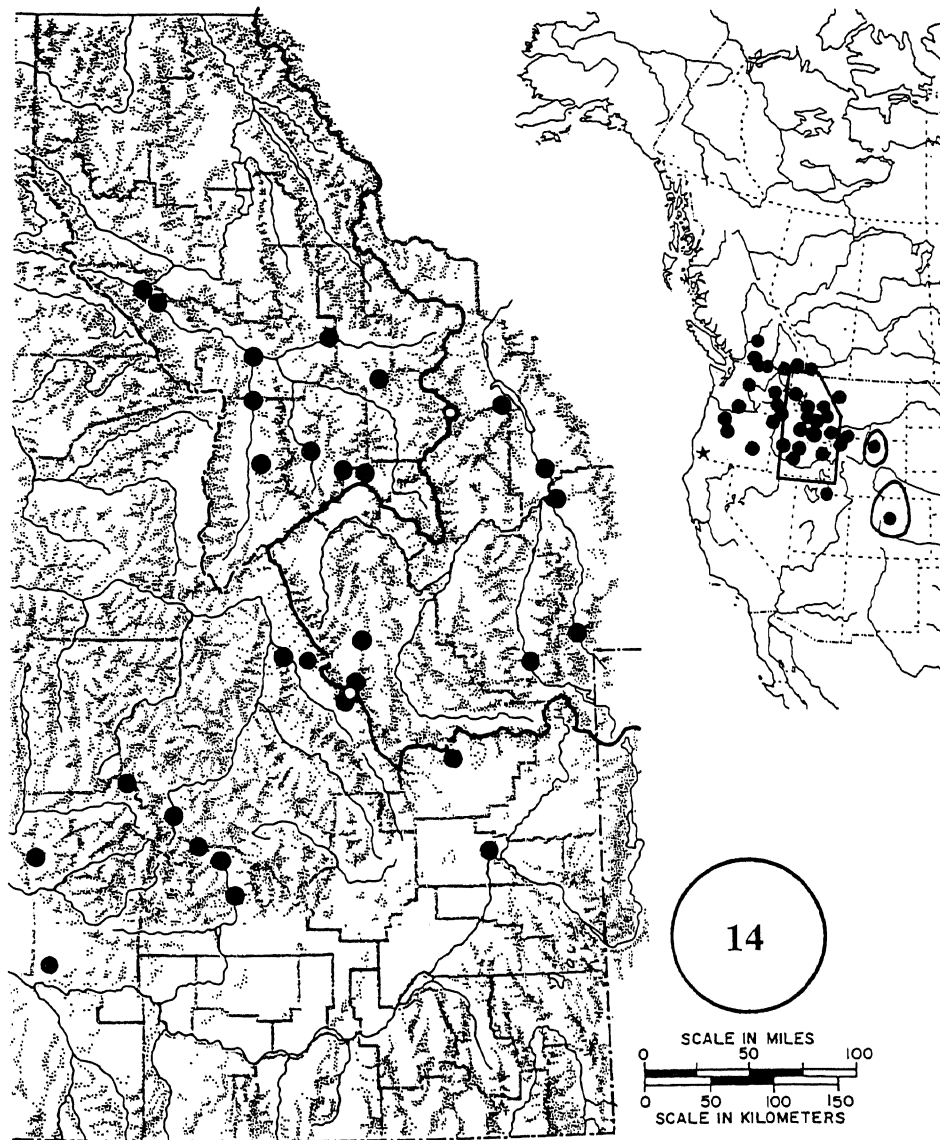


Figure 14. Distribution of the leafhoppers *Sorhoanus debilis* (circles) and *Sorhoanus virilis* (star). Box: area of detail; ovals: populations confined to mountains; open circle, sample from pass.

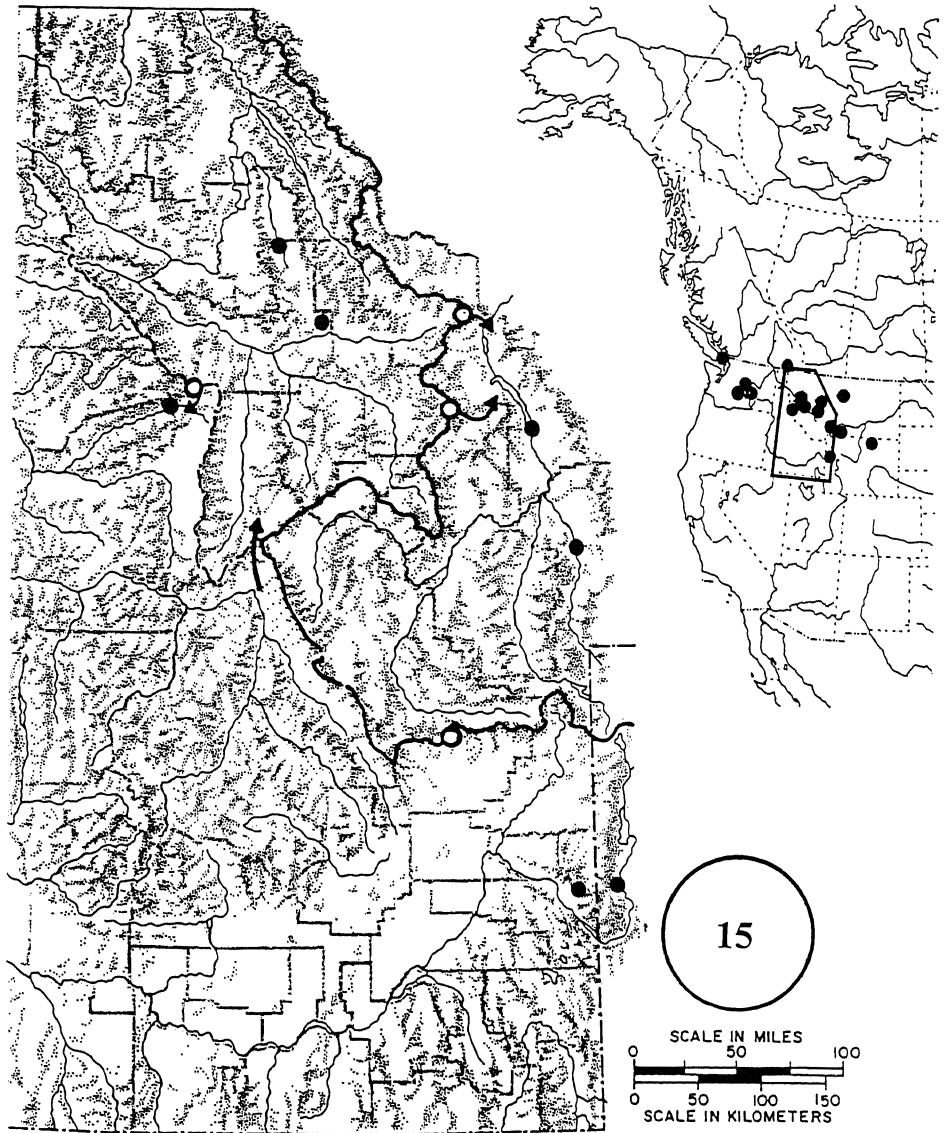


Figure 15. Distribution of the leafhopper *Endria montana*. Box, area of detail; arrows, inferred dispersal route across Lost Trail, Lolo, Rogers and MacDonald passes (open circles).

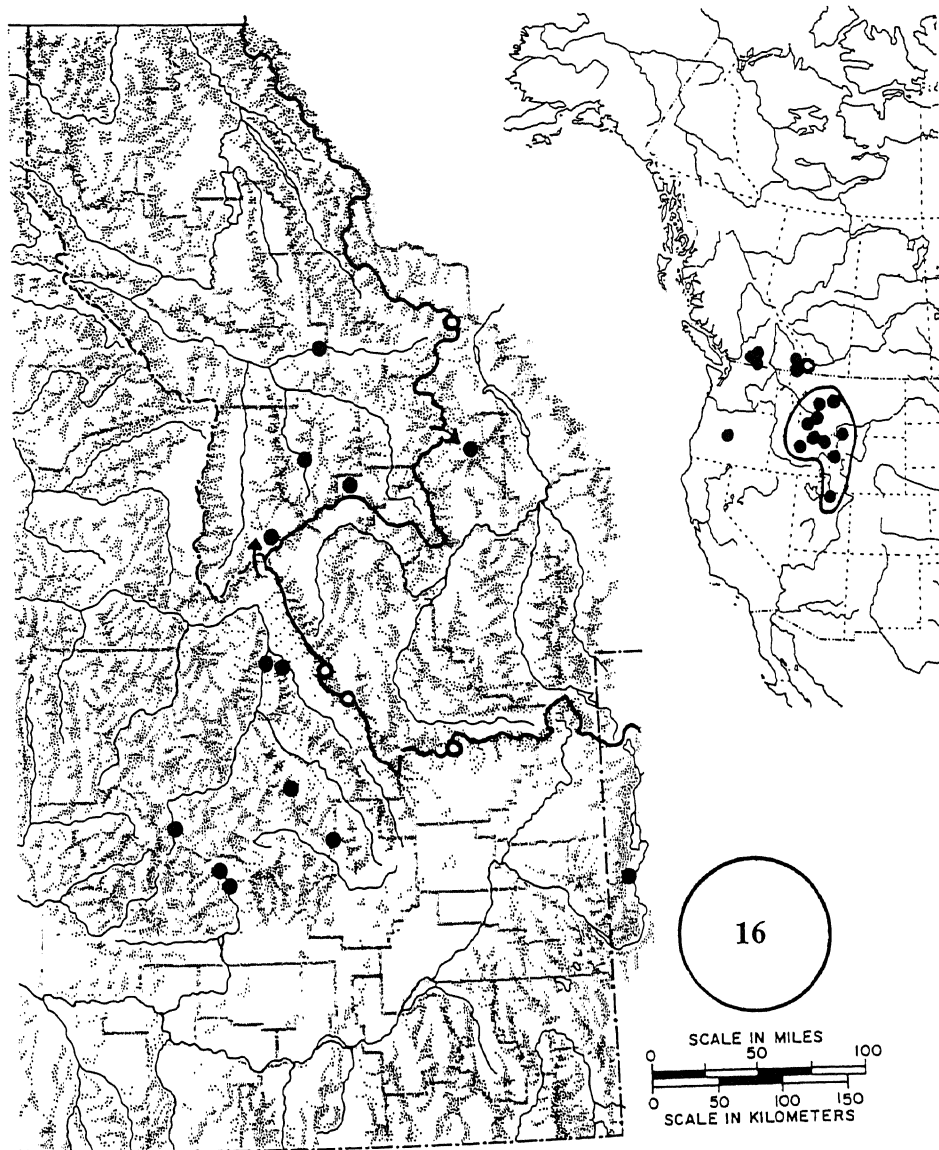


Figure 16. Distribution of the leafhopper *Orocastus pinnipenis*. Outline, eastern populations confined to mountains; open circles, taken in passes; arrows, inferred dispersal routes through Lost Trail and MacDonald passes.

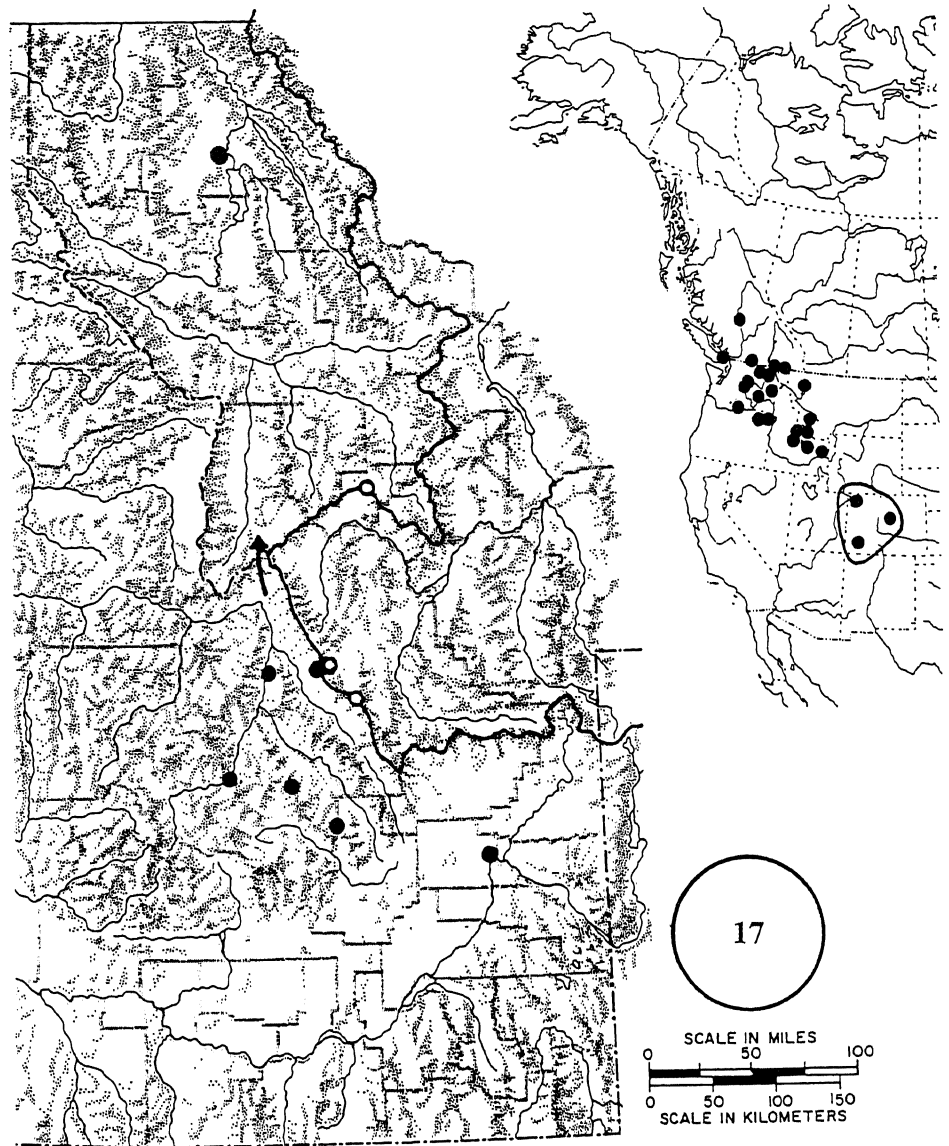


Figure 17. Distribution of the leafhopper *Psammotettix attenuens*. Outline, populations confined to mountains; open circles, samples taken in passes; arrow, inferred dispersal route through Lost Trail Pass.

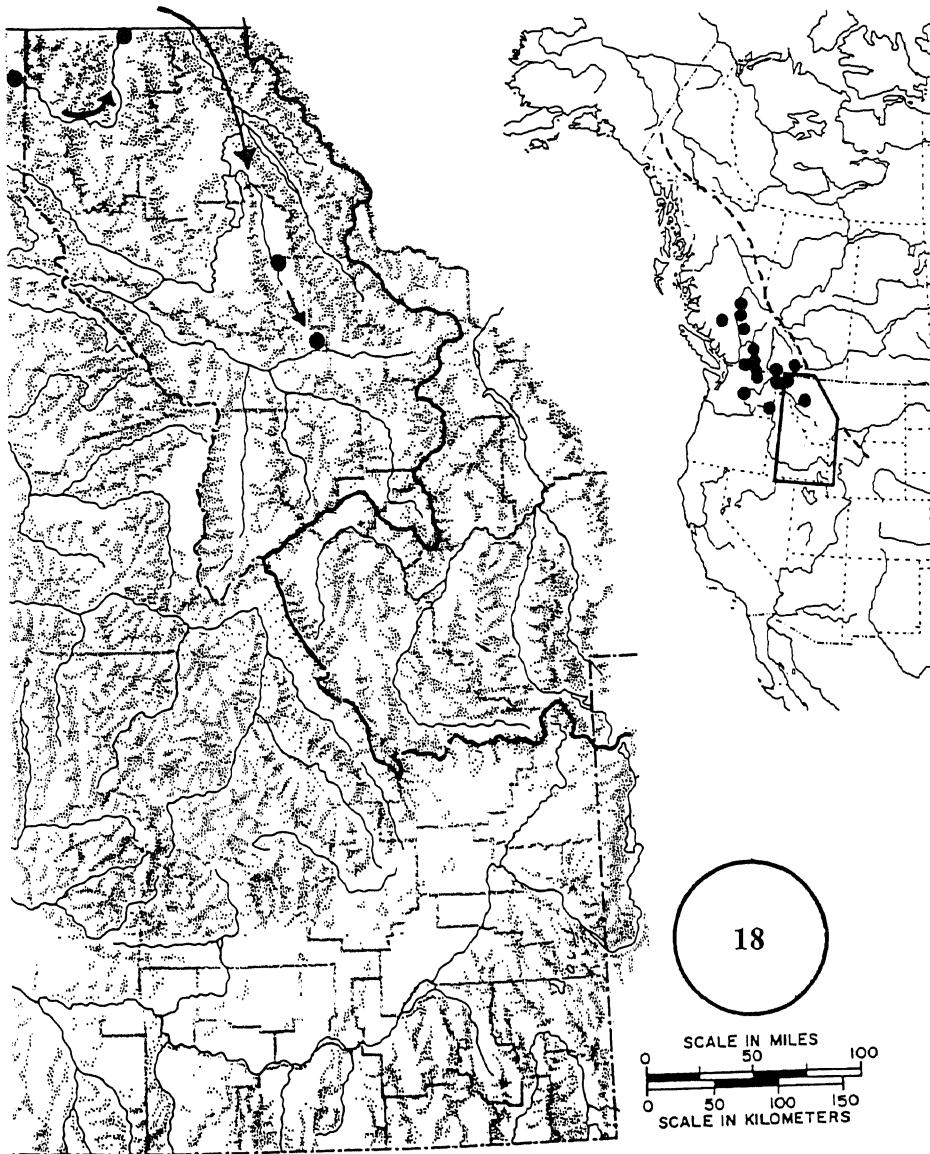


Figure 18. Distribution of the leafhopper *Cuerna* spp. west of 101°W. Box, area of detail; dashed line, western extent of *C. septentrionalis*; filled circle, *C. cuesta*; arrows, inferred dispersal route.

Figure 19 (following page). Distribution of glacial-age patterned ground (stippled) in the PNW and probable glacial refugia of relict populations of the flightless genus *Errhomus* (stars). 1, *E. picturatus*; 2, *E. serratus obliteratus*; 3, *E. reflexus*; 4, *E. serratus instabilis*; 5, *E. satus*; 6, *E. praedictus*; 7, *E. paradoxus*; 8, *E. winguatt*; 9, *E. ochoco*; 10, *E. calvus*; 11, *E. josephi*; 12, *E. pallidus*; 13, *E. bractus*; 14, *E. rivalis*; 15, *E. solus*; 16, *E. camensis*. Circled: species that have shifted to non-balsamroot hosts. All species shown in modern sites, except for 3, 10, 11 and 15 which are shown with contracted ranges.

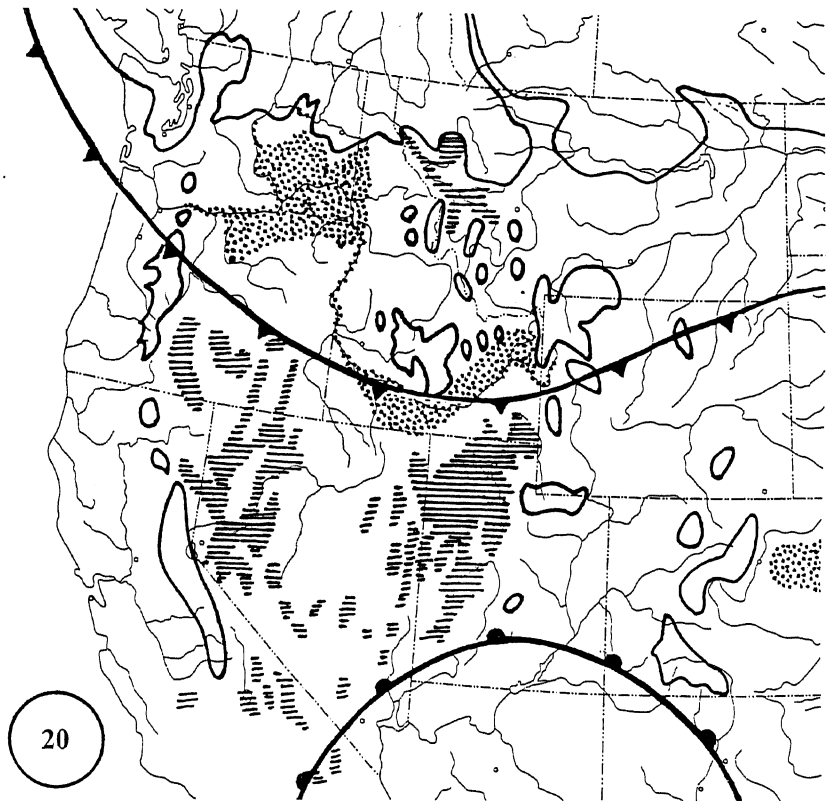
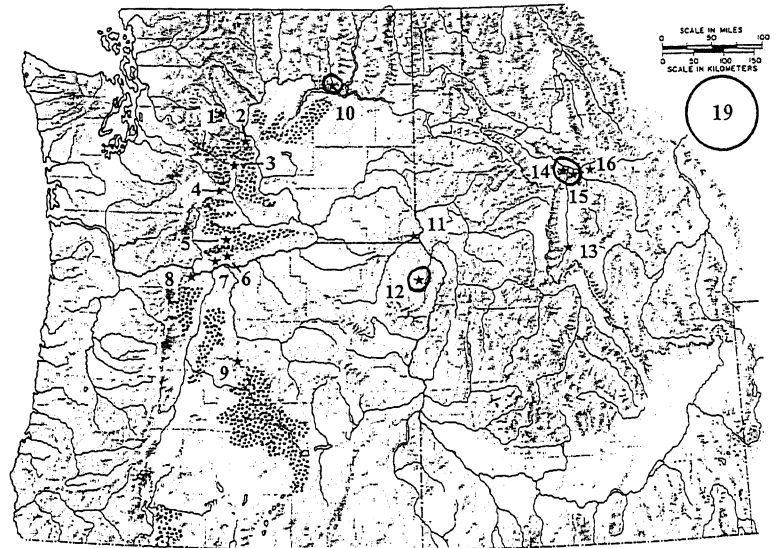


Figure 20. Hypothetical summer monsoon over PNW and areas to the south during the height of Pleistocene glaciation, showing permanent high pressure system (cold front) over WA, ID and MT and permanent low pressure system (warm front) over AZ; prevailing winds between these would be east to west (reverse of winter direction), bringing wetter than normal conditions to UT, NV and southern OR. Outline, ice cover; stippled, loess deposits and canyons; striped, glacial-age lakes.