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BIOSYSTEMATICS
OF THE
GRYLLOBLATTODEA

by

JOSEPH WILLIAM KAMP

B.A. (1951), M.A. (1961)
California State University at Chico

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Department of Zoology

The University of British Columbia
Vancouver 8, Canada

Date Sept 10, 1970

ABSTRACT

The North American Grylloblattidae are either hygrophilic occupants of the alpine-subalpine or facultative cavernicoles of lava ice caves. The research indicates that the habitats preferred by Grylloblatta must be cold and moist but not wet. The preferred alpine-subalpine hypolithion was found to be beneath stones 50 to 150 cm. buried 20 to 50 cm. deep in the substrate. Grylloblatta also temporarily occupied glaciers, snow fields, rotting logs and borders of glacial springs. The optimum microclimate in the alpine-subalpine habitats was within - 3 to + 6° C. with a humidity above 70 per cent. Humidity evidently governs the occupancy of the hypolithion more than temperature. The insect will not inhabit hypolithion with relative humidities less than 70 per cent, regardless of temperature.

The cavernicolous habitat for Grylloblatta is a micro-environment limited to a few ice caves in lava fields. Sufficient ice must be present to maintain a spring-to-fall temperature of - 3 to + 8° C. and over 80 per cent relative humidity. During the winter the ice cave is recharged with cold air below the tolerance of Grylloblatta at which time the insect inhabits the hypolithion.

The temperature preference of Grylloblatta, established in the laboratory, was between - 3.5 and + 5° C. at 90 to 99 per cent relative humidity, - 2.2 to + 4.5° C. at

relative humidities between 70 and 90 per cent, and - 1.1 to + 1.6° C. at 50 to 70 per cent relative humidities. Temperature tolerance at humidities above 95 per cent ranges between - 4 and + 11° C. Four-hour exposure to + 16° C. and one-hour exposure at - 5.5° C. produces 50 per cent mortality. Lethal extremes were - 8° C. and + 23° C. All stages of the insect were found to be active year around with no dormant period. The mean freezing point depression of the hemolymph was measured at - 0.98° C., therefore, the insect remains active in a supercooled state.

Twenty-six new populations were found during this research, extending the distribution from the Yukon-British Columbia border to the southern Sierra Nevada of California. Five new species and three new subspecies are here described. The distributional data indicate the presence of four divergent groups characterized by isolated endemic populations or species. The present disjunct distribution and zoogeography have been fundamentally influenced by the geologic and climatic events of the late Pleistocene. Further, regional and sometimes highly localized volcanic activity during the post Pleistocene, the warm dry Hypsithermal period, and the re-birth of summit and cirque glaciers, commencing approximately 2500 years ago, have affected the distributional patterns of Grylloblatta. The recent zoogeography of the various species and populations in western North America is discussed.

A comparative lipid analysis of Grylloblattidae and six other insects from related orders, and with varying temperature preferences, shows differences in fatty acid composition. The composition in Grylloblatta is more like that in Dermaptera, but the affinity is as remote as is demonstrated in the numerical analysis. Analysis of Grylloblatta shows 65.8 per cent of the total fatty acids are unsaturated, 91 per cent of which have melting points below its maximum tolerated temperature. These data clearly indicate the low temperature adaptation of Grylloblatta; such composition is not seen in the warmer tolerance forms.

In a numerical analysis of 164 external and internal morphological characters in Grylloblatta and seven other related orthopteroid insects, Dermaptera has the closest affinity to the Grylloblatta. The phenetic affinities and relationships of the Grylloblatta, as shown in the analysis, place the taxon at the ordinal level. The most acceptable systematic treatment of this group is as the order Grylloblattodea.

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ADDENDUM

None of the new names used in this thesis has any status in zoological nomenclature until such time as they are published in accordance with the provisions of the International Code of Zoological Nomenclature. They are used in the thesis only for convenience. In final publication different names may be used.



Grylloblatta occidentalis occidentalis

adult female

three times adult size

I. GENERAL INTRODUCTION

Few insects discovered in the 20th century have stimulated wider interest among entomologists than the Grylloblattodea. The first two specimens discovered at Banff, Alberta, by E. M. Walker in 1913, were described by him the following year as Grylloblatta campodeiformis, in a new family of Orthoptera, the Grylloblattidae (Walker, 1914). At that time the order Orthoptera was a "catch all" assemblage of insects of such diverse forms as the cockroaches, mantids, stick insects, earwigs, grasshoppers and crickets.

Grylloblatta campodeiformis is the emblem of the Entomological Society of Canada and is of special interest on three accounts, namely (1) its peculiar structure and hence taxonomic and evolutionary affinities, (2) its peculiar habits and temperature tolerance, and (3) its peculiar zoogeographic distribution.

Walker (1914) described Grylloblatta as a wingless insect with a head resembling that of an earwig, eyes like those of a termite, and antennae like those of Phasmida. Such a peculiar combination of morphological features to many suggests an ancient or primitive taxon. Thus, Walker (1937) called Grylloblatta a living fossil and the possible representative of some ancestral line leading to modern orthopteroids, while Zeuner (1945) considered it a recent

living Protorthoptera.

There has been much speculation and divergence of opinion concerning its taxonomic position and phylogenetic affinities. Expert orthopterists have been unable to agree on its status and relationships, and individual authors have been troubled by its systematic placement over the years. Thus, Walker (1933) considered the Grylloblattidae to have close affinity to the Saltatoria (grasshoppers), but by 1938 he placed it between the Blattaria (cockroaches) and the Saltatoria, and later placed it nearest to the living Ensifera (crickets, katydids). (Walker, 1943).

Crampton (1915) considered that Grylloblatta occupied a position intermediate between the Dermaptera (earwigs) and Isoptera (termites), and believed it to be the living representative of the common ancestor of the Gryllidae and Tettigoniidae (long-horned grasshoppers). In the course of 16 papers by Crampton (1915-1938) on the affinities of Grylloblatta, he associated it with literally every order of the orthopteroids. Imms (1927) placed Grylloblatta nearer to the Dictyoptera, while Snodgrass (1937) believed it had affinities with Blattaria and Orthoptera.

One of the aims of this study was to clarify the affinities of the Grylloblattidae. This was attempted by a numerical analysis of the information provided by morphological characters present in the orthopteroids and by a study of the lipid chemical characteristics. The avail-

ability of living Grylloblatta material enabled me to identify morphological structures not readily discernible in preserved materials.

The most recent studies, using large numbers of morphological characters to assess evolutionary affinities in the orthopteroids, are those of Giles (1963) and Blackith and Blackith (1968). Based solely on drawings, Blackith and Blackith (1968) considered Grylloblatta to be closest to the Ensifera (Orthoptera). Giles (1963), using a single specimen of Grylloblatta, considered it to be closest to the Dermaptera.

Biochemical taxonomy is now a favored area of study and many constituents of the body are available for this research. Since lipids have been used in the past in this context (Fast, 1970) and since they are of importance in determining certain physiological attributes of insects, their study in Grylloblatta and other orthopteroids and lower insects permits a two-fold use of the same data.

The Grylloblattodea occur in cold and moist habitats in Siberia, Japan and western North America. They are found on glaciers, beneath stones on the fringe of snow patches, on moist talus slopes, in rotting logs and in ice caves. The distributions are very disjunct and the taxonomy of the North American forms is most confused. Grylloblatta has long been considered by entomologists to be one of the rarest of all insects. At the beginning of this study fewer than 75 adult specimens (the majority being

Grylloblatta campodeiformis campodeiformis) were in the major entomological collections of the world. Only a few years ago the world's largest insect collection, in the British Museum (Natural History), possessed a single specimen (G. c. campodeiformis) and it was treated with the same care and "reverence" as the Museum's Dodo and Archaeopteryx.

The discovery of many new populations of Grylloblatta, and the collection of well over 500 adults and numerous larvae from many types of habitat, permitted a study of distribution, habitats, and the biology in a depth not previously attainable. In order to undertake these studies in depth, however, a thorough systematic study of all material was essential. Only in this way could satisfactory identifications be obtained and accurate comparisons of data be made. Thus, it was necessary in the course of the research to describe five new species, three new subspecies, and to change the taxonomic position of two species. This taxonomic work is in Appendix I.

The discovery of these new taxa and many new populations made it possible to describe and discuss the present distribution as a direct result of Pleistocene or Neoglacial activity. Therefore, I have discussed the Rocky Mountain Cordillera, Coast-Cascade and Sierra Nevada distribution, and the implications of the Pleistocene post Pleistocene climates on the present occurrence of Grylloblatta. This

could only be completed, however, after data on (1) the hypolithion and cavernicolous habitats, (2) the bioclimatic requirements of various species both in the microhabitats and in the laboratory, and (3) the seasonal activity of Grylloblatta in alpine and cave habitats had been obtained.

Finally, the availability of a cryophilic form made it possible to investigate the relationship between environmental temperature and the lipid composition of insects. The literature reports on the effects of temperature and degree of lipid saturation are in conflict. This seems to be due to the fact that all studies have been performed by acclimation of a species to different environmental temperature regimes. Therefore, a comparative lipid analysis was performed on six different orthopteroid orders: two orders with high temperature preference, three with a temperate though variable preference, and one with a cold preference. My analysis was also used as a tool to indicate evolutionary relationships among these six taxa.

In summary then, this thesis is concerned with the biosystematics of the Grylloblattodea. It is concerned with the habitats, the temperature and humidity preferences, the distribution and zoogeography. The systematic affinity of the taxon is considered and the peculiarities of the lipid composition are discussed with reference both to the phylogenetic relationships and the habitats occupied by the taxon.

II. HABITAT AND BIOCLIMATIC REQUIREMENTS OF GRYLLOBLATTA SPECIES

Introduction

The typical environmental niche reported for the North American Grylloblatta is the alpine-subalpine life zone (Walker, 1914; Caudell, 1923; Ford, 1926; Silvestri, 1931; Gurney, 1937, 1948, 1961), but it does occur at low elevations (Campbell, 1949; Kamp, 1963). The genus has also been reported as a facultative cavernicole (Kamp, 1970). The hypolithion and cavernicolous situations seem to be the resident areas, and the insects range only temporarily into other habitats while foraging for food.

I. The Hypolithion Habitat

Grylloblatta occurs in the hypolithion of the alpine biome. The term alpine zone, as used in this thesis, follows Swan (1968). He states that the alpine zone begins at the forest line, which is the highest elevation where trees are the dominant flora type either in continuous stands or in groups, and that the upper limit of the alpine zone is the highest elevation where the biota are dependent upon local autotrophic plants as the base for nutrition. Thus defined, the alpine zone is the same as eualpine, high alpine, nival, eunival, high altitude, Canadian and

Hudsonian in the literature.

The lower limits of the alpine zone in western North America can be less than 1000 feet in elevation in the Yukon, to over 10,000 feet in the southern Sierra Nevada and Rocky Mountains. The altitude depends upon a number of physical factors: latitude, massiveness of the mountain range, direction of slope, gradient of slope, extent and duration of winter snow cover, temperature, humidity, type of soil, moisture and prevailing winds.

The subalpine, as here used, is a subdivision of the alpine zone extending from forest line to tree line. Tree line is the upper limit of trees that are generally scattered over open ground cover. The subalpine is a transitional region of the alpine zone where the environment changes from that of the forest to that of the alpine.

The climatic factors interacting on organisms in the alpine include:

1. High transparency of the air;
2. Low atmospheric temperatures;
3. Reduced evaporation from exposed surfaces;
4. Reduced water vapor tension correlated with reduced atmospheric pressure;
5. Greatly increased intensity of the ultraviolet radiation;
6. Increased rates of insolation and radiation;
7. Wide differences in atmospheric and ground temperatures resulting in large diurnal and nocturnal fluctuations;

8. Snow cover than insulates against aridity, low temperature, ultraviolet radiation, and governs substrate moisture and temperature.

Snow cover, particularly the winter snow cover, is perhaps the most important environmental condition that makes life possible here on a year around basis. The snow cover exerts an ameliorating influence on the extremes of atmospheric temperature fluctuations. In winter the snow forms a protective blanket against low temperatures and desiccation, and prevents ground freezing. A foot of snow (30 cm.) will provide enough insulation from an air temperature of -12°C . to prevent freezing of the ground (Landsberg, 1962). The insulation effectiveness increases as the density of the snow increases.

In the late spring and early summer the atmospheric and soil temperatures do not rise as rapidly as expected under conditions of high transparency and aridity of the alpine atmosphere. Snow has a very low heat conductivity (0.01 cal/cm/degree) and a very high albedo (80-90 per cent reflection) (Sellers, 1967). With snow cover most of the sun's energy (heat) is reflected back and, of the remainder, a large percentage is lost as latent heat in the melting of the snow. The slow melting of the snow allows a gradual increase in soil temperature rather than an abrupt increase, as experienced on bare soils or rock. Snow counteracts the high insolation and aridity of the

alpine by replacing soil moisture and increasing humidities. Without the presence of some snow cover in the alpine zone and its ameliorating effects on the atmospheric conditions, only the most cold-hardy arthropods could inhabit this area.

However, many insects, not particularly cold-hardy, do live in the alpine area. They can do this by largely avoiding the open exposed environments. They live in unexposed and somewhat protected areas such as under mats of vegetation, the the first few millimeters or centimeters of the soil, under stones or rocks or in other underground cavities.

Within these special microhabitats, special microclimates prevail, which, although largely a product of and dependent on the atmospheric conditions above, are much less severe and more stable than in the open alpine area. These special microhabitats, with their rather constant microclimates, heavily dependent on the snow cover, provide a wide variety of niches for a great many different types of insect.

It is evident that it is the hypolithic microhabitat in the alpine that is the most favored by insects, since it is here that one finds the greatest diversity and the highest populations. By definition, the hypolithic habitat includes all the underground cavities and narrow spaces under the many stones and boulders that are more or less deeply buried in the ground.

Schonborn (1961) has described the stratification of the hypolithion in Europe and Asia. He states that stones about 100 to 400 cm.² and 20 cm. thick form the most stable hypolithion. The first layer is on the undersurface of the stone and is 5 to 10 mm. thick; the character species are predominantly zoophagous. The second layer is that of the floor of the substrate under the boulder. The depth of this layer depends upon the nature of the soil, the percolation of melt-water and the vegetation of the locality. It is usually 20.- 30 mm. deep. The arthropod community of this layer is usually feeding on detritus. The third layer underneath the substrate contains more or less decomposed plant debris and ranges up to 40 mm. in thickness. This third layer may be taken as the base of the food pyramid of the hypolithic community and is largely composed of phytophagous forms or detritus feeders, dominated by Collembola. The first and second layers are also the resting places for nocturnal Diptera that must contribute substantially to the diet of the carnivorous species.

The hypolithion is characterized by a conspicuous discontinuity of distribution. It is only prevalent in older consolidated slopes that have adequate soil to hold the stones or boulders sufficiently long for the subsurface environment to evolve. The development of this environment results from decay of vegetable matter, mechanical activity of animals and melt-water. At the elevations associated with this habitat in the alpine zone, there are

many areas of unconsolidated talus slopes with loosely lying stones that often slide or roll down. These areas afford a very temporary hypolithion which is generally not occupied by other than transients.

II. The Cavernicolous Habitat

The cavernicolous niche for Grylloblatta is a micro-environment limited to the ice caves in the lava plateaus of western North America. These caves occur in Oregon, California and Washington, and Grylloblatta occupy them as troglophilic inhabitants.

Geologically, the lava caves in western North America are late Pliocene or Pleistocene in age and are tubes or tunnels in fissure flows of pahoehoe basalts (Williams, 1957; Walker, Peterson and Greene, 1967; Greeley, 1971).

The caves were formed either by superheated gases that blew through lava that was still viscous and underlay the cooling crusted surfaces, or by cracks and fissures that formed at the advancing front of the flows. Such fronts were followed by an outpouring or draining of liquid veins or conduits which left a hollow void or tube. It is common to find two or more caverns in the same system, and a few systems are multi-leveled with as many as five stories (Kamp, 1963; Greeley, 1971). The caverns range in size from small grottos to cavities more than two miles long, 16 m. in height, and up

to 26 m. wide (Halliday, 1959; Greeley, 1970). Not all caves contain ice, and probably less than 10 per cent house persistent ice. Balch (1900) has suggested that the cave ice represents remnants of the Ice Age.

Ecologically, the western ice caves are located in the Upper Sonoran with a dominant flora of Ceanothus, Artemisia, and Juniperus, with scattered Pinus contorta and P. ponderosa that grade into thick stands of these pines in the Transition. Total moisture from rain and snow rarely exceeds 12 inches per year, with 50 per cent lost by evaporation (Sellers, 1967).

The classification of cavernicole organisms is based upon the fauna of the limestone caves in Europe that have a homeothermic environment. The classification was established by Schiodte (1849) and Schiner (1853) and was introduced to North America by Packard (1888). Today in North America it is used with little modification for the fauna of limestone and lava caves.

Troglobites are animals found only in caves and are so modified that rudimentations of structure restrict them to a cave existence. Troglophiles are animals found frequently in caves, reproducing there, and completing their life cycle underground but not necessarily in the cave. Troglloxenes are animals often found in caves, but not completing their whole life cycle underground.

The Microenvironment and Microclimate
of Grylloblatta Habitats

Grylloblatta are not universally distributed throughout the alpine-subalpine areas of western North America. They occur in only some of the ice caves associated with the volcanic regions of the Cordilleran. These insects appear to have particular microclimatic requirements that are to be found in only limited areas. Since these microenvironments have not been studied in detail in the Nearctic, one of the aims of the present research was to obtain detailed microclimatic data from the alpine-subalpine hypolithion and the cavernicolous habitat in localities where Grylloblatta are found.

I. Materials and Methods

The alpine-subalpine habitats at McKenzie Pass, Crater Lake, Mt. Hood, Bachelor Butte and Sunshine Shelter, all in the Cascade Range, Oregon, and at Athabaska Glacier, Jasper National Park, Alberta, were selected for study. These sites were chosen because all have populations of Grylloblatta, are centrally located in the Cascade or Rocky Cordillera, and government weather records covering at least 10 years are available.

Temperatures were recorded using thermographs (Ryan Instruments, model D-45; J. P. Friez and Sons, model 594).

Maximum-minimum thermometers (Six-type, Taylor Instruments) were used in areas where thermographs could not be reached to service throughout the year due to snow conditions. Additional substrate temperatures were obtained while collecting Grylloblatta specimens. These data were combined with government weather bureau records to construct monthly profiles.

Humidity recordings were obtained by thermohygrographs (J. P. Friez and Sons, model 594; Edney-Short Mason Ltd., model 215) and lithium chloride hygrosensors (Hygrodynamics, models 15-1810, 4-4821KW). Humidities were recorded beneath the rocks of the hypolithion with a micro-aspiration psychrometer (J. P. Friez and Sons).

South Ice Cave and Edison Ice Cave, Deschutes National Forest, Oregon, were selected for study of the cavernicolous habitat since they are lava ice caves with resident populations of Grylloblatta. Other caves in California, Oregon and Washington were also examined periodically.

Temperature and humidity records, limited in time but covering the seasons of the year, were obtained from South Ice Cave between 1963 and 1971. In addition, isolated temperature and humidity measurements were made in the other ice caves in California, Oregon and Washington.

To obtain long term temperature data ten 45-day continuous record thermographs (Ryan Instrument, model D-45) were installed in the different speleological zones of

South Ice Cave. Air temperatures were recorded 25 cm. above the rocks. Rock and air temperatures were recorded from June, 1970, to March, 1971. Spot data collected previously for April and May filled in a year's record. Relative humidity measurements were obtained twice a month for each temperature site with the help and cooperation of local forest service personnel. By the use of posted markers, the amounts of melting and formation of ice were recorded at monthly intervals throughout the year. Simultaneously, light measurements were obtained using a Gossen Lunasix meter.

II. Results

A. The Alpine-Subalpine Habitat

1. Microhabitat

The usual microhabitat of Grylloblatta in the alpine-subalpine was found to be that of cavities beneath stones and boulders which are more or less buried in the ground. Most insects were found under isolated rocks 50 to 150 cm. in diameter and buried to a depth of about 30 cm. They occasionally were taken beneath small rocks 5 to 10 cm. in diameter (scree), and in talus slopes 50 or more feet deep that contain rocks of all sizes (Fig. 1). In all cases

Figure 1. Examples of various Grylloblatta habitats:
upper left, alpine-subalpine hypolithion,
Mt. Hood, Oregon; upper right, entrance to
South Ice Cave, Oregon; lower left, alpine
hypolithion around glacier borders, Athabaska
Glacier, Jasper National Park; lower right,
typical hypolithic cavity with snow margin
(ruler 15 cm. long), 5200 feet, Mt. Baker,
Washington.



the substrate was subirrigated by melt water. On occasion Grylloblatta was found to occupy the spaces beneath decaying bark and in or beneath fallen logs.

In the alpine-subalpine Grylloblatta were found to seasonally occupy different sites. They inhabited the hypolithic spaces deep in the talus or beneath the largest boulders in summer and winter and were found in other areas only in the late spring and fall.

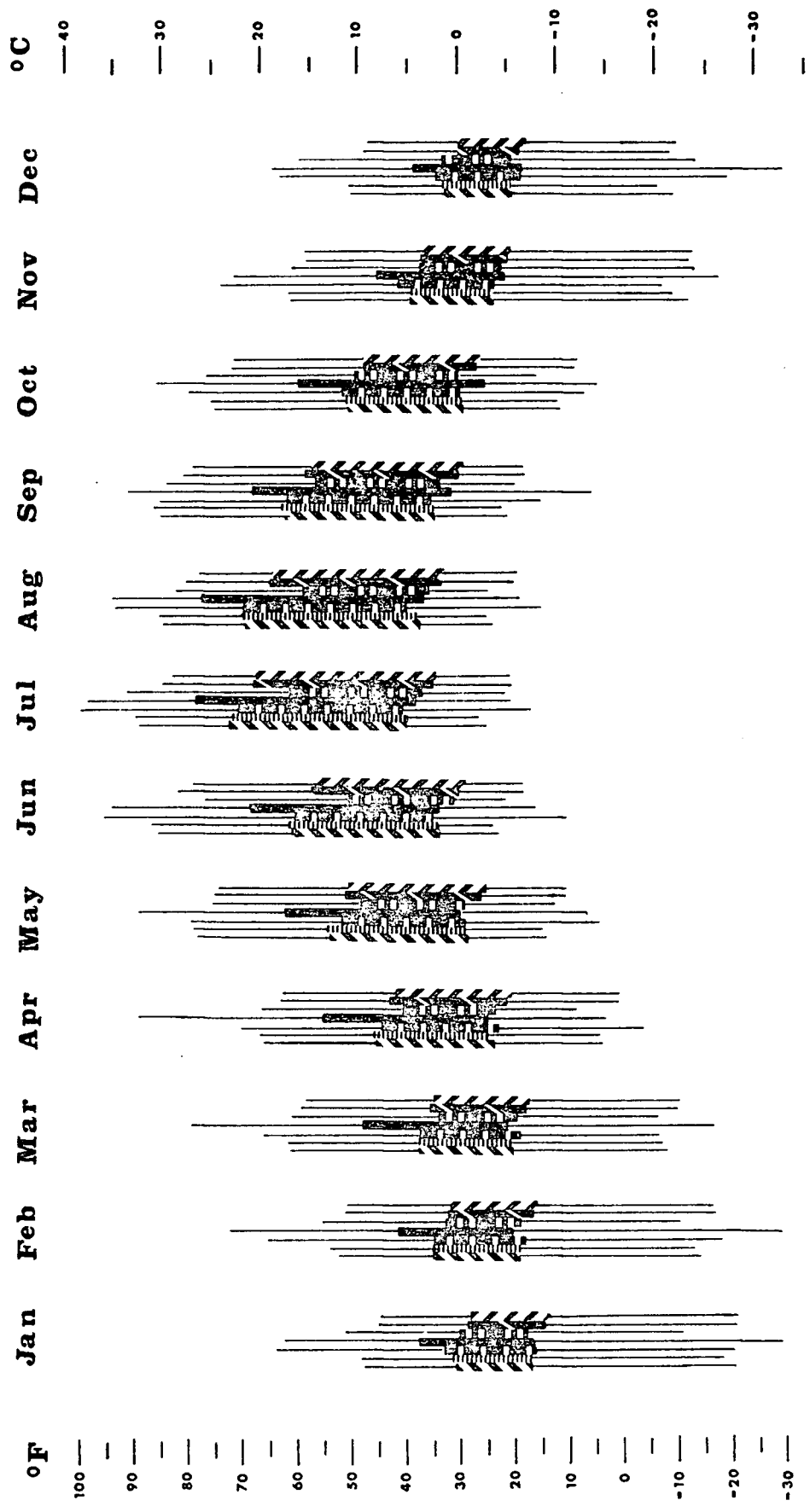
2. Microclimate

The microclimate in the hypolithion was found to be more uniform than the surface climate. While the surface air temperatures were subject to wide circadian, seasonal and yearly fluctuations, the temperatures of the hypolithion occupied by the Grylloblatta fluctuated only slightly.

Figure 2 presents the yearly air temperature profile for five alpine-subalpine sites. Yearly surface air temperatures ranged from -40°C . to $+40^{\circ}\text{C}$. and a circadian range in excess of 30 degrees was noted. In contrast to this, the greatest yearly temperature range recorded in the hypolithion preferred by the Grylloblatta was 10 degrees. In the alpine, atmospheric relative humidity ranged from less than 10 per cent to saturation. A summer alpine humidity fluctuation in excess of 80 per cent frequently occurred in a few hours.

Figure 2. Monthly atmospheric temperature of alpine-subalpine habitats of Grylloblatta in Oregon (1969 to 1971). Wide bar = mean minimum and maximum temperatures; narrow bar = absolute minimum and maximum temperatures; solid vertical bar to right of °C. scale = preferred temperature range of Grylloblatta, and narrow hatched bar = tolerable temperature limits of Grylloblatta. Locality key to graph as follows:

- ▧ McKenzie Pass 5,325 ft.
- ▦ Edison Ice Cave 5,200 ft.
- Crater Lake 6,475 ft.
- ▩ South Ice Cave 5,050 ft.
- Timberline, Mt. Hood 6,000 ft.
- ▧ Bachelor Butte, Century Drive 6,450 ft.
- ▧ Sunshine, North Sister 6,600 ft.



The microclimate in the hypolithic spaces occupied by the Grylloblatta was found to vary and to depend on the size of the rock, substrate ground water, snow cover, surface temperature and exposure.

The hypolithic microclimate beneath boulders (50-150 cm. in diameter and 20-50 cm. thick) partially buried 30 cm. or more deep was the most uniform throughout the year. When this type of hypolithion was inhabited by Grylloblatta the yearly extreme range was - 3 to + 6° C. The hypolithion temperature was found to rise slowly from around 0° C. in the summer to a maximum of + 6° C. in late September or early October. The temperature within the microhabitat then decreased rapidly to the minimum, when the air temperature went below 0° C. in the fall. This cooling of the hypolithion continued until the snow cover provided insulation from further drop in temperature. In the alpine-subalpine where Grylloblatta occurred the cooling ceased by mid-December. The hypolithic temperature then remained between - 3 and + 1° C. throughout the winter and spring.

In the years when there was reduced or delayed snow cover, the temperature in this type of hypolithic space fell below - 3° C. and the insects were found to move to the deeper hypolithion below the freezing zone. Only when the hypolithic temperature reached between - 3 and 0° C. again did Grylloblatta re-occupy the spaces.

Field records indicate that a humidity no lower than

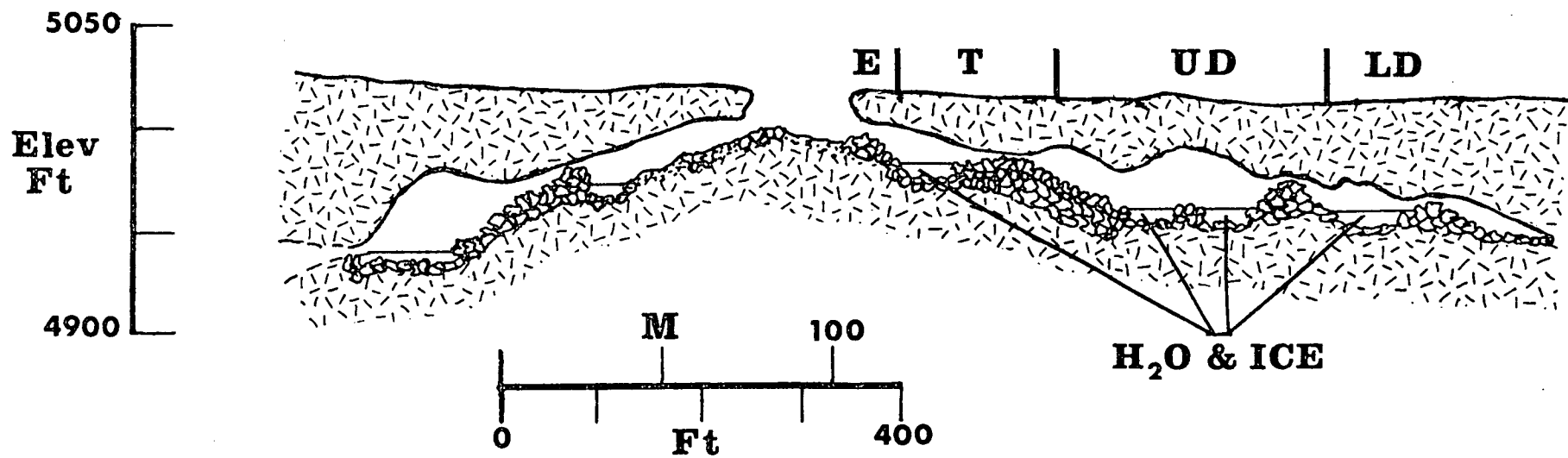
70 per cent must be present in combination with the - 3 to + 6° C. temperature range for Grylloblatta to inhabit the alpine hypolithion. The humidity in the microclimate preferred by the Grylloblatta was found to fluctuate on a yearly cycle. Beneath the large boulders the humidity inhabited by Grylloblatta ranged between 90 and 100 per cent during the spring season. As the hypolithic temperatures slowly rose during the summer and fall seasons the humidity gradually decreased. When the humidity was below 70 per cent the Grylloblatta were found to leave the hypolithion even if the temperature remained below + 6° C. In the late fall the hypolithic humidity remained at the yearly minimum until the temperature decreased and the rain and first snows increased the moisture. The hypolithic humidity then rose to at least 90 per cent and persisted at this level through the winter. In response to the melting of the snow pack the maximum humidity in the alpine hypolithion was found to occur in the late spring.

B. The Cave Habitat

1. Microhabitats of the Ice Cave

Ecologically, the ice caves may be divided into four zones (Fig. 3): 1) entrance zone, 2) twilight zone, 3) upper dark zone, and 4) lower dark zone. The distribution of the

Figure 3. South Ice Cave, Oregon. Profile to scale indicating limits of entrance (E), twilight (T), upper dark (UD) and lower dark (LD) ecological zones. Two recorders in each zone for air and rock temperatures.



fauna and the gradation of one zone into the other are transitional and depend upon the season.

a. Entrance Zone

The entrance zone substrate is composed of ceiling and walls, spallated rocks and boulders interspaced by large amounts of wind- or water-borne soil and organic detritus. Biotically, the entrance zone is the richest of the four zones. The walls and ceiling are covered with lichens and the substrate is littered with plant and animal material transported by Erithizon, Citellus, Neotoma, Peromyscus and a variety of birds. The fauna of this zone are facultative troglophiles and will also be found in non-cave habitats. It contains, in addition to the above rodents and birds, an invertebrate fauna of Arachnida, Diplopoda and Insecta. Examples are spiders, harvestmen, millipedes, moths, mosquitoes and Collembola. This zone grades into the twilight zone that exhibits less organic material in the substrate. This material decreases in amount with increase in distance from the entrance.

b. Twilight Zone

The twilight zone receives only indirect light of low intensity. Biotically, it contains the nests and caches of rodents, a thin moss cover, and growth of fungi

on decaying organic material. The fauna, in addition to the same fauna of the entrance zone, contains Campodeidae, facultative Grylloblatta, Machilidae and Coleoptera.

This zone is also used by many organisms as a retreat from extremes of surface temperature. During the hot summer and early fall the local bird and mammal fauna retreat here from midday until dusk and they utilize the small pools of melt or drip water present in this twilight zone. In periods of very hot, dry weather Diptera and Lepidoptera invade this zone as well.

The following two zones are speleologically described as one zone, the dark zone. Biologically, however, the dark zone is divisible into two, as follows.

c. Upper Dark Zone

The upper dark zone may receive indirect light of very low intensity, less than .016 foot candles (.172 lumens/ sq. m.) for an hour or less during the early morning or near sunset. The length of light exposure depends on the entrance orientation and amount of ceiling collapse in the twilight and entrance zones.

Biotically, this zone is inhabited by small rodents. Rodent nests are always present and in some caves very large nests and caches of twigs, pine cones and grass occur that are evidently deposited by pack rats, Douglas squirrels

and porcupines. Plant flora is limited to fungi growing on organic material. The Arthropoda are the dominant fauna, composed of Campodeidae, Machilidae, Collembola, Grylloblatta, Diplopoda and Arachnida. During the fall there may be large numbers of dead Lepidoptera and Diptera killed by the cold and these are utilized as food by the other Arthropoda. Chiroptera use this zone during the diurnal period and may in certain caves hibernate here during the winter.

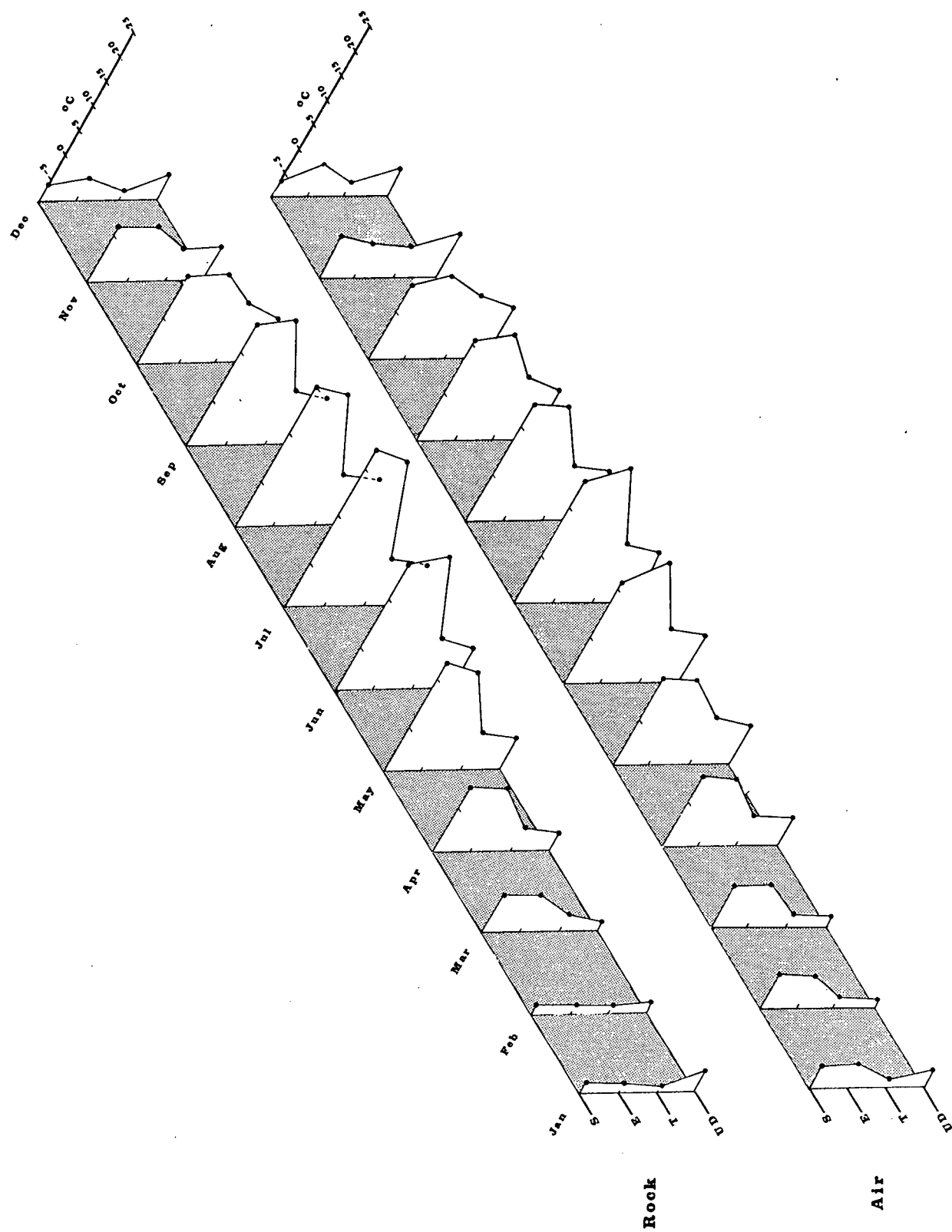
d. Lower Dark Zone

This microhabitat is a region of permanent darkness with little atmospheric exchange throughout the year. Organic material is very limited and is restricted to the droppings of wandering rodents. Fungi and molds are the exclusive flora and are restricted to the scat. The fauna is limited to Campodeidae, Diplopoda and Arachnida.

2. Microclimate of the Ice Cave Habitats

The field data obtained (Figs. 2 and 4) show that the microclimate of the caves is in general more stable than that of the surface climate. While the air temperatures and humidities in the outer zones of the cave environment fluctuated with the external conditions, the substrate

Figure 4. South Ice Cave, Oregon. Monthly temperature profile of rock and cave air showing latent response of rock temperature to that of air (April, 1970, to March, 1971). S = surface, E = entrance zone, T = twilight zone, UD = upper dark zone.



and atmosphere 5 cm. above the substrate in the deeper zones were much more uniform.

a. Temperature

Figure 4 presents the mean monthly temperature profiles obtained from South Ice Cave. Temperatures recorded at South Ice Cave of the different biospeleological habitats agree with those obtained from other ice caves in California, Oregon and Washington. I therefore believe the yearly temperature profile of South Ice Cave to be representative of the temperatures found in most western North American lava caves containing ice that persists for a number of years.

The atmospheric temperatures of the twilight and dark zones were below 0° C. from November to May. The rock temperatures of these zones were generally a few degrees colder than the air temperatures. Rock temperatures in these zones were -15° C. in late winter. The rock did not remain at such temperatures but slowly rose in the spring and summer as it lost cooling power to the slowly warming atmosphere. By late summer and early fall, rock temperatures were between -3 and $+3.5^{\circ}$ C., depending on the distance from the cave entrance, proximity to ice, the mass of ice in the zone, and the heat flow through the ceiling and underlying rock.

The temperatures in the entrance zone varied greatly,

both seasonally and daily. This zone is continually under the influence of the external climatic fluctuations. From January through May this zone was in equilibrium with the temperature means of the external environment. From June through October the air temperatures of the entrance zone were generally higher than the mean maxima of the external temperatures. With the lowering of the external temperatures during November, the entrance rock temperature approached equilibrium with the external conditions. The mean air temperature in this zone dropped below the outside mean during November. In December there was a lag of the entrance zone rock and air temperatures behind the external temperatures.

Thus, there was a definite lag in cave temperatures compared with surface temperatures. Seasonal values in the cave responded as a dampened phase shift of the annual surface temperature curves. In winter, when the external temperature fell below that of the cave atmosphere, colder, dense air entered the cave and replaced the warmer cave air. Repeated influxes of colder air lowered the cave temperature and gradually the outer ecological zones of the cave came into equilibrium with the mean outside winter temperature. The deeper ecological zones fell below the outside mean and remained below the outside mean throughout the rest of the winter.

The repeated charges of cold that lower the twilight and upper dark zone temperatures during the winter caused

those areas to remain relatively stable during the spring and early summer. A gradual increase of temperature occurred during the warmest seasons and the microhabitat temperatures in the deeper zone of the cave rose to a maximum of 5° C.

b. Ice

The formation of new ice in the cave was dependent on the simultaneous presence of water and below- 0° C. rock temperatures. The usual source of the water was seepage of rain and snow melt through the overlying rock; in rare cases running water was the primary source. In winter the cave received little or no seepage from the frozen surface and at this time the relative humidity fell below 10 per cent. In general, during the winter the amount of ice present represented the ice and melt water that remained at the end of the fall season. However, wind-blown snow contributed to ice build-up in the entrance zone during the winter in some years.

Ice accumulated in the lava caves only during the spring and early summer. Only during an exceptional year did small amounts of ice accumulate during the late fall. A warm (above 0° C.) rainy period following an initial below- 0° C. cooling of the rock surface resulted in seepage being transformed into ice.

During the fall usually the dry cold circulating air caused evaporation of most of the water formed by summer melting of the ice before it could freeze. During the spring warmer external air circulating through these caves raised the rock temperature above 0° C. so rapidly that seepage from runoff did not always form ice. In the spring, ice formation was found to vary and this depended upon surface temperatures, time of ground thaw, and the amounts of rain and melt water.

Cave ice was found to vary from thin sheets a few mm. thick to glaciers 2 to 5 m. in depth, up to 15 m. wide and 50 m. long. In some depressions, "lakes", ice was found and there was from 30 to 60 cm. of water on top during late summer and early fall.

Ice is not perpetual, but only transitional, in most of the lava caves studied in the west. In caves with active circulation, ice only lasted 1 to 2 years and it was only in those caves with a static or passive circulation that cave ice persists for years.

The exact age of persistent ice is unknown in the west beyond the 150 years of recorded history, since none of the current dating methods have been applied to western cave ice.

c. Humidity

Ice cave humidities were also found to be seasonally

cyclic. In the twilight and upper dark zones of South Ice Cave from November to March all water vapor was frozen by the below-0° C. temperatures and this caused a drop in humidity. At the onset of the winter season the humidity of these zones was usually above 80 per cent. It fell to 10 per cent or less by January and the microhabitat was very dry until the spring surface thaw.

There was a rapid rise of humidity during the spring melt of April and May. The humidity was noted to rise in a 2-week period from 10 per cent or less to over 80 per cent. The humidity then stabilized around 80 per cent for a short period as the seepage of melting snow diminished. From June to September seepage from spring and summer rain and the gradual melting of ice caused the humidity to rise to 90 per cent or more. This same cycle was present in other western lava ice caves (personal observation).

It must be re-stated that the temperature and humidity patterns presented here are for the rock and the bottom 25 cm. of the atmosphere. I took the climatic data from this region for it is the active zone for almost all of the cavernicolous fauna. Stratification of temperature and humidity occurs in the cave atmosphere, with temperatures increasing and humidities decreasing from floor to ceiling.

III. Discussion and Summary

Grylloblatta has been found on glaciers (J. G. Edward, personal communication), at the borders of springs (Henson, 1957a), beneath stones on the fringe of snow patches (Gurney, 1937, 1948, 1953, 1961), under stones (Ford, 1926; Gurney, 1937, 1961), boulders or logs firmly embedded in the ground (Mills and Pepper, 1937; Kamp, 1963), in moist rock slides (Gurney, 1937, 1948; Campbell, 1949; Chapman, 1953), in rotting logs (Henson, 1957a; Kamp, 1963; Gagné, 1968) and in ice caves (Kamp, 1953, 1963, 1970). These insects have definite humidity and temperature requirements (Mills and Pepper, 1937).

The present research indicates that the habitats preferred by Grylloblatta must be cold, but not too cold, and moist, but not wet. Such cold and moist habitats, that are more or less stable and permanent, occur in isolated regions of the alpine-subalpine.

The hypolithion above timberline is composed of a wide variety of microenvironments. Each type of microenvironment has a unique microclimate more or less directly influenced by the capricious alpine-subalpine climate. The cavities beneath stones or boulders, 50 to 150 cm. in diameter and 20 to 50 cm. thick, typically provide the optimum conditions for Grylloblatta in the alpine-subalpine. The temperature-humidity conditions of such hypolithic cavities fluctuate minimally during the day, and seasonal

fluctuations beneath the larger boulders are neither abrupt nor extreme.

This type of hypolithion has a yearly extreme temperature range of -3° to $+6^{\circ}$ C. and a humidity above 70 per cent. Seasonal variations are hardly evident, with winter and spring temperatures between -3° and $+1^{\circ}$ C. The temperature slowly rises during the summer, reaching the maximum by late September or early October. The temperature then decreases rapidly to the minimum until the snow cover provides sufficient insulation from further drop in temperature. The most important physical factor of the hypolithion that makes possible habitation by Grylloblatta is snow cover. It provides insulation against the intense winter atmospheric cold and aridity and is the source for the gradual development of the hypolithic cavity and climate.

However, the humidity of the alpine-subalpine hypolithion microhabitat preferred by Grylloblatta fluctuates on a yearly cycle. It ranges between 90 per cent and saturation during the spring. As the temperature slowly rises during the summer and fall, the humidity gradually decreases, evidently reaching the minimum tolerated by Grylloblatta in the early fall. The first rains and snow, coupled with decreasing temperatures during the late fall, raise the humidity to approximately 90 per cent where it persists throughout the winter. Snow melt in the spring then raises the humidity to the maximum level.

Humidity seems to govern the occupancy of the hypolithion by Grylloblatta more than temperature. The insect will not inhabit any hypolithion with relative humidity less than 70 per cent, regardless of the temperature. Mills and Pepper (1937) have earlier reported that the optimum humidity is around 100 per cent, and Henson (1957b) noted an almost saturated humidity is required.

Chapman (1953) has stated that it is moisture, rather than altitude, that is important to Grylloblatta. The fact that these insects occur at Kamloops, British Columbia, in talus slopes at 1400 feet (Campbell, 1949) and in the talus at 3195 feet on the North Fork of the Feather River (Kamp, 1963) would seem to bear this out. Here, as in many other localities, they can only be found in the late fall - early spring, when cool moist surface conditions prevail. While Campbell (1949) collected specimens out in dry conditions in the fall, this is most unusual.

The cavernicolous habitat for Grylloblatta is a micro-environment limited to the ice caves in the lava fields (Kamp, 1953, 1963, 1970). Grylloblatta is not found in all ice caves, but only in those with sufficient quantity of persistent ice to maintain a spring-to-fall temperature range of -3° to $+5^{\circ}$ C. and over 80 per cent relative humidity. These conditions are comparable to those prevailing in the alpine-subalpine hypolithion cavities.

In contrast to the narrow yearly fluctuations of the hypolithic microclimate, the cavernicolous habitat occupied

by Grylloblatta undergoes a drastic change in the winter. This winter change is so great that it renders the cavernicolous environment uninhabitable by Grylloblatta. During the winter the cave atmosphere is recharged with cold air and it is this cold recharge which makes the cave an unsuitable environment for Grylloblatta at this time of year. The insects are forced out onto the surface, into a habitat which they certainly cannot tolerate at any other time of the year.

The present study thus confirms that Grylloblatta has particular temperature and humidity requirements, which no doubt in part account for the rather spotted distribution of the genus in western North America (Gurney, 1937; Kamp, 1963). It is likely that this insect is not as rare as often stated. Instead, the insect has particular environmental requirements that are either not often met with in the field, or not recognized by entomologists searching for these insects. This, together with their predaceous habit that tends to space them out (Mills and Pepper, 1937; Campbell, 1949; Gagné, 1968) and the fact that they appear photonegative and active mostly at night (Ford, 1926) has resulted, at times, in little success when searching for specimens.

The insect is active all winter and does not have a dormant period (Mills and Pepper, 1937; Henson, 1957a). It, thus, is active also when most entomologists think there is little about to be collected in the field.

Activity of Grylloblatta in Alpine and Cave Habitats

I. Introduction

The activity of Grylloblatta in the hypolithic habitat has received little attention in the literature. What has been published is incidental to taxonomic descriptions or reports of laboratory cultures (Ford, 1926; Campbell, 1949; Gurney, 1953, 1961). The most extensive description of field activity is a report of the winter activity of G. c. campodeiformis from Kamloops, British Columbia (Campbell, 1949). Activity in the cavernicolous habitat has been limited to the general accounts of Kamp (1963, 1970).

II. Methods

Observations were made of the activity of the insects in the specific habitats at seasonal intervals throughout the year. The vertical and horizontal movement within the habitat was recorded as the seasonal macroclimate affects the environmental conditions within the hypolithion and cave.

III. Results

A. Activity in Alpine Habitats

The seasonal hypolithic activity of Grylloblatta temporarily varied in response to climatic conditions, extent and depth of hypolithion, latitude, slope and elevation. Winter snowfall and the spring and summer temperatures were the most important factors regulating yearly activity within the alpine-subalpine habitats.

Most of the species and populations of Grylloblatta distributed in the Cordillera were found to follow the same general yearly activity pattern. The insects were active throughout the year in different depths of the hypolithion in response to the surface climate.

1. Winter Season

Insects were found beneath rocks buried at shallow depths or on the surface beneath the snow pack. In certain localities, where the slope and exposure or below-normal snowfall tended to produce isolated accumulations of snow, most of the Grylloblatta population was active below the freezing zone in the hypolithion. The insects did not tend to aggregate beneath the isolated snow patches except in a shale or sandstone substrate.

This lack of aggregation is not surprising since adult and older instars were found to be extremely antagonistic toward other individuals and are cannibalistic. Except for 5 pairs in copulo, more than one individual was never found under a rock or within $1\frac{1}{2}$ feet of another during collections

of approximately 1000 individuals. On occasion, during dull overcaste days without wind and with temperatures between 0 and + 5° C., individuals were taken on the snow surface.

Two isolated populations were found only during the late fall and winter seasons. Grylloblatta barberi (Feather River, Plumas Co., California) and G. c. campodeiformis (Mt. Paul, Kamloops, British Columbia) occurred at elevations below 2000 feet. Field observations indicate that they both were active in the upper 3 to 5 feet of the hypolithion between October and February. Temperature measurements and collecting suggest that this depth of habitat could not be tolerated by the insects during the rest of the year and they retreat into the substrate. The talus slopes of Mt. Paul receive little winter snow and temperatures may be below - 30° C. Winter collecting indicates that the Grylloblatta population here migrates below the freezing level in the hypolithion and is only active in the upper portions where air temperatures are between - 5° C. and + 6° C. with no wind.

2. Spring Season

In most years the winter snow pack persisted until late spring at localities studied above 5000 feet. The Grylloblatta were found to occupy the same regions of the hypolithion during this period as they do in the winter.

As atmospheric surface temperatures rose there seemed to be increased snow surface activity. With the increased abundance of flying insects the Grylloblatta became active foragers on the snow surface during the early evening. Nocturnal surface activity was restricted to air temperatures between - 2 and + 5° C. and a humidity over 75 per cent. The insects retreated beneath the snow within minutes if the temperature dropped a few degrees or a light wind came up to lower the humidity.

In the subalpine, when the snow melted into isolated banks or patches during May and June, Grylloblatta was found in the shallow hypolithion, in fallen logs, and under small stones and in mosses at the snow edge. Grylloblatta was not found under large rocks or in shallow gravel embedded in mud or running water. Grylloblatta preferred a hypolithion that was moist but not wet. The early nymphal stage was found in wetter conditions than were the larger instars or adult forms. Short periods of contact with water did not have an adverse effect on these insects. Most stages of Grylloblatta were observed to walk through shallow pools or melt rivulets, and even under water for short distances. Three hours of submergence have no apparent adverse effect on adults, but four hours of submergence appear to be lethal. The penultimate instar can withstand 2 hours of submergence while 5 minutes of exposure beneath water appears lethal to the first instar.

3. Summer Season

In the alpine-subalpine habitats Grylloblatta occurred beneath the larger rocks deeply buried in subirrigated slopes, the smaller rocks at the snow edge, or deep within large rotting logs.

All stages were found nocturnally active on persistent snow fields or glacier margins within the limits of temperature and humidity stated previously. Nocturnal foraging began between 9:30 and 10:00 P. M. and rarely continued after 1:00 A. M.

4. Fall Season

The locations of the insects within the hypolithion during early fall were found to depend largely on the amount of winter snow pack and late spring and summer temperatures. In normal years Grylloblatta were usually found beneath rocks 2 to 3 feet in diameter which were partially buried at least $1\frac{1}{2}$ feet deep in subirrigated slopes. They were active between the smaller rocks that were buried beneath $1\frac{1}{2}$ feet or more of the vegetation mat. During this period nocturnal surface activity decreased because of the reduced amounts of snow and the shorter intervals of optimum temperatures and humidities.

The substrate depth of activity during the late fall in the hypolithion was found to depend solely on the time

of the first persistent snow. In the normal years snow depth was sufficient to insulate the shallow regions of habitat against below-0° C. temperatures and Grylloblatta was active in the same portions as during late summer. With periods of below-0° C. temperatures before the first snow the insects retreated deep into the habitat.

With the arrival of the first snow Grylloblatta were found beneath the smallest rock, above the surface in tree stumps and in damp moss in the diurnal period. When rain or snowfall occurred with temperatures between - 3 and + 6° C., all stages of the insect were at times found active on the surface. Nocturnal activity was never observed in late November and early December. The first instar nymphs were only found after the first snow in the fall. By mid-winter the second instar was captured. This has also been reported by Ford (1926) and Walker (1937). The limited presence of the first instar suggests that hatching of the eggs takes place after exposure to the first combination of below-0° C. temperature and snow.

On occasion Grylloblatta were found to be active beneath bark or small rocks that were covered with a trace of snow and when the atmospheric temperatures were down to - 10° C. These occasions were always preceded by higher air temperatures and some snow melt.

B. Activity in Cave Habitats

In the Bend area, Grylloblatta were found to be troglophilic cavernicoles except in winter months. During the winter when there was below-freezing temperatures and low humidities in the caves, the insects were not present in this habitat. As the temperatures and humidities fell, the arthropod fauna was found to migrate toward the surface, where they were found as typical hypolithions under rocks below the frost depth. During the spring, as the surface temperatures slowly rose, the insects migrated downward, eventually reaching the cave environment. Arachnida and Diplopoda were the first to re-occupy the twilight and upper dark zones of the cave, usually by mid-April. Evidently these groups are not as restricted by the humidities of the environment as Grylloblatta for they were also the last to migrate out during the late fall.

When humidities reached 80 per cent and percolating melt water had moistened the rock surfaces, Grylloblatta returned to the upper dark zone, usually in late May or early June, where they remained until the next winter.

Most years the hypolithion became very dry and warm by mid-April (Fig. 4) and then was not inhabited by the Grylloblatta. These insects invaded the various outer ecological zones of the cave in sequence, moving to the next deeper as the previous one became uninhabitable.

By March the Grylloblatta were active in the moss and shallow hypolithion of the surface adjacent to the entrance. The length of time this area was occupied appeared to depend on the temperature, rainfall and melt water runoff. In normal years this region became very dry and warm by mid-April and the insects retreated deeper into the lower entrance zone. During the nocturnal period the Grylloblatta were observed to search for food in the upper regions of the entrance and on the surface, especially on melting snow banks. This surface and entrance activity was evidently governed by humidity rather than by temperature, for night-time temperatures were usually around or below freezing at this time of the year. The Grylloblatta were only active on those nights when the humidity was above 75 per cent and in still air. A slight breeze and drop of the humidity was found to induce the Grylloblatta to retreat within minutes to the lower regions of the entrance zone.

In May, when there was a sharp temperature rise in the entrance zone (Fig. 4), the insects moved into the twilight and upper dark zones. These zones were occupied then until late October or November, at which time the Grylloblatta evacuated the cave environment rapidly. They then became occupants of the hypolithion.

During the winter months Grylloblatta were active in the hypolithion below the frost zone regardless of the surface temperature. Insects were observed and collected

1 m. below the surface when the air temperature was - 12 to - 20° C. In mild periods of the winter, especially during and immediately after wet snow storms when temperatures were slightly above zero, the insects were often active on the snow surface. The Grylloblatta, found in the high lava plateaus of western North America, for most of the year were thus true cavernicolous troglophiles. When the cave environment became unfavorable, they then became hypolithions.

IV. Discussion and Summary

The hypolithic activity of Grylloblatta in the alpine-subalpine of the western Cordillera temporarily varies in response to the effects of the climatic conditions. The insect is restricted to certain parts of the hypolithion and shows limited surface activity, probably because of its narrow temperature-humidity optimum. Snow depth and spring-summer temperatures are the most important factors regulating yearly activity.

Grylloblatta do not hibernate (Mills and Pepper, 1937; Henson, 1957a, 1957b) and, hence, are dependent on adequate snow cover for protection against the atmospheric cold and low humidities of the winter season. When

snow depth is sufficient to insulate against extreme dryness and cold the Grylloblatta are active in the shallow hypolithion and ground surface beneath the snow.

Adequate snow pack during the spring and early summer provides the low temperatures and high humidities necessary to the insect and it remains active in the hypolithion and beneath the snow. As the snow melts during the summer, diurnal activity is restricted to the deeper hypolithion that is subirrigated by melt water. Here, during the highest summer temperatures, 15 to 20 feet below the surface, high humidity, ice, and air temperature around 0° C. are often present (Kamp, 1963).

Fall season is the most critical for the Grylloblatta. In the western Cordillera the early fall is generally the driest and warmest season. During this period the insects will only be active deep in the hypolithion. Some snow is necessary during the later fall as protection against the rapidly falling temperatures.

Surface activity may take place at any season of the year, but is limited to a range of - 2 to + 5° C. and at least 75 per cent humidity, but is usually restricted to the nocturnal period. Winter snow surface activity has been reported by Fletsch (1947), Campbell (1949) and Gurney (1953), but they did not give details of the snow surface microclimatic conditions that permit such activity.

Cavernicolous species are typical hypolithic inhabitants

during the winter when the cave environment is too cold and dry. In the spring, when cave temperatures slowly rise, the insect re-enters the cavernicolous habitat, occupying each deeper zone as the more shallow one becomes too dry or warm.

Temperature and Humidity Preference of Grylloblatta

I. Introduction

It is often stated in the literature that the preferred habitat of Grylloblatta is cool and damp. The few temperature-humidity preferenda and the optimum and lethal limits reported are conflicting. Mills and Pepper (1937) reported an optimum of $+ 3.7^{\circ}$ C., a preferendum between $+ 0.1$ and $+ 15.5^{\circ}$ C., with lethal limits about $- 6.2^{\circ}$ C. and $+ 27.8^{\circ}$ C. A preference range between $- 2.5^{\circ}$ C. and $+ 11.3^{\circ}$ C. was stated by Edwards and Nutting (1950). Henson (1957b) published an optimum of $+ 1.0^{\circ}$ C. and a preference range between $- 3.0$ and $+ 5.0^{\circ}$ C. Humidity requirements are inferred to be 100 per cent. In the test procedures described by each there was no statement of the humidity at the time of testing nor any control of the relative per cent. In the above studies the insect tested was G. c. campodeiformis, collected from Gallatin Canyon, Montana.

Field data of temperatures at times of collection have been reported to be $- 9.44$ to $+ 15.56^{\circ}$ C. by Campbell (1949), $- 1.8$ to $+ 7.22^{\circ}$ C. by Kamp (1963), and

+ 1.1° C. by Chapman (1953). These temperatures were from four different species of Grylloblatta, ranging from British Columbia to Montana and California.

From these apparent contradictions, the questions arise as to whether the differences are due to experimental conditions, acclimatization of test specimens, seasonal responses, nutrition, age, or the varying preferences by different species and populations. In an attempt to answer these questions, I investigated the temperature-humidity responses under controlled laboratory conditions.

II. Materials and Methods

The fundamental principle underlying these studies is that of attempting to simulate in the laboratory the spectrum of natural conditions under which Grylloblatta have been observed or have been reported to encounter in their natural habitats. Accordingly, four criteria were established for these experimental procedures: 1) use of a multiple rather than a single factor approach, 2) use of gradients of temperatures and humidities comparable to those in the habitat, 3) use of different populations and species, and 4) use of insects of known sex, length of time in captivity, nutrition, and holding temperatures and humidities.

A. Experimental Chamber

I designed and built a multiple factor environmental gradient chamber. The chamber is a highly modified and specialized design based in part, in terms of operating principles, on the circular gradient chamber of Pratt, Collins and Witherspoon (1957).

Pratt's chamber is of ideal design for work on flying insects at ambient or higher temperatures. In working at temperatures ranging around 0° C. and humidities of 70 per cent and higher, many physical problems are encountered. The manufacturer's published data for transparent plexiglass and its resistance to fluids are not valid in the range of -25 to $+15^{\circ}$ C.

The solutions generally used to establish and maintain relative humidity become toxic to the insects and to the sensors used to record humidity. In atmospheres of high relative humidity, as the dew point of the atmosphere is reached by lowering the temperature, condensation, fog and rain form in the chamber.

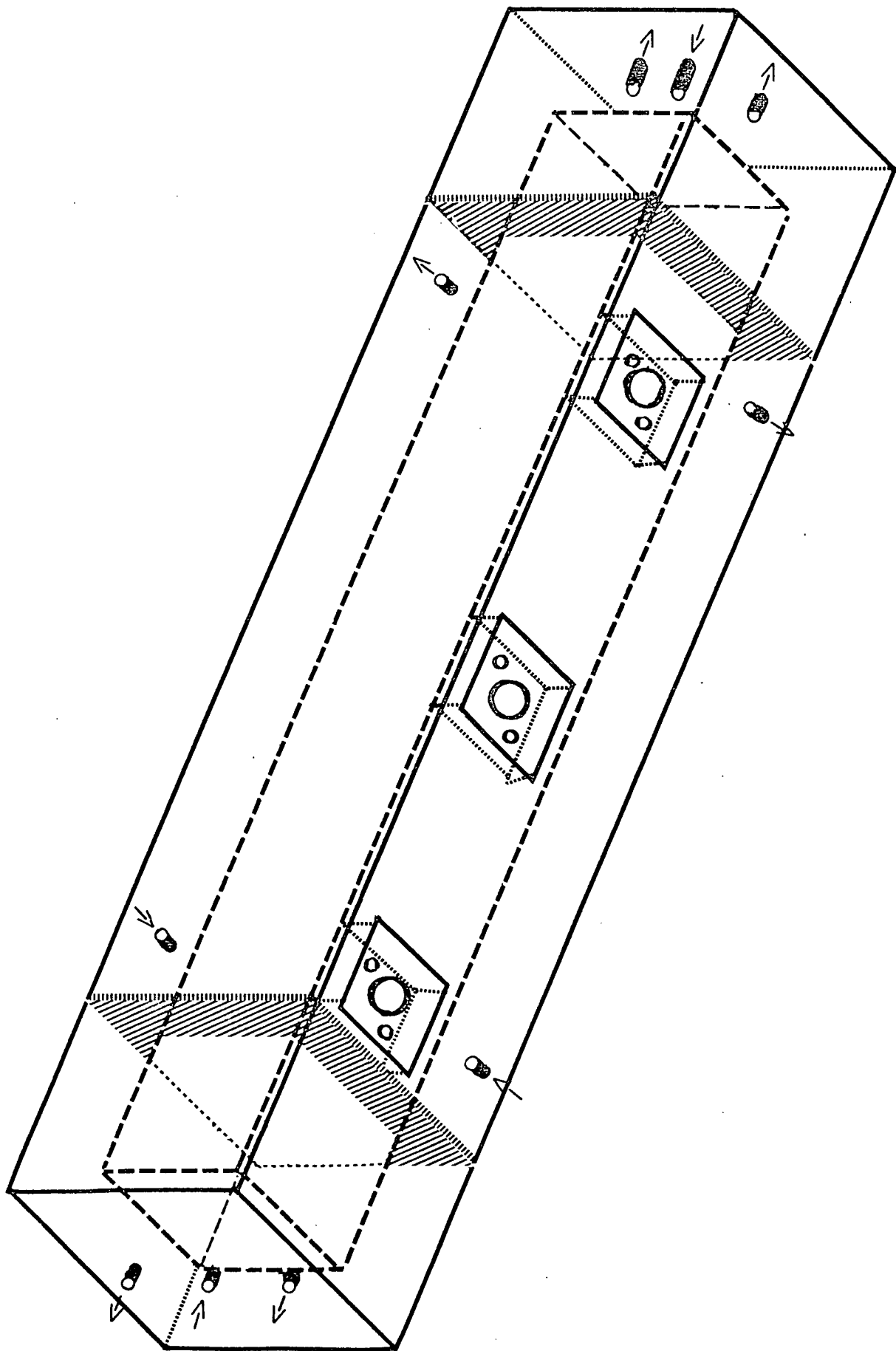
The test chamber I used was a rectangular transparent plexiglass tube (15 x 15 x 138 cm. and 1.25 cm. thick) surrounded by separate heat exchangers lengthwise and at either end for temperature control. Each heat exchanger had

separate inlet and outlet pipes (Fig. 5). Three access ports were spaced equidistantly on the top for insertion of insects and sensing elements. Solution boxes for humidity control were at either end. The entire test chamber was housed in a 6 x 3 x 2 -foot refrigerated cabinet. Three circulating pumps (Gebruber-Haake 2-model, FS 1-model HK) were outside the cabinet and connected to the heat exchangers by insulated tubing.

Temperature gradients were established and maintained by the circulation of soya oil and a saturated solution of NaCl through the two end heat exchangers. The temperature of these heat exchangers was higher and lower than the maximum and minimum temperature of the gradient for a given test. The temperature of the liquid in the lengthwise heat exchanger was that of the mid-point of the gradient desired. The temperature of the refrigerator cabinet was usually maintained at or below the mid-point of the gradient.

By varying the choice of temperatures and the flow rates in and out of the heat exchangers, it was possible to establish an atmospheric temperature gradient of 10 to 15° C. in the inner chamber in 4 to 10 hours. The lower the desired gradient was in temperature, the longer the time necessary to establish the gradient. Once the gradient was established and stable it held from 4 to

Figure 5. Transparent view of temperature-humidity chamber. Arrows indicate direction of flow for temperature control into the three separate heat exchangers. Heat exchangers are separated by hatched partitions in diagram. Three access ports located on top for insertion of sensors and specimens. Scale is 1/10 actual size.



8 hours over a temperature spectrum of -15 to $+20^{\circ}\text{C}$. The flow rate of the cold heat exchanger was 2 to 3 times that of the higher heat exchanger. The flow rate in the middle heat exchanger was adjusted to be $1/3$ to $1/4$ that of the high exchanger. It was possible to maintain a gradient for 12 to 24 hours by periodic adjustment of temperature and flow rates of each heat exchanger. Temperatures were recorded along the gradient with 6 equally spaced YSI Type 4 thermistors calibrated to 0.2°C .

Over the range of temperatures that were tolerated by Grylloblatta, the regulation of relative humidity was the most difficult operation of the chamber. It was not hard to establish and maintain a gradient of humidity of 10 to 15 per cent within the range of 40 to 80 per cent relative humidity at a temperature gradient above $+10^{\circ}\text{C}$. Below $+10^{\circ}\text{C}$., when the vapor pressure approached saturation (humidities of 95 per cent and higher), at the dew point temperature and below condensation, fog and rhime formation caused rapid shifts in the relative humidity in the closed system.

Mixtures of glycerol-water were found to be preferable to salt solutions in establishing humidity gradients in this chamber. Glycerol-water mixtures maintained the desired humidity over the longer periods of time and were relatively non-toxic to Grylloblatta and the humidity sensors were not seriously affected by these chemicals. The concentrations of glycerol to water for a given humidity were found by trial and error. Data available regarding

concentrations of glycerol-water mixtures for a specific humidity were based on an air volume of 1 liter, a very large surface-to-air ratio (Stokes and Robinson, 1949; Winston and Bates, 1960).

For humidity gradients from 90 to 99 per cent relative humidity, the bottom of the chamber was lined with $\frac{1}{2}$ -inch thick sponge rubber and saturated with distilled water. A gradient of 90 to 99 per cent was possible with the arrangement over a temperature range of -5 to $+10^{\circ}$ C. for periods of 2 hours. Lower humidity gradients of 20 per cent were possible for periods of four hours, using glycerol-water mixtures. Relative humidity was recorded in the chamber using 3 equally spaced narrow range hygrosensors (Hygro Dynamics Co., type H-3) individually calibrated to ± 1.5 per cent relative humidity from -10 to $+60^{\circ}$ C.

B. Test Methods

Specimens of adult Grylloblatta campodeiformis campodeiformis Walker were collected from Athabaska, Jasper National Park, Alberta, at an elevation of 7100 feet. Specimens of Grylloblatta lavacola were obtained from McKenzie Pass, Cascade Mountains, Oregon. The specimens were transported to the laboratory in individual containers at 95 + per cent humidity and at 0 to $+4^{\circ}$ C. They were then held under the same conditions in environmental cabinets (Controlled Environment Ltd.) until needed and

also between the test periods.

Specimens were tested a) within seven days of capture, and b) over a period of four months, for possible temperature acclimatization. Individuals were exposed to the following temperature gradients: 1) - 8 to + 5° C., 2) - 5 to + 10° C., 3) + 5 to + 20° C. Each temperature gradient was tested with the following humidity gradients: 1) 50 to 70 per cent relative humidity, 2) 70 to 90 per cent relative humidity, 3) 90 to 99 per cent relative humidity. Each insect was exposed only to one combination per day and returned to the holding humidity and temperature in the laboratory environmental chamber.

For the experiments, the insects were placed in the center of the test chamber, which in most trials was the mid-point of the temperature gradient being tested. Since Grylloblatta become very agitated and hyperactive upon handling, a ten minute period was allowed before recording position in the gradient. During this period the insect would rapidly explore the entire length of the test chamber regardless of the temperature-humidity gradient it encountered.

The insect's position in the gradient was recorded every 10 minutes for 30 minutes. The insect was then made to move from the last zone recorded and then its position was recorded again after 10 minutes. These time periods were chosen for it was observed that the insects would position themselves in the most tolerable portion of the gradient within 10 to 20 minutes and then stay within that

narrow range. In an attempt to determine whether fatigue and/or habituation were influencing the initial rest point, the insects were made to make another choice after 30 minutes.

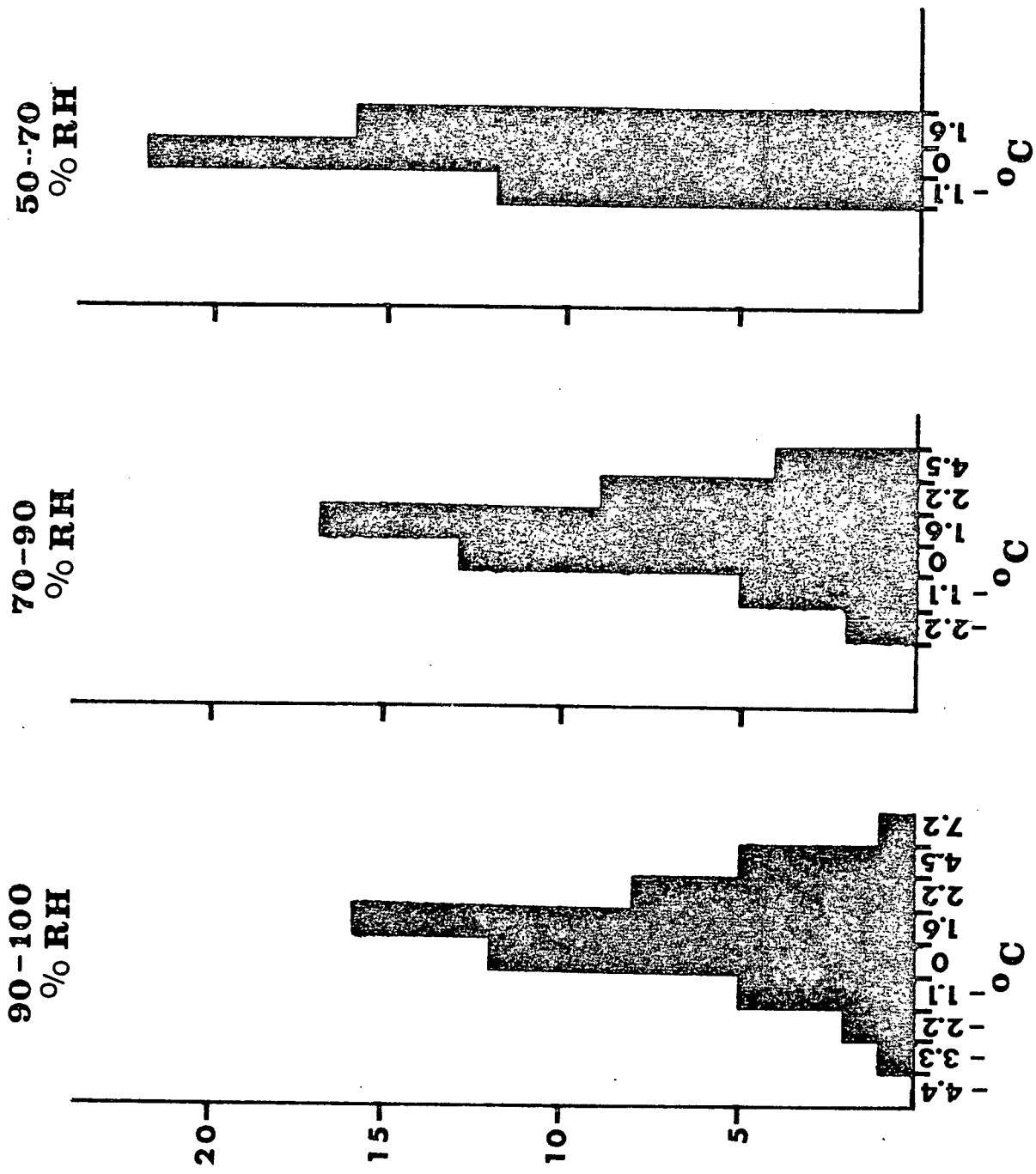
III. Results

A total of 50 adult Grylloblatta were tested in each gradient of temperature-humidity. Twenty females and five males were used of G. lavacola and twenty-two females and three males of G. c. campodeiformis.

At a temperature-humidity gradient of -8 to $+5^{\circ}$ C. and 90 to 99 per cent relative humidity, no individuals preferred a temperature below -3.5° C. Over the temperature range of -3.5 to $+5^{\circ}$ C., an approximately normal distribution curve was recorded. Thirty-eight insects preferred a temperature range between 0 and $+2.22^{\circ}$ C., with sixteen preferring about $+1.67^{\circ}$ C. Testing at the same temperature gradient and a humidity gradient between 70 and 90 per cent, the distribution was compressed between -2.22 to $+4.50^{\circ}$ C., with thirty individuals preferring between 0 and $+1.67^{\circ}$ C. At a humidity gradient of 50 to 70 per cent, only a narrow temperature range was chosen (between -1.11 and $+1.67^{\circ}$ C.) by all individuals (Fig. 6).

In a test temperature gradient of -5 to $+10^{\circ}$ C. and at the above three humidity gradients, the insects showed very little change from that exhibited at -8 to $+5^{\circ}$ C. One female specimen of G. lavacola preferred a temperature

Figure 6. Temperature response of adult Grylloblatta campodeiformis and G. lavacola to various controlled relative humidity ranges. Fifty trials were used for each range.



around $+ 7^{\circ}$ C. Over the other humidity gradient of 70 to 90 and 50 to 70 per cent, no statistical changes were found. During testing in a temperature gradient of $+ 5$ to $- 20^{\circ}$ C., all individuals were recorded within $+ 5$ to $+ 6^{\circ}$ C., regardless of the humidity gradient.

Figure 6 is a summary of total individuals tested at the various gradients. No individuals were exposed to humidities below 50 per cent. I observed, both in the field and in the laboratory, that individuals exposed to lower relative humidities, even for very short periods, underwent rapid dessication and a 50 per cent mortality.

With the sole exception of the female G. lavacola that chose a temperature of about $+ 7^{\circ}$ C., no difference was detectable between the two species or between sexes. Grylloblatta campodeiformis campodeiformis specimens were collected 685 miles north of G. lavacola and 2000 feet higher in elevation. One would possibly expect some differences in temperature and humidity tolerances between these populations, yet test results were identical.

IV. Discussion and Summary

Laboratory temperature preference data many times do not represent the actual habitat preferences of the organism. The apparent discrepancies of some reports are undoubtedly due to acclimation to pre-experimental conditions, wide range of preference, seasonal responses, nutrition, age,

varying populations and species preferences, inadequate test chamber or methods, no control of humidity, and lack of field data for comparison. Mills and Pepper (1937), for example, did not take humidity into account in their temperature gradient.

An observation chamber in which one can control simultaneously gradients of temperature and humidity does present some problems of design and operation. However, the design I used functioned admirably over the ranges tested, that is the ranges found in the natural habitat. It has also been used with success by others testing amphibia and various orders of insects (Licht, unpubl.; Scudder, unpubl.). The parameters of age, sex, nutrition and acclimation were carefully controlled in the present experiments.

The temperature preference of Grylloblatta in this study, like that observed in earlier studies (Mills and Pepper, 1937; Edwards and Nutting, 1950; Henson, 1957b) is much lower than that found in the majority of insects (Mills and Pepper, 1937; Wigglesworth, 1965; Heath et al, 1971). This is not surprising in an insect that is active throughout the winter at high elevations.

Both species of Grylloblatta studied at 90 to 99 per cent relative humidity preferred a temperature between - 3.5 and + 5° C., the optimum being + 1.67° C. These data agree with the temperature preference reported by Henson (1957b) with a saturated atmosphere. At no stage

in the experiments did the preferred temperature range expand significantly above + 5° C. Thus, when the gradient was + 5 to + 20° C. and the relative humidities between 90 and 99 per cent, 70 and 90 per cent, or 50 and 70 per cent, the insects preferred the + 5 to + 6° C. area.

Since the Grylloblatta used by Henson (1957b) were G. c. campodeiformis, and those in this study were G. c. campodeiformis from Athabaska, Alberta, and G. lavacola from McKenzie Pass, Oregon, and since all showed a similar temperature preference, it would seem that the various species and populations of Grylloblatta in western North America might have similar requirements. Although one female G. lavacola showed a preference for + 7° C., this is still close to the rest of the data obtained.

The findings of Mills and Pepper (1937) for G. c. campodeiformis from Gallatin Canyon, Montana, differ significantly from the present results. They found the optimum to be + 3.7° C. and the normal range of preference from + 0.1 to + 15.5° C. While it is possible that they were using insects with quite different attributes, it is also possible that their data are in error because they did not control or evidently attempt to consider the humidity conditions in their experimental set-up. This omission is one that is frequent in much of the early work on insect temperature preference, and has been stated to be a factor producing erroneous results (White and Zar, 1968).

Edwards and Nutting (1950) stated the preference range in G. c. campodeiformis (material obtained from Pepper) to be $- 2.5$ to $+ 11.3^{\circ}$ C., since between these temperatures the insects remained quiet in the respirometers used in their experiments. While this range is somewhat closer to the range obtained in the present study and by Henson (1957b), it still seems rather high. Again, the insects may be different to those used herein, and humidity was evidently not taken into account. However, these data were not obtained in gradient preference experiments and so should not be taken for close comparison with other findings.

Until more populations of Grylloblatta are studied in detail , with full cognisance of the importance of the humidity-temperature interaction in these insects, it is not possible to state categorically that all Grylloblatta have the same requirements. Indeed, in situations where two species coexist, as in Edison Ice Cave and McKenzie Pass, it could well be that they differ in their temperature requirements, since one of the factors permitting coexistence in closely related species can be a difference in temperature preferences or optima (Heath et al, 1971; Jamieson, 1973). The most recent data suggest that Grylloblatta in western North America do have similar temperature-humidity preferences, and it would be instructive to study coexisting species and other populations, such as those at Kamloops, British Columbia, where they occur

at 1400 feet in an area that is normally quite hot and dry. Unfortunately, material from such populations was not available for inclusion in the present research.

The preference range of -3.5 to $+5^{\circ}$ C. obtained in the laboratory seems to coincide almost exactly with the range of temperatures normally encountered in the hypolithion and cavernicolous microhabitats that Grylloblatta occupy. The field data showed the hypolithion to remain over the year between -3 and $+6^{\circ}$ C. with a humidity over 70 per cent, and the cavernicolous habitats, when occupied in the spring, summer and fall, had the same range. Chapman (1953), from field collections, considered that the optimum was $+1.1^{\circ}$ C. and Kamp (1963) has previously reported the range as between -1.8 and $+7.22^{\circ}$ C. in the field. The figures given by Campbell (1949), namely -9.44 to $+15.56^{\circ}$ C., would appear to be too wide and perhaps based on general environmental temperatures rather than on the microenvironment in which the insects live.

Finally of note is the narrowing of the preference temperature range as the humidity decreases. This same phenomenon has been found in various species of woodlice (Tracheoniscus) (White and Zar, 1968) and is evidently a response that can lead to a reduction in water loss by evaporation. The integument of Grylloblatta is a thin cuticle with very extensive membraneous areas. Field and laboratory observations confirm that Grylloblatta is

extremely susceptible to dehydration, even over the preferred temperature range, when the humidity falls below 70 per cent.

While warmer air can hold more water vapor than colder air, the vapor pressure is also higher for warmer air. For example, maximum vapor pressure (saturation) at + 5° C. is 6.54 mm. Hg. and is 4.58 mm. Hg. at 0° C. (Landsberg, 1962). When the air is lower than saturation, the diffusion gradient would be from the insect to the air and the organism would lose water. Grylloblatta, by moving to a lower temperature when exposed to humidities below 70 per cent, decreases the vapor pressure deficit (saturation deficit) and an equilibrium relative humidity condition is found higher than the atmospheric humidity around the insect by the process of vapor pressure stabilization (Sellers, 1967). For conservation of water at low atmospheric humidities, the saturation deficit at a given temperature is of greater importance to survival than relative humidity alone. Therefore, Grylloblatta decreases the range of temperature preference as humidity decreases and this changes the saturation deficit which reduces water loss from the body of the insect.

Temperature Tolerance and Lethal Limits of Grylloblatta

I. Introduction

The temperature-humidity experiments showed that two species of Grylloblatta have a temperature preference between about - 4 and + 7° C. and a humidity preference of greater than 90 per cent. These experiments, which allowed free choice of temperature and humidity, do not demonstrate the full range of temperature in which Grylloblatta can survive.

Previous studies have set the upper lethal limit in G. c. campodeiformis as + 27.8 ± 1° C., and the lower limit as - 6.2° C. (Mills and Pepper, 1937). However, Edwards and Nutting (1950) set the upper limit at + 20.5° C. and Campbell (1949) states that they freeze at - 3.5° C. (+ 26° F.). There is obviously some disagreement. Since it has been suggested that the temperature preferences reported in the literature may be in error, the extremes of temperature survival need verification. This is important because the extremes of high or low temperature may govern their distribution to a considerable degree.

II. Materials and Methods

In an attempt to establish parameters of tolerance

to temperatures and lethal limits, the following procedure was employed.

The test equipment utilized a Gebruder-Haake constant temperature circulator and a small transparent chamber immersed in the circulator bath. The circulator was controlled by a variable thermoregulator accurate to 0.05° C. and operated over a range of -35 to $+100^{\circ}$ C. A saturated solution of NaCl was used in the bath as the heat exchanger.

The test chamber for the insects was constructed of 25 mil milar plastic $1\frac{1}{2} \times 3 \times 5$ inches and was sealed to maintain humidity. This chamber was lined with $\frac{1}{4}$ -inch sponge rubber on the bottom and 1-inch on all sides. The sponge rubber, when saturated with distilled water, provided a humidity of 95 per cent and also insulated the insects from contact with temperatures differing from the chamber atmosphere. A YSI thermistor, calibrated to 0.05° C. from -10 to $+25^{\circ}$ C. with a 10-second response time, monitored the chamber air temperature.

The Grylloblatta were chosen at random from the series used in the preference experiments. I believe the choice to be valid for I found no change in response, at least over the range tested, to have taken place during the four-month test period.

Prior to a given test run, the atmospheric temperature of the immersed test chamber was adjusted to the same temperature as the housing container for the insect ($+2$ to $+4^{\circ}$ C.). The insect was allowed to explore and to

become adjusted to the chamber for 10 minutes after being placed in it. The atmospheric temperature of the chamber was changed at a constant rate of 1° C. per 2.5 minutes. Temperatures and reactions of the insect were recorded every minute.

"Normal activity" of Grylloblatta was recorded when the insect exhibited the following behavior: body slightly elevated above substrate, slow measured walking, antennae moving and touching some object as if exploring surroundings, cerci straight or with slight downward curve. "Decreased activity" was typified by: sternum on substrate, antennae limp or not moving, cerci relaxed. "Increased activity" was defined as: rapid non-directional movement over substrate, sternum greatly elevated, rapid waving of antennae. "Hyperactivity" was defined as being an intensified pattern of the increased activity with an upward arching of the entire abdomen. Paralysis was shown by: little or no response to an external stimulus, entire sternal region on substrate, legs laterally extended. Spasm or tetany was defined as an uncontrolled jerking and twitching of legs and antennae. Death was preceded by a tetany in which the insect assumed almost normal posture and then slowly fell over on the pleural region, with rigid legs and no recovery if removed from that temperature.

III. Results

Under the test parameters as the temperature increased

the insects exhibited normal activity until a temperature of $+ 6.5 \pm 0.2^{\circ}$ C. was reached. From $+ 6.8$ to $+ 11^{\circ}$ C. $\pm 0.1^{\circ}$ C., the activity was reduced. Increased activity began at $+ 11.5 \pm 0.3^{\circ}$ C. and progressively intensified when it became hyperactive at $+ 16^{\circ}$ C. The insects were hyperactive over the temperature range of $+ 16$ to $+ 21.0 \pm 0.5^{\circ}$ C. At $+ 22^{\circ}$ C. the insects were paralyzed and death took place between $+ 23.0^{\circ}$ C. and $+ 23.3^{\circ}$ C. (Fig. 7). Shortage of specimens prevented extensive study of short term acclimation in these insects.

The insects exposed to decreasing temperatures remained normally active to $- 2.2^{\circ}$ C. Activity was reduced between $- 2.2$ and $- 4^{\circ}$ C. $\pm 0.5^{\circ}$ C. The insects become increasingly active during the period of temperature between $- 4.0$ and $- 5.5^{\circ}$ C. $\pm 0.5^{\circ}$ C. The insects experienced a sudden paralysis at $- 5.5^{\circ}$ C. and a tetany and spasms between $- 6.5$ and $- 7^{\circ}$ C. with death following between $- 7.5$ and $- 8.0^{\circ}$ C. Insects were also exposed to various temperatures for long term survival in the zone of fatal high temperature. The results are presented in Table I and Figure 7.

IV. Discussion and Summary

Sudden changes of climatic condition in the alpine-subalpine are common. A thirty-degree change in temperature within an hour is not unusual and the humidity can also change as rapidly. Hence, Grylloblatta can be exposed to temperatures and humidities beyond the preferenda

Figure 7. Temperature tolerance and lethal limits of adult Grylloblatta campodeiformis and G. lavacola when exposed to 1° C. temperature change each $2\frac{1}{2}$ minutes. Solid bar = length of tolerable exposure; oblique hatched bar = occurrence of 50 per cent mortality; narrow bar = longevity from 50 to 100 per cent mortality; vertical hatched bar = survival through test period. Alphabetical letters indicate the activity behavior and temperature range shown in Table 1.

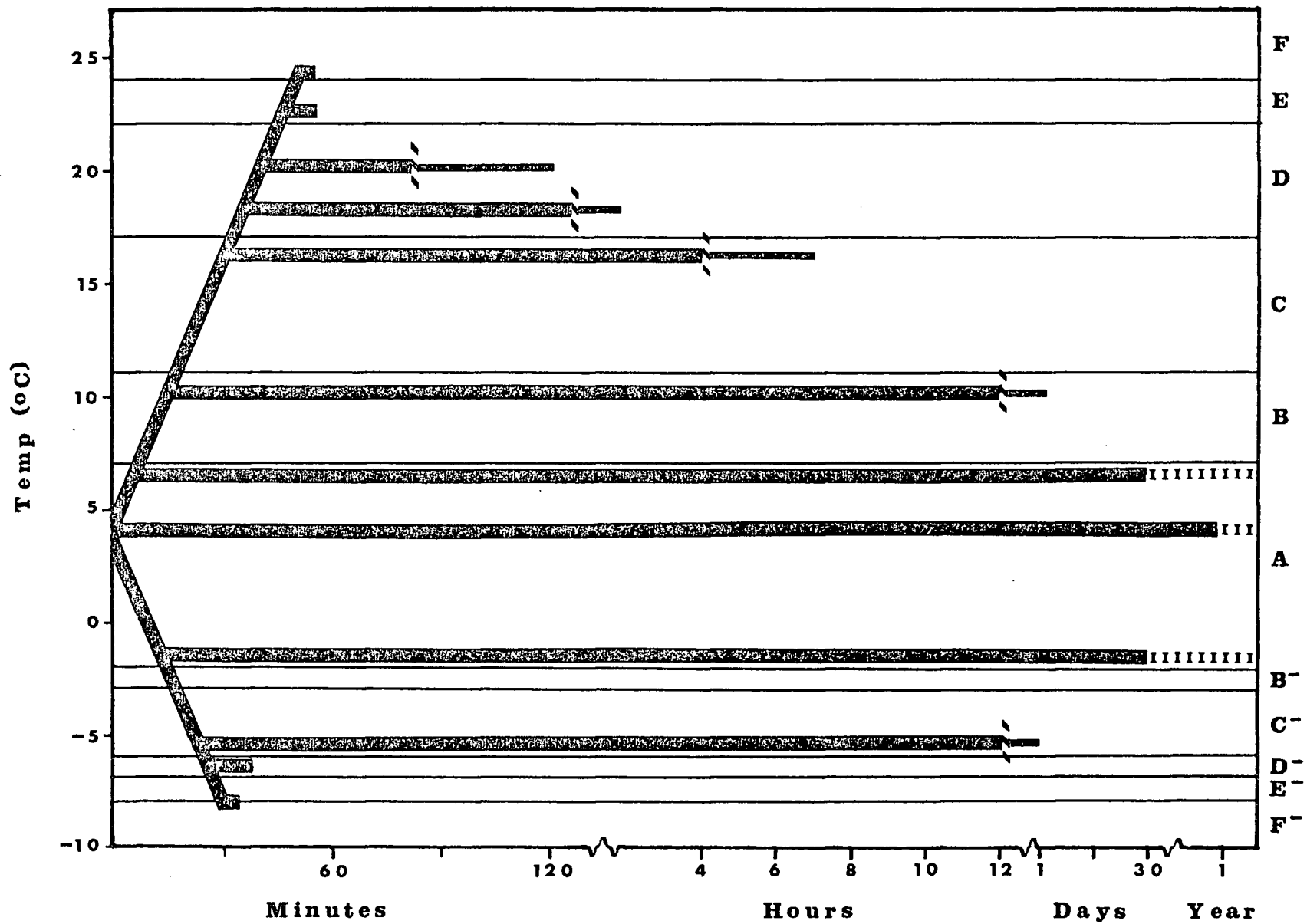


TABLE I

Temperature Tolerance and Limits of Grylloblatta

<u>Tolerance and Lethal Limits*</u> (1° C. shift/2.5 minutes)	<u>Long Term Exposure</u> (mortality in per cent)
A Normal activity -2.2 to -6.8° C.	+ 10° C. for 12 hours - 50% for 24 hours - 100%
B- Decreased activity -2.2 to - 4° C.	+ 16° C. for 4 hours - 50% for 7 hours - 100%
C- Increased activity - 4 to - 5.5° C.	+ 18° C. for 1½ hours - 50% for 2½ hours - 100%
D- Paralysis - 5.5 to - 6° C.	+ 20° C. for 40 min. - 50% for 2 hours - 100%
E- Spasm tetany - 6.5 to - 7° C	+ 22° C. for 1 min. - 75% for 10 min. - 100%
F- Death - 7.5 to - 8° C.	+ 23.5° C. for 1 min. - 100%
B Increased activity + 6.8 to + 11° C.	

*Alphabetical letters refer to those in Figure 7.

C Increased activity

+ 11 to + 16° C.

D Hyperactivity

+ 16 to + 21° C.

E Paralysis

+ 22° C.

F Death

+ 23 to + 24° C.

should they venture out from their regular microhabitats. This they do quite often for they come out, for example, to forage on snow fields or on glaciers at night, where they can capture prey numbed by the cold (Ford, 1926). They are then often caught by a sudden change in temperature and perish.

Grylloblatta can maintain activity over a wider range of temperature than the preferred range. In humidities of 95 + per cent the range of activity was between - 4 and + 11° C. in contrast to the preferred choice of - 3.5 to + 5° C. These results are in agreement with the data obtained by Edwards and Nutting (1950). Activity was reduced at the extremes, but Grylloblatta can survive at + 10° C. and at - 4° C. for at least six hours without mortality. Activity increased between + 11 and + 16° C. and also between - 4 and - 5.5° C. This increased activity exhibited in the small test chamber was undoubtedly a searching mechanism for a more tolerable temperature. There is evidence for this hypothesis in that an exposure of four hours at + 16° C. caused 50 per cent mortality and increased to 100 per cent within seven hours. The time of exposure to - 5.5° C. that caused mortality was shorter than the higher temperature with 50 per cent mortality within one hour.

Paralysis from exposures to below-zero temperatures is reversible if the insect can reach - 4° C. within five

minutes. Grylloblatta, paralyzed by exposure to high temperatures (ie. + 22° C.), cannot recover and a one-minute exposure is lethal to most individuals.

Thus, the short term survival data suggest an upper limit of about + 23° C. and a lower limit of - 8° C. These results are not greatly different from those obtained by Mills and Pepper (1937), although their upper limit would appear to be too high. The results in the present thesis were obtained with a 95 per cent relative humidity; the humidity in the Mills and Pepper (1937) experiments is unknown.

The upper limit of + 20.5° C., stated by Edwards and Nutting (1950), was based on a 1½-hour exposure period and so cannot be compared with the short term exposure results of the present study. However, the long term exposure data obtained in the present research agree almost exactly with the above figure, for at + 20° C. Grylloblatta survived only for about two hours. There would thus seem to be no great discrepancy in the general temperature extremes said to be tolerated by these insects: the experimental methods each time must be taken into account.

These data indicate that Grylloblatta is a cryophilic form with a narrow range of temperature and humidity tolerance. The fact that the hemolymph has a freezing point depression of 0.98° C. (unpublished data) bears this out. However, the depression is not as great as in such cold-hardy insects as Bracon cephi (Salt, 1959). Further,

it is of interest to note that, while Grylloblatta shows a respiration maximum at $+ 20^{\circ}$ C., there is no metabolic adjustment to temperature in this insect. The slope of the temperature-metabolism curve is the same as for Thermobia domestica which has a temperature optimum of $+ 37.5^{\circ}$ C. (Edwards and Nutting, 1950).

III. SYSTEMATICS, DISTRIBUTION AND ZOOGEOGRAPHY

Introduction

Knowledge of the family Grylloblattidae has grown slowly since the original description. It now contains three genera, namely, Grylloblatta Walker, 1914, Grylloblattina Bei-Bienko, 1951, and Galloisiana Caudell, 1924, and fifteen species.

The early described forms, such as Grylloblatta campodeiformis campodeiformis Walker, 1914, Grylloblatta barberi Caudell, 1924, Galloisiana notabilis Silvertri, 1927, Grylloblatta campodeiformis occidentalis Silvestri, 1931, and Grylloblatta sculleni Gurney, 1937, were based on immature stages or adult females as type material. Such species and descriptions, based on a few females or immature specimens, is not surprising since Grylloblattidae have long been considered among the rarest of the insects.

The description of species and subspecies from female and immature specimens has caused some confusion regarding the validity of some populations, for topotype adults and especially adult males are still unknown for some. Immature stages of most species are exceedingly difficult, if not impossible, to differentiate from each other. In addition, adult females possess few taxonomic characters of discriminatory value at the species level. It has been increasingly

evident that taxonomy and systematics must be based on males since the male genitalia are of great importance having many specific characters (Gurney, 1961; Kamp, 1963).

The known distribution of Grylloblattidae suggests that they are limited to the eastern Palaearctic and western Nearctic faunal regions of the world. A more limiting descriptive faunal region would be the Cordilleran complex of the Pacific rim. It is, of course, not impossible that Grylloblattidae may eventually be found in some other parts of the world. The discovery of Grylloblattidae elsewhere would be surprising, since there has been widespread interest in the group, and many competent entomologists have searched most areas of the world for these insects.

Mani (1968) and his associates have found no evidence of the group in the Cordillera of the Himalaya-Pamir complex. Bei-Bienko (1951) and Sharov (1968) have literally combed the U. S. S. R. without finding a single population except for one form found in the Maritime-Siberian region of the Pacific. I and many others have searched the alps and ice caves of Europe and the arctic of North America and others have looked during expeditions in South America without finding a single specimen. In addition, the fact that no insect at all nearly related to the group has ever been found is evidence of the restricted and scattered distribution, and is suggestive of the fact that these insects

must be the last survivors of an ecologically highly specialized nearly extinct group.

The separation of the Palaearctic and Nearctic genera was probably not a very recent event (Gurney, 1961). There has been intermittent land connection between North America and Asia throughout the geological ages (Simpson, 1947) and in the absence of fossil evidence, it is impossible to say at what time the range of the family was continuous.

If the family is confined to mountainous hypolithion and lava ice cave habitat, as the present evidence indicates, and is not present in the regions of continuous permafrost of the arctic or subarctic low elevations, it is somewhat improbable that the group crossed the land bridges connecting Alaska and Siberia at various times during the Pliocene and Pleistocene epochs.

Before this study knowledge of the family showed that there were nine species of Grylloblatta in the western Nearctic Cordillera, a single species, Grylloblattina djakonovi, in the Primuryo Territory, 90 miles east of Vladivostok, Mariames, Siberia, U. S. S. R., and six species of Galloisiana on the Japan Archipelago.

Since the Grylloblattodea are unknown in the fossil record, any attempt to decipher the distributional history of the genus Grylloblatta cannot be based on paleontological data. The present distribution and zoogeography can only be understood by reference to the climatic, geographic

and geological changes that have taken place in the past. Since it has been noted in the previous section of the thesis that this requires very detailed study of these factors for each population and since I have had first-hand experience only in western North America, only the Nearctic distribution can be adequately considered herein.

Materials and Methods

The distribution of all populations of Grylloblatta in western North America was mapped. Material from as many of these localities as possible was then obtained and studied taxonomically. Further collecting then in these same localities and at likely intermediate stations was then undertaken. From these studies, the taxonomy of the Nearctic Grylloblatta was clarified and the possible systematic relationships were established. Detailed distributions for each species could then be determined.

Results

The Nearctic Species

Fifteen species and five subspecies have been recognized in the present research (Table II). From morphological features, such as size, number of antennal segments,

TABLE II

List of Species and Subspecies of Grylloblatta

- Grylloblatta campodeiformis campodeiformis Walker 1914
- Grylloblatta campodeiformis athapaska ssp.n.
- Grylloblatta campodeiformis nahanni ssp.n.
- Grylloblatta scudderi sp.n.
- Grylloblatta occidentalis Silvestri 1931
- Grylloblatta skagitensis sp.n.
- Grylloblatta chirugica Gurney 1961
- Grylloblatta hoodalles sp.n.
- Grylloblatta sculleni sculleni Gurney 1937
- Grylloblatta sculleni cryocola ssp.n.
- Grylloblatta lavacola sp.n.
- Grylloblatta paulinai sp.n.
- Grylloblatta rothi Gurney 1953
- Grylloblatta gurneyi Kamp 1963
- Grylloblatta chandleri Kamp 1963
- Grylloblatta barberi Caudell 1924
- Grylloblatta washoa Gurney 1961
- Grylloblatta bifractrilecta Gurney 1953

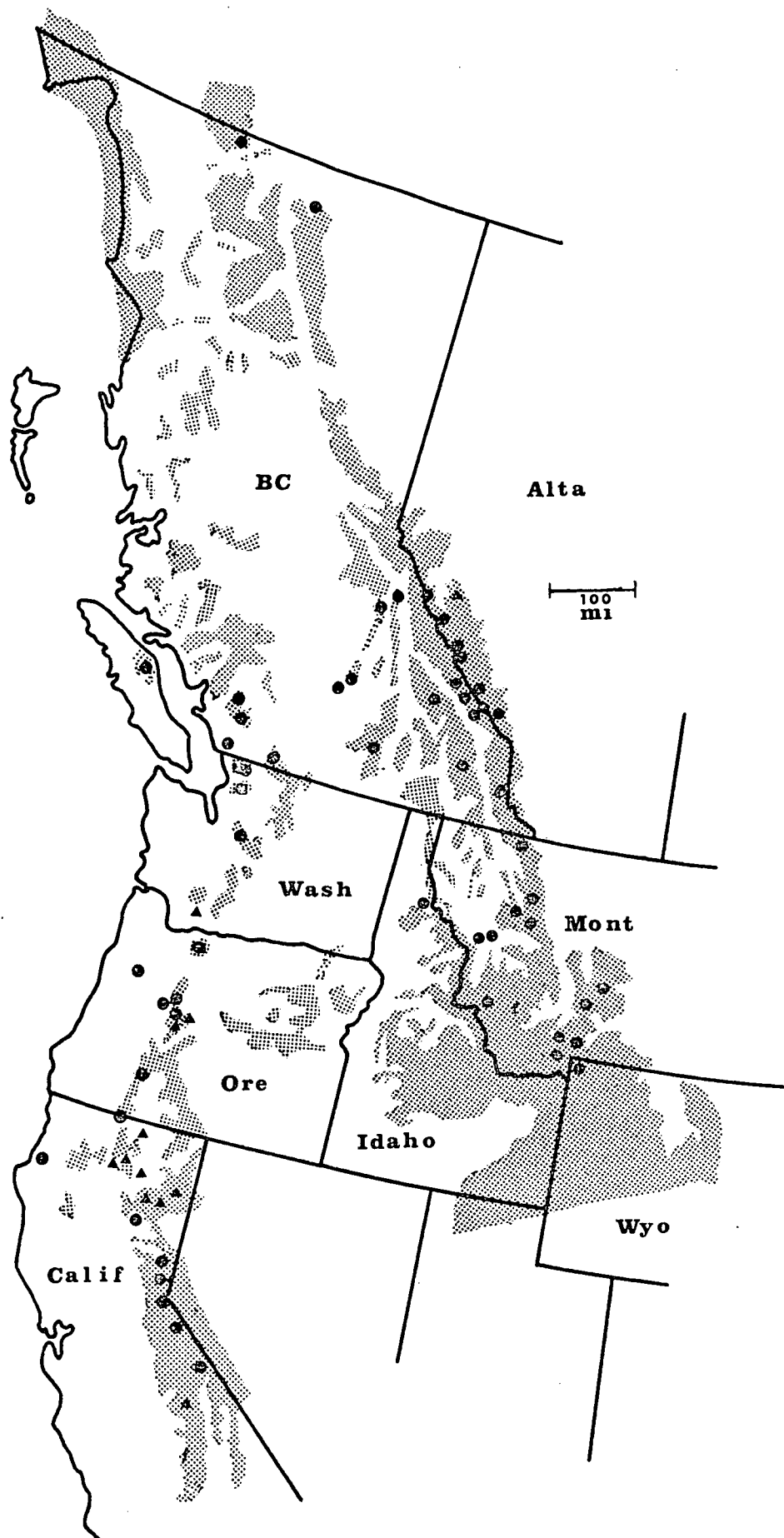
shape of pronotum, length and shape of ovipositor, and symmetry of male genitalia, the taxa can be separated into groups as follows: 1) G. occidentalis and G. scudderi, 2) G. skagitensis and the Mt. Rainier population, 3) G. chirugica, 4) G. hoodalles and G. rothi, 5) G. paulina, G. lavacola and the Mary's Peak population, 6) G. sculleni and G. s. cryocola, 7) G. gurneyi, G. barberi, G. chandleri, Mt. Shasta, Mt. Elwell and Sierra Butte populations, 8) G. washoa, G. bifractrilecta, Yosemite, Convict Basin, and Sequoia populations, and 9) G. campodeiformis campodeiformis, G. c. athapaska and G. c. nahanni.

The Nearctic Distribution

The necessity of a specialized habitat has produced a scattered distribution of the Nearctic Grylloblattidae limited to western North America. Grylloblatta are usually found above 5000 feet elevation in the Rocky Mountain and Cascade Cordillera of Canada and the United States and in the Cascade and Sierra Nevada Cordillera and its associated plateaus of Washington, Oregon and California (Fig. 8).

Distribution data for Western Hemisphere Grylloblatta points to the presence of three divergent groups characterized by isolated endemic populations or species.

Figure 8. 5000-foot elevation contour of the Cordillera of western North America is indicated by stippled areas. Solid circles = hypolithic localities of Grylloblatta; solid triangles = cavernicolous localities of Grylloblatta.



The genus is distributed from the Upper Convict Basin in the Sierra Nevada of California, along the major ranges to the Cassiar Range on the Yukon-British Columbia border, and north from Yellowstone National Park, Wyoming, to the end of the Canadian Rocky Mountains (Fig. 9).

Individual populations or species distribution may be very limited. The distribution may be as small as a single cave system or one side of a mountain peak or canyon, or may be large and occupy a chain along a mountain range.

One species group is found in the Rocky Mountain Cordillera of Canada and Montana, northern Wyoming and eastern Idaho.

The Coast-Cascade Cordillera group of species extends from Mt. Garibaldi, British Columbia, south to Crater Lake, Oregon, and east-southeast into the Modoc Plateau of the Basin Range province in California. This group occupies rocks mainly composed of various types of basalts. The ranges are predominantly composed of volcanics of late Tertiary (Miocene and Pliocene) and Pleistocene age (Peck, 1960).

The third group of species occurs in the Sierra Nevada of California from Mt. Elwell in the north to the Sequoia National Park in the southern portion of the range. This group of species occurs chiefly in substrate of granitic origin and the present range is from diastrophism of upper Miocene to present (King, 1958, 1959).

Figure 9. Species distribution of Grylloblatta localities.

Insert A = Oregon Cascade Mountain and high desert; insert B = Canadian Rocky Mountain localities.

Key to Grylloblatta species and localities:

1. G. sp., May's Hole (Cave), Sequoia National Park, California.
2. G. sp., Convict Basin, California
3. G. bifractrilecta, Sonora Pass, California
4. G. washoa, Echo Summit, California
5. G. sp., Sierra Buttes, California
6. G. sp., Mt. Elwell, California
7. G. barberi, North Fork Feather River, California
8. G. sp., Ice Cave, Plumas Co., California
9. G. sp., Ice Cave, Griffith Meadows, California
10. G. chandleri, Ice Cave, Eagle Lake, California
11. G. sp., Ice Cave, Siskiyou Co., California
12. G. sp., Mt. Shasta, California
13. G. sp., Ice Cave, Siskiyou Co., California
14. G. sp., Blue Lake, California
15. G. gurneyi, Ice Cave, Lava Beds National Monument, California
16. G. sp., Mt. Ashland, Oregon
17. G. rothi, Crater Lake, Oregon
18. G. sp., Mary's Peak, Coast Range, Oregon
19. G. hoodalles n. sp., Mt. Hood, Oregon
20. G. chirugica, Ape Cave, Skamania Co., Washington
21. G. sp., Mt. Rainier, Washington

Figure 9 continued

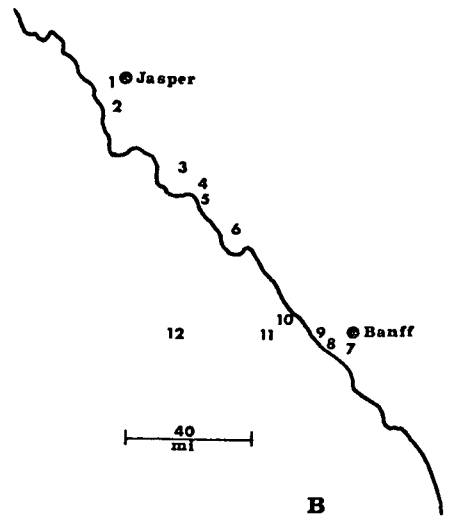
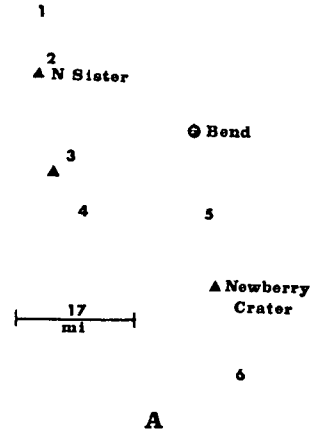
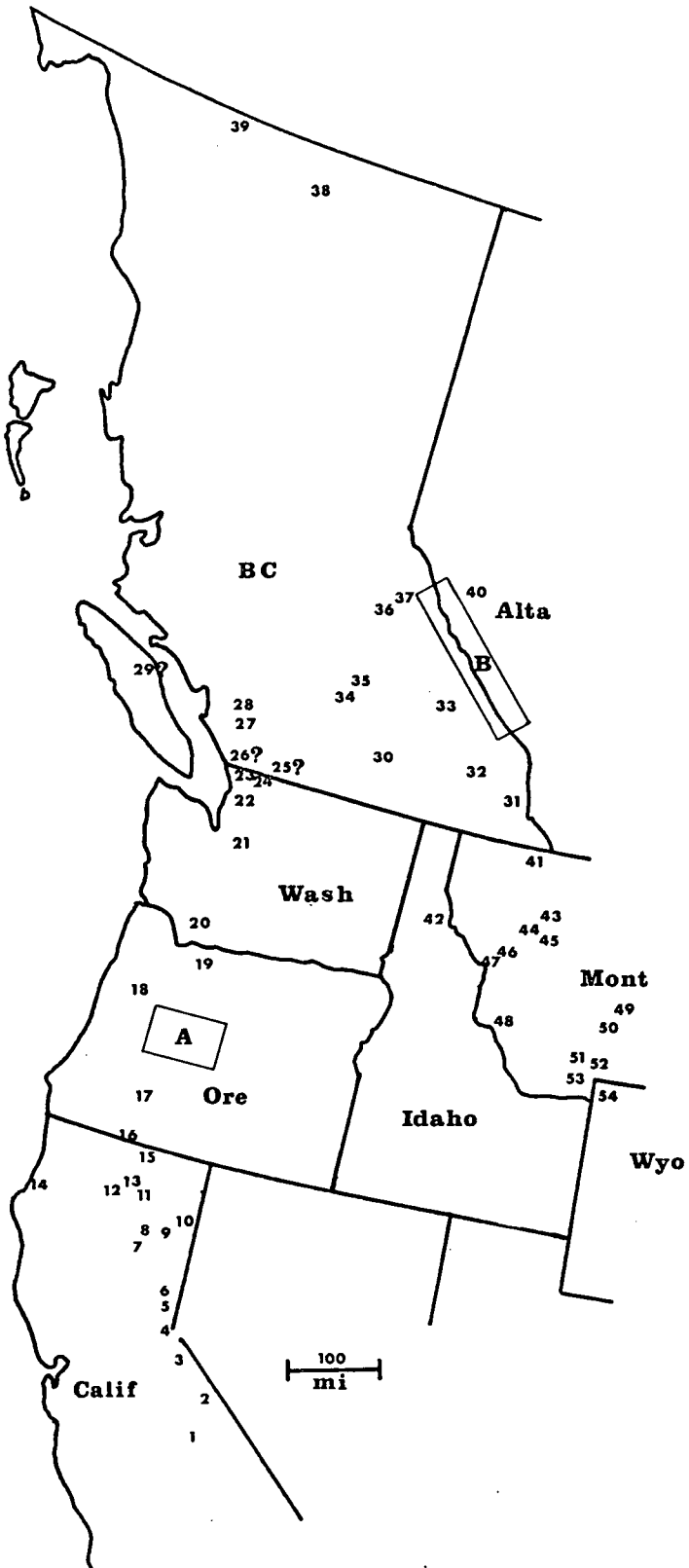
22. G. skagitensis n. sp., Glacier Peak, Washington
23. G. occidentalis, Mt. Baker, Washington
24. G. occidentalis, Hanagen Peak, Washington
25. G. sp., Timberline Valley, Manning Park, British Columbia
26. Report from Grouse Mountain, British Columbia (doubtful)
27. G. scudderi n. sp., Mt. Garibaldi, British Columbia
28. G. scudderi n. sp., Wedge Peak, British Columbia
29. Report from Forbidden Plateau, Vancouver Island, British Columbia (doubtful)
- 30-37. G. campodeiformis campodeiformis
38. G. campodeiformis athapaska n. ssp., Mt. St. Paul, British Columbia
39. G. campodeiformis nahanni n. ssp., Cassiar, British Columbia
- 40-54. G. campodeiformis campodeiformis

Insert A

1. G. lavacola n. sp., McKenzie Pass, Oregon
2. G. sculleni sculleni stat. nov., North Sister, Oregon
3. G. sculleni cryocola n. ssp., Edison Ice Cave, Oregon
4. G. rothi, Bachelor Butte, Oregon
5. G. sp., Ice Cave, Deschutes Co., Oregon
6. G. paulinai n. sp., South Ice Cave, Oregon

Insert B

- 1-12. G. campodeiformis campodeiformis



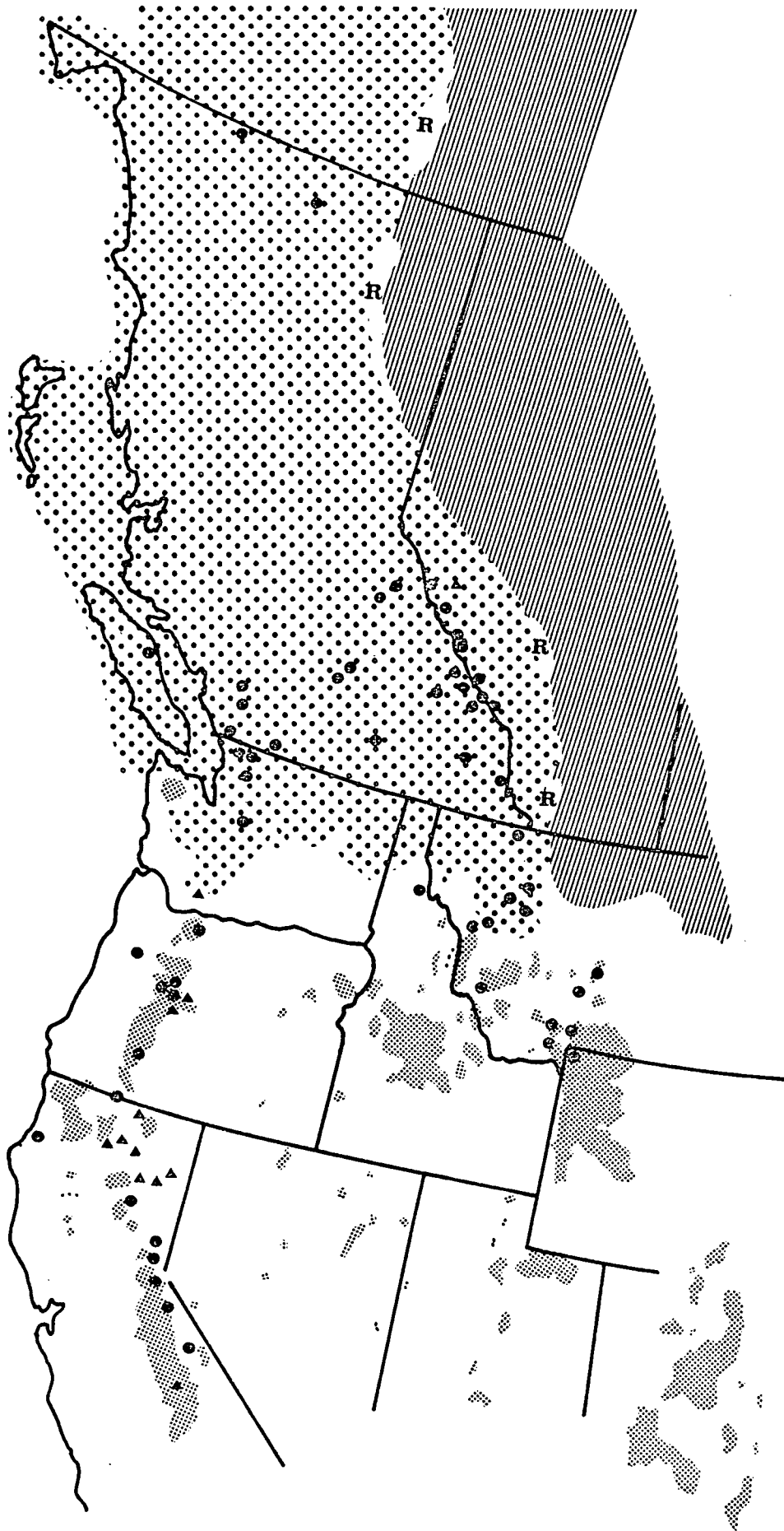
I have no evidence that the different groups are selective for habitats in substrate of different geologic origin. It is most likely that the different groups occupy these ranges because of historical reasons and because now these areas are the only tolerable habitats present. The rock types occupied indicate no more than the geologic origin of the individual ranges.

Zoogeography

I. The Rocky Mountain Cordilleran Group

The entire distribution of the Canadian population of the Rocky Mountain Cordilleran group lies within the area covered by the late Pleistocene Cordilleran Glacier complex (Flint, 1947). The Cordilleran Ice Sheet formed through coalescence of piedmont and valley glaciers in the Rocky Mountains and Cascade Range of Canada and flowed south into the United States, extending south as three major lobes to about $47^{\circ} 30'$ latitude (Fig. 10) (Miller, 1958; Williams, 1961; Richmond, 1964). Nunataks projected a few hundred feet above it. The surface sloped 15 to 50 feet/mile (3 to 10 meters/km) (Flint, 1935) from an altitude of over 8500 feet in central British Columbia to 7300 feet (2200 m) at the Canada-United States border and the British Columbia-Yukon boundary. At the Canada-United States border ice was

Figure 10. Maximum extent of Late Pleistocene glaciation in western North America, modified in part from Flint (1957) and Canadian Geological Survey (1958). Large stipples = extent of Cordilleran ice sheet; vertical hatch = extent of Keewatin ice sheet; small stipples = extent of mountain glaciation; R = possible ice-free refugia; solid circles = hypolithic localities of Grylloblatta; solid triangles = cavernicolous localities of Grylloblatta.



3500-5000 feet (1000-15000 m) thick over major valleys, to an altitude of about 2000 feet (600 m) with its southern limits in Montana and Washington (Flint, 1957; Canadian Geological Survey, 1958).

Four or five major periods of glaciation separated by interglaciations are recognized for the whole Pleistocene in this region. The late Pleistocene (last glaciation) is subdivided into at least three stades, or minor advances, separated by brief interstades (Alden, 1953; Richmond, 1965).

Numerous isolated populations of Grylloblatta campodeiformis campodeiformis occur along the Cordilleran crest with the type locality being Sulphur Mt., Banff National Park, Alberta (Fig. 9 B). The known populations scattered along the mountain chain might possibly reflect incomplete sampling of the habitat: there may be many undiscovered populations. There are many areas that are remote and only accessible after long hikes or a great deal of technical climbing.

A scattered distributional pattern is, however, probably the true picture of G. c. campodeiformis in the Rocky Mountain Cordilleran complex. Over the past five years I and others (R. E. Leech, E. R. MacDonald, L. Bartlett and J. Gordon Edwards) have visited most of the areas between known localities. The combined efforts have yielded less than six new populations and the spotty distribution seems to be a fact.

The range of individual populations varies from less than 100 yards to approximately $\frac{1}{2}$ -mile area. In no instance have longer continuous distributions been discovered.

I believe that this "pocket" distribution is due to local or micro-topography and its effects on the micro-climate conditions. Around such centers of populations within a short distance other areas of apparently suitable habitat may be present, yet the insect will not be found in them.

Ecological or geographical features such as a different face of a slope, a glacial outwash stream, a moraine, flat open area of alpine, lack of soil between rocks, seem to function as effective barriers to colonization of adjacent suitable habitat. These barriers which may be only a few yards in breadth seem to be barriers to dispersal and colonization to this apterous, photonegative, cryobionic G. c. campodeiformis. The populations appear to be more or less effectively isolated from each other.

Such "pocket" distribution is not unique among the Insecta. All the various orders found in the different mountainous regions of the world have forms exhibiting similar discontinuity of distribution. It reaches its highest development in the Himalayas where 98 per cent of the Dermaptera, 95 per cent of the Coleoptera, and over 80 per cent of the Orthoptera exhibit such isolation (Mani, 1968). Much the same isolation in very limited ranges is also known for flightless grasshoppers along the west coast of North America (Cohn and Cantrall, pers. comm.). Populations a few miles apart maintain species and subspecies integrity.

I have not been able to obtain any field evidence for the presence or absence of gene flow between populations of G. c. campodeiformis occurring within a short distance of one another. Further, the size of populations is not known: too few specimens are available for mark and recapture techniques and the animals' habits are not conducive to sequential sampling. The state of the "art" of discovering populations and the collections of individuals did not develop early enough in this project to permit field studies on movement and interbreeding. It is now possible to conduct such long term study and I hope to instigate this in the near future.

From geologic evidence the regions currently occupied by the Canadian Rocky G. c. campodeiformis were subjected to successive massive glaciation during the Pleistocene. From this evidence the following questions arise. Are the present-day Grylloblatta descendants of pre-Pleistocene inhabitants and did they survive the last Cordilleran glaciation, or are they new arrivals following the ice recession?

Four hypotheses are immediately available. Each hypothesis has its proponents when applied to the present distribution of the various flora and fauna of the Rocky Mountains. (1) The populations have continuously occupied the region during Pleistocene glaciation and the present distribution is little changed. (2) The populations survived the Pleistocene glacial episodes in some local ice-free refugia and invaded the present habitats as the ice receded. (3) The

different populations retreated to local nunataks that projected above the ice sheet during glacial periods and later spread out from them. (4) The fauna retreated north or south beyond the ice sheet borders and the present distribution is of post Pleistocene origin. We can consider each of these in turn.

(1) Continuous habitation of the region by the G. c. campodeiformis is totally invalid. Grylloblatta do occupy the hypolithion under snow fields and under favorable conditions may feed on the peripheral surface of glaciers, but long term survival under or on an ice sheet would be impossible. The movement of glacier ice abrades to bedrock or below and removes all unconsolidated substrate. The action of valley and cirque glacier ice deposits material as lateral or terminal moraines. The continual movement and building of moraines by active glaciers make the substrate uninhabitable for Grylloblatta.

While Grylloblatta do actively search for food for short periods under favorable conditions on the margins of small glaciers, continual occupation is not possible. The circadian temperature and humidity fluctuations are beyond the extremes tolerated by the organisms (see other sections of thesis). Nocturnal foraging by Grylloblatta on small snow fields a few hundred feet in diameter has been noted, but any rapid fluctuations of temperature and humidity can be lethal. I have observed on numerous occasions while collecting on snow fields at night that a few degree fall in temperature or slight wind movement will cause the Grylloblatta to retreat

within 15-20 minutes to the hypolithion. During such conditions individuals far from the snow field margins become stupified and die. It is usually possible on large snow fields where Grylloblatta forage to find a few dead individuals next morning that did not safely retreat to the hypolithion.

If present free air temperature gradients can be extrapolated to paleoclimates the mean summer temperatures during the late Pleistocene glacial maxima were up to 9° C. (17.5° F.) cooler than the present temperature of the region (Heusser, 1964; Richmond, 1965). Since the present mean for the region at 5000 feet is approximately 2° C. (35.6° F.) (Meteorological Division, Department of Transport, 1970) continual glacier surface survival by Grylloblatta seems highly improbable.

It can be hypothesized that late Pleistocene Grylloblatta had a lower temperature-humidity tolerance than the present forms and could survive glacial maxima temperatures. It seems most likely that if such a lowered tolerance were present during the Pleistocene, natural selection would have been for retention of this attribute rather than against it, for in the present habitat occupied by these insects it would still be an advantageous physiological feature.

(2) Late Pleistocene glaciation survival in ice-free refugia is a possibility for at least a few of the Canadian Rocky Mountain Grylloblatta. However, survival in ice refugia close to or matching the present distribution is highly improbable.

The Keewatin and Cordilleran ice sheets are generally

considered to have been at times in continuous contact throughout most of the region east of the Cordilleran crest. Extensive reworking of tills, outwashes, and moraines has made it difficult to determine the limits and absolute zones of contact. There is some evidence for at least two and possibly as many as six refugia lying between the two ice sheet complexes (Canadian Geological Association, 1958). A small refugium is thought to have existed during the late Pleistocene in the Pincher Creek-Macleod (Porcupine Hills), Alberta, region (Canadian Geological Association, 1958) (Fig. 10).

Southeast of Edmonton in the Buffalo Lake Region, Bretz (1943) has mapped end moraines whose arrangement suggests that a deglaciated zone existed between the Cordilleran and Keewatin ice sheets. Halliday and Brown (1943), in their study of the present distribution of pine trees in Canada, speculate that this region could have been a refugium for the western pine species. Hansen (1949), from analysis of bog pollen profiles, has also recognized the possibility that pre-late Pleistocene forests existed in an ice-free belt in the same area.

The Fernie population of G. c. campodeiformis may possibly have inhabited the Pincher Creek-Macleod (Porcupine Hills) refugium during late Pleistocene. However, the same species is known from Jasper National Park, Alberta, to Yellowstone National Park, Wyoming. I suggest that while the Fernie population may have occupied this refugium during late Pleistocene, it is unlikely to be the nucleus or parent popula-

tion from which the present total distribution of the species has been derived. Further, the possibility that this Fernie population did not find refuge in the Pincher Creek-Macleod region must be considered. The region, even if not glaciated, was subjected to extensive outwash of till and silts from both ice sheets (Horberg, 1952). Present populations of Grylloblatta do not inhabit such mixtures of unconsolidated material. The area, thought not to have been glaciated, is limited in size with little elevation change and it is probable that a suitable habitat did not exist. The present site of the population is separated from the refugium area by the Flathead River valley which contained an extrusive southern lobe of the Continental Ice Sheet that projected approximately 100 miles into Montana. The ice sheet recessions at the beginning of the post Pleistocene are believed to have been by stagnation and melting instead of by frontal retreat (Rice, 1936; Nasmith, 1962). Stagnation melting freed the highland, but ice remained for possibly hundreds of years in the valleys of the Flathead and Stillwater drainages. In light of the present distributional pattern and the systematics of the species, the Fernie population could well be an early post Pleistocene migrant along the Flathead and Whitefish ranges from a southern center of late Pleistocene G. c. campodeiformis.

The present distribution pattern of the G. c. campodeiformis does not support late Pleistocene occupation in the questionably deglaciated Buffalo Lake region. If this area was the center of late Pleistocene survival

and the Banff-Jasper populations are migrants from the region, it would suggest the presence of populations up the only possible migration route, the Saskatchewan River. It is true that suitable climate and habitat exist above Nordegg, yet no populations of G. c. campodeiformis have been discovered in this drainage.

Considering late Pleistocene and post Pleistocene geological data, the present distribution pattern, and the systematics of G. c. campodeiformis, I suggest that the genus did not occupy the Buffalo Lake region. A late Pleistocene habitation in an ice-free refugium in the north is most likely for the northern British Columbia species of Grylloblatta.

The Summit Lake (Lat. 58° 45' N.) subspecies of Grylloblatta is found some 450 miles northwest of the G. c. campodeiformis populations in Jasper National Park. In this context it should be noted that the main Canadian Rocky Mountain Cordillera decreases in elevation to the north and is interrupted by major river drainages, such as the Fraser, Parsnip, and especially the Peace River: the extensive interior valleys present major geographical barriers.

The Cassiar- Mt. McDame subspecies of G. campodeiformis, found on the east slopes of the Cassiar Range, is presently isolated from the Summit Lake species. The climatic conditions that exist in the Liard Plain, the Dease and Liard rivers and tributaries, and the Rocky Mountains, tend to maintain this isolation.

Two large, unglaciated refugia existed west of the Mackenzie River during late Pleistocene (Canadian Geological Association, 1958). Topography and geological evidence suggest that the southern unglaciated area of the Liard and Nahanni ranges, extending north to the Canyon Range west of Fort Liard and Fort Simpson, was the most likely refugium for these populations during the late Pleistocene. (Fig. 10).

As the ice sheets receded from the highlands along the Liard and Fort Nelson rivers migration routes would have been available, permitting refugium populations to reach the present localities of Cassiar and Summit Lake. Morphological features indicate a close relationship of these populations to G. c. campodeiformis. The topography of the terrain and the distance separating the northern group from G. c. campodeiformis predicates against post Pleistocene migration of the northern forms from the south.

The close relationship, however, does suggest a pre-late Pleistocene common origin with a disjunct isolation of the northern group during late Pleistocene in the refugium. A future discovery of Grylloblatta from the Liard or Nahanni ranges would substantiate this hypothesis. Based on observations and collections I have made during trips into the Fort Nelson and Peace River valley, I doubt that Grylloblatta will be discovered from the area.

(3) Survival during Pleistocene glaciation on nunataks projecting above the ice sheets is frequently suggested as an explanation of present distribution patterns for the flora

and fauna of western Canada (see McCabe and Cowan, 1945; Calder and Savile, 1959; Mathias and Constance, 1959). The present climatic conditions that exist on nunataks above the small ice fields, Wapta and Columbia (Jasper-Banff National Parks), coupled with field observations suggest that only those organisms most resistant to extreme cold and dessication could survive any extended period of time.

The bare rock substrate on such projections is frozen throughout the year except for a few small areas on the west-southwest face that are sheltered from wind and thaw during July and August. Air temperature may rise a few degrees above 0° C. during these months, but the peaks are buffeted by cold katabatic wind which counteracts the above zero temperatures. During July and August, 1969, I climbed Mt. Columbia, Mt. Athabaska, and the Twin mountains, nunataks above the Columbia Ice Field, and found no animal life and observed only the rare crusteous lichens.

One would assume that present conditions on such nunataks are ameliorated from those that existed during massive Cordilleran and Continental glaciations. If life is marginal today on such areas it was even more so during the Pleistocene. Even if conditions were less severe during the Pleistocene than present, evidence from the narrow range of temperature and humidity tolerated by Grylloblatta would indicate again that these insects would not be present. In addition, the widespread distribution of the species in the Rocky Mountain Cordillera does not suggest late Pleistocene survival on nunatak refugia. I am inclined to believe that

those who propose Pleistocene nunatak survival have never studied the nature of the environment there.

(4) A late Pleistocene occupation of habitats south of the Cordilleran and Keewatin ice fronts in Montana and Idaho must be considered, with the present distribution being established during or soon after ice recession (ca. 9000 years ago).

Nine populations of G. c. campodeiformis are known from localities south of the maximum Pleistocene ice advances in Montana and Wyoming (Fig. 10). Five other populations of the species occur in regions that had a periglacial climate on the margins of the Flathead and Lewis lobes of the Cordilleran Ice Sheet in northern Montana and Idaho.

The present distribution of the species along the crest of the Rocky Mountain Cordillera from Yellowstone, Wyoming, to Jasper, Alberta, and the concentration of present populations south of the maximum ice advance, suggest that Montana was the center of the late Pleistocene G. c. campodeiformis distribution. Thus, the present distribution is a result of migrations along ice-free highlands during glacial recession some 9000 years ago.

II. Coast-Cascade Group

The distribution of Grylloblattidae in the Coast-Cascade Cordillera is restricted, with few exceptions, to

the major stratovolcanoes or ice caves in plateau lava fields. Each inhabited peak and cave system has a characteristic species or subspecies usually allopatric with other Grylloblatta. They are separated by climatic or geographic barriers, such as elevation, river canyons and lava fields. Every known species now occurs in a locality which was within the maximum extent of late Pleistocene glaciation or the periglacial zone surrounding such glaciation (Figs. 9 A and 10).

The Coast-Cascade Cordillera, though usually treated as a single physiographic unit, can be considered as five major subdivisions. These correlate with the known distribution and systematics of the Grylloblatta and show individual regional Pleistocene-post Pleistocene geological and climatic changes. These subdivisions are: 1. The Northern Cascades, extending from Garibaldi-Wedge Peak, British Columbia, south to Mt. St. Helens, Washington; 2. The High Cascades, a narrow belt of summit volcanoes beginning with Mt. Hood and including the Three Sisters-Bachelor Peak complex; 3. The Southern Cascades, comprising Crater Lake, Mt. Shasta and Mt. Lassen; 4. Plateau and Basin ranges, lying east of the Cascades and including the Columbia, High Desert and Modoc plateaus; 5. Secondary ranges, including portions of the Coast and Klamath ranges.

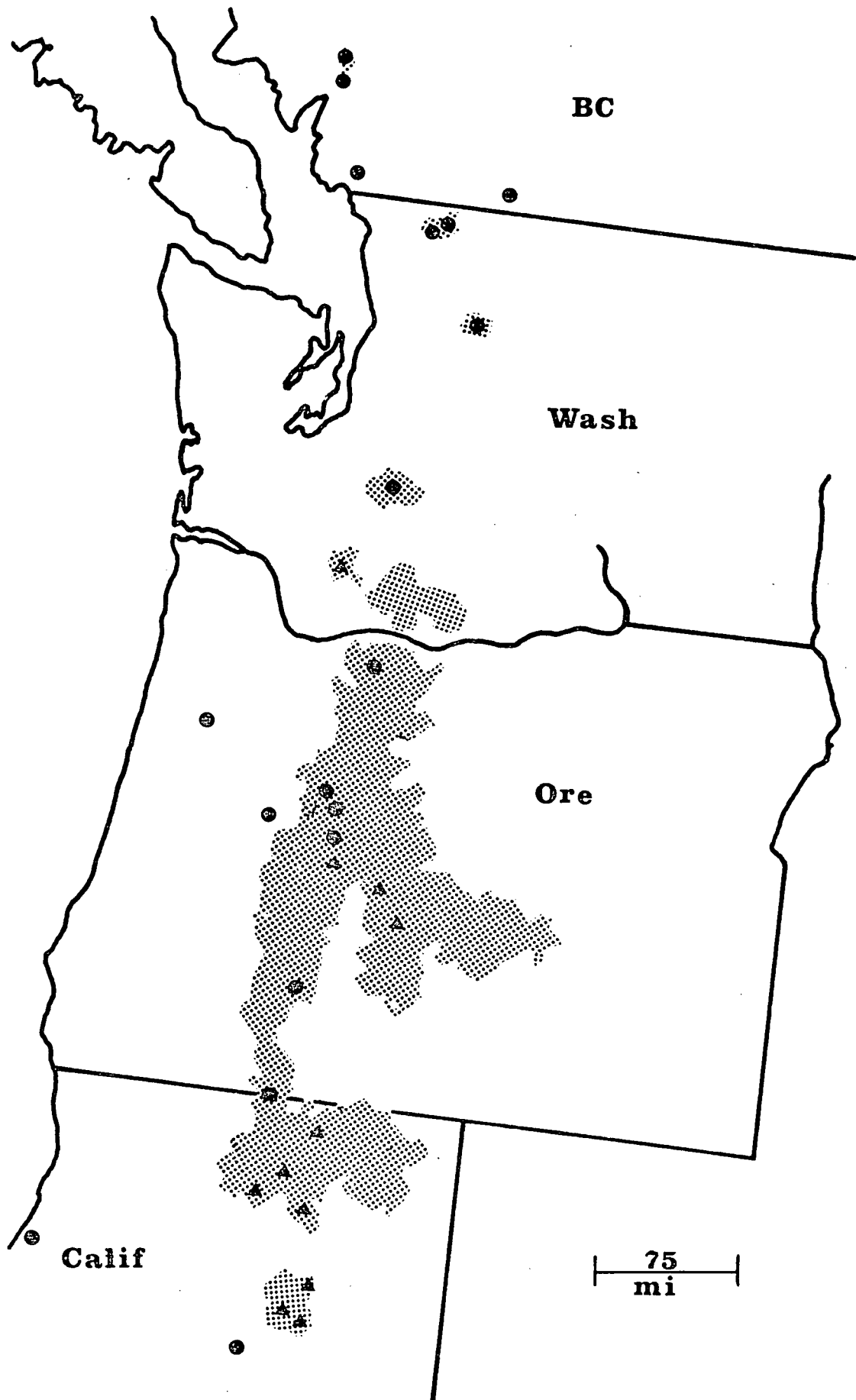
The Quaternary (Pleistocene-post Pleistocene) history of the Cordillera is exceedingly varied and includes such events as repeated alpine glacial advances, invasion of the Northern Cascades by the Cordilleran Ice Sheet, catastrophic

floods released by glacier-dammed lakes and covering wide expanses, and the building of numerous stratovolcanoes and huge fissure flows of lava covering hundreds of square miles (Fig. 11).

The Cascade Range is 100-160 km. wide and extensive areas along the crest are 1200 m. (4000 ft.) in elevation. Towering 1000-4000 m. (3000-10,000 ft.) above the average crestline are 12 large stratovolcanoes. Most of these volcanoes lie west of the crest and form the headwaters of the many major rivers that drain the east and west slopes of the mountains. These major peaks, because of their elevation above the average crestline and the east-west dissection of the total range by the major drainage systems, function as evolutionary islands for the Grylloblattidae.

The most extensive record of Pleistocene glaciation is recognized in Washington, where glacial strata representing at least four major glaciations, are interbedded with non-glacial deposits. The stratigraphic evidence for each major glaciation includes records of at least two glacier fluctuations for each period (Armstrong et al, 1965; Crandell, 1965). The records of Pleistocene glaciation and climatic changes are not as well documented for the southern portion of the range. Nevertheless, geological formations indicate Pleistocene glaciation along the entire range. This consisted of the Cordilleran Ice Sheet, with its origin in the Coast Mountains of British Columbia, invading northern Washington on either side of the Cascades; there were broad valley and piedmont glaciers flowing down the major drainage with the

Figure 11. Quaternary to Recent volcanics of Coast-Cascade Range indicated by stippled areas; solid circles = hypolithic localities of Grylloblatta; solid triangles = cavernicolous localities of Grylloblatta.



crestline covered by expansive ice fields and ice caps.

The early and middle Pleistocene is recorded to have had two major glaciations, each with two or more advances of the Puget Lobe of the Cordilleran Ice Sheet, extending approximately 170 miles south of the British Columbia-Washington border to the vicinity of Mt. St. Helens (Crandell, 1963; Snavely et al, 1958). Each of these major advances was contemporary with the formation of ice fields at higher elevations.

Three glacial episodes occurred during the late Pleistocene. The last, the Fraser Glaciation, occurred between 25,000 and 11,000 years ago. During the earlier two episodes of the late Pleistocene, large valley and piedmont glaciers covered the lowland south of the Puget Lobe and were fed by vast ice fields and ice caps that mantled the entire length of the Cascade Range. Mountain glaciation is thought to have been of lesser extent during the Fraser period, although ice fields and ice caps again covered the areas now occupied by the Grylloblattidae.

During the Fraser Glaciation alpine glaciers in British Columbia formed the Puget Lobe which invaded Washington about 22,000 years ago and reached their maximum advance 50 miles south of Seattle between 15,000 and 13,000 years B. P. (Crandell, 1963; Heusser, 1964).

This glacial episode, the Vashon Stade, was followed by the Everson nonglacial interval that terminated about 11,500 years ago and had a climate cooler and more moist than the

present. A short-lived Sumas Stade followed with the re-advance of the Cordilleran Ice Sheet and the rebirth of mountain glaciers and ended with the disappearance of the ice sheet and mountain glaciation approximately 11,000 years B. P.

At the time the Puget Lobe reached its maximum extent during the Vashon Stade, alpine glaciers in the Cascades had greatly decreased in size or had disappeared (Cary and Carlston, 1937). The recession of alpine glaciers in the Cascade Range while the Cordilleran Ice Sheet continued to expand is thought to have been the effect of a climatic change of regional distribution prior to the maximum expansion of the Puget Lobe (Mathews, 1951). Mathews (1951) suggested that this change resulted in increasing temperature and caused the wasting of the mountain glaciers. The increase of temperature could have resulted in greater precipitation on the ice sheet, because its size and elevation maintained a local cold climate on the ice surface and continued to expand.

During the Sumas readvance of the Puget Lobe, about 11,500 years ago, there was a temporary return to cold climatic conditions in the mountains and the rebirth of alpine and cirque glaciers. Sumas mountain glaciation is indicated by morainal and till features lying on nonglacial deposits and covered by two distinctive volcanic ash layers. The volcanic ash falls are from Glacier Peak, Washington, with a tentative date about 11,000 years B. P. (Fryxell, 1965) and from the widespread Mazama ash from Crater Lake,

Oregon, of 6600 years B. P. in age (Powers and Wilcox, 1964).

Two mountain glacier episodes are known for the post Pleistocene, the older advance during Neoglacial beginning about 3500 to 2000 years ago. During the younger advance, starting at least 700 years ago, various glaciers on the major peaks reached maximum stage, ranging from 600 to 100 years B. P. The Cascade glaciers have since been undergoing an inconsistent pattern of recession and advance and this continued to the present day (Harrison, 1956a, 1956b; Sigafos and Hendricks, 1961).

The analysis of pollens from nonglacial deposits suggests that the interglacial climates were at least 2° C. cooler (yearly mean) and were much moister than present (Heusser, 1964). Summer mean temperatures during the very late Pleistocene (Fraser Glaciation) are considered to have been at least 6-9° C. below the present (Mullineaux, Waldron and Rubin, 1965).

The present distribution of Grylloblatta in the Coast-Cascade Cordillera is a direct result of the various episodes in the late Pleistocene advances and recessions of mountain crest ice fields and ice caps. Late Pleistocene centers of Grylloblatta survival were below the summit ice sheet and between the valley and piedmont glaciers fed from the Cordillera.

1. Northern Cascade Group

The Grylloblattidae occurring in the northern portion of the Cordillera are: Grylloblatta scudderi, Wedge Peak, British Columbia; Grylloblatta occidentalis, vicinity of Mt. Baker, Washington; Grylloblatta skagitensis, Glacier Peak, Washington; and Grylloblatta chirugica, Ape Cave, Skamania Co., Washington. In addition, from the north and east slopes of Mt. Rainier I discovered Grylloblatta in October, 1969. From the morphological characters of the adult females, I believe this population to be a new species. I have not as yet named it as such for adult males are still unknown.

There are literature reports of Grylloblatta species occurring on the Forbidden Plateau, Vancouver Island (Buckell, 1930; Spencer, 1945). Spencer (1945) also reports that the genus has been found on Grouse Mountain, north of Vancouver, British Columbia. A single female is reported from Garibaldi Peak, British Columbia (Walker, 1937). In the B. C. Provincial Museum collection there is a single adult female Grylloblatta from Timberline Valley, Manning Park. The condition of the specimen does not allow comparison with Grylloblatta occidentalis or G. scudderi. Except for the Garibaldi and Manning Park specimens, there is reason to believe that these are hearsay records for they have not been substantiated by material. However, I believe that eventually Grylloblatta will be discovered

from more localities in southwestern British Columbia.

The Northern Cascade species of Grylloblatta, except for G. chirugica, occur in localities which were covered by the Cordilleran Ice Sheet, ice fields and crest ice caps during Fraser Glaciation about 25,000 to 10,000 years ago.

Ape Cave on the slope of Mt. St. Helens (type locality of G. chirugica) has been the scene of repeated post Pleistocene lava, ash and mud flows. Some of this activity is as recent as 1802, 1831, 1842 and 1854 (Lawrence, 1954; Heusser, 1960). These and earlier eruptions have reworked or obliterated all trace of late Pleistocene glaciation to the extent that only Neoglacial and recent features are known.

Grylloblatta scudderi occurs in the alpine zone about 6000 feet on the north and east slopes of Wedge Peak, Garibaldi Mt., British Columbia. The returns from six different collecting trips by Topping, Bartlett and myself indicate that this is a very sparse population.

Late Pleistocene glacial evidence indicates that Grylloblatta scudderi could not have occurred in the region prior to the Sumas Stade about 11,500 to 11,000 years B.P. The present population is undoubtedly from stock that survived the extensive late Pleistocene glaciation south of the ice front. The very small population would tentatively suggest post Pleistocene migration during the Neoglacial period about 3500 to 2000 years ago from parent stock in the vicinity of Mt. Baker.

The broad expanse of the Fraser River and delta has been an effective topogeographical barrier for many species. This

major barrier tends to rule out a postglacial migration directly from the southern regions of the range, unless Neoglacial climate was much colder than present records indicate. A post Pleistocene dispersal route from the south to the present locality is suggested. The elevations through the Manning Park Cascades, the Lillooet Range, are such that suitable climatic conditions must have existed along the coast during Neoglacial times. Any future discovery of Grylloblatta populations from either the Grouse Mountain-Mt. Seymour area or the Manning-Lillooet region could greatly contribute to our understanding of the distribution and systematic relationship of Grylloblatta scudderi.

Irrespective of late or post Pleistocene origin, the species did not occur in its present locality during the greater portion of the Fraser Glaciation. Nunatak survival for the genus above the Cordilleran Ice Sheet is not considered possible for reasons presented earlier.

Grylloblatta occidentalis is known from Mt. Baker and from surrounding mountains within a vicinity of 15 miles. Populations of limited distribution are known from Mts. Winchester, Goat, Table, Herman, Hannegan, Shuksan and Baker. Morphological examination of a limited series indicates that the species is composed of three subspecies that are isolated from each other by topographical features.

The populations in the Skagit Range, which occur on Winchester Mountain, Serfrit Mountain, Goat Mountain and Hannegan Peak, are found above 5200 feet and form one

subspecies group. The Skagit Range is a small subsidiary chain of the above peaks branching northwesterly off the main Cascade crestline. The populations in the Skagit Range are topographically isolated from other populations in the region by the Nooksack River flowing to the west and the Chilliwack River draining the eastern slopes. The canyons cut by these rivers and their tributaries almost isolate this part of the Cascade crest. The elevations of the ridges, low mountains and foothills between the Skagit Range subspecies and the populations in the Mt. Shuksan complex, average below 3000 feet with the bottom of the river canyons between 1000-2000 feet. The lower elevations are much too dry and the temperature too high to be tolerated by Grylloblatta during most of a yearly season. Suitable hypolithion habitat is scarce and generally covered by erosional silts and persistent snow does not exist. While the Skagit Range and Mt. Shuksan populations are only 7 miles apart, the climatic and topogeographical barriers seem to be effective and are presumed to have been in existence long enough for morphological differentiation to have taken place.

The Mt. Shuksan populations occurring on Mt. Herman, Table Mountain and across the Kulshan Ridge to Mt. Shuksan constitute a further subspecies. These populations are morphologically distinct from those on the 6000-8000 foot slope of Mt. Baker which are another subspecies.

The topography to the south and west of the Shuksan

complex is at an elevation that the climatic conditions most of the year would be a possible effective barrier for interchange with the Mt. Baker subspecies. From Table Mountain, lying in the center of the Shuksan subspecies range, Ptarmigan Ridge leads southwest directly to Mt. Baker. Ptarmigan Ridge has small patches of snow which persist throughout the year and the lower portions toward Table Mountain are composed of substrate which appears to be ideal habitat for Grylloblatta. Yet G. occidentalis is not found anywhere along the 5 miles between Table Mountain and Mt. Baker.

The ancestral population of G. occidentalis most likely survived the late Pleistocene west or southwest of Mt. Baker between mountain ice and the Fraser Lobe. The present Mt. Baker subspecies populations are found only on the western and northwestern facing slopes. Flowing down from the summit ice field of Mt. Baker to the northeast along the upper portion of Ptarmigan Ridge are Manning, Rainbow and Park Glaciers. Below the glaciers the upper portion of the ridge is composed of earlier moraines and till which are unconsolidated and subject to avalanche. This loose, moving rock evidently is not a suitable habitat and acts as a barrier between the two subspecies.

I believe that these three morphologically distinct population groups are subspecies, although I have no evidence that gene flow does not occur between them. It is possible that during exceptional years of much greater snow fall and a long cool spring, the peripheral populations of each sub-

species may come in contact. A long cool spring preceded by very heavy snow could allow the snow cover to exist across the lower elevations well into the normal summer conditions. Under such climatic conditions local populations could spread out and meet; short distances only separate the three groups.

The Mt. Baker G. occidentalis are presently isolated from G. scudderi by the climatic and major topographical barriers previously discussed. They are also separated by 50 miles from G. skagitensis on Glacier Peak. Both of these stratovolcanoes are 20 to 40 miles west of the Cascade crest-line. Most of the topography in the 50 miles of separation is below 3000 feet in elevation and dry during the late spring through fall seasons. The wide valleys of the Skagit, Sauk, Stehekin and Suiattle rivers, with elevations below 1500 feet, are the major topographical barriers. The heads of the valley and river drainages lack suitable, moist, cool hypolithion. The 50-mile separation with a lack of suitable hypolithion and the present temperature-humidity conditions in the lowlands would appear to be an effective barrier between the two species, if habitat and temperature-humidity tolerance is constant throughout the genus.

Grylloblatta skagitensis occurs in the compound cirque basin between Kennedy Glacier, Glacier Ridge and the headwaters of the White Chuck River. The basin between 6000-9000 feet in elevation contains large permanent snow fields through the summer and fall. The entire basin substrate is a hypolithion in material of Neoglacial or younger age.

The basin was ice-covered during the Fraser Glaciation and the present glaciers and morainal features are all of Neoglacial age (ca. 3500-2000 years B. P.). Glacier Peak experienced a major eruption of pumice and ash near the time of the Sumas Stade ice retreat. This pumice and ash covered the slopes to a depth of a meter or more and are recorded as far east as Montana (Wilcox, 1965). If alpine glaciers disappeared about 11,500 years ago, as suggested by Mathews (1951) and Crandell (1963), any hypolithion occupied then by G. skagitensis would have been destroyed. The hypolithion inhabited by the insects is thus less than 3500 years old, the maximum age of the current glaciers. The upper elevations of the basin are presently the sites of much avalanche activity of snow, ice and rock.

The sequence of volcanism, Fraser advance and recession, and Neoglacial events suggests recent invasion of the present habitat. The pioneering stock of G. skagitensis certainly did not come from the west for that region was either under an ice sheet or too hot and dry during the later Hypsithermal interval (ca. 9000-3500 years ago.). The only possible areas of survival during Fraser Glaciation and Hypsithermal times are to the east or south near Mt. Rainier.

Discovery of Grylloblatta from the Cascade crest east of Glacier Peak would help to clarify the origin of the present populations. The discovery of more males and females from Mt. Rainier would certainly contribute to the knowledge of the relationship and phylogeny of G. skagitensis.

I speculate that populations of Grylloblatta occur above Holden in the Chilon mountains and in the eastern Glacier Peak Wilderness Area. Numerous independent trips by Mr. Bartlett and myself, searching for Grylloblatta in the mountains between Glacier Peak and Mt. Rainier, have failed to produce any populations. Glacier Peak is well isolated by distance and topography from both G. occidentalis to the north and the undescribed Mt. Rainier populations.

Between Glacier Peak and Mt. Rainier, a 90-mile expanse, the Cascade Range decreases in elevation and breadth. The highest peaks are less than 6000 feet except for three near Mt. Rainier that exceed this elevation. This portion of the Cascade Range is divided by two major drainage systems: the Skykomish River flowing west through Stevens Pass at 4000 foot elevation and the Wenatchee River draining the eastern slopes of the range. The headwater canyons overlap in Stevens Pass at 4061-foot elevation. Further south toward Mt. Rainier, the Cascade Range is divided by an even lower pass, the Snoqualmie, 3010 feet above sea level. In between these low passes a dozen other river systems have dissected both slopes with deep canyons.

The combination of late Pleistocene glacial evidence, the lower elevations of the dissected intervening portion of the Cascade Range, the inferred climate during Hypsithermal and Neoglacial periods, and field data, strongly suggest separation between Glacier Peak and the Mt. Rainier Grylloblatta for at least 40,000 years.

The Mt. Rainier Grylloblatta are found on the northern and eastern slopes in Cayuse and Chinook pass hypolithion habitats above 4600 feet. They occur up to 7500 feet elevation on the older moraines of Emmons Glacier. This occurrence at elevations below those from which they are generally known from localities in the ranges, is undoubtedly due to the much cooler more moist summer climate of the north and east slopes of Mt. Rainier. This localized cool summer climate seems to be the effect of the topography of the mountain and of many glaciers extending to lower elevations.

Mt. Rainier was continually glaciated during late Pleistocene. While the Puget Lobe during Fraser Glaciation did not overrun the western slopes, the earlier Salmon Springs Stade (ca. 35,000 years ago) did meet the ice cap existing on the mountain. The regional snowline (the elevation above which snow accumulated and forms ice fields) (Matthes, 1940) in the mountains near Rainier was approximately 3100 feet (1000 m.) during Fraser Glaciation about 25,000 to 9000 years ago. Glaciers from the ice fields of Mt. Rainier extended to lower elevations in the river valleys and covered the regions now inhabited by the Grylloblatta. The extent of glaciation on Mt. Rainier decreased during the middle portion of the Fraser episode. A rigorous cold climate returned to Mt. Rainier before the end of the Sumas Stade with the formation of cirque and valley glaciers extending below 4000 feet around 11,000 years ago (Crandell et al, 1962).

Glaciers and persistent snow fields disappeared during the Hypsithermal interval on Mt. Rainier. The present large glaciers are of Neoglacial origin and not older than 3500 years. Glacial activity has continued to the present with major advances occurring during the 14th and 15th centuries and again in the 1850's, and then reached or covered the present habitat of the insects (Harrison, 1956a; Sigafos and Hendricks, 1961).

Post Pleistocene volcanic activity of Mt. Rainier is recognized by ash deposits and mud flows in the locality of the Grylloblatta between 2300-2000 years ago (Crandell et al., 1962). Extensive mud flows are recorded in modern time covering the habitat (Fiske, Hopson, and Waters, 1963).

The populations on Mt. Rainier must thus be very recent inhabitants of the present habitats. The parent stock could have survived at least the last portion of late Pleistocene glaciation on the western slopes in an area between the summit ice fields and the Cordilleran Puget Lobe in the coastal plain. Continual survival during the entire late Pleistocene in the upper region of the American River east of Chinook Pass is a possibility. The present distribution would support the existence of Pleistocene refugia on the eastern slope of Mt. Rainier.

Grylloblatta chirugica, known from Ape Cave and other ice caves on the southern slopes of Mt. St. Helens, occurs in habitats no older than the late Pleistocene (Verhoogen, 1937). In fact, most of the present cone and surrounding

lava fields appear to be of postglacial origin and less than 12,000 years old (Lawrence and Lawrence, 1959; Mullineaux, 1964). Mt. St. Helens has been the most active of the northern Cascade stratovolcanoes during the post Pleistocene. The last 1000 years have been a period of violent activity with major eruptions of lava, pumice, and mud as recently as 1854. The entire area of the lava fields surrounding the peak are mantled with pumice varying in depth from 1 to 6 feet. The eruption of 1843 deposited ash $\frac{1}{2}$ -inch deep 93 miles away at The Dalles, Oregon.

Between Mt. Rainier and the Columbia River the Cascade Range reaches its lowest crest elevation. The entire region is covered with glacial outwash or extensive lava fields and possesses a climate too dry and hot for post Pleistocene habitation by G. chirugica.

The region was not extensively glaciated during the late Pleistocene for glacierization was restricted to Mt. Adams, Mt. St. Helens, and the crestline. The entire region certainly must have had a periglacial climate under the influence of the Cascade ice fields to the north and south.

During late Pleistocene, 40,000 to 9000 years ago, climatic conditions were probably ideal anywhere in the area for Grylloblatta. However, at the termination of the last glaciation and the return for a 5000-6000 year period of much warmer dry conditions (the Hypsithermal), Grylloblatta chirugica were undoubtedly forced to retreat to the only habitat tolerable, namely, the ice caves. Occupation of

the higher elevations and alpine on Mt. St. Helens was not possible owing to continual volcanic activity.

Grylloblatta chirugica, or ancestral species, has undoubtedly existed in the region since at least the late Pleistocene. Geological and paleobotanical information suggest much the same cycles of climatic conditions for the entire Quaternary 1,000,000+ years (Emiliani, 1955; Flint, 1957; Martin and Harrell, 1957). Therefore, the present stock may have inhabited the general region for a considerable length of time.

The topographical barrier of the Columbia River and the nature of the insect's morphology show a long isolation and no relationship to Grylloblatta on Mt. Rainier or Mt. Hood.

The present distribution of the Northern Cascade species of Grylloblatta is of a post Pleistocene origin and no older than 9000 years. The present populations of Grylloblatta scudderi, Grylloblatta occidentalis and Grylloblatta skagitensis are derived from ancestral stock which lived during the late Pleistocene south or east of the ice fronts and reached the present localities as the ice receded at the beginning of post Pleistocene (ca. 10,000 years ago). The present distribution of G. scudderi may be as recent as the Neoglacial (ca. 3500-2000 years ago).

2. High Cascade Group

The Mt. Hood Grylloblatta are geographically isolated by the Columbia River Gorge from G. chirugica found in the lava caves on the slopes of Mt. St. Helens. The Columbia River has functioned as an effective barrier to northern migration to many animal species (e.g. Amphibia, see Stebbins, 1949; Lowe, 1950).

The Columbia River Gorge barrier evidently has been in effect throughout the Pleistocene. Certainly it was a very effective barrier during periods of late Pleistocene when the gorge was repeatedly swept rim to rim by catastrophic floods arising in eastern Idaho and western Montana (Richmond, 1965).

The population of Grylloblatta hoodalles is presently isolated from G. rothi, G. lavacola and G. s. sculleni in the Three Sisters complex by the Warm Springs Plateau and the lowlands between Mt. Hood and Mt. Jefferson. Other barriers to population interchange exist, such as the deep canyons of the Salmon, Clackamas and Matolius rivers.

The present temperature in these lower areas is such that Grylloblatta could not survive except during the short periods of mid-winter. This has been an effective barrier to the taxon since at least the beginning of the post Pleistocene (ca. 8500 B. P.). Even during the coldest of

Neoglaciation, temperature means were not appreciably lower than today. Populations could exist in this area if they inhabited lava ice caves, but currently none has been found.

Mt. Hood was extensively glaciated during the Fraser Glaciation of the late Pleistocene. The severity of the glaciation is exemplified by the possible plucking of at least 600 vertical feet from the summit and possibly more from the slope (Wise, 1964a, 1964b). The mountain was almost completely ice covered with terminal moraines below 4500 feet (Crandell, 1965; Wise, 1966).

Ice completely covered the High Cascades from Ollalie Butte just south of Mt. Hood to Mt. McLoughlin near the Oregon-California border during Fraser Glaciation (Thayer, 1939; Crandell, 1965) (Fig. 10). During that time the present barrier between the more southern Cascade species of Grylloblatta and the Mt. Hood species did not exist. This region would have experienced a periglacial climate during Fraser Glaciation since it is between the extensive ice cap of the Cascades and that of Mt. Hood.

In fact this southern peripheral zone may well have been of post Pleistocene origin for the present species on Mt. Hood. As the ice retreated toward Mt. Hood the Grylloblatta may have followed the front, the population eventually then finding the only tolerable habitat at the beginning of the Hypsithermal on the slopes of Mt. Hood. Evidence

for this southern origin of the present population is its close relationship with G. rothi found at south Broken Top in the High Cascades.

The G. hoodalles at Timberline Lodge, 6000-foot elevation, Mt. Hood, has occupied this locality for less than 1700 years. The southeast flank of Mt. Hood experienced a huge mud and water flow mixed with eruptive hornblende andesite debris about 1670 B. P. \pm 200 years (Lawrence and Lawrence, 1959; Wise, 1966). This mud-andesite flow completely covered the whole southwest flank of Mt. Hood, being many feet deep as far as the 3800-foot elevation on Zigzag River. The source of this material is believed to have been the last eruptive phase of Mt. Hood and the breaching of a crater lake of 1/3-mile diameter and 800 feet deep. The flow completely buried large trees and denuded the upper slopes.

The present habitat of the Grylloblatta is in this unsorted debris beneath rotten logs and large buried rocks. Search by myself and biologists of the U. S. Forest Service has failed to locate any other populations of G. hoodalles on the mountain.

I do not believe that the genus migrated to the mountain before 1670 B. P. The present population must have moved to the unsorted material from some other region of the mountain since 1670 \pm 200 years B. P. The unsorted material of glacial flows and boulders of all sizes create an ideal hypolithion not found in other areas of the south

slopes. Extensive erosion on the other flanks of the mountain of Recent origin may have destroyed the original post Pleistocene habitat.

I seriously doubt that this is the only population of G. hoodalles on Mt. Hood. I feel that investigations during the summer will turn up at least one more at Cloud Cap on the east slope about 6800-foot elevation. Should additional populations be found in the future, they will be geographically isolated from each other by the unstable canyons present on all flanks.

The Grylloblatta that occur in the Three Sisters region are the most concentrated group of species of the entire genus in North America. Within an area of sixty by thirty miles are found G. s. sculleni, G. rothi, G. lavacola, G. s. cryocola and G. paulinai, plus two cavernicolous populations of uncertain systematic relationships. Grylloblatta s. sculleni, G. rothi and G. lavacola are sympatric in the Three Sisters, McKenzie Pass-Belknap lava fields region. Grylloblatta paulinai is an allopatric and troglomorphic cavernicolous form. A peripheral population of G. lavacola is sympatric with G. s. cryocola in the Edison Ice Cave system for at least a portion of the yearly climate cycle and is thought to exist sympatrically with G. rothi.

The Three Sisters complex is composed of extinct individual volcanic cones that range in elevation from 7045 to 10,854 feet with such picturesque names as North Sister, Middle Sister, South Sister, Little Brother, Husband, Wife, Bachelor and Broken Top. Hodge (1925), in describing the

geology of the region, visualized these volcanic cones to be Pleistocene remnants of a single huge mountain over 18,000 feet high which he called Mt. Multnomah. In later more detailed work, Williams (1957) considered these to be of individual volcanic origin of Pleistocene or younger age. Today most geologists follow Williams' theory. In any event, there has been almost continuous volcanic activity on or around the peaks throughout the entire span of the Pleistocene, and this continued during the post Pleistocene until less than 2000 years ago (Williams, 1957; Peck, 1960).

Evidence of early and middle Pleistocene glaciation is unknown for the High Cascades. The sequence of events, documented for the Northern Cascades and the Sierra Nevada to the south, is inferred to have taken place in the Three Sisters region (Williams, 1942, 1944; Flint, 1947; Peck, 1960). Late Pleistocene glaciation is well documented with glacial stades correlated in age with the Northern Cascades and the Sierra Nevada (Heusser, 1966). The Fraser Glaciation in the High Cascades was widespread. The entire range was covered with summit ice fields 500-1000 feet thick at an elevation of 5000 feet and deeper over the high peaks (Thayer, 1939; Williams, 1942, 1957). Lobes from the summit ice fields extended far down the east slopes transporting boulder erratics of crest origin over 80 miles into the present high desert (Williams, 1957; Allison, 1966).

Summit ice field lobes extended down the valleys on the western slopes to the Willamette lowlands around 2000 to 2500 feet in elevation. Earlier late Pleistocene

glaciation entered the lowlands, transporting erratics across the valley as far west as Monmouth and Corvallis (Allison, 1935, 1936).

There are fifteen major glaciers and numerous snow fields of Neoglacial or Recent origin flowing from subsummit ice fields on North Sister, Middle Sister, South Sister, Bachelor and Broken Top. These peaks have populations of Grylloblatta occurring on the lower slopes which range up to the present terminal moraines of the glaciers between 7500 and 8000 feet.

Most traces of late Pleistocene glaciation have been obliterated on these peaks by the extensive post Pleistocene volcanism and Neoglacial ice movement. North Sister is the oldest of the complex and is considered to be early or middle Pleistocene in age, having lost one-fourth of its mass during late Fraser Glaciation. Middle Sister, South Sister, Broken Top and Bachelor are thought to be perhaps middle but most likely late Pleistocene in age, with growth extending well into the post Pleistocene. Summit craters exist on all of these peaks and the slopes show erosion attributed only to the present glaciers (Williams, 1942, 1957).

McKenzie Pass, immediately north of the Three Sisters, is composed of extensive lava fields of Neoglacial or younger age and the area is dominated by Belknap Crater. The 6800-foot high Belknap Crater is the primary source of the extensive lava flow that covered some 50 square miles and which flowed down the pass to 4000 feet and covered the lower

slopes of North Sister to an elevation of 6500 feet. This flow, hundreds of feet thick, completely covered the late Pleistocene headwaters of the McKenzie River and is dated 3000 years B. P. (Baldwin, 1964). There are younger isolated fissure flows that form steptoes (islands) in the 3000-year old Belknap Crater flow.

Grylloblatta s. sculleni occurs in the basin between North Sister and Middle Sister. The type locality at Scott Camp, 6600 feet, is in consolidated old talus of morainal hypolithion below Renfrew Glacier. This species has been taken from over 8000 feet in this basin north, down the slopes of North Sister, to the Belknap lava fields where it occurs sympatrically with G. rothi and G. lavacola.

Grylloblatta lavacola inhabits the Belknap lava fields and is distributed along the southeastern margins of the flows from Windy Point (4909 feet) to Condon Butte (5030 feet) and up the lavas covering the slope of North Sister.

The type locality of Grylloblatta rothi is Happy Valley (6450 feet) located below Crook Glacier on Broken Top. This is a species of wide distribution, occurring at 7000 feet on Bachelor 6 miles south and through the Three Sisters to McKenzie Pass, 15 miles southwest of Broken Top.

Grylloblatta s. cryocola is a cavernicolous subspecies from the Edison Ice Cave system, 5 miles southeast of Bachelor. The Edison Ice Cave system formed in a pressure ridge on a post Pleistocene basaltic fissure flow from the southeastern flank of Bachelor. A 6888 year B. P. age is assigned to Bachelor and the Edison flow is possibly the

same age (Taylor, 1965). Grylloblatta s. cryocola is seasonally troglophilic in the caves or hypolithion in the substrate above and around the caverns. It occurs sympatrically with G. lavacola in the twilight and entrance zone portions of the cave system. Grylloblatta s. cryocola is restricted to the cave area but G. lavacola appears to be a disjunct population in this area, being unknown from Bachelor, Broken Top or Middle Sister.

The present localities of Grylloblatta in the Three Sisters complex were covered by late Pleistocene (23,000-9000 years B. P.) ice fields or glaciers. The present ranges are all located in post Pleistocene and younger lava fields or in hypolithion of Neoglacial to Recent origin.

The ancestral populations of these species were undoubtedly forced out of the region by late Pleistocene ice advance. The present distribution suggests a retreat both to the east and west beyond the ice fronts and in the periglacial zone. As late Pleistocene ice receded in the High Cascades, approximately 11,000 to 9000 years ago, the parent stocks probably followed the retreating ice and peripheral zone back to the higher elevations near the vicinity of the Three Sisters.

An eastern retreat and subsequent return is evidenced by Grylloblatta paulinae from South Ice Cave, located in the high desert lavas to the east. A western late Pleistocene retreat and early post Pleistocene return is documented by the discovery of a new species of Grylloblatta on Mary's

Peak near the western borders of the Willamette lowlands and Coast Range. Both South Ice Cave and Mary's Peak are located within the late Pleistocene periglacial zone, as indicated by fossil ice wedges in their vicinity.

The present distributions of the species of Grylloblatta in this region of the High Cascades must have formed after the post-volcanic and Neoglaciation periods that began approximately 3500 years ago. Based on the present sympatric distribution and the fact that no hybrid populations have been discovered, I hypothesize that the parental populations were the same species as found today.

3. Southern Cascade Group

The Southern Cascade Grylloblattidae are known only from Crater Lake, Oregon, Mt. Shasta and the vicinity of Mt. Lassen, California. The mountains, isolated from the main range by extensive low elevation lava fields, are the southern extension of the major volcanic peaks which dominate the Cascade Range. Major volcanic activity took place throughout the Pleistocene and has continued to Recent time, with Mt. Lassen erupting in 1914 and active until 1917 (Williams, 1932a, 1942; Anderson, 1941). In addition, each was the site of local ice caps and glaciers during the various glaciations of the Pleistocene and Neoglacial.

Mt. Shasta (14,164 feet) has currently active glaciers and

both Mt. Lassen (10,466 feet) and Crater Lake (6000 to 8300 feet) have large snow fields which last throughout the year.

Grylloblatta rothi was reported by Gurney (1953) from Crater Lake. Two specimens, tentatively identified as Grylloblatta gurneyi, are known from Mt. Shasta. Grylloblatta barberi and Grylloblatta chandleri, while not occurring on Mt. Lassen, are found within the periglacial zone that existed around the Mt. Lassen ice shield during Tioga (Fraser) Glaciation (Williams, 1932b; Anderson, 1941). Eagle Lake, Lassen Co., the type locality for G. chandleri, is 30 miles east of Mt. Lassen. The type locality of G. barberi is 20 miles southeast of Lassen in the north fork of the Feather River. An isolated population of Grylloblatta occurs in Wilson Ice Cave located within the southern boundary of Tioga Glaciation on Mt. Lassen.

The present Crater Lake is situated in a caldera formed when the top of approximately 12,500-foot Mt. Mazama collapsed 6453 \pm 250 years ago (Powers and Wilcox, 1964). Mt. Mazama was mantled by extensive ice fields during the late Pleistocene, volcanic activity also occurring at this time (Williams, 1942). It is thought that just prior to the mountain collapse which formed the lake caldera, a violent explosion took place, depositing pumice 30-40 feet deep as far as 30-45 miles to the north and east. Some of this ash and pumice was wind-borne to central Montana and Alberta (Williams, 1942; Wilcox, 1965).

The localities around the Crater Lake rim where Grylloblatta is now found were covered many feet deep by the hot

pumice and huge avalanches of mud and lava resulting from the rapidly melting glaciers during the explosion. Before the Hypsithermal period, during which the crater formed, the localities were extensively glaciated and ice-covered during Fraser Glaciation (ca. 23,000-12,000 years ago).

It seems unlikely that Grylloblatta inhabited Mt. Mazama during the late Pleistocene in light of the widespread occurrence of ice fields and glaciers and the periodic volcanic activity. At least once during the late Pleistocene Mt. Mazama was covered by the ice sheet which mantled the entire Oregon Cascades as far south as Mt. McLaughlin (Crandell, 1965) (Fig. 10)

The possibility that Grylloblatta inhabited some areas on Mt. Mazama in the time between ice recession and about 6600 years ago must be considered. The almost continuous volcanic activity during the period tends to negate this possibility. If Grylloblatta did not occupy Mt. Mazama during the late Pleistocene and 6600 years ago, where did the parental population survive this period? Other species of Grylloblatta are known from the south in the vicinity of Mt.

Shasta, the Lava Beds National Monument and Medicine Lake Highlands. These numerous northern California populations, of which many are cavernicolous, are not closely related systematically to G. rothi. The northern California species form a distinct group seemingly restricted to the lava in the Modoc Plateau and southern terminus of the Cascades.

The Crater Lake Grylloblatta, probably subspecific with

G. rothi, undoubtedly came from the same ancestral stock. The parental stocks of each modern form most likely inhabited the high desert plateau east of the ice fields covering the Three Sisters complex and Mt. Mazama. They then returned, following the receding periglacial zone, into the High and Southern Cascades. I believe the Crater Lake populations migrated to their present localities sometime after the caldera formation from the northeast and most likely during Neoglaciatio (ca. 3500-2000 years ago). The discovery of additional populations on Mt. Thielson, Diamond Peak, the Twins and Maiden Peak, between the Three Sisters and Crater Lake, would substantiate this hypothesis.

The Crater Lake Grylloblatta are presently isolated from the species in the Modoc Plateau by the Klamath Marsh and dry rabbit brush scrublands. This Crater Lake population is also rather effectively isolated from the Klamath Mountain population to the southwest by the low elevations associated with the Rogue River drainage and the Grants Pass-Medford Valley. The drainage canyons of the Willamette, Deschutes and Umpqua rivers virtually divide the low crest of the Cascade Range between Crater Lake and the High Cascade system. In addition, just north of the Crater Lake rim exists a pumice desert some 10 miles wide which, until historical times, was apparently devoid of plant life.

The identification of the Crater Lake population as G. rothi by Gurney (1953) was based on a single female which was declared the allotype. The holotype is from Broken Top,

over 90 miles north. This association of holotype and allotype was based on the shortness of the cercal segments, these being the only specimens then known. I have since collected Grylloblatta of both sexes from various localities on the rim of Crater Lake and believe that these populations are not typical G. rothi. Any future discovery of Grylloblatta between Crater Lake and Broken Top would be highly important, since it might lead to a decision regarding the exact identity of the Crater Lake Grylloblatta.

The parental populations of both the Mt. Shasta and Mt. Lassen species undoubtedly inhabited regions within the periglacial zone and possibly occupied all the Modoc Plateau and Medicine Lake Highlands. They are conspecific with, or closely related to, other species now occurring within ice caves of the plateau lava fields (Kamp, 1963).

4. Modoc Plateau-Basin Range Group

The Grylloblatta in the Modoc Plateau-Basin Ranges are cavernicolous species found in the numerous ice caves of the lava fields. Grylloblatta chandleri, with type locality as Eagle Lake, ranges into the ice caves on the eastern slope of Mt. Lassen. Almost every ice cave explored between Eagle Lake and the Medicine Lake Highlands contains populations of Grylloblatta. North of these highlands, G. gurneyi occurs in many of the ice caves in the Lava Beds National Monument.

Geologically, the Modoc Plateau is a basaltic block

3000-5000 feet high, surrounded by numerous volcanoes 1000-2000 feet higher. On the western edge it borders the Southern Cascades. During the late Pleistocene Tioga Stage of glaciation, local ice caps and mountain glaciers were present on the highest peaks, especially the Medicine Lake Highlands between the Lava Beds National Monument and Eagle Lake-Mt. Lassen region (Stearns, 1929; Blackwelder, 1931; Peacock, 1931; Williams, 1932a, 1932b).

A discussion of the late Pleistocene-post Pleistocene distribution and phylogenetic relationships of the species in this area is given by Kamp (1963).

5a. Coast Range Group

The only known Grylloblatta from the Coast Range is a new species which occurs on the upper elevations of Mary's Peak, 14 miles west of Corvallis, Oregon. In the Coast Range of western Washington and Oregon the crestline is below 3000 feet, but a few summits, such as Mary's Peak, are over 4000 feet in elevation. Glaciation during the Fraser Stage of late Pleistocene was apparently restricted to cirque glaciers on the protected eastern side of the highest peaks (Baldwin and Roberts, 1952). Mary's Peak was the site of such local glaciation during the late Pleistocene. The eastern region of the Coast Range around Mary's Peak was also apparently affected by the climate present in the periglacial zone and the valley glaciers which carried erratics derived from the High Cascades to a few miles

west of Corvallis.

This isolated species of Grylloblatta is most probably a remnant of Grylloblatta displaced to the west by the extensive ice fields and valley glaciers from the High Cascades to the east. As ice receded with the advent of the Hypsithermal interval, a segment of the population may have retreated to the present locality of Mary's Peak.

The present distribution of this species is restricted to the eastern slopes between 3000 feet and the 4100-foot summit. A regional storm pattern deposits larger depths of snow on the east side of the Peak where it may persist in sheltered areas well into the fall.

5b. Klamath Mountain Group

Grylloblatta is known from the Klamath Mountains near the Oregon-California boundary. A single specimen was found on the Siskiyou Summit, 4464 feet, 14 miles south of Ashland, Oregon, in a typical hypolithion situation.

The Klamath Mountains are a very rugged region somewhat higher in elevation than the Coast Range. Clusters of high peaks, 6000-9000 feet in altitude, rise above the general levels which are between 2700 and 4000 feet in elevation. The narrow canyon floors of the many rivers are less than 900-2200 feet above sea level, even in the center of the range, giving the mountains a precipitous relief of 3200-6600 feet.

Evidence of widespread late Pleistocene Tioga Glaciation is known from above 3000 feet for the Klamath and Trinity Ranges (Flint, 1947; Wells, Hotz and Carter, 1949). This glaciation of cirques, valley glaciers and summit ice fields may have extended east to the Sacramento River Canyon. This is near the western border of the glaciation present in the Mt. Shasta region of the Southern Cascades (California State Water Resources, 1959; Sharp, 1960).

I have not seen the specimen in the U. S. National Museum collection and A. B. Gurney has not been able to determine the species, nor its relationship (Gurney, pers. comm.) It is not surprising that Grylloblatta occurs in the Klamath Mountains considering the proximity to the range of the northern California and southern Oregon species. The Klamath-Trinity mountains are in an area of heavy snow-fall which persists throughout the year in the highest elevations and even in summer is under the influence of northern Pacific storm systems.

Dr. Gurney, members of the California Department of Entomology, and I searched in the region of Grizzly Peak in 1964. This region, of high alpine and large cirque basins, contains the only glacier in the mountain range. We did not discover Grylloblatta at that time, though we did find new forms of high altitude Orthoptera such as Boonacris, Melanoplus and Napaia. We feel confident that Grylloblatta occurs in the region and south on higher peaks of the Trinity Range.

The Siskiyou Summit material is presently isolated

both topographically and climatically from other species. Additional material will probably establish a close relationship to the extreme southern Cascade-Modoc Plateau species.

III. The Sierra Nevada Group

From the standpoint of systematics and distribution, the Sierra Nevada Grylloblatta are a diverse fauna. Seven areas containing Grylloblatta are known for the Sierra Nevada, scattered in local "pockets" from the northern terminus south along the crest below Sequoia National Park, a distance of 300 miles.

Grylloblatta washoa is described from 7382 feet on Echo Pass Summit, Eldorado Co., south of Lake Tahoe.

Grylloblatta bifratrilecta is known from the 9000-10,000 foot level of Sonora Pass, 50 miles southeast of Lake Tahoe.

A new species (Gurney, pers. comm.) is found on the Badger Pass-Glacier Peak region of Yosemite National Park between 6000 and 7500 feet in altitude.

A single female has been found at 12,000 feet in the Upper Convict Basin near Devil's Postpile National Monument, 70 miles southeast of Sonora Pass. The southernmost population is from May's Hole, Sequoia National Park, Tulare Co.

From the northern Sierra Nevada I discovered two new species, one from 8587-foot Mt. Elwell, 60 miles southeast of Mt. Lassen, and another from the 6000-7000 foot elevation in the Sierra Butte, 10 miles south of

Yuba Pass located approximately halfway between Mt. Lassen and Lake Tahoe.

The apparently disjunct distribution of this group along the Sierra Nevada is probably a consequence of incomplete collecting. There are few accessible passes through the high elevations of the range and there has been much searching perhaps in the wrong habitat. In fact, the lack of habitat knowledge impeded my collecting success during the two weeks I spent in the region in 1967. A number of entomologists in the past 10 years have looked for Grylloblatta during their other collecting. These records were based on the descriptions of either the Rocky Mountain habitat or that of G. sculleni in loose talus at the foot of glaciers. I firmly believe that Grylloblatta populations will be found the length of the range as far south as Walker Pass, west of Death Valley, and possibly in the San Gorgonio-San Jacinto ranges of southern California.

Present systematic data suggest that possibly two groups of species are distributed in the Sierra Nevada: a northern group of large size, long, many-segmented antennae, very long legs and symmetrical male genitalia, occurring from Lake Tahoe to the vicinity of the closely related Modoc Plateau-Southern Cascades species, and a southern group of small size, short, less segmented antennae and moderately asymmetrical male genitalia, from Lake Tahoe to Kings Canyon National Park.

The Sierra Nevada is a gigantic westward-tilted fault

block up to 14,000 feet in elevation. Its eastern slope is an abrupt wall of 15-35° slope rising in 5 miles from 2800 to 11,000 feet above the basin and range province. It has an average crestline altitude of over 7500 feet. The western slope descends from the crest to an altitude of 300-600 feet at its foot in a distance of 50-60 miles. The numerous streams and rivers have cut narrow gorges 2000-7000 feet deep. A region 35 miles wide along the 350-mile crest was intensely glaciated during the Pleistocene (Blackwelder, 1931; Averill, 1937; Wahrhaftig and Birman, 1965).

Six major glaciations have been recognized in the Sierra Nevada for the Pleistocene, and three smaller advances are known for the Neoglacial period. The Tioga Glaciation is correlated for the late Pleistocene and is equal to the Pinedale Glaciation in the Rocky Mountains and the Fraser Glaciation in the Coast-Cascade ranges (Matthes, 1930; Blackwelder, 1931; Birman, 1957, 1964; Thompson and White, 1964).

The Sierra Nevada at the present time contains only a few cirque glaciers on the sheltered north slope above 10,500 feet near Lake Tahoe and above 13,000 feet between Sequoia-King's Canyon National Parks. Climatic snowline is 14,000 feet in the Sequoia-King's Canyon area and 7000 to 9000 feet in the northern portions (Flint, 1957). The climate is very seasonal, with 90 per cent of the precipitation in the winter, and is controlled more by topography than by latitude.

Precipitation ranges from 90 inches in the north to only 55 inches in the southern regions. Precipitation increases 2 to 4 inches for each 300-foot rise, reaching a maximum at about 5000-6000 feet in the central part of the range. At higher elevations 86 per cent of the precipitation falls as snow, and this reaches an average depth of 34 feet on Donner Summit. The east side of the Sierra Nevada is in a rain shadow and has a high desert condition of little rain and snow.

Summer temperatures range from 15-100° F. and during the winter from -30° to about 55° F. (U. S. Weather Bureau, 1964). The season's snow, which begins in October, has usually disappeared by August except for small banks and fields at the highest elevations (Dale, 1959).

In the late Pleistocene a fairly continuous complex of ice fields formed along the crest, with glaciers descending both slopes. The direction of the descending glaciers was closely controlled by the present drainage patterns and general topography which had been previously established. Snowline was approximately 2000 feet lower during the glacial maxima than it is at present.

During Tioga Glaciation ice fields were thicker in the southern and central regions between 37-38° latitude than elsewhere in the range. To the north the lower elevations of the crest resulted in a smaller volume, and at the southern terminus, higher temperatures kept ice volumes restricted to the highest elevations (Flint, 1957).

The larger glaciers that descended from the crest ice

fields were only about 10 miles long on the eastern slope and as much as 65 miles long on the western side of the range. In the southern Lake Tahoe region the glaciers descended to altitudes of 3000-4000 feet on the east (the floor of the Basin Range) and 1800-3000 feet to the west (Blackwelder, 1931; Putnam, 1960; Birman, 1964). In the north glaciers seldom exceeded 25 miles in length and rarely descended below 3200 feet. However, the northern ice flowed into the middle fork of the Feather River, 10 miles north of Mt. Elwell (Averill, 1937).

The known localities of the Sierra Nevada Grylloblatta are restricted to the higher summits and isolated peaks which rise well above the crestline. Each species is isolated from others by the climate of the intervening elevations, the river canyons and glaciated topography. As an example, between G. washoa and G. bifratrilecta the range is divided by three passes and four major rivers. The new species in Yosemite is separated from G. bifratrilecta by the Yosemite Valley and the 3000-foot deep Merced River Canyon.

The southern Grylloblatta species are well isolated topographically from the others by the Kern Canyon and King's River Gorge, each 6000-7000 feet deep. The northern two populations are separated from each other by the much lower elevation of the crestline. The drier, warmer conditions of the low elevations isolate this northern group from the other Sierra Nevada species.

The ancestors of the present Sierra Nevada species

probably inhabited the western slopes of the range below the ice fields and glacier fronts during the late Pleistocene. A post Pleistocene return to the vicinity of the present localities probably occurred, being restricted by the existing drainage and topography and valley glaciers which persisted longer than the glaciers on the intervening highlands. Their persistence well into the post Pleistocene probably channeled migration between the canyons to the present localities, for these all lie between the major passes and canyons.

The northern forms may have retreated either to the north or west and then returned during ice recession. The close systematic relationships between these northern Sierra Nevada populations and those of the Modoc Plateau-Southern Cascades suggest a possible common Pleistocene origin.

Discussion and Summary

The interpretation of present distributional patterns of Grylloblatta is hindered by the complete void in the fossil record. As in other such studies (Beirne, 1952), the conclusions arrived at on the origin and history of the Grylloblattodea in western North America are those that appear the most probable when all known aspects of the biology, distribution and taxonomy of the animals, and all available information on past climatic, vegetational and geographical changes in the area are taken into account.

These conclusions are, however, a matter of personal opinion and so may be somewhat controversial.

The reconstructions are based almost completely on deductive evidence. Such evidence is often capable of several interpretations, but the conclusions drawn herein are those that appear most likely with the present data.

The further we retreat into past histories of distribution, the more tenuous and incomplete indirect evidence becomes, especially in the western Cordillera. The Pleistocene is represented by five major ice ages in the west and the last major advance has obscured most evidences of earlier stades. Hence, most indirect evidence is available for only the last 25,000 to 40,000 years.

The late Pleistocene and post Pleistocene geologic and climatic events have been found to be useful in the analysis of present patterns of distribution and speciation of other terrestrial organisms. It has been recognized for many years that the Pleistocene glaciation played an important role in the present distribution of animals.

In western North America, for example, Hubbs and Miller (1948) used such data for the understanding of the distribution of fish in the Great Basin. Blair (1958, 1959, 1963) and Thurlow (1961) found Pleistocene and post Pleistocene events had pronounced influence on the distribution and speciation of the Amphibia.

The Pleistocene- post Pleistocene has been found to have had an important influence on the present distribution

of western Reptilia (Smith, 1957), birds (Mengel, 1964) and mammals (Peterson, 1955). The same periods have influenced the present distribution of invertebrates, especially the Insecta (Ricker, 1964; Howden, 1966).

The basic argument in the above papers is that glaciation was the most important influence. The premise is that glacial advances were accompanied by climatic effects far south of continental glacial borders and at lower elevations than evidence from terminal moraines would indicate for cirque and mountain glaciation. The climatic effects produced the cold region, or zone, known as the Periglacial (Boreal) of Flint (1957) and Brum-schwieler (1962).

The degree of displacement has been argued pro and con, with some plant ecologists (e.g. Braun, 1955) arguing strongly against any significant displacement. However, evidence of widespread displacement in the west can be documented from botanical work. Wendorf (1961), using pollen analysis, indicates a boreal woodland of Pinus and Picea 15,000 to 22,500 years ago for eastern New Mexico and western Texas; these areas today are xerophytic desert shrub and cacti. Martin (1963) finds the Mohave Desert of California with a Juniperus and Pinus forest and the southeastern region of Arizona containing a forest of Pinus ponderosa and Abies; these regions are presently arid desert grass and shrub flora.

When the continental ice sheets of the Pleistocene disappeared, it is usually assumed that the deglaciated areas were repopulated by species previously persisting north (Yukon-Mackenzie valleys) or south of the ice. This was undoubtedly true for highly mobile species where success for dispersal was not influenced by the vagaries of the post-glacial terrain and climate. This theory poses problems when applied to such an organism as Grylloblatta which is apterous, has a very slow growth rate, and is restricted to a narrow range of temperature and humidity.

Pleistocene survival in refugia has been proposed many times for species with low dispersal powers. Such a theory would seem very applicable to Grylloblatta. Evidences of refugia within and between the Cordilleran and Keewatin ice sheets are incomplete and in many cases contradictory. Some of the proposed refugia are mantled with glacial outwash which would seemingly restrict the amounts of suitable hypolithic habitat for the insect. Nunatak survival during the Pleistocene was not possible for Grylloblatta. It is reasonable to assume that the present environmental conditions on nunataks projecting above small ice fields are no more severe today than during the massive Pleistocene glaciation.

Thus, while two theories have been advanced to explain the distribution of organisms since the Pleistocene, namely, 1) survival north and south of the ice sheets and post

Pleistocene invasion into areas that were ice-covered, and 2) survival within the glaciated areas in ice-free refugia, either can be applied to explain the present distribution of those species of Grylloblatta which occur within the boundaries of continental glaciation. The Coast-Cascade and Sierra Nevada distributions of Grylloblatta can be explained by late Pleistocene survival at elevations below the borders of the summit ice sheets.

The presence of a single species of Grylloblatta occurring throughout the Rocky Mountain Cordillera, and the present distribution of many populations south of the margins of maximum ice advance, indicate late Pleistocene survival of G. c. campodeiformis in Montana and Wyoming. The present distribution of G. c. campodeiformis along the crest of the Rocky Mountain Cordillera regions north of the boundaries of continental glaciation suggests migration along highlands during glacial recession some 9000 years ago.

The distribution pattern and present isolation suggest late Pleistocene survival of G. c. athapaska and G. c. nahanni in the refugia of the Liard and Nahanni ranges. The close relationship of these subspecies further suggests a pre-late Pleistocene common origin with isolation of G. c. athapaska and G. c. nahanni during late Pleistocene.

The present distribution and taxonomic relationships of G. scudderi and G. occidentalis plus geologic evidence indicate a late Pleistocene survival south of the Cordilleran

ice sheet and between the Fraser lobe and summit ice fields. The very small population of G. scudderi and the assumed subspecies distribution of G. occidentalis tentatively suggest some dispersal as recent as Neoglacial, beginning 3500 to 2000 years ago.

The sequence of volcanism, Fraser advance and recession, and Neoglacial events suggest a recent distribution of G. skagitensis that occurs in the Glacier Peak region. The pioneering stock of the present population most likely survived the late Pleistocene and Hypsithermal periods to the east of Glacier Peak or south toward Mt. Rainier.

The continual glaciation since late Pleistocene and the post Pleistocene volcanic activity in the locality of the Mt. Rainier Grylloblatta suggest that these are very recent inhabitants in their present locality.

The current isolation of G. chirugica to the ice caves in the lava fields of Mt. St. Helens and the past geologic and climatic history of the region indicate a late Pleistocene distribution approximately 8000 to 9000 years old. Grylloblatta were probably hypolithion inhabitants in the region during the late Pleistocene, 40,000 to 9000 years ago. However, with the termination of late Pleistocene glaciation and the beginning of the Hypsithermal period, G. chirugica were forced to retreat to the ice caves.

The distribution of Grylloblatta species in the High Cascades depicts a pattern of insular species and a center

of recent sympatric distribution in the hypolithion of the alpine-subalpine.

The present distribution must have formed after the volcanic and Neoglacial periods that began approximately 3500 years ago. The number of species and the presence of sympatric forms suggest systematic differentiation well in the past.

The Southern Cascade and Modoc Plateau-Basin Range Grylloblatta are presently insular populations restricted to the major volcanic peaks or ice caves of the lava deserts. The general cavernicolous distribution predates the Hypsithermal interval with possibly some short distance dispersal during the Neoglacial.

The isolation of the alpine-subalpine species was most certainly pre-Hypsithermal. The present distribution of that species on the major peaks has taken place since the cessation of Hypsithermal-Neoglacial volcanic activity. The fact that many of the isolated populations are conspecific also indicates a rather recent dispersal to the present habitats.

The distribution patterns in the Sierra Nevada shows scattered "pockets" of Grylloblatta existing the length of the range. Taxonomically, there are two distinct groups in the Cordillera: a northern group more closely related to the Southern Cascade-Modoc-Basin Range species, and a southern species group. The northern populations most likely occupied the plateau regions to the north during

late Pleistocene, the present distribution being established on glacial recession and probably with no Neoglacial re-adjustment.

The topographical isolation of the different species suggests systematic differentiation before the late Pleistocene.

BY NUMERICAL ANALYSIS

Introduction

It is now generally agreed that the Grylloblattodea should be placed in the orthopteroid group of insects with the Dictyoptera, Phasmida, Orthoptera, Isoptera, Plecoptera, Embioptera and Zoraptera. These constitute a closely related group of exopterygotes, the Polyneoptera of Martynov (1938). The relative position of the grylloblattids within the orthopteroid complex has never been settled satisfactorily.

From the phylogenetic standpoint, the Grylloblattidae are of exceptional interest in that they combine a mosaic of features found in the other orthopteroids, as well as unique morphological characters that are viewed as primitive and restricted to the taxon. For example, the head is dermapteroid, the eyes are isopteroid, and the antennae are like Timea (Phasmida). The legs and tarsi are similar to the Dictyoptera and Isoptera. The ovipositor resembles the Tettigoniidae (Orthoptera), but is less developed, while the male genitalia are asymmetrical and resemble in part those of the Dictyoptera. The cerci of both sexes are like those found only in the Dictyoptera. Characters unique to the Grylloblattidae include the lack of a

subgenital plate in the female and the occurrence of three free thoracic segments that have retained their primitive muscular connections. The ventral nerve cord is composed of seven free pairs of abdominal ganglia, as compared with five or six in the other orthopteroids. The presence of sternal spinae following all three thoracic segments differs from all other living orthopteroids in which a third spina is absent.

The possession of a combination of characters that are exhibited also in other groups has made it difficult to settle the taxonomic position of the Grylloblattidae. The phenetic and phylogenetic affinities of the taxon to the other orthopteroids have given rise to much speculation and divergence of opinion.

In the original description, Walker (1914) treated Grylloblatta as the type genus of a new family within the Orthoptera (sen. lat.). Crampton (1915) elevated Grylloblattidae to ordinal status as Notoptera. Other subordinal and ordinal names proposed include Grylloblattaria (Bruner, 1915), Grylloblattoidea (Brues and Melander, 1915), and Grylloblattodea (Brues and Melander, 1932). Much confusion exists in the literature since all the above names are used in various parts of the world. In North America the Grylloblattodea¹ is usually placed within the Orthoptera

¹ Grylloblattodea is adopted here as the correct name, following the suggestion of Essig (1942:105, footnote)

(e.g. by Borror and DeLong, 1971).

The evolutionary affinities have been the subject of many publications. Walker (1933) considered Grylloblattidae to have a close affinity to the ancestor of the Saltatoria of the Orthoptera. After further morphological studies (Walker, 1938), he placed them between Blattaria (Dictyoptera) and the Saltatoria (Orthoptera), and later he placed them nearest to the living Ensifera (sen. str.) (Walker, 1943).

Crampton (1915) considered that Grylloblatta occupies a position intermediate between the Dermaptera and Isoptera and thought it to be the nearest living representative of the common ancestors of the Gryllidae and Tettigoniidae. Crampton (1917) later changed his mind and considered Grylloblatta to be intermediate between the mantids and embiids as well as possibly related to the Orthoptera (sen. str.) and Phasmida. A detailed discussion of Crampton's sixteen papers (1915-1938) on the affinities of Grylloblatta is not necessary. In the course of his work he associated Grylloblatta with literally every order of orthopteroids.

Imms (1927) placed Grylloblatta nearer to the Dictyoptera than to the Saltatoria, while Snodgrass (1937) declared its affinities to be with both the Blattaria and the Orthoptera. Zeuner (1939, 1945) went so far as to call them "recent, living Protorthoptera," and Walker (1937) called Grylloblatta a "living fossil" and a representative

of some line ancestral to modern orthopteroids.

The orthopteroid fossil record gives no indication of the affinities of the Grylloblattidae. The Ensifera, Blattaria and Protorthoptera are known from the Carboniferous, the Caelifera and Phasmida from the Triassic, the Dermaptera from the Jurassic and the Mantodea from the Tertiary (Crowson et al, 1967). No fossil record of the Grylloblattodea is presently known.

Considerable confusion exists about the taxonomic status and the affinities of the taxon. Many of the opinions are purely speculative, and most of the above authors restricted the basis of their opinions to the anatomical features of particular interest to them at the time of publication; often only a single character was considered.

The historical confusion of the systematic position of the taxon has made it necessary to attempt to clarify the affinities of the Grylloblattodea. What seemed to be needed was not so much another consensus of the opinions of earlier workers, but a synthesis of information provided by the morphological characters that are available in the orthopteroids.

To compare various orthopteroid groups at the family, or higher, taxonomic level, using a wide range of anatomical characters, presents many difficulties, both practical and theoretical. Only the advent of high speed computers has

made it possible to assess large masses of comparative data in a reasonable length of time.

Since the pioneering work of Bordas (1898), many authors have commented on the desirability of basing comparisons between various groups of the orthopteroid insects on a wide range of characters. To date, only two quantitative assessments of the affinities of the higher orthopteran taxa have been attempted (Giles, 1963; Blackith and Blackith, 1968). Both studies superficially discussed the affinities of Grylloblattidae. Blackith and Blackith (1968) had to rely upon drawings of Grylloblatta, and from their numerical analysis considered the taxon to have greatest affinity to the Ensifera. Grylloblatta was not included in the cladograms and dendrograms by Blackith and Blackith (1968). In a later presentation of orthopteroid affinities (Blackith and Reymont, 1971), Grylloblatta was not discussed.

Materials and Methods

Detailed presentation of the various methods employed in numerical taxonomic analysis can be found in Sokal and Sneath (1963) and Blackith and Reymont (1971). At the subfamily level or below, there is much to recommend the use of counts of discrete variables and/or linear measurements (Blackith, 1965). At the family level or above, the need is mainly to make the measures somehow represent the

groups under comparison. Almost all the applications of such numerical techniques have been to comparisons at the generic level or below.

The largest number of studies, in which numerical taxonomic comparisons among insects have been made, use counts of dissimilarities based on the methods of Sokal and Sneath (1963). The more recent approach by Camin and Sokal (1965), considered by the authors to be phylogenetic, requires that the investigator can so order, by weighting if necessary, multi-state characters that his sequence of states follows the evolutionary sequence. I find the Camin-Sokal approach questionable because analysis must be preceded by judgments on the phylogeny that can influence the results.

In my study a non-weighted analysis was employed. It was based in part on that of Edwards and Cavalli-Sforza (1964, 1965), which utilizes a count of the number of dissimilarities among the various groups in the chosen suite of characters. This is followed by a cluster analysis to yield the shortest connection (generalized distance) between clusters (Prim, 1957), and the distance between clusters is employed to construct the subdivisions of the suite of characters into the branches of the dendrogram.

An alternate method was also used to check the reliability of the analysis of dissimilarities that show possible affinity. This involved the development of a

similarity index by cluster analysis of matching characters. This allowed the construction of a dendrogram in which the lengths of the arms are equal to the similarities and the branching equals the smallest distance coefficient between a cluster pair. Such a dendrogram shows phenetic relationships based on degree of matching characters.

The anatomical characters employed by Giles (1963) and Blackith and Blackith (1968) were used in my analysis, with modifications necessary to include Grylloblattidae. A total of 80 attributes were adapted from Blackith and Blackith (1968), and include features of the integument, nervous system, alimentary canal, circulatory system and musculature. Eighty-four of the 283 characters originally considered by Giles (1963) in the analysis of the dermapteran affinities were chosen; these were limited to the external morphology (Appendix II). Since the characters used in each suite were not chosen at random, and characters with attributes shared by all of the groups would be of no discriminatory value, a posteriori weighting is inevitable (Blackith and Reymont, 1971).

I used fresh material wherever possible and supplemented it with descriptions from the literature. The complete delineation of all species in any taxonomic hierarchy would require the examination of an impracticable number of organisms. I used one species as the "exemplar," the term employed by Sokal and Sneath (1963), of a higher

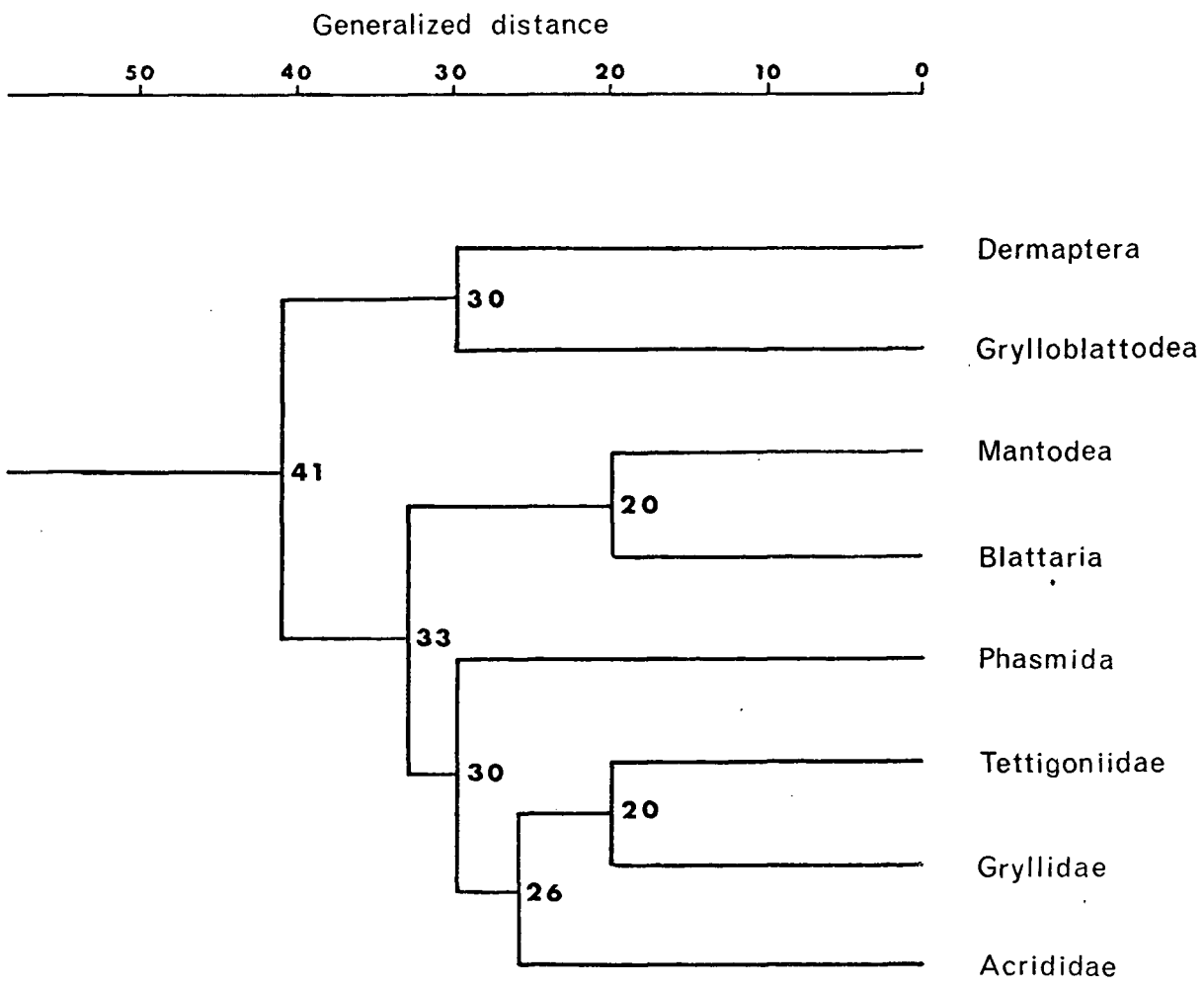
taxon. The risk that such "exemplars" might deviate widely from the means for their taxa must always be recognized. My analysis was based on material from the Mantodea (Stagmomantis carolina), Blattaria (Periplaneta americana), Dermaptera (Anisolabis maritima), Phasmida (Anisomorpha sp.), Tettigoniidae (Ceuthophilus sp.), Gryllidae (Gryllus assimilis), Acrididae (Locusta migratoria) and Grylloblattodea (Grylloblatta campodeiformis).

The suites of characters were transformed into Fortran IV by Mr. Borden and the basic data matrix computed on an IBM 1130. The program may be obtained from Mr. Borden, Computer Center, Zoology Department, University of British Columbia.

Results

Figure 12 presents the analysis of the number of dissimilarities of 84 external morphological characters based on the shortest connection network between clusters. The arrangement of the insects does not signify linear phylogenetic relationships. The dendrograms are a two-dimensional representation of a multi-dimension model and the position of the branching is the significant feature in showing degrees of phenetic relationships. For example, Figure 12 implies that the Acrididae has a greater similarity to the Phasmida than to either the Tettigoniidae or the

Figure 12. Dendrogram showing dissimilarity analysis of 84 external characters, modified from Giles (1963). Numbers at branchings equal generalized distance between clusters based on shortest connection network of Prim (1957).



Prim: shortest connection network (84 characters)

Gryllidae. The dendrogram also shows that the Phasmida and the Dictyoptera (Mantodea and Blattaria) are more like Grylloblattodea and Dermaptera than either is to the Ensifera (Tettigoniidae and Gryllidae) or to the Caelifera (Acrididae). Therefore, the dendrogram is a diagram of only phenetic relationships, and any attempt to read the branching as "earlier" or "later" evolutionary occurrences depends upon the assumption of equal, or nearly equal, evolutionary rates, evidences of which are unknown in these taxa.

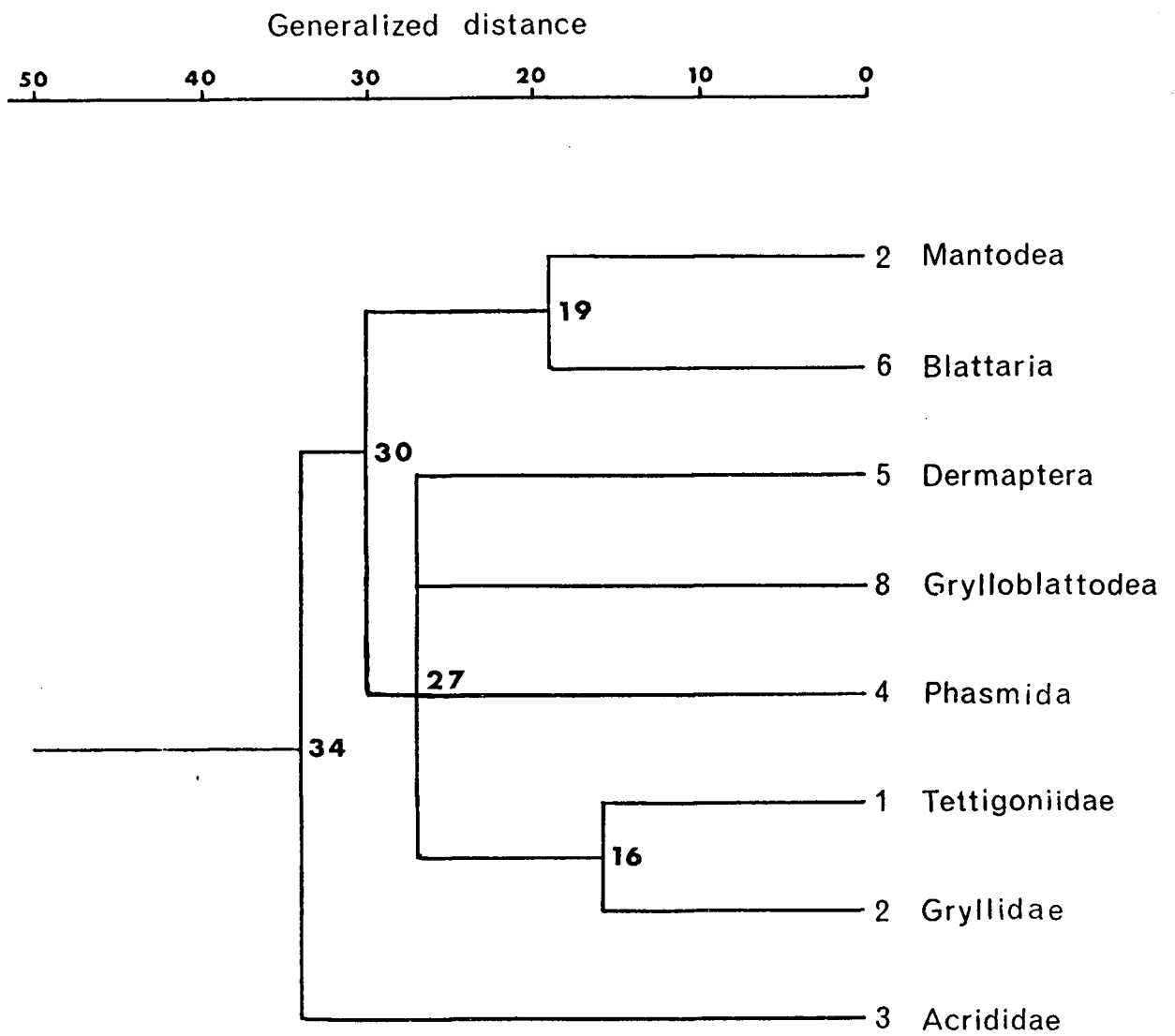
The dendrogram agrees in part with conventional classification of the groups (Imms, 1957). For example, the Tettigoniidae and Gryllidae branch at a generalized distance of 20, which, in the dendrogram, corresponds to the superfamily level. Modern classification places these two groups as superfamilies of the suborder Ensifera (Imms, 1957). The generalized distance of the branching of the Caelifera and Ensifera corresponds to the suborder level. The generalized distance of the Dermaptera, Phasmida, Orthoptera and Dictyoptera equals the ordinal level in this dendrogram. The presently classified suborders, Mantodea and Blattaria, are depicted at a dissimilarity distance equal to the superfamily in this analysis of external characters. The Grylloblattodea, considered by many to belong to the order Orthoptera, branches at the level of order.

Figure 13 represents an analysis of dissimilarities, using a suite of 80 characters chosen from both external and internal anatomy. The Dictyoptera branch from the other taxa at the ordinal level, but differ from Figure 12 by showing closer phenetic affinities to the Dermaptera and Grylloblattodea. In the analysis shown in Figure 13, the Acrididae (Caelifera) branch at the greatest generalized distance and shows little affinity to the Ensifera.

The changes in the degree of phenetic affinity of the groups in the two dendrograms graphically illustrate the danger of conferring relationships based on a single suite of features.

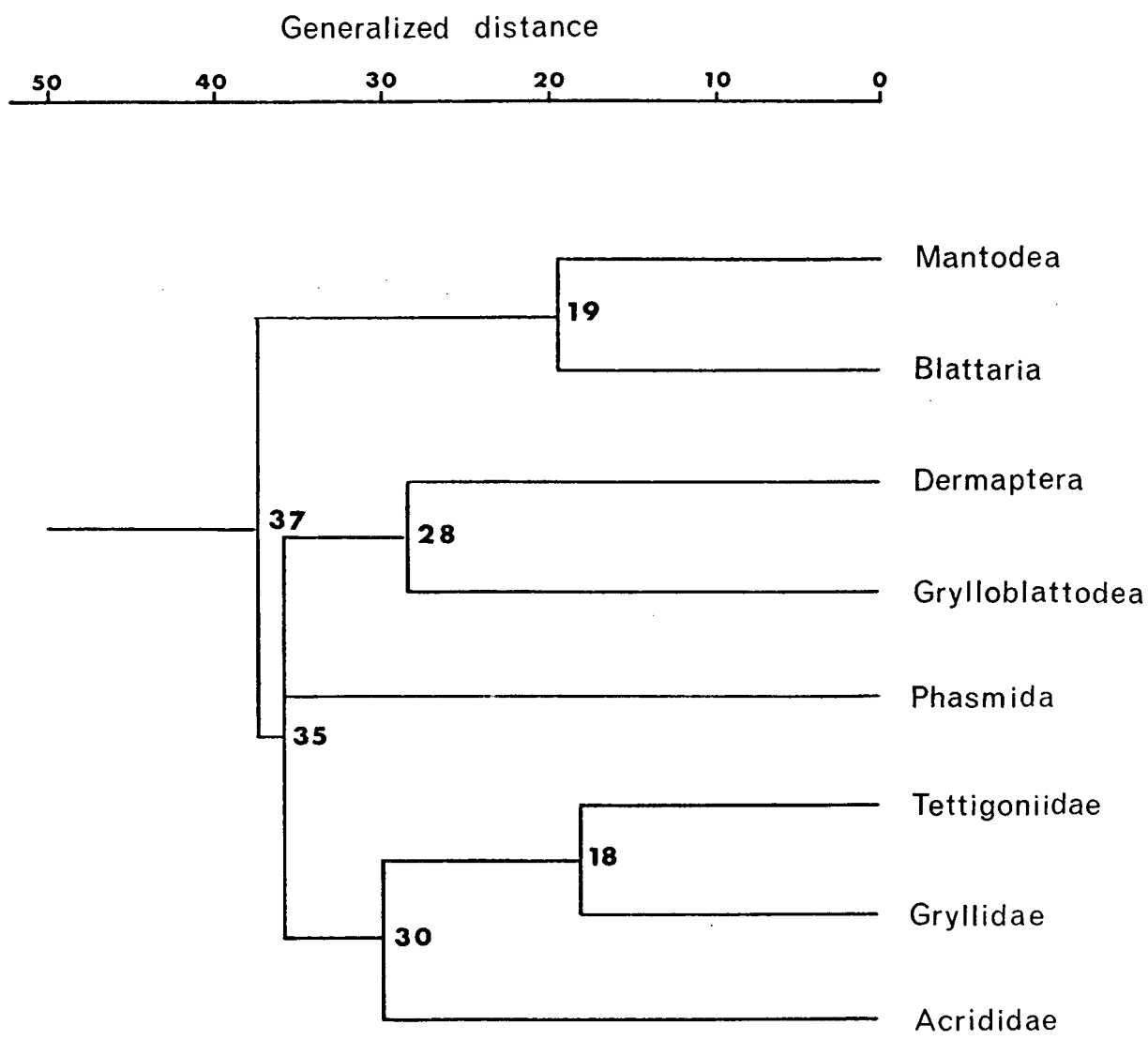
Figure 14 is an analysis combining the suites of characters (164) used in Figures 12 and 13. This dendrogram depicts a compromise between the different degrees of affinity suggested in Figures 12 and 13. The generalized distances, equivalent to taxonomic ranking, do not change appreciably. The Dictyoptera branch at the greatest generalized distance, representing less phenetic affinities to the other taxa than shown in Figures 12 and 13. In Figure 14, the Mantodea and Blattaria again remain at the superfamily level. The Acrididae (Caelifera) agrees in the phenetic affinity to the Ensifera, as in Figure 12. The greater generalized distance of ordinal levels in Figure 14 suggests subordinal status for Grylloblattodea and Dermaptera that is equal to the Ensifera and Caelifera in the Orthoptera.

Figure 13. Dendrogram showing dissimilarity analysis of 80 external and internal characters, modified from Blackith and Blackith (1968). Same construction as in Figure 12.



Prim:shortest connection network (80 characters)

Figure 14. Dendrogram showing dissimilarity analysis of 164 characters, combining those used in Figures 12 and 13. Same construction as in Figure 12.

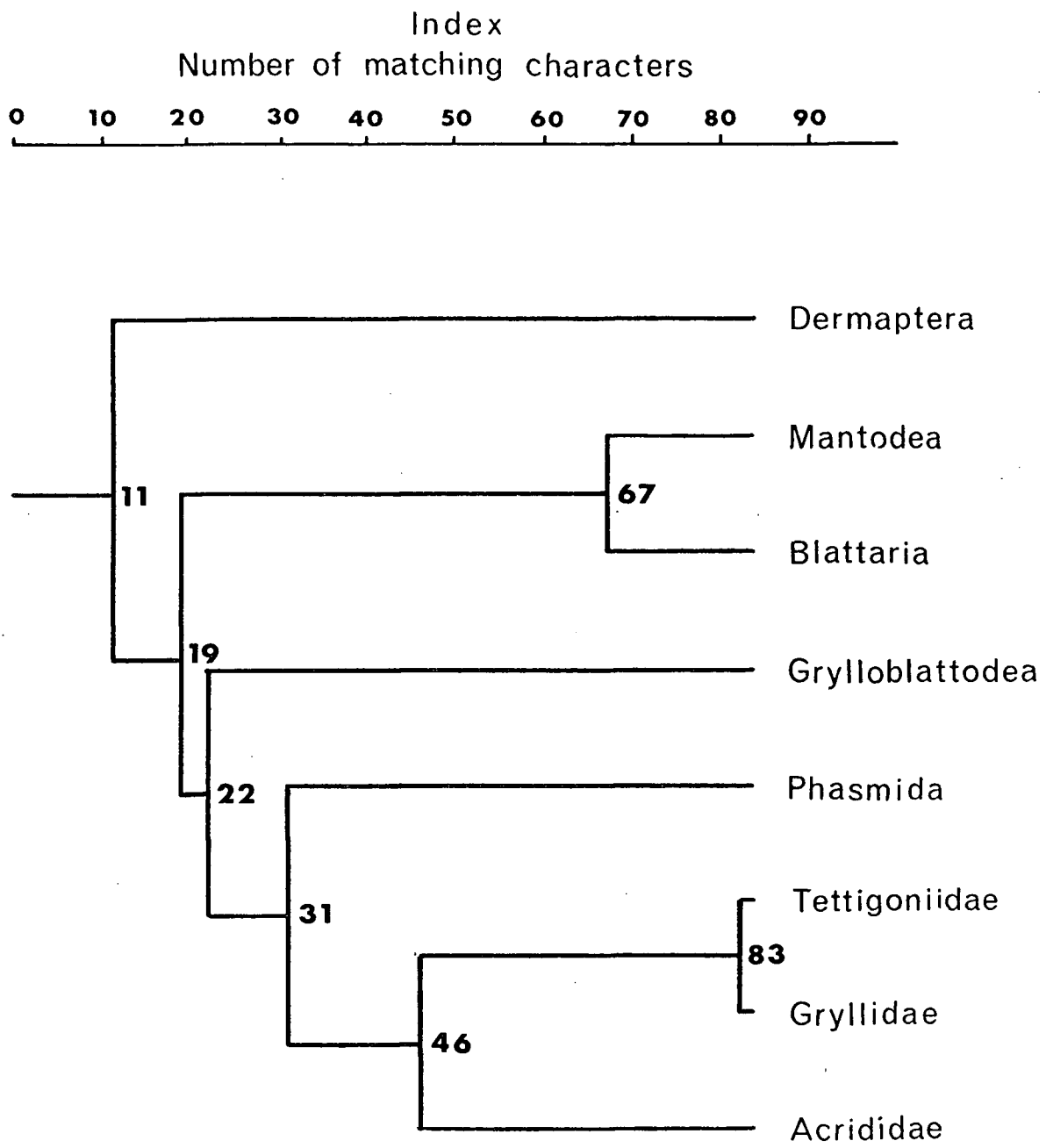


Prim: shortest connection network (164 characters)

Figure 15 represents the phenetic affinities obtained by a similarity analysis of the 84 external characters used in Figure 12. The Ensifera agree with Figure 12, which is a dissimilarity analysis. The Acrididae, (Caelifera) and Ensifera depict possible subordinal position in Figure 15. In Figure 15 the Phasmida is as in Figure 12, in that it shows similarity to the Orthoptera, but shows closer affinities to the Grylloblattodea and the Dictyoptera, even though the common phenetic affinities are the same in each figure. The phenetic relationship of the Dictyoptera is in general agreement with Figure 12. The number of matching characters between the Mantodea and the Blattaria (78 per cent) hardly justifies subordinal status as now ranked in conventional classification. In Figure 15 the Dermaptera shares only 13 per cent of the characters with the other orthopteroids. The Grylloblattodea departs radically from the dissimilarity analysis of Figure 12, in which the taxon branches from a base shared with the Dermaptera. Figure 15 places the Grylloblattodea intermediate in phenetic affinity between the Dictyoptera and the Phasmida-Orthoptera branches, as suggested by Walker (1938). He later changed his mind (Walker, 1943) and placed it nearer to the Ensifera.

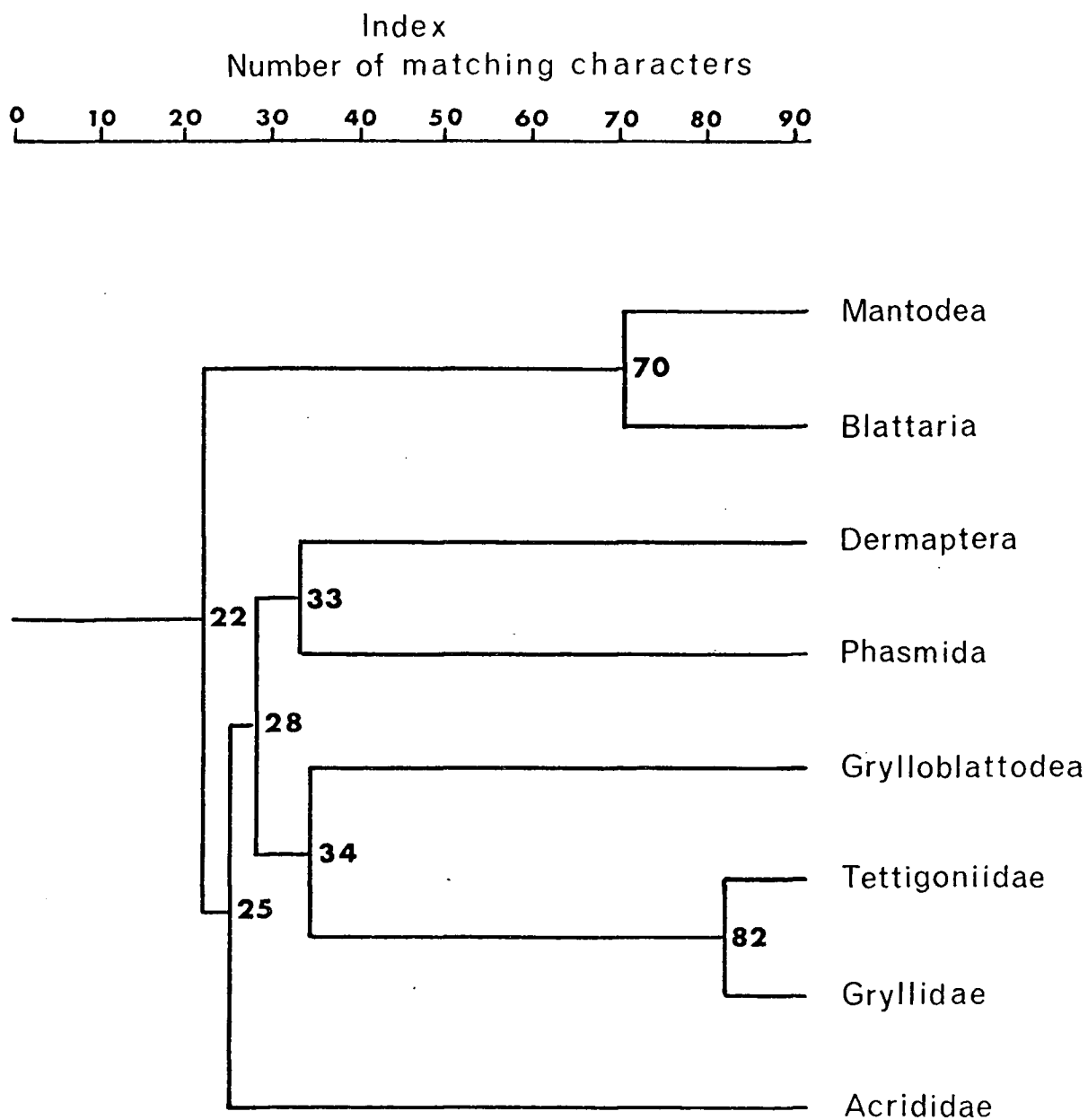
Figure 16 is a similarity index of the 80 external and internal characters also used in Figure 13. The Mantodea-Blattaria again share over 75 per cent of the characters. The affinity of the Dictyoptera to the other groups is in

Figure 15. Dendrogram showing similarity analysis of 84 external characters used in Figure 12. Length of each arm equals number of similarities and branching equals shortest distance coefficient between a cluster pair.



Similarity index (84 characters)

Figure 16. Dendrogram showing similarity analysis of 80 external and internal characters used in Figure 13. Same construction as in Figure 15.

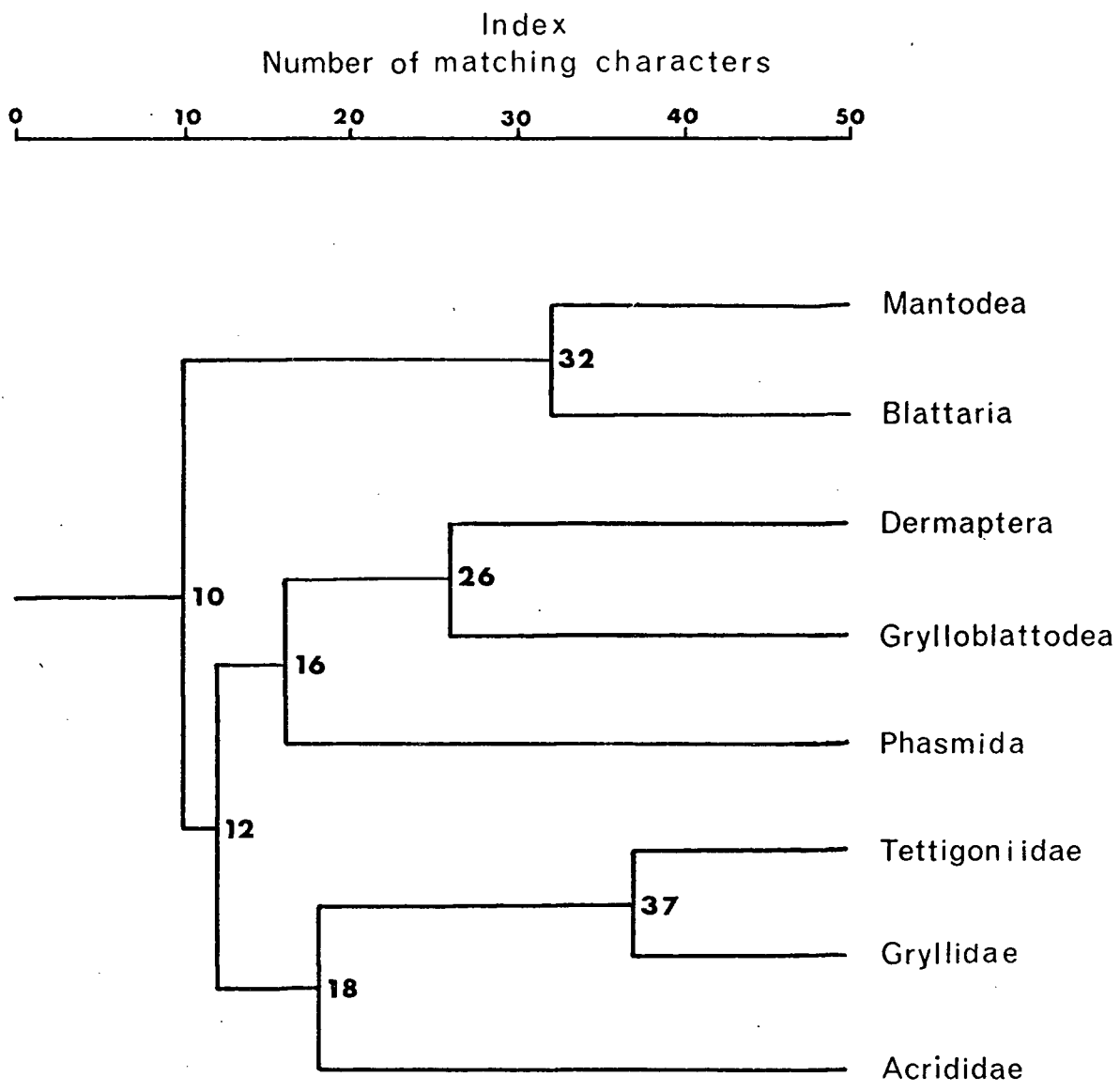


Similarity index (80 characters)

general agreement with the other dendrograms. The Acrididae shows few similarities with the Ensifera, and this agrees with Figure 13. In light of present knowledge and the usually accepted classification of the relationship of the Ensifera and Caelifera as suborders of the Orthoptera, this placement is to be suspect. The position of Phasmida is in general agreement with the other dendrograms which use the same suite of characters and have close affinities to the Dermaptera. Grylloblattodea show some affinity to the Ensifera, but have closer affinities to the Dermaptera and Phasmida.

Figure 17 presents a dendrogram of a similarity analysis of the combined suites of characters as used in Figure 14. The dendrogram of 164 characters is again a compromise of the dendrograms for each separate suite. The branches of the similarity index are comparable to the generalized distances shown in Figure 14. The Orthoptera branch from the common base which also leads to the Dermaptera, Grylloblattodea, and Phasmida; whereas, in Figure 15, the common affinity is with the Phasmida. In Figure 16 the Ensifera have the closest affinity to the Grylloblattodea. In Figure 17 the Dermaptera and Grylloblattodea have closer affinities to each other than to the other taxa, and these agree with the relationships shown in Figure 15. The small number of characters in common would seem to warrant at least subordinal rank. The affinities of the Dictyoptera are in

Figure 17. Dendrogram showing similarity analysis of 164 characters used in Figure 14. Same construction as in Figure 15.



Similarity index (164 characters)

agreement with present knowledge of the group. The Acrididae shows less phenetic affinity to the Ensifera than would be expected from the current taxonomic groupings of the Orthoptera.

Discussion

An attempt has been made to determine the relationship of the Grylloblattodea to the other orthopteroid orders by an objective method using a large number of morphological characters.

Although the dendrograms of this study are not fully consistent in taxonomic hierarchy, they present a pattern of affinities that some current opinions (e.g. Sharov, 1968) would support as a reasonable account of orthopteroid phenetic relationships. For example, the Tettigoniidae and Gryllidae show a high affinity to each other in all dendrograms. This implied relationship is consistent with their position in several recent taxonomic works (Brues, Melander, and Carpenter, 1954; Borror and DeLong, 1971). The percentage of similarities and the generalized distance for the Ensifera are at a level consistent with the accepted subordinal status of the taxon (Borror and DeLong, 1971).

The phenetic relationship of the Caelifera to the Ensifera in Figures 14 and 17 might be at a higher taxonomic

level than would be acceptable by some authors (Ander, 1939; Rehn, 1952). In Figures 13 and 16 the remote affinity of the Caelifera to the orthopteroid stem at, or below, the ordinal level is certainly not in accordance with the current systematic concepts of the relationships between the Ensifera and Caelifera. Possibly the use of a suite of characters chosen from both the internal and external morphology has made the Caelifera more distinctive than previously suspected. This tenuous affinity was also found by Blackith and Blackith (1968) in their analysis of Australian orthopteroids. In a study of redundancy and non-selective (no change) characters, Le Quesne (1972) chose from the 92 characters used by Blackith and Blackith (1968) only those that behaved as if they were uniquely derived. In an analysis based on Le Quesne's criteria, 20 to 26 characters out of the original suite were used by Le Quesne (1972) in a re-assessment of phenetic relationships in the orthopteroids. The dendrogram that he constructed did not differ in detail from the earlier analysis (Blackith and Blackith, 1968). Le Quesne (1972) inferred that there has been a considerable degree of repetition in the evolution of the orthopteran group. These analyses suggest that a possible re-evaluation of the systematic relationships of the Ensifera and Caelifera is needed.

The close association of the Dictyoptera in my dendro-

grams does not agree with Rehn (1951). The Blattaria and Mantodea show over 75 per cent similarity of characters (Figures 15, 16, and 17) and a close generalized distance from each other in the remaining dendrograms. One might regard them as more appropriately treated at the superfamily level instead of at the current subordinal rank. This close agreement of affinities was also found by Blackith and Blackith (1968) in their study of Australian orthopteroids.

The close association of the Grylloblattodea with the Dermaptera in my analysis does not agree with that of Borror and DeLong (1971). It is not necessary, however, to read any phylogenetic implications into this phenetic similarity. Neither the Grylloblattodea nor the Dermaptera should be considered as ancestral to the other, and whether they shared close evolutionary lineage is debatable. A surprising feature is the close phenetic affinity of the Phasmida, Dermaptera and Grylloblattodea. Tentatively, then, one could assimilate the complex into a single higher taxon.

At the present time there is no agreement among authorities about the higher classification of the orthopteroids. I do not advocate, at present, any wholesale upgrading of taxa, but am simply drawing attention to the use of numerical methods of investigation as a start for a consistency of orthopteroid taxonomy.

Modern classifications of the orthopteroids consider Dictyoptera, Dermaptera, Orthoptera and Phasmida as orders. The phenetic affinities and relationships of the Grylloblattodea, as shown in the dendrograms here presented, place the taxon at the ordinal, rather than family, rank. In order to achieve some degree of consistency in the hierarchial ranking among the orthopteroids, derived from morphological affinities, I support the proposition that the most acceptable systematic rank of the Grylloblattodea is that of an order.

I. Introduction

Composition of insect lipids is a topic of considerable current interest, and a number of excellent reviews of the subject have appeared in the last decade (Fast, 1964, 1970; Gilby, 1965; Gilmour, 1965, 1966). The lipids of insects generally show a similarity in composition to those found in other animals. The existing knowledge reveals that the insect lipid metabolism is for the most part similar to that of vertebrates (Gilmour, 1966; Kinsella, 1966a).

The quantitative and qualitative composition of the fatty acids in insect lipids have received extensive attention since gas-liquid chromatography became available for microanalysis. Unfortunately, the majority of studies reported the fatty acid composition of total or neutral and/or polar lipid fractions. The reports of specific lipid classes are predominantly for triglycerides and phospholipids (ie. Lambremont, Blum and Schrader, 1964; Fast, 1966; Harlow, Lumb and Wood, 1969; Beenakkers and Scheres, 1971).

Nevertheless, certain generalizations have been put forth: 1) there are species-specific differences, both qualitative and quantitative, in the major lipid classes and in fatty acid composition; 2) while species differences

are apparent, there is present a specific composition pattern of fatty acids for many higher taxa in the Insecta; 3) many insects are unable to synthesize linoleic (18^2) and linolenic (18^3) acids and these are required in the diet (Hilditch and Williams, 1964; House, 1965; Lambremont, Stein and Bennett, 1965); 4) the composition of fatty acids in insect lipids varies depending on the fatty acids present in the diet (Lambremont, Blum and Schrader, 1964; Nelson and Sukkestad, 1968; Schaefer, 1968; Vanderzant, 1968); 5) there is a correlation between environmental temperature and fatty acid composition. Earlier works reviewed by Fast (1964) suggest the saturation of the fatty acids increases with temperature, or conversely, lipids in insects living at, or acclimated to, lower temperatures have more unsaturated fatty acids.

The literature on insects supports, with rare exceptions, specific species and higher taxa differences of lipid and fatty acid composition. There are as many exceptions reported for dietary requirements, fatty acid- diet relationship and effects of temperature on fatty acid composition as there are substantiating studies. Major exceptions to essential dietary requirements of 18^2 and 18^3 may be found in the aphids (Strong, 1963; Bowie and Cameron, 1965), coccids (Tamaki and Kawai, 1968), certain Diptera and Lepidoptera (Chippendale, Beck and Strong, 1964; Fast, 1966; Vanderzant, 1968). Numerous reports suggesting that diet does not directly affect fatty acid composition are

known (ie. Gilmour, 1961; Saha, Randell and Riegert, 1966; Keith, 1967; Nakasone and Ito, 1967; Moore and Taft, 1970; Lipsitz and McFarlane, 1971; Carter, Dinus and Smythe, 1972). In general, it might be stated that if dietary fatty acids do affect the fatty acid composition of the insect, it is usually only the triglyceride fraction, and synthesis can take place to supply essential fatty acids not present in the diet.

The effects of environmental temperatures on fatty acid composition has been reviewed in insects by Fast (1966) and on vertebrates by Knipprath and Mead (1968). The majority of studies confirm a correlation between temperature and degree of saturation of the fatty acids (Takata and Harwood, 1964; Keith, 1966; Knipprath and Mead, 1968; Zar, 1968; Baranska and Wlodawer, 1969; Schaefer and Washino, 1969). Van Handel (1966), Buffington and Zar (1968) and Fast (1970) report exceptions to the correlation and object to the postulate that at low temperatures organisms attempt to maintain a constant liquidity by use of lower melting unsaturated fatty acids. The insect studies cited have been conducted either on whole insects that overwinter as adults in hibernation, or eggs, or pupae, or on tissue containing triglycerides. In addition, the majority of studies have been to acclimatization to either high or low temperatures. To my knowledge, no insect has been investigated that does not hibernate or does not pupate. Nor have there been any comparative studies between insect

species which normally live under different temperature conditions.

When I considered the various hypotheses and counter-hypotheses, as discussed previously, Grylloblatta seemed to be an ideal insect to use in the investigation of the various aspects presented. It is generally accepted that there are similar patterns of lipid and fatty acid composition within a given family or order. As stated earlier, the systematic and phylogenetic position of the Grylloblatta in the orthopteroid insects has been uncertain.

I performed a comparative lipid and fatty acid analysis between Grylloblatta, Thysanura, Blattaria and Orthoptera for the following reasons: 1) as a physiological comparison to augment my numerical morphological comparative study; 2) the lipid and fatty acid composition of Grylloblattodea has not been investigated, nor has that of any of the more "primitive" orthopteroids; 3) Grylloblatta is active throughout its entire life cycle within a narrow temperature range much lower than the majority of insects.

II. Materials and Methods

The insects used in this analysis are all females and are as follows: Isoptera (Zootermopsis angusticollis, adult alate primary reproductives, Galiano Island, British Columbia, collected by G. G. E. Scudder), Dictyoptera, Blattaria (Periplaneta americana, one week old adults,

U. B. C. Department of Zoology culture), Orthoptera, Ensifera (Gryllus assimilis, adults, Macdonald College culture, V. R. Vickery, Quebec), Dermaptera (Anisolabis maritima, adult, Mandarte Island, British Columbia, Ian Robertson, collector), Thysanura, Machilidae (Pedetontus sp., Puget Sound, Washington, T. Carefoot, collector), Grylloblattodea (Grylloblatta campodeiformis campodeiformis, Jasper National Park, Alberta, and Grylloblatta lavacola, McKenzie Pass, Oregon, J. W. Kamp, collector).

Prior to the extraction of the total lipids, food was withheld from the specimens for 48 to 72 hours. Any foreign particles were removed from the integument with compressed air. The specimens were then frozen in a tared vial over solid carbon dioxide and weighed.

1. Extraction and Purification

The extraction of the lipids was by a modification of the Folch, Lees, Sloane-Stanley (1957) procedure which I found through experimentation to give the most satisfactory yield of the complex lipids present in insects. All the reagents used were either chromatographic or pesticide grades and checked for lipo-contaminants by gas chromatography. Solvents were evaporated under vacuum at temperatures less than + 5° C. The insects were homogenized for 30 minutes at 0° C. with 20 volumes chloroform:methanol (2:1 v/v) and filtered through a micropore funnel. The homogenate was then further homogenized and extracted

with 10 volumes chloroform: methanol (1:2 v/v) and 10 volumes chloroform: methanol (7:1 v/v). The filtrates were combined and partitioned by the addition of 1/5 the total filtrate volume of cold 0.9 per cent NaCl solution. The upper phase containing methanol, water, NaCl, proteins, amino acids and carbohydrates was removed. The inter and lower phases were rinsed three times with chloroform: methanol: 0.9 per cent saline (3:47:48 v/v/v) and the chloroform-lipid phase extracted. To ensure complete removal of the saline and thus to prevent oxidation, the lipid-chloroform phase was desiccated with anhydrous magnesium sulfate under refrigeration, then evaporated under vacuum, dissolved in 20 ml. chloroform and stored at -10° C. in nitrogen until further processed.

2. Separation of Lipid Classes

Three 0.5 ml. aliquots of the total lipid extract were used for gravimetric determination of the lipids extracted. The remaining extract was separated on a silicic acid column (1.5 x 14 cm.) into a neutral fraction eluted with 200 ml. cold chloroform and a polar fraction eluted with 200 ml. cold chloroform: methanol (1:1 v/v) (Morris, 1961). The eluates were then vacuum-evaporated to dryness, dissolved in 20 ml. petroleum ether and three 0.5 ml. aliquots weighed for each fraction. The neutral lipid fraction was then separated into triglycerides, diglycerides, monoglycerides, free fatty acids, hydro-

carbons, esters and sterol classes on a Florisil, hydrated 7 per cent, column (1.5 x 15 cm.) according to the method of Carroll (1961). The efficiency of separation into classes was monitored by thin-layer chromatography (Mangold, 1965). The solvent-lipid class mixtures were then refrigerated, while drying over magnesium sulfate, in a nitrogen atmosphere. The solvents of the lipid classes were vacuum-evaporated, lipids dissolved in 20 ml. of petroleum ether, aliquots taken for quantification and stored at -10° C. under nitrogen until saponification and methylation.

3. Analysis of Fatty Acids by Gas Chromatography

Aliquots of the tri-, di- and monoglyceride and free fatty acid classes were saponified with 0.5 N methanolic sodium hydroxide, esterified with boron fluoride-methanol 14 per cent w/v using the procedure of Metcalfe, Schmitz and Pelka (1966). The fatty acid methyl esters were dissolved in spectroanalyzed n-hexane for separation by gas chromatography.

Qualitative and quantitative analyses of the fatty acid methyl esters present in the four classes were performed on a Varian-Aerograph Model 1820 Gas Chromatograph equipped with dual differential flows ionization detectors. Columns, 6 or 12 feet long, 1/8-inch outside diameter, of stainless steel, packed with 20 per cent DEGS (diethylene

glycol succinate) on DMCS-chromosorb W, 60/80 mesh, maintained at + 200° C. and a carrier gas flow at 40 ml./ min. of N₂. Methyl esters of fatty acid standards for comparative purposes were purchased from Analabs, Inc., Connecticut, and Applied Science Laboratories, California. Chromatograph peaks were identified by comparison with retention time of the standards. Unknown peaks were tentatively identified by a plot of log relative retention time versus number of carbon atoms (James, 1959). Quantification as per cent/weight were made with a Disc Integrator coupled to a recorder output.

III. Results and Comparisons

The fatty acid composition of free fatty acids (FFA), mono-, di- and triglycerides of the six insect taxa analyzed, are shown in Table III and Figures 18, 19, 20, 21, 22 and 23.

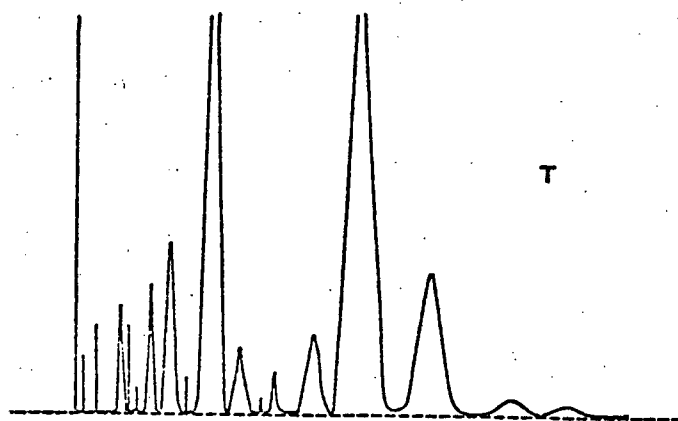
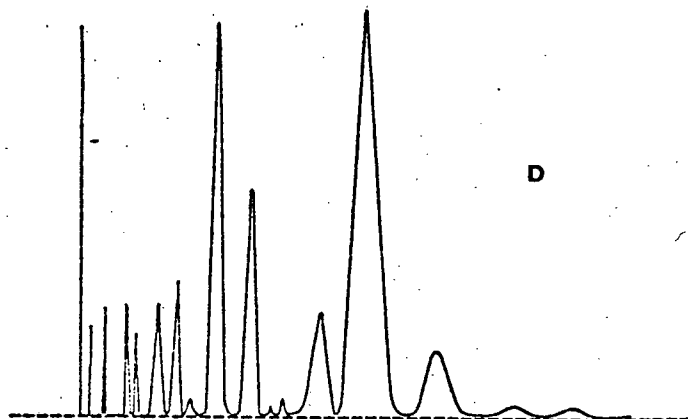
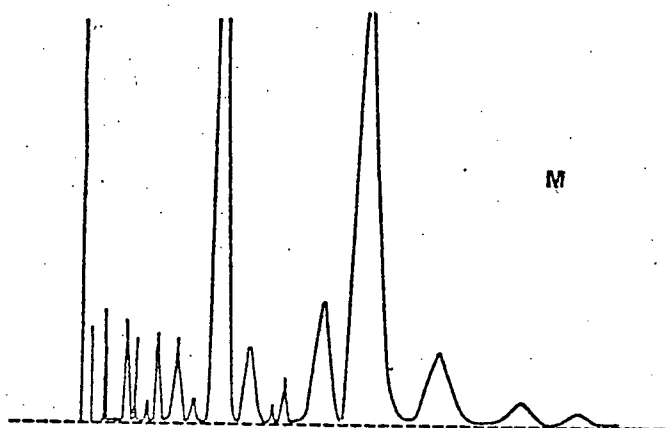
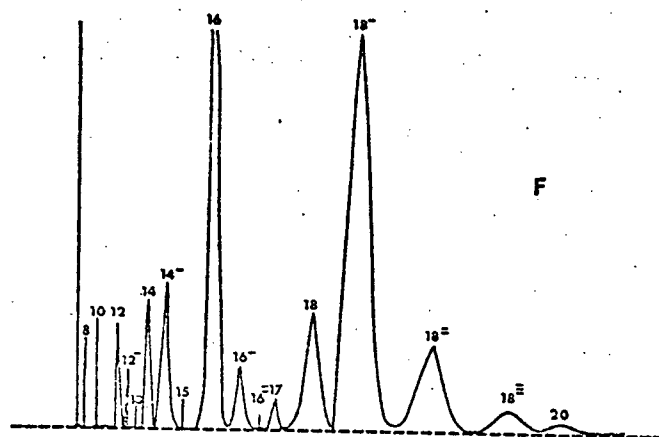
1. *Order Thysanura (Pedetontus) (Fig. 18)

The fatty acids present in the FFA and glycerides of Pedetontus (Thysanura) resemble those of Lepisma saccharins (Thysanura) (Kinsella, 1969). Quantitatively, Pedetontus displays differences from those reported for Lepisma saccharina and Thermobia domestica (Fast, 1970). These quantitative differences are reasonable considering other reports of generic differences (Fast, 1964) and that the

* Thysanura sensu. lat.utilized in this thesis.

Figure 18. Representative chromatograms of Pedetontus.

F: free fatty acid fraction, M: monoglyceride fraction, D: diglyceride fraction, T: triglyceride fraction. Baseline drift corrected; attenuation intervals not indicated. Number equals carbon number of fatty acid and superscript equals number of unsaturated bonds in molecule.



fatty acid content of the esters and phospholipids in Pedetontus were not determined. Like the majority of the literature reports on fatty acids (Fast, 1970), only the chain lengths of 14 to 18 carbons were quantified for Thermobia domestica.

The large proportion (52.9 %) of oleic (18:1) and palmitic (16:0) acid agrees with reports of other insects except the aphids and coccids (Fast, 1970). The major fatty acids present in the Insecta: myristic (14:0), palmitic (16:0), palmitoleic (16:1), stearic (18:0), oleic (18:1), linoleic (18:2) and linolenic (18:3), comprised 83.6 % of the fatty acid content of FFA and mono-, di- and triglycerides in Pedetontus. The unsaturated fatty acids make up 59.4 % of the total, with the unsaturated 18-carbon fatty acids predominating.

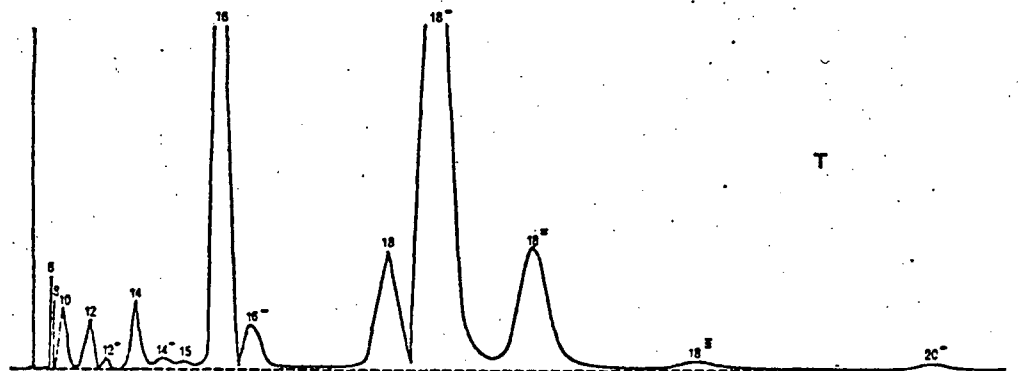
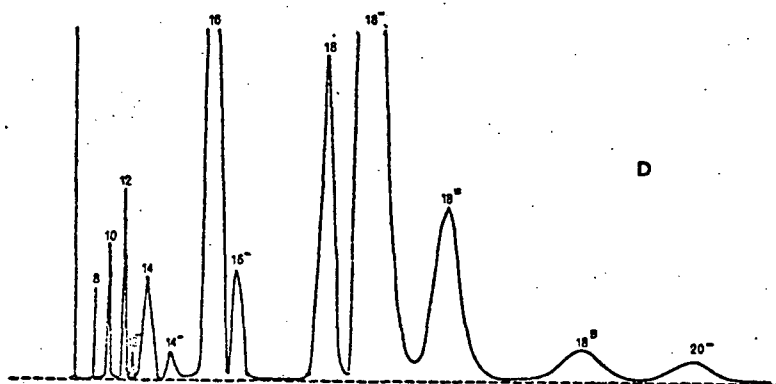
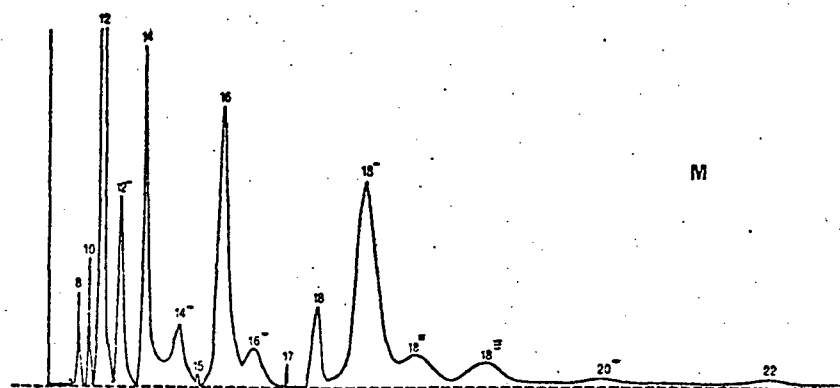
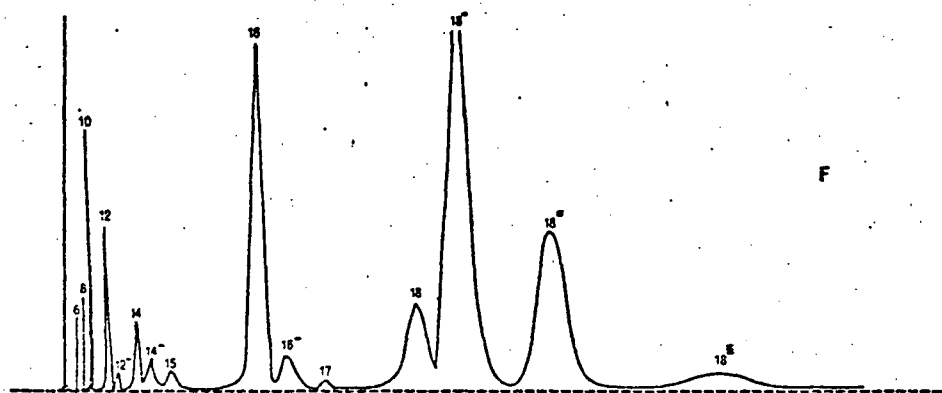
In Pedetontus the unsaturated acids, excluding the 18-carbon fatty acids, represent 13.6 % of the FFA, with 7.2 % as myristoleic (14:1), 12.9 % of the monoglycerides including 6.7 % palmitoleic (16:1), 19.2 % of the diglycerides including 10.3 % as palmitoleic acid, and 11.35 % of the triglycerides mainly as myristoleic (9.3 %). The concentration of myristoleic and palmitoleic acids, higher than those of most insects, is difficult to explain since little is known of the fatty acid metabolism in Thysanura. In fact, little is known about lipid metabolism and fatty acid biosynthesis of Insecta; that reported is indirect evidence supporting hypotheses extrapolated from lipid

research of microorganisms and vertebrates. The amounts of 14:1 and 16:1 approach those concentrations reported for some Diptera (Culicidae) (Van Handel, 1966) and Hemiptera (Aphididae) (Tamaki and Kawai, 1968).

2. Order Blattaria (Periplaneta) (Fig. 19)

The fatty acid composition in Periplaneta americana from the University of British Columbia culture closely resembles that of Blattella germanica (Krishnan, 1968) and the P. americana used by Kinsella (1966b). Quantification of my analysis differs for the reasons discussed under Pedetontus sp. Oleic acid (18:1) was the largest component in the lipid classes analyzed and accounts for 29.5 to 40.9 % (mean, 36.31 %) of the total fatty acid fraction. The major fatty acids, myristic, palmitic, palmitoleic, stearic, oleic, linoleic and linolenic, represent 89.6 % of the fatty acids. Unsaturated acids were represented as a mean content of 60.7 % of the total, ranging from 53.7 % in the monoglyceride fraction to 64.8 % in the triglycerides. The unsaturated 18-carbon fatty acids comprised 88.5 % of the total unsaturated fatty acids present in the classes analyzed. The remaining unsaturated acids, represented by linderic (12:1), myristoleic (14:1), palmitoleic (16:1), eicosenoic (20:1) and erucic (22:1), composed 22.1 % of the FFA, 9.9 % of the monoglycerides, 8.3 % of the diglycerides and 5.7 % of the triglyceride

Figure 19. Representative baseline-corrected chromatograms of Periplaneta americana. Legends as in Figure 18.

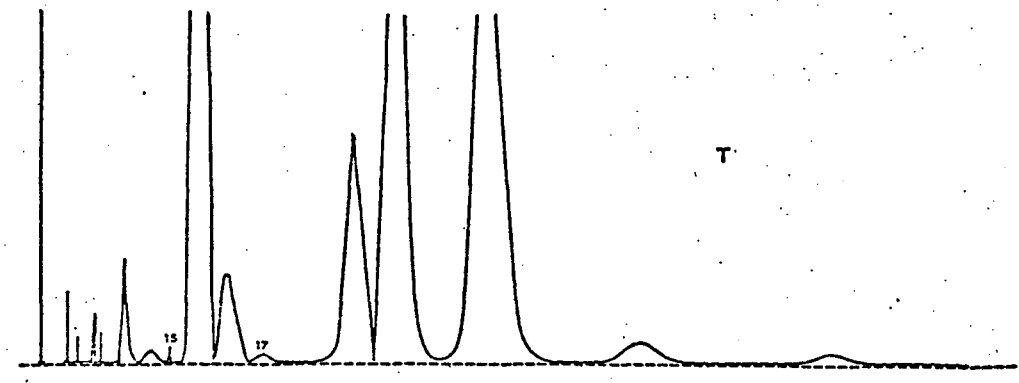
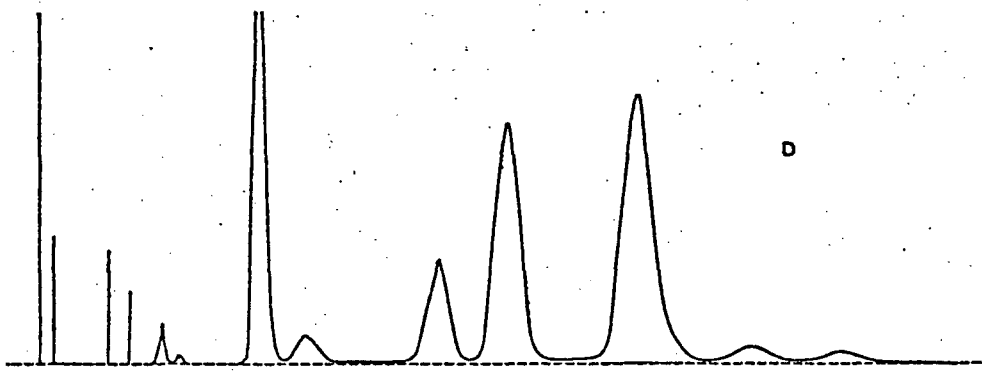
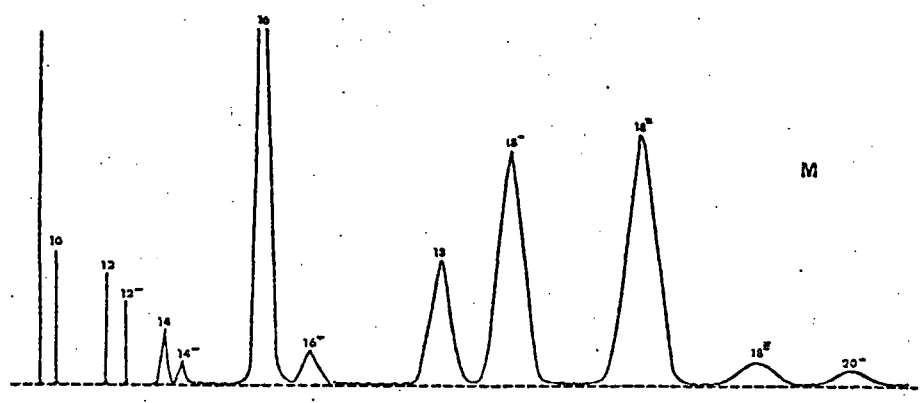
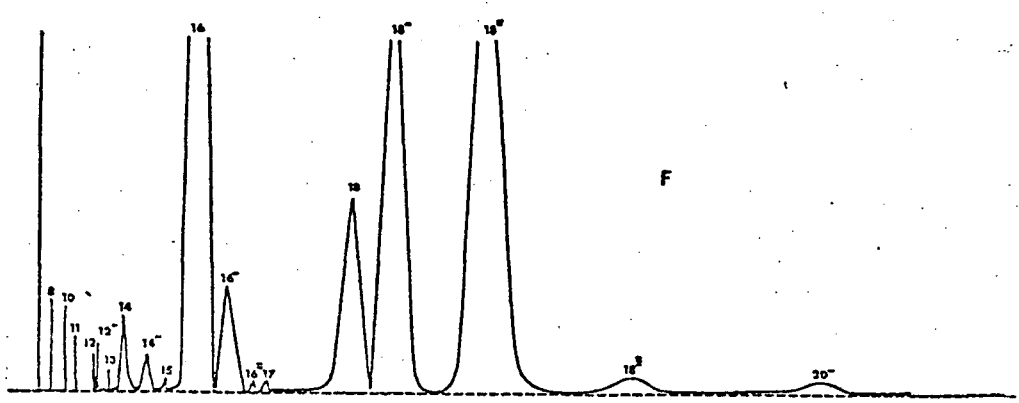


fraction. The long chain fatty acids, 20:1 and 22:1, are not found in the FFA fraction and account for 1.83 % of the total fatty acid content. These results closely resemble those of 13 other species of Blattella as listed in Fast (1970).

3. Order Orthoptera (Gryllus) (Fig. 20)

My fatty acid analysis of Gryllus assimilis resembles literature reports of other Gryllidae (Fast, 1967; Young, 1967; Hutchins and Martin, 1968a). The major fatty acids present in the four classes are myristic, palmitic, palmitoleic, stearic, oleic, linoleic, and linolenic, which average 97.5 % of the total composition, with linoleic representing 32.98 %. The mean percentage of unsaturated fatty acids present in the four classes is 66.45 %, being the highest in the six orders of insects I investigated. The 18-carbon unsaturated acids comprise 86.3 % of the total unsaturated fatty acids. Oleic (18:1), linoleic (18:2), and linolenic (18:3) constitute 53.8 % of the total fatty acids present in the FFA, 62.6 % of the monoglyceride, 65.7 % of the diglyceride, and 57.2 % of the triglyceride fraction. Gryllus assimilis has more of 18:1, 18:2, and 18:3 in the monoglyceride and diglyceride fractions than the other orders and the concentrations in the FFA and triglyceride fractions are only exceeded by Periplaneta. Gryllus assimilis differs from the other orders investigated in that linoleic

Figure 20. Representative baseline-corrected chromatograms of Gryllus assimilis. Legends as in Figure 18.

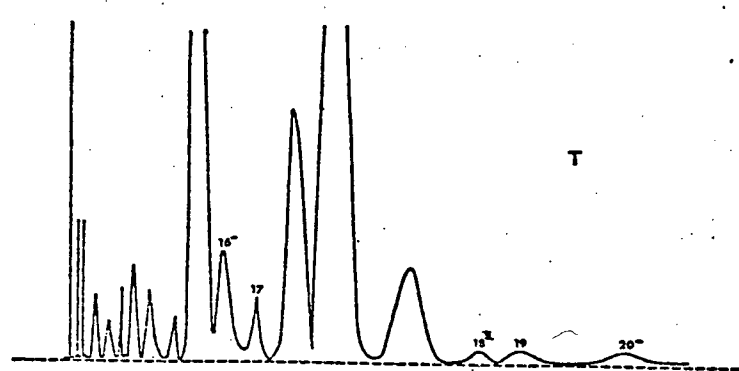
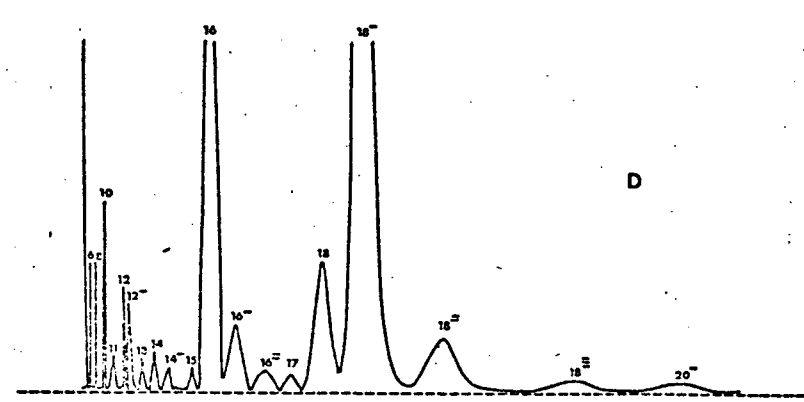
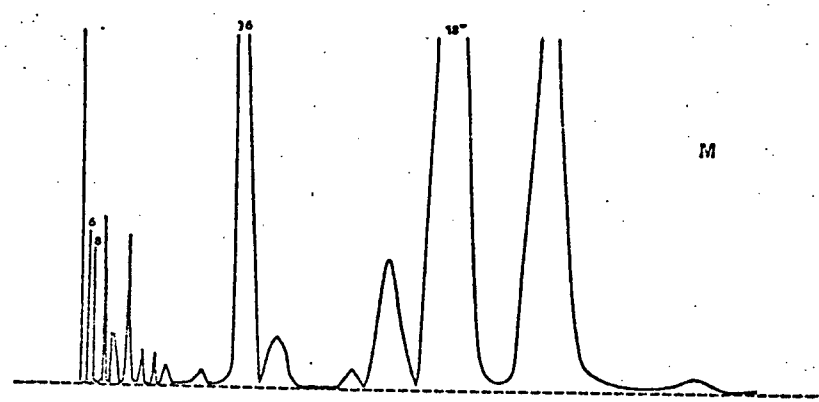
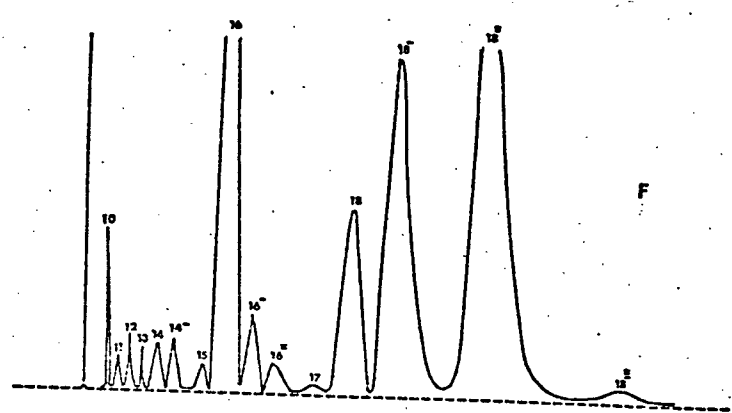


acid (18:2) is the predominant component of the FFA and glyceride fractions. The Gryllidae and Tettigoniidae seem to differ from the other Orthoptera in respect to linoleic acid concentrations. Fast (1967) reported that Gryllus bimaculatus contained greater amounts of linoleic acid than oleic and this was found also in the Tettigoniidae, Scudderia furcata (Young, 1967). The high concentration of linoleic acid may be a possible reflection of dietary intake or the metabolic need for a low melting point, highly mobile long chain fatty acid.

4. Order Isoptera (Zootermopsis) (Fig. 21)

Twenty fatty acids were detected in the isopteran, Zootermopsis angusticollis. The fatty acid composition differs from the subterranean termites, Reticulitermes flavipes (Young, 1967; Carter, Dinus and Smythe, 1972), and is much like Macrotermes falciger, the African fungus-growing termite (Cmelik, 1972). The major components, myristic (14:0), palmitic (16:0), palmitoleic (16:1), stearic (18:0), oleic (18:1) and linoleic (18:2), make up 80.9 % of the total fatty acids present. The carbon-18 series of oleic and linoleic are the major unsaturated fatty acids present. The minor unsaturated components are lauroleic? (12:1), myristoleic (14:1), palmitoleic (16:1), hexadecadienoic (16:2), linoleic (18:3) and eicosenoic (20:1), and make up 12.6 % of the FFA fraction, 6.8 % of the monoglycerides, 13.3 % of the diglycerides and 12 % of the triglycerides.

Figure 21. Representative baseline-corrected chromatograms of Zootermopsis angusticollis. Legends as in Figure 18.

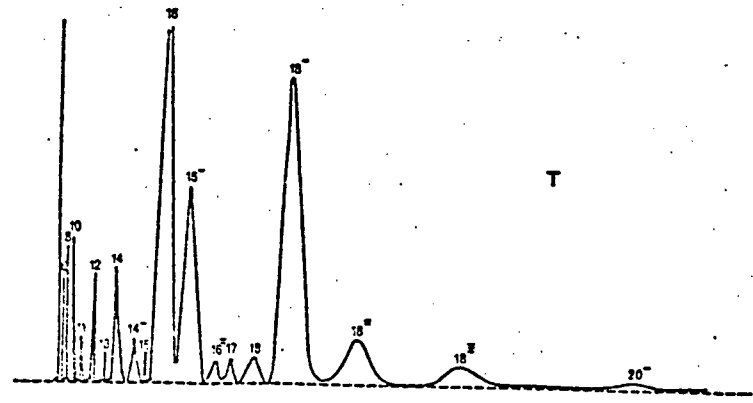
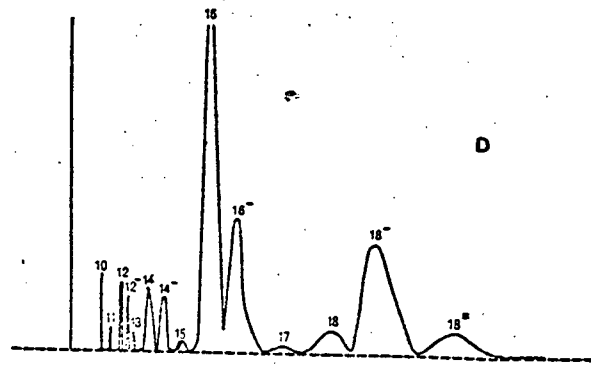
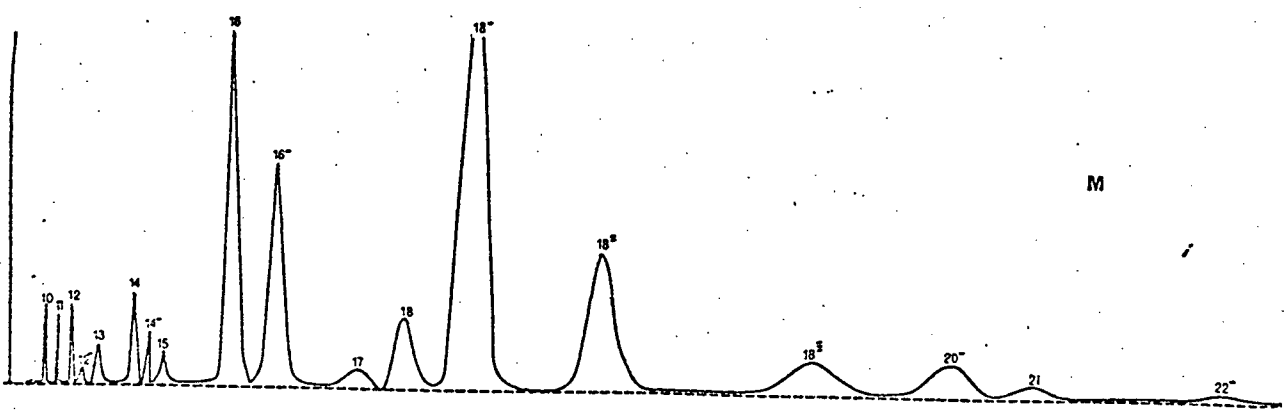
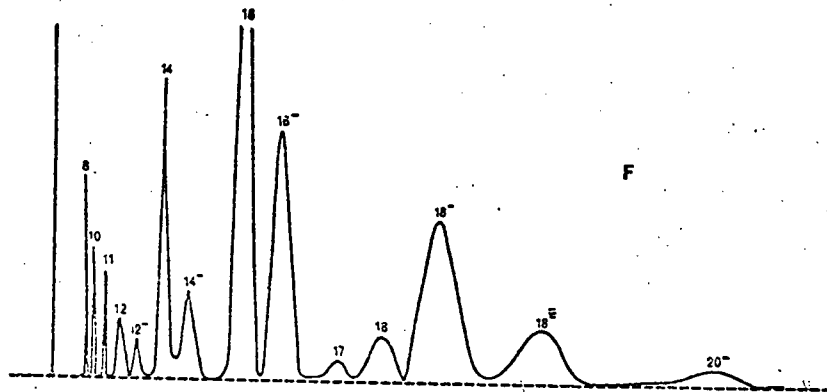


The presence of hexadecadienoic acid (16:2) in the FFA and diglyceride fractions is difficult to explain. Cmelik (1972) found 16:2 to be present in all fractions of the fungus-feeding termite but offered no explanation. It is possible that 16:2 is a product of oxidation via acetyl CoA and the Malonyl pathway from linoleic acid (18:2). This has been suggested by Wakil (1961) to be the mechanism in the rat, and Keith (1967) believes this is also true for Drosophila. The presence of 16:2 in both Macrotermes and Zootermopsis, which either feed on fungi or on rotting wood containing fungal mycelia, suggests to me that hirogenic acid is of dietary origin. Since hirogenic acid is found in only the FFA and diglycerid fractions, this adds support for a dietary origin, for these two fractions function primarily as transport and synthesis components.

5. Order Dermaptera (Anisolabis) (Fig. 22)

Twenty-one straight chain fatty acids (C6 to C22:1) were identified from the dermapteran, Anisolabis maritima. The presence of 6 other compounds was detected which may be in the branched or hydroxy fatty acids. The major fatty acids present in the combined fractions were myristic (14:0), palmitic (16:0), palmitoleic (16:1), stearic (18:0), oleic (18:1), linoleic (18:2) and linolenic (18:3) and account for 85.8 % of the total fatty acid composition. Unsaturated fatty acids average 65.3 %, with 71.3 % in the

Figure 22. Representative baseline-corrected chromatograms of Anisolabis maritima. Legends as in Figure 18.



triglycerides, 67.6 % in the monoglycerides, 56.0 % in the diglycerides and 54.8 % in the FFA fraction. The amounts of unsaturated acids present is exceeded in this comparative analysis by the Gryllus that contain 66.45 % and Grylloblatta that contain 65.8 % of the total fraction. The unsaturated 18-carbon chain fatty acids average 40.4 % of the total fractions and are present in lower concentrations than in the other orders.

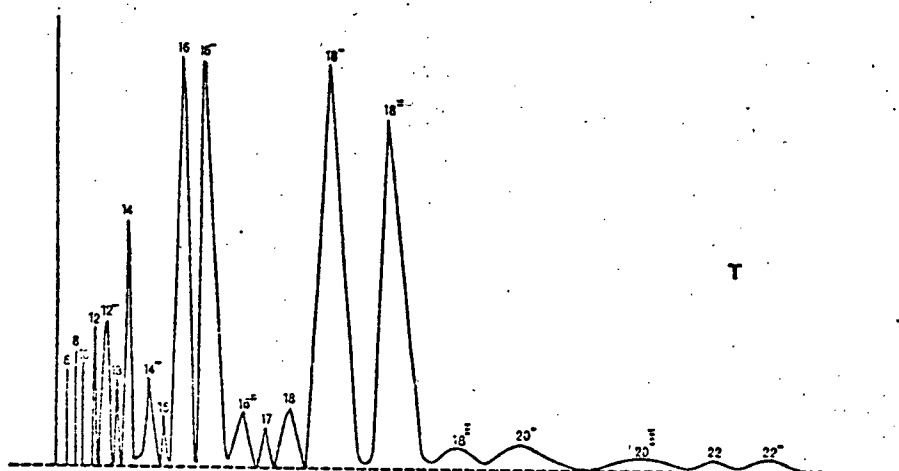
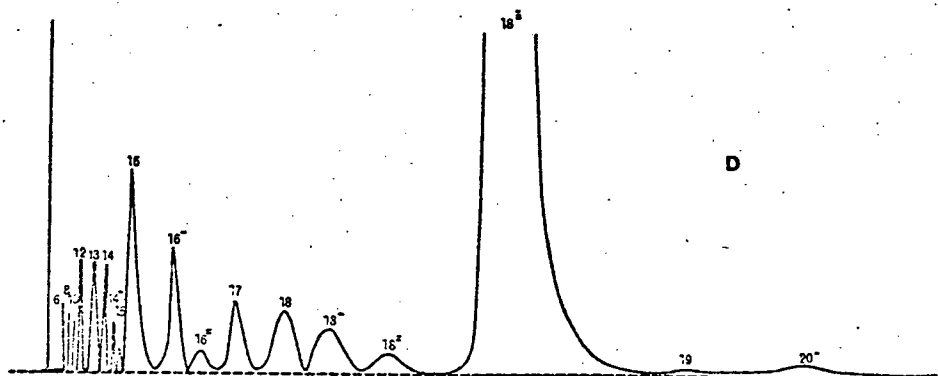
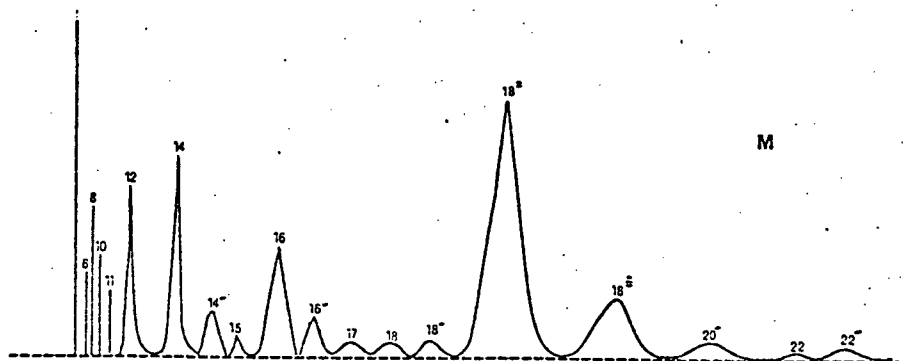
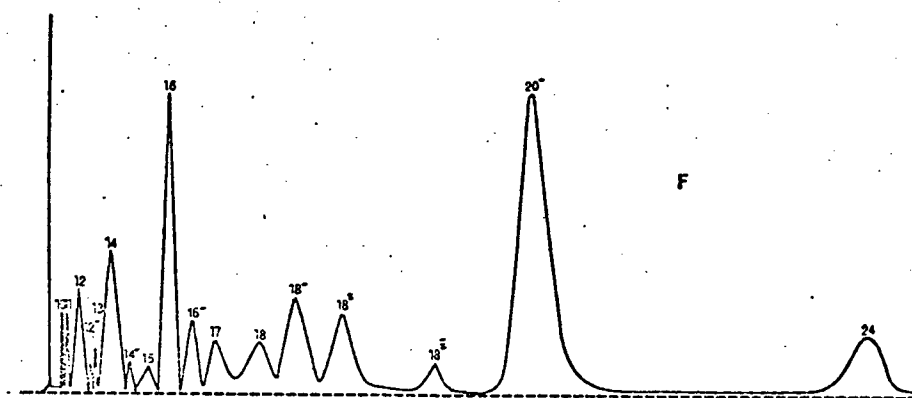
Of note are the small amounts of the polyunsaturated 18 carbons which are necessary for growth and metamorphosis. The low amounts of 18:2 and 18:3 are reflected by the large concentrations of palmitoleic acid (16:1) present in Anisolabis FFA and glyceride fractions. The condition of low 18:2 and 18:3 and high 16:1 is characteristic of the Diptera (Schaefer and Washino, 1969; Fast, 1970) and has been observed in the cockroach (McGuire and Gussin, 1967) and in moths (Schaefer, 1968). The significance of this condition is not certain and there are conflicting hypotheses that it is a dietary and a non-dietary fatty acid synthesis phenomenon (Fast, 1970; Madariaga et al. 1972). Since nothing is known of the fatty acid composition of the Anisolabis diet, no conclusions can be drawn. Nevertheless, I suggest a tentative hypothesis for the condition in Anisolabis. Municio et al (1971) have shown that certain Diptera are capable of synthesizing saturated and mono-saturated fatty acids independently of the fatty acid composition of the diet. In Anisolabis 16:1 compensates

for a lack of 18-polyunsaturated acids and palmitoleic acid is a synthesis product of mitochondria or oxidation of a fatty alcohol C14:0 (Lambremont, 1972) and is desaturated to 16:0 and then elongated to 18:0 or 18:1 as Keith (1967) found to happen in Drosophila. This method would then account for the elevated concentrations of 16:0 (palmitic acid) present in Anisolabis. The high concentration of 16:1 and 18:1 may be of environmental significance to the genus as will be discussed later.

6. Order Grylloblattodea (Grylloblatta) (Fig. 23)

Twenty-four fatty acids were identified in Grylloblatta lavacola and range in chain length from 6 to 24 carbons. Six other unidentified compounds were present and most likely are branched, hydroxy fatty acids or fatty alcohols. The composition of the major fatty acids in the four fractions differs from the other orders analyzed. Myristic (14:0), palmitic (16:0), palmitoleic (16:1), stearic (18:0), oleic (18:1), linoleic (18:2) and linolenic (18:3) account for only 69.1 % of the total fatty acid composition in contrast to the 82 + to 97 % found in the other orders tested in this study. The other major fatty acids present are myristoleic (14:1) and the unusual occurrence of eicosenoic (gandoic) (20:1) and lignoceric (24:0). Unsaturated fatty acids make up 65.8 % of the total present in the four fractions and this percentage

Figure 23. Representative baseline-corrected chromatograms of Grylloblatta lavacola. Legends as in Figure 18.



is exceeded only by the Gryllus. The unsaturated 18-carbon fatty acids average 41.1 % of the total acid composition, with concentrations of 19.6 % FFA, 37.9 % of triglycerides, 48.8 % of monoglycerides and 58.4 % of the diglyceride fraction. Lignoceric (24:0) has not been reported previously as occurring in insects and its presence is difficult to explain from current knowledge of lipid synthesis and metabolism in the Insecta.

There is an intriguing possibility which warrants further investigation. Faurot-Bouchet and Michel (1964) discovered in Coccidae natural occurring esters of fatty acids with carbon chain lengths of 16 to 34. They identified these esters and fatty alcohols (24 to 30 carbons) from cuticular waxes. Shikata (1960) and Amin (1960) showed that lepidopteran waxes consisted of a mixture of fatty acid esters and alcohols of chain lengths C16 to C34. Lignoceric acid (C24) in the Grylloblatta is found only in the FFA fraction and therefore may be an oxidation product of a cuticular waxy ester or a precursor by mitochondrial synthesis to cuticular wax components. There is also the suggestion (Hutchins and Martin, 1968b) that a C24 could be a cleavage of an alkan or olefinic hydrocarbon or a possible precursor to the formation of such compounds. My temperature-humidity experiments show that as environmental temperature rises a higher humidity is sought by the Grylloblatta. The integument of Grylloblatta has few areas of heavy scleritization usually associated with insects, being limited to

appendages, head capsule and the tergal segments. The remaining cuticle is thin and in areas transparent.

The fatty acids present in Grylloblatta, such as erucic (22:1), behenic (22:0), eicosenoic (20:1), heptadecanoic (17:0), pentadecanoic (15:0), undecanoic (11:0) and nonanoic (9:0), are not generally reported as occurring in Insecta. The few exceptions where these fatty acids are reported (Lindsay and Barlow, 1970; Yendol, 1970; Blomquist et al, 1972; Thompson and Barlow, 1972) may well prove to be the rule. Recent studies of insect cuticular waxes and hydrocarbons (Bursell and Clements, 1967; Hutchins and Martin, 1968b; Blomquist et al, 1972) suggest that these compounds are most likely associated with the synthesis of waxes, hydrocarbons and esters in the cuticle. As shown by Thompson and Barlow (1972), undecanoic (11:0) and nonanoic (9:0) acids are formed by stearic (18:0) and acetate, elongated to 20:0, attenuated to 20:1, and oxidated to C11:0 and C9:0. Erucic (22:1), behenic (22:0) and heptadecanoic (17:0) acids have been reported to be associated with secondary alcohols and wax esters in the orthopteran, Melanplus (Blomquist et al, 1972). In Grylloblatta these compounds are formed at much higher concentrations than reported for other insects. Few insects are active at the temperatures preferred by the Grylloblatta. The higher concentrations of these compounds in Grylloblatta suggest that they may be essential components of the cuticle to combat water loss.

at temperatures around 0° C.

IV. Discussion of Environmental and Systematic Relationships Demonstrated by Lipid Analysis

The conflicting evidence of the effects of environmental temperature on fatty acid composition in insects may be due to the fact that the studies were concerned with changes from acclimation to different varying temperatures. I know of no studies where the saturation or unsaturation of the fatty acid composition has been analyzed from insects with different habitat temperatures.

The insect orders used in this study have, in general, different temperature preferences. Periplaneta americana is a warm-preferring form and is indigenous from subtropical America. It is also able to survive in the colder temperate regions in artificial habitats such as human habitations. The thysanuran, Pedetontus, occurs in a temperate maritime climate, but is only found in the cracks and crevices of the shore cliffs during the warmer seasons of the year when habitat temperatures are in the range of + 25 to + 50° C. The maritime earwig, Anisolabis maritima, inhabits ocean beaches just above high tide mark and escapes the lower temperatures of the northern coastal climate by retreating under stones and beneath decaying vegetation. I found, when maintaining cultures in the laboratory, that + 10° C. is the approximate lower limit of tolerance. Zootermopsis angusticollis, the Pacific coast coniferous dampwood, or "rottenwood", termite, occurs from British Columbia to Baja

California. While often found at high elevations and occurring in areas of wide temperature variation, it is, nevertheless, a warm-adapted species. The heat of decay within the wood maintains a rather uniform temperature between $+ 15$ and $+ 25^{\circ}$ C. Gryllus assimilis, the field cricket, is a wide-ranging species, occurring from the middle of South America and extends throughout most of North America. This genus seems to be of wide temperature tolerance, but does escape freezing temperatures by overwintering as nymphs or retreating into burrows or vegetation. Grylloblatta is a cryophilic form restricted to an optimum temperature range of $- 3$ to $+ 6^{\circ}$ C. The insect does not hibernate and is active at temperatures that are generally lethal to most insects.

If lower temperatures are correlated with higher concentrations of the unsaturated fatty acids that have lower melting points than saturated ones, it should be evident in this series of insects. In addition, the melting points of the total fatty acids present should also reflect to some degree temperature preferences or tolerances.

For Grylloblatta $+ 10^{\circ}$ C. is the maximum limit for any long term survival. Therefore, when considering the liquidity of the fatty acids, I chose the $+ 10^{\circ}$ C. melting point as the reference point.

The total per cent of fatty acids present in the four classes analyzed with a melting point above $+ 10^{\circ}$ C. is as follows:

Total Per Cent Fatty Acids

with M.P. above + 10° C.

<u>Pedetontus</u>	76.0	S.E.0.11	<u>Zootermopsis</u>	70.4	S.E.0.02
<u>Periplaneta</u>	75.0	0.02	<u>Gryllus</u>	58.4	0.02
<u>Anisolabis</u>	71.5	0.10	<u>Grylloblatta</u>	43.1	0.11

The percentages above + 10° C. are in excellent agreement with habitat temperatures. Pedetontus and Periplaneta are the two most thermophilic of the orders and form a group distinct from the others. Anisolabis and Zootermopsis are both maritime forms and are exposed to a wider range of moderate habitat temperatures. These, too, form a pair with a somewhat lower per cent of above + 10° C. melting point fatty acids. Gryllus forms a distinct entity, as might be predicted by its wide range and exposure to varying temperature fluctuations. The only strictly cryophilic form of this group, Grylloblatta, contains merely 43.1 % of the fatty acids that have a melting point at + 10° C. or higher. This is consistent with the habitat temperatures if Grylloblatta is to remain highly active.

The percentage of unsaturated fatty acids present in the different orders tested do not present the same distinct pattern as found in the melting point of fatty acids present. The total per cent of unsaturated fatty acids is as follows:

TABLE V

Total Per Cent Unsaturated Fatty Acids			
<u>Pedetontus</u>	59.4	0.01	<u>Anisolabis</u> 65.3 0.05
<u>Periplaneta</u>	61.0	0.02	<u>Grylloblatta</u> 65.8 0.10
<u>Zootermopsis</u>	63.0	0.05	<u>Gryllus</u> 66.4 0.01

Pedetontus and Periplaneta again form a group and is what would be expected if higher environmental temperatures are correlated with higher percentages of saturated fatty acids. Zootermopsis is also consistent with a moderately temperate form. The pattern changes here in that Anisolabis, Gryllus and Grylloblatta all form a group, yet have widely differing temperature preferences.

Environmental temperatures are correlated with the degree of saturation of the fatty acids present in the insects if one considers the melting points of the unsaturated fatty acids. The total per cent of unsaturated fatty acids with a melting point above $+10^{\circ}$ C. is as follows:

TABLE VI

Total Per Cent Unsaturated Fatty Acids			
With M. P. Above $+10^{\circ}$ C.			
<u>Periplaneta</u>	36.3	0.05	<u>Zootermopsis</u> 35.3 0.01
<u>Pedetontus</u>	35.3	0.01	<u>Anisolabis</u> 33.2 0.05
<u>Gryllus</u>	25.0	0.01	<u>Grylloblatta</u> 8.9 0.02

The order groupings are once again consistent with habitat temperatures. From these data the environmental temperatures do appear to affect the degree or percentages of saturated-unsaturated fatty acids present in the organism. The conflicting data of previous reports might be in agreement if the temperature tolerances of the different insects tested were taken into consideration.

The overall quantitative and qualitative patterns of fatty acids in the orders analyzed agree with the fatty acid composition found in other insects. Each order has its own distinct composition as has been found in other studies. Nevertheless, Grylloblatta and Anisolabis, while each possesses a distinct composition, more closely resemble each other than the other orders analyzed. This closer relationship is consistent with the morphological relationships presented earlier.

VI. DISCUSSION AND CONCLUSIONS

As noted in the general introduction to this thesis, the Grylloblattodea are of interest owing to their structure and systematic position, their low temperature-high humidity preference and winter activity, and their disjunct distribution and zoogeography. These three aspects have been considered in the present research, but much remains to be done.

With respect to the climatic tolerance, my research has shown that the two species of Grylloblatta studied have a preferred temperature of - 3.5 to + 5° C. at 90 to 99 per cent relative humidity, a result in general agreement with the results obtained by Henson (1957b). The upper and lower lethal limits are correspondingly low and it is clear that Grylloblatta is like other winter-active insects such as Boreus (Mecoptera), Chionea (Diptera) (Chapman, 1954; Hågvar, 1971) and the carabid Pterostichus brevicornis (Coleoptera) (Baust and Miller, 1971, 1972) in this respect.

In such insects, it is evident that there must have been evolutionary adaptations to temperature, permitting them to move, feed, grow and reproduce at temperatures much lower than those preferred by the majority of other insects.

In the present study, while the physiological basis of this low temperature-high humidity preference was not

selected as a main line of investigation, the data on lipid composition have produced evidence relevant to environmental physiology and temperature preference of Grylloblatta. My analysis shows that the unsaturated fatty acids account for 65.8 per cent of the total fatty acids in Grylloblatta, of which only 8.9 per cent have melting points above $+ 10^{\circ}$ C. In the temperate forms analyzed, unsaturated fatty acids with melting points above $+ 10^{\circ}$ C. range from 25 to 36 per cent. The percentage of fatty acids that are liquid at or below the maximum tolerated temperature suggests a physiological mechanism is present in Grylloblatta that allows mobility of the insect and continued intra- and intercellular transport at low temperatures. The high concentration of liquid fatty acids may also function as an "antifreeze" mechanism which retards freezing and nucleation of body water.

In the future, it would be worthwhile to examine the temperature preference and tolerance of coexisting species to see if there are adaptations in this parameter permitting them to live together, as documented in other insects (Heath et al, 1971; Jamieson, 1973). The immature stages should also be studied since different instars in a life cycle may show different preferences or optima (Sherman and Watt, 1973). Many other aspects of the physiology would be worthwhile pursuing, glycerol content

and enzyme functions being two that seem appropriate.

In general, in insects cryoprotectants either increase cold resistance by greatly lowering freezing or supercooling points, without affording protection in the event of ice formation, or they allow varying degrees of cold protection without necessarily profoundly lowering freezing or supercooling points (Baust and Miller, 1972). The former, which frequently involves specific behavioral responses resulting in the reduction of nucleation agents (Salt, 1961, 1968), seems not to occur in Grylloblatta, as this insect is active and feeds during winter. Salt (1968) found cessation of feeding was an important behavior reducing, for example, nucleation agents in the gut, etc. In Grylloblatta, as in Pterostichus brevicornis (Baust and Miller, 1972), the cryoprotectant probably does not greatly influence the freezing and supercooling points. Here, the glycerol content and changes would be worthy of study, since these have been shown to have a pronounced cryoprotectant function (Salt, 1961; Sømme, 1964; Baust and Miller, 1971, 1972). In this context, one of the potential sources of glycerol might be the lipids. The ready conversion of neutral fats to glycerol and their component fatty acids, either by enzyme mediation or acid hydrolysis, could be important (Baust and Miller, 1972).

The adaptation to low-temperature living by Grylloblatta undoubtedly involves either quantitative changes in enzymes

or changes in the type of particular enzymes. Studies of such biochemical adaptations have received considerable attention in cold-acclimated animals (Somero and Hochachka, 1971; Sømme, 1972) and in fishes showing evolutionary cold adaptation (Somero, Giese and Wohlschlag, 1968), but to date similar studies in evolutionary cold-adapted insects do not seem to have been undertaken. Grylloblatta would be an ideal subject to study in this context, perhaps in preference to Borens or Chionea because of its larger size. Certainly, one might expect in this insect the production of enzymes which are particularly well suited for function at the temperature to which they are adapted (see Somero and Hochachka, 1971).

The narrow temperature-humidity tolerance of Grylloblatta seriously restricts the habitat that this genus can occupy. Only the alpine-subalpine hypolithion and the ice cave environment seem to provide the required conditions on a more or less permanent basis. Even in these habitats, however, the microenvironments are not universally available, for in the alpine-subalpine, it would seem that only under stones or boulders, 50-150 m. in diameter and 30-50 cm. thick, do the required relatively constant temperature and high humidity occur. Such a limitation and dependence upon particular stone size is well known in the hypolithion community (Hågvar and Østbye, 1972). Likewise, ice caves are highly variable (Halliday, 1954), but only

certain ones are known to contain populations of Grylloblatta (Kamp, 1970). Here again, only under certain conditions and at certain times of the year, do the required temperature-humidity conditions occur.

With the narrow temperature-humidity tolerance of Grylloblatta documented, with the limited availability of permanent microhabitats evident, and the knowledge that much of the present Nearctic range of Grylloblatta was glaciated during the Pleistocene (Hubbs and Miller, 1948), it is obvious that the distribution patterns in western North America have been greatly changed in the past. The present distribution pattern has been fundamentally influenced by the geologic and climatic events of the Pleistocene. Further, the regional, and sometimes, highly localized, volcanic activity during the post Pleistocene, the warm dry period (Hypsithermal), and the rebirth of summit and cirque glaciers, commencing approximately 2500 years ago, must have profoundly affected the distribution patterns of Grylloblatta.

It would seem that the present distribution of Grylloblatta in the Coast-Cascade Cordilleran has been strongly influenced by volcanism in the post Pleistocene. The distribution suggests two centers of dispersal for the northern Coast-Cascade species: one somewhere east of the Cordilleran crest between Mt. Baker and Glacier Peak, and the other east of the summit between Glacier Peak and Mt. Rainier.

The current distribution of Grylloblatta and the events of the post Pleistocene indicate that there was no single center of post Pleistocene dispersal for species in the High Cascade-Basin ranges or the Sierra Nevada. The post Pleistocene pockets of dispersal were probably many and migration controlled by regional topography and volcanism.

The early post Pleistocene center of dispersal for Grylloblatta campodeiformis campodeiformis was probably south of the Cordilleran-Keewatin ice sheet in Montana, with subsequent northward migration to the barriers of the Peace River region.

The present distribution pattern and systematics within Grylloblatta suggest that the northern Great Basin and Columbia Basin have been effective barriers to dispersal between the Rocky Mountains and the Cascades. These basins and ranges have evidently acted as barriers since the beginning of the late Pleistocene and possibly throughout the various episodes of the Quaternary periods. The effectiveness of the barriers is reflected by the present distribution of Grylloblatta on the western fringe of the Columbia and Great Basins and its absence elsewhere in the basins.

Grylloblatta is absent east of the Rocky Mountain Cordilleran. During the late Pleistocene a zone of suitable climate south of the Keewatin Ice Sheet probably extended eastward across the Central Plains, but lack of suitable habitat there seems to have prevented dispersal to eastern mountain ranges.

The deficit of Grylloblatta material south of Yellowstone National Park along the Rocky Mountain crest is, I believe, due to lack of investigation in suitable areas. Further research should concentrate in this area.

Grylloblatta appear to be absent north of the southern Cassiar and Liard ranges. This may be due in part to insufficient field investigation; however, I believe the taxon will not be found north of the -5° C. isotherm or in widespread permafrost. The permanently frozen deeper substrate and the freezing and thawing of the surface layer of the permafrost would preclude occupancy of the available hypolithion by Grylloblatta. In the northern portions of its range, G. c. campodeiformis does not occupy areas of relic or discontinuous permafrost, even though suitably sized rock is present. Grylloblatta may occur in the mountain ranges on the Gulf of Alaska, such as the Coast, St. Elias, Wrangell, Chugach and McKinley ranges, for these areas are influenced by the maritime climate and permafrost is not widespread. Relic populations are found at the British Columbia-Yukon border, not far from the more southern of these localities. Discovery of Alaskan populations may shed some light on the relationship of Grylloblatta to the Asian genera, Grylloblattinia and Galloisiana. Such relationships have not yet been discussed in detail, and the interpretation of the zoogeography of the Grylloblattodea as a whole is also a task for the future. For this, a fuller knowledge of the phylogeny of the order, the orthop-

teroids and the Insecta is essential. So far, the data here are too sparse.

While early phylogenetic speculations related the Grylloblattodea to almost every order of the Orthopteroidea over the years, the recent phenetic analyses have suggested affinities with the Dermaptera (Giles, 1963) and the Ensifera (Blackith and Blackith, 1968). The analysis undertaken in the present thesis indicate a phenetic affinity of Grylloblatta to the Dermaptera and Phasmida, but this does not settle the phylogenetic problem. Perhaps not until fossils are discovered will this be feasible.

It is possible that fossil Grylloblattodea do exist and have been overlooked by paleontologists. Most fossil insects consist of fragments such as wing, sclerite and head capsule. Nymphs and adult males of Grylloblatta can easily be mistaken for larvae of staphylinid or lamellicorn Coleoptera. For example, 7 specimens, adults of both sexes and nymphs, collected between 1906 and 1910 and in the Rocky Mountain Park Museum and the Canadian National Collection, were not recognized as Grylloblatta until 1916 (Walker, 1919). The first specimens of Grylloblattodea discovered in Russia were collected in 1935 and were identified as coleopterous larvae. They were not recognized and described as Grylloblattodea until 1951 (Sharov, 1968). I have found over a dozen museum specimens of Grylloblatta which had not been recognized as grylloblattids. Hence, if fossil Grylloblattodea has been found, the identity may be shrouded by lack of recognition.

There is no doubt that the Grylloblattodea are among the most important of the insects for understanding the phylogeny of the Pterygota. They not only combine in their morphology numerous "ancestral" features that occur in six other orthopteroid orders, but they also possess a number of features not found in other pterygote insects.

The oldest known insect fossils are the winged Archaeoptera of the Devonian (Rohdendorf, 1961). Other pterygote fossils belong to the Protorthoptera, Protoblattodea, Paleodictyoptera and Blattodea and occur in the Carboniferous, but not until the Upper Carboniferous do apterygote fossils occur in the form of the Monura (Rohdendorf et al, 1961).

The modern Grylloblattodea are generally considered to be secondarily apterous or neotenic (Walker, 1914; Crampton, 1915; Caudell, 1923, 1924; Imms, 1957; Sharov, 1968), having supposedly evolved from some early winged form. In the examination of Grylloblatta for characters used in the numerical analysis, I found a number of morphological features in the thorax that suggest a primarily apterous structure. The three thoracic terga are freely movable upon one another and are progressively shorter and less differentiated posteriorly. The intersegmental muscles are well developed and retain the primitive connection to a single tergal antecosta. The meso- and metaterga show no evidence of being divided into a prescutum, scutum, scutellum and postnotum. These same structural conditions

are found in the apterygote orders, Thysanura and Diplura, and are absent in adult pterygote orders. The phragmata are absent in the Grylloblatta thorax, the longitudinal dorsal muscles are flat and less developed than in other pterygotes, tergo-sternal muscles are absent, and the tergo-pleural muscles are attached to the pleural areas. In contrast, winged Pterygota have small pleuro-alar flexors attached to the pleural ridge. The thoracic pleura of Grylloblatta are on a primitive plan and retain the apterygote condition. The pleura are thinly sclerotized except along the pleural sutures and the point of origin of the pleural arms. The epimeron is in the original position of the apterygote anopleurite. The precoxal and postcoxal bridges, which are present in the typical wing-bearing segment, are absent in Grylloblatta. The pleural ridge bears a minute terminal expansion which may possibly be a precursor of a pleural alar process. The pleural arms (pleural apophyses) are not attached to the pleural ridge as in other Pterygota. The sternal regions are largely membranous and each segment has a spinasternum. The presence of a third spinasternum is unknown for other Pterygota. The sternal features resemble the Apterygota and are not suggestive of even feeble fliers such as Blatta.

The general structures of the thoracic sclerites and their musculature indicate a primary apterous condition in Grylloblatta, unless regressive mutations and saltations

have occurred throughout the thorax. Such large-scale regression of structures associated with wings is not known from secondary apterous orthopteroids. It can be argued that the Grylloblattodea are neotenous and only adult in the genitalia and internal reproductive system. However, the thoracic morphology suggests that the Grylloblattodea might be a modern relic of an ancient non-winged stock. Certainly, this aspect bears further investigation in the future. Nevertheless, whether primarily apterous or not, a common phylogenetic relationship of Grylloblattodea with other orthopteroids must be remote, probably dating back to the pre-Cretaceous. In this respect then, one can agree with Walker (1937) in considering Grylloblatta one of the few living fossils in the Insecta.

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APPENDIX I
SYSTEMATICS OF GRYLLOBLATTA
CONSIDERED

Grylloblatta sculleni sculleni Gurney

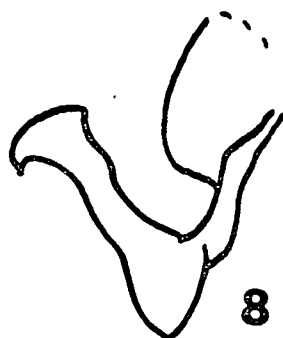
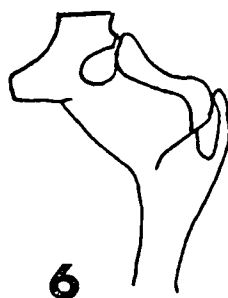
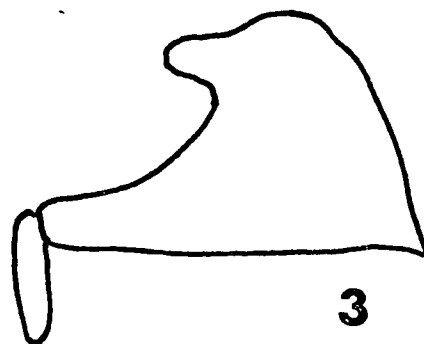
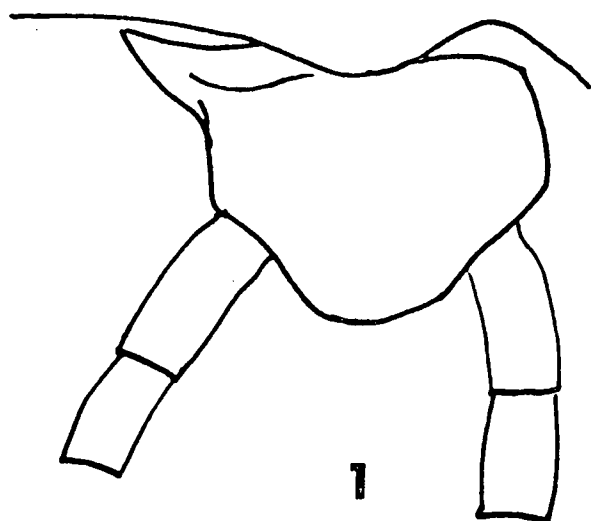
Grylloblatta sculleni Gurney, 1937 (Pan-Pacific Entomologist, 13(4):159-171). Type locality: Scott Camp, about 6600 feet, Three Sisters, Cascade Mountains, Oregon. Date: July 12, 1936. Collector: H. A. Scullen. Habitat: beneath small loose talus. Holotype: adult female, No. 52017, U. S. National Museum. Allotype: unknown. Paratypes: 2 adult females, U. S. National Museum. Topotypes: 4 adult males, unaccessioned, U. S. National Museum (1), Oregon State University Collection (2), J. W. Kamp Collection (1). Topotype locality: Three Sisters (North Sister), 6500 feet, Cascade Mountains, Lane Co., Oregon. Date: July 22, 1970. Collector: J. W. Kamp.

Description of male topotype:

Size large for males of genus; body and leg pubescence dark and conspicuous with many stout spine-like setae; antennae long, each 18 mm. and as long as total body-head length; 40 antennal segments left, 32 right (broken); 3rd antennal segment less than 1.2 times as long as 2nd.

Pronotum (Fig. 24-9) with lateral margins slightly convergent as in G. skagitensis and G. chandleri, anterior margin bearing setae, two rows of setae on dorsum; legs long with many rows of spine-like dark brown setae; leg ratios (length divided by width): protibia, 9.25; profemur, 4.04;

Figure 24 . Grylloblatta sculleni sculleni



metatibia, 13.64; metafemur, 7.12.

Supra-anal plate (Fig. 24-1) symmetrical to 10th abdominal tergum, plate with lateral margins nearly equal, antero-lateral corners normally concealed beneath tergum; cerci long, about one-half antennal length, distal third of each segment with stout setae; left gonocoxa wider at base than long, with heavy fringe of weak setae, stylus double-tapered as in G. chandleri; right gonocoxa (Figs. 24-2,3) with ventral margin nearly straight, antero-dorsal margin gently rounded to meet clasper-like process.

Principal copulatory sclerite (Figs. 24-6,7) with dorso-lateral lobe extending laterally from main arm, dorsal processes and apical lip short and more rounded than other species; first secondary accessory sclerite as in Figure 24-5; second accessory sclerite as in Figure 24-4, with tip recurving

Color: dorsum and head light tan-brown; legs and venter slightly lighter approaching dry straw.

Measurements (length in mm.): pronotum, 3.30; eye, 0.60; protibia, 3.70; profemur, 4.25; metatibia, 6.55; metafemur, 5.70. Measurements (width in mm.): head, 3.15; pronotum, 2.65; protibia, 0.40; profemur, 1.05; metatibia, 0.48; metafemur, 0.80.

Collected at night on large persistent snowfield on Belknap Crater lava fields, Scott Pass, south slope of North Sister.

The male of G. s. sculleni has been unknown until now. With this the other material from the High Cascades can now be determined.

The discovery of another subspecies, G. s. cryocola, warrants recognition of the nominate form as G. s. sculleni.

Additional material:

Two males, collected at night on McKenzie Pass, 2 miles west northwest, on July 18, 1971, by J. W. Kamp.

Grylloblatta skagitensis n. sp.

Type locality: Glacier Basin, 5500 feet, Glacier Peak, Snokomish Co., Washington. Date: September 15, 1969.

Collector: L. Bartlett. Habitat: persistent snow fields.

Holotype: adult male, unaccessioned, U. S. National Museum.

Allotype: adult female, same data, unaccessioned, U. S.

National Museum. Paratypes: 1 adult male and 9 adult females, unaccessioned, University of Idaho collection.

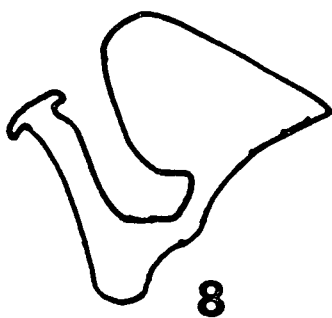
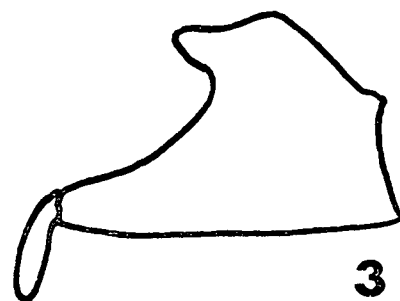
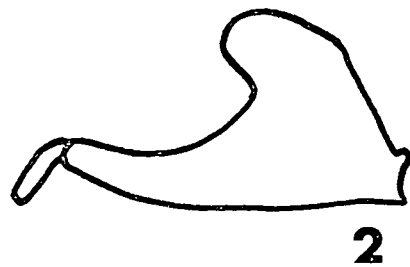
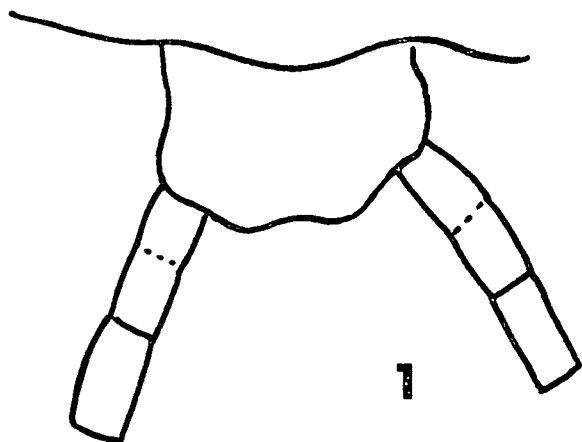
Description of male holotype:

Size medium for genus; finely pubescent; major body setae conspicuous as in G. scudderi; lateral end of posterior margins of abdominal terga with a single row of well developed setae (lacking in G. scudderi); 32 antennal segments left (broken), 37 right.

Pronotum (Fig. 25-9) with lateral margins noticeably convergent posteriorly, more so than in G. scudderi, and postero-lateral angles distinctly obtuse; leg ratios (length divided by width): protibia, 5.85; profemur, 3.34; metatibia, 12.83; metafemur, 5.37.

Supra-anal plate of the 10th abdominal tergum (Fig. 25-1)

Figure 25 Grylloblatta skagitensis n. sp.



borne symmetrically; with postero-lateral margins weakly asymmetrical, right margin more obtuse-angulate than left; right cercus insertion anterior to left, posterior margin of supra-anal plate slightly obtuse emarginate; right gonocoxa shaped as in Figure 25-3, stylus 4 times as long as wide and attached to base; oblique view of right gonocoxa with arcuate margin below thumblike process forming acute angle with lobe.

Principal copulatory sclerite (Figs. 25-6,7) with short copulatory process, apex of process mesoemarginate, dorsolateral and ventrolateral lobes greatly expanded laterally from main body of sclerite; secondary accessory sclerite 1 as in Figure 25-5, as wide as long and approaching that of G. rothi; secondary accessory sclerite 2 (Fig. 25-4) with beak almost straight and narrower than in G. occidentalis, and larger than in G. scudderi; cerci with dark major setae on distal portion each segment; sclerotized basal portion right phallomere as in Figure 25-8.

Color: medium suede brown; sterna, legs, cerci, antennae, light buff.

Measurements (length in mm.): pronotum, 2.8; protibia, 2.87; profemur, 3.18; metatibia, 4.75; metafemur, 4.41. Measurements (width in mm.): head, 2.55; pronotum, 2.25; protibia, 0.49; profemur, 0.95; metatibia, 0.37; metafemur, 0.83.

Description of female allotype:

Differs from male in usual sexual features and is larger with more elongate legs; 36 antennal segments left,

33 right; 3rd antennal segment less than 1.8 times as long as 2nd.

Head wider than pronotum; pronotum with lateral margins slightly convergent posteriorly, postero-lateral margins almost acute, differing from G. scudderi and G. occidentalis, posterior margin doubly arcuate, each side with transverse sulcus; major body setae very conspicuous; leg ratios (length divided by width): protibia, 7.00; profemur, 3.60; metatibia, 13.78; metafemur, 5.62; legs with many strong setae.

Ovipositor: ventral valves with short stout setae on distal third; dorsal valves only slightly arcuate.

Color: as in male.

Measurements (length in mm.): pronotum, 3.32; protibia, 3.30; profemur, 3.78; metatibia, 5.65; metafemur, 5.01; ovipositor, 4.35. Measurements (width in mm.): head, 3.10; pronotum, 2.92; protibia, 0.47; profemur, 1.05; metatibia, 0.41; metafemur, 0.89.

Description of paratypes:

Collected at type locality between 5000-7500 feet.

Paratype male differs slightly from holotype in absolute measurements as follows: (length in mm.): pronotum, 2.80; protibia, 2.85; profemur, 3.22; metatibia, 4.78; metafemur, 4.40; (width in mm.): head, 2.50; pronotum, 2.27; protibia, 0.46; profemur, 0.98; metatibia, 0.40; metafemur, 0.85. Antennal segments of male 36, right and left. Antennal segments of females range from 35 to 37.

General comments:

Grylloblatta skagitensis resembles G. scudderi and G. occidentalis upon gross examination. Grylloblatta skagitensis males may be distinguished from G. scudderi and G. occidentalis by the details of the primary and secondary copulatory sclerites. It differs from G. scudderi by having a shorter pronotum, different tibia ratios, and in general shape of supra-anal plate and right gonocoxa.

The majority of specimens were collected at night, between 10 pm. and midnight, as they foraged on large persistent snow fields. Other material was obtained in nearby hypolithion.

The specific name refers to the Skagit Indian tribe which has occupied the Skagit River drainage for centuries. In some of the Skagit legends Glacier Peak is referred to as a spirit that rumbles and speaks, undoubtedly because of its volcanic activity.

Grylloblatta scudderi n. sp.

Type locality: Whistler Mountain, 6400 feet, Garibaldi Provincial Park, British Columbia. Date: July 13, 1970. Collectors: L. Bartlett and J. W. Kamp. Habitat: alpine on snow. Holotype: adult male, unaccessioned, Canadian National Collection. Allotype: adult female, same data, unaccessioned, Spencer Entomological Museum, University of British Columbia. Paratypes: none.

Description of male holotype:

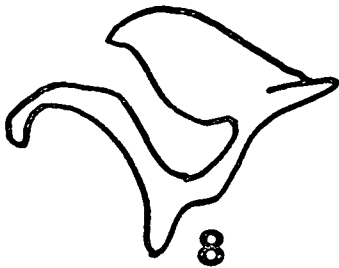
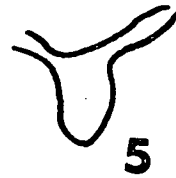
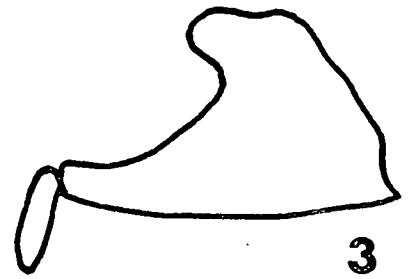
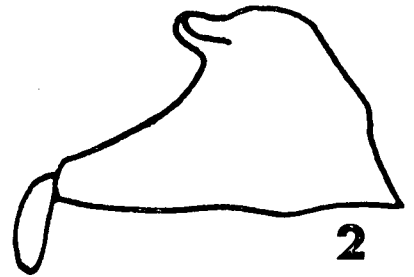
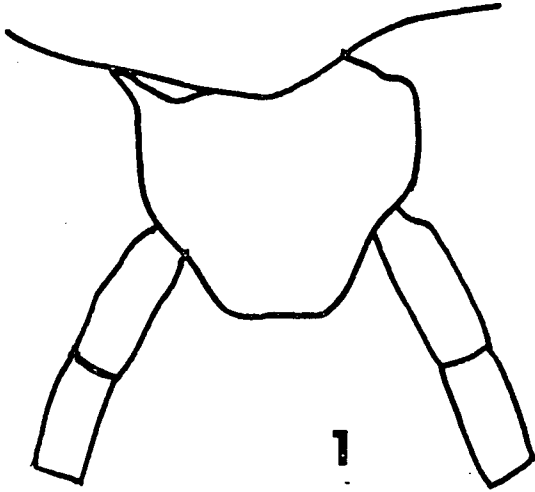
Larger than G. campodeiformis but equal in size to G. skagitensis; body and legs densely clothed with fine tan pubescence; major body setae more conspicuous than in G. campodeiformis, but about as in G. skagitensis; 35 antennal segments left; 37 right.

Pronotum (Fig. 26-9) longer than head width, with lateral margins only slightly convergent (as in G. campodeiformis), postero-lateral angle nearly acute; leg ratios (length divided by width): protibia, 7.62; profemur, 3.31; metatibia, 14.84; metafemur, 5.09; tibia proportionately longer than in G. occidentalis or G. skagitensis.

Supra-anal plate symmetrical to the 10th abdominal tergum (Fig. 26-1), lateral and posterior margins symmetrical, lateral margins gently concave toward posterior; cerci insertion opposed; right gonocoxa shaped as in Figure 26-3, stylus 3 times as long as wide and attached basally to gonocoxa; right gonocoxa in lateral oblique view as in Figure 26-2, clasper not as wide as in G. skagitensis or in G. campodeiformis.

Principal copulatory sclerite (Figs. 26-6,7) differing from that of G. skagitensis in that apex of copulatory process is not emarginate, but has apex more pronounced and dorsal cap more expanded than in G. campodeiformis or G. occidentalis, dorso-lateral lobe alate; apical process of secondary accessory copulatory sclerite as in Figure 25-5; accessory sclerite 2 (Fig. 26-4) with apex more sharply

Figure 26. Grylloblatta scudderi n. sp.



constricted than in G. occidentalis and G. skagitensis; basal scleritized portion of right phallomere as in Figure 26-8.

Color: head and thorax grayish-tan; abdomen light gray; legs straw.

Measurements (length in mm.): pronotum, 2.67; protibia, 2.82; profemur, 3.15; metatibia, 4.75; metafemur, 3.82. Measurements (width in mm.): head, 2.50; pronotum, 2.22; protibia, 0.37; profemur, 0.95; metatibia, 0.32; metafemur, 0.75.

Description of female allotype:

Size medium for genus but smaller than G. occidentalis; major body setae less prominent than in other species; 36 antennal segments left and right; antennal segments smaller than in G. skagitensis or G. occidentalis but about as in G. campodeiformis.

Head as wide as pronotum length; pronotum with lateral margin less emarginate than in G. skagitensis; leg ratios (length divided by width): protibia, 7.67; profemur, 3.31; metatibia, 13.85; metafemur, 5.17.

Ovipositor: short, dorsal valves reaching to distal margin of segment 4 of cercus; ventral valves moderately curved throughout length.

Color: as in male.

Measurements (length in mm.): pronotum, 2.90; protibia, 2.80; profemur, 3.15; metatibia, 4.85; metafemur, 4.40; ovipositor, 3.00. Measurements (width in mm.): head, 2.67;

pronotum, 2.32; protibia, 0.36; profemur, 0.95; metatibia, 0.35; metafemur, 0.85.

General comments:

Grylloblatta scudderi males can be distinguished from those of G. occidentalis and G. skagitensis by the shape and details of the supra-anal plate and right gonocoxa. It may also be separated from other species by details of the copulatory sclerite. Female G. scudderi may be separated from other species by the short ovipositor and pronotal shape.

Holotype and allotype specimens were collected on a large persistent snow field lying in a cirque approximately 1000 feet below a glacier. The air temperature on the snow field was 5° C. colder than the air and snow fields outside the cirque. Much colder air from the higher elevations flowed off the glacier and was funnelled by the topography into the cirque over the snow field. Searching on other snow fields failed to find any additional specimens. Nine nymphs (3 males, 6 females) were collected from the hypolithion immediately adjacent to the cirque snow field.

It is a pleasure to name this new species for Dr. G. G. E. Scudder, whose sustained interest and encouragement are deeply appreciated.

Grylloblatta paulinae n. sp.

Grylloblatta sp. Kamp, 1970 (Annales de Speleologie,

25(1):223-230). Type locality: South Ice Cave, 5000 feet (T. 23, S; R. 14E, Sec. 18, N.E. $\frac{1}{4}$; U. S. G. S. Newberry Crater Quadrangle), Deschutes National Forest, Lake Co., Oregon. Date: November 21, 1968. Collector: J. W. Kamp. Habitat: cavernicolous. Holotype: adult male, unaccessioned, U. S. National Museum. Allotype: adult female, same data except collected July 22, 1963, unaccessioned, U. S. National Museum. Paratypes: 4 adult males and 5 adult females, unaccessioned, 1 each sex, Oregon State University collection and remainder J. W. Kamp collection.

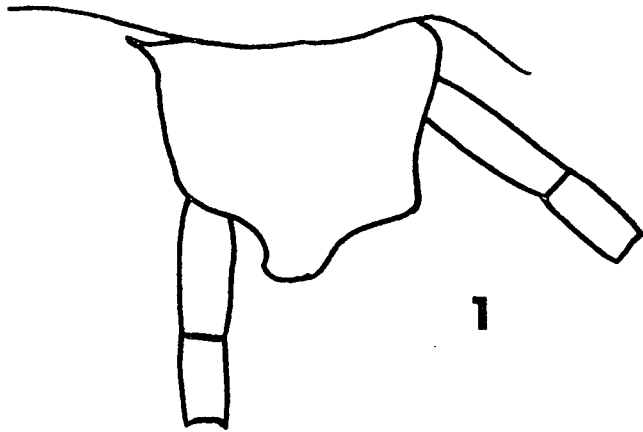
Description of male holotype:

Size large for genus; very fine dense body pubescence inconspicuous; major setae sparse except on legs; setae less than in G. skagitensis; antennae shorter than in G. chirugica and about as long as thorax and abdomen combined; 35 antennal segments left, 36 right.

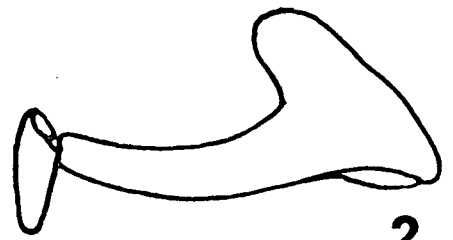
Head as wide as pronotum is long and larger than in G. skagitensis or G. rothi; pronotum (Fig. 27-9) with lateral margins converging less posteriorly than in G. skagitensis or G. sculleni, postero-lateral margin weakly obtuse, posterior margin slightly arcuate between postero-lateral angle and mid-line; leg ratios (length divided by width): protibia, 5.88; profemur, 2.91; metatibia, 4.65; metafemur, 4.70.

Supra-anal plate slightly asymmetrical to 10th abdominal tergum (Fig. 27-1); supra-anal plate with left posterior lobe almost acute to postero-lateral margin, lobe

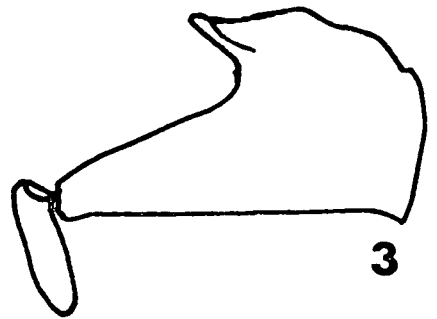
Figure 27. Grylloblatta paulinae n. sp.



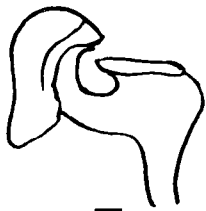
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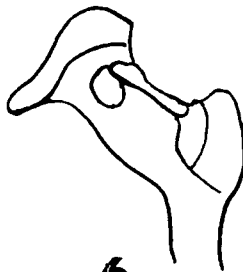
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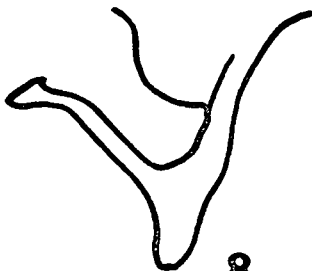
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shorter and more acute than in G. rothi; right gonocoxa (Fig. 27-3) with anterior margin arcus half ellipsoid; clasper acute to dorsal margin, slightly recurved at apex, and laterally expanded; ventral margin of gonocoxa straight in lateral oblique view as in Figure 27-2, narrow distal arm with wide clasper.

Principal copulatory sclerite (Figs. 27-6,7) with dorso-lateral lobe expanded and over half the length of lateral margin below dorsal cap; apex of dorsal process less than half length of cap; ventro-lateral lobe short, slightly pointed; secondary accessory sclerites as in Figures 27-4,5; accessory sclerite 2 (Fig. 27-4) with short apex, shorter than in other species; accessory sclerite (Fig. 27-5) longer and more pointed than in G. chirugica; sclerotized basal portion of right phallomere as in Figure 27-8.

Color: dorsum and head light brown; legs and venter pale straw.

Measurements (length in mm.): pronotum, 3.00; protibia, 3.00; profemur, 3.50. Measurements (width in mm.): head, 3.00; pronotum, 2.42; protibia, 0.51; profemur, 1.20; metatibia, 0.42; metafemur, 0.85.

Description of female allotype:

Size large for females of genus, larger than holotype or paratype males; fewer major setae than in G. sculleni or G. skagitensis, with very fine pubescence and sparse major setae; antennae with 35 segments each; third antennal

segment 1.25 times the length of second; second antennal segment longer than in G. chirugica, G. sculleni and G. rothi; antennae as long as thorax and abdomen combined, shorter than in G. sculleni.

Head as wide as pronotum length; pronotum with lateral margins nearly straight as in G. sculleni, but postero-lateral angle decidedly obtuse, differing from G. sculleni and G. chirugica; leg ratios (length divided by width): protibia, 8.33; profemur, 3.68; metatibia, 12.12; metafemur, 6.71; ratios proportionately greater than in G. chirugica and G. rothi; pro- and metatibia proportionately longer than in G. sculleni but pro-and metafemur shorter.

Ovipositor: ventral valves bear short stout setae along entire length; valves long and tapering, reaching base of seventh cercal segment; ovipositor much longer than in G. sculleni, G. chirugica or G. skagitensis.

Color: as in male.

Measurements (length in mm.): pronotum, 3.00; protibia, 3.00; profemur, 3.50; metatibia, 4.85; metafemur, 4.70; ovipositor, 4.50. Measurements (width in mm.): head, 3.00; pronotum, 2.55; protibia, 0.36; profemur, 0.95; metatibia, 0.40; metafemur, 0.70.

Description of paratypes:

Length Measurements of Paratypes (Range and Mean)

	<u>Males</u>	<u>Females</u>
Pronotum	2.98-3.00 (2.99)	2.92-3.00 (2.93)
Protibia	2.85-3.00 (2.92)	2.90-3.00 (2.95)
Profemur	3.50-3.58 (3.54)	3.40-3.50 (3.49)

Metatibia	4.65-4.80 (4.72)	4.75-4.95 (4.82)
Metafemur	4.70 (4.70)	4.50-4.70 (4.61)
Ovipositor		4.35-4.45 (4.43)

General comments:

The shape of the supra-anal plate separates G. paulinai from all other species except G. rothi and G. lavacola. Grylloblatta paulinai differs from G. rothi in the number of antennal segments, shape and details of right gonocoxa, primary copulatory sclerite and secondary accessory sclerites; G. paulinai differs from G. lavacola in the details of the supra-anal plate, right gonocoxa and sclerites of the genitalia.

Grylloblatta paulinai is restricted to South Ice Cave or the hypolithion in the immediate vicinity. The species occupies the cave except during the winter when the temperatures and humidities fall below the lethal limits for the insect.

This species is named after the cattle rustler renegade Indian Chief, Paulina, of the Walapi Tribe of the Snake Indian nation. The renegade title was declared by white men when he and his band would not be forced onto a reservation with their natural enemy, the Warm Springs Tribe. Chief Paulina was killed in ambush on April 25, 1867, for stealing a few cattle to feed his starving band. Since the type locality, South Ice Cave, occurs on the southeast slope of Paulina Mountain, it seems fitting to recognize this brave individual once again by naming this new species after him.

Grylloblatta campodeiformis athapaska n. ssp.

Type locality: Mt. St. Paul, 4925 feet, Summit Lake, Stone Mountain Provincial Park, British Columbia. Date: August 26, 1962. Collector: R. E. Leech. Habitat: east slope of hypolithion. Holotype: adult male, unaccessioned, Canadian National Collection. Allotype: adult female, same locality data except collected at 5400 feet, unaccessioned, Canadian National Collection. Paratypes: none.

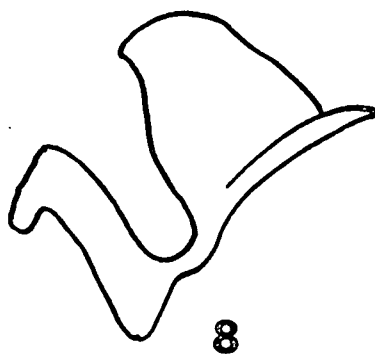
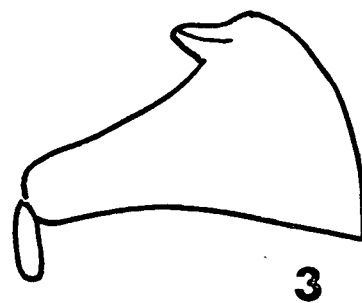
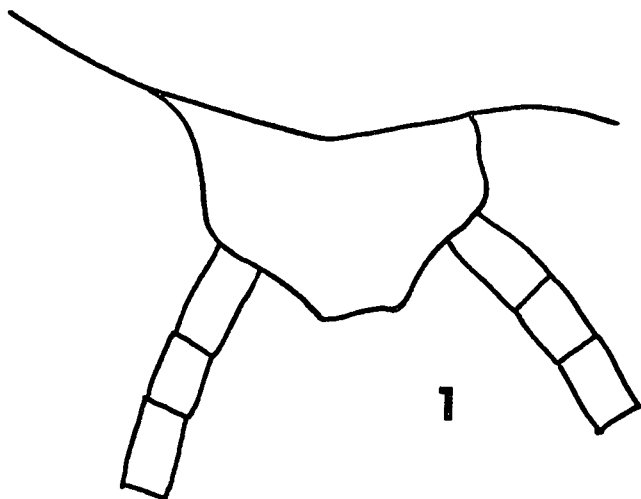
Description of male holotype:

Size as in G. c. campodeiformis; body pubescence pale and less conspicuous than in type of species; 29 antennal segments left, 28 right (broken); individual antennal segments longer than in G. c. campodeiformis from Jasper National Park.

Pronotal length shorter than in Jasper population of G. c. campodeiformis, being nearly square and with lateral margins less convergent than in topotypic material (Fig. 28-9); postero-lateral angle of pronotum approximately acute; leg ratios: (length divided by width): protibia, 6.09; profemur, 2.73; metatibia, 10.00; metafemur, 5.45; legs shorter in proportion than in G. c. campodeiformis.

Supra-anal plate (Fig. 28-1) slightly asymmetrical to 10th abdominal segment; tergum shape as in type (Fig. 28-1); right gonocoxa (Figs. 28-2,3) differing in detail from that of G. c. campodeiformis, anterior margin a smooth ellipse rather than obtuse angulate as in Jasper G.c. campodeiformis specimens; stylus length twice

Figure 28. Grylloblatta campodeiformis athapaska n. ssp.



width, shorter and elipsoid rather than tapering as in G. c. campodeiformis.

Principal copulatory sclerite (Figs. 28-6,7) differing in details from G. c. campodeiformis with apex of dorsal process pyramid-shaped rather than beak-like, dorso-lateral lobe less alatus than normal for topotype material, ventro-lateral lobe short and equal to dorso-lateral lobe length, less dilated and more alatus than in G. c. campodeiformis; secondary accessory sclerites differing as in Figures 28-4,5.

Color: not certain for specimen has faded in preserving.

Measurements (length in mm.): pronotum, 2.59; protibia, 2.50; profemur, 2.73; metatibia, 4.00; metafemur, 3.71; cercus, 4.50. Measurements (width in mm.): head, 2.71; pronotum, 2.60; protibia, 0.41; profemur, 1.00; metatibia, 0.40; metafemur, 0.68.

Description of female allotype:

Size equal to topotypic Jasper material; 29 antennal segments each; leg ratios (length divided by width): protibia, 5.50; profemur, 3.50; metatibia, 9.15; metafemur, 5.07; protibia, metatibia and metafemur much shorter in proportion than Jasper female G. c. campodeiformis; basal tarsomere subequal in length to next three tarsi whereas tarsomere equal to next three in Jasper G. c. campodeiformis.

Pronotum robust and almost square in shape, lateral margins almost straight rather than converging as in G. c. campodeiformis.

Ovipositor: shorter and more robust than in G. c. campodeiformis, with ventral valves markedly curved over distal 1/3; cerci short with 6 cercal segments and equal to length of dorsal blades of ovipositor; dorsal blades of ovipositor equal to 5 segments in the Jasper G. c. campodeiformis.

Color: head, thorax and abdomen dark tan suede; venter and legs medium straw.

Measurements (length in mm.): pronotum, 2.72; protibia, 2.20; profemur, 2.80; metatibia, 3.00; metafemur, 3.60; ovipositor, 3.00; cerci, 4.40. Measurements (width in mm.): head, 2.80; pronotum, 2.45; protibia, 0.40; profemur, 0.80; metatibia, 0.40; metafemur, 0.71.

General comments:

Grylloblatta campodeiformis athapaska can be distinguished from G. c. campodeiformis by the shorter, more square, pronotum and by the absolute measurements and proportional ratios of the legs. Males of G. c. athapaska differ in essential details of the principal copulatory sclerite and the secondary accessory sclerites. Female G. c. athapaska are distinguished by the shortness of the cerci and ovipositor blades.

Mt. St. Paul, the type locality, is over 450 miles north of the last known Rocky Mountain Cordilleran population of G. c. campodeiformis (from Whistler Mt., Jasper National Park). The two subspecies are isolated from each

other by the broad, low Peace River plateau. Survey collecting between the two populations by R. E. Leech and E. E. MacDonald and my own survey trips indicated that suitable hypolithion habitats over the plateau were extremely rare, and no additional populations of Grylloblatta have been discovered.

I believe that G. c. athapaska is a late Pleistocene relict that has survived in the refugium along the Nahan and Liard ranges.

The subspecies is named after the native language of the Indian nation that inhabited northern British Columbia and the Yukon and Northwest Territories.

Grylloblatta campodeiformis nahanni n. ssp.

Type locality: Mt. McDame, 5400 feet, Cassiar Mountain Range, Cassiar, British Columbia. Date: September 17, 1969. Collector: J. W. Kamp. Habitat: hypolithion near snow bank. Holotype: adult male, unaccessioned, Canadian National Collection. Allotype: adult female, Limestone Peak, 6000 feet, Cassiar Mountain Range, collected September 16, 1969, by J. W. Kamp in hypolithion in snowstorm, unaccessioned, Spencer Entomological Museum, University of British Columbia. Paratypes: none.

Description of male holotype:

Size larger than G. c. athapaska; pubescence conspicuous; major setae prominent; 24 antennal segments left (broken),

29 right; third antennal segment 1.5 time the length of second segment.

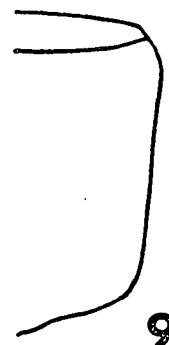
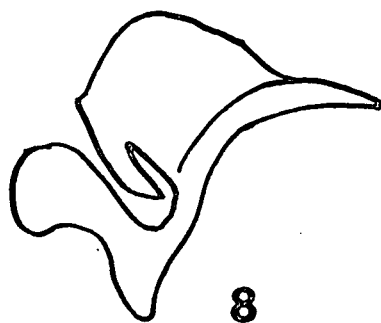
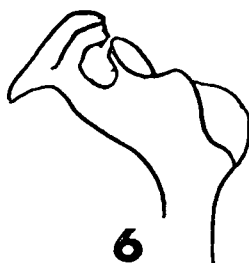
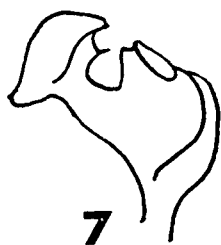
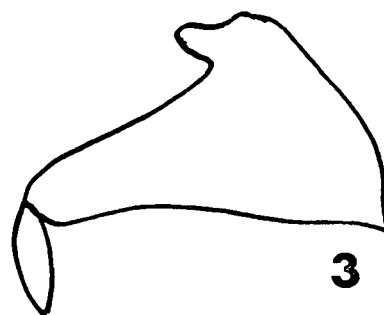
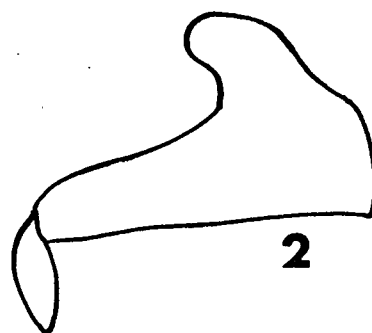
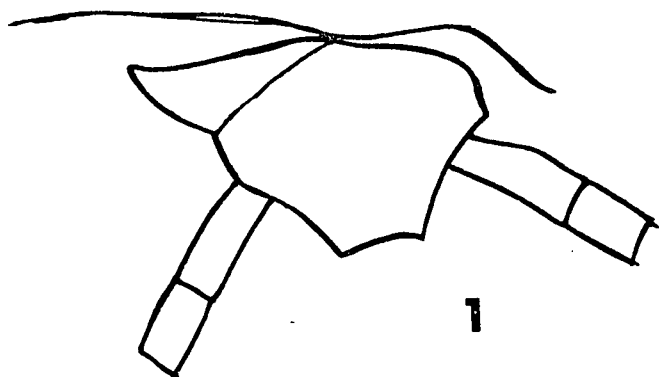
Pronotal length about equal to head width and longer than in G. c. athapaska; lateral margins of pronotum noticeably convergent, approaching G. c. campodeiformis specimens from Jasper National Park; pronotum wider in proportion to length than in G. c. campodeiformis and not square as in G. c. athapaska; leg ratios (length divided by width): protibia, 5.33; profemur, 2.75; metatibia, 10.62; meta-femur, 6.55; metatibia and femur longer than in G. c. athapaska; metatibia longer than in G. c. campodeiformis from Jasper National Park.

Supra-anal plate slightly asymmetrical to 10th abdominal tergum (Fig. 29-1); differs from other subspecies in details of lateral and posterior margins (Fig. 28-1); right gonocoxa (Figs. 29-2,3) with clasper process more obliquely expanded than in other subspecies.

Principal copulatory sclerite (Figs. 29-6,7) differing in details from G. c. campodeiformis and G. c. athapaska, apex of dorsal cap long and recurving, dorso-lateral lobe as in Jasper G. c. campodeiformis, but with greater lateral expansion of lobe; secondary accessory sclerite 1 (Fig. 29-5) wider and more rounded than in other forms; accessory sclerite 2 with constricted neck (Fig. 29-4); basal sclerite portion of right phallomere (Fig. 29-8) more as in G. c. athapaska.

Color: head and thorax medium tan; abdomen grayish-tan;

Figure 29. Grylloblatta campodeiformis nahanni n.ssp.



venter and legs medium straw.

Measurements (length in mm.): pronotum, 2.80; protibia, 2.40; profemur, 2.70; metatibia, 4.25; metafemur, 3.43; cerci, 4.80. Measurements (width in mm.): head, 2.81; pronotum, 2.48; protibia, 0.45; profemur, 0.98; metatibia, 0.40; metafemur, 0.60.

Description of female allotype:

Larger than females of Jasper G. c. campodeiformis; 29 antennal segments left and right.

Pronotum length about equal to head; pronotum wider in proportion than in G. c. campodeiformis, shape being between square appearance of G. c. athapaska and rectangular shape of G. c. campodeiformis; lateral margins of pronotum slightly convergent, but less so than in G. c. campodeiformis material from Jasper; pronotum not as straight as in G. c. athapaska; basal tarsomere of metatarsus subequal in length to next three tarsomeres, as in G. c. athapaska; legs longer than in other subspecies; leg ratios (length divided by width): protibia, 6.08; profemur, 3.06; metatibia, 11.07; metafemur, 5.33.

Ovipositor: short; dorsal valves about as in G. c. athapaska; cerci longer than in other subspecies.

Color: head, thorax and abdomen golden brown; legs and ventral region pale straw.

Measurements (length in mm.): pronotum, 3.05; protibia, 2.80; profemur, 3.11; metatibia, 4.43; metafemur,

4.00; ovipositor, 3.00; cerci, 5.00. Measurements (width in mm.): head, 3.18; pronotum, 2.70; protibia, 0.45; profemur, 0.88; metatibia, 0.40; metafemur, 0.75.

General comments:

Grylloblatta campodeiformis nahanni may be distinguished from G. c. campodeiformis by the length of the ovipositor and differs from the other subspecies by the longer cerci and legs in both sexes. Males can be distinguished from males of G. c. campodeiformis and G. c. athapaska by the details of the principal copulatory sclerite and secondary accessory sclerites. In some features G. c. nahanni is intermediate between Jasper material of G. c. campodeiformis and Mt. St. Paul material of G. c. athapaska.

The Cassiar region of Cassiar Mountain Range, the type locality for G. c. nahanni, is approximately 200 miles west-northwest of the type locality of G. c. athapaska. The two localities are separated by the intervening Liard Plain. For relationships between G. c. athapaska and G. c. nahanni and their possible late Pleistocene origin see the section on distribution.

Grylloblatta campodeiformis nahanni is named after the Nahanni Indian Tribe which still inhabits the region. These natives were a great source of information to me regarding the habitat of this insect and reported seeing a strange "bug" on Limestone Peak.

Grylloblatta sculleni cryocola n. ssp.

Type locality: Edison Ice Cave, 5200 feet, (T. 19S; R. 9E.; Sec. 14, S.E. $\frac{1}{4}$; U. S. Forest Service map); Deschutes National Forest, Deschutes Co., Oregon. Date: November 15, 1970. Collector: J. W. Kamp. Habitat: dark zone on cave ice. Holotype: adult male, unaccessioned, U. S. National Museum. Allotype: adult female, same locality data, collected July 20, 1962, by J. W. Kamp, unaccessioned, U. S. National Museum. Paratypes: 1 adult male and 5 adult females, J. W. Kamp collection.

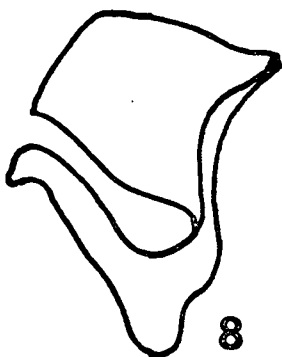
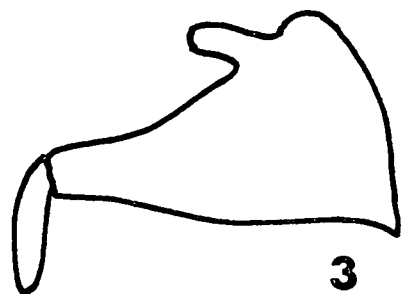
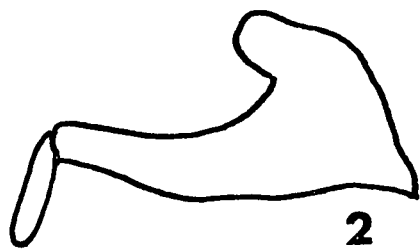
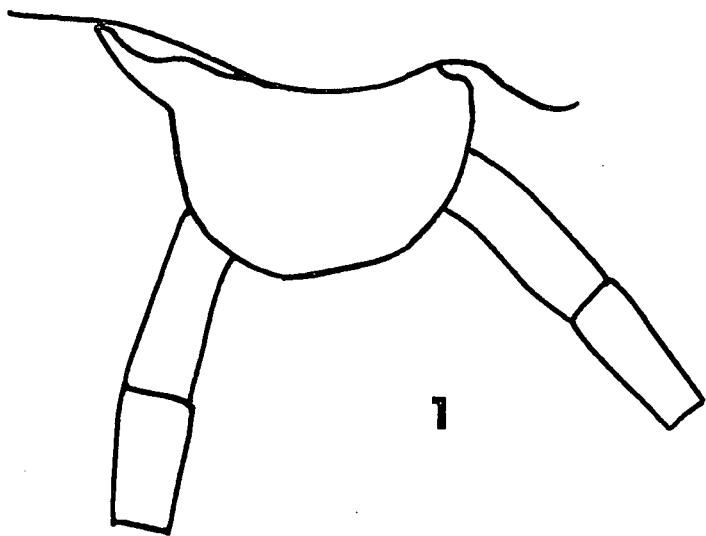
Description of male holotype:

Size medium for males of genus, smaller than G. s. sculleni; pubescence and major setae as in G. s. sculleni; antennae as long as in G. s. sculleni, longer than total head-body length; third antennal segment longer than in G. s. sculleni; third antennal segment equal to combined lengths of segments 4 and 5 (cf. subequal in G. s. sculleni); 40 antennal segments left and right.

Pronotal length 1.2 times head width and proportionately longer than in G. s. sculleni; legs long; leg ratios (length divided by width): protibia, 8.72; profemur, 4.50; metatibia, 13.80; metafemur, 6.66; legs longer and wider than in G. s. sculleni.

Supra-anal plate (Fig. 30-1) symmetrical to 10th abdominal tergum, plate differing from that of G. s. sculleni; plate moderately curvate around postero-lateral

Figure 30. Grylloblatta sculleni cryocola n. ssp.



margins, convex rather than concave as in G. s. sculleni; cercal length as in G. s. sculleni; right gonocoxa (Figs. 30-2-3) with slightly arcuate ventral margin, antero-dorsal margins abruptly recurving to meet clasper; in lateral oblique view clasper narrower than in G. s. sculleni.

Principal copulatory sclerite (Figs. 30-6,7) differing in details of apex and dorso-lateral, ventro-lateral lobes; secondary accessory sclerite 1 (Fig. 30-5) much longer than in G. s. sculleni; accessory sclerite 2 with apex long and not recurved as in G. s. sculleni; distal portion of sclerotized region of right phallomere (Fig. 30-8) gently rounded, while pointed in G. s. sculleni.

Description of female allotype:

Size as large as in G. s. sculleni; 41 antennal segments right and left.

Pronotum proportionately wider than in topotype G. s. sculleni material; postero-lateral angle of pronotum more obtuse than in G. s. sculleni and somewhat acute; lateral margin of pronotum straight for anterior $3/4$ of length, then converging noticeably; legs longer than in G. s. sculleni; leg ratios (length divided by width): protibia, 9.28; profemur, 4.50; metatibia, 13.89; metafemur, 8.00; legs proportionately longer except metatibia and with greater proportional length than in G. s. sculleni (mean leg ratios of 6 topotype G. s. sculleni: protibia, 7.84; profemur, 3.83; metatibia, 14.15; metafemur, 6.21).

Ovipositor: length of dorsal valves about equal to

those of G. s. sculleni; ventral valves of ovipositor more acute in curve than in G. s. sculleni; cerci longer than in G. s. sculleni.

Color: head and dorsal thorax-abdomen very pale straw; ventral surface and legs dry yellow.

Measurements (length in mm.): pronotum, 3.70; protibia, 4.18; profemur, 4.50; metatibia, 6.67; metafemur, 6.00; cerci, 9.25; ovipositor, 3.70. Measurements (width in mm.): head, 3.35; pronotum, 2.85; protibia, 0.45; profemur, 1.00; metatibia, 0.48; metafemur, 0.75.

Description of paratypes:

Thirty-nine to 41 antennal segments.

Ratios of Leg Measurements of 5 Paratype Females

	<u>Range</u>	<u>Mean</u>
Protibia	8.33-9.22	8.63
Profemur	3.97-4.59	4.33
Metatibia	13.30-14.78	13.91
Metafemur	7.46-8.00	7.81

General comments:

Grylloblatta sculleni cryocola females are very difficult to distinguish from those of G. s. sculleni. Grylloblatta sculleni cryocola differs in the greater length of the protibia, profemur and metafemur. The leg ratios are greater than in G. s. sculleni. Grylloblatta sculleni cryocola is much lighter in color than is G. s. sculleni and has longer cerci. Males of G. s. cryocola may be distinguished by the details of the genital sclerites.

Grylloblatta sculleni cryocola is restricted to Edison Ice Cave and the hypolithion in the immediate vicinity. It occurs sympatrically with G. rothi. Grylloblatta sculleni cryocola was not found to be sympatric with G. rothi in other localities and it was not found in the higher elevations of the Three Sisters Mountains.

Grylloblatta hoodalles n. sp.

Type locality: Mt. Hood, 5900 feet, junction of Phlox Point and Timberline roads, Oregon. Date: June 18, 1970. Collector: J. W. Kamp. Habitat: hypolithion. Holotype: adult male, unaccessioned, U. S. National Museum. Allotype: adult female, same data except collected June 18, 1970. Paratypes: 1 adult male and 4 adult females, J. W. Kamp collection.

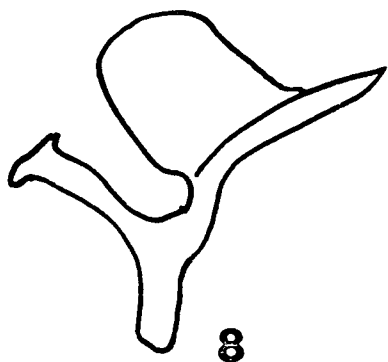
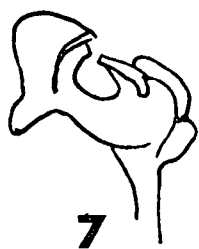
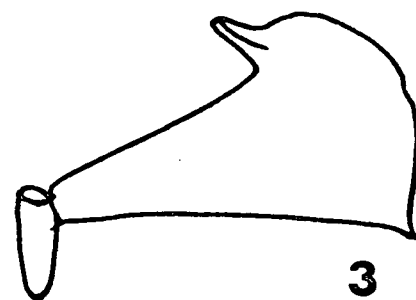
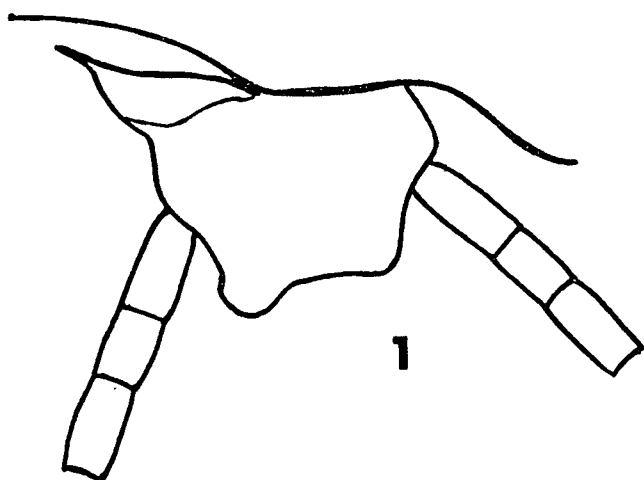
Description of male holotype:

Small for genus; smaller than G. chirugica and more resembling size of G. rothi; fine body pubescence conspicuous; 30 antennal segments left, 24 right; legs short and stout, more so than in topotypic G. rothi.

Pronotum shorter than in G. rothi; leg ratios (length divided by width): protibia, 5.04; profemur, 2.72; metatibia, 9.52; metafemur, 3.96.

Supra-anal plate (Fig. 31-1) is asymmetrical with base of left cercus posterior to right, as in G. rothi; plate shorter than in G. rothi, with left apical lobe less

Figure 31. Grylloblatta hoodalles n. sp.



developed; left gonocoxa as broad as long; right gonocoxa with clasper process (Fig. 31-3) more angulate to dorsal margin than in G. rothi; in lateral oblique view (Fig. 31-2) clasper more expanded than in G. rothi, with posterior arm of gonocoxa narrower; stylus borne on basal $1/3$, length 2 times width.

Principal copulatory sclerite (Figs. 31-6,7) differing in details from G. rothi; apex of dorsal process of this sclerite shorter and more curved than in topotypic G. rothi material, dorso-lateral lobe 1.5 times that of G. rothi, straighter in profile and more laterally expanded, in oblique view (Fig. 31-7) ventro-lateral lobe with acute ventral point lacking as in G. rothi; secondary accessory sclerite 1 (Fig. 31-5) short, globular with basal constriction differing from the longer tapering sclerite of G. rothi; accessory sclerite 2 differs in details of head-like portion and apex of beak; dorsal sclerotized portion of right phallomere (Fig. 31-8) longer and thinner than in G. rothi.

Color: darker than G. rothi; general body medium brown; ventral abdomen, legs and cerci lighter buff.

Measurements (length in mm.): pronotum, 2.75; protibia, 2.52; profemur, 3.00; metatibia, 4.00; metafemur, 3.77. Measurements (width in mm.): head, 2.78; pronotum, 2.40; protibia, 0.50; profemur, 1.10; metatibia, 0.42; metafemur, 0.95.

Description of female allotype:

Thorax and abdomen short compared to G. rothi; thorax 1/5 longer in G. rothi; 22 antennal segments left (broken), 30 segments right; third antennal segment less than 2 times length of second and shorter than in G. rothi; antennae short, 3/4 length of topotypic G. rothi; segments of antennae short, terminal segments smaller than in any other form and less than $\frac{1}{2}$ length of terminal segments of G. rothi.

Head and pronotum small compared to those of G. rothi; posterior margins of pronotum obtuse rather than di-emarginate as in G. rothi; legs short and robust; leg ratios (length divided by width): protibia, 5.34; profemur, 2.95; metatibia, 10.00; metafemur, 4.44.

Ovipositor: length of dorsal blade about equal to that of G. rothi; cerci shorter than in G. rothi; dorsal valve of ovipositor reaching middle of 8th cercal segment.

Color: general body color about as in G. rothi; abdominal terga grayish-brown, darker than in G. rothi.

Measurements (length in mm.): pronotum, 3.00; protibia, 2.51; profemur, 2.95; metatibia, 4.00; metafemur, 3.87; ovipositor, 3.62. Measurements (width in mm.): head, 3.00; pronotum, 2.50; protibia, 0.47; profemur, 1.00; metatibia, 0.40; metafemur, 0.87.

Description of paratypes:

Agree with type material in leg ratios and details of genitalia.

General comments:

Grylloblatta hoodalles may be distinguished from G.

rothi by the short robust legs and the general details in the description.

The type locality, near Timberline Lodge, is in an unsorted debris from an eruption thought to be less than 1000 years old (see discussion of distribution). Grylloblatta hoodalles is geographically isolated from G. rothi by the low intervening elevations of the Cascade Range. It seems to be restricted to the isolated stratovolcano (Mt. Hood), for no populations have been found between the type locality and the Three Sisters Mountains.

The species name refers to Mt. Hood in The Dalles region of the Columbia River.

Grylloblatta lavacola n. sp.

Type locality: Belknap Crater Lava Fields, 5384 feet, (T. 15S; R. 8E., U. S. Geological Survey Topographic Map, Three Sisters Quadrangle), McKenzie Pass, Mt. Washington Wilderness Area, Cascade Mountains, Oregon. Date: June 18, 1970. Collector: J. W. Kamp. Habitat: collected on snow field at night. Holotype: adult male, unaccessioned, U. S. National Museum. Allotype: adult female, same data except collected July 18, 1971, by J. M. Taylor, unaccessioned, U. S. National Museum. Paratypes: 4 adult males and 12 adult females, J. W. Kamp collection.

Description of male holotype:

Size large for genus, as large as G. s. sculleni; body

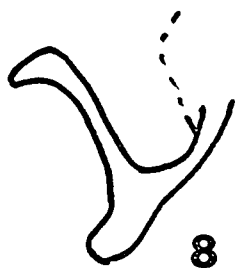
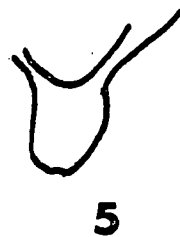
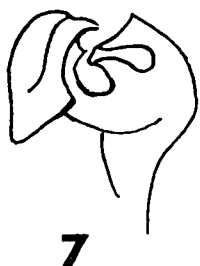
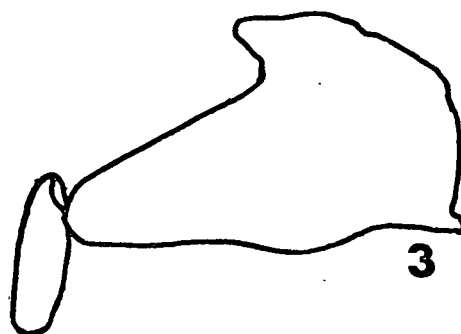
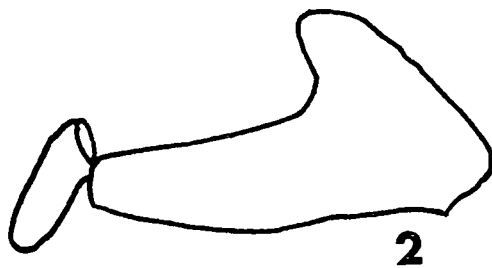
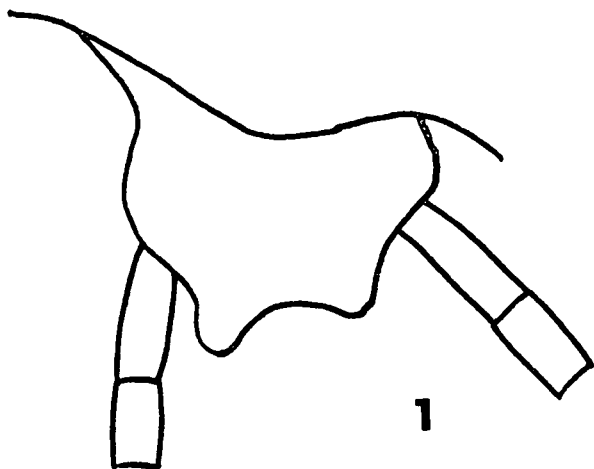
and legs densely clothed with fine pubescence; major setae less conspicuous than in G. s. sculleni; antennae longer than in G. rothi; antenna about 14.5 mm.; 34 antennal segments left, 33 right; third segment 1.2 times as long as second.

Head width equal to pronotal length; pronotum larger than in G. s. sculleni; pronotum (Fig. 32-9) with lateral margins moderately converging, more than in G. s. sculleni; dorsum of pronotum lacking rows of setae typical of G. s. sculleni; legs longer than in G. rothi; leg ratios (length divided by width): protibia, 5.72; profemur, 3.34; metatibia, 11.11; metafemur, 4.80.

Supra-anal plate (Fig. 32-1) asymmetrical to 10th abdominal tergum; left lobe on posterior margin of plate well developed, larger than in G. rothi, and right margin with lobe as long as left lobe in G. rothi; cerci about $\frac{1}{2}$ antennal length, longer than in G. rothi, and about $\frac{2}{3}$ length of G. s. sculleni; left gonocoxa wider at base than long, heavily pubescent with scattered setae, lacking in G. s. sculleni and G. rothi; right gonocoxa (Figs. 32-2,3) has general shape of that of G. rothi, anterior margin more curved than in G. rothi and much like that found in G. s. sculleni; stylus on gonocoxa borne laterally on basal third.

Principal copulatory sclerite as in Figures 32-6,7 differing in details from G. rothi; dorso-lateral lobe of sclerite shorter than that of G. rothi and expanded laterally, dorsal processes and apical lip approaching that of G. s.

Figure 32. Grylloblatta lavacola n. sp.



sculleni; secondary accessory sclerite 1 (Fig. 32-5) shorter and wider than that of G. rothi found in the Three Sisters Mountains; second accessory sclerite (Fig. 32-4) with shorter beak-like apex than in G. rothi.

Color: medium brown body; legs and antennae medium straw.

Measurements (length in mm.): pronotum, 3.40; protibia, 3.15; profemur, 3.75; metatibia, 5.00; metafemur, 5.05. Measurements (width in mm.): head, 3.35; pronotum, 2.90; protibia, 0.55; profemur, 1.30; metatibia, 0.45; metafemur, 1.05.

Description of female allotype:

Larger than G. rothi, and approaching G. s. sculleni in size; major setae well developed, but less conspicuous than in G. s. sculleni; 34 antennal segments right and left; third segment 1.2 times length of second.

Pronotum with noticeably converging lateral margins, postero-lateral margin obtuse; leg ratios (length divided by width): protibia, 7.44; profemur, 3.04; metatibia, 11.30; metafemur, 4.89.

Ovipositor: dorsal valves longer than in G. s. sculleni, without marked curvature to ventral blades; dorsal valves reaching to middle of sixth cercal segment; cerci shorter than in G. s. sculleni and each segment longer than in G. rothi.

Color: head-thorax medium brown; abdomen grayish-tan; legs light brown.

Measurements (length in mm.): pronotum, 3.45; protibia, 3.50; profemur, 3.65; metatibia, 5.10; metafemur, 4.75; ovipositor, 4.05. Measurements (width in mm.): head, 3.30; pronotum, 2.90; protibia, 0.47; profemur, 1.20; metatibia, 0.45; metafemur, 0.97.

Description of paratypes:

Agree in ratios and measurements with holotype and allotype. Do not approximate either G. rothi or G. s. sculleni from the McKenzie Pass-Three Sisters region.

General comments:

Grylloblatta lavacola occurs sympatrically with both G. s. sculleni and G. rothi in the Belknap Crater Lava fields. Grylloblatta lavacola seems to be limited to the lavas and is the most numerous species.

Grylloblatta occidentalis, Silvesteri,

Grylloblatta campodeiformis occidentalis Silvesteri,

1931 (Trans. Amer. Ent. Soc., 57:291-295)

The type locality is Mt. Baker, Washington, and it was originally described from a nymphal male. The subsequent discovery of Grylloblatta scudderi and G. skagitensis and additional material of G. c. campodeiformis shows that G. c. occidentalis is not a subspecies of G. campodeiformis. It is closely related to G. scudderi, from Garibaldi Provincial Park, British Columbia, and to G. skagitensis, from Glacier Peak, Washington. Based on the differences of male genitalia figured by Gurney (1948), number of

antennal segments, and proportional and absolute measurements, I believe this population warrants specific status as G. occidentalis.

TABLE VII

84 EXTERNAL CHARACTERS OF THE ORTHOPTEROIDS

(Modified from Giles, 1963)

No.	Character	Dermaptera	Grylloblattodea	Tettigoniidae	Gryllidae	Acrididae	Phasmida	Blattaria	Mantodea
HEAD AND NECK									
1	Ocelli absent	X	X	0	0	0	0	0	0
2	Pleurostomal sulci angulate	X	X	X	X	X	0	X	0
3	Subocular sulci	X	0	0	X	X	0	X	0
4	Epistomal sulcus complete	X	X	0	X	X	X	0	X
5	Antennal sockets near mandibular articulations	X	X	0	0	0	X	0	0
6	Antennal sulcus and anterior tentorial pit confluent	X	X	0	0	0	0	0	0
7	Tentorial body entire anteriorly	X	X	X	X	X	X	0	0
8	Tentorial body imperforate	X	X	X	X	X	X	0	0
9	Tentorial body elongate	X	X	0	X	X	0	0	0
10	Anterior tentorial arms twisted	X	X	0	X	0	0	X	0
11	Dorsal tentorial arms stout	X	X	0	X	X	X	0	0
12	Tentorial maculae near eyes	X	0	0	0	0	X	0	0
13	Dorsal tentorial arms arise from body	X	X	0	X	0	0	X	X

14	Antennae short	X	X	0	0	X	X	0	0
15	Tip of labrum membranous	X	X	0	X	0	X	X	X
16	Mandibles with two apical teeth	X	X	0	0	0	0	0	0
17	Membranous area basally on inner edge of mandibles	X	X	X	X	X	X	0	0
18	Lacinia with two apical teeth	X	0	0	0	0	X	X	X
19	Galea cylindrical	X	X	X	X	0	0	0	0
20	Maxillary palps not membranous distally	X	X	0	0	0	X	0	X
21	Labrostipes mesially divided	X	X	0	0	0	0	X	X
22	Paraglossae cylindrical	X	X	0	0	0	0	0	0
23	Labial palps sclerotized distally	X	X	0	0	0	X	0	X
24	Dorsal cervical sclerite	X	0	X	X	0	X	X	X
25	Anterior ventral cervical sclerite narrow	X	0	0	0	0	0	X	X
26	Posterior ventral cervical sclerite wide	X	0	0	0	X	0	0	0
27	Posterior lateral cervical sclerites	X	X	0	0	X	X	X	X
28	Posterior lateral cervical not articulated with prothorax	X	0	X	X	0	0	0	0

THORAX

PROTHORAX

Pleural Regions

29	Generally well sclerotized	X	X	0	0	0	0	X	X
30	Cryptopleury absent	X	0	0	0	0	X	X	X
31	Pleural apophysis fused to sternal apophysis	X	0	0	0	X	0	X	0
32	Pleuro-coxal articulation an- terior to trochantino-coxal	X	X	0	0	0	0	X	X
33	Anterior edge of trochantin rolled	X	X	X	0	0	0	0	X
34	Accessory coxal plate	X	0	X	X	X	0	X	0
35	Postpleural sclerite	X	0	0	X	0	X	X	X

Sternum

36	Presternum absent	X	X	0	0	0	X	X	X
37	Sternellum	X	0	X	X	X	X	X	X
38	Sternacostal suture absent	X	X	0	X	0	0	X	0
39	Separate sclerites for pits	X	X	0	0	0	0	0	0
40	Separate spinasternite	X	X	X	X	0	0	X	0
41	Spina smaller than meso- thoracic spina	X	X	X	X	X	X	0	0

Leg

42	Coxae of each segment wide apart	X	X	X	0	X	X	0	0
43	Coxae wider than long	X	0	X	X	X	X	0	0
44	Three tarsal segments on all legs	X	0	0	0	0	0	0	0

MESOTHORAX

Tergum

- 45 Phragmata absent or very
 small X X 0 X 0 0 X X
- 46 Tegmina X 0 X X X X X X

Pleural Regions

- 47 Pleural apophysis joined by
 muscle to sternal apophysis X X X 0 0 X X X
- 48 Pleuro-coxal articulation an-
 terior to trochantino-coxal X X X X X 0 0 X
- 49 Anterior edge of trochantin
 rolled X X X X X 0 0 X
- 50 Precoxale a separate sclerite X X 0 X 0 X X X
- 51 Accessory coxal plate X 0 0 X X X X 0
- 52 Peritremal sclerite absent X 0 X X 0 0 0 0
- 53 Postpleural sclerite X 0 0 0 0 X X X

Sternum

- 54 Sternellum absent X X 0 0 0 0 0 0
- 55 Sternacostal suture absent X X X X 0 0 0 0
- 56 Separate spinasternite X X 0 0 0 0 X 0

Leg

- 57 Mesothoracic and metathoracic
 coxae wider than long X X X X X X 0 0

METATHORAX

Tergum

- 58 Phragmata large X 0 X X X X 0 X

Pleural Regions

- 59 Episternum and epimeron
 nearly horizontal X X 0 0 0 0 0 0
- 60 Pleural ridge without
 apophysis X 0 0 0 0 0 0 0
- 61 Pleuro-coxal articulation pos-
 terior to trochantino-coxal X 0 X X X X 0 0
- 62 Anterior edge of trochantin
 rolled X X X X X X 0 X
- 63 Precoxale fused with
 basisternum X 0 0 0 0 0 0 0
- 64 Accessory coxal plate X 0 0 X 0 X X 0

Sternum

- 65 Two sternal pits X X 0 0 X 0 X 0

Leg

- 66 Roughly same length as front
 and middle legs X X 0 0 0 X X X

GENERAL

- 67 Sterna overlap: pro-/meso-/
 metasternum X X 0 0 0 0 X 0

- 68 Intersegmental sclerites
 small X X X X X X X X

ABDOMEN

GENERAL

- 69 Abdomen dorso-ventrally
 compressed X X 0 0 0 X X X

Tergum

- 70 Antecosta forms distinct
ridge X X 0 0 0 X 0 0

Pleural Regions

- 71 Entirely membranous X X X X X 0 0 0
72 Spiracles in membrane X X X X 0 0 0 0

PREGENITAL SEGMENTS

Segment 1, ♂ and ♀

- 73 Tergum I has large phragmata X 0 X 0 X X 0 0
74 Tergum I smaller than other
terga X 0 X X 0 0 X X
75 Sternum I absent X 0 0 0 0 0 0 0
76 Pleural regions membranous X X 0 0 0 0 X X
77 Spiracle I largely surrounded
by tergum I X 0 0 0 X 0 X X

GENITAL SEGMENTS

Segment 9, ♂

- 78 Tergum IX approximately size
of generalized tergum X X 0 0 0 X 0 0
79 Styli absent from subgenital
plate X X 0 X X X 0 0

Segment 7, ♀

- 80 Sternum 7 is long subgenital
plate X 0 0 0 0 0 X X

Segment 8, ♀

- 81 Pleural region membranous X X X X X 0 0 0

POSTGENITAL SEGMENTS

Segment 10, ♂ and ♀

82 Tergum X large, well

sclerotized

X X X X 0 X 0 0

Paraprocts

83 Well sclerotized, conspicuous

plates

X 0 0 X X X X X

Epiproct

84 Well sclerotized

X 0 0 X X X 0 0

TABLE VIII

80 EXTERNAL AND INTERNAL CHARACTERS OF THE ORTHOPTEROIDS
(Modified from Blackith and Blackith, 1968)

No.	Character	Dermaptera	Grylloblattodea	Tettigoniidae	Gryllidae	Acrididae	Phasmida	Blattaria	Mantodea
HEAD AND NECK									
1	Fewer than 30 antennal segments present	X	0	0	0	X	0	0	0
2	Lateral ocelli present in apterous	0	0	0	X	0	0	X	X
3	Frontal suture absent	X	0	X	0	0	0	0	0
4	Post frontal suture absent	0	X	X	X	X	0	X	0
5	Epistomal suture absent	0	0	0	0	0	0	X	0
6	Subantennal suture absent	X	X	X	X	0	X	0	X
7	Subocular suture absent	0	X	X	0	0	0	0	X
8	Genoepicranial suture absent	0	X	0	X	X	0	X	X
9	Keel on hypopharynx present	0	0	0	0	X	0	0	0
10	Mesal hook on torma absent	0	0	0	0	X	0	0	0
11	Superlinguae absent	0	0	X	X	X	X	X	X
12	Salivary cup impactor present	0	0	0	0	X	0	0	0
13	Glossae not well developed	X	0	0	0	X	0	X	X
14	Dorsal sclerites on cervix absent	0	X	X	0	X	X	0	0

15	Ventral sclerites on cervix								
	absent	0	0	0	0	X	X	0	0
	THORAX AND LEGS								
16	Pleurosternal suture absent								
	in adult	0	0	0	0	X	0	0	0
17	Mesal prosternal process								
	present	0	X	0	0	0	0	0	0
18	Trochantin in metathorax								
	absent	0	0	X	0	0	X	0	0
19	Dorsal tibial spur or spurs								
	present on hind legs	0	0	0	X	X	0	X	0
20	Ventral tibial spur or spurs								
	present	0	X	X	X	X	0	X	X
21	Hind tarsi with fewer than								
	4 segments	X	0	0	X	X	0	0	0
22	Hind tarsi with fewer than								
	5 segments	X	0	X	X	X	0	0	0
23	Arolia present	0	0	0	0	X	X	X	0
24	Brunner's organ present	0	0	0	0	X	0	0	0
25	Tympanum present on fore								
	tibia	0	0	X	X	0	0	0	0
	ABDOMEN AND GENITALIA								
26	Dorsal sulcus well developed	0	0	0	0	0	0	0	0
27	Spiracles not in tergites	X	X	X	X	0	X	X	X
28	Cerci unsegmented	X	0	X	X	X	X	0	0
29	Lateral apodemes present on								
	sternites	X	0	0	0	X	0	0	0

30	Tympanum present on first segment	0	0	0	0	X	0	0	0
31	Dorsal pouch present	0	0	0	0	X	0	0	0
32	Male genitalia strongly asymmetric	X	X	0	0	0	0	X	X

MUSCULAR CHARACTERS HEAD AND NECK

33	Labial retractor absent	0	0	0	0	X	0	0	0
34	No muscles attached to ventral cervical sclerites of membrane	0	0	0	0	0	X	0	X

THORAX AND LEGS

35	Crossed prosternals to first cervical sclerites present	0	X	X	X	X	0	0	X
36	Tergopleurals in meso or metathorax absent	0	0	X	X	X	0	0	0
37	Lateral intersegmentals in prothorax absent	0	0	0	0	0	0	0	X
38	Lateral intersegmentals in meso or metathorax absent	0	0	X	0	X	0	0	0
39	Muscle joining meso and metapophyses present	X	X	X	X	X	0	X	X
40	Ventral transverse furcals absent	X	0	X	X	X	0	X	X
41	Reducers of fore femora not well developed	0	0	0	0	0	X	0	0

ABDOMEN AND GENITALIA

42	Two spiracular muscles								
	present	X	0	X	X	X	0	X	X
43	Antagonistic muscle arising								
	from sternum	X	0	X	X	X	0	0	0
44	Transverse sternals on								
	anterior segments absent	X	X	0	0	0	X	X	X
45	Paradorsal present	0	0	0	0	X	0	0	0
46	Sternopleurals absent	X	0	0	0	0	X	X	X
47	Tergopleurals absent	X	0	X	0	X	0	X	0
48	No muscles joining sternite or								
	pleural sclerite to tergite								
	cephalad	X	0	X	X	X	X	0	0
49	Tergosternals in 2 or more								
	bands	X	X	X	0	X	0	0	X
50	Internal longitudinal tergals								
	banded	X	0	0	0	X	X	0	X
51	Alary muscles not more than								
	10	0	0	0	0	X	0	0	0
52	Alary muscles not more than								
	11	X	0	0	X	X	X	0	0
NEURAL CHARACTERS									
53	Posterior recurrent nerve								
	single	X	X	0	0	0	X	X	X
54	Mandibular nerves close to								
	circumesophageal								
	connectives	X	X	X	X	X	X	0	0

55	Corpora allata large and separate from subesophageal ganglion	0	0	X	X	X	0	X	X
56	More than 1 abdominal ganglion fused to third thoracic ganglion	0	0	0	X	X	0	0	X
57	More than 2 abdominal ganglia fused to third thoracic ganglion	0	0	0	0	X	0	0	X
58	Not more than 4 abdominal ganglia free	0	0	0	0	0	0	0	X
59	Not more than 5 abdominal ganglia free	0	0	0	X	X	0	0	X
60	Not more than 6 abdominal ganglia free	0	0	X	X	X	X	X	X
61	Circumesophageal connectives pass through hole in body of tentorium	0	0	0	0	0	0	X	X

INTESTINAL CHARACTERS

62	Intima of proventriculus without 6 longitudinal folds	0	X	0	0	0	X	0	0
63	Neck of proventriculus not tubular	0	0	0	0	0	0	X	X
64	Proventriculus globular in part	0	X	X	X	0	0	0	0

65	V-shaped plates in cardiac valve	0	0	0	0	X	0	0	0
66	Gastric caeca two or more	0	X	X	X	X	0	X	X
67	Gastric caeca six or more	0	0	0	0	X	0	X	X
68	Gastric caeca eight or more	0	0	0	0	0	0	X	X

OTHER CHARACTERS

69	Phytophagous insects of elongate form	0	0	0	0	0	X	0	0
70	Segmental vessels in thorax present	0	0	0	0	0	0	X	0
71	Ovariolo ligaments arise in thorax	X	X	0	0	X	0	0	X
72	Paired incurrent ostia absent in thorax	0	0	0	0	0	X	0	0
73	Fewer than 3 incurrent ostia in thorax	X	X	X	X	0	X	0	0
74	Phagocytic organs present in abdomen	0	0	X	X	0	0	0	0
75	Segmental vessels present in abdomen	0	0	0	0	0	0	X	X
76	Ovariolo ligaments arise in abdomen	0	0	X	X	0	X	0	0
77	Male accessory glands few (less than 15 pairs) and not convoluted	0	X	0	0	0	X	0	0
78	Testis confined to terminal segments	0	0	0	0	0	0	0	X

79	Ootheca formed	0	0	0	0	X	0	X	X
80	Subgenital plate in female	X	0	X	X	X	X	X	X