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Title: THE LEAFHOPPER GENUS GIPRUS  
(HOMOPTERA:CICADELLIDAE)

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Abstract approved: \_\_\_\_\_  
Paul Oman

Members of the deltocephaline leafhopper genus Giprus Oman live on grasses, primarily in the desert-scrub, chaparral, and marine sand dune communities of western North America. Of 16 known species, 10 are undescribed. Recharacterization of the genus results in exclusion of Laevicephalus incongruus Oman. Differentiation of species is primarily dependent on male genital structures; characterization of species is through illustration, verbal description, and a diagnostic key. Intraspecific variation noted is primarily of two types: size and color variation in two dune-inhabiting species, and variation in shape and size of accessory aedeagal processes of G. siskiyou (Oman). The fifth instar nymph of Giprus is characterized. It is concluded that the distributional patterns of the Oregon species of Giprus are not determined by host associations.

The Leafhopper Genus Giprus  
(Homoptera:Cicadellidae)

by

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## TABLE OF CONTENTS

INTRODUCTION	1
MATERIALS AND METHODS	4
GENERIC CHARACTERISTICS	9
RELATIONSHIP TO OTHER GENERA	11
MORPHOLOGICAL DIFFERENTIATION AND COMPARISON OF SPECIES	13
INFRASPECIFIC VARIATION	20
KEY TO SPECIES	29
DESCRIPTIONS OF SPECIES	33
DISTRIBUTION, HABITAT, AND HOST PLANTS	51
LIFE CYCLE	64
PHYLOGENY WITHIN <u>GIPRUS</u>	68
FUTURE AREAS OF RESEARCH	72
ILLUSTRATIONS	73
BIBLIOGRAPHY	85
APPENDIX	88
INDEX TO GENERA AND SPECIES	89

## LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Ratio of head width (W) to head length (L) for all species of <u>Giprus</u>	19
2. Lengths of <u>Giprus</u> W and <u>Giprus</u> P.	22
2a. Mean length of <u>Giprus</u> W at 4.0 km N Waldport 1967-1971.	22
2b. Mean length of <u>Giprus</u> W at each site in 1971.	22
2c. Mean length of <u>Giprus</u> P at each site in 1971.	22
3. Species groups of <u>Giprus</u> based on the structure of the male genitalia.	69
4. <u>Giprus siskiyou</u> : forewing	77
5. <u>Giprus</u> M : fifth instar nymph	77
6. <u>Giprus siskiyou</u> : head	77
7. <u>Giprus</u> W : head	77
8. <u>Giprus</u> C : female 7th sternum	78
9. <u>Giprus cinerosus</u> : female 7th sternum	78
10. <u>Giprus</u> R : female 7th sternum	78
11. <u>Giprus</u> T : female 7th sternum	78
12. <u>Giprus</u> S : female 7th sternum	78
13. <u>Giprus joaquinus</u> : female 7th sternum	78
14. <u>Giprus</u> M : female 7th sternum	78
15. <u>Giprus angelus</u> : female 7th sternum	78
16. <u>Giprus</u> V : female 7th sternum	78

<u>Figure</u>		<u>Page</u>
17	<u>Giprus pacificus</u> : female 7th sternum	78
18	<u>Giprus</u> W ; female 7th sternum	79
19	<u>Giprus</u> G : female 7th sternum	79
20	<u>Giprus</u> P : female 7th sternum	79
21	<u>Giprus siskiyou</u> : female 7th sternum	79
22	<u>Giprus cartwrighti</u> : female 7th sternum	79
23	<u>Giprus siskiyou</u> : male genital capsule	79
24	<u>Giprus</u> W : male genital capsule	79
25	<u>Giprus</u> R : male genital capsule	79
26	<u>Giprus</u> V : male genital capsule	79
27	<u>Giprus cartwrighti</u> : male genital capsule	79
28	<u>Giprus cinerosus</u> : connective and aedeagus	80
29	<u>Laevicephalus sylvestris</u> (Osborn & Ball) : connective and aedeagus	80
30	<u>Laevicephalus incongruus</u> : connective, style, and aedeagus	80
31	<u>Giprus siskiyou</u> (Mt. Shasta, California) : connective, style, and aedeagus	80
32	<u>Giprus siskiyou</u> (15 miles NE Alturas, California): connective, style, and aedeagus	81
33	<u>Giprus siskiyou</u> (Cliffdell, Washington): connective, style and aedeagus	81
34	<u>Giprus siskiyou</u> (11 miles E Frenchglen, Oregon) : connective, style, and aedeagus	81
35	<u>Giprus</u> W : connective, style, and aedeagus	81

<u>Figure</u>		<u>Page</u>
37	<u>Giprus joaquinus</u> : connective, style, and aedeagus	81
38	<u>Giprus</u> D : connective, style, and aedeagus	82
39	<u>Giprus angelus</u> : connective, style, and aedeagus	82
40	<u>Giprus</u> V : connective, style, and aedeagus	82
41	<u>Giprus</u> P : connective, style, and aedeagus	82
42	<u>Giprus</u> M : connective, style, and aedeagus	82
43	<u>Giprus</u> S : connective, style, and aedeagus	82
44	<u>Giprus</u> T (Tehachapi Pass, California) : connective, style, and aedeagus	83
45	<u>Giprus</u> T (Mill Valley, California) : connective, style, and aedeagus	83
46	<u>Giprus pacificus</u> : connective, style, and aedeagus	83
47	<u>Giprus</u> C : connective, style, and aedeagus	83
48	<u>Giprus</u> R : connective, style, and aedeagus	83
49	<u>Giprus cinerosus</u> : connective, style, and aedeagus	83
50	<u>Giprus cartwrighti</u> : connective, style, and aedeagus	83
51-67	<u>Giprus siskiyou</u> (3 miles S Weed, California) : apex of aedeagus	84
68-87	<u>Giprus siskiyou</u> (36 miles E Klamath Falls, Oregon): apex of aedeagus	84



## LIST OF TABLES

<u>Table</u>		<u>Page</u>
1.	Summary of length data for all species of <u>Giprus</u>	21
2.	Climatic data for recording stations closest to collecting sites of <u>Giprus</u> V, <u>Giprus</u> M and <u>G. siskiyou</u>	56
3.	Climatic data for selected Pacific Coast recording stations.	60
4.	Dates of collection of <u>Giprus</u> W at Waldport (all years).	65
5.	Collection of <u>Giprus</u> by week.	66

THE LEAFHOPPER GENUS GIPRUS  
(HOMOPTERA:CICADELLIDAE)

INTRODUCTION

Members of the genus Giprus (Oman) are slender, small to medium-sized leafhoppers, cinereous to amber in color, and frequently with blackish-brown markings on the wings and head. They inhabit western North America, occurring in climatic zones ranging from coastal to continental at latitudes from 32° N to 47° N at elevations from sea level to 1981 m. The genus is associated with various species of grasses, usually in chaparral, desert scrub, or sagebrush communities. Giprus is placed in the Subfamily Deltocephalinae, Tribe Deltocephalini. It is a member of that group of deltocephaline leafhoppers characterized by a linear connective and an articulation between the connective and the aedeagus and is closely related to several other grassland genera (Laevicephalus DeLong, Lemellus Oman, Sorhoanus Ribaut, Verdanus Oman, and Cazenus Oman).

This study summarizes present knowledge of the taxonomy, distribution, biology, and ecology of Giprus. It identifies areas where further study is needed in order to understand the phylogeny of the group and the factors responsible for the evolution of a large number of species in a relatively small geographic area.

Taxonomic literature dealing with members of the genus Giprus

provides an excellent illustration of the gradual restriction of generic concepts in the Cicadellidae which has occurred in the past half century. The first known species was described by Van Duzee (1892) as Deltocephalus cinerosus. At that time, the genus Deltocephalus Burmeister was a large, poorly defined group containing many diverse elements. DeLong (1926), recognizing the need to divide Deltocephalus into compact, more easily definable groups, erected a number of subgenera. The subgenus Laevicephalus, in which D. cinerosus was placed, was distinguished by its wing venation, color, curvature of the vertex, and the angle of the vertex and the front. When Laevicephalus was elevated to generic status in 1929 by DeLong and Slesman, it was noted that the genus contained species with a great diversity of genitalic structures. In 1937 Oman recognized and characterized, primarily on the basis of the male genitalia, a "cinerosus group" of Laevicephalus which included L. cinerosus and five additional species: L. angelus Oman, L. pacificus Oman, L. joaquinus Oman, L. siskiyou Oman, and L. incongruus Oman. In 1949 Oman removed the "cinerosus group" and L. cartwrighti, which he had described in 1932, from Laevicephalus and erected the genus Giprus to contain them.

Although no significant contributions to our knowledge of Giprus have been made since 1949, numerous studies of the leafhopper fauna of the grasslands of Europe and Asia by Emel'yanov (1964) and others

have produced no evidence that Giprus occurs outside the Nearctic region. The discovery of what appeared to be a series of new species of Giprus in 1968-69 led to renewed interest in the genus. The questions arose as to whether the previously held concept of species as applied to Giprus was too narrow and as to whether these new forms were discrete species or extreme infraspecific variants of other species. This study was undertaken in order to gain a better understanding of the circumscription of species in Giprus and in part involved a study of infraspecific variation to determine the range of variation that could be expected within a population. An attempt was also made to determine the factors responsible for the apparently limited distribution of some of the species. As preliminary investigations had suggested that different species of Giprus were collected from different species of grasses, it was initially postulated that the distribution of each species of Giprus might be dependent upon the distribution of the grass on which it fed, and that each species had a single grass species as host.

## MATERIALS AND METHODS

Over 3,000 specimens, including one holotype and 87 paratypes of seven species, were examined during the course of this study. Most specimens were collected specifically for this project by Paul Oman, Chandra Viraktamath, and Jane Sawbridge. Other sources of specimens were the United States National Museum of Natural History, California Academy of Sciences, University of Kansas, University of Arizona, and the University of California at Davis.

Field work was undertaken with several main objectives. As it was deemed desirable to obtain large samples of populations at each collection site to permit studies of infraspecific variation, samples of 50 or more specimens were taken whenever possible on each visit to a site. Field work was also necessary in order to obtain first hand knowledge of habitats and to determine host associations. A result rather than a primary objective of the field work was a greatly improved knowledge of the distribution of the genus and the addition of several new species. G. siskiyou was studied by making a north-south transect (170 km; 12 sites) between Mt. Ashland, Oregon and 54.7 km north of Redding, Shasta County, California and an east-west transect (233 km; 14 sites) between Cedarville, Modoc County, California and Klamath River, Siskiyou County, California. The purpose of this method of sampling was to

determine whether previously observed variation in G. siskiyou was topoclinal or ecoclinal in nature.

I examined habitats of G. siskiyou, G. cartwrighti, and Giprus species R, V, T, P, W, S, G, and M. Habitats of the remaining species, except for that of Giprus D were examined by Dr. Oman. Deductions regarding habitat associations were based on large samples where possible. When only one site was observed or when a site from which only a few specimens were collected is described, the limitations of the data are noted. Host associations were determined by selective sweeping of grass inflorescences. Grasses from which Giprus was taken were sampled at each collection site. They were dried, mounted on heavy paper, and identified using Hitchcock (1950). In addition, color photographs were taken of the general habitat and host plants in many localities.

Annual precipitation, mean July maximum temperature, and mean January minimum temperature are given for the recording stations nearest to sites where Giprus was collected. As records were not taken at actual collection sites, the available climatic data indicate only general conditions in a given area.

Most adult specimens were preserved dry and mounted on points; some were initially preserved in alcohol, then processed with cellosolve (24 hours) and xylene (2 hours) before being dried and mounted on points. A few adults and most nymphs were

preserved in alcohol and not mounted.

Genitalia were prepared for study by teasing the abdomens from the insects with two microdissecting needles, then heating the abdomens in 10% KOH for approximately five minutes until the KOH was just below the boiling point. They were then rinsed in water before being transferred to glycerine for observation, dissection, and storage. The styles, connective, and aedeagus were removed from the genital capsule for close examination by severing the dorsal attachment of the aedeagus to the tenth segment and the ventral attachments of the styles to the plates. The seventh sternum of the female was removed from the rest of the abdomen for detailed examination. Cleared and dissected abdomens were stored in plastic microvials attached below the insect on the pin.

A micrometer disc ruled in 0.1 mm squares, placed in an ocular of a stereoscopic microscope and drawing paper with a 1/2 inch square grid were used to prepare drawings. Anatomical details were checked with a compound microscope at 150 x. Internal male genitalia and the female seventh sternum were magnified 50 x for drawing; male plates were drawn from dry specimens at 30 x. The wing was removed from the insect, placed between two glass slides, and drawn at 30 x. Details of venation were checked with a compound microscope at 150 x. All drawings of homologous structures were made to the same scale. Drawings of the internal male genitalia

show a dorsal view of the connective, aedeagus, and left style; the right style is omitted. In addition, a lateral view of the aedeagus as seen from the left side is shown.

Measurements were made with an American Optical Filar Micrometer Model No. 426. Total body length was measured as the distance from the apex of the crown to the wing tips. Median length of the head and its width immediately anterior to the eyes were measured and the ratio of width (W) to length (L) computed for each individual in a sample. The mean of the W/L values for a sample (usually 10 of each species) was computed and assigned as the W/L value for the species.

The aedeagi of specimens of G. siskiyou collected at many sites over several years were compared in a study of infraspecific variation in that species. In order to determine the amount of infraspecific variation present in a population at a given time, individuals in series collected at a single site on the same day were compared. Two such samples were studied, one from near Weed, California, in the north-south transect and one from near Bly, Oregon in the east-west transect. Infraspecific variation in G. siskiyou was documented by drawings.

Comparative morphology was used as the primary basis for classification and species discrimination; field observation of populations was used as additional evidence to supplement and reinforce



conclusions.

Holotypes are or will be deposited in the United States National Museum of Natural History, except where otherwise indicated in connection with the species descriptions. All specimens designated as paratypes of new species were collected on the same day and at the same locality as the holotype.

## GENERIC CHARACTERISTICS

The external morphology of species of Giprus is sufficiently distinctive to allow easy differentiation of the genus from most other species of related genera.

The head is approximately twice as long medially as the shortest distance between the eyes, giving the head a more or less pointed appearance which is accentuated by oblique blackish-brown dashes on each anterolateral submargin of the crown. Other pigmentation may be present in varying degrees on the crown and pronotum. The ratio of the head width immediately anterior to the eyes to the median length of the head is between 1.20 and 1.30 in most species.

Significant wing characters are the small appendix, inner anteapical cell usually closed basally, and the central anteapical cell usually constricted (Figure 4). Wings are transparent with ground color cinereous to amber in all species except G. cartwrighti which has a greenish-gold ground color. In most species, at least some individuals have blackish-brown markings within the borders of the wing cells.

Members of the genus Giprus range from 2.80 mm to 4.82 mm in length with the majority of representatives of each species between 3.50 mm and 4.50 mm long. Males tend to be slightly smaller than females although there is frequently an overlap so that the smallest

female in a sample may be smaller than the largest male.

Important internal and external characters of the genitalia include heavily setose pygoferes, broad male plates, a large triangular valve, an aedeagus with a basal submembranous hoodlike extension for attachment to the tenth segment, and an aedeagal shaft arising from a point dorsad of the point of articulation of the phallobase and the connective. The seventh sternum of the female has a median incision and two pairs of dentate projections on the posterior margin.

Fifth instar Giprus nymphs (Figure 5) are cream colored with extensive light brown to blackish-brown markings on the head, pronotum, wing pads, and abdominal dorsum. The abdominal venter has fewer dark markings. The eyes, head, and body of nymphs frequently have a reddish tinge.

## RELATIONSHIP TO OTHER GENERA

While Oman (1949) placed Giprus in close association with Lemellus, Sorhoanus, Verdanus, Cazenus, and Laevicephalus, it most closely resembles Laevicephalus and the two are probably derived from a common ancestor. Many of the external characters used to differentiate between Laevicephalus and Giprus are actually found to some extent in both genera. The only character which will unequivocally discriminate between Giprus and Laevicephalus is the structure of the aedeagus. In Giprus, the connective is articulated with a ventral projection of the phallobase and the aedeagal shaft extends posteriorly from the phallobase dorsad to the point of articulation with the connective (Figure 28), whereas in Laevicephalus the articulation of the connective and the phallobase is directly in line with the aedeagal shaft (Figure 29).

Comparison of aedeagi allows easy discrimination of Giprus from other closely related genera. Lemellus has an asymmetrical aedeagal shaft while a symmetrical aedeagal shaft is present in all Giprus. Sorhoanus, Verdanus, and Cazenus are similar to Laevicephalus in having the aedeagal shaft directly in line with the point of articulation between the connective and the phallobase. Psammotettix is externally similar to Giprus and may be confused with it when representatives of both genera occur together as in the

coastal sand dunes and in southern Oregon. By recourse to genitalic characters, they are easily separated as Psammotettix has a connective longer than the aedeagus. The male plates and female seventh sternum are also distinctive.

Laevcephalus incongruus, a species which Oman (1949) placed in Giprus, has several characteristics which make it atypical of Giprus; it is conspicuously larger than members of the genus Giprus; the posterior margin of the female seventh sternum is emarginate; and most significantly, the structure of the aedeagus is unlike that of species of Giprus (Figure 30). The aedeagus of L. incongruus is more like that of Laevcephalus than that of Giprus, as the point of articulation of the connective and the phallobase is directly opposite the shaft of the aedeagus. For this reason, I am removing L. incongruus from Giprus and returning it to Laevcephalus.

## MORPHOLOGICAL DIFFERENTIATION AND COMPARISON OF SPECIES

A number of morphological characters have been examined for their usefulness in discriminating between species of Giprus.

Male genital plates of Giprus do not show characters which allow easy species differentiation as their shape, size, and alignment may be similar for several species which have markedly different internal structures. G. cartwrighti, the only species to have plates which are distinct enough to be unmistakable, has elongate, gradually tapering plates with acute, diverging apices (Figure 27). The other fifteen species can be grouped according to three plate types. The type characteristic of most species is that in which the plates are contiguous for their entire length and have acute apices (Figure 23). Those species with this plate formation are G. angelus, G. pacificus, G. joaquinus, G. siskiyou, and Giprus species M, P, S, and T. The second type is that in which the plates are broadly rounded, contiguous for only part of their length, diverging posteriorly, and abruptly narrowing in some to acute apices (Figure 25). Species in this category are G. cinerosus and Giprus species C, R, and D. Three species are intermediate with respect to plate characteristics. Giprus W (Figure 24) and Giprus G have broadly rounded plates which are contiguous for half their length and which then separate and gradually

taper posteriorly to form acute apices. Giprus V (Figure 26), while basically similar to Giprus W and Giprus G, differs from them in that the plates are contiguous almost to the apex and the apices are sub-acute and only slightly divergent.

In Giprus, interspecific variation is most evident in the internal male genitalia, especially the aedeagus. Length, curvature, and thickness of the shaft, and position and number of paired processes must be considered. Six species, G. cinerosus (Figure 49), G. pacificus (Figure 46), Giprus C (Figure 47), Giprus R (Figure 48), Giprus S (Figure 43), and Giprus T (Figures 44, 45), have a pair of elongate processes at some point on the shaft. This group can be further divided into three subgroups: G. cinerosus and Giprus R with three pairs of processes and a long straight aedeagus; G. pacificus and Giprus C with two pairs of processes of which the elongate pair originates considerably basad of the apex, and with a thickened or slightly sinuate aedeagal shaft; and Giprus S and Giprus T with the elongate processes originating at or near the apex of the aedeagus. A second group is associated because the aedeagus is relatively short and stout, each has more than one pair of aedeagal processes, all pairs of processes are short, and there is some tendency toward enlargement of the aedeagal apex. G. angelus (Figure 39), Giprus M (Figure 42), Giprus V (Figure 40), and Giprus P (Figure 41) belong in this group. Several species have a single

pair of processes or have two pairs of very short processes. G. joaquinus (Figure 37), Giprus D (Figure 38), Giprus W (Figure 36), Giprus G (Figure 35), and G. siskiyou (Figures 31, 32, 33, 34) belong in this group. G. siskiyou differs from all other species of Giprus in that it possesses a pair of lateral flanges basad of the dorsal processes. G. cartwrighti (Figure 50), while possessing only one pair of minute aedeagal processes, has a sinuate aedeagus found in no other Giprus species and for this reason is placed in a group by itself. Slightly decurved aedeagal shafts occur in Giprus W and Giprus joaquinus while Giprus D has an extremely decurved aedeagal shaft.

The styles are basically similar in all species of Giprus. Differences are most noticeable in the shape of the tips and their size relative to the style as a whole. The number of teeth on the style tips is variable even between sides of the same specimen. Style tips that are fairly broad and flat with the teeth in a straight or almost straight line are the most common type and occur in G. cinerosus, G. pacificus, G. joaquinus, and Giprus species T, R, C, W, and P.

The structure of the posterior margin of the seventh sternum of the female has been used by many workers in delimiting genera and species of deltocephaline leafhoppers. It is not a useful specific character for Giprus because several species have an almost



identical posterior margin to the seventh sternum. External examination of the female seventh sternum of dried specimens results in positive identification of species in only two instances: G. cartwrighti (Figure 22) can be recognized because the posterior margin of the seventh sternum is semi-circular in shape and the median incision is short and narrow; G. joaquinus (Figure 13) is the only species to have the posterior margin of the seventh sternum elongate medially so that its median length is about three times that at the lateral margin. All other species of Giprus (Figures 8-12, 14-21) appear so similar externally that it is impossible to identify them by the shape of the seventh sternum.

A search for characters useful for species differentiation of female specimens led to study of the structure of the dorsal extension of the seventh sternum. Readio (1922, p. 219), in describing the genitalic structure of female Cuerna costalis (Fabricius) (as Oncometopia lateralis) noted that

Dorsad of the sternum of segment seven is an invaginated pocket in which the bases of the valves of the ovipositor are located. Its ventral side is formed by the apical portion of the seventh sternum and a membrane arising from the dorsal surface of this sclerite and extending cephalad to its base. The dorsal side of the pocket is formed by a membrane which is continuous with the membrane of the ventral side, and which extends caudad to the eighth sterna with which it connects. The greater part of this dorsal membrane is strongly chitinized, but medially it is apparently divided by a narrow, clear line which expands apically into the entirely membranous apex connecting with the eighth sterna. Laterally this pocket is bounded by the

continuation of the dorsal membrane to the seventh and eighth pleura. The anterior portions of these lateral membranes are strongly chitinized and curve mesad ventrally.

A similar condition appears to exist in Giprus. The dorsal extension of the seventh sternum appears to be a single sclerotized structure in some species and a pair of such structures loosely held together by a membrane in others. The dorsal extension is attached to the ventral portion of the seventh sternum posteriomedially between the outer pair of dentate projections. The posterior portion of the ventral part of the seventh sternum is unpigmented; the heavily sclerotized dorsal extension gives the posterior margin of the seventh sternum its characteristic color pattern. So far the dorsal extension of the seventh sternum appears to be useful only in separating the externally similar G. angelus (Figure 15) females from female G. cinerosus (Figure 9), Giprus T (Figure 11), Giprus R (Figure 10) and Giprus C (Figure 8). G. angelus is the only one of these southern California species to have a fused dorsal extension of the seventh sternum.

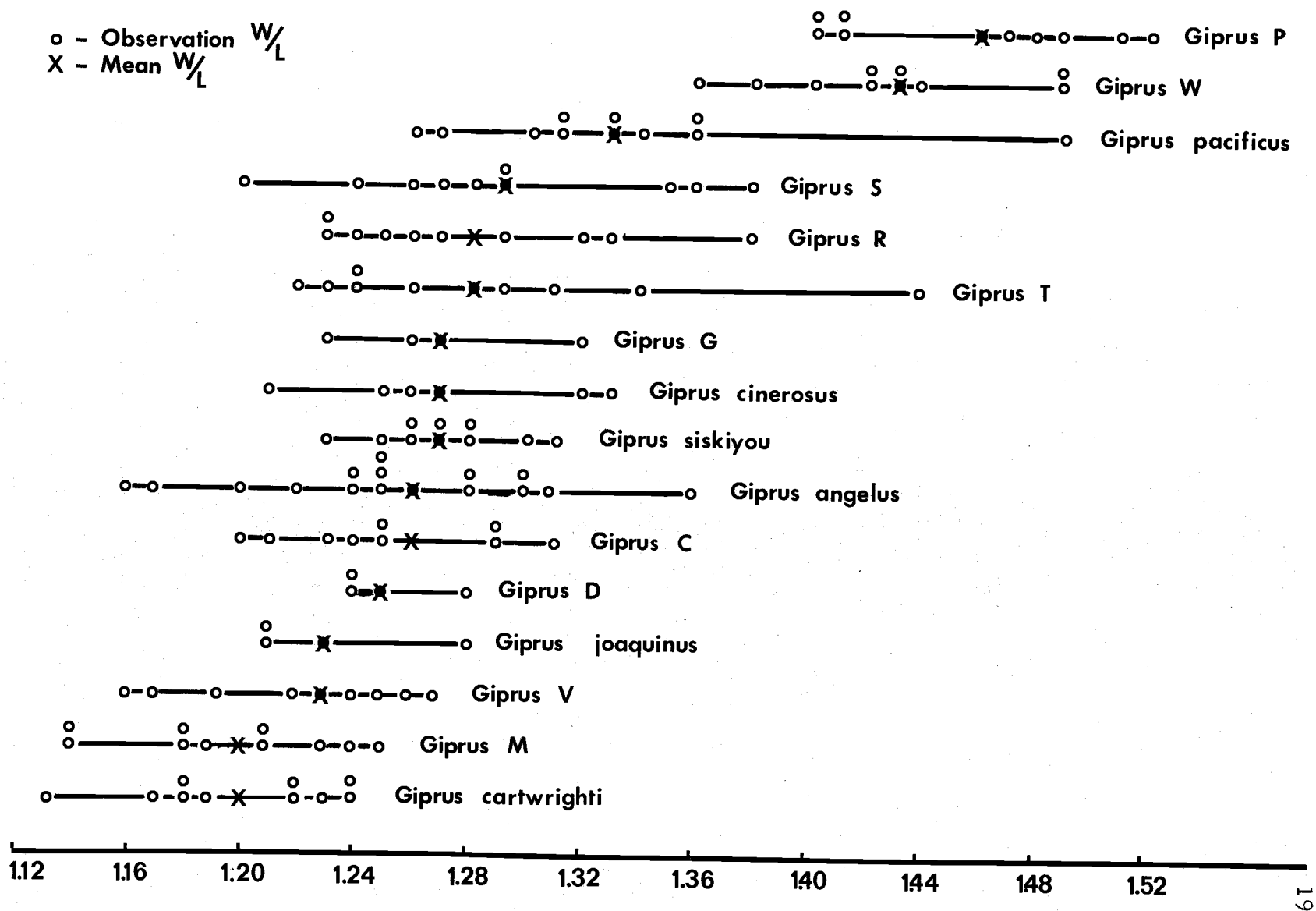
Observed differences in head shape raised the question of whether such differences would be useful in species differentiation. Mean W/L values ranged from 1.20 for G. cartwrighti and Giprus M indicating a very pointed head to 1.43 and 1.46 for Giprus W and Giprus P respectively (Figure 7) indicating a blunt head. It is notable that the latter two species and G. pacificus all occupy coastal habitats.

This may be either an adaptation to the coastal habitat or an indication of possible evolutionary pathways within the genus. As these coastal species are otherwise so different morphologically that they are presumed not to be closely related, the former explanation seems more plausible although what the adaptive advantage could be is unknown. Head shape, while useful as an indicator of habitat, is not a suitable character for species determination because there is too much overlap of values between species (Figure 1).

In addition to the aforementioned characters, total body length, degree of pigmentation of the wings, and wing venation were considered for their possible usefulness in discriminating between species. In each case considerable infraspecific variation and overlap between species were found and it appeared that these characters were not reliable for distinguishing between species.

Figure 1. Ratio of head width (W) to head length  
(L) for all species of Giprus

o - Observation  $W/L$   
 X - Mean  $W/L$



## INFRASPECIFIC VARIATION

Intraspecific variation is evident in many structural characters of Giprus. Variations in overall size of the insect, pattern and degree of pigmentation of the head and wings, shape and pigmentation of the female seventh sternum, wing venation, and the structure of the tip of the aedeagus have been examined in this study.

The maximum and minimum length values (Table 1) for each sex of each species indicate the range of variation in size within the species. Studies of size variation in female Giprus W and Giprus P show that in each species there exist some populations consisting of very large individuals and some populations consisting of very small individuals (Figures 2b and 2c). A study of samples from a single locality collected over a five year period shows that individuals collected in 1971 were significantly larger than those collected in other years (Figure 2a). Since size is apparently unrelated to species affinity of Giprus P and Giprus W, it must be dependent upon environmental factors or on inherent genetic differences between populations. As different sizes occur in different years at the same locality, the latter explanation alone is unlikely. Variations in the size of individuals collected at different sites or in different years at the same site may be a reflection of differences in diet or microclimate. Harries and Douglass (1948) report that in the beet leafhopper,

Table 1. Summary of length data for all species of Giprus

Species	<u>Sex</u>			
	♀	♂		
	Min. (mm)	Max. (mm)	Min. (mm)	Max. (mm)
<u>Giprus siskiyou</u>	3.76	4.58	3.50	4.32
<u>Giprus G</u>	4.26	4.49	4.12 (1 only)	4.12
<u>Giprus V</u>	4.00	4.23	3.77	4.07
<u>Giprus M</u>	3.91	4.41	3.71	4.07
<u>Giprus P</u>	3.66	3.96	3.84	3.96
<u>Giprus D</u>	4.82 (1 only)	4.82	4.08	4.36
<u>Giprus cinerosus</u>	4.30	4.31	3.91	4.17
<u>Giprus R</u>	3.59	3.88	3.29	3.50
<u>Giprus T</u>	3.95	4.21	3.65	4.20
<u>Giprus S</u>	3.73	4.12	3.51	4.13
<u>Giprus pacificus</u>	3.23	3.26	2.81	3.01
<u>Giprus C</u>	3.79	4.03	3.53	3.93
<u>Giprus angelus</u>	3.59	4.04	3.79	4.05
<u>Giprus joaquinus</u>	4.11	4.28	3.95 (1 only)	3.95
<u>Giprus W</u>	3.68	3.96	3.30	3.86
<u>Giprus cartwrighti</u>	4.01	4.54	3.87	4.19

n = 10 except where indicated

Figure 2.        Lengths of Giprus W and Giprus P.

Figure 2a.        Mean length of Giprus W at 4.0 km N Waldport.

- (1) 1968 (n=8)
- (2) 1967 (n=8)
- (3) 1970 (n=30)
- (4) 1969 (n=25)
- (5) 1971 (n=30)

Figure 2b.        Mean length of Giprus W at each site in 1971.

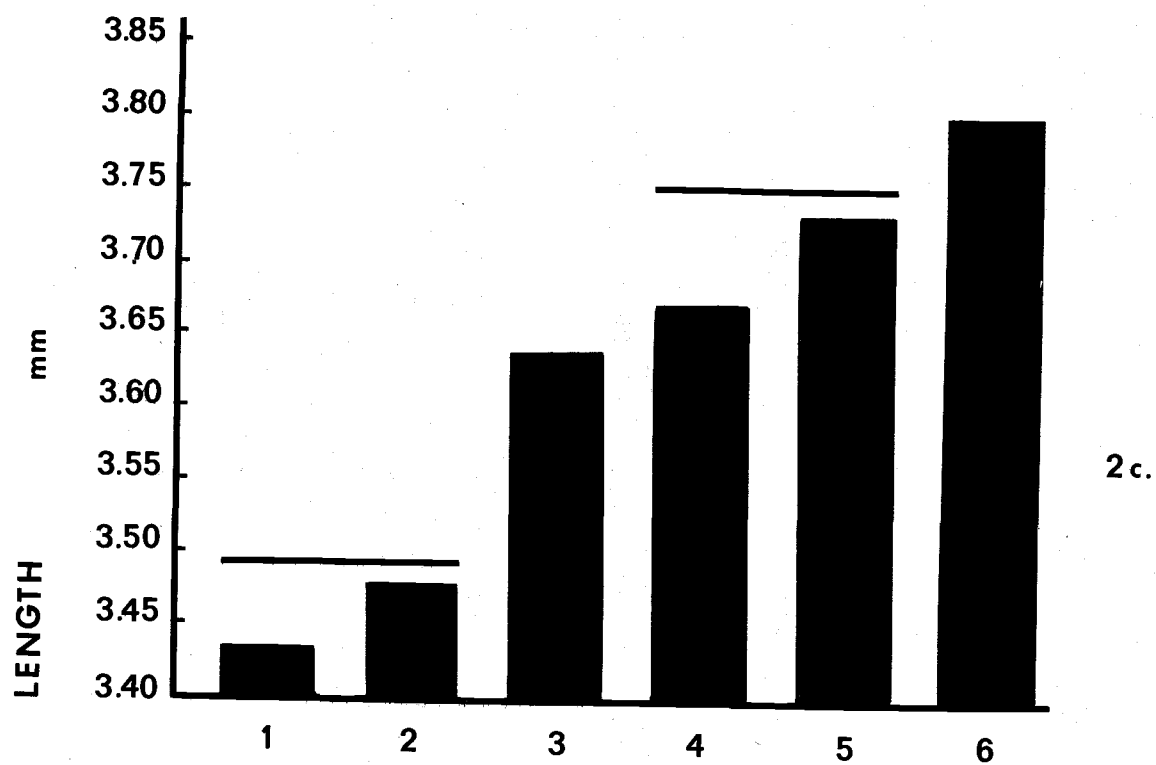
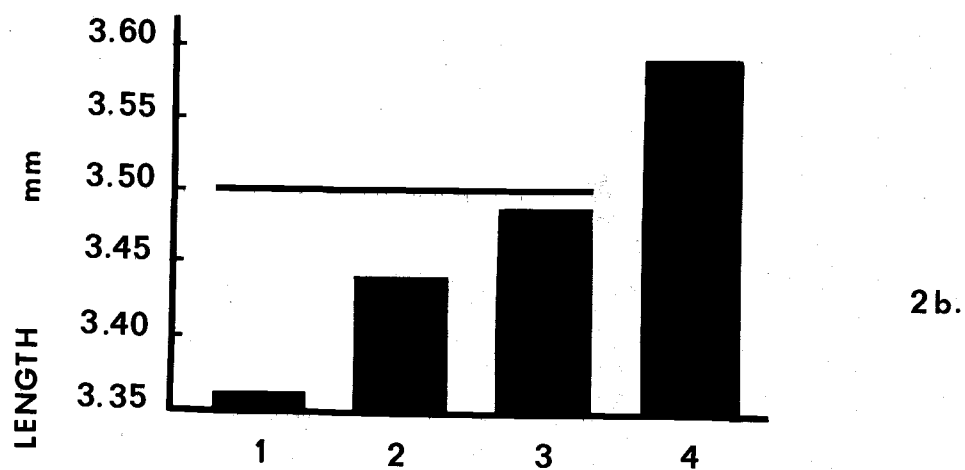
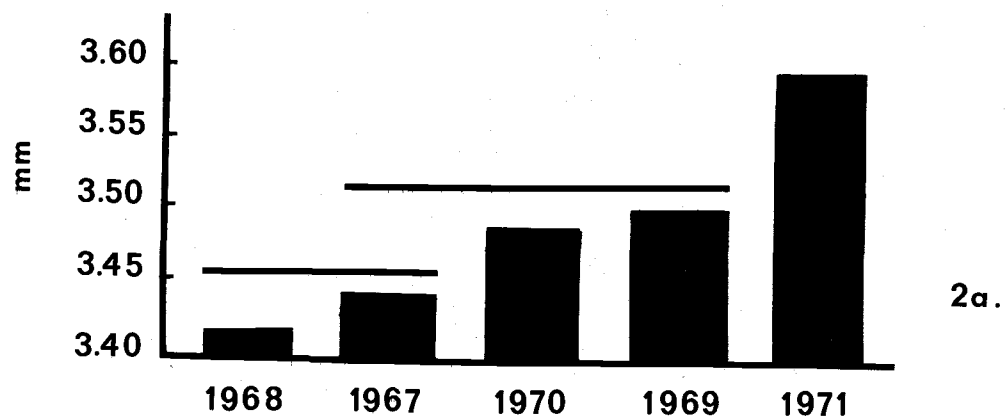
- (1) 9.6 km S Brookings (n=10).
- (2) 13.7 km N Florence (n=30).
- (3) 8.0 km S Bandon (n=15).
- (4) 4.0 km N Waldport (n=30).

Figure 2c.        Mean length of Giprus P at each site in 1971.

- (1) 17.7 km S Reedsport (n=10).
- (2) 12.9 km S Florence (n=22).
- (3) 16.1 km N Pacific City (n=30).
- (4) 17.7 km S Florence (n=30).
- (5) Nehalem Bay State Park (n=30).
- (6) 1.6 km S Newport (n=30).

A bar connecting two means indicates that they are not significantly different at the 0.01 level of significance.





Circulifer tenellus (Baker) (as Eutettix tenellus), nymphs which developed during the summer or under warm conditions in a controlled environment were smaller than nymphs developing in the fall or under cooler conditions in a controlled environment. Climatic data for Newport, Oregon, the closest recording station to the site 4.0 km N Waldport, show that temperatures in May and June 1971 were an average of  $1.8^{\circ}\text{C}$  below normal temperatures for those months and temperatures in July 1971 were an average of  $0.7^{\circ}\text{C}$  below normal temperatures for July (U. S. Weather Bureau, 1971). Temperatures at Newport in the same months of 1967-1970 were not below normal. Thus, temperature records support the hypothesis that the size of the insects at a given site in a given year is determined by temperature conditions during their developmental stages.

Pigmentation of Ciprus may also be affected by environmental conditions. The basic head markings are oblique blackish-brown dashes on the anterolateral submargin of the crown. These may be supplemented by other patches of pigment. Dark or light appearance of the wings depends on the number of cells with fuscous markings and the percentage of each cell so covered. Color ranges from wings with no fuscous markings to wings with all cells heavily pigmented by fuscous markings. The wing illustrated (Figure 4) is of average darkness.

Studies of the beet leafhopper, Circulifer tenellus, (Harries and

Douglass, 1948) have shown that temperature during the final nymphal instar has a direct effect on the coloration of the adult. As the temperature at which the nymph develops is decreased, the color of the adult becomes darker. Harries and Douglass also found that light, atmospheric moisture, sexual development, and age do not affect the color of adults and that temperature during the adult stage does not affect color. It seems likely that temperature is producing similar effects in Giprus. G. siskiyou shows considerable infraspecific color variation between individuals from different populations. G. siskiyou from Mt. Ashland are the darkest Giprus known, yet some other populations are quite pale. In a single Giprus W or Giprus P population, color frequently ranges from pale amber to almost as dark as G. siskiyou from Mt. Ashland. This phenomenon could be explained as a response to small climatic differences within the dunes. If a nymph developed in a part of the dunes where, because of close proximity to trees bordering the dunes or because of the slope on which the host was located, temperatures were lower, it would become a darker adult than a nymph developing on unshaded dunes receiving maximum exposure to the sun and consequently higher temperatures. It is probable that mature Giprus move around more than nymphs so that a mixture of shades eventually occurs throughout the dunes.

The venation of the wings of leafhoppers has been used

extensively in the past to distinguish between genera but is often unreliable because variation frequently occurs. While the forewings of all species of Giprus adhere to the basic wing venation pattern (Figure 4), numerous variations occur and frequently the two wings of the same insect are dissimilar. The most commonly observed variation involves extra crossveins in the costal region; extra crossveins also occur in the discal and anteapical cells. The outer anteapical cell is variable in size and may be as large as the central anteapical cell, minute, or occasionally absent. In the latter case, the costal cell was very broad, suggesting that the  $R_4 + 5$  vein was incomplete so that the outer anteapical cell was open on the side nearest the costal margin. The apical cells may be divided, probably representing separation of normally fused longitudinal veins (e. g.  $R_4 + 5$ ). Other variations include the inner anteapical cell open basally and the central anteapical cell not constricted.

The seventh sternum of the female also varies within each species. Variation most frequently involves the degree of pigmentation of the dorsal extension of the seventh sternum and the shape of the two pairs of dentate projections from the posterior margin of the sternum. Parasitism by dryinid wasps is fairly common among these leafhoppers and apparently can alter the shape of the genital segment.

As species of Giprus can be readily distinguished only by the

structure of the aedeagus, the taxonomically most significant infraspecific variation is that involving aedeagal structure. Through studies of infraspecific variation we can determine whether populations occurring in limited geographic areas and showing certain morphological differences between them are actually discrete species or extremes of infraspecific variation.

A study of two samples of populations, one from south of Weed, California and the other from 58 km east of Klamath Falls, Oregon, shows that there is considerable variation in the gross structure of the tip of the aedeagus of G. siskiyou. While the dorsal processes are more or less constant throughout the samples dissected, noticeable variation occurs in the position and degree of development of the lateral flanges. They range from slight lateral protrusions which merely suggest the presence of flanges (Figures 66, 67, 86) to well developed structures (Figures 51, 52, 68, 69, 70). Figure 68 illustrates extreme development of the lateral flanges. The lateral flanges exhibit greater asymmetry than is usually found amongst the aedeagal structures of Giprus. One of the more extreme asymmetrical conditions is illustrated in Figure 63. Variation also occurs in the position of the lateral flanges on the shaft relative to the dorsal processes. Figures 51, 52, and 61 show specimens which have the lateral flanges projecting only slightly basad of the dorsal processes while Figures 53 and 69 show individuals with the lateral

flanges extended considerably basad of the dorsal processes.

Figure 87 illustrates a specimen which did not have the heavy pigmentation characteristic of the others. This may be a sign of developmental aberrations which have led to the poorly developed apical notch in this individual.

The variation shown in these samples is highly significant because it indicates that structures such as those seen in specimens from southcentral Washington (Figure 33), Steens Mountain, Oregon (Figure 34), and northeastern California (Figure 32), fall within the demonstrable range of variation of G. siskiyou. A single specimen (Figure 68) from 58 km east of Klamath Falls, Oregon shows greater development of the lateral flanges than is shown in any of the individuals from isolated populations.

Oman (1937), in his original description of G. siskiyou, noted only a single pair of aedeagal processes and made no mention of the presence of lateral flanges. The individual illustrated in his paper was probably one of the extremes showing little or no development of the lateral flanges. Because of their variable shape, position, and size, and the possibility that they may not be evident in all individuals, the lateral flanges should not be considered important characters in defining G. siskiyou.

Although only five Giprus C males have been examined, considerable infraspecific variation is evident and further investigation

of infraspecific variation in this species is highly desirable. One specimen appears to have two very small dorsal processes originating at the bases of the dorsal elongate processes. Another specimen is markedly asymmetrical with the processes on the right joined to the aedeagus basad of those on the left. The angle between the elongate dorsal processes and the aedeagal shaft is also variable. Variation in the angle formed by the lateral processes and the aedeagal shaft is seen in G. pacificus.

Other species of Giprus show far less infraspecific variation in the aedeagal structures of individuals taken from a single population.

Structural variation between widely separated populations of the same species is noticeable. Specimens of Giprus T from Tehachapi Pass, California (Figure 44) and from the Highland District of Santa Cruz County, California, have straight elongate processes and ventral processes with acute apices. Specimens of Giprus T from Mill Valley, California (Figure 45) have distinctly sinuate elongate processes and ventral processes with blunt apices. Minor differences also occur between specimens of Giprus S collected in southern Utah and northern Nevada. Specimens from intervening localities may show such differences to be part of the normal range of variation in these species.

KEY TO THE SPECIES OF GIPRUS

- 1      Aedeagus approximately 3 times the length of the connective, slender, and sinuate, with minute apical processes (Figure 50); male plates attenuate with diverging apices (Figure 27); 7th sternum of female approximately semicircular with small median incision  
(Figure 22) . . . . . Giprus cartwrighti
- 1'      Aedeagus no more than two times the length of the connective; male plates short and stout (Figures 23-25); 7th sternum of female not as above . . . . . 2
- 2(1')      Aedeagus with at least one pair of elongate retrorse processes (Figures 44, 45, 46) that diverge obliquely from the longitudinal axis of the shaft; if longest pair of processes is less than 1/3 the length of aedeagal shaft, then they originate considerably basad of the apex . . . . . 3
- 2'      Aedeagus without elongate retrorse processes; aedeagal armature consisting of stout, retrorse, dentate processes; lateral flanges; or slightly elongate processes (Figures 38, 39) that originate near the apex . . . . . 8
- 3(2)      Aedeagus with one pair of straight or sinuate lateral or lateroventral elongate processes arising at or near the apex and no more than one other pair of processes . . . . . 4



- 3' Aedeagus with three pairs of processes, or if only two, then the slightly elongate pair originates considerably basad of the apex . . . . . 5
- 4(3) Aedeagus with a single pair of elongate, sinuate, latero-ventral apical processes about  $3/4$  the length of the aedeagal shaft; no ventral processes . . . . . Giprus S.
- 4' Two pairs of aedeagal processes: short ventral processes originating at the base of the elongate lateral processes and curving mesad (Figures 44, 45); lateral processes either straight or sinuate in lateral view . . . . . Giprus T
- 5(3') Aedeagus with three pairs of processes: one pair short and ventral, one pair elongate and lateral, and one pair very short and dorsal . . . . . 6
- 5' Aedeagus with fewer than three pairs of processes . . . . 7
- 6(5) All pairs of processes apparently originating at the same point on the aedeagal shaft; ventral processes not visible in dorsal view (Figure 49) . . . . . Giprus cinerosus
- 6' Elongate processes clearly originating basad of the other processes; ventral processes extending slightly laterad and therefore visible in dorsal view (Figure 48) . . . . Giprus R
- 7(5') Aedeagus with dorsal and lateral processes only; shaft stout and straight (Figure 47) . . . . . Giprus C

- 7' Aedeagus with lateral and lateroventral processes only;  
shaft somewhat sinuate (Figure 46) . . . . Giprus pacificus
- 8(2') Aedeagus with a single pair of lateroventral  
processes . . . . . 9
- 8' Aedeagus with more than one pair of processes or  
processes not as above . . . . . 10
- 9(8) Aedeagal shaft slender, slightly decurved, and with apex  
acute in dorsal view (Figure 36) . . . . . Giprus W
- 9' Aedeagal shaft straight with apex broadly rounded in dorsal  
view (Figure 35) . . . . . Giprus G
- 10(8') Aedeagus with a single pair of dorsal processes combined  
with a pair of more or less well developed (and at times  
asymmetrical) lateral flanges (Figures 31-34)  
. . . . . Giprus siskiyou
- 10' Aedeagus with more than one pair of processes; no lateral  
flanges . . . . . 11
- 11(10') Aedeagus with two pairs of processes . . . . . 12
- 11' Aedeagus with more than two pairs of processes . . . . . 14
- 12(11) Aedeagal shaft strongly decurved with dorsal and lateral  
processes well developed; shaft fairly stout  
(Figure 38) . . . . . Giprus D
- 12' Aedeagal shaft not strongly decurved; if slightly decurved  
the processes are very small . . . . . 13

- 13(12') Aedeagus with dorsolateral and ventrolateral processes  
very small (Figure 37); female 7th sternum much longer  
medially than laterally (Figure 13) . . . . . Giprus joaquinus
- 13' Aedeagus with dorsal and lateroventral processes well  
developed (Figure 39) . . . . . Giprus angelus
- 14(11') Aedeagus with a thin pair of lateral processes arising  
distinctly basad of the bulbous apex (Figure 41)  
. . . . . Giprus P
- 14' Aedeagus without such a thin pair of lateral  
processes . . . . . 15
- 15(14') In dorsal view aedeagus four times as long as greatest width  
of apical processes; in lateral view apical processes  
oriented obliquely to the longitudinal axis of the  
aedeagal shaft . . . . . Giprus M
- 15' In dorsal view aedeagus twice as long as greatest width  
of apical processes; in lateral view apical processes  
essentially transverse to the longitudinal axis of the  
aedeagal shaft . . . . . Giprus V

Giprus cartwrighti (Oman)

Figures 22, 50

Laevicephalus cartwrighti Oman 1932 p. 90

LENGTH: ♀ : 4.01 mm - 4.54 mm; ♂ : 3.87 mm - 4.19 mm

HEAD SHAPE: W/L = 1.20

FEMALE 7TH STERNUM: Dorsal extensions separate and posterior margin semicircular; dentate projections on posterior margin equal in length and projecting only slightly.

MALE GENITALIA: Plates elongate and gradually tapering to acute, diverging apices. Aedeagus whip-like, sinuate, and with minute apical processes. Styles flared near tip.

HOLOTYPE: ♂, Sloughouse, California, May 19, 1931. USNM No. 44240.

DISTRIBUTION (MAP 1): CALIFORNIA: Butte County: Oroville; Fresno County; Coalinga; Kern County: Tehachapi Pass, Monterey County: Bryson; San Bernardino County: 3.2 km S Rock Camp, L. Arrowhead; San Joaquin County: Lockeford; Santa Clara County: Los Gatos Canyon; Siskiyou County: 25.7 km E Klamath River, 18.5 km N Weed, 25.1 km N Yreka, 0.8 km E Yreka. OREGON: Jackson County: 5.1 km S Ruch, Agate Desert, Agate Lake, Upper Table Rock N of Medford.

(April-December)

HOSTS: Unknown, usually collected in mixed grassland.

Giprus siskiyou (Oman)

Figures 4, 6, 21, 31, 32, 33, 34, 51-87

Laevicephalus siskiyou Oman 1937 p. 478

LENGTH: ♀ : 3.76 mm - 4.58 mm; ♂ : 3.50 mm - 4.32 mm

HEAD SHAPE: W/L = 1.27

FEMALE 7TH STERNUM: Dorsal extensions separate; inner pair of denate projections on posterior margin shorter than outer pair.

MALE GENITALIA: Plates contiguous for their entire length; apices acute. Aedeagus with one pair of dorsal processes near apex. Lateral flanges basad of processes may be more or less well developed and are often asymmetrical. Style tips small and blunt. Aedeagal apex notched in lateral profile.

HOLOTYPE: ♂, Mt. Shasta City, California, June 29, 1935.

USNM No. 52205.

DISTRIBUTION (MAP 3): CALIFORNIA: Modoc County: 24.1 km NE Alturas, 11.3 km NE Alturas, Fandango Pass 1829 m; Shasta County: 20.9 km S Castella, 3.2 km S Castella, Castella; Siskiyou County: Bray, 26.1 km N Yreka, 21.6 km N Yreka, 0.8 km E Yreka, 25.7 km E Klamath River, 1.8 km E Klamath River, 18.5 km N Weed, N of Weed,

4.8 km S Weed, Mt. Shasta City, S of Mt. Shasta City,

Dunsmuir. NEVADA: Ormsby County: Carson City.

OREGON: Jackson County: Mt. Ashland 1402 m, Mt. Ash-

land 1250 m, Siskiyou Summit, Pinehurst; Klamath County:

30.6 km W Klamath Falls, Klamath Falls, 35.4 km E Klamath

Falls, 48.3 km E Klamath Falls 57.9 km E Klamath Falls,

9.6 km E Bly; Harney County: 17.7 km E Frenchglen.

WASHINGTON: Kittitas County: Cliffdell; Pierce County:

Mt. Rainier (Cottonwood Flats), Yakima County: Naches,

40.2 km S Toppenish, 57.9 km S Toppenish. (May-July)

HOSTS: Stipa lemmoni (Vas.) Scribn., Poa sp., Bromus sp. (one  
locality), Sitanion jubatum J. G. Sm. (one locality).

Giprus G sp. n.

Figures 19, 35

LENGTH: ♀: 4.26 mm - 4.49 mm; ♂: 4.12 mm

HEAD SHAPE: W/L = 1.27

FEMALE 7TH STERNUM: Dorsal extensions separate; inner and outer pairs of dentate projections on posterior margin of equal length.

MALE GENITALIA: Plates contiguous at base but separating posteriorly into acute, diverging apices. Aedeagus with one pair of short, lateroventrally projecting apical processes; apex broadly rounded in dorsal view. Style tips slender and elongate.

HOLOTYPE: ♂, 3.2 km (2 mi) E Gasquet, California, July 10, 1971.

USNM No. \_\_\_\_\_.

PARATYPES: 3 ♀

DISTRIBUTION (MAP 3): CALIFORNIA: Del Norte County: 3.2 km E Gasquet. (July)

HOST: Unknown



Giprus W sp. n.

Figures 7, 18, 36

LENGTH: ♀: 3.68 mm - 3.96 mm; ♂: 3.30 mm - 3.86 mm

HEAD SHAPE: W/L = 1.43

FEMALE 7TH STERNUM: Dorsal extensions separate; both pairs of dentate projections on posterior margin of equal length.

MALE GENITALIA: Plates contiguous at base but separating posteriorly into acute, diverging apices. Aedeagal shaft slightly decurved and supporting a single pair of lateroventrally projecting processes. Apex of aedeagus acute. Styles broad at tips.

HOLOTYPE: ♂, 4.0 km (2.5 mi) N Waldport, Oregon, July 3, 1970,

USNM No. \_\_\_\_\_

PARATYPES: 21 ♀, 23 ♂

DISTRIBUTION (MAP 1): OREGON: Coos County: 8.0 km S Bandon;

Curry County: 9.6 km S Brookings; Lane County: 13.7 km N

Florence; Lincoln County: 4.0 km N Waldport (July-September)

HOSTS: Poa macrantha Vas., Festuca rubra L.

Giprus joaquinus (Oman)

Figures 13, 37

Laevicephalus joaquinus Oman 1937, p. 478.

LENGTH: ♀ : 4.12 mm; ♂: 3.95 mm

HEAD SHAPE: W/L = 1.23

FEMALE 7TH STERNUM: Elongate medially, about three times the length at the lateral margin. Dorsal extensions fused.

MALE GENITALIA: Plates contiguous for their entire length; apices acute. Aedeagus long and slightly decurved with two pairs of small apical processes, one pair dorsal and the other ventral. Style tips broad and flat.

HOLOTYPE: ♂, Califa, California, June 12, 1935. USNM No. 52207.

DISTRIBUTION (MAP 2): CALIFORNIA: Madera County: Califa. (June)

HOST: Unknown

Giprus D sp. n.

Figure 38

LENGTH: ♀ : 4.82 mm; ♂ : 4.08 mm - 4.36 mm

HEAD SHAPE: W/L = 1.25

FEMALE 7TH STERNUM: No record; only female has abdomen missing.

MALE GENITALIA: Plates broadly rounded and contiguous for most of their length but separating posteriorly. Aedeagus strongly decurved and supporting two pairs of short, narrow, apical processes, one pair originating dorsally and the other laterally. Styles with blunt tips.

HOLOTYPE: ♂, Grass Valley, California, May 18, 1930. California Academy of Sciences.

PARATYPES: 1 ♀, 1 ♂.

DISTRIBUTION (MAP 2): CALIFORNIA: Nevada County: Grass Valley; Placer County: Dutch Flat. (May-June).

HOST: Unknown

Giprus angelus (Oman)

Figures 15, 39

Laevicephalus angelus Oman 1937 p. 478.

LENGTH: ♀: 3.59 mm - 4.04 mm; ♂: 3.79 mm - 4.05 mm

HEAD SHAPE: W/L = 1.26

FEMALE 7TH STERNUM: Dorsal extension fused; inner pair of dentate projections on posterior margin shorter than outer pair.

MALE GENITALIA: Plates contiguous for their entire length; apices acute. Aedeagus with two pairs of apical processes, one pair dorsal and the other lateroventral. Style tips blunt.

HOLOTYPE: ♂, above Mint Canyon, California, June 8, 1935.

USNM No. 52206.

DISTRIBUTION (MAP 3): CALIFORNIA: Los Angeles County: Mint Canyon; Monterey County: Salinas. (June)

HOST: Unknown

Giprus V sp. n.

Figures 16, 40

LENGTH: ♀ : 4.00 mm - 4.23 mm; ♂ : 3.77 mm - 4.07 mm

HEAD SHAPE: W/L = 1.23

FEMALE 7TH STERNUM: Dorsal extension fused; inner pair of dentate projections on posterior margin much shorter than outer pair.

MALE GENITALIA: Plates broadly rounded and contiguous at base but separating posteriorly into subacute, slightly diverging apices. Aedeagus short, stout, broadest at the apex, and with three pairs of short apical processes: one pair latero-ventral, one pair lateral, and one pair dorsal. Styles short and broad with blunt tips.

HOLOTYPE: ♂, Sams Valley, Oregon, May 15, 1970. USNM No.

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PARATYPES: 14 ♀, 15 ♂.

DISTRIBUTION (MAP 2): OREGON: Jackson County: Sams Valley.

(May-June)

HOSTS: Stipa lemmonii, Poa scabrella (Thurb.) Benth. ex Vasey.

Giprus P sp. n.

Figures 20, 41

LENGTH: ♀: 3.66 mm - 3.96 mm; ♂: 3.84 mm - 3.96 mm

HEAD SHAPE: W/L = 1.46

FEMALE 7TH STERNUM: Dorsal projections separate; inner pair of dentate projections on posterior margin shorter than outer pair.

MALE GENITALIA: Plates contiguous for their entire length; apices acute. Aedeagus with bulbous apex produced into a pair of lateroventral processes. A pair of thin laterodorsally projecting processes originate basad of the bulbous apex. Style tips broad.

HOLOTYPE: ♂, 16.1 km (10 mi) N Pacific City, Oregon, July 20, 1971. USNM No. \_\_\_\_\_

PARATYPES: 65 ♀, 38 ♂.

DISTRIBUTION (MAP 3): OREGON: Coos County: 17.7 km S Reedsport; Douglas County: 17.7 km S Florence; Lane County: 12.9 km S Florence; Lincoln County: 1.6 km S Newport; Tillamook County: Nehalem Bay State Park, 16.1 km N Pacific City, 1.6 km N Pacific City. (July-August)

HOSTS: Festuca rubra, Poa macrantha

Giprus M sp. n.

Figures 5, 14, 42

LENGTH: ♀: 3.91 mm - 4.41 mm; ♂: 3.71 mm - 4.07 mm

HEAD SHAPE: W/L = 1.20

FEMALE 7TH STERNUM: Dorsal extension fused; inner pair of dentate projections on posterior margin almost as long as outer pair.

MALE GENITALIA: Plates contiguous for their entire length; apices acute. Aedeagus short with three pairs of apical processes: one pair dorsal, one pair lateral, and one pair ventral. Aedeagus broadly rounded apically. Styles with small, flared tips.

HOLOTYPE: ♂, Merlin, Oregon, May 27, 1970. USNM NO. \_\_\_\_\_

PARATYPES: 17 ♀, 15 ♂.

DISTRIBUTION (MAP 1): OREGON, Josephine County: Merlin (May-June).

HOST: Danthonia californica Boland var. americana (Scribn.)

Hitchc. ?

Giprus cinerosus (Van Duzee)

Figures 9, 28, 49

Deltocephalus cinerosus Van Duzee, 1892 p. 305

Laevicephalus cinerosus (Van Duzee)

LENGTH: ♀: 4.30 mm - 4.31 mm; ♂: 3.91 mm - 4.17 mm

HEAD SHAPE: W/L = 1.27

FEMALE 7TH STERNUM: Lateral margins short; dorsal extensions separate; inner pair of dentate projections on posterior margin slightly shorter than outer pair.

MALE GENITALIA: Plates broadly rounded, separate for half their length and abruptly narrowing posteriorly to small acute apices. Aedeagus with three pairs of apical processes all originating at the same point on the shaft: a short ventral pair, an elongate lateral pair, and a short dorsal pair. Style tips broad.

LECTOTYPE: ♂, California. Iowa State University.

DISTRIBUTION (MAP 2): CALIFORNIA: Los Angeles County;

Orange County: Newport Beach; Riverside County: Perris;

San Diego County: El Cajon, Pala, Witch Creek. (February-May)

HOST: Unknown



Giprus R sp. n.

Figures 10, 25, 48

LENGTH: ♀ ; 3.59 mm - 3.88 mm; ♂ : 3.29 mm - 3.50 mm

HEAD SHAPE: W/L = 1.28

FEMALE 7TH STERNUM: Dorsal extensions separate; inner pair of dentate projections on posterior margin longer than outer pair.

MALE GENITALIA: Plates broadly rounded, contiguous for half their length, and abruptly narrowing posteriorly to acute apices. Aedeagus with three pairs of processes: a short ventral pair; an elongate lateral pair arising basad of the ventral pair, and a very short dorsal pair. Style tips broad.

HOLOTYPE: ♂, 4.8 km (3 mi) N Rosamond, California, March 23, 1971. USNM No. \_\_\_\_\_

PARATYPES: 20 ♀, 39 ♂.

DISTRIBUTION (MAP 2): CALIFORNIA: Los Angeles County:

4.8 km S Lancaster; 4.8 km N Rosamond. (March-April)

HOSTS: Stipa speciosa Trin. & Rupr., Oryzopsis sp.

Giprus T sp. n.

Figures 11, 44, 45

LENGTH: ♀ : 3.95 mm - 4.21 mm; ♂ : 3.65 mm - 4.20 mm

HEAD SHAPE: W/L = 1.28

FEMALE 7TH STERNUM: Dorsal extensions separate; dentate projections on posterior margin of equal length.

MALE GENITALIA: Plates contiguous for their entire length; apices acute. Aedeagus with a pair of straight or sinuate laterally projecting processes from which arise a pair of ventral processes which curve toward the midline.

HOLOTYPE: ♂, 27 mi SE Bakersfield, California, March 23, 1971.

USNM No. \_\_\_\_\_

PARATYPES: 9 ♀, 12 ♂.

DISTRIBUTION (MAP 3): CALIFORNIA: Kern County: Tehachapi

Pass 579 m & 823 m; Marin County: Mill Valley; Napa County:

32 km N St. Helena; Santa Cruz County: Highland District.

(March-June)

HOST: Unknown

Giprus S sp. n.

Figures 12, 43

LENGTH: ♀ : 3.73 mm - 4.12 mm; ♂ : 3.51 mm - 4.13 mm

HEAD SHAPE: W/L = 1.29

FEMALE 7TH STERNUM: Dorsal extensions separate; inner pair of dentate projections on posterior margin shorter than outer pair.

MALE GENITALIA: Plates contiguous for their entire length; apices acute. Aedeagus short and slightly sinuate with one pair of sinuate processes originating lateroventrally and extending basally approximately 3/4 of the length of the aedeagal shaft.

HOLOTYPE: ♂, 6.4 km (4 mi) N Winnemucca, Nevada, June 23, 1971. USNM No. \_\_\_\_\_

PARATYPES: 2 ♀, 1 ♂.

DISTRIBUTION (MAP 1): NEVADA: Humboldt County: Winnemucca, 6.4 km N Winnemucca, 16.1 km N Winnemucca. UTAH: Washington County: St. George. March (Utah) - June (Nevada)

HOST: Unknown

Giprus C sp. n.

Figures 8, 47

LENGTH: ♀ : 3.79 mm - 4.03 mm; ♂ : 3.53 mm - 3.93 mm

HEAD SHAPE: W/L = 1.26

FEMALE 7TH STERNUM: Dorsal extensions separate: inner pair of dentate projections on posterior margin shorter than outer pair.

MALE GENITALIA: Plates broadly rounded, contiguous for half their length, and separating posteriorly to acute, diverging apices. Aedeagus with somewhat elongate dorsal processes arising more than 1/3 of the distance from the apex to the base and with lateroventral processes arising near the apex.

Aedeagal shaft somewhat stout. Style tips broad.

HOLOTYPE: ♂, 1.6 km (1 mi) NW top of Cajon Pass, California,  
April 23, 1971 USNM No. \_\_\_\_\_

PARATYPES: 11 ♀, 4 ♂.

DISTRIBUTION (MAP 1): CALIFORNIA: San Bernardino County:  
1.6 km NW top of Cajon Pass (April)

HOST: Stipa speciosa

Giprus pacificus (Oman)

Figures 17, 46

Laevicephalus pacificus Oman 1937 p. 477.

LENGTH: ♀ : 3.23 mm - 3.26 mm; ♂ : 2.81 mm - 3.01 mm

HEAD SHAPE: W/L = 1.33.

FEMALE 7TH STERNUM: Dorsal extensions separate; inner pair of dentate projections on posterior margin as long as outer pair; median incision short.

MALE GENITALIA: Plates contiguous for their entire length; apices acute. Aedeagus sinuate with two pairs of processes; a somewhat elongate lateral pair arising at a point about 1/3 of the distance from the apex of the aedeagus to the base and a short ventral pair arising near the apex. Styles broad at tips.

HOLOTYPE: ♂, Montara, California, June 13, 1935, USNM No. 52204.

DISTRIBUTION (MAP 2): CALIFORNIA: Alameda County: Bay Farm; San Mateo County: Montara. (May-June)

HOST: Unknown.

## DISTRIBUTION, HABITAT, AND HOST PLANTS

The accumulation of distribution, habitat, and host plant data is a first step from which more comprehensive studies of the biology of an insect may be undertaken. As in any attempt to generalize, one of the major problems encountered in endeavoring to describe habitat, host plants, and distribution of a species is that collection of only a few specimens may lead to false assumptions. For example, several interpretations might be made of the fact that only three G. cinerosus were collected at Newport Beach, California; only four Giprus G at Gasquet, California; and only nine G. joaquinus at Califa, California. Assuming that the habitat sampled was indeed the natural habitat of the species, these individuals might represent the beginning or end of what is a larger population at its peak, or they might have been collected at the edge of a large population. However, the occurrence of a few specimens at a locality might also be the result of chance invasion of the habitat during random dispersal. Temporarily suitable climatic conditions may allow the development of small populations which are viable for only one or a few seasons. Alternatively, adverse conditions such as drought or destruction of the natural habitat may force the insects to abandon one habitat and move to a different area.

Determination of hosts of Giprus is complicated by the

occurrence of a single species of Giprus on two or more genera of grasses, and by instances of a single species of grass hosting one species of Giprus at one locality and another species of Giprus at another locality. In this discussion the host is defined as a plant on which both nymphs and adults occur with a high frequency.

The only valid bases for describing habitats and host preferences are continued field observation of large populations over a number of seasons and rearing of the insects in the laboratory. As long term habitat observation was not possible for most of the species discussed, and laboratory rearings attempted were unsuccessful, the information presented here should be taken as a general indication of the apparent conditions required for survival of the species, rather than as a definitive description of the habitat or host requirements.

Giprus siskiyou occurs over a wider geographic area (Map 3) than any other member of the genus except G. cartwrighti as well as over a considerable range of altitudes. It occurs from a low elevation of 701 m at Dunsmuir and Hornbrook, California to a high elevation of 1981 m on Steens Mountain, Oregon. G. siskiyou also occurs in two major habitat types: chaparral communities in southwestern Oregon and northern California, and shrub-steppe communities east of the Cascade Range.

"Chaparral" is the term applied to communities of scrub

vegetation consisting of dense stands of evergreen (usually) shrubs with extensive root systems and small, thick, heavily cutinized leaves borne on rigid twigs and branches; communities are frequently dominated by one species (Detling, 1961). The climatic requirements for chaparral vegetation are low annual precipitation (250-760 mm) of which less than 20% is summer rainfall and no more than a moderate difference between seasonal temperature extremes (Cooper, 1922). In Oregon, high precipitation limits chaparral vegetation mainly to the Rogue River Valley and south, although isolated patches of chaparral occur further north in the Umpqua River Valley (Detling, 1961). The chaparral of southwestern Oregon and northwestern California is dominated by Ceanothus cuneatus Nutt. Either Arctostaphylos viscida Parry or A. canescens Eastw. (depending on the soil type) is the second most common plant and is found in more mesic conditions than sites where C. cuneatus is the only shrub present (Detling, 1961).

C. cuneatus was present at nine of the eleven sites where G. siskiyou was collected in northwestern California; Arctostaphylos sp. was present at five localities. Other common species were Pinus ponderosa Dougl. (6 localities), Quercus sp. (6 localities), and Stipa lemmonii (5 localities).

East of the Cascades, G. siskiyou is most frequently found in shrub-steppe communities. Shrub-steppes, which in eastern Oregon



are mostly covered by Artemisia communities, are characterized by low annual precipitation (190-610 mm), warm-to-hot dry summers, and cold winters (Franklin and Dyrness, 1969). Artemisia sp. is recorded at eight of the ten localities where G. siskiyou was collected in southeastern Oregon. Other frequently occurring shrubs and trees are Juniperus sp. (occidentalis Hook. ?) (7 localities), Chrysothamnus nauseosus (Pall) Britt. (7 localities), C. viscidiflorus (Hook.) Nutt. (4 localities), and Purshia tridentata (Pursh) DC. (3 localities). At Steens Mountain, Oregon G. siskiyou was found 30 m above the Juniperus occidentalis belt. At 40.2 km and 57.9 km south of Toppenish, Washington, G. siskiyou was collected in Artemisia associations; P. tridentata was also present at both localities.

G. siskiyou was taken from Stipa lemmonii at a total of seven sites and from Poa sp. at four sites; south of Toppenish, Washington, G. siskiyou was on Sitanion jubatum (Oman, field notes: June 26, 1969). At other localities it was taken by general sweeping and the host was undetermined.

In view of the discontinuity in records of occurrence of G. siskiyou, it is interesting to speculate on how isolated populations came to be present in southcentral Washington, on Steens Mountain, Oregon, and in the Sierra Nevada. A possible explanation of how G. siskiyou may have migrated to southcentral Washington from the Siskiyou Mountain region is suggested by the botanical studies of

Detling (1961). His theory is based on Hansen's (1947) findings that from about 8000 years ago until about 4000 years ago there existed a warm, dry period in the northwest. Detling believes that during that period the chaparral vegetation now characteristic of southwestern Oregon and northwestern California extended as far north as the valleys of southwestern Washington and east via the Columbia Gorge into southcentral Washington. Drought conditions of the Columbia Gorge did not permit shrub species of the chaparral to migrate above the gorge but herbaceous species were able to move into this area. It is possible, then, that G. siskiyou migrated northward with the chaparral vegetation into southcentral Washington via the Willamette Valley and the Columbia Gorge. As cooler, moister climatic conditions returned west of the Cascades, oak woodlands and conifer forests became dominant and, except for certain relict islands of chaparral vegetation in the Willamette Valley (Detling, 1953), chaparral vegetation was confined to the region south of the Umpqua River Valley. Of these relict islands of chaparral vegetation in the Willamette Valley, Marys Peak has been examined thoroughly and no G. siskiyou has been found. G. siskiyou would presumably have been eliminated from those areas where the climate became unsuitable; excess precipitation is probably the limiting factor barring Giprus from inhabiting the Willamette Valley. According to Detling, the only area which retained chaparral herbs was the

area above the Columbia Gorge and comparison of climatic data indicates conditions similar to those of southern Oregon (Table 2). Thus it appears reasonable that G. siskiyou could also survive in that area. Detling's theory provides a possible explanation for the absence of Giprus from most of central and eastern Oregon. Failure to find Giprus at The Dalles, Prineville, Bend, Lapine, Silver Lake, Summer Lake, or Christmas Lake, Oregon in what appear to be suitable habitats is negative evidence supporting the theory that Giprus moved northward west of the Cascade Range.

Table 2. Climatic data for recording stations closest to collecting sites of Giprus V, Giprus M and G. siskiyou.

Locality	Annual Precipitation (mm)	Mean July Max. (°C)	Mean Jan. Min. (°C)
Alturas Calif.	326.6	31.2	-9.0
Carson City, Nev.	282.2	38.4	-4.2
Ellensburg, Wash.	210.3	28.9	-9.3
Grants Pass, Oreg.	789.2	32.3	-0.3
Klamath Falls, Oreg.	357.1	29.6	-6.4
Lakeview, Oreg.	366.8	29.2	-8.0
Medford, Oreg.	536.4	32.0	-1.9
Mt. Shasta City, Calif.	924.3	29.4	-4.1
Yakima, Washington	199.6	31.3	-8.7
Yreka, Calif.	444.0	33.1	-4.6

(U. S. Weather Bureau, 1960)

G. siskiyou most probably reached Steens Mountain from southcentral Oregon where the species is widespread. The Steens

Mountain site is only 169 km from Fandango Pass, California where G. siskiyou is known to occur and less than 193 km from Bly, Oregon where a larger population is present.

The occurrence of G. siskiyou at Carson City, Nevada may represent more than an isolated population. The region east of the southern Cascade Range between Alturas, California and Carson City has not been searched for Giprus; other populations may occur in this area, and possibly even farther south.

Two other species are found in the chaparral communities of the Rogue River Valley. Giprus V (Map 2) is from Sams Valley, Oregon at the base of Table Rock north of Medford, Oregon, 42.2 km east of Merlin, Oregon where Giprus M (Map 1) occurs, and only 64 km north of Mt. Ashland, Oregon, the most northerly site where G. siskiyou has been found west of the Cascades. Ceanothus cuneatus is the dominant shrub in the lower areas of the slight slope on which Giprus V is found; Arctostaphylos viscida becomes plentiful farther uphill. Giprus V was collected from the heads of Stipa lemmonii and from Poa scabrella. At Merlin, C. cuneatus is again the most common shrub with Arctostaphylos sp., Quercus garryana Dougl., and Arbutus menziesii Pursh. also present. Giprus M was collected from an area where Danthonia californica var. americana was the most common grass, but the untimely destruction of the habitat has prevented further observation to determine whether this is the host.

The question arises as to why there should be three allopatric species within such a small area. A difference in climate appears most likely to be the isolating factor. There is no apparent geographic barrier preventing G. siskiyou from extending its range into the Rogue River Valley from Mt. Ashland. Climatic data (Table 2) show that annual precipitation and mean July maximum temperature at Medford and Grants Pass fall within the range found at G. siskiyou sites, but that the January mean minimum temperature is lower for G. siskiyou sites, possibly indicating adaptation for lower temperatures in the egg stage of G. siskiyou. On the other hand, it is entirely possible that the microclimates of the actual sites where Giprus has been collected are so different from the climates of the nearest recording stations, that to depend on data from the recording stations is misleading.

Giprus G (Map 3) was taken on short, extremely dry grass (unidentifiable due to its poor condition) amongst the boulders on the banks of the Smith River 3.2 km east of Gasquet, California. This is a dry woodland area with Ceanothus sp. present and may not be the natural habitat of Giprus G but rather an enforced habitat due to the dry conditions found late in the season.

The central Oregon Coast, inhabited by Giprus W (Map 1) and Giprus P (Map 2), is characterized by mild temperatures and abundant precipitation. Temperature fluctuation between the warmest

and coolest months is moderate. While summer precipitation is only 4-7% of the annual total, low summer evaporation rates due to cool temperatures prevent moisture deficiency in plants (Wiedemann, Dennis, and Smith, 1969). A great number of small-scale climatic modifications are found on the dunes.

The sand dune species of Giprus almost always occur on the lee side of foredunes or on the slopes of higher dunes farther inland. Vegetation may be sparse and consist only of the host grasses, Festuca rubra, and Poa macrantha as at the site 16.1 km north of Pacific City, Oregon, or Lathyrus sp., Tanacetum camphoratum Less., and Glehnia leiocarpa Math. may occur along with the host grasses. Giprus P was collected from a pure stand of F. rubra at the site 12.9 km south of Florence.

The occurrence records for Giprus W and Giprus P are interesting and puzzling. These two coastal species occur from the California border in the south (Giprus W) to Nehalem Bay in the north (Giprus P). Similar sand dune habitats farther north along the coast between Cannon Beach and Astoria, Oregon, on Long Beach Peninsula, Washington, and at Wickininnish Beach (Pacific Rim National Park), British Columbia have been searched for populations of Giprus W and Giprus P but so far without success. However, it is interesting to note that a species of Psammotettix associated with Giprus W and Giprus P along the central Oregon Coast was abundant at these

northern sites. While an increase in latitude may partly explain the absence of Giprus from northern areas, precipitation and temperature extremes (except for Wickininnish Beach (Pacific Rim National has very high precipitation) are much the same in the areas where Giprus is present and absent (Table 3).

Table 3. Climatic data for selected Pacific Coast recording stations.

Locality	Annual Precipitation (mm)	Mean July Max. (°C)	Mean Jan. Min. (°C)
Astoria, Oreg.	1966.7	20.5	-1.1
Bandon, Oreg.	1423.4	16.5	3.3
Brookings, Oreg.	2067.8	19.3	4.4
Newport, Oreg.	1682.2	17.7	3.2
North Bend, Oreg.	1570.2	19.1	3.6
Reedsport, Oreg.	1874.6	20.7	2.9
Seaside, Oreg.	2024.4	19.6	2.5
Tillamook, Oreg.	2272.0	20.2	1.8
Long Beach, Wash.	1240.0	16.2	3.2
Tofino, Airport, B. C.	3196.1	18.5	2.1

(U. S. Weather Bureau, 1965)

The ranges of Giprus P, which has the more northerly distribution, and Giprus W, which has the more southerly distribution, overlap extensively on the central Oregon Coast. As the two species have never been found at the same site, it could be speculated that micro-climatic factors of the individual sites determine the distribution of each species in the region of species overlap. Conversely, the distributions of the two species may be entirely random as a result

of chance invasion of the dune habitat. In view of the great dissimilarity of internal structures, it is very unlikely that one species was derived from the other, so it is probable that invasions of the dune habitat took place at different times.

Giprus S is known from the area of northern Nevada which Billings (1951) calls the sagebrush-grass zone of the Great Basin, and from southwest Utah just outside the limits of the Great Basin (Map 1). Habitat data are available only for the two collecting sites at Winnemucca, Nevada. At these sites, Giprus S was taken in the Artemisia sp. - Chrysothamnus nauseosus association. Both males and females were taken at 1368 m elevation on the northeast side of a steep slope and a single male was taken at a second site at the eastern edge of the sand dunes at the base of the hill. The climates of the Nevada and Utah sites differ in that Winnemucca has greater precipitation and lower temperatures than St. George, Utah (U. S. Weather Bureau, 1965a, c). That Giprus S is able to survive at both localities indicates a certain amount of adaptability of the species.

Giprus R occurs in the western Mojave Desert of California (Map 2) where mean annual precipitation is 76-152 mm, 80% of which falls between November 1 and April 30; summers are hot with daily maximum temperatures averaging 38° C or higher; winters are cold with an average annual minimum of -9.5° C; strong winds are common



in the spring and fall (Twisselmann, 1967). The habitat of Giprus R is characterized by the presence of Yucca brevifolia Engelm. in Wats., Grayia spinosa (Hook) Moq., Atriplex sp., Tetradymia canescens DC., Coreopsis sp., Larrea divaricata Cav., Stipa speciosa, and Oryzopsis sp. Some of the plants found at these collecting sites are listed by Twisselmann (1967) as being members of the Creosote Bush Association and some as being members of the Arid Shrub Association. The site 67.2 km east of Palmdale, California is probably more typical of the Creosote Bush Association while the Rosamond, California site where Larrea divaricata was not present in the actual collecting area may be a transition zone between the Creosote Bush Association and the Arid Shrub Association. Nymphs and adults of Giprus R were taken from Stipa speciosa and Oryzopsis sp.

While Giprus T is found in widely separated parts of California (Map 3), habitat data are available only for the collection site at 823 m elevation in Tehachapi Pass. At this locality nymphs and adults were taken from a mixed stand of Bromus sp. and Avena sp. Crataegus sp. and Pinus sabiana Dougl. were in the immediate vicinity of the densest part of the population with Quercus sp. slightly farther downhill.

G. cinerosus (Map 2) was observed in the field on one occasion

when three individuals were taken at the margin of the estuary at Newport Beach, California (Oman, field notes, April 24, 1971). No host or habitat data are available for other sites where G. cinerosus has been collected.

Giprus C (Map 1) was collected in a single locality at Cajon Pass, California in the transition between a Yucca brevifolia belt and a Juniperus sp. belt. Also present were Eriogonium fasciculatum Benth., Salvia dorii (Kell.) Abrams subsp. carnosa (Dougl. ex Jeps.) Abrams, and Stipa speciosa. Specimens were collected from the latter (Oman, field notes, April 23, 1971).

G. cartwrighti has a range extending from southern California to southern Oregon (Map 1). Typically it is found in flat, shrubless, open areas with mixed short grass and forb cover such as occurs at Agate Desert north of Medford, Oregon. Occasionally G. cartwrighti is found in the chaparral association and on sloping land as at 0.8 km east of Yreka, California where G. siskiyou and G. cartwrighti occur together.

Only borrowed specimens of G. angelus (Map 3), G. joaquinus (Map 2), G. pacificus (Map 2), and Giprus D (Map 2) were examined and no host nor habitat data are available for these species. In addition, there are a number of female specimens, mostly from California, that cannot be assigned to species because they were not associated with males (Appendix B).

## LIFE CYCLE

Giprus have been collected during every month except January, October, and November, with most species present between March and August (Table 5). Only G. cartwrighti has been collected as adults in December. Adults of species of southern California and Utah are present earlier in the year while interior species farther north are present in May and June, and those of the central Oregon Coast are not abundant until July.

Available evidence from field collection suggests that Giprus (with the possible exception of G. cartwrighti) is univoltine. Collection of Giprus W over a period of five seasons on the Oregon Coast near Waldport indicates that eggs hatch in June, and that adults are present from July onwards (Oman, field notes, July 3, 1970). Giprus W is most abundant in this locality in the first half of July. As the season progresses, males die off first and the number of females decreases until by October no Giprus W remain. Data for Giprus V on May 1, 1970 when only males were collected suggest that males mature first. The absence of males when G. cartwrighti was collected at Los Gatos Canyon, California on December 8, 1938, suggests that this was the end of a season.

Table 4. Dates of collection of Giprus W at Waldport (all years).

April 13	July 1	3	10	19	23	August 5	20	31	Sept. 15	Oct 1
none	♀♂n	♀♂n	♀♂	♀♂	♀	♀♂	♀♂	♀	♀	none
n - nymphs present				♀ - adult females present				♂ - adult males present		

Diapause can be defined as physiologically enforced arrested development by means of which a species synchronizes its development with the appropriate seasons or adapts to adverse conditions (Chapman, 1969). Diapause occurs in response to environmental stimuli which regularly precede the adverse conditions rather than as a direct result of the adverse conditions (Danielevskii, 1965). Photoperiod, temperature, water, and diet may stimulate the onset of diapause; diapause is usually terminated by exposure to cold temperatures (Harvey, 1962). Obligatory diapause, where every individual in every generation enters diapause usually results in a univoltine life cycle (Chapman, 1969).

From these studies of other insects, one can infer several things about diapause in Giprus. Diapause probably accounts for the absence of adult Giprus for most of the year. Since nymphs and adults are present for only a short time, diapause almost certainly occurs in the egg stage. As Giprus is apparently univoltine, diapause is probably obligatory. The adverse conditions which are most likely

Table 5. Collection of Giprus by week.

	Feb 5-11 12-18	Mar 11-17 18-24	Apr 25-31 1-7	8-14 15-21	May 22-28 29-5	6-12 13-19	June 20-26 27-2	3-9 10-16	17-23 24-30	July 1-7 8-14	15-21 22-28	Aug 29-4 5-11	12-18 19-25	Sep 26-1 2-8	9-15	Dec 8
<u>G. cinerosus</u>	♂ ♂		♀♂	♀♂			♀♂									
<u>Giprus T</u>		♀♂ ♀♂n			♀♂		♂									
<u>Giprus S</u>		♀ ♀	♀	♂♀				♀	♀♂							
<u>Giprus R</u>		♀♂n		♀♂												
<u>G. cartwrighti</u>				♀♂	♀♂ ♂	♀♂ ♀♂n	♀ ♀♂									♀
<u>Giprus C</u>					♀♂											
<u>Giprus V</u>					♂	♀♂ ♀♂n	♀♂ ♀		♀♂ ♀							
<u>Giprus M</u>						♀♂ ♀♂	♀♂		♀♂							
<u>G. pacificus</u>						♀♂		♀♂								
<u>G. siskiyou</u>							♀♂n		♀♂ ♀♂	♀♂ ♀♂						
<u>Giprus D</u>						♀♂	♂									
<u>G. angelus</u>								♀♂	♂							
<u>G. joaquinus</u>								♀♂								
<u>Giprus W</u>										♀♂n ♀♂	♀♂ ♀	♀♂	♀♂ ♀		♀	
<u>Giprus P</u>										♀♂n ♀♂n	♀♂n	♀♂				
<u>Giprus G</u>										♀♂						

♀ adult females present  
♂ adult males present  
n nymphs present

to require diapause in Giprus are lack of water and food due to drying of the host grasses and cold winter temperatures in many parts of Giprus' range.

## PHYLOGENY

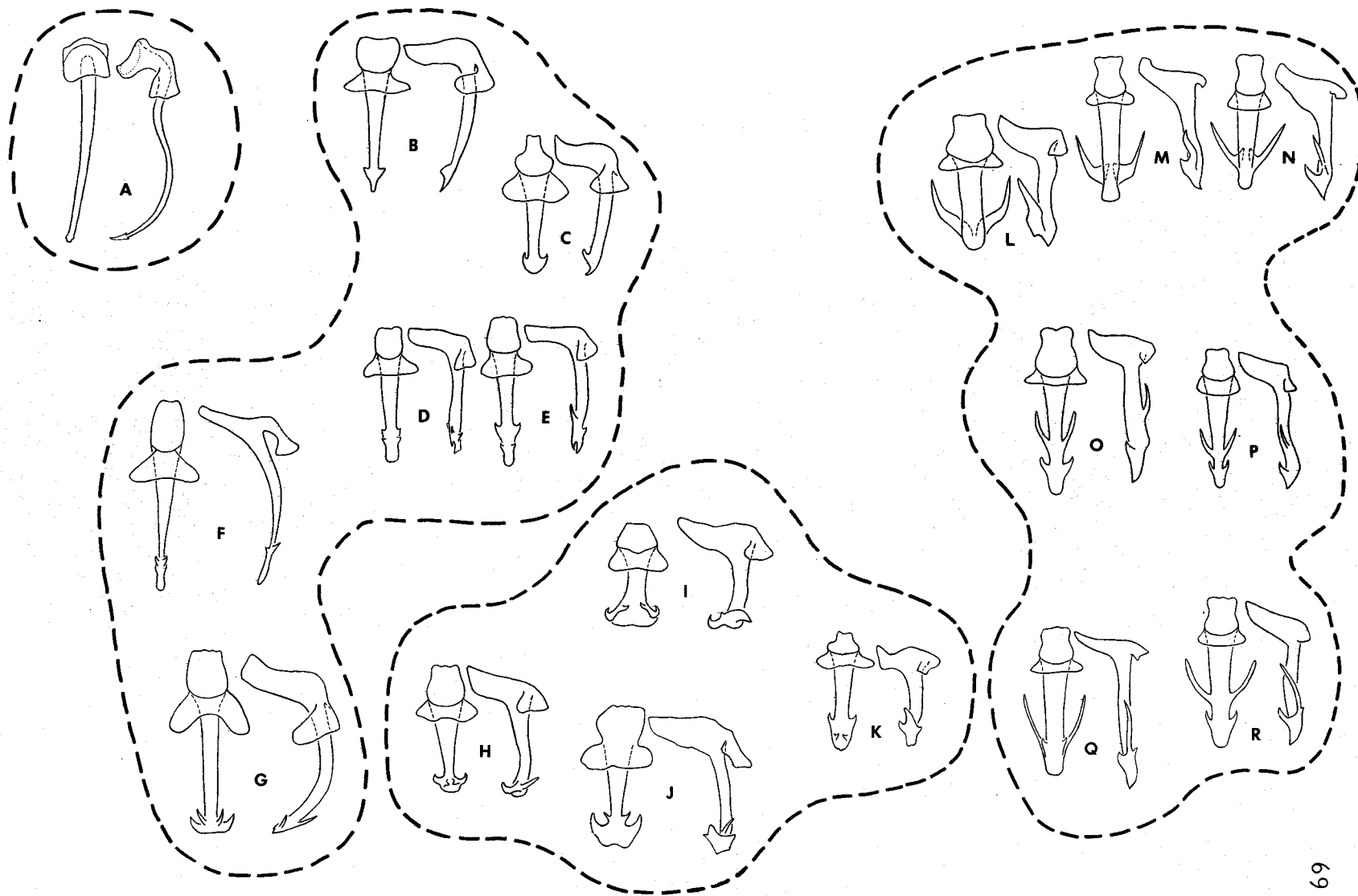
Because of the scarcity of fossils, no good evidence of evolutionary pathways within the Cicadellidae exists and speculation as to the derivation of genera and species must be based on our knowledge of present day insects. Morphological, physiological, ethological, ecological, and geographical evidence may be used to support theories of the relationships between species. In Giprus, only morphology, distribution, and ecology have been studied at all, and data for the latter are not complete enough to serve as the basis for phylogenetic speculation. Hence, morphological evidence is used for this purpose. Because size and color are too similar in many species to contribute to a grouping scheme, species groups of Giprus are based primarily on the structure of the aedeagus (Figure 3). The weakness of such a scheme is that it depends almost entirely on morphology. A morphologically based species group may occur over a wide geographic area and overlap geographically with members of another species group, but within each group most species occur in the same geographic area.

In Figure 3 G. cartwrighti is set apart from other Giprus for several reasons which when taken together suggest that it is not closely related to other species in the genus. The external genitalia of both males and females, and the sinuate aedeagus, are

Figure 3. Species groups of Giprus based on the structure of the male genitalia.

- A G. cartwrighti
- B Giprus W
- C Giprus G
- D G. siskiyou
- E G. siskiyou
- F G. joaquinus
- G Giprus D
- H G. angelus
- I Giprus V
- J Giprus P
- K Giprus M
- L Giprus S
- M Giprus T
- N Giprus T
- O Giprus C
- P G. pacificus
- Q G. cinerosus
- R Giprus R





characteristic of Laevicephalus. However, the position of the aedeagal shaft relative to the connective places the species in Giprus. Thus, I suggest that G. cartwrighti was derived from the Laevicephalus - Giprus line at about the time the two lines differentiated. As supporting evidence, it might be noted that the only instances where two species of Giprus occur together are those where G. cartwrighti is one of a sympatric pair, suggesting that G. cartwrighti and other species do not compete ecologically to such an extent as to allow only one to exist at a given locality. Also, G. cartwrighti is most frequently encountered in open grassland habitats such as those favored by Laevicephalus.

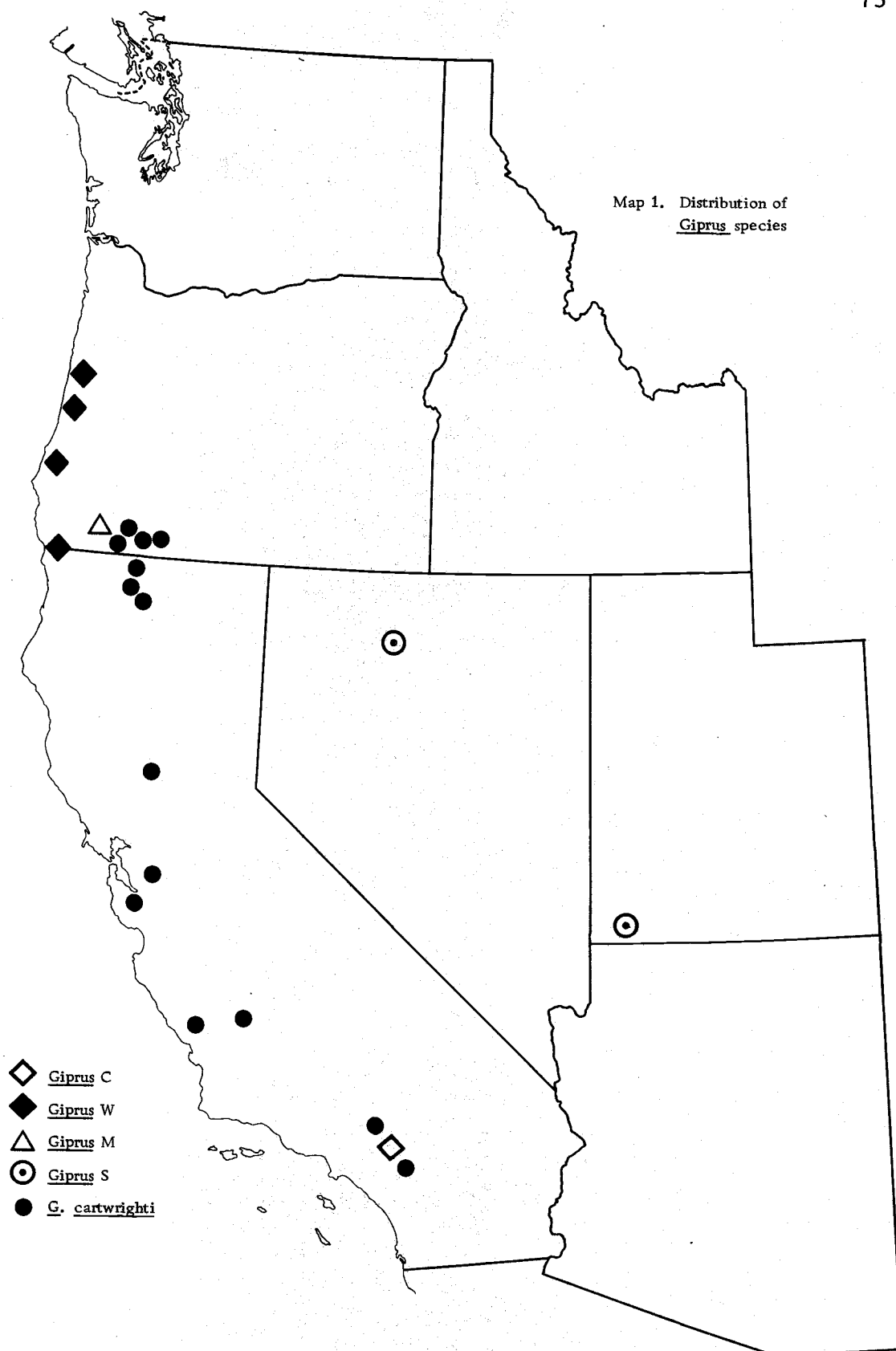
G. siskiyou is not only the structurally most variable species but has been taken from a greater variety of host plants and over a greater geographic area than any other species except G. cartwrighti. While extension of the range is probably a recent occurrence, the structural and ecological plasticity of this species suggest that within G. siskiyou lies the potential for further speciation, and possibly the root of past speciation. While it would be presumptuous to assume that G. siskiyou might have given rise to all other species of Giprus, it could conceivably be the ancestor of Giprus V, Giprus M, and Giprus G, all of which occur close to the center of G. siskiyou's distribution and in similar habitats.

Since there is little apparent structural difference among the

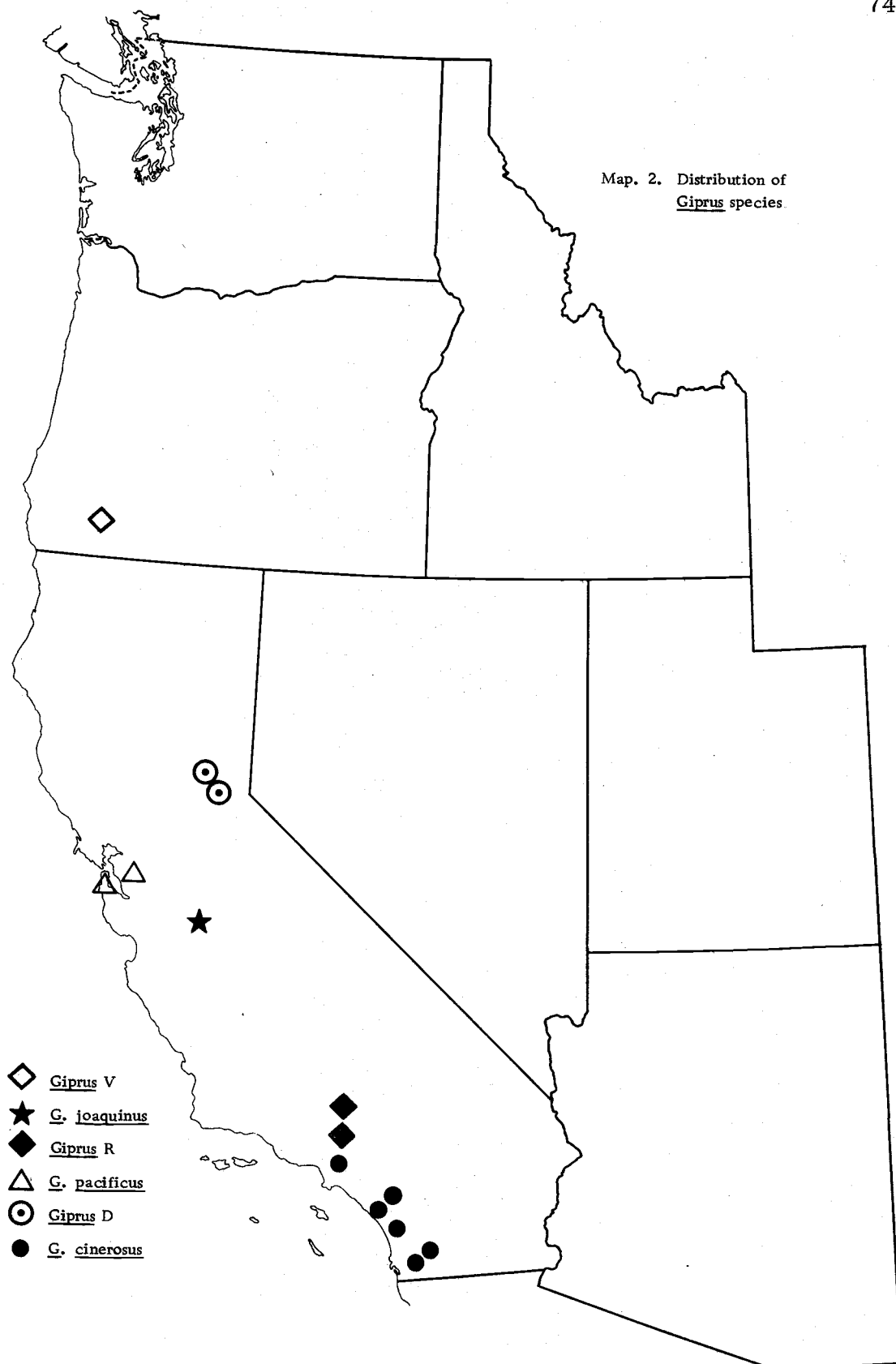
females of the different species of Giprus and the males differ mainly in aedeagal embellishments, most species may have been evolved, not because they held some adaptive advantage over the parent species, but as a result of mutation or inbreeding in the limited gene pool of a population which had become isolated from the parent population. This would explain the existence of many species with limited distributions which differ structurally from their neighbours only by characters of the shape, curvature, and processes of the aedeagus.

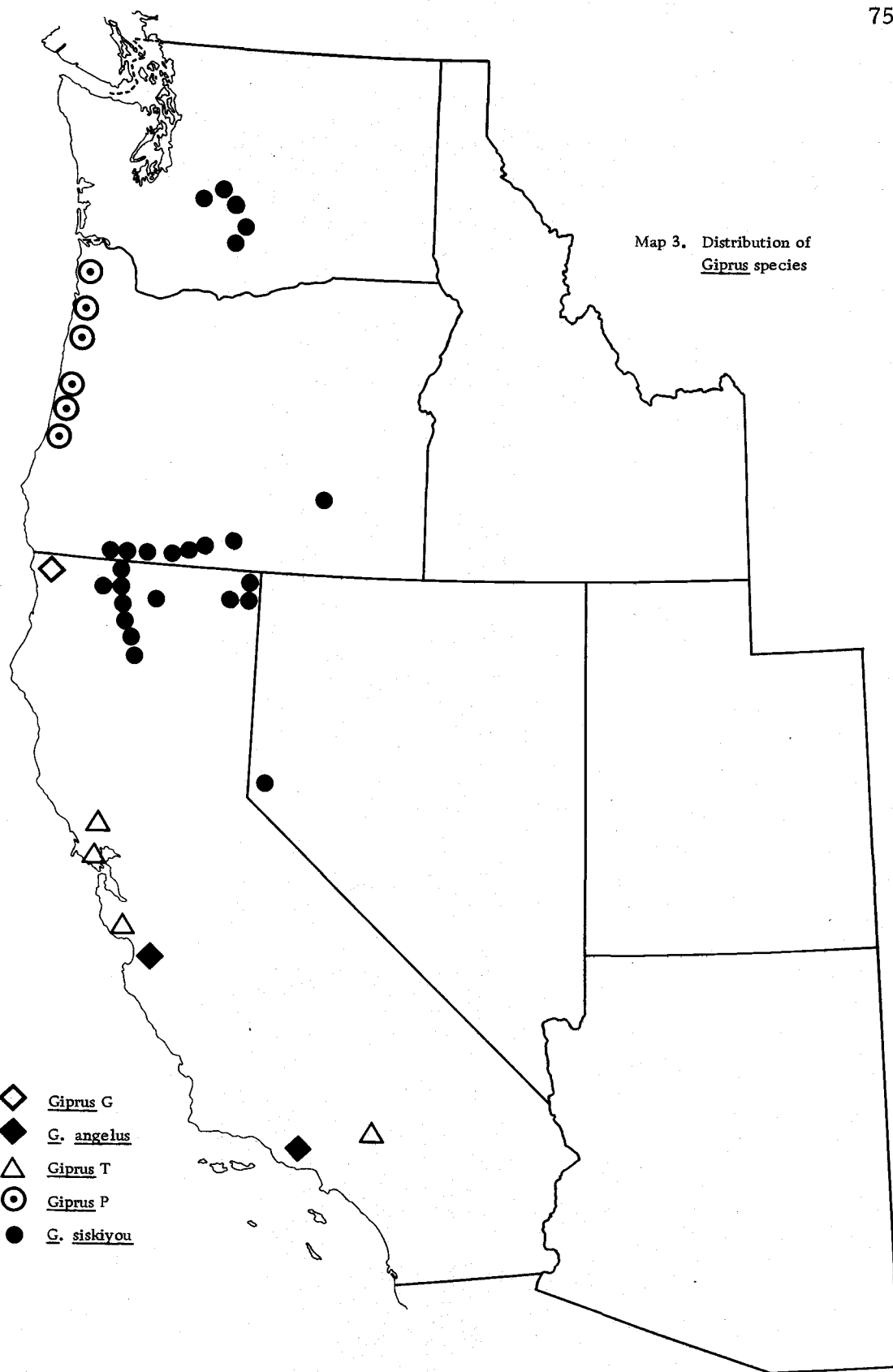
## FUTURE AREAS OF RESEARCH

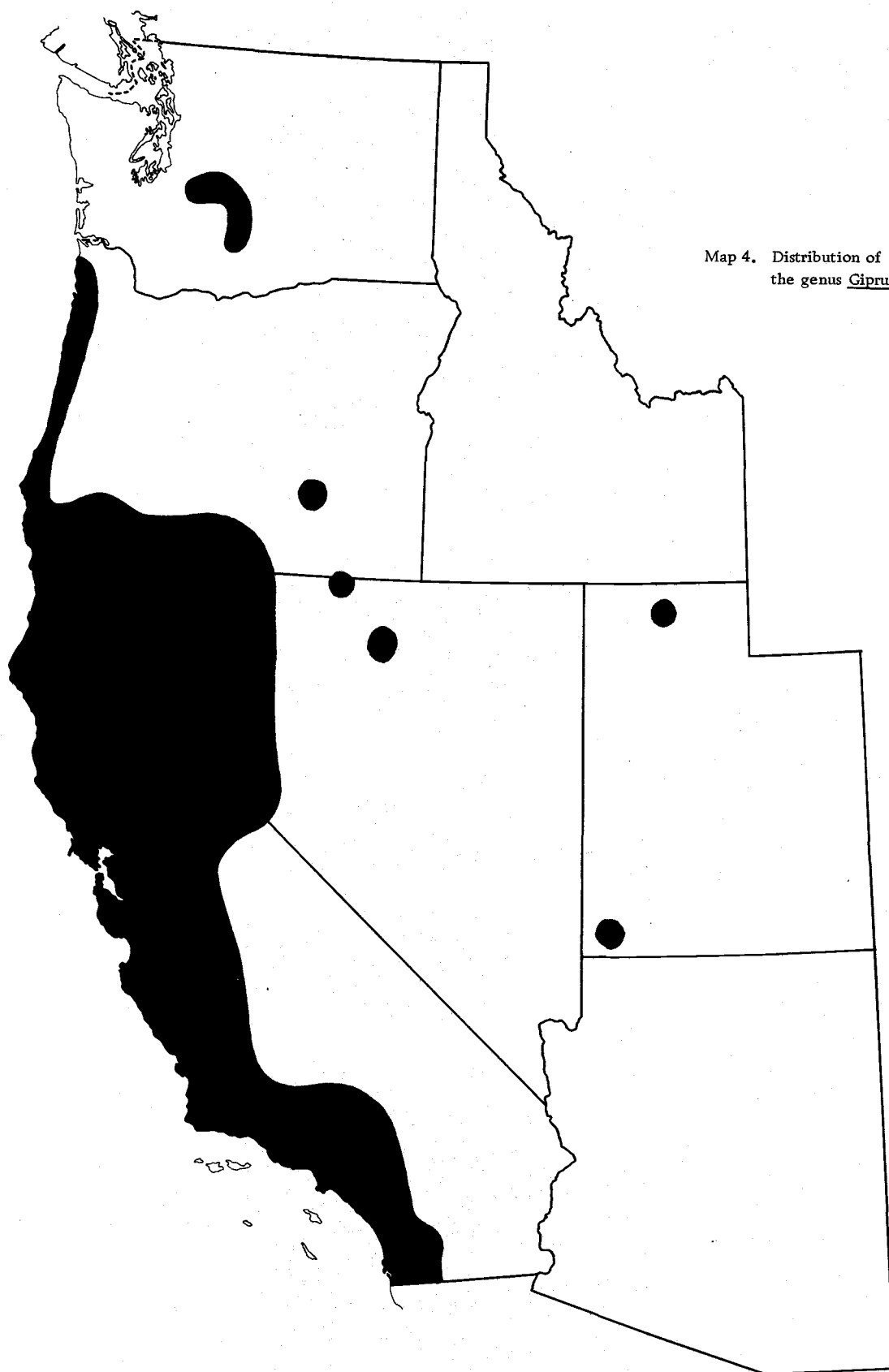
This study has brought to light many areas where further investigation is needed before we can fully understand the species concept as applied to Giprus and the possible evolutionary pathways within the genus. Concentrated field work should provide more accurate knowledge of the distributions of known species and would probably uncover new species, especially in California, Nevada, and Utah where large areas have not yet been searched for Giprus. More detailed investigations of the vegetation and climate of habitats where Giprus occurs, regular sampling of populations, and long term observation of both large and small populations should provide much information useful in biological studies of the genus. A record of climatic conditions (temperature and precipitation) at actual collection sites will allow more accurate comparison of climatic conditions within and among sites. As yet it is not known where the eggs are laid and only fifth instar nymphs have been observed. Laboratory rearings would establish host preferences and supply information about the behavior of the adults and nymphs, duration of nymphal instars, and diapause in Giprus.



Map. 2. Distribution of  
Giprus species.



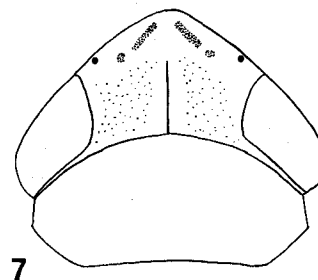
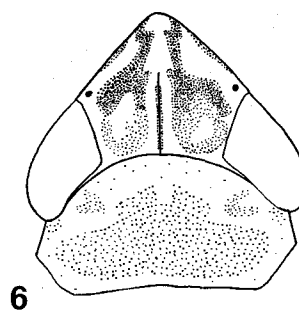
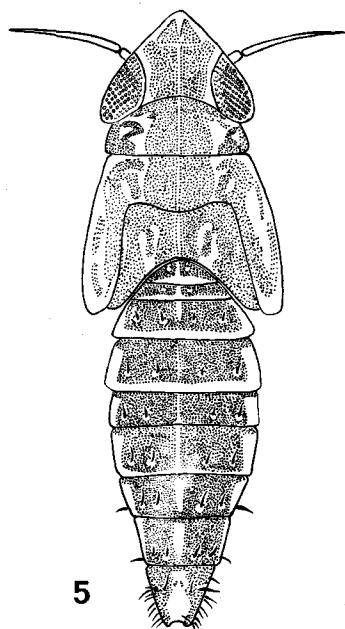
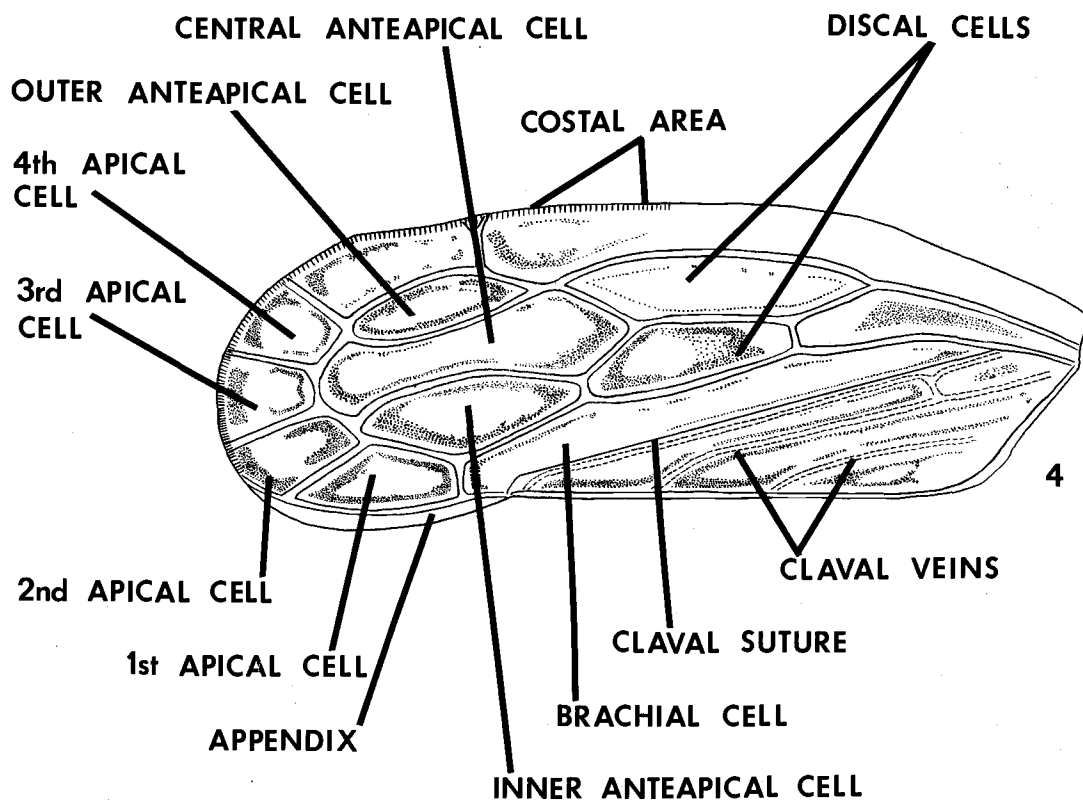






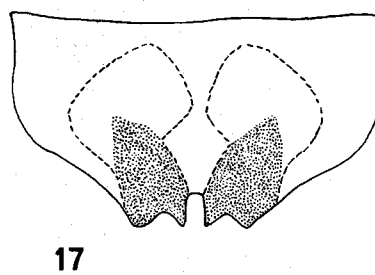
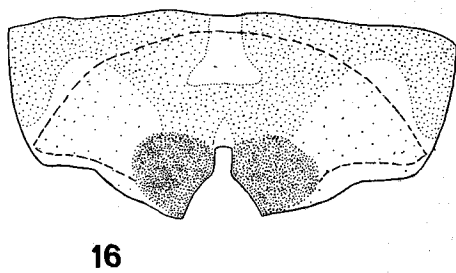
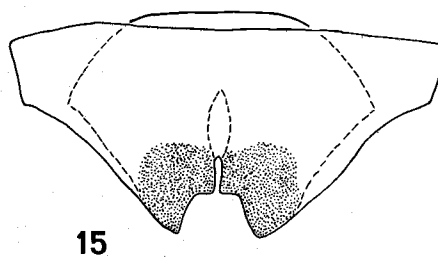
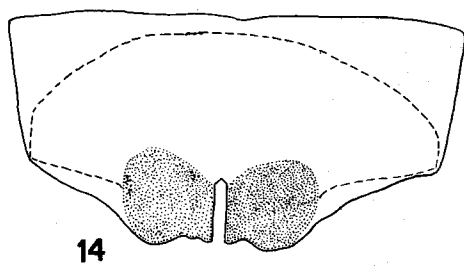
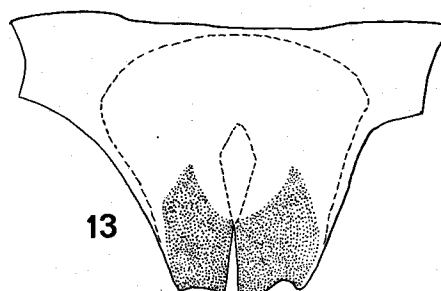
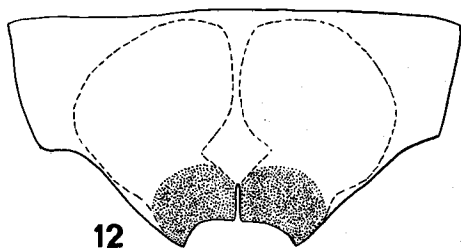
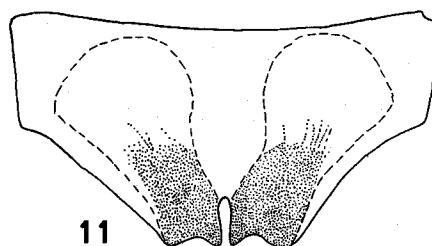
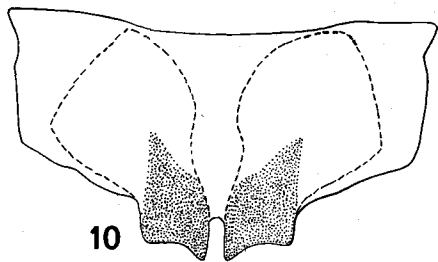
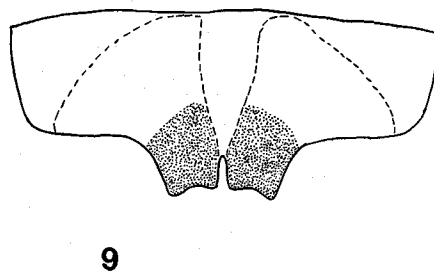
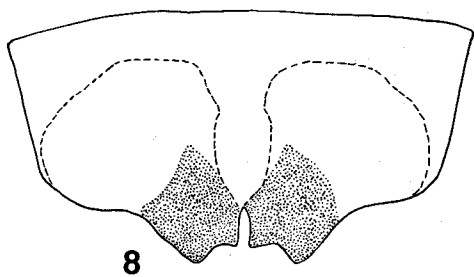
Figure

- 4     Giprus siskiyou : forewing
- 5     Giprus M : fifth instar nymph
- 6     Giprus siskiyou : head
- 7     Giprus W : head



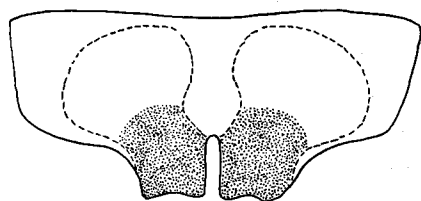
Figure

- 8     Giprus C : female 7th sternum
- 9     Giprus cinerosus : female 7th sternum
- 10    Giprus R : female 7th sternum
- 11    Giprus T : female 7th sternum
- 12    Giprus S : female 7th sternum
- 13    Giprus joaquinus : female 7th sternum
- 14    Giprus M : female 7th sternum
- 15    Giprus angelus : female 7th sternum
- 16    Giprus V : female 7th sternum
- 17    Giprus pacificus : female 7th sternum

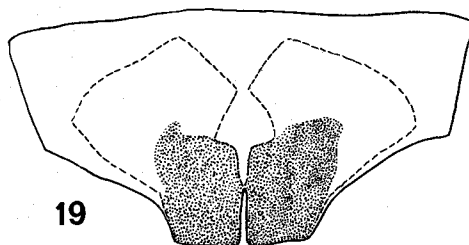


Figure

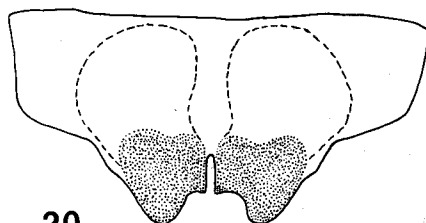
- 18 Giprus W : female 7th sternum
- 19 Giprus G : female 7th sternum
- 20 Giprus P : female 7th sternum
- 21 Giprus siskiyou : female 7th sternum
- 22 Giprus cartwrighti : female 7th sternum
- 23 Giprus siskiyou : male genital capsule
- 24 Giprus W : male genital capsule
- 25 Giprus R : male genital capsule
- 26 Giprus V : male genital capsule
- 27 Giprus cartwrighti : male genital capsule



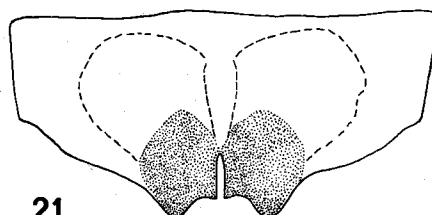
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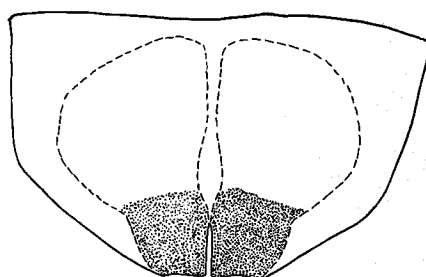
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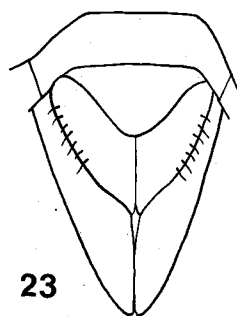
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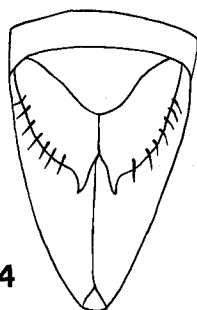
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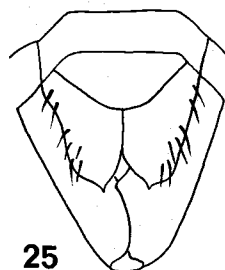
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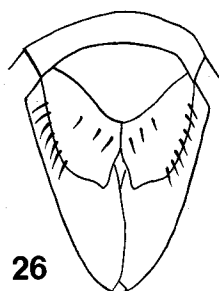
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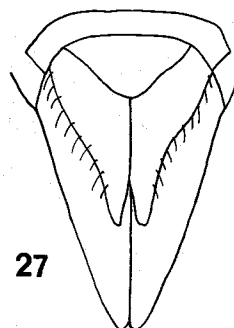
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Figure

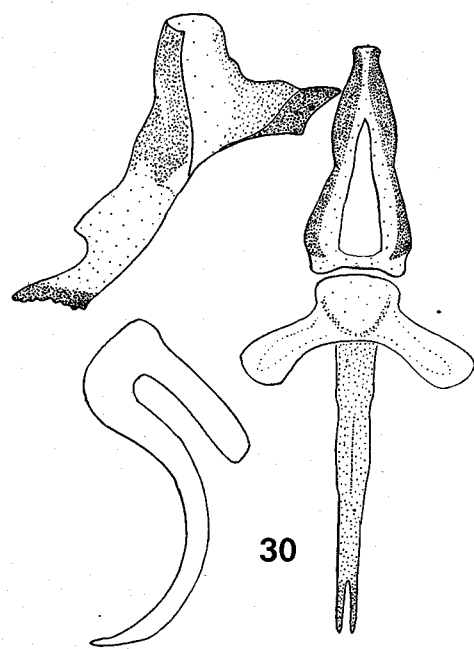
- 28     Giprus cinerosus : connective and aedeagus
- 29     Laevicephalus sylvestris (Osborn & Ball) :  
         connective and aedeagus
- 30     Laevicephalus incongruus : connective, style,  
         and aedeagus
- 31     Giprus siskiyou (Mt. Shasta, California) :  
         connective, style, and aedeagus



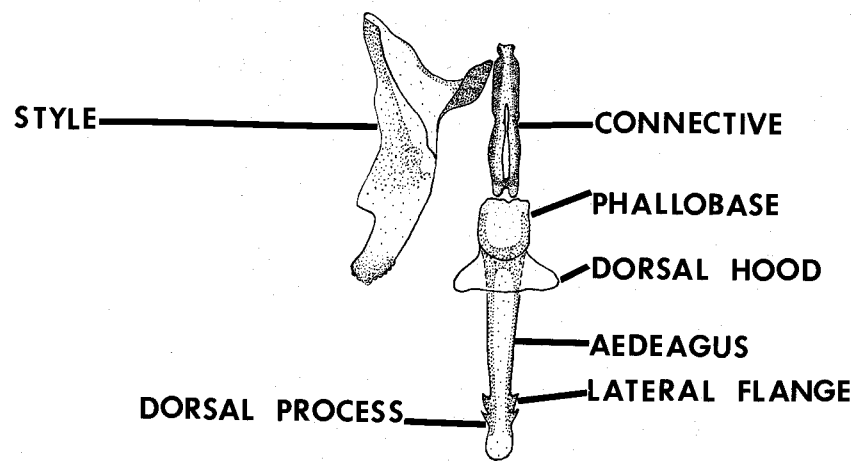
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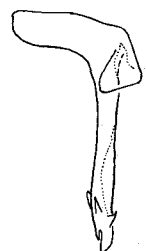
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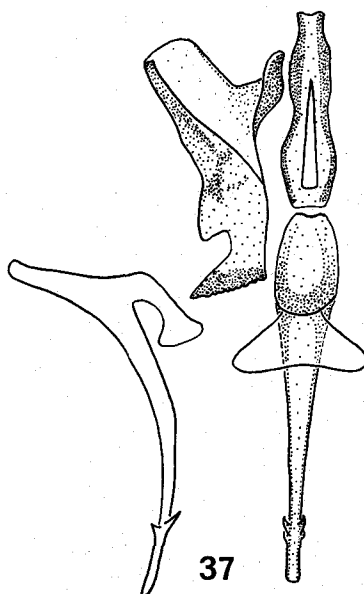
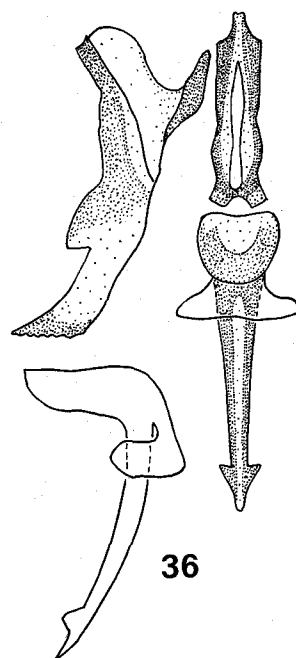
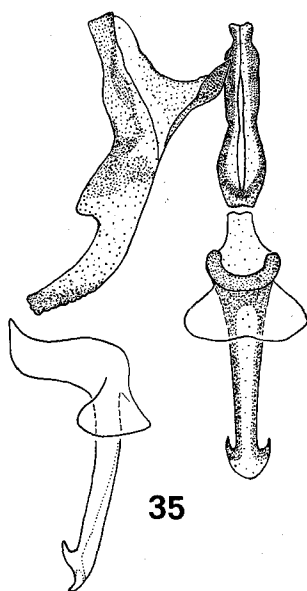
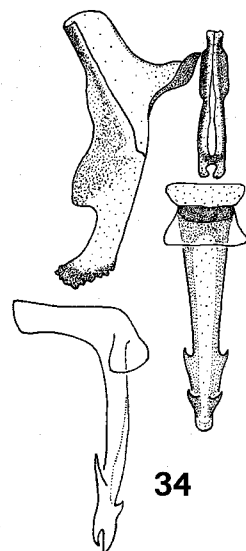
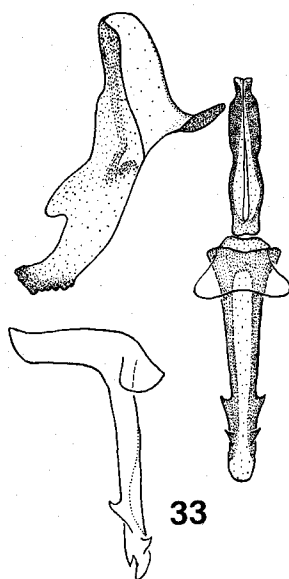
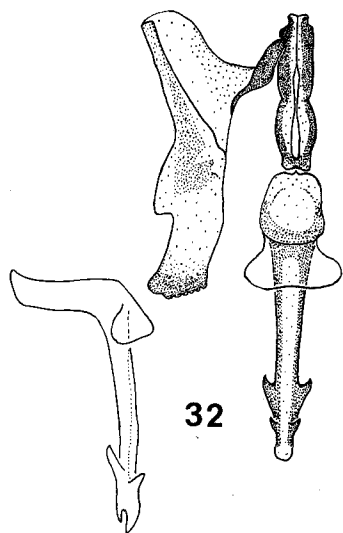
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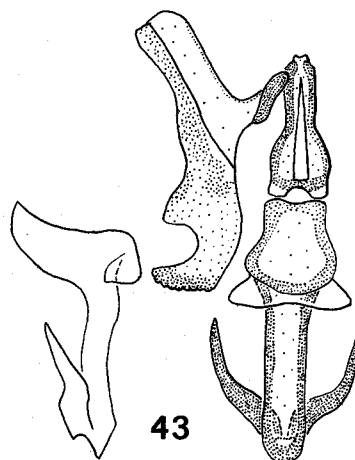
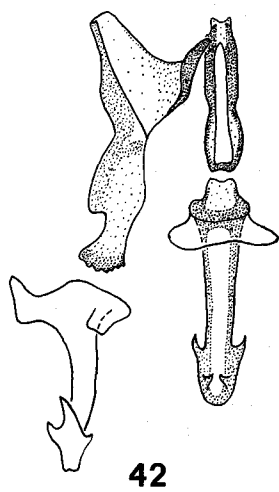
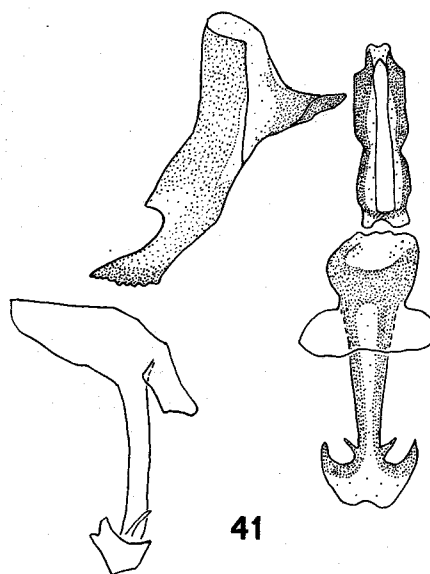
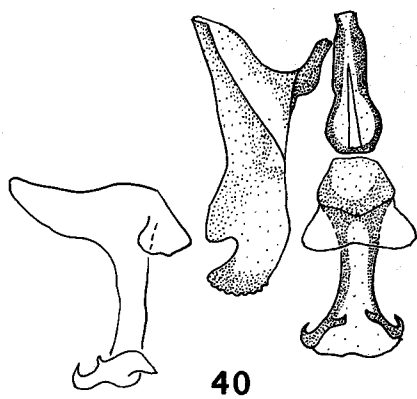
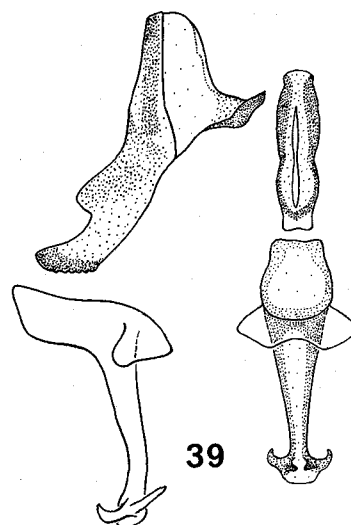
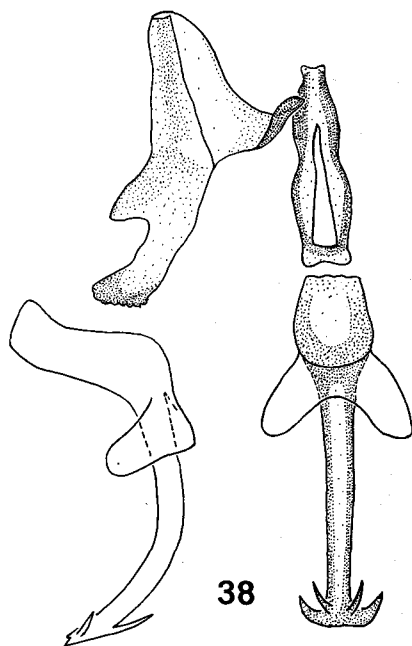
Figure

- 32 Giprus siskiyou (15 miles NE Alturas, California) : connective, style, and aedeagus
- 33 Giprus siskiyou (Cliffdell, Washington) : connective, style, and aedeagus
- 34 Giprus siskiyou (11 miles E Frenchglen, Oregon) : connective, style, and aedeagus
- 35 Giprus G : connective, style, and aedeagus
- 36 Giprus W : connective, style, and aedeagus
- 37 Giprus joaquinus : connective, style, and aedeagus



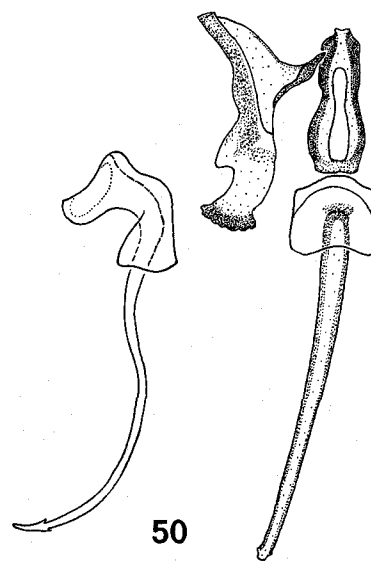
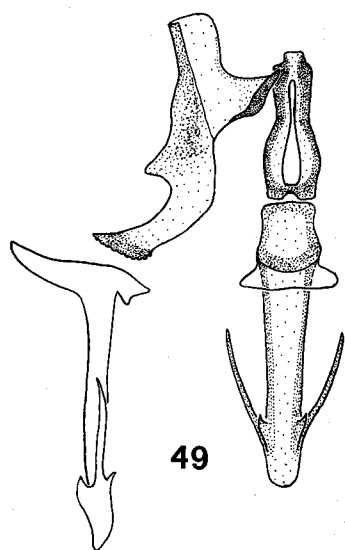
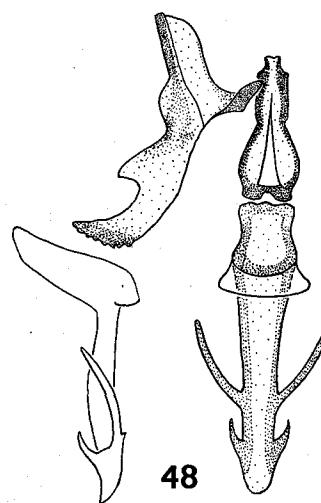
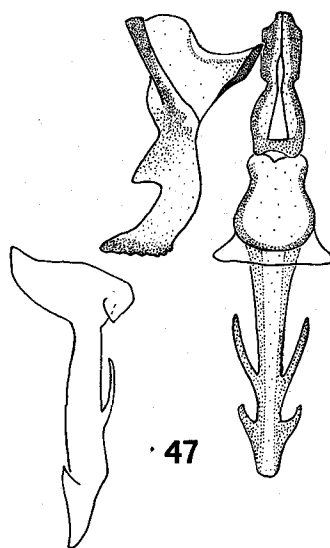
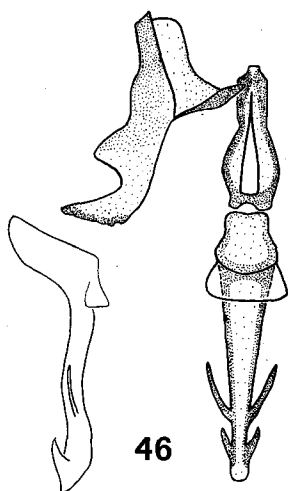
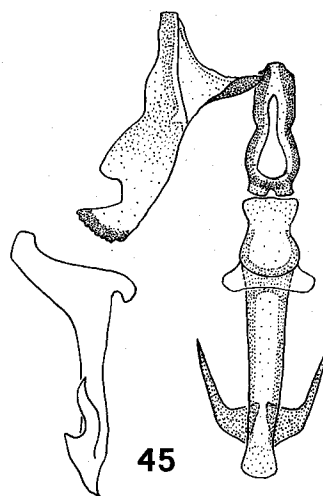
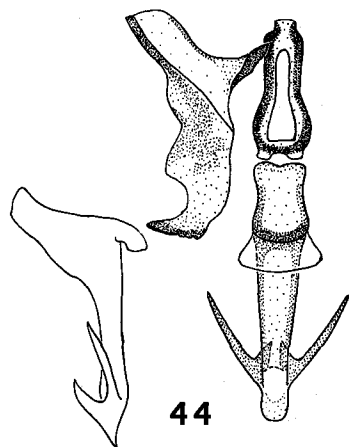
Figure

- 38     Giprus D : connective, style, and aedeagus
- 39     Giprus angelus : connective, style, and  
         aedeagus
- 40     Giprus V : connective, style, and aedeagus
- 41     Giprus P : connective, style, and aedeagus
- 42     Giprus M : connective, style, and aedeagus
- 43     Giprus S : connective, style, and aedeagus



Figure

- 44     Giprus T (Tehachapi Pass, California) :  
         connective, style, and aedeagus
- 45     Giprus T (Mill Valley, California) :  
         connective, style, and aedeagus
- 46     Giprus pacificus : connective, style, and  
         aedeagus
- 47     Giprus C : connective, style, and aedeagus
- 48     Giprus R : connective, style, and aedeagus
- 49     Giprus cinerosus : connective, style, and  
         aedeagus
- 50     Giprus cartwrighti : connective, style, and  
         aedeagus

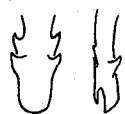


Figure

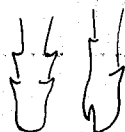
- 51-67    Giprus siskiyou (3 miles S Weed, California) :  
apex of aedeagus,
- 68-87    Giprus siskiyou (36 miles E Klamath Falls) :  
apex of aedeagus



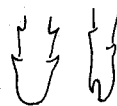
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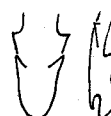
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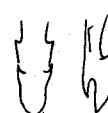
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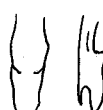
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## APPENDIX

## APPENDIX-LIST OF UNIDENTIFIED FEMALE SPECIMENS

STATE	COUNTY	LOCALITY	DATE
CALIFORNIA	Kern	Tehachapi Pass 3900'	III-23-71
	Kern	Poso Creek	VI-5-29
	Lake	N Fork Cache Cr. Hwy 20	V-14-61
	Los Angeles	Tanbark Flat	VI-26-52
	Los Angeles	Saugus	VI-7-35
	Los Angeles	-	IV-2-16
	Los Angeles	-	March
	Los Angeles	-	April
	Los Angeles	Pasadena	IV-6-09
	Marin	Golden Gate	VII-17-33
	Mendocino	11 mi E Calpella	VI-18-59
	Mendocino	Hopland	V-9-26
	Monterey	Bradley	V-23-20
	Monterey	Jolon	V-11-59
	Riverside	Perris	VI-5-35
	Riverside	Riverside	IV-28-71
	Riverside	Riverside	IV-29-71
	San Bernardino	1/2 mi NE Devore 2200'	IV-29-71
	San Bernardino	Cajon Pass	VI-6-35
	San Diego	-	IV-2-16
	San Diego	Warner Springs	VI-3-35
	San Diego	Del Mar	VI-2-35
	San Diego	Newton	VI-1-35
	San Diego	San Diego	IV-25-20
	San Diego	San Diego	V-24-13
	San Diego	San Diego	IV-23-20
	San Luis Obispo	Atascadero	IV-22-32
	Santa Barbara	Santa Maria	-
	Santa Clara	San Jose	IV-9-31
	Santa Cruz	Santa Cruz	VI-18-17
	Ventura	Foster Park	IV-13-06
	Yolo	Davis	V-7-51
NEVADA	Humboldt	3 mi S Denio	V-21-71
	Humboldt	3 mi S Denio	VI-23-71
UTAH	Boxelder	3 mi SW Lampo	VI-11-33

## INDEX TO GENERA AND SPECIES

<u>angelus</u> (Oman), <u>Giprus</u> . . . . .	41
C (species, new), <u>Giprus</u> . . . . .	49
<u>cartwrighti</u> (Oman), <u>Giprus</u> . . . . .	33
<u>Cazen</u> Oman . . . . .	11
<u>cinerosus</u> (Van Duzee), <u>Giprus</u> . . . . .	45
D (species, new), <u>Giprus</u> . . . . .	40
G (species, new), <u>Giprus</u> . . . . .	37
<u>Giprus</u> Oman . . . . .	9
<u>incongruus</u> Oman, <u>Laeviccephalus</u> . . . . .	12
<u>joaquinus</u> (Oman), <u>Giprus</u> . . . . .	31
<u>Laeviccephalus</u> DeLong . . . . .	11
<u>Lemellus</u> Oman . . . . .	11
M (species, new), <u>Giprus</u> . . . . .	44
P (species, new), <u>Giprus</u> . . . . .	43
<u>pacificus</u> (Oman), <u>Giprus</u> . . . . .	50
<u>Psammotettix</u> Haupt . . . . .	11
R (species, new), <u>Giprus</u> . . . . .	46
S (species, new), <u>Giprus</u> . . . . .	48
<u>siskiyou</u> (Oman), <u>Giprus</u> . . . . .	35
<u>Sorhoanus</u> Ribaut . . . . .	11
T (species, new), <u>Giprus</u> . . . . .	47
V (species, new), <u>Giprus</u> . . . . .	42
<u>Verdanus</u> Oman . . . . .	11
W (species, new) <u>Giprus</u> . . . . .	38