A Revision of the Nearctic Species of the *Cicindela sylvatica* group (Coleoptera: Cicindelidae)

by

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ABSTRACT

Interspecific and intraspecific variation of *C. longilabris* Say and *C. nebraskana* Casey were studied by means of discriminant analysis of morphometric data and univariate analysis of qualitative characters of adult specimens. The geographic variation of male and female genitalic structures of *C. longilabris* and *C. nebraskana* was studied and compared with that of the Palearctic species of the *sylvatica* group: *C. sylvatica* Linnaeus, *C. granulata* Gebler, *C. japana* Motschulsky, *C. gemmata* Faldermann, *C. soluta* Dejean and *C. lacteola* Pallas. Soil associations of the two Nearctic species were investigated.

C. longilabris is a boreal and montane forest species occurring on Podzolic soils in eastern North America and Luvisolic and Brunisolic soils of coniferous forests in western North America as well as in boreal forest-grassland transition areas. Three subspecies are recognized: *C. l. longilabris* Say, found across the boreal zone from Newfoundland and New England to Alaska, *C. l. laurentii* Schaupp, in the Rocky mountain areas of the United States, including isolated populations in northern New Mexico, eastern Arizona, northern Arizona and southwestern Utah, and *C. l. perviridis* Schaupp, found in the Sierra Nevada and Cascade Mountains of California, Oregon and Washington. An area of hybridization occurs in southwestern Alberta, southeastern British Columbia, eastern Washington, Idaho and northwestern Montana where the three subspecies converge geographically. *C. nebraskana* is a monotypic species which occurs on Chernozemic soils of prairie grasslands and grassland-forest transition zones of western North America.

The three year life cycle of *C. longilabris* is described. Two winters are passed in the larval stage and one winter in the adult stage before mating and oviposition occur. The egg stage and first, second and third stage larvae of *C. longilabris* are described.

A reconstructed phylogeny is presented in which three species pairs are evident, *C. soluta-C. gemmata*, *C. sylvatica-C. granulata*, and *C. longilabris-C. nebraskana*, with *C. japana* being most closely related to the *soluta-gemmata* sibling species, and *C. lacteola* having been derived earlier in the evolution of the whole group.

This thesis is an original composition, based on research carried out by the author, and has not been previously submitted for credit toward any degree or diploma. Where the work of others has been included, it has been so acknowledged and appropriately cited.

Timothy G. Spanton

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TABLE OF CONTENTS

TABLE OF CONTENTS (Cont'd.)

LIST OF TABLES

LIST OF TABLES (Cont'd.)

LIST OF TABLES (Cont'd.)

LIST OF TABLES (Cont'd.)

LIST OF FIGURES

FIGURE

LIST OF FIGURES (Cont'd.)

LIST OF FIGURES (Cont'd).

LIST OF FIGURES (Cont'd.)

INTRODUCTION

Many North American species of tiger beetles have extensive geographic ranges and exhibit a large amount of intraspecific variation especially in such obvious characters as colour and pattern of markings of the elytra (Willis 1967). Many typologists in the last century and early part of this century have described individual variants as species or subspecies without understanding the large degree of variation present in these beetles (Willis 1967). As a result there has been much synonymy and confusion over the status of the plethora of formally named taxa.

The descriptive and classificatory phases of the study (alpha and beta taxonomy) of the North American tiger beetles is fairly complete, it is only in the last twenty years that studies of intraspecific variation, or gamma taxonomy have been conducted. Freitag studied the geographic variation, distribution and revised the taxonomy of the North American species of the *Cicindela maritima* group of tiger beetles. Willis (1967) studied the geographic variation and ecology of a diverse group of *Cicindela* species occurring in saline habitats in the central United States, Gaumer (1977) studied intraspecific variation and taxonomy of adults and larvae of *C. formosa*, and Kaulbars (1982) studied the morphological and ecological variation of the species of the *sexguttata* species group of *Cicindela*.

Wallis (1961) confused many of the intraspecific categories of *C. longilabris* and *C. nebraskana* but indicated that his understanding of these species was based on few specimens and suggested that this group required additional study. Leffler and Pearson (1976) indicated that a revision of *C. nebraskana* and *C. longilabris* was required to sort out the nomenclature of the group.

The immature stages and life histories of a number of tiger beetle species have been studied (Shelford, 1908; Criddle 1907, 1910; Hamilton 1925; Willis, 1967, among others) but the life histories of *C. longilabris* and *C. nebraskana* are largely unknown. The larvae of *C. longilabris* are known only from one second instar specimen (Leffler 1979) and the larvae of *C. nebraskana* are known only from one third instar specimen and three exuviae (Leffler 1979).

The objectives of this study were: to determine if *C. longilabris* and *C. nebraskana* are distinct species; to investigate the pattern of intraspecific variation in the complex; determine what, if any intraspecific groupings of populations warranted formal subspecific recognition; determine which of the available names should apply to any subspecies recognized; and to investigate the life history of *C. longilabris* and describe as many of the immature life stages as possible.

MATERIALS AND METHODS

Adult specimens and loaning institutions

More than 6,210 adult specimens were examined in the course of this study, of these 1357 specimens were used in the numerical analyses.

Most of these specimens were obtained on loan from the following institutions and private collections. I have used standard acronyms for collections of insects as proposed by Heppner and Lamas (1982), wherever possible.

AAM	Alan and Anne Morgan, Departments of Earth Sciences and Biology respectively, University of Waterloo, Waterloo, Ontario N2L 3G1
AMNH	American Museum of Natural History, New York, New York 10024 L. H. Herman
BGSU	Bowling Green State University, Bowling Green, Ohio 43403 R. C. Graves
CAS	California Academy of Sciences, San Francisco, California 94118 D. H. Kavanaugh
CDF	Clifford D. Ferris, P. O. Box 3351 University Station, Laramie, Wyoming 82071
CMP	Carnegie Museum of Natural History, Pittsburgh, Pa. 15213 R. L. Davidson, G. Ekis
CNC	Canadian National Collection if Insects, Biosystematics Research Institute, Ottawa, Ontario K1A 0C6 J. E. H. Martin

CSU	Colorado State University, Fort Collins, Colorado 80523 H. E. Evans
CU	Cornell University, Ithaca, New York 14853 L. L. Pechuman, Q. D. Wheeler
ISU	Iowa State University, Ames, Iowa 50011 R. E. Lewis
KSU	Kansas State University, Manhattan, Kansas 66506 H. D. Blocker
MPM	Milwaukee Public Museum, Milwaukee, Wisconsin 53233 G. R. Noonan
MSU	Montana State University, Boseman, Montana 59717 S. Rose
MUN	Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9 D. J. Larson
NAU	Northern Arizona University, Flagstaff, Arizona 86001 C. D. Johnson
NCSR	Northern Carolina University, Raleigh, N. C. 27650 C. Parron
NDSU	North Dakota State University, Fargo, N. D. 58105 E. U. Balsbaugh
OKS	Oklahoma State University Natural and Cultural History Museum, Stillwater W. A. Drew
PSU	Pennsylvania State University, University Park, Pa 16802 D. L. Pearson
PUL	Purdue University, Lafayette, Indiana 47907 A. Provonsha
REA	Robert E. Acciavatti, 2111 Cherry Street, Morgantown, W. V. 26505
SMEK	Snow Museum of Entomology, University of Kansas, Lawrence 66045 G. W. Byers

UAE	University of Alberta, Edmonton, Alberta G. E. Ball
UAF	University of Arkansas, Fayetteville, Arkansas. 72701 R. Chenowith, C. Carlton
UBC	University of British Columbia, Vancouver, B.C. S. G. Cannings
UIM	University of Idaho, Moscow, Idaho 83843 W. F. Barr
UMAA	University of Michigan, Ann Arbor, Michigan 48109 T. E. Moore, M. F. O'Brien
UMW	University of Manitoba, Winnipeg, Manitoba R3T 2N2 T. D. Galloway
UNM	University of New Mexico, Albuquerque, N. M. 87131 C. S. Crawford
UOG	University of Guelph, Guelph, Ontario. N1G 2W1 D. Pengelly, S. Marshall
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560 T. L. Erwin
USU	Utah State University, Logan, Utah 84322 W. J. Hanson
UV	University of Vermont, Burlington, Vermont R. T. Bell
UWM	University of Wisconsin, Madison, Wisconsin 53706 S. Krauth
WJ	Walter Johnson, 2917 16th Avenue South, Minneapolis MN. 55407
WSU	Washington State University, Pullman, WA. 99164 R. Zack

Characters and Measurements

The following adult characters were used in this study.

1. Total head width across the widest point on the eyes (hw)(Fig. 1)
2. Length of labrum including the median tooth (ll)(Fig. 1)
3. Width of labrum (lw) (Fig. 1)

4. Ratio: length of labrum/width of labrum (ll/lw)
5. Colour of labrum (lcol)

   I arbitrarily assigned three states for this character.

   1) uniformly pale in colour, or pale except for a darkened apical edge.
   2) apical edge or midrib broadly darkened or mottled.
   3) uniformly dark brown or black.

   The setal pattern on the labrum was used as another character. The number of setae in each of four locations on the frontal surface of the labrum was indicated (Fig. 2).

6. Number of setae in position 1 (ls1)
7. Number of setae in position 2 (ls2)
8. Number of setae in position 3 (ls3)
9. Number of setae in position 4 (ls4)
10. Number of sensory setae on the first segment (scape) of the left antenna (Fig. 3) (ssl)
11. Number of sensory setae on the scape of the right antenna (ssr)
12. Number of other setae on the scape of the left antenna (osl)
13. Number of other setae on the scape of the right antenna (osr)
14. Pronotal width (pw) Fig. 4)
15. Pronotal length (pl) (Fig. 4)
16. Ratio: pronotal width/pronotal length (pw/pl)
17. Mesothoracic femur length (fl) (Fig. 5)

   The left mesothoracic leg was chosen preferentially. Where the left was missing, the same measurement from the right leg was used. The mesothoracic leg was chosen because prothoracic and metathoracic legs were more frequently missing from pinned specimens.

18. Mesothoracic tibia length (tl) (Fig. 5)
19. Ratio: mesofemur length/mesotibia length (fl/tl)
20. Length of left elytron (el) (Fig. 6)

    This was measured from the apex of the scutellum along the medial edge of the elytron to its apex.

21. Width of left elytron at its widest point (ew) (Fig. 6)

    This was measured with the beetle held in a horizontal plane. If the specimen was canted to one side it would produce a slightly greater measurement. This was difficult to measure accurately as many specimens were pinned at odd angles.

22. Ratio: head width/pronotal width (hw/pw)
23. Ratio: Elytral width/elytral length (ew/el)
24. Ratio: femur length/elytral length (fl/el)
25. Per cent of elytral surface covered by light markings or maculations. This was estimated in a manner very similar to that used by Gaumer (1977). A series of specimens representing the range of variation present in *C. nebraskana* and *C. longilabris* was selected. A drawing was made of the left elytron of each specimen. A polar planimeter was used to determine the percentage of each elytron covered by the maculations. Subsequently, these drawings were used as standards of comparison for

estimating the percentage to the nearest one of six categories: 1%, 2%, 5%, 10%, 20% and 30% (Fig. 7).

26. The configuration of the humeral lunule (hl)

I recognized the following six states of this character (Fig. 8)

0) humeral lunule absent
1) one humeral dot present at shoulder of the elytron
2) one subhumeral dot present
3) both humeral dots present
4) humeral lunule complete or nearly so
5) humeral lunule complete and connected to marginal line

27. The configuration of the middle band (mb)

Specimens were categorized as being closest to one of the following states of this character (Fig. 9).

0) middle band completely absent
1) middle band barely discernible, or broken into two pieces
2) middle band present and with angle of bend > 45° , and not touching lateral margin of the elytron
3) band complete, touching lateral edge of elytron and with angle of bend > 45°
4) band present, not touching lateral margin of elytron and elbow < 45°
5) middle band complete, touching lateral margin of elytron and elbow < 45°
6) band complete, touching lateral margin of elytron, with marginal line well developed

28. Apical lunule character states (al)

The following states were recognized in the degree of development of the apical lunule (Fig. 10)

0) apical lunule entirely absent
1) apical lunule consists of small subapical dot
2) apical lunule consists of large subapical dot
3) apical lunule complete or nearly so
4) lunule complete and with dot expanded and extending far anteriorly
5) apical lunule continuous with marginal line

29. Colour of dorsal surface of elytra (ec)(Table 1)

30. Colour of proepisternum (pc) (Table 2)

31. Colour of ventral surface of abdomen (vc) (Table 3)

Tables 1 - 3 contain a vernacular description of a colour condition, the character state number and corresponding name and number from the ISCC-National Bureau of Standards Colour Charts (Kelly and Judd, 1965). For each of characters 29, 30, and 31 a small series of specimens was chosen to represent the range of variation found in the *C. longilabris* species complex. These standard specimens were compared with the ISCC-National Bureau of Standards Colour Charts (Kelly and Judd, 1965) and the corresponding colour name and number were noted. If a specimen did not closely match any one colour, the two or three colours closest to it were noted. Subsequently, each studied specimen was compared against standard specimens and designated as being closest to one of the representative colour categories.

TABLE 1. Designated states for colour of the dorsal surface of elytra of *C. longilabris* and *C. nebraskana*.

Vernacular description	Code	ISCC-NBS* Number	ISCC-NBS Name
Black	1	267	Black
Dark Brown	2	65	Brownish Black
Mid Brown to Bronze	3	56	Deep Brown
Olive Green	4	108 or 111	Dark Olive Dark Grayish Olive
Green	5	142	Deep Green
Blue Green	6	174	Dark Greenish Blue
Dark Blue	7	183	Dark Blue

* Kelly and Judd, 1965.

TABLE 2. Designated states for colour of the proepisternum of *C. longilabris* and *C. nebraskana*.

Vernacular Description	Code	ISCC-NBS[*] Number	ISCC-NBS Names
Shining Black	1	267	Black
Black and Green	2	267 and 142	Black and Deep Green
Metallic Green	3	142	Deep Green
Metallic Green and Blue, or Metallic Green and Purple	4	142 and 183 or 142 and 197	Deep Green and Deep Blue, or Deep Green and Deep Purplish Blue
Blue and/or Purple Predominantly	5	183 and/or 197	Deep Blue and/or Deep Purplish Blue
Bronze and Metallic Green or Bronze and Purple in combination	6	75 and 142 or 75 and 197	Deep Yellowish Brown and Deep Green or Deep Yellowish Brown and Deep Purplish Blue
Bronze to Chestnut Brown Predominantly	7	75 and 56	Deep Yellowish Brown to Deep Brown

[*] Kelly and Judd, 1965.

TABLE 3. Designated states for colour of the venter of the abdomen of *C. longilabris* and *C. nebraskana*.

Vernacular description	Code	ISCC-NBS Number	ISCC-NBS Names
Black	1	267	Black
Black and Green	2	267 and 142	Black and Deep Green
Metallic Green	3	142	Deep Green
Metallic Green and Blue or Metallic Green and Purple	4	142 and 183 or 142 and 197	Deep Green and Deep Blue or Deep Green and Deep Purplish Blue
Blue and/or Purple Predominantly	5	183 and/or 197	Deep Blue and/or Deep Purplish Blue
Brown and Metallic Green or Brown and Metallic purple	6	56 and 142 or 56 and 197	Deep Brown and Deep Green or Deep Brown and Deep Purplish Blue
Brown Predominantly	7	56	Deep Brown

* Kelly and Judd, 1965.

One difficulty with this method is that many of the colours of tiger beetles are structural (Shelford, 1917) and have a metallic sheen, whereas those of the standard colour charts are opaque. The colour of the dorsal surface of elytra was designated a single colour state. In the case of colour of the proepisternum and venter of the abdomen, each character state was frequently a mosaic of more than one colour, which added to the problem.

Measurements and character states were taken from adult specimens from 60 different localities across the range of the species complex, 12 population samples of *C. nebraskana* and 48 of *C. longilabris* (Fig. 11, Table 4). An effort was made to choose larger population samples from localities throughout the ranges of the two species. While only small samples were available for many localities they were analyzed with the knowledge that they may have been atypical because of biased sampling by collectors. Occasionally, especially with commonly occurring species, collectors overlook typical specimens in favour of unusual forms.

Numerical Analysis of Morphometric Data

In the numerical analysis of morphometric data sexual dimorphism was examined in each of the species complexes. Males were compared against females for each of the variables with the use of a one-way analysis of variance procedure as described by Kim and Kohout (1975). With the proability of a type one error set at 0.05, significant sexual dimorphism was found in both complexes of *C. nebraskana* and *C. longilabris*. Females of both complexes showed significantly larger measurements in head width, labrum width and length, pronotal width and length and elytral width and length, suggesting that females of both species are significantly larger in overall size. In all subsequent analyses of morphometric data males and females were treated separately. All analyses were performed with the use of a Vax 11/780 computer.

Discriminant analyses based on the above series of measurements were performed to investigate relative differences among population samples. The discriminant procedure used was described by Klecka (1975) and was taken from the Statistical Package for the Social Sciences for Vax/VMS, Version M, Release 8.1, May 1, 1981.

The minimum level of tolerance for rejection of characters from the analysis was 0.001. Canonical discriminant function scores for each test are presented in Tables 5 and 6. Tests of the statistical significance of the distances between group centroids for each discriminant test are reported in Tables 7 - 36. The variables selected in each discriminant test are indicated in Table 37.

A linear discriminant function is a combination of character scores which discriminates between groups much better than one character taken singly (Sneath and Sokal, 1973). For this reason significance levels of 0.05 or 0.01 are not useful in this type of analysis. The latter level of significance would identify minor population differences which are not taxonomically useful. Neighbouring populations which appear to be extremely similar were often shown to be significantly different beyond the 0.01 level by these analyses.

Discriminant analyses were used to examine relative relationships between populations with little regard to absolute differences. Under these circumstances a significance level of 0.001 was selected as the minimum requirement indicative of a taxonomic category. However, no taxonomic decisions were based entirely on the evidence of discriminant analysis.

Once the discriminant tests had been applied to determine seemingly important population groupings, additional one way analyses of variance were performed using the procedure described in Kim and Kohout (1975). This was done to investigate the statistical differences in those variables which scored highest in the discriminant functions.

Analysis of colour and pattern of markings

Colour analysis was demonstrated with the use of pie graphs on distribution maps (Figs. 12 - 19) in a manner similar to that used by Freitag (1965), Willis (1967) and Gaumer (1977). Average states of additional characters for each population sample are summarized in Table 38 and were indicated with symbols on maps (Figs. 20 - 27) in a way similar to that used by Goulet and Baum (1981, 1982).

Dissections of Male and Female Genitalia

The genitalia of male and female specimens of widely distributed populations of *C. nebraskana* and *C. longilabris* were examined for structures of taxonomic importance. In addition males and females of 6 Palearctic species were dissected and examined to determine relationships between the species of the *C. sylvatica* group as a whole. In all 170 genitalic dissections were performed.

To study the genitalia, a beetle was first relaxed in hot water. A pair of fine forceps was used to pull out the genitalic armature which was cleared in a hot solution of 10% potassium hydroxide for approximately 10 minutes and washed in water. Dissections were done with the use of a Wild M5 dissecting microscope at 15x and 31x and drawings were made with the aid of an attached drawing tube at magnifications of 31x and 62.5x.

Soil Associations

Collecting localities taken from specimen label data were located as accurately as possible on soil maps to determine if a relationship exists between the distribution of dominant soil types and the distribution of the different forms of the *C. sylvatica* group in North America. National scale and state soil maps were used for this purpose. Conversions between the United States and Canadian systems of soil classification were done as accurately as possible with tables provided in Clayton et al (1977). Descriptions of soil types were followed in Clayton et al (1977) for the Canadian classification and in Soil Survey Staff (1960, 1967) for the American system.

Dates of collection were also recorded from specimen labels and used to plot histograms of frequency of capture versus date to investigate seasonality in adults of *C. longilabris* and *C. nebraskana*.

Label data were also used for compiling distribution lists and plotting distribution maps of the North American species.

Field Methods

Adult specimens were collected with an insect net and killed in an ethyl acetate jar and either pinned the same day or transferred to 70% ethanol for temporary storage. Larvae were collected in one of two ways. The "lie in wait" method involved waiting near the mouth of an open larval burrow until the larva appeared near the surface, at which time a small shovel was driven at an angle under the larva, cutting off its escape route. The other method was to dig the larva out with a hand trowel. As larvae of *C. longilabris* were often found at depths up to 60 cm it was usually helpful to insert a long piece of flexible grass into the burrow until the larva was felt at the bottom. A hole was then dug beside the stalk of grass until the larva was encountered. Larvae were either preserved directly in 70% ethanol or placed alive in a glass vial with a small amount of soil for transport back to the laboratory.

Samples of soil were collected from larval sites and transported to the laboratory where they were thoroughly dried in an oven and, if necessary rolled gently with a rolling pin to break up any aggregations which formed during drying. Each sample was then shaken through a standard sieve series with sieve sizes 2.0 mm, 0.50 mm, 0.25 mm, 0.125 mm, 0.063 mm and 0.037 mm to determine the distribution of soil particle sizes.

Study Sites

One site was located in the Thunder Bay district near the East Bay of Dog Lake, 1 - 5 km W of highway 527 and 50 km N of highway 17. It was used primarily as a source of specimens, both for mating experiments and rearing of larvae. Some observations of activity patterns were conducted at this site. The species *C. longilabris* was found along logging roads that run through second growth forest in an area of sandy soil where the dominant trees were Trembling Aspen (*Populus tremuloides* Michx.) and Jack Pine (*Pinus banksiana* Lamb.) and through an area of slightly more gravelly soil with Trembling Aspen, Jack Pine and Spruce (*Picea* sp.). Ground cover varied from bare soil on the road surface to patchy distributions of bare soil, mosses and lichens, some grasses, wild strawberry (*Fragaria virginiana*) and leaf litter.

The other study site at Stanley Hill Cemetery on highway 17, 16 km west of Thunder Bay, Ontario, included some of the grounds of the cemetery, a small sandy area along the edge of forested land across the highway from the cemetery and a part of a pasture bordering the cemetery on the east side. This was an area of sandy soil with vegetation cover ranging from mixed forest of predominantly Trembling Aspen and Jack Pine to old field habitat and bare soil.

A bare road surface ran along the edge of the field which at one end was in close proximity to Jack Pine trees and it runs farther into an open field habitat at the other end. This road was marked at intervals of approximately 5 meters for a distance of 800 meters.

A multiple mark and recapture study was conducted at this site through the course of the summer to investigate the mobility and relative abundance of the adult beetles. Beetles were searched for visually and captured with a net. Marks were placed on the elytra in the form of small dots of Testor's model enamel paint, which has been used successfully in mark and recapture studies of tiger beetles (Willis, 1974; Palmer, 1976; Kaulbars, 1982) and by a number of other workers on other insects (Southwood 1978). Using 6 locations on each elytron where spots could be placed and six colours of paint, 468 different combinations of marks were possible with no individual bearing more than two spots. Each beetle was captured, marked and released at the same site and its sex, location and date of capture were recorded. Each capture session consisted of one survey from one end of the 800 meters of marked road surface to the other and back again. On days when few beetles were captured this took approximately 2 hours, when beetles were numerous a capture session was limited to 3 hours in duration. An attempt was made to conduct weekly capture/recapture sessions throughout the summer, however, because these beetles are not active in cool or rainy weather a weekly schedule could not be strictly followed. Instead these sessions were conducted mainly on sunny, warm days.

The chronology of larval development was studied at the Stanley Hill study site by marking burrows. A golf tee numbered with a waterproof ink marker was placed 2 cm north of each burrow, and the developmental stage noted. This is easy to do as in *C. longilabris* and many other tiger beetle species, the size of the head and pronotum of the larvae and therefore the diameter of the burrow it inhabits occur in 3 discreet size categories corresponding to the 3 larval instars. Burrows were checked at intervals of a few days to a week throughout the summer. Newly found burrows were marked and each burrow was noted as being open or closed, and if open, the instar stage was recorded.

In the middle to latter half of the summer, 1st instar larval burrows began to appear in numbers too large for all to be marked with golf tees. At this time visual counts were made of open burrows in each stage of development at intervals of a few days to a week to gather further information on the seasonality of the larval stages.

Some observations were made of activity patterns, attempted and successful prey captures and copulatory behaviour. The latter was observed both in the field and the laboratory. Such observations were timed approximately with a wrist watch and recorded.

Rearing Techniques

Live adults were kept in glass terraria approximately 15 cm x 40 cm x 25 cm in size, the bottoms of which were covered to a depth of 3 - 6 cm with soil taken from the site where the beetles were captured. A petrie dish filled to the level of the rim with soil was placed in the shallow end of each terrarium and periodically filled with water. In this way soil moisture available to the beetles ranged from wet at one end to dry at the higher end. Two to three adults of both sexes were placed in each terrarium. Initially mortality due to cannibalism was high until clumps of mosses, grasses and leaf litter from the beetles natural habitat were added to the terraria. The tiger beetles immediately used the leaf litter for cover or dug shallow burrows under the clumps of grass or moss. Aggressive encounters were greatly reduced in number after these modifications. The beetles were fed primarily flour beetles (*Tribolium* sp.) supplemented occasionally with assorted arthropods from sweep-netting.

First instar larvae which appeared in the terraria subsequent to mating and oviposition, and other larvae dug from the field were reared in glass tubes approximately 2 cm in diameter by 30 cm long in a manner similar to that described by Palmer (1979). The rearing tubes were plugged at the bottom with wet cotton balls or crumpled paper towelling and filled to a depth of 20 - 25 cm with soil from the site where the larvae were collected, or in the case of those produced in the laboratory, where their parents were collected. The rearing tubes were stood on end in a plastic bucket and the soil kept slightly moist with water added to the bucket and occasionally applied to the surface with a plant sprayer. Soil moisture was carefully regulated to minimize mould growth. In a few cases mould developed and specimens were lost.

First instar larvae of *Cicindela* were fed early instar larvae of *Tribolium* sp. and second and third instar tiger beetle larvae were fed late instar, pupae and adult *Tribolium*.

Mating and rearing experiments in the laboratory were carried out at an ambient temperature of approximately 20°C, with fluorescent lighting which was generally on during the day and off at night. No attempt was made to approximate naturally occurring photoperiod, temperature or humidity. Palmer (1979) noted that fecundity of some species of tiger beetles is reduced under laboratory conditions and suggested that temperature may be important in egg production. Reproduction success may have been increased if laboratory conditions more closely approximated the warm daytime temperatures, cool nights and long photoperiod typical of summer in the natural environment.

Criteria for species and subspecies

Species concepts have been discussed by Simpson (1961) and Mayr (1969) among many others. The subspecies category has been discussed by many workers including Mayr (1969), Edwards (1954), Parkes (1955), and Smith and White (1965) in favour of its use and by Wilson and Brown (1953), Gosline (1954), Hubbell (1954) and Owen (1963), among others, opposed to its use. It is here felt that the subspecies category, as stated by Mayr (1969), is a useful if arbitrary device for classifying population samples in geographically variable species.

In the absence of direct breeding evidence, relationships between phena in this study were inferred, based on holomorphological evidence with emphasis on adult morphology and supplemented with some ecological and distributional data. Sympatric forms which show little or no intergradation in at least one character are considered specifically distinct. Allopatric forms which intergrade clinally over a fairly wide zone of contact are considered subspecies if sufficient morphological difference exists between the forms. Allopatric populations which are completely isolated geographically are considered subspecies if they differ only in colour or colour pattern.

TABLE 4. Population samples of *C. longilabris* and *C. nebraskana* used in numerical and colour analyses (Fig. 11).

SPECIES	CODE	LOCALITY	MALES	FEMALES
C. nebraskana	AB1	Alberta: Lethbridge	11	9
	AB2	Alberta: 16 km. E. Patricia	8	3
	BC1	British Columbia: Oliver	11	21
	BC2	British Columbia: Chilcotin	15	16
	CA1	California: Tuolumne/Mono Co. Sonora Pass	11	12
	ID1	Idaho: Moscow Mountain	15	15
	MB1	Manitoba: Ninette	3	5
	MT1	Montana: Bozeman	10	16
	UT1	Utah: Lake Co. Mill Creek Canyon	3	6
	WA1	Washington: Bkm. W. Cle Elum	8	6
	WY1	Wyoming: Park Co. Clay Butte	4	6
	WY2	Wyoming: Sublette Co. Lower Green River Lake	12 3	18 6
C. longilabris	AB3	Alberta: Fawcett	12	12
	AB4	Alberta: McMurray	17	6
	AB5	Alberta: 7.2 km. N. Banff	13	18
	AB6	Alberta: 20 km W. Beaver Mines	19	16
	AB7	Alberta: Wm. A. Switzer Prov. Park 12 km. N. Hinton	4	14
	AZ1	Arizona: Kaibab Nat. Forest Kaibab Lodge vicinity	10	20
	AZ2	Arizona: Apache Co. White Mtns & Escudilla Mtns. area	6	18
	BC3	British Columbia: Creston	16	14
	CA2	California: Tuolumne/Mono Co. Tioga Pass	13	15
	CA3	California: Tuolumne/Mono Co. Sonora Pass	15	15
	CA4	California: Yosemite Nat. Park Saddlebag Lake	8	24
	CO1	Colorado: Mineral Co., Creede	14	16
	CO2	Colorado: Pitkin/Lake Co., Independence Pass	17	19

TABLE 4 (Cont'd)

SPECIES	CODE	LOCALITY	MALES	FEMALES
C. longilabris	MB2	Manitoba: Riding Mtn. Nat. Park	5	3
	MB3	Manitoba: Norway House	8	7
	MB4	Manitoba: Gillam	27	34
	MI1	Michigan: Houghton Co. Oskar	18	12
	MT2	Montana: 19 km. S. Neihart	4	5
	NB1	New Brunswick: Various Localities	4	7
	NF1	Newfoundland: Gander	26	24
	NF2	Newfoundland: Harmon Field	21	10
	NH1	New Hampshire: Twin Mtn.	11	22
	NM1	New Mexico: Sandoval Co. Jemez Mtns.	10	6
	NM2	New Mexico: Bernallilo Co. Sandia Crest	7	7
	NS1	Nova Scotia: Various localities	3	6
	NT1	Northwest Territories: Yellowknife	7	10
	NT2	Northwest Territories: Fort Smith	16	16
	ON1	Ontario: Kenora vicinity	16	23
	ON2	Ontario: Maynooth	-	6
	OR1	Oregon: Lost Prairie Campground Nr. Sweethome	6	11
	OR2	Oregon: Blue Mtns. Bone Springs	10	13
	QB1	Quebec: Thunder River (Riviere aux Tonneres)	8	10
	QB2	Quebec: Forestville	11	11
	QB3	Quebec: Mont Albert	7	11
	QB4	Quebec: Duparquet	15	15
	SD1	South Dakota: Black Hills Sturgis-Lead	8	11
	SK1	Saskatchewan: Torch River	13	10
	SK2	Saskatchewan: Big River	8	1
	SK3	Saskatchewan: Hudson Bay	16	6
	UT2	Utah: San Juan Co. Abajo Mtns.	6	5

TABLE 4. (Cont'd)

SPECIES	CODE	LOCALITY	MALES	FEMALES
C. longilabris	UT3	Utah: Iron Co. 5 km. S. Cedar Breaks Nat. Mon.	8	8
	WA2	Washington: Olympic Nat. Park	24	30
	WA3	Washington: Chelan Co. Stevens Pass	27	5
	WY3	Wyoming: Medicine Bow Mtns. 13 km. N. Centennial	5	6
	YK1	Yukon: Whitehorse	8	9
	YK2	Yukon: Watson Lake	5	2
	YK3	Yukon: Rampart House	3	4
	YK4	Yukon: Dawson	1	4
	TOTAL		647	710

RESULTS AND DISCUSSION

Discriminant Analysis

Figure 11 and Table 4 indicate the population samples used in these analyses. Tables 5 and 6 indicate the canonical discriminant functions derived in each of the tests and Tables 7 to 36 present F statistics and associated significance levels for comparisons between groups. Table 37 indicates which variables were selected by the discriminant program in each of the tests.

Due to the number of variables analyzed and the sample sizes the discriminant procedure used has sufficient power to show up differences which may be called statistically significant between most of the population samples investigated. I feel that such statistical differences are minor and not taxonomically meaningful. A significance level of 0.0001 was arbitrarily chosen as the minimum degree of morphometric difference between groups for taxonomic status. However, the discriminant tests of morphometric data were not used as the sole criterion for taxonomic decisions. Populations were treated as members of the same taxon where a difference between them was indicated by a discriminant analysis to be significant at the above mentioned minimum levels, but where there was a lack of supporting evidence based on qualitative characters, soil associations or other distributional/zoogeographical factors.

Discriminant analysis Tests 1 and 2 (Table 5) compared specimens from the island of Newfoundland (NF) with specimens from Ontario (ON), Quebec (QB) and Manitoba (MB). In Test 1 for male specimens, function 1 separates NF from QB, ON and MB at a significance level beyond 0.0001. The variables ll, lw, ew and prct (Table 37) contribute the greatest amount to the variation in discriminant function 1. Newfoundland males have on average, a longer and wider labrum, wider elytra and are more heavily maculated than those of the mainland populations. Table 7 indicates F statistics and significance levels for comparisons between these groups. The NF group is significantly different from each of the three mainland groups beyond the 0.0001 level, whereas the mainland groups in this test do not differ from each other significantly at the 0.0001 level.

Test 2 (Table 5) compares females of the above four groups. In this test Function 1 separates between NF and the mainland populations. The variables prct and el make the largest contribution to function 1 (Table 37). Newfoundland females have, on average longer elytra and are more heavily maculated than the mainland populations. F statistics and significance levels between groups of females (Table 8) also show NF to be significantly different beyond the 0.0001 level from each of the other three groups. ON and QB do not differ significantly from MB.

Tests 3 and 4 (Tables 5, 9 and 10) were conducted to investigate variation among population samples from Gander, Nfld. (NF1), Harmon Field, Nfld. (NF2), Thunder River, Quebec (QB2) and Mont Albert, Quebec (QB3) (Fig. 11). In test 3, for males, two discriminant functions were derived which dealt with a significant amount of variation (Table 5). Function 1 scored the two Quebec populations close together, with NF2 having an intermediate value and NF1 scored farthest from the Quebec populations. Function 2 scored NF1 and QB3 closer together near the mid range of the scale, with QB3 and NF2 farthest apart at either end of the range of values. In both functions, measurements of the labrum and pronotum contributed most to the functions (Table 37). Again, males from Newfoundland were found to have a larger labrum and a larger pronotum. These differences reflect a difference in overall body size, those specimens on the island being larger on average. It is a commonly occurring phenomenon, for island populations of animals to be different in size and Lindroth (1963) indicated that a number of species of carabid beetles are noticeably larger in body size on the island of Newfoundland than are their mainland populations.

The F statistics and associated significances between groups (Table 9) indicate a discordant pattern of variation. Males from NF1 are different from QB2 and QB3 at a significance level beyond 0.0001, whereas NF2 males are not significantly different from QB3 males at a 0.01 level. NF1 males and NF2 males differ from each other significantly beyond the 0.0001 level. This greater statistical difference between populations from Newfoundland than between NF2 and QB3 would seem to refute any subspecific status for Newfoundland populations, based on morphometric characters.

Test 4 (Table 5) dealing with female specimens also produced 2 functions dealing with a significant amount of variation (at or beyond 0.0001 level). Function 1 separates most strongly between NF1 and QB2 at opposite ends of the range of values with NF2 and QB3 having very similar scores, intermediate on the scale. Function 2 scores QB2, NF1 and NF2 close together with QB3 distinctly separate from the former three. Femur length, tibia length are the variables contributing the greatest amount of variation to Function 1 and 2 for females of these four populations. The multivariate F statistics and associated significances for Test 4 (Table 10) indicate that females of NF2 do not differ from those of QB2 and QB3 significantly at the 0.001 level. The F statistics and significance level between NF1 and NF2 is comparable to that between NF2 and the Quebec populations. These relative differences based on morphometric characters would not warrant any subspecific distinction between the populations on Newfoundland and those of the mainland.

A series of discriminant tests were conducted to compare population samples in the Rocky Mountain area of the United States where populations are highly variable and the pattern of variation is complex.

Tests 5 and 6 (Tables 11 and 12) compare population samples from southwestern Alberta (AB6), Montana (MT2), south Wyoming (WY3), and central Colorado (CO2). In Test 5 using male specimens, function 1 separates between these four populations (Table 5), however, the variation expressed in this function is not clinal in a north-south direction. The AB6 population is more similar to the WY3 and CO2 populations than it is to MT2 which is its closer neighbour geographically. Test 5 (Table 11) shows the males of AB6 are significantly different from the CO2 and MT2 males at a significance level of 0.0001, however they are not different from WY3 at the 0.001 level. WY3 males are not significantly different from either the AB6 males or the CO2 males at the 0.001 level, however they are statistically different at the 0.0001 level from MT2, which in this analysis is their nearest neighbour to the north. This pattern of variation appears rather discordant between these populations.

Test 6 compared females of the same populations. Functions 1 and 2 (Table 5) both produce significant separation between these groups. Function 1 in this case indicates a clinal difference north to south with AB6 scoring farthest on the scale from CO2, the "typical" *C. longilabris laurentii* form as described by Schaupp (1884). Function 2 in Test 6 is also highly significant (p = 0.0001) and indicates a different pattern of variation, scoring AB6 closer to CO2 than either WY3 or MT2. The multivariate F statistics and significances in Table 12 for female specimens, indicate that from south to north, CO2 is not significantly different from WY3 (0.0024), WY3 is not significantly different from MT2 (0.0387), but MT2 is significantly different from AB6 beyond the 0.0001 level. This suggests that the difference between AB6 and the other populations is greater than are the differences among the west central Montana (MT2), southern Wyoming (WY3) and central Colorado (CO2) populations.

Tests 7 and 8 (Tables 13 and 14) compare a sample from what appears to be a geographically isolated population in the Black Hills of South Dakota (SD) with samples of the Rocky Mountain form from central Colorado(CO2) and the Medicine Bow Mountains of southern Wyoming (WY3). Table 5 shows that for both males and females, function 1 is significant beyond the 0.0001 level in differentiating these populations and the 2nd function is not significant at the 0.05 level. Table 13 showing F statistics and significance levels indicates males of WY3 and CO2 are not significantly different at the 0.01 level. This is not surprising as the montane forest habitat is continuous in a coarse geographical sense between central Colorado and southern Wyoming. The same table also indicates that the difference between SD and WY3 males is not significant at the 0.01 level. The significant difference between CO2 males and SD males (p = 0.0000) could reflect the greater geographical distance between the sampled populations. Table 14 comparing females indicates that CO2 and WY3 are significantly different beyond the 0.0001 level, and the F statistic comparing SD and WY3 is significant to the 0.0003 level. Discriminant tests 7 and 8 seem to indicate that there is more difference between the South Dakota population and the nearest sampled Rocky Mountain population than there is between population samples from within the Rocky Mountain region.

Tests 9 and 10 (Tables 15 and 16) compare population samples from central Colorado, Independence Pass (CO2), southern Colorado, Creede (CO1), the Jemez Mountains of northern New Mexico, west of the Rio Grande (NM2) and the Sandia Mountains in northern New Mexico, east of the Rio Grande (NM3). This was done to compare the New Mexico populations with the typical *C. l. laurentii* from Colorado and to determine if the Rio Grande is a significant barrier to gene flow between the two New Mexico populations. In Test 9 using male specimens, the first two discriminant functions (Table 5) are significant beyond the 0.0001 level, and separate between all four populations very well. Table 15 showing F statistics and significance levels for pairs of the Colorado and New Mexico samples of males, indicates the two New Mexico populations are not significantly different at the 0.001 level. All the other populations differ from each other significantly at the 0.0001 level. Table 16 for female specimens also shows the two New Mexico samples to be significantly different at the 0.0004 level, and each of the comparisons between pairs of these four populations shows significant difference beyond the 0.0001 level.

Both Tests 9 and 10 indicate that there is less difference between the New Mexico populations than between the Colorado populations. If the Rio Grande is a barrier between the populations east and west of it in New Mexico, it is less important a block to gene flow between populations than is effected by the greater geographic distances between CO1, CO2 and the New Mexico populations.

Tests 11 and 12 (Tables 17 and 18) were conducted to compare the above mentioned Colorado populations with populations from the Abajo Mountains in southeastern Utah (UT2) and the Cedar Breaks vicinity in southwestern Utah (UT3). Both Utah populations are found in areas of montane forest habitat isolated from other populations of the species by areas of lower elevation and drier habitat.

In Test 11 (Table 5) the first two discriminant functions are significant beyond the 0.0001 level and show a discordant pattern of variation between the groups. CO2 and UT3 are farthest apart geographically (Fig. 11) yet function 1 scores them closest together. CO1, CO2 and UT2 are closer together geographically (Fig. 11), yet these populations score farther apart in discriminant function 1. Table 17 indicates a similarly discordant pattern of variation between males of these populations.

Test 12 for females of the same four populations also shows two discriminant functions dealing with a significant level of variation (beyond 0.0001 level, Table 5). Table 18 for Test 12 indicates UT2 and UT3 are not significantly different at the 0.01 level. This suggests that the approximately 250 km of arid, unsuitable habitat and the Colorado

River Valley separating these populations does not form a significant barrier to gene flow. This table also shows CO1 and CO2 to be significantly different beyond the 0.0001 level, which is surprising for two reasons. Both forms share the colouration and increased maculation of the typical *C. l. laurentii* form and the montane forest habitat is fairly continuous, in a coarse geographic sense between these two sites. In an east-west direction, Test 12 (Table 18) shows the degree of difference between CO1 and UT2 is not significant at the 0.001 level, but the difference between CO1 and UT3 is significant to the 0.0001 level. This latter difference probably reflects the greater geographical distance separating the populations.

Tests 13 and 14 compared populations from the Kaibab Plateau in northern Arizona (AZ1) with UT2 and UT3 from Utah. In test 13 (Table 19) using male specimens, there is no significant difference between AZ1 and UT2, whereas statistical differences are greater between AZ1 and UT3 and between UT2 and UT3. This is surprising as the former pair of populations are on opposite sides of the Colorado River Valley and are separated by a greater geographical distance than are AZ1 and UT3. Female specimens of these populations do not exhibit the same pattern (Table 20).

Tests 15 and 16 compared populations from the Kaibab Plateau in northern Arizona (AZ1), White Mountains of Apache Co. in eastern Arizone, and the lumped populations of Colorado (CO) and New Mexico (NM). In Test 15 (Table 5) comparing males, all three discriminant functions deal with a highly significant amount of variation. The F statistics (Table 21) indicate AZ1 and AZ2 are not significantly different from each other at the 0.001 level. Any other two of these 4 populations are significantly different from each other beyond the 0.0001 level. Test 16 comparing females (Table 5) also shows three highly significant functions separating the groups. The F statistics and associated significances for this test (Table 22) show all of these 4 groups to be different from each other beyond the 0.0001 level.

Tests 9 to 16 suggest a complex pattern of relationships and a degree of genetic isolation among populations of the Colorado Plateau, Northern New Mexico, White Mountains of eastern Arizona, Kaibab Plateau in northern Arizona, Cedar Breaks area in S. W. Utah and Abajo Mountains in S. E. Utah. Such a pattern is what one would expect given the fragmented distribution of the montane forest habitat in isolated areas at the southern end of the Rocky Mountain region (National Atlas of the United States of America, 1970). *C. longilabris* is a boreal and montane forest species. Its geographic range (Fig. 79) corresponds well with the Canadian and Hudsonian faunal zones as presented by Muesbeck and Krombein (1952). Each of the above mentioned localities is in an area of the Canadian faunal zone, surrounded and separated from the others by areas of transition and upper Sonoran faunal zones (Muesbeck and Krombein 1952).

The next 8 tests were conducted to investigate the populations in the Cascade Mountains and the Sierra Nevada from southern British Columbia through Washington, Oregon to California.

Tests 17 and 18 compare two populations in Washington State, Olympic National Park (WA2), and Stevens Pass in Chelan Co. (WA3), with populations from Creston, British Columbia (BC3), and south western Alberta, 20 km W. of Beaver Mines (AB5). In Table 5, test 17 comparing males shows 1 function significant beyond the 0.0001 level which separates the groups in a discordant manner, scoring BC3 closest to WA3 and AB5 closest to WA2 even though this latter pair of populations are most geographically distant of the 4. Functions 2 and 3 also show discordant variation patterns, each one weakly separating the groups. The F statistics and associated significances for test 17 (Table 23) indicate the only differences between pairs of groups which is significant beyond the 0.001 level is between WA2 and WA3, which are geographically the closest together of the 4 in this comparison.

Test number 18, using female specimens of the same 4 population samples produced two functions significant beyond the 0.0001 level (Table 5). Function 1 scores WA2 and WA3 closest together with BC3 intermediate in score and AB5 scoring farthest from the Washington populations. Function 2 shows a discordant pattern of variation, with AB5 scoring closest to WA3. The F statistics comparing pairs of groups (Table 24) for test 18 shows each group to be different from each other group at the 0.0001 level except for WA2 and WA3. Females of the two Washington populations are not significantly different from each other at the 0.001 level.

Test 19 and 20 compared the two Washington populations mentioned above with specimens from two localities in Oregon, Lost Prairie Campground near Sweethome in Linne Co. (OR1), and Bone Springs in the Blue Mountains of Umatilla Co. (OR2). Test 19 using female specimens produced two highly significant discriminant functions, significant beyond the 0.0001 level (Table 5). Function one scores the two Oregon samples close together with theper cent of the elytra covered in maculations being the variable making the largest contribution to the function.

Function 2 (Table 5) shows a strange pattern of variation in that WA2 and WA3 scored closest together, both having intermediate values in the range of discriminant scores while OR1 and OR2 scored farthest apart from each other at opposite ends of the scale. The F values for test 19 (Table 25) indicate that WA2 and WA3 are not significantly different from each other at the 0.001 level. This is probably due to the geographical proximity of these two localities. The greater level of significance (Table 25) comparing other pairs of populations in this test is probably due to the greater geographic separation between them. Test 20 using male specimens of the same 4 populations also produced two discriminant functions significant beyond the 0.0001 level. The F values and associated significances (Table 26) indicate WA2 and WA3 are not different at the 0.001 level and the same highly significant differences exist between other pairs of populations within this group of 4.

Tests 21 and 22 compare WA2, OR1 and OR2 with a population from Tioga Pass, California (CA2). Test 21 with male specimens produced two discriminant functions dealing with a highly significant degree of variation ($p < 0.0001$) (Table 5). The figures in Table 27 indicate OR1 and OR2 are not significantly different from each other at the 0.001 level. All of the other populations in this test are significantly different from each other beyond the 0.0001 level. Table 28 for test 22 using female specimens indicates all of the 4 populations differ from each other significantly beyond the 0.0001 level.

Tests 23 and 24 compared the lumped populations from Washington

(Wa) with the lumped populations from Oregon (OR) and California (CA), representing the named forms *C. l. columbiana* Casey 1924, *C. l. ostenta* Casey 1913, and *C. l. perviridis* Schaupp 1884, respectively.

In test 23, comparing males, two highly significant discriminant functions were derived which separated very well between the groups (Table 5). As shown in Table 29 for males, each of these three groups differs significantly from each other beyond the 0.0001 level. In Table 30, comparing females for the same three groups, the results are similar, all three groups differ significantly from every other beyond the 0.0001 level. The significant statistical differences between CA, OR, and WA are probably due to the geographical distance between the sampled localities. Judging by the distribution of *C. longilabris* through this region (Fig. 79), it seems likely that these forms are genetically continuous between southern British Columbia and central California. It is possible that a study of numerous population samples throughout the Pacific region would show some continuity of relationship between these forms.

Tests 25 and 26 were done to compare three large groupings of population samples. One was the lumped populations of the Rocky mountain States from Montana to Arizona and New Mexico, another the lumped population samples of the Cascades and Sierra Nevada from southern British Columbia to east central California, and a third the nominal form from across the boreal zone in its broadest sense in the northern part of the continent.

In test 25, comparing male specimens, two functions were derived dealing with a significant amount of variation (sign beyond the 0.0001 level). Table 31 for test 25 indicates multivariate F figures between

Test 26 comparing female specimens produced very similar results. Two highly significant discriminant functions were produced (Table 5). One function set the Pacific form apart from the other two and the second function separated the Rocky Mountain group from the Pacific and Boreal forms. Table 32 shows any two group comparison between these three to have an F statistic that is significant beyond the 0.0001 level. Both male and female specimens show highly significant statistical differences between these three groups, beyond the minimum significance level (0.0001) here chosen for taxonomic purposes.

The variables contributing the most to the discrimination between the above three groups were pronotal width (pw), pronotal length (pl), per cent of elytral surface covered with maculations (prct), head width (hw), length of mesothoracic tibia (tl) and elytral width (ew) (Table 37). A one-way analysis of variance was performed to investigate the statistical differences in each of these measurements between the three groups in question. For males, all three groups were statistically different from each other in pw ($F = 27.958$, $p = 0.0001$, sign. at 0.05 by Scheffe's procedure) and hw ($F = 25.710$, $p = 0.001$, sign. at 0.05 by Scheffe's procedure). For both of these variables males of the Boreal group measured the largest and the Pacific group measured the smallest. Similarly for females, a one-way analysis of variance showed that each of the groups is different from the others based on the variables pw ($F = 57.793$, $p = 0.0001$, sign. at 0.05 by Scheffe's procedure) and hw ($F = 52.201$, $p = 0.0001$, sign. at 0.05 by Scheffe's procedure). For both variables, females of the Boreal form had the largest average measurement and the Pacific form was the smallest of the three. These statistics probably reflect the overall size differences with the nominate form being largest, the Rocky Mountain form being smaller, on average and the Pacific form being the smallest.

The boreal form has a proportionately shorter, wider pronotum than the other two groups evidenced by the statistical difference in the variable pl/pw (one-way anova Males: F = 42.165, p = 0.0001, sign at 0.05 by Scheffe's procedure; Females: F= 36.908, p = 0.0001, sign at 0.005 by Scheffe's procedure).

Per cent of the elytral surface covered with maculations was another discriminating variable which shows statistical differences between the groups. A one-way anova of male specimens indicated that the boreal group is less maculate than are the other two groups (F = 43.175, p = 0.0001, sign at 0.05 by Scheffe's test). The same test with female specimens showed the boreal form to be least maculate, the Rocky Mtn. group more so and the pacific group the most maculate, on average (F = 55.577, p = 0.0001, sign at 0.05 by Scheffe's procedure).

Discriminant tests 27 and 28 were performed to compare population samples of *C. nebraskana* from east of the Rocky Mtns. with those west of the divide. Leffler (1979) in studying tiger beetles of the pacific Northwest states recognized two subspecies, *C. n. nebraskana* from east of the divide and *C. n. chamberlaini* from west of the divide, based primarily on a statistical difference in head width, the eastern populations having the narrowest heads with intermediate populations occurring near the divide in eastern Idaho and northwestern Wyoming. Test 27 (Tables 6, 33) for male specimens, produced a discriminant function which separated between the eastern and western populations significant beyond the 0.0001 level.

The variables contributing most to the discriminant function were, in order of importance fl and el (Table 37). Hw was not selected in this analysis. Test 28 using female specimens also separated between the groups significant beyond the 0.0001 level (Tables 6, 36). In this discriminant function the variables contributing most to the variation were, in order of importance fl and hw.

Using one-way analyses of variance these with the probability of a type one error set at 0.01, for both males and females, the western populations of *C. nebraskana* had significantly longer mesofemur ~~lengths,~~ on average, and larger elytra than the eastern populations. No differences in other measurements significant at the 0.05 level were found between the eastern and western forms of *C. nebraskana*.

Discriminant tests 29 and 30 were done to compare *C. longilabris* with *C. nebraskana*. As Tables 6 and 35 indicate, for test 29 comparing male specimens a discriminant function was derived which separated the two groups very well. The multivariate F ratio was 39.988, significant beyond the 0.0001 level. The variables contributing most to the discriminant functions were ll, lw, ll/lw, prct, hw/pw, lcol, and ls2 (Table 37).

The discriminant function derived in test 30 between females of the two species was also highly significant (Table 6). The multivariate F ratio was significant beyond the 0.0001 level (Table 36). The variables most effective in separating the females of the species were prct, lw, lcol, ll/lw, pw, ls2, and osr (Table 37).

Using a one-way analysis of variance with the probability of a type one error set at 0.001, males and females of *C. longilabris*, as compared to those of *C. nebraskana*, were found to have a significantly longer and wider labrum, longer labrum in proportion to length, and they are more maculate, and have proportionally wider heads, in relation to pronotal width. While males and females of *C. nebraskana* were found to have significantly more non-sensory setae on the scape of the antenna (Fig. 3) than *C. longilabris*, they could not be individually identified on that basis, as the range for *C. nebraskana* is 1 - 7 and for *C. longilabris* it is 0 - 8.

TABLE 5. Canonical discriminant functions evaluated at group centroids for discriminant analyses of *C. longilabris*.

TEST	SEX	GROUP	FUNCTION 1	SIGN.	FUNCTION 2	SIGN.	FUNCTION 3	SIGN.
1	M	NF	1.50447		0.10389		-0.11024	
		QB	-0.54713		-0.66181		-0.07796	
		ON	1.46495		0.62022		-0.83300	
		MB	-0.62092	0.0000	0.30818	0.0007	0.54264	0.0118
2	F	NF	1.23770		-0.27416		0.15491	
		QB	-0.04590		0.65663		0.07562	
		ON	-1.31731		-0.36636		0.07562	
		MB	-0.35960	0.0000	-0.18288	0.0008	-0.53029	0.0255
3	M	NF1	-1.47603		0.34675		0.14078	
		NF2	0.42626		-1.17008		-0.38365	
		QB3	1.76261		-0.26151		1.36885	
		QB2	1.55336	0.0000	1.58061	0.0001	-0.47121	0.0796
4	F	NF1	-1.03027		0.26421		0.23094	
		NF2	0.48235		0.32265		-1.52325	
		QB3	0.45092		-1.76087		0.07403	
		QB2	2.29503	0.0000	0.65092	0.0001	0.59693	0.0087
5	M	AB6	1.00629		1.11885		0.21340	
		MT2	3.97995		-2.40156		0.41489	
		WY3	-0.25666		-0.27851		-2.52338	
		CO2	-1.92646	0.0000	-0.53768	0.0000	0.41859	0.0030
6	F	AB6	-2.97788		1.17719		-	
		MT2	-1.30577		-4.02785		-	
		WY3	-0.09169		-1.15608		-	
		CO2	2.72354	0.0000	0.49568	0.0001	-	-
7	M	SD1	-4.64296		-0.50687			
		WY3	-0.50943		1.98964			
		CO2	2.33475	0.0000	-0.34666	0.1133		

TABLE 5. (Cont'd)

TEST	SEX	GROUP	FUNCTION 1	SIGN.	FUNCTION 2	SIGN.	FUNCTION 3	SIGN.
8	F	SD	4.58970					
		WY3	1.29735					
		CO2	-2.82532	0.0000				
9	M	CO2	0.99471		-1.48198		-0.15956	
		CO1	1.65177		1.45321		0.39330	
		NM1	-2.19463		1.02074		-1.73605	
		NM2	-3.83817	0.0000	-0.18224	0.0000	1.08894	0.0119
10	F	CO2	1.90040		-2.24976			
		CO1	1.70876		2.55167			
		NM1	-3.96863		2.07228			
		NM2	-6.22924	0.0000	-1.20609	0.0000		
11	M	CO1	0.66186		-1.51311		0.57218	
		CO2	-1.36747		-0.08774		-0.68947	
		UT2	3.23520		1.16558		-0.80103	
		UT3	-0.67878	0.0000	1.96019	0.0000	1.06459	0.0217
12	F	CO1	2.13700		-0.73862		0.11328	
		CO2	-1.94474		-0.55063		0.06162	
		UT2	0.28454		1.40495		-2.19150	
		UT3	0.19078	0.0000	2.17930	0.0000	1.13917	0.0042
13	M	AZ1	-1.79330		1.19043			
		UT2	-1.35183		-2.17416			
		UT3	3.2550	0.0000	0.14258	0.0070		
14	F	AZ1	-1.41689		0.14151			
		UT2	1.83524		-2.60665			
		UT3	2.73738	0.0000	1.45756	0.0002		
15	M	AZ1	0.13085		-1.91721		1.50960	
		AZ2	0.95029		-3.56755		-1.54645	
		CO	1.46635		1.04926		-0.07873	
		NM	-3.08631	0.0000	0.47355	0.0000	-0.19862	0.0026

TABLE 5 (Cont'd.)

TEST	SEX	GROUP	FUNCTION 1	SIGN.	FUNCTION 2	SIGN.	FUNCTION 3	SIGN.
16	F	AZ1	-1.41254		1.06969		1.37545	
		AZ2	0.28015		1.56243		-1.39183	
		CO	2.31152		-0.68513		0.10926	
		NM	-3.66227	0.0000	-1.96556	0.0000	-0.48309	0.0000
17	M	AB5	0.64021		0.07681		-1.33454	
		BC3	-0.06441		1.15340		0.29512	
		WA2	0.79147		-0.42574		0.45819	
		WA3	-0.96181	0.0000	-0.34929	0.0006	-0.03994	0.0070
18	F	AB5	2.18785		0.65324		-0.31884	
		BC3	0.57672		-1.73228		0.25492	
		WA2	-1.19315		0.45355		0.39589	
		WA3	-2.52235	0.0000	-0.43460	0.0000	-2.34365	0.0048
19	F	WA2	2.29534		0.44680		-0.21752	
		WA3	0.53768		-0.90667		2.67438	
		OR1	-1.94902		-2.94783		-0.39117	
		OR2	-3.93970	0.0000	1.92464	0.0000	-0.00721	0.0134
20	M	WA2	-1.16132		0.29135		0.56615	
		WA3	-0.19293		-0.30871		-0.75424	
		OR1	2.41583		1.99641		-0.13952	
		OR2	2.04366	0.0000	-1.21602	0.0000	0.76217	0.0030
21	M	WA2	0.06838		1.67293		-	
		OR1	-1.78721		-2.68806		-	
		OR2	-4.40994		-0.79712		-	
		CA2	3.75166	0.0000	-1.29600	0.0000	-	0.1646
22	F	WA2	0.97274		2.07583		0.35008	
		OR1	-1.75585		-2.78124		1.57788	
		OR2	-5.01774		0.10852		-1.13278	
		CA2	3.42118	0.0000	-2.06052	0.0000	-0.92771	0.0000

TABLE 5 (Cont'd)

TEST	SEX	GROUP	FUNCTION 1	SIGN.	FUNCTION 2	SIGN.	FUNCTION 3	SIGN.
23	M	WA	-1.19849		0.71185			
		OR	-1.71588		-2.08296			
		CA	2.51949	0.0000	-0.12788	0.0000		
24	F	WA	0.08908		2.17924			
		OR	4.09752		-1.03891			
		CA	-1.90554	0.0000	-0.94157	0.0000		
25	M	Boreal	-0.67659		0.14247			
		Pacific	1.02706		0.48910			
		Rocky Mtn	0.39649	0.0000	-0.91121	0.0000		
26	F	Boreal	-0.68318		0.30761			
		Pacific	1.19464		0.45284			
		Rocky Mtn	0.12659	0.0000	-1.00810	0.0000		

TABLE 6. Canonical discriminant functions evaluated at group centroids for discriminant analyses of the *C. longilabris/nebraskana* complex.

TEST	SEX	GROUP	FUNCTION 1	SIGN.
27	M	*C. nebraskana* W.	0.94882	
		C. nebraskana E.	-1.18602	0.0000
28	F	*C. nebraskana* W.	0.88205	
		C. nebraskana E.	-1.15877	0.0000
29	M	*C. nebraskana*	-2.02870	
		C. longilabris	0.40574	0.0000
30	F	*C. nebraskana*	1.87920	
		C. longilabris	-0.42643	0.0000

TABLE 7. Test 1, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from ON, QB, MB and NF populations.

Each F statistic has 11 and 130 degrees of freedom.

GROUP	MB	NF	ON
NF	9.0942* 0.0000+		
ON	2.6068 0.0049	9.6797 0.0000	
QB	2.2757 0.0142	8.8662 0.0000	2.9690 0.0015

TABLE 8. Test 2, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from ON, QB, MB and NF populations.

Each F statistic has 11 and 130 degrees of freedom.

GROUP	MB	NF	ON
NF	6.2102* 0.0000+		
ON	3.0459 0.0015	10.681 0.0000	
QB	2.4519 0.0097	5.3447 0.0000	4.5953 0.0000

TABLE 9. Test 3, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from NF1, FN2, QB2 and QB3 populations.

Each F statistic has 11 and 51.0 degrees of freedom.

GROUP	NF1	NF2	QB2
NF2	5.4696* 0.0000+		
QB2	6.5061 0.0000	4.8526 0.0000	
QB3	5.1840 0.0000	2.2677 0.0243	2.2184 0.0276

TABLE 10. Test 4, F statistics* and associated significance levels + between groups of females of *C. longilabris* from NF1, NF2, QB2 and QB3 populations.

Each F statistic has 11 and 52 degrees of freedom.

GROUP	NF1	NF2	QB2
NF2	3.1630* 0.0024+		
QB2	7.1868 0.0000	3.1506 0.0025	
QB3	4.0046 0.0003	2.7531 0.0069	3.9801 0.0003

TABLE 11. Test 5, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from AB6, CO2, MT2 and WY3 populations.

Each F statistic has 10 and 31.0 degrees of freedom.

GROUP	AB6	CO2	MT2
CO2	7.7157* 0.0000+		
MT2	5.3965 0.0001	9.6265 0.0000	
WY3	3.3473 0.0047	3.4466 0.0039	5.3543 0.0001

TABLE 12. Test 6, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from AB6, CO2, MT2 and WY3 populations.

Each F statistic has 12 and 30 degrees of freedom.

GROUP	AB6	CO2	MT2
CO2	16.853* 0.0000+		
MT2	6.8916 0.0000	8.9868 0.0000	
WY3	4.1033 0.0008	3.5363 0.0024	2.2102 0.0387

TABLE 13. Test 7, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from SD1, WY3, and C02 populations.

Each F statistic has 10 and 18 degrees of freedom.

GROUP	C02	SD
SD	17.667* 0.0000+	
WY3	3.4895 0.0103	4.7833 0.0020

TABLE 14. Test 8, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from SD1, WY3 and C02 populations.

Each F statistic has 7 and 26 degrees of freedom.

GROUP	C02	SD
SD	41.862* 0.0000+	
WY3	10.187 0.0000	6.0584 0.0003

TABLE 15. Test 9, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from C01, C02, NM2 and NM3 populations.

Each F statistic has 10 and 31 degrees of freedom.

GROUP	C01	C02	NM2
C02	5.5649* 0.0001+		
NM2	6.3524 0.0000	6.5030 0.0000	
NM3	12.043 0.0000	10.223 0.0000	3.0369 0.0085

TABLE 16. Test 10, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from C01, C02, NM2 and NM3 populations.

Each F statistic has 12 and 32.0 degrees of freedom.

GROUP	C01	C02	NM2
C02	12.693* 0.0000+		
NM2	9.0431 0.0000	13.770 0.0000	
NM3	23.377 0.0000	21.781 0.0000	4.4303 0.0004

TABLE 17. Test 11, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from C01, C02, UT2 and UT3 populations.

Each F statistic has 10 and 32 degrees of freedom.

GROUP	C01	C02	UT2
C02	4.6389* 0.0004+		
UT2	5.1400 0.0002	7.8806 0.0000	
UT3	5.6039 0.0001	3.2884 0.0050	5.1997 0.0002

TABLE 18. Test 12, F statistics* and associated significance levels+ between groups of females of *C. longilabris* C01, C02, UT2 and UT3 populations.

Each F statistic has 10 and 34 degrees of freedom.

GROUP	C01	C02	UT2
C02	11.468* 0.0000+		
UT2	4.0178 0.0011	4.3413 0.0006	
UT3	5.1419 0.0001	5.3286 0.0001	2.6987 0.0150

TABLE 19. Test 13, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from AZ1 UT2, and UT3 populations.

Each F statistic has 8 and 14 degrees of freedom.

GROUP	AZ1	UT2
UT2	3.5985* 0.0177+	
UT3	9.8476 0.0001	7.5985 0.0006

TABLE 20. Test 14, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from AZ1, UT2 and UT3 populations.

Each F statistic has 8 and 14.0 degrees of freedom.

GROUP	AZ1	UT2
UT2	8.2160* 0.0000+	
UT3	11.156 0.0000	5.7274 0.0006

TABLE 21. Test 15, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from AZ1, AZ2, CO, and NM populations.

Each F statistic has 12 and 49.0 degrees of freedom.

GROUP	AZ1	AZ2	CO
AZ2	3.2500* 0.0017+		
CO	6.7441 0.0000	8.1203 0.0000	
NM	8.1346 0.0000	10.395 0.0000	15.754 0.0000

TABLE 22. Test 16, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from AZ1, AZ2, CO and NM populations.

Each F statistic has 12 and 71.0 degrees of freedom.

GROUP	AZ1	AZ2	CO
AZ2	6.2772* 0.0000+		
CO	17.036 0.0000	12.026 0.0000	
NM	10.075 0.0000	13.455 0.0000	25.767 0.0000

TABLE 23. Test 17, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from AB5, BC3, WA2 and WA3 populations.

Each F statistic has 10 and 64.0 degrees of freedom.

GROUP	AB5	BC3	WA2
BC3	2.4639* 0.0146+		
WA2	2.3074 0.0219	2.7377 0.0072	
WA3	2.9980 0.0037	2.7576 0.0068	3.6413 0.0007

TABLE 24. Test 18, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from AB5, BC3, WA2 and WA3 populations.

Each F statistic has 10 and 50.0 degrees of freedom.

GROUP	AB5	BC3	WA2
BC3	5.3787* 0.0000+		
WA2	10.883 0.0000	6.0324 0.0000	
WA3	7.5380 0.0000	4.6766 0.0001	2.9970 0.0049

TABLE 25. Test 19, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from OR1, OR2, WA2 and WA3 populations.

Each F statistic has 12 and 41.0 degrees of freedom.

GROUP	OR1	OR2	WA2
OR2	10.502* 0.0000+		
WA2	15.494 0.0000	22.923 0.0000	
WA3	3.8061 0.0006	6.9492 0.0000	3.0682 0.0036

TABLE 26. Test 20, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from OR1, OR2, WA2 and WA3 populations.

Each F statistic has 9 and 53.0 degrees of freedom.

GROUP	OR1	OR2	WA2
OR2	3.9172* 0.0007+		
WA2	7.5075 0.0000	7.9508 0.0000	
WA3	5.8815 0.0000	5.2442 0.0000	3.6642 0.0013

TABLE 27. Test 21, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from WA2, OR1, OR2, and CA2 populations.

Each F statistic has 12 and 37.0 degrees of freedom.

GROUP	CA1	OR1	OR2
OR1	9.3348* 0.0000+		
OR2	22.903 0.0000	3.4314 0.0019	
WA2	12.314 0.0000	7.2812 0.0000	11.435 0.0000

TABLE 28. Test 22, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from WA2, OR1, OR2, and CA2 populations.

Each F statistic has 12 and 52.0 degrees of freedom.

GROUP	CA1	OR1	OR2
OR1	14.666* 0.0000+		
OR2	34.833 0.0000	10.397 0.0000	
WA2	16.822 0.0000	17.852 0.0000	24.494 0.0000

TABLE 29. Test 23, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from CA, OR, and WA populations.

Each F statistic has 10 and 87 degrees of freedom.

GROUP	CA	OR
OR	20.526* 0.0000+	
WA	26.646 0.0000	8.447 0.0000

TABLE 30. Test 24, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from CA, OR, and WA populations.

Each F statistic has 17 and 35 degrees of freedom.

GROUP	CA	OR
OR	42.579* 0.0000+	
WA	20.481 0.0000	26.688 0.0000

TABLE 31. Test 25, F statistics* and associated significance levels+ between males from lumped population samples of *C. longilabris* from the Rocky Mountain States, Pacific Region and the Boreal Region.

Each F statistic has 12 and 431 degrees of freedom.

GROUP	BOREAL ZONE	PACIFIC REGION
Pacific region	18.885* 0.0000+	
Rocky Mtn. Region	12.662 0.0000	10.140 0.0000

TABLE 32. Test 26, F statistics* and associated significance levels+ between females from the lumped population samples of *C. longilabris* from the Rocky Mountain States, Pacific Region, and Boreal Region.

Each F statistic has 12 and 464 degrees of freedom.

GROUP	BOREAL ZONE	PACIFIC REGION
Pacific Region	22.872* 0.0000+	
Rocky Mtn. Region	15.807 0.0000	16.323 0.0000

TABLE 33. Test 27, F statistics* and associated significance levels+ between males of *C. nebraskana* from lumped populations from west of the continental divide and east of the continental divide.

Each F statistic has 9 and 89 degrees of freedom.

GROUP	WEST
East	11.358* 0.0000+

TABLE 34. Test 28, F statistics* and associated significance levels+ between females of *C. nebraskana* from lumped populations from west of the continental divide and east of the continental divide.

Each F statistic has 8 and 109 degrees of freedom.

GROUP	WEST
East	14.166* 0.0000+

TABLE 35. Test 29, F statistics* and associated significance levels+ between males of *C. longilabris* and *C. nebraskana*.

Each F statistic has 12 and 581 degrees of freedom.

GROUP	*C. nebraskana*
C. longilabris	39.988* 0.0000+

TABLE 36. Test 30, F statistics* and associated significance levels+ between females of *C. longilabris* and *C. nebraskana*.

Each F statistic has 10 and 627 degrees of freedom.

GROUP	*C. nebraskana*
C. longilabris	50.403* 0.0000+

TABLE 37. Variables (as described in the Materials and Methods section) selected in discriminant analysis of *Cicindela longilabris/nebraskana*. The 'X' indicates variables that failed the minimum tolerance test (minimum tolerance = 0.001). The '+' indicates variables selected to maximize the Mahalanobis Distance between groups.

Test	Sex	hw	ll	lw	lcol	ls1	ls2	ls3	ls4	ssl	ssr	osl	osr	pw	pl	fl	tl	el	ew	prct	ll/lw	pl/pw	hw/pw	fl/tl	ew/el	fl/el
1	M		+	+			+			+					+		+	+	+	+	+	+				
2	F		+			+	+	+	+							X	+	+		+			+	+		
3	M		+	+		+	+							+	+		+			+	+	+			+	
4	F		+	X			+	+						+		+	+			+	+			+	+	
5	M	+		+			+			+		+		+	+					+		+	X		+	
6	F	+				+	+				+		+				+	+	+	+	+	+			X	+
7	M	+							+	+	+	+	+						+	+		+			+	
8	F	+						+	+		+	+								+					+	
9	M			+		+	+		+	+					+					+	+		+			+
10	F	+	+			X	+	+		+	+				+				+	+	+					+
11	M	+	+			+	+							+				+		+			X	+	+	+
12	F		+			X		+	+	+	+			+	+		+		+	+		X				
13	M	X		+		+	+								+			+		+		+	+			
14	F			+		X	+		+			+								+		+		+		
15	M	+	+						+	+			+	X	+	+			+	+		+	+		+	

TABLE 37 (Cont'd.)

Test	Sex	hw	ll	lw	lcol	ls1	ls2	ls3	ls4	ssl	ssr	osl	osr	pw	pl	fl	tl	el	ew	prct	ll/lw	pl/pw	hw/pw	fl/tl	ew/el	fl/el
16	F	+	+			+		+				+		X	+				+	+	+	+	+			+
17	M			+		+	+					+				+			+	+	+	+	+			
18	F		+					+		+	+	+				+	+		+	+			+	X		
19	F	+	+	+		+	+	+			+	+			+			+		+				+		
20	M		+			+						+	+	+	+		+			+		+				
21	M					+		+	+		+	+	+	+	+		+			+			+			+
22	F			+			+		+		+	+		+	+	+	+	+		+		+		X		
23	M	+					+				+		+	+	+			+	+	+		+				
24	F	+					+		+			+		+		+			+	+		+	+		+	+
25	M	+	+				+		+			+		+	+	+	+		+	+		+				
26	F	+		+			+				+	+	+		+	+			+	+		+	+			
27	M				+	+	+		+				+			+			+					+	+	
28	F	+	+			+				+		+			+	+			+							
29	M		+	+	+		+			+	+		+					+		+	+	+	+			
30	F			+	+		+		+		+		+	+						+	+					+

Colour and Pattern of Markings

Figure 12 presents the frequency of occurrence of three categories of labrum colour for females of each population of *C. longilabris*. In most samples, all females had light coloured labra, in some of the populations a significant fraction of females exhibited labra which were intermediate in colour, mottled, or darkened along the outside edge and midrib. In a small number of population samples a small fraction of females had dark coloured labra. There appears to be no geographic pattern to the variation in this character in *C. longilabris*. Figure 13 indicates the frequency of occurrence of character states of female labrum colour in population samples of *C. nebraskana*. This character is highly variable between populations.

In samples from southern Alberta (AB1, AB2) (Table 4, Fig. 11), and eastern California (CA1), the dark coloured labrum predominates. In the Wyoming populations (WA1, WA2) the vast majority of female specimens have light coloured labra, and in the rest of the populations the three character states are represented in varying frequencies between the two extremes. There appears to be no pattern to the variation in this character in *C. nebraskana*. Overall, among *C. nebraskana* females 44.8% had light coloured labra, 30.6% were intermediate in character and 24.6% were black (total, n = 134). Among *C. longilabris* females labra were light in 90.3%, intermediate in character in 8.2% and black in colour in 1.5% of specimens (n = 586).

Among male specimens of *C. nebraskana* 82.6% had light labra, 15.6% intermediate, and 1.8% black (n = 109), and among *C. longilabris* males the corresponding figures were 97.6% light labra, 1.8% intermediate, and 0.6% dark (n = 538).

Figure 14 shows the frequency of occurrence of colours of the proepisternum of *C. longilabris*. This character is variable across the range of the species, but in most populations, specimens with green and black, green, green and blue, or bronze and green coloured proepisterna (character states 2 - 7, Table 2), make up the largest fraction of samples. Figure 15 shows the frequency of occurrence of proepisternal colour states in population samples of *C. nebraskana*. In this species the proepisterna in most of the populations are black colour, with notable exceptions being the Wyoming populations (WY1 and WY2) and the northern Utah population (UT1), in each of which specimens with bronze coloured proepisterna (character states 6, 7 Figure 15), make up a large fraction of the sample.

Figure 16 presents frequency of occurrence of colours on the ventral surface of the abdomen in *C. longilabris*. This character is variable throughout the species, but metallic greens and mixtures of metallic greens, blues and bronze colour (character states 3, 4, 6, Table 3) predominate in most populations.

In contrast, Figure 17 shows the frequency of occurrence of various colours of the venter of the abdomen in specimens of *C. nebraskana*. In the majority of population samples, black (character state 1, Table 3) is the most frequent colour of the ventral surface, with blue and purple (Character state 5) and bronze (states 6, 7), comprising large fractions of some of the samples. The UT1 sample is peculiar in having a large number of specimens with black and green abdominal colouring (character state 2, Fig. 17).

Figure 18 shows the frequency of occurrence of colours of the elytra of *C. longilabris*. This character is highly variable throughout the range of the species. The blue-green and dark blue colour (states 6 and 7, Table 1) occurred so rarely that they did not show up as a fraction of any of the sampled populations.

Green specimens predominate in the Newfoundland populations (Fig. 18), of *C. longilabris*. The mainland specimens across eastern North America are almost all black or dark brown in dorsal colouration. In the western part of the continent elytral colour is more variable. In the Rocky mountains of the western United States dark brown, bronze and olive green (character states 2, 3, and 4) specimens predominate and in the Pacific region from California to Washington State, bright green coloured specimens are most numerous. In *C. nebraskana* (Fig. 19), black coloured specimens are in the overwhelming majority with dark brown and bronze elytra occurring in small fractions of the populations.

Figures 20 and 21 show the average percentage of the elytral surface covered with maculations (Fig. 7), in *C. longilabris* and *C. nebraskana*. In the former species (Fig. 20), most of the specimens of the boreal zone have an average between 1 and 5% of their elytral surface covered with maculations. This percentage increases greatly in specimens of some populations of the Pacific and Rocky Mountain regions of the United States.

In *C. nebraskana* (Fig. 21), most of the specimens have an average less than one percent of the elytral surface area covered with maculations. The exceptions are the ID1 and WY2 samples which have an average 1.2 and 1.6% respectively of their elytral surface covered with light markings.

Figures 22 - 27 and Table 38 present weighted mean values of characters of the elytral markings for population samples of *C. longilabris* and *C. nebraskana*. Figure 22 presents weighted mean character values of the humeral lunule (Figs. 6, 8) for population samples of *C. longilabris*. In most populations of this species the humeral lunule is usually present as one or two distinct dots or else is present as a complete lunule (Fig. 8). Figure 23 presents the weighted mean character values of the humeral lunule for samples of *C. nebraskana*. In all samples of this species, the humeral lunule is entirely lacking in most specimens.

Figure 24 presents the weighted mean character values of the middle band (Figs. 6, 8) for *C. longilabris*. In most population samples from the boreal zone, the middle band is either indistinctly present (state 1, Fig. 9) or is complete, but quite thin (state 2, Fig. 9). The middle band is more developed in the southern Rocky Mountain region and in the Pacific coast states. Figure 25 presents weighted average character values of the middle band (Fig. 9) for samples of *C. nebraskana*. In a majority of the populations the middle band is lacking completely in most specimens. In BC1, WA1, ID1, WY2 and MB1 (Fig. 11) the middle band is either incompletely present or is present as a thin line (states 1 and 2, Fig. 9) in most specimens.

Figure 26 presents weighted mean character values of the apical lunule of samples of *C. longilabris*. In some populations in the Atlantic region of Canada (QB1, NF2, NB1, NS1, Fig. 11), the apical lunule is

TABLE 38. Weighted mean values of characters prct, hl, mb, al for samples of *C. nebraskana* and *C. longilabris*. Characters are defined in the Materials and Methods section and indicated in Fig. 4, 5, 6, and 6. Locality codes are defined in Table 4 and illustrated in Figure 11.

	Population	prct	hl	mb	al
C. nebraskana	AB1	0.5	0.00	0.05	0.00
	AB2	0.5	0.09	0.09	0.00
	BC1	0.6	0.00	1.22	0.13
	BC2	0.9	0.55	0.71	0.13
	CA1	0.6	0.00	0.96	0.04
	ID1	1.2	0.03	1.40	0.26
	MB1	0.7	0.38	1.00	0.38
	MT1	0.5	0.04	0.27	0.00
	UT1	0.7	0.00	0.89	0.11
	WA1	0.7	0.64	1.36	0.14
	WY1	0.5	0.10	0.10	0.00
	WY2	1.6	0.20	1.80	0.13
C. longilabris	AB3	2.9	2.21	1.54	0.75
	AB4	4.6	2.87	1.83	1.13
	AB5	4.5	2.13	2.36	0.94
	AB6	4.0	1.94	2.06	1.06
	AB7	2.7	2.44	1.78	0.89
	AZ1	4.1	2.20	2.17	1.67
	AZ2	5.9	2.79	3.54	1.33
	BC3	4.8	1.97	2.33	1.13
	CA2	11.2	3.86	4.75	2.57
	CA3	10.2	3.87	3.23	3.00
	CA4	10.7	4.00	4.25	2.47
	CO1	8.5	2.53	3.53	3.07
	CO2	11.4	3.36	4.64	3.50
	MB2	1.8	1.50	1.25	0.38
	MB3	3.2	2.5	1.7	0.7
	MB4	3.2	2.53	1.8	0.82
	MI1	3.2	2.70	1.43	0.90
	MT2	3.7	2.40	2.44	1.10
	NB1	3.1	2.3	1.6	1.0
	NF1	4.3	2.82	1.98	0.98
	NF2	4.8	3.00	2.00	1.13
	NH1	3.2	2.36	1.70	0.85
	NM1	1.7	0.75	1.38	0.50
	NM2	1.0	0.29	0.57	0.21
	NS1	1.4	2.90	1.90	1.10
	NT1	3.4	2.35	1.65	0.94
	NT2	3.6	2.38	1.88	0.75
	ON1	1.7	1.82	1.39	0.67

TABLE 38 (Cont'd)

	Population	prct	hl	mb	al
C. longilabris	ON2	0.8	1.33	0.67	0.17
	OR1	2.0	0.59	3.77	1.06
	OR2	1.0	0.13	1.87	0.22
	QB1	4.8	3.11	2.0	1.06
	QB2	3.4	2.82	1.73	0.82
	QB3	3.0	2.17	1.78	0.94
	QB4	2.8	2.43	1.63	0.87
	SO1	2.6	1.32	1.47	0.63
	SK1	3.4	2.34	1.74	0.74
	SK2	2.7	2.44	1.44	0.56
	SK3	3.1	1.91	1.68	0.82
	UT2	9.1	3.36	3.36	2.27
	UT3	18.8	5.00	6.00	4.06
	WA2	7.9	3.80	4.93	2.28
	WA3	5.5	3.13	3.69	1.81
	WY3	5.8	3.63	3.36	2.09
	YK1-4	3.2	2.69	1.86	1.22

typically present as a dot of varying size (states 1 - 2, Fig. 10). In most of the samples from across the boreal zone the apical lunule is usually missing completely (state 0, Fig. 10) or is present as a dot of varying size (states 1, 2, Fig. 10). The apical lunule is more developed in many populations of the southern Rocky Mountains and Pacific regions, but is quite variable between populations.

Figure 27 shows weighted mean character values for the apical lunule (Fig. 10) of samples of *C. nebraskana*. In all population samples of this species the apical lunule is lacking in the majority of specimens any may be present as a small dot (character state 1, Fig. 11) in a few specimens.

Genitalia of the *Cicindela sylvatica* group

Structures of the genitalia of both sexes of tiger beetles are in some cases specifically distinct and aid in identification and reconstruction of phylogeny as demonstrated by Horn (1930) Mandl (1935, 1936, 1937, 1954, 1956, 1967, 1970, 1974), Papp (1952), Rivalier (1950, 1954, 1957, 1961, 1963), Rumpp (1957), Freitag (1965), Wallis (1961), Leffler (1979), and Kaulbars (1982) for males, and Tanner (1927), Freitag (1966, 1972, 1979) and Kaulbars (1982) for females.

Rivalier (1950, 1954) in classifying the Palearctic and Nearctic *Cicindela* concluded that *C. longilabris* (which presumably included *C. nebraskana*) and the Palearctic species *C. soluta* Dejean, *C. lacteola* Pallas, *C. japana* Motschulsky, *C. gemmata* Faldermann, *C. sylvatica* Linnaeus and *C. granulata* Gebler form a group of closely related species based on similarities of the sclerotized structures of the internal sac of the male aedeagus.

Previously the male genitalia of *C. soluta* and its geographic variation were studied by Mandl (1936), and Papp (1952) figured the male genitalia of *C. longilabris*. Mandl (1970) examined the male genitalia of *C. sylvatica* and described a new subspecies, *C. sylvatica reiseri*, based partly on slight differences in the sclerites of the internal sac.

Drawings of the ventral view, in its retracted state and left lateral view of the male aedeagus and the sclerites of the internal sac are here presented for a number of populations of *C. longilabris* (Figs. 28 - 39), *C. nebraskana* (Figs. 40 - 43) and for the six Palearctic species

(Figs. 44 - 49) of the *sylvatica* group of Rivalier (1950, 1954). Drawings of the female genitalia are presented for various populations of *C. longilabris* (Figs. 50 - 47), *C. nebraskana* (Figs. 58 - 60) and for the six Palearctic species in the group (Figs 61 - 66). The nomenclature applied here follows Rivalier (1950, 1954) and Freitag (1965) for males and Freitag (1966, 1972) for females.

Figures 28 - 39 present male genitalia of various populations of *C. longilabris*. The median lobe of the aedeagus is of moderate length, curved in lateral view, with lateral flanges at the apical fourth of its length which converge towards the apex producing a ventrally curved point (Fig. 29). The left lateral apical flange is usually slightly more pronounced than that on the right. The parameres (Fig. 29) are usually two-thirds to three quarters of the length of the median lobe and taper to thin pointed apices. In all of the approximately 90 examined specimens of the *C. sylvatica* group the right paramere is shorter than the left. In 23 measured specimens the right paramere averaged 85% of the length of the left with a range of 78% to 99%. Figure 28 shows the arrangement of sclerites in the internal sac of the aedeagus of *C. longilabris*. The numbered sclerites are probably homologous with the correspondingly numbered structures of the internal sac in the *C. maritima* group as described by Freitag (1965) and the *C. sexguttata* group as described by Kaulbars (1982). The largest is number 5, the median tooth, "la grande dente" of Rivalier (1950). The flagellum, "le flagelle" of Rivalier (sclerite 4, Figs. 28, 29), is a long, tapering sigmoid shaped structure, thickened at its base, and pointed apically.

A small sclerite (3) "le clou" of Rivalier lies ventral to the base of the flagellum. The large curved sclerite 2, "la pièce arciforme" of Rivalier (1950) and a smaller twisted sclerite 6 "la baguette" of Rivalier lie dorsally in the internal sac (Fig. 28).

Figures 29 and 30 present the male genitalia of *C. longilabris* from Newfoundland. The shape of the aedeagus and configuration of sclerites of the internal sac are typical of the species. The median lobe is large in size which is consistent with the slightly larger average body size of Newfoundland specimens. Figure 31 shows a genitalia configuration typical of the species, in a specimen from Forestville, Quebec. Again the large size is consistent with the large specimen from which the aedeagus was dissected. Figure 32 shows a smaller specimen from Whitehorse, Yukon territory with slightly exaggerated lateral flanges on the aedeagus. This character varies greatly among specimens within populations and does not show any consistent difference between populations.

Specimens from Creede, Colorado (Fig. 33), Sheep's Crossing, Apache Co., Arizona (Fig. 34), the Kaibab Plateau, Arizona (Fig. 35), Cedar Breaks in southwestern Utah (Fig. 36), and Olympic National Park in Washington (Fig. 37), are not different in size and shape of the aedeagus or sclerites of the internal sac, relative to individual differences to be seen within these populations. The slightly smaller size of genitalia of specimens from Lost Prairie Campground in Oregon (Fig. 38), and Sonora Pass in California (Fig. 39), are consistent with the smaller average body size of beetles in the Pacific coast states as discussed in the morphometric analysis.

Male genitalia of ~~species~~ specimens of *C. nebraskana* from Mill Creek Canyon, Utah (Fig. 40), Sonora Pass California (Fig. 41), Oliver, BC (Fig. 42) and Patricia, Alberta (Fig. 43) exhibit inter-population variation no greater than intrapopulation variation. There may be slightly more pronounced flanges of the median lobe in *C. nebraskana* than in *C. longilabris*, but larger series of specimens would have to be examined to adequately test that hypothesis.

Norman Rumpp has found a statistical difference in the size of the genitalia between *C. nebraskana* and *C. longilabris* where the species are sympatric in east central California. The former has a longer aedeagus and longer median tooth of the internal sac, consistent with the larger overall body size of *C. nebraskana* relative to the smaller form of *C. longilabris* which occurs in the area (Rumpp, unpublished data).

Figure 44 shows the male genitalia of *C. sylvatica*. The median lobe of the aedeagus is distinctly different from *C. longilabris* and *C. nebraskana* in its long narrow apex. The flagellum (sclerite 4) of *C. sylvatica* is short and stout and the tooth (sclerite 5) lacks the expanded base evident in the two Nearctic species. Sclerites 1, 2, and 6 (Fig. 44) are relatively small in size.

The male genitalia of *C. granulata* (Fig. 45) are distinguished by the thick median lobe with an acutely pointed apex and the stout flagellum which is not greatly thickened at its base, relative to that of *C. longilabris* (Figs. 28 - 39), *C. nebraskana* (Figs. 40 - 43) or

C. sylvatica (Fig. 44).

The median lobe of *C. japana* is intermediate in shape between that of *C. longilabris* or *C. nebraskana* (Figs. 28 - 43) and the narrower, elongated shape of *C. sylvatica* (Fig. 44). The sclerites of the internal sac distinguish *C. japana* (Fig. 46). Sclerite a (Fig. 46) could be the result of a fusion of the flagellum (sclerite 4) and sclerite 1, but this is uncertain. Sclerites 2 and 3 (Fig. 46) are small in size and sclerite 5 is probably a reduced median tooth. The homology of sclerite b in Figure 46 is uncertain.

The male genitalia of *C. gemmata* are shown in Figure 47. The median lobe of the aedeagus is large, consistent with the large size of the beetle and is greatly curved in lateral view. The most notable character is the sclerite cluster of the internal sac (Fig. 47).

The male genitalia of *C. soluta* (Fig. 48) are smaller in size, consistent with the small body size of the beetle, and are unique among the species of the *sylvatica* group in the shape of the projection at the apex of the aedeagus. The sclerite cluster of the internal sac (Fig. 48) is similar to the sclerite cluster of *C. gemmata* (Fig. 47). Structures C in Figures 47 and 48 could possibly be the median tooth (sclerite 5) reduced in size and lacking the enlarged base present in *C. longilabris* (Figs. 27 - 39). The homologies of other sclerites of the internal sac of *C. gemmata* and *C. soluta* are unclear.

The male genitalia of *C. lacteola* (Fig. 49) are distinct in the size and shape of the median lobe of the aedeagus and in the semi-circular ring of sclerites in the internal sac which probably represent an enlargement and breaking up of sclerite 2. Sclerite 5 (Fig. 49), the median tooth of the internal sac in *C. lacteola* is different in shape from that of other species in the *sylvatica* group.

Figures 50 - 57 show the female genitalia of *C. longilabris*. Specimens from Harmon Field, Nfld. (Fig. 50), Forestville, Quebec (Fig. 51) and Whitehorse, Yukon (Fig. 52) show the size and shape of the oviduct sclerite, second gonacoxae, second gonapophyses, sternum 8 and syntergum 9 and 10, typical of *C. longilabris*. Figure 52 shows slightly shorter second gonapophyses with more rounded species and slightly more rounded points at the apex of sternum 8. This is due to wear and is well within the range of variation found within local populations. I have seen older female specimens with second gonapophyses worn to half the length of those shown in Figures 50 and 51. Specimens from Creede, Colorado (Fig. 53) and Cedar Breaks, Utah (Fig. 54) show a slightly more pronounced ventral notch of the second gonacoxae than is shown in Figures 50 - 52. This, however, is also a character which varies within populations. Specimens from the Kaibab Plateau of Arizona (Fig. 55) have an oviduct sclerite wider and more rounded than is typical of *C. longilabris*. Specimens from Sheep's Crossing, Apache Co., Arizona (Fig. 56) and Lost Prairie Campground, Oregon (Fig. 57) show no variation greater than one would find within a population.

The female genitalia of *C. nebraskana* (Figs. 58, 59 and 60) and *C. longilabris* are not clearly separable. The specimen from Oliver, BC (Fig. 59) is an example of an old female with very worn second gonopophyses which appeared scratched and abraded.

The female genitalia of the Palearctic species of *C. sylvatica* (Fig. 61) show no characters that are distinctly different from *C. longilabris* and *C. nebraskana*, although syntergum 9 and 10 of the former species is slightly more rounded.

The female genitalia of the Palearctic species *C. granulata* (Fig. 62) are distinct in having a relatively short, wide oviduct sclerite, two small sclerotized structures visible in the right side of the bursa copulatrix and a slightly narrower syntergum 9 and 10 with lateral margins straighter than that of *C. sylvatica*.

The female genitalia of *C. japana* (Fig. 63) are distinguished by the combination of a large oviduct sclerite, a small, square shaped, lightly sclerotized field in the membrane between the second gonacoxae, and very rounded apices of sternum 8. The rounding of the apices of sternum 8 of this specimen (Fig. 63) may be due largely to wear, as there are no setae on the apices and the second gonapophyses showed signs of much abrasion. The few female specimens of *C. japana* I was able to examine were all old and worn.

The female genitalia of *C. gemmata* (Fig. 64) are distinct in the wide, rounded, slightly triangular shaped oviduct sclerite and the notched shape of the second gonapophyses.

The female genitalia of *C. soluta* are distinguishable by several characters (Fig. 65). The shape of the oviduct sclerite is uniquely different from other species of this group, there is a pronounced point on the medial edge of the second gonacoxae immediately above the notch, the second gonapophyses have a notched shape to their lateral edge, sternum 8 is uniquely shaped at its apex with one distinct seta at a notch at the apex on each side, and the lateral portions of syntergum 9 and 10 are more rounded in shape than other species of this group. The notched shape of the lateral edge of the second gonapophyses of *C. soluta* (Fig. 65) suggest a close relationship with *C. granulata* (Fig. 64).

The female genitalia of *C. lacteola* (Fig. 66) are distinct in the truncated setose apices of sternum 8, and the 3 small dark heavily sclerotized structures inside the bursa copulatrix.

The number of setae on the ventral surface of the second gonapophyses does not appear to be a useful character in distinguishing species of the *sylvatica* group due to its variability. In *C. longilabris* this varies from 0 in some individuals to 4 in others and often differs between the right and left sides of the same individual (Figs. 54, 55, 56).

The egg of *C. longilabris*

Descriptions of the egg state of species of *Cicindela* have been published by Moore (1906) for *C. repanda* Dejean, Shelford (1908) for *C. purpurea* Olivier, Huie (1915) for the European species *C. campestris* Linnaeus, Willis (1967) for *C. circumpicta* LaFerté, *C. ducdecimguttata* Dejean, *C. nevadica* LeConte, and *C. togata*LaFerté, Hori (1982) for *C. japonica* Thunberg, and Kaulbars (1982) for *C. denikei* Brown. These descriptions indicate that the eggs of *Cicindela* are similar, lacking any obvious character differences except for size, the larger beetles usually having larger eggs. Willis (1967) observed a fine reticulate pattern on the shiny surface of the chorion of the egg of *C. togata* at high power. Moore (1906), Huie (1959), Zikan (1929) and Willis (1967) noted that the eggs of *Cicindela* are sticky at one end or are fastened to the substrate by a short stalk.

I succeeded in finding only one egg of *C. longilabris* from a mating in the laboratory which measured 2.2 mm long by 1.2 mm at its greatest diameter and not appreciably wider at one end than the other. It had a shiny transparent chorion and a pale creamy coloured embryo within (Fig. 67).

Larvae of *C. longilabris*

George Horn (1878) described the larvae of one species of each of the genera of North American tiger beetles with the species *C. repanda* representing *Cicindela*. Shelford (1908) briefly described larvae of 12 species of *Cicindela* with notes on life histories and biology. Hamilton (1925) published detailed descriptions of the larvae of a large number of cicindelid species of 6 genera, 34 of them from the genus *Cicindela*. Willis (1967) published descriptions of four additional species. Larvae of *C. nebraskana* and *C. longilabris* were not among those described by any of the above authors. Leffler (1979) described the third instar larva of *C. nebraskana*. He also described a single second instar larva from an area of hybridization between the Rocky Mountain form *C. longilabris laurentii* and the Pacific coast form *C. l. perviridis*.

As larval descriptions have traditionally been based on the third instar (Hamilton, 1925; Willis, 1967) and some of the characters in these descriptions vary between instars of a species and between individuals of the same instar, it seems appropriate to redescribe the larval stages of *C. longilabris* beginning with the 3rd instar.

Series of specimens of all three instars of *C. l. longilabris* were reared from laboratory mating of adult specimens collected in the Thunder Bay District of Ontario. The format used for the descriptions of the larvae follows that used by Hamilton (1925) and Willis (1967).

Third instar larva of *C. longilabris longilabris* (Figs. 68 - 72)

Material available: Twelve specimens were reared from matings of captive adults. Eight of the specimens were killed and preserved the day the descriptions were done. Twelve exuviae of larvae that had been reared to the adult stage were collected in Thunder Bay, Ontario.

Colour: Head, pronotum and clypeus bronzy black with some metallic reflections varying from green to cupreous to bronzy in some specimens; labrum black or very nearly so; mandibles rufous basally to black in distal protion; antennae dark brown to black; maxillae rufous to medium brown frequently with apical segments of palpus and galea dark brown black; genae rufous posteriorly to dark brown or black anteriorly; mesonotum dark grayish brown anteriorly to light brown posteriorly; metanotum slightly lighter brown than mesonotum; legs somewhat variable, shading from light to dark brown; sclerotized areas on abdomen yellowish brown; setae on head and pronotal surface brown some white setae around lateral margins of pronotum; setae on remainder of body brown.

Head: Diameter of stemma I approximately equal to diameter of stemma II and approximately equal to interstemmatal distance (slightly variable); frontoclypeolabral area approximately as wide as long, or very nearly so (somewhat variable); U-shaped ridge on caudal part of frons with 2 setae; distal segment of antenna approximately 0.7 as long as penultimate segment, penultimate segment about 0.6 as long as 2nd segment, proximal segment approximately 0.8 as long as 2nd segment; proximal segment of antennae with 8 setae; 2nd with 8 or 9 setae; penultimate segment with 2 setae; distal segment with 2 or 3 obvious setae and sometimes 1 - 3 very minute setae; maxilla with 3 setae on mesal edge of basal segment of galea and 5 setae on distal segment, maxillary palpus 3 segmented; 2nd segment of maxillary palpus with 2 setae, 0 setae on proximal and distal segments; basal segment of labial palpus with 3 small ventrodistal spines flanked on each side by two setae; distal segment of labial palpus with 1 setae; ligula usually with 4 or sometime 5 setae; labio-stipites with 2 long distinct setae and 2 minute setae (Figs. 68, 69).

Pronotum: Cephalolateral angles projecting as far anteriorly as mesal edge; lateral margins slightly carinate; setae on disc of pronotum usually 7 on each half (variable 6 - 8) (Fig. 68).

Abdomen: Sclerotized areas distinct; secondary setae numerous, less than one half as long as primary setae; ventral elevations of 9th abdominal sternum usually with 4 distinct setae (occasionally 3 large and one smaller); pygopod bearing a variable number of primary setae (16 - 20); median hooks of 5th segment with 2 - 4 setae (usually 3); inner hooks with central spine approximately 1/3 the length of the entire hook and with two setae at shoulder of hook at least twice as long as spine (Figs. 70 - 72).

Measurements: Total length of body, 12 - 20 mm (likely to vary greatly with the nutritional state of the individual and length of time since last moult); diameter of stemma I 0.28 - 0.30 mm.; diameter of stemma II 0.25 - 0.29 mm; distance between stemma I and stemma II 0.26 - 0.33 mm.; length of frontoclypeolabral area 1.8 - 1.9 mm.; length of pronotum 2.0 - 2.2 mm.; width of pronotum 3.44 - 3.61 mm.

Second instar larva of *C. longilabris longilabris*

Material available: Twelve specimens were reared from matings of captive adult *C. longilabris longilabris* collected in the Thunder Bay District. Seven of these specimens were killed and preserved the day the descriptions were written.

Colour: Head, pronotum and clypeus bronze-black with metallic reflections of green or cupreous; labrum also bronze; mandibles rufous brown at base to black apically; antennae dark brown to black; maxillae brown; genae light rufous brown posteriorly to black anteriorly; mesonotum dark grayish brown anteriorly to light brown posteriorly; metanotum slightly lighter than mesonotum; legs variable from light brown in some individuals to dark brown in others; sclerotized areas on abdomen yellowish brown; setae on head and pronotal surface brown; setae on margin of pronotum light brown; setae on remainder of body brown.

Head: Diameter of stemma I approximately equal to diameter of stemma II and approximately equal to interstemmatal distance (slightly variable); frontoclypeolabral area approximately as wide as long; U-shaped ridge on caudal part of frons with 2 setae; relative proportion of sizes of antennal segments approximately as in the 3rd instar larvae; proximal segment of antenna with 5 - 6 antenna with 5 - 6 setae; distal segment with 3 setae; mesal edge of basal segment of maxillary galea with 2 setae; distal segment of galea with 5 setae; maxillary palpus 3 segmented; 2nd segment with 2 setae; basal and distal segments with 0 setae; basal segment of labial palp with 3 small ventrodistal spines flanked on mesal side by 1 setae, on the lateral side with 2 setae; distal segment of labial palpus with 1 setae; ligula with 4 setae; labio-stipites with only 2 long setae visible.

Pronotum: Cephalolateral angles projecting as far anteriorly as mesal edge; lateral margins slightly carinate; setae on disc of pronotum 7 in number.

Abdomen: Sclerotized areas distinct; secondary setae less than half as long as primary setae; ventral elevations of 9th abdominal sternum usually with 4 setae (occasionally with 3 distinct setae and 1 smaller one); pygopod bearing 18 - 20 setae; median hooks of 5th segment with 2 setae; inner hooks with central spine approximately half the length of the entire hook and with 2 setae at shoulder of hook approximately twice as long as spine.

Measurements: Total length of body 10 - 14 mm.; length of pronotum 1.26 - 1.40 mm.; width of pronotum 2.04 - 2.36 mm.

First instar larva of *C. longilabris longilabris*

Material available: Five specimens were reared in laboratory mating of captive adult *C. longilabris longilabris* collected in the Thunder Bay District of Ontario.

Colour: Head, pronotum, and clypeus bronze-black with some metallic reflections of cupreous or green; labrum also bronze; mandibles lighter in colour than in 2nd or 3rd instar, light brown proximally to dark brown distally; maxillae light brown; distal segment of galea dark brown; genae rufous; mesonotum grey-brown, metanotum light gray-brown; legs light to medium gray-brown; sclerotized areas on abdomen almost transparent; setae on head and pronotal surface very light brown; setae on remainder of body very light brown.

Relative body proportions and arrangement of setae almost identical to 2nd and 3rd instars with the following differences: Number of setae around lateral margin of pronotum greatly reduced, proximal segment of antennae with 0 setae; 2nd segment of antennae with 2 setae; penultimate segment with 2 setae; distal segment with 3 primary setae, and in some individuals 2 smaller setae visible; mesal edge of basal segment of maxillary galea with 1 setae; basal segment of labial palp with 3 ventrodistal spines; flanking setae not developed; median hooks on dorsum of 5th abdominal segment with only 1 setae each; inner hooks not well developed, spine approximately 2/3 the entire length of hook; pygopod usually with 12 sometimes 14 setae surrounding it.

Measurements: Total length 4.7 - 7.1 mm.; length of pronotum 0.78 - 0.84 mm.; width of pronotum 1.34 - 1.46 mm.

The three larval instars differ from each other in the following ways:

1. Size: The size of head and pronotum appears to occur in distinct size classes, as is evident for many other soil inhabitating tiger beetles in the work of Shelford (1908), Hamilton (1925), Willis (1967), Palmer (1978, Palmer and Gorrick (1979).

   The overall body size or abdominal size probably varies with nutritional state and the length of time the larva has had to grow since its most recent moult, which has been shown for *C. repanda* (Palmer and Gorrick 1979), and for *C. japonica* (Hori, 1982).
2. Colour of labrum: Because the metallic lustres are structural colours, they vary somewhat with the age of the individual as was shown by Shelford (1917). These colours also vary with different preserving fluids.
3. There is a difference in the number of setae on the median hooks of the 5th abdominal segment between the instars. 1st instars have 1, 2nd instars 2, and 3rd instars usually 3 but this can be variable between 2 and 4 in number.

4. The number of setae on the mesal margin of the basal segment of the maxillary galea is 1 in 1st instars, 2 in 2nd's and 3 in 3rd instars as was noted by Leffler (1979).
5. Fewer setae are evident on each of the antennal segments in the earlier instars as indicated in the above descriptions. The 3rd instar larva of *C. longilabris* keys out to step 18 of Hamilton's (1925) key, with one possible obstacle at step 8, where the variability in the number of setae on the median hook of the 5th abdominal segment could cause problems. As stated above, most 3rd instar larvae have 3 setae on the median hook, but some 3rd's and all earlier instars have a smaller number. Once keyed to step 18 of Hamilton's key, *C. longilabris* larvae can be separated from those of *C. tranquebarica* and *C. silvicola* by the following key:

1. Pronotal surface with a number (less than 25) of small secondary setae in addition to primary setae .... *C. tranquebarica*
1. Pronotal surface with secondary setae numbering 2 or 1 2
    2. Pronotal surface with 2 setae on each side in addition to the 6 primary setae; distance between ocelli I and II greater than the diameter of ocellus II; occurs in the Old World .. *C. silvicola*
    2. Pronotal surface with 1 seta on each half in addition to the 6 primary setae; distance between

stemmata I and II approximately equal to diameter of stemmata I and II; occurs in North America .... *C. longilabris*

Life History

The life histor~~y~~ies of a number of cicindelid species have been described. Enock (1903) and Huie (1915) worked out the four year cycle of the Palearctic species *C. campestris* (Fig. 73). Criddle (1907, 1910) studied the life histories of *C. formosa* Say, *C. limbata* Say, *C. limbalis* Klug and *C. lengi* Horn. Shelford (1908) determined the life cycles of *C. purpurea*, *C. limbalis*, *C. formosa*, *C. hirticollis* Say, *C. punctulata* Olivier, *C. sexguttata* Fabricius and *C. lepida* LeConte, and outlined partial life cycles for other species. Willis (1967) provided some information on the life cycle of *C. circumpicta*, *C. duodecimguttata*, *C. togata* and *C. willistoni* LeConte, and information concerning adult seasonality of *C. rapanda*, *C. cuprascens* LeConte, *C. macra* LeConte and *C. hirticollis* Say. The life history of the Palearctic species *C. japonica* was studied by Hori (1982). Zikan (1929) described partial life cycles and larval stages for a number of Brazilian species in several different genera of tiger beetles. Cazier (1942) summarized the limited information on *Omus*, and Palmer (1976) studied the life cycle of *Pseudoxychila tarsalis* Bates.

Shelford (1908) in studying *Cicindela* species in the vicinity of Chicago identified three life cycle patterns (Fig. 73):

1. A one year cycle such as in *C. punctulata* in which the eggs are laid in mid-summer and larvae usually attain 3rd instar by fall, hibernate as 3rd instars, pupate the following June; adults emerge in early July and become sexually mature very soon, mate and die within two months.

2. A two year cycle such as in *C. lepida* Dejean in which the eggs are laid in mid-summer, attain 2nd instar by fall, hibernate as 2nd instars, moult to 3rd instar in the second summer, hibernate again and pupate the following spring, adults emerge early in the third summer, become sexually mature very quickly and mate and die in two or three months.
3. A two year cycle such as in *C. purpurea* in which the eggs are laid in June, larvae attain 3rd stage by fall and hibernate the first winter, pupate the following summer, adults emerge late in the second summer, hibernate the second winter and emerge the next spring, mate and die. Larval life lasts 13 months, the adult stage lasts twelve to thirteen months.

Shelford (1908) indicated that temperature, moisture, and food influence the duration of the larval stadia. Some of the species, which Shelford had found to have a two year cycle as in pattern 3 in the Chicago area, were found by Criddle (1910) to have 3 year cycles farther north in Manitoba, where the larval life was prolonged over another winter. This is probably caused by shorter summer seasons which limit total food intake and delay progress through the larval stages. The work of Palmer and Gorrick (1979) and Hori (1982) indicates that the larvae of tiger beetles must attain a threshold body mass before moulting to the next stage can occur.

No studies of the chronology of *C. longilabris* or *C. nebraskana* through their immature stages have been published and information regarding adult seasonality of these species is limited. Leffler's (1979) observations based on the unworn look of the elytra of adult *C. longilabris perviridis* collected in late summer, indicate that the adults must emerge late in summer, overwinter and become sexually mature the following spring and based on adult specimens collected in September which appeared teneral, he notes that the same pattern of adult seasonality is the case for *C. nebraskana*. Dunn (1978) provided a frequency histogram of *C. longilabris* specimens captured in New Hampshire which showed that adults were most frequently collected during the month of August.

My data regarding the adult seasonality of these two species is consistent with the findings of Dunn (1978) and Leffler (1979).

Figure 74 indicates the total number of adult *C. longilabris* taken in each capture session at the Stanley Hill study site in 1982. No attempt was made to estimate absolute population size. Only relative abundance at different times of the season was observed. June 5, 15, and September 2 were cool overcast and rainy days when few beetles were active. The overall curve is a bimodal pattern. The number of specimens captured in the August 24 session does not adequately represent the abundance of *C. longilabris* on that date. The technique used to mark and record the location and date of capture of each individual required a handling time which limited the total number that could be processed in one capture session. Specimens were so numerous on that day that with each step 8 or 10 adult specimens of *C. longilabris* could be seen to fly in many directions, and a few times 2 or 3 specimens were captured in one drop of the net. At other times of the season when the beetles were not so numerous the upper limit on the number of individuals which could be captured, marked, recorded and released was not approached.

Seventy-six per cent of the individuals captured on August 10 were teneral, 59% of those captured on August 17th were teneral and 66% of those captured on August 24th were teneral, indicating that the majority of specimens collected at that time of year had emerged from the pupal stage within a very few days previous to their capture. The fact that very few of the specimens collected in May appeared teneral, combined with the frequency of capture data (Fig. 74) indicates that *C. longilabris* overwinters in the imago state.

The sex ratio of males to females of all adults of *C. longilabris* captured in May 1982 was 1.74: 1 (n = 85). In June this ratio was 1.22:1 (n = 60), in July 1.57 : 1 (n = 18), in August 1.17 : 1 (n = 117) and in September 0.81 : 1 (n = 38). Freitag (1965) in examining seasonal changes in sex ratios of *C. oregona* and *C. duodecimguttata* found that females outnumbered males early in the season and males are more numerous than females late in the season. The above data suggest that the reverse is true in *C. longilabris*. However, the above ratios may not be indicative of the actual sex ratios of the species. Kaulbars (1982) indicated that males of *C. denikei* were more numerous in prime open foraging areas during breeding season and at any given time a percentage of females were ovipositing in sites outside of the foraging areas. Similar behavioural differences between males and females may bias observed ratios of *C. longilabris*.

Pairs of adult *C. longilabris* at the Stanley Hill site were occasionally observed *in copulo* during June and July. No mating pairs were seen after July 19th or any time during August or September. This is consistent with the hypothesis that the adults emerging in late summer do not reach sexual maturity until the following spring.

Figure 75 presents the frequency of capture of adult *C. longilabris* by date of collection from the label data of borrowed specimens collected in Canada. A bimodal pattern is weakly evident with population peaks in June and late August. There is probably a bias in these figures due to the fact that insect collectors are usually more active in temperate climates during summer months. This may account for the relatively large numbers indicated for the month of July at a time of year when the relative abundance of *C. longilabris* was seen to decline at the Stanley Hill site (Fig. 74). With a sufficient number of insect collectors in the field, specimens will be collected even if their abundance is low. It is a common habit among collectors to collect only a few specimens of a common form when encountered regardless of its abundance.

Figure 76 presents the frequency of capture of adult *C. longilabris* from label data of borrowed specimens collected in the Pacific coast states of Washington, Oregon, and California and suggests a bimodal pattern of adult seasonal abundance. The large peak in the first half of July probably reflects the time of year when collectors are most active, and the second peak in September when collecting is greatly reduced is probably indicative of a late summer emergence of adults from the pupal stage.

Figure 77 presents the same type of histogram based on specimens from Utah, Colorado, Arizona and New Mexico. A bimodal frequency distribution is presented with the greatest numbers occurring in early August. The pattern of seasonality of adults of *C. longilabris* is similar throughout its range, with some differences in the timing of late season emergence. In Canada the late season peak in numbers occurs in the latter half of August (Figs. 74, 75), in the southern Rocky Mountain region this seems to occur in the early half of August (Fig. 77), and in the Pacific coast states in early September (Fig. 76).

Figure 78 presents the frequency of capture of *C. nebraskana* adults by date from label data of borrowed specimens. This species appears to be less abundant during mid summer and experiences a population peak in late summer. Thus *C. nebraskana* probably has a life cycle in which adults emerge in late summer and overwinter before mating the following spring and early summer.

The marking of larval burrows and subsequent observations of development in size and condition of the burrows at the Stanley Hill site in the summer of 1982 yielded three patterns of seasonality.

Third instar burrows marked in May and early June all disappeared after approximately mid June. Specimens either died, had their burrows disturbed or closed their burrows, pupated and later emerged as adults without leaving signs of having done so. In some cases the burrows and golf tees marking them were disturbed by off-road motorcycles and lawn mowers.

Seven 3rd instar larvae dug from their burrows and placed in rearing tubes in May pupated in June and emerged as adults of *C.l. longilabris* in late July. These burrows were closed between the active 3rd instar stage and emergence of the adult for an average of 46 days, ranging from 39 to 62 days. The specimens were probably not in the pupal stage all of that time. Actual duration of the pupal stage is not known as it was not observed directly.

The majority of specimens marked as 2nd instars at the Stanley Hill site in May and June were not successfully followed through the season, presumably due to mortality. Those followed through the season were found to have attained 4rd instar by early June. They continued to feed for most of the summer and were still in the 3rd instar stage in the third week of September. They would presumably have overwintered in this stage if left in the ground to do so.

First instar larvae appeared in the second week of July and were found in increasingly large numbers throughout July. The majority were not followed through the duration of the summer, probably due to a high mortality rate. Those which were successfully followed through the summer had attained the 2nd instar stage by the first or second week of September and presumably overwintered in the 2nd stage.

One first instar larva found in early May at the Stanley Hill site had probably overwintered. It was probably an individual which had not acquired sufficient body size to moult to 2nd instar before its first winter. Such variant specimens are to be expected.

These data indicate that the entire life cycle of *C. longilabris* is three years in duration. Figure 73 presents the chronology of the three year cycle of *C. longilabris* compared with the cycles of other species studied by previous authors (Shelford, 1908; Huie, 1915).

If the chronology of the life cycle was rigid for all individuals, *C. longilabris* would consist of three distinct populations each genetically and temporally isolated from the other two. Many workers (Shelford, 1908; Willis, 1967; Palmer, 1976) have indicated that some variability occurs in the timing of appearance of the life stages in many species of tiger beetles. Hori (1982), in studying *C. japonica* in which the seasonality of the adult stage is similar to that of *C. longilabris* indicated that a small number of the adults emerging in late summer achieve sexual maturity quickly and a small amount of oviposition occurs in late summer and early fall. An intensive study of the population dynamics of *C. longilabris* would probably reveal a similar amount of variability in the timing of life stages. The presence of slow developing larvae as mentioned above, and a small amount of late season mating would maintain a genetic connection between year classes.

It is unlikely that the life cycle of *C. longilabris* is less than three years in duration anywhere in the geographic range of the species. Even in the southern part of its range in Arizona, New Mexico, Utah and Colorado the same pattern of adult seasonality occurs (Fig. 77); here the beetles inhabit montane forest at·high elevations where the duration and temperature ranges of the seasons roughly approximate that of the boreal forest zone farther north. It is quite possible however, that the cycle may take a year longer in the more northern part of its range. Just as some species of *Cicindela* which have 2 year cycles in the vicinity of Chicago (Shelford 1908) were found to have 3 year cycles in Manitoba (Criddle 1910), the larvae of *C. longilabris* may take an extra year to develop in the northern part of its range where it approaches tree line and the southern limit of continuous permafrost (Fig. 79), and where the summer season is significantly shorter. This is of course hypothetical and the life history would have to be studied in various parts of the range of the species to test the hypothesis.

Soil Associations

Leffler (1979) contended that edaphic factors are among the most important limits in defining tiger beetle habitats. The female chooses the oviposition site (Shelford, 1907) and the entire larva stage is spent in a burrow in the soil. Many species are restricted to soils of particular types, clay, sand, or alkali-encrusted among others. Kaulbars (1982) found that soil type seemed to be a limiting factor in the distribution of some of the forms of the *Cicindela sexguttata* species group.

Leffler (1979) found a correlation between the length of the second gonapophyses of the female genitalic armature used in oviposition and the particle size of soil inhabited among 15 species of *Cicindela*. He concluded that species with long narrow styli are found in soils with a high proportion of sand and those with short stout styli inhabit soils with a high clay content, adding the cautionary note that recently eclo~~d~~sed individuals should be examined for such a test, as digging activity can greatly wear down the length of the styli making them much shorter and more blunt in older individuals. If this is the case it raises the question of whether eggs laid by an older female might be laid in soil of a slightly different texture and at a different depth in the soil than eggs laid earlier in the life of the same adult female, and whether there might be, therefore, a differential survival rate between the early and late eggs. If such differential survivorship occurs it would be a strong selective force favouring individuals laid at a certain stage in the life of the adult female thus tending to stabilize a given life cycle pattern for a given species. Intensive field studies of oviposition site selection by females and subsequent larval survivorship would have to be undertaken to answer these questions.

Leffler (1979) also concluded that the mean ratio of breadth/length of the styli of the 2nd gonapophysis is not statistically significantly different between *C. longilabris* (X = 56.75) and *C. nebraskana* (X = 56.95). According to Leffler's (1979) hypothesized relationship between the dimensions of the 2nd gonapophyses and soil texture, one would not expect a significant difference in the particle size distribution of the soils inhabited by these two species. Leffler (1979) however, indicated that there is such a difference. He stated that five samples of soil from *C. longilabris* collecting sites are clayey soils with a mean of 28.6% sand, in contrast with five samples of soil from *C. nebraskana* collecting sites all from sandy clay with a mean of 50% sand.

My data are more consistent with Leffler's (1979) indicated similarities between the dimensions of the 2nd gonapophyses of these two species. Using 0.63 mm diameter as the border between sand and gravel ($>$ 0.63 mm diameter) and silt and clay ($<$ 0.63 mm diameter), samples taken from widely distributed *C. longilabris* collecting sites averaged 82% sand and gravel and 3 samples from *C. nebraskana* sites averaged 83% sand and gravel. In each case gravel (particles $>$ 2.0 mm diameter) made up a very small fraction. Although the sample sizes are too small to be conclusive, these data suggest that both species occur on sandy soils in which silt and clay are very small components.

It is quite possible that edaphic factors other than particle size, such as pH, electroconductivity, moisture and temperature of soil, the amount of organic matter present and chemical make-up are important in the distribution of the two species.

By plotting collecting localities from specimen label data on soil maps comparisons were made between the distribution of the different forms of *C. longilabris* and *C. nebraskana* and that of major dominant soil types at the order and great group level of classification.

In eastern North America the great majority of locality records of *C. longilabris* fell on map units indicating Humo-Ferric Podzols as the dominant soil type (Soil Conservation Service, 1967; Soils of Canada, 1972). Soils of the Podzolic order, in the Canadian classification are well to imperfectly drained mineral soils which typically develop under coniferous or mixed forest or heath vegetation and characteristically have complexes of soluble organic matter and compounds of aluminum and iron leached from the surface layers and deposited in the B or subsurface horizon (Clayton et al, 1977). The Humo-Ferric great group is very widely distributed in Canada being the dominant soil type in all podzolic map units indicated on the Soils of Canada (1972) map. Humo-Ferric Podzols occur mainly on well drained sites and are characterized by B horizons in which accumulations of aluminum and iron colloids are considered most significant to their properties and the organic matter content of the B Horizon is less than 10% (Clayton et al, 1977).

Table 39 shows that the percentage of locality records of *C. longilabris longilabris* falling on map units where Humo-Ferric Podzols are dominant was 74% in Newfoundland, 81% in the other Atlantic Provinces, 72% in Ontario, 63% in Quebec and Labrador and 100% in the New England states of Maine, Vermont and New Hampshire. In all of these areas most of the remaining localities are in areas dominated by Luvisols or Brunisols. In New York State 9 of 10 collecting sites were in the area of the Adirondack Mountains where Humo-Ferric Podzols are dominant. One specimen was collected in the southern Catskill Mountains in an area where Eutric Brunisols are dominant. This is the southernmost record of *C. longilabris* in eastern North America.

In Michigan 85% of collecting records fell on map units where Podzols are dominant, in the northern half of the state. In Wisconsin 58% of the locality records are from areas where Podzols dominate, in the northern quarter of the state. Another 31% of the records from Wisconsin appear to occur on Orthic Regosols which are soils with horizons too poorly developed to be classified in any other soil order (Clayton et al, 1977). In Minnesota 27% of the locality records occurred on map units where Podzols are dominant but another 53% are from areas where Gray Luvisols are dominant. Gray Luvisols are well to imperfectly drained mineral soils that have developed under the influence of the decomposition of forest vegetation in mild to cold climates and have silicate clay as the major accumulation product in the B or subsurface horizon (Clayton et al, 1977).

The majority of collecting records for *C. l. longilabris* in eastern North America occur in areas where Humo-Ferric Podzols are dominant and the southern limit of the distribution of this form in the

TABLE 39. Relative frequency (%), and absolute frequency (in brackets), of occurrence of locality records of *Cicindela longilabris* on dominant soil types as indicated by soil maps (see test for references of soil maps

	AK	NB, NS PE	AZ	BC	CA	CO	ID	MI	MN	MT	NV	ME, NH VT
Brown Chernozem					2%(1)		6%(2)				100%(1)	
Dark Brown Chernozem			80%(8)			3%(2)						
Black Chernozem										23%(6)		
Dark Gray Chernozem												
Brown Solonetz												
Black Solonetz												
Solod												
Gray Brown Luvisol							19%(7)					
Gray Luvisol		19%(4)		24%(5)	96%(46)	87%(68)		6%(3)	53%(16)	38%(10)		
Humo-Ferric Podzol		81%(17)		43%(9)				85%(46)	27%(8)			100%(4
Melanic Brunisol										35%(9)		
Eutric Brunisol				9.4%(2)			64%(23)					
Distric Brunisol												
Orthic Regosol			20%(2)			5%(4)		2%(1)	13%(4)			
Cumulic Regosol												
Cryic Regosol												
Rockland				4.7%(1)								
Humic Gleysol				4.7%(1)				4%(2)				
Gleysol	100%(2)							2%(1)				
Cryic Gleysol												
Fibrisol&Mesisol												
Cryic Fibrisol												
Borderline Cases				14.2%(3)	2%(1)	5%(4)	11%(4)	2%(1)	0.7%(2)	4%(1)		
N =	(2)	(21)	(10)	(21)	(48)	(78)	(36)	(53)	(30)	(26)	(1)	(4

TABLE 39 (Cont'd.)

	NF	NM	NY	NT	ON	OR	AB,MB SK	QB	SD	UT	WA	WI	WY	YK
Brown Chernozem						51%(24)								
Dark Brown Chernozem							2.6%(2)			100%(25)	9%(2)		14%(1)	
Black Chernozem							25%(19)							
Dark Gray Chernozem							5.3%(4)							
Brown Solonetz		22%(2)												
Black Solonetz														
Solod							1.3%(1)							
Gray Brown Luvisol						15%(7)						4%(1)		
Gray Luvisol	22%(5)	78%(7)			4%(2)		25%(19)	1.5%(1)	100%(9)			8%(2)	86%(6)	
Humo-Ferric Podzol	74%(17)		90%(9)		72%(36)		5.3%(4)	63%(41)				58%(15)		
Melanic Brunisol					6%(3)			14%(9)						
Eutric Brunisol				25%(1)		28%(13)	1.3%(1)				91%(21)			80%(12)
Distric Brunisol			10%(1)		6%(3)			7.7%(5)						
Orthic Regosol												31%(8)		
Cumulic Regosol														
Cryic Regosol														
Rockland				25%(1)			13.2%(10)	1.5%(1)						20%(3)
Humic Gleysol					2%(1)			1.5%(1)						
Gleysol				25%(1)	2%(1)			1.5%(1)						
Cryic Gleysol														
Fibrisol&Mesisol					6%(3)		15.8%(12)	1.5%(1)						
Cryic Fibrisol							1.3%(1)	1.5&(1)						
Borderline Cases	4.3%(1)			25%(1)	2%(1)	6.3%(3)	3.9%(3)	6.2%(4)						
N =		(9)	(10)	(4)	(50)	(47)	(76)	(65)	(9)	(25)	(23)	(26)	(7)	

eastern half of this continent approximates the southern limit of Humo-Ferric Podzols as the dominant soil type. This could be a limiting factor for other tiger beetles as Graves (1965) has shown that the northern limit of the distribution of *Cicindela scutellaris lecontei* Haldeman corresponds closely with the southern limit of *C. l. longilabris* across Ontario, Michigan, Wisconsin and Minnesota.

In the western part of the boreal forest podzols give way to a complex pattern of Luvisols, Brunisols and Podzols as dominant soil types under forest and heath vegetation cover (Clayton et al, 1977).

Table 39 indicates that locality records of *C. l. longilabris* across the prairie provinces appear to fall on a variety of soil types ranging from map units where organic soils dominate such as Fibrisols and Mesisols (15% of records) to Rockland (13.2%). Areas with Gray Luvisols dominant accounted for 25% of the cases in the prairie provinces, Humo-Ferric Podzols accounted for only 5.3%.

A large number of records occur in areas of dominantly Black Chernozems (25%) and Dark Gray Chernozems (5.3%)(Table 39). These are soils which occur in a broad band from south central and eastern Manitoba northwestwards through Saskatchewan to its northern apex in central Alberta and from there southward in a narrow zone paralleling the east slopes of the Rocky Mountains and crossing the border into the United States. These soils are typical of the Aspen Parkland or Fescue Prairie zone which is transitional between the treeless grassland of the Mixed prairie and the true Boreal forest (Clayton et al, 1977). Luvisols occur as subdominant soils in many areas of the Aspen

Parkland transition zone (Clayton et al, 1977). The reason such a large number of the collecting records of a primarily boreal form such as *C. l. longilabris* occur in this transition zone is probably because it is closer to centres of human population and is therefore more heavily collected than in the boreal zone farther north.

In the Northwest Territories the records are very few in number and are scattered in map areas indicating Eutric Brunisols, Gleysols and Rockland as dominant soil types. It is quite unlikely that the larvae of *C. longilabris* would occur in gleysols, which are defined by Clayton et al (1977) as poorly drained mineral soils whose profiles reflect the influence of being waterlogged and are under reducing conditions due to lack of aeration either continuously or for a large part of the year. It is also unlikely that the larvae of this species could pass their life cycle on rockland, but they are probably found in localized areas of better drained mineral soils of forests.

In the Yukon, 80% of the records of this species are from areas where Eutric Brunisols are dominant. The Brunisolic order of soils are a broad grouping of imperfectly to well drained soils developed under the influence of forest, alpine or tundra vegetation, occurring under climatic conditions ranging from Mesic to Arctic and widely varying moisture regimes (Clayton et al, 1977). The processes of leaching and weathering are weakly developed in Brunisols, so they tend to reflect the chemical characteristics, especially the base status and acidity of the parent material. Eutric Brunisols are base-saturated soils developed under forest or alpine vegetation and usually occur on basic or calcareous parent materials (Clayton et al, 1977).

In the Rocky Mountain States *C. longilabris* is found in the Canadian zone forest on associations of Luvisols, Brunisols, and Podzols. In Idaho 64% of the records were from map areas indicating associations of dominant Brunisols and Sub dominant Humo-Ferric Podzols, and 19% were from areas where Gray-Brown Luvisols are dominant. In Montana the majority of localities were from soils which typically develop under forest conditions (Montana General Soil Map, 1978); 35% were from associations of dominant Brunisols and subdominant Podzols and 38% were from associations of dominant Gray Luvisols and Subdominant Humo-Ferric Podzols.

In Wyoming 86% of localities fell on map units where Gray Luvisols were the dominant soil type. In South Dakota all of the localities fell within the Black Hills area in the southwest part of the state where the dominant soil type is Grey Luvisols similar to the Luvisols of central Colorado, northwestern Wyoming and western Montana (Soil Associations of South Dakota, 1971). The Black Hills in South Dakota also have a dominant vegetation cover of montane forest similar to that of the Rocky Mountain region (National Atlas of the United States of America, 1970).

Two records in South Dakota are peculiar. Pierre, S. D. is in an area that is shown as dominantly Chernozemic soils at the map scale used (Soil Associations of South Dakota, 1971) and is removed by a distance of more than 200 km from the Black Hills. Brookings, S. D. is approximately 500 km distant from the Black Hills, and only 300 km distant from the nearest records of *C. longilabris* in central Minnesota. If there is a genetic connection between the Minnesota populations and those of the Black Hills of South Dakota via small disjunct patches of suitable habitat it would explain why specimens from the Black Hills have reduced maculation from the Rocky Mountain forms and on average, a darker brown dorsal colouration. It is more likely, however, that the specimens in questions are abnormally maculate specimens of *C. nebraskana* having some metallic green colour on their ventral surfaces and an elytral texture intermediate between that typical of either species.

Of the locality records of *C. longilabris* from Colorado, 87% were on map units indicating associations of dominant Gray Luvisols and subdominant Podzols typical of the montane coniferous forest (Colorado General Soil Map, 1976). Seven of nine localities in New Mexico where *C. longilabris* has been taken occur on map units indicating a dominant soil type of Gray Luvisols associated with Humo-Ferric Podzols. The other two localities, Soccorro Co., South Baldy Pk., and Bernallilo Co., Sandia Mtns. are in small areas of National Forest at high altitudes and could be local sites of Luvisolic or Podzolic soils which do not show up at the map scale used (New Mexico General Soil Map, 1974).

The data in Table 39 suggest that *C. longilabris* in the Rocky Mountain States occurs primarily in montane forest areas on associations of dominantly Luvisolic and subdominant Podzolic soils. This trend is not evident in Utah and Arizona at the map scales used (Utah General Soil Map, 1973; Soil Conservation Service, 1967).

In Utah, soil associations are unclear partly due to map scale and partly due to difficulties in converting between U. S. and Canadian soil terminology. On the national scale of mapping (Soil Conservation Service, 1967) all of the locality records of *C. longilabris* occur in areas where the dominant soils are Mollisols in the U. S. classification most of which correspond with Chernozems in the Canadian classification. However, most of the localities when plotted on the Utah General Soil Map (1973) fell on areas where Argic Cryoborolls dominate, which are soils of the Mollisolic order which develop in cold climates and have an argillic, or subsurface horizon of clay accumulation (Soil Survey Staff, 1960). This is a characteristic more typical of the Luvisolic soils which develop under forest cover, using the Canadian classification (Clayton et al, 1977). I have collected *C. longilabris* in the vicinity of Cedar Breaks in S. W. Utah at elevations of 3000 meters in areas of montane forest where the soil would not be described as chernozemic.

The majority of locality records from Arizona also fell on map units indicating Chernozems as the dominant soil type. This is also due to the map scale used. This species has been collected in only three areas of this state, the Escudilla and White Mountains of Southern Apache County, the San Francisco Mountains north of Flagstaff and the Kaibab Plateau north of the Grande Canyon. In the Kaibab area and Apache County these beetles are only found in areas of Engelmann Spruce (*Picea engelmannii*), and Subalpine Fir (*Abies lasiocarpa*) forest where the soil is probably Luvisolic or Podzolic but are too limited geographically to show up on a soil map.

In British Columbia locality records of *C. longilabris* fell on map units indicating as dominant soil types: Podzols (43%), Gray Luvisols (24%) and Eutric Brunisols (9.4%) (Table 39).

In the Pacific Coast States most of the localities seem to occur on associations of Brunisols and Luvisols (Table 39). In Washington state 91% fell on map units where Brunisols are dominant (Chapin 1979), and in California 96% of the collecting records fell on associations of dominant Luvisols and subdominant Brunisols of steep mountainous, forested terrain in the Sierra Nevada and the southern Cascade Mountains.

In Oregon 28% of collecting records fell on areas where Brunisols are dominant and 15% on areas where Luvisols are dominant but are associated with subdominant Brunisols. The fact that 51% of the localities fell on map units indicating Chernozemic soils as dominant is probably due once again to a problem of map scale. The areas of montane forest habitat in the northeastern and southeastern parts of this stage where Brunisols or Luvisols may well occur are much too limited geographically to show up on the General Soil Map of Oregon (1977) as a dominant soil type.

There seems to be a weak trend for *C. longilabris* to occur primarily on associations of Brunisols and Luvisols in the Pacific Region with Brunisols being the dominant soil type inhabited in the Cascade and Coast ranges in Washington and Oregon and Luvisols being the dominant order of soils inhabited in the Sierra Nevadas of California. In the Rocky Mountain region *C. longilabris* appears to occur primarily on associations of Luvisolic and Podzolic soils, and in the Rocky Mountain and Pacific regions its distribution follows that of montane forest habitat with populations in the two regions being largely separated by the arid areas of the Great Basin of Nevada, western Utah, southern Idaho and southeastern Oregon.

Soil associations of *Cicindela nebraskana* are noticeably different from *C. longilabris*. The majority of collecting records of *C. nebraskana* fell on map units where Chernozemic soils are dominant (Table 40). In the Canadian classification (Clayton et al, 1977) Chernozemic soils are well to imperfectly drained soils of good structure with dark coloured virgin or cultivated A horizons, overlying subsurface horizons of high base saturation. These soils develop within areas of cool to cold continental climates, their humus enriched A horizons are developed and maintained by cyclic growth and decay of xerophytic to mesophytic grasses and forbs typical of grasslands or transitional grassland-forest communities. They are typical of the Canadian prairies and rangelands of interior British Columbia (Clayton et al, 1977), which are the areas in Canada where *C. nebraskana* occurs (Fig. 11).

In Manitoba 82% of the collecting localities of this species occurred on the dominantly Black Chernozemic soils of the transition zone between treeless prairie and boreal forest. The vast majority of Chernozemic soils in Manitoba are of the Black Chernozemic great group (Soils of Canada 1972). In Alberta and Saskatchewan collecting localities of *C. nebraskana* are spread across areas where Brown, Dark Brown and Black Chernozemic great groups are dominant. A small number of cases (7%) in Alberta fall on areas where Brown Solonetz soils are dominant. Brown

TABLE 40. Relative frequency (%), and absolute frequency (in brackets) of occurrence of locality records of *C. nebraskana* on dominant soil types as indicated by soil maps (see text for references of soil maps).

	AB	BC	CA	CO	ID	MB	MT	ND	OR	SK	SD	UT	WA	WY
Brown Chernozem	28%(8)	11%(5)			68%(30)				100%(12)	37%(7)		74%(26)	55%(17)	
Dark Brown "	10%(3)	20%(9)			2.3%(1)		76%(22)	94%(16)		21%(4)			13%(4)	47%(13
Black Chernozem	34%(11)	9%(4)				82%(9)	(1)			37%(7)				
Dark Gray		11%(5)												
Brown Solonetz	7%(2)		60%(3)											
Black Solonetz														
Solod														
Gray Brown Luvisol			40%(2)		7%(3)									
Gray Luvisol		17%(8)					10%(3)				100%(1)			21%(6
Humo-Ferric Podzol		4%(2)												
Ferro-Humic Podzol														
Melanic Brunisol														
Eutric Brunisol					20.4%(9)								19.2%(6)	7%(2
Distric Brunisol		20%(9)												
Orthic Regosol						9%(1)	7%(2)	6%(1)				17%(6)	3.2%(1)	18%(5
Cumulic Regosol														
Cryic Regosol														
Rockland														
Humic Gleysol		2%(1)											6.4%(2)	
Gleysol														
Cryic Gleysol														
Fibrisol&Mesisol														
Cryic Fibrisol														
Dominantly Icefields														
Borderline Cases	18%(5)	6%(3)		100%(1)	2.3%(1)	9%(1)	3.5%(1)	0		5%(1)		9%(3)	3.2%(1)	7%(2
N =	(29)	(46)	(5)	(1)	(44)	(11)	(29)	(17)	(12)	(19)	(1)	(35)	(31)	(28

Solonetz soils have a development of A horizons very similar to those of Brown Chernozems, but are salty or alkaline, either from a saline parent material or from saturation by external saline waters. Solonetz soils usually develop under grasses and forbs (Clayton et al 1977).

In North Dakota 94% of localities where *C. nebraskana* has been collected fell on map areas where Dark Brown Chernozemic soils are dominant, and in Montana 76% fell on map units where Dark Brown Chernozems are dominant and 3.5 % on areas where Black Chernozems are dominant.

In British Columbia 51% of the locality records of this species fell on map units where Chernozemic soils are dominant. The remaining localities were scattered among areas where Luvisols, Brunisols, Podzols of Gleysols are dominant. Chernozemic soils are dominant in an extremely small fraction of the geographical area of British Columbia (Soils of Canada 1972). It would seem unlikely that a fraction as large as 51% of the locality records would occur on such an area unless there was such a habitat preference in *C. nebraskana*. Most of the records of this species in B.C. occur in or near the Fraser and Thompson River valleys, the Okanagan Valley and the Kootenay Valley, which are the areas of the province where Chernozemic soils are found (Clayton et al 1977) (Fig. 11). The error involved in inferring anything about soil associations in southern British Columbia is due to the map scale used (Soils of Canada 1972) being inadequate for the complex pattern of mountains and valleys which produce large changes in geomorphology, vegetation, and soils over small distances. I feel these inaccuracies tend to seriously mask any trend which would be more apparent at a finer scale.

In Washington State 68% of locality records of *C. nebraskana* are on map areas indicating the dominant soil type to be Chernozemic (Chapin 1979). This is in sharp contrast to the 91% of the *C. longilabris* records from this state which fell on map units indicating Brunisols as dominant.

In Oregon 100% of the locality records of *C. nebraskana* fell on map units dominated by Chernozemic soils (Table 40), (General Soil Map of Oregon, 1977).

Of the few records I have seen of this species from California, three occur on map units indicating that dry desert soils (probably Regosols) are dominant in the White Mountains of Mono County. Two localities, Sonora Pass and Sonora Peak area, Mono and Tuolumne Counties, fell on map units indicating dominantly Luvisolic soils, but are very close to the borderline between this forest soil type and a map unit that is dominantly desert soils. At the map scale used for an area of mountainous terrain, five locality records are inconclusive.

The only record of *C. nebraskana* from Nevada, Elko Co., Montello in the northeast corner of the state, appears to be on the borderline between areas which are dominantly Chernozems and dry Regosolic soils.

Approximately 70% of the locality records in Idaho occurred on map areas which are dominantly Chernozems. Only about 1/2 of the map area of Idaho is dominantly Chernozemic in soil type, suggesting a habitat preference of *C. nebraskana* for soils of that order.

In Utah 74% of the locality records of this species fell on areas of dominantly Brown Chernozems (Utah General Soil Map 1973). In Wyoming 47%

of the records fell on areas dominated by Chernozemic soils and an additional 18% occurred on map areas which are dominantly dry Regosolic soils (Wyoming General Soil Map, 1975).

To sum up, throughout most of the ranges of *C. longilabris* and *C. nebraskana* a separation between the species can be seen to occur at the level of soil orders. The former occurs almost exclusively in areas of Podzolic soils in the eastern half of the continent and on Luvisols, Brunisols and Podzols, soils of montane and subalpine forest and alpine or arctic meadows in the west. In contrast, *C. nebraskana* occurs primarily on Chernozemic soils of grasslands and grassland-forest transition zones. Across the Canadian prairies the ranges of the two species are sympatric in a broad zone occurring in the area where Black Chernozems are dominant in the Aspen-Oak and Aspen Grove transition zone between prairie grassland and boreal forest (Rowe, 1972; Clayton et al, 1977).

More field study of these species is required to elucidate the nature of the ecological separation which is apparent from the above comparisons of distribution data and soil maps. This is especially true in the mountainous areas of the Pacific states and southern British Columbia where the two species can occasionally be taken at the same localities (Leffler and Pearson, 1976; Norman Rumpp, Pers. Comm.). Leffler and Pearson (1976) have indicated that the form they refer to as *C. longilabris ostenta* occurs in the Hudsonian and Alpine-Arctic life zones of the Olympic Peninsula and Cascade Mountains in Washington State, whereas *C. nebraskana* approximately follows the distribution of the Ponderosa Pine-Bunchgrass vegetation association in that state.

Within *C. longilabris* a weak separation can be seen in the western United States between the Cascades and Sierra Nevada where the beetles occur primarily on Brunisolic soils and associations of Brunisols and Luvisols, and the Rocky Mountain region where the beetles occur on Luvisols and associations of Luvisols and Podzols. The arid soils of the great basin of Nevada, western Utah, southern Idaho and western Oregon seems to function as a partial geographic barrier between the forms.

CLASSIFICATION

The species *Cicindela longilabris* Say

Cicindela longilabris longilabris Say 1824, p. 268 (type locality Silver Islet, Sibley Prov. Pk. Ontario here designated). LeConte 1848, p. 178; 1960, p. 33 and 1961, p. 338. Leng 1902, p. 119. Harris 1911, p. 20. Horn 1915, p. 377; 1928, p. 11 and 1930, p. 82. Rivalier 1954, p. 252. Lindroth 1955, p. 19; 1963, p. 93. Wallis 1961, p. 46. Graves 1963, p. 501; 1965, p. 67. Leffler 1979, p. 467, 470. Boyd and Associates 1982, p. 6.

Cicindela albilabris Kirby 1837, p. 12 (type locality - "Taken in Lat. 64° and also in Canada..."). Emmons 1854, p. 36.

Cicindela longilabris albilabris, LeConte 1848, p. 178; 1860, p. 33. Casey 1913, p. 17.

Cicindela longilabris novaterrae Leng 1918, p. 141 (type locality - Bay St. George, Newfoundland). Wallis 1961, p. 46. Boyd and Associates 1982, p. 6.

Cicindela oslari terracensis Casey 1924, p. 13 (type locality - Terrace, British Columbia).

Cicindela var. *nebraskana*, Horn 1928, p. 11.

Cicindela longilabris laurentii Schaupp 1884, p. 87 (type locality - Colorado). Leng 1902, p. 121. Harris 1911, p. 20. Casey 1913, p. 20. Leffler 1979, p. 474. Boyd and Associates 1982, p. 6.

Cicindela longilabris oslari Leng 1902, p. 121 (type locality - San Francisco, San Miguel Mountains, Colorado). Harris 1911, p. 20. Boyd and Associates 1982, p. 6.

Cicindela longilabris vestalia Leng 1902, p. 121 (type locality - Maiden, Montana).

Cicindela oslari densissima Casey 1924, p. 12 (locality unrecorded "probably Colorado").

Cicindela oslari estesiana Casey 1924, p. 13 (type locality - Colorado).

Cicindela laurenti Casey 1924, p. 13. Tanner 1929, p. 82. Dahl 1941, p. 189.

Cicindela montana laurenti Wallis 1961, No. 65, Plate 3.

Cicindela longilabris perviridis Schaupp 1884, p. 87 (type locality - California, Oregon, Utah and Newfoundland). Harris 1911, p. 20. Horn 1915, p. 377 and 1930, p. 82. Leffler 1979, p. 477. Boyd and Associates 1982, p. 6.

Cicindela perviridis, Leng 1902, p. 122.

Cicindela ostenta, Casey 1913, p. 17 (type locality - California).

Cicindela perviridis placerensis, Casey 1913, p. 18 (type locality - Placer Co., California).

Cicindela ostenta columbiana, Casey 1924, p. 13 (type locality - British Columbia).

Cicindela montana perviridis, Wallis 1961. p. 50.

Cicindela longilabris ostenta, Leffler and Pearson 1976, p. 29. Boyd and Associates 1982, p. 6.

Cicindela longilabris laurentii X *Cicindela longilabris perviridis*

Cicindela montana oslari, Wallis 1961, p. 50.

Cicindela montana laurenti, Wallis 1961, p. 50.

Cicindela longilabris oslari, Leffler and Pearson 1976, p. 29.

Recognition

The convex and elongate labrum, bald, broadly excavated head and non-serrate elytral apices are sufficient to distinguish adult specimens of *C. longilabris* and *C. nebraskana* from those of all other North American species of *Cicindela*.

Adults of *C. longilabris* can be distinguished from those of *C. nebraskana* by the more coarse, frequently confluent, granulate punctations on the elytral surface, usually metallic green abdomen, at least in part, of combination of metallic green, green and blue or green and bronze, pattern of maculations of the elytra including, in most specimens, a humeral and/or post humeral spot, or complete humeral lunule, a sloping, elbowed middle band and an apical lunule varying from a subapical spot to an entire apical lunule. The labrum of *C. longilabris* is light coloured in 90.3%, intermediate or mottled in 8.2% and black in 1.5% of female specimens and light in 97.6% intermediate or mottled in 1.8% and dark in 0.6% of male specimens. For descriptions of *C. longilabris* see Say (1824), Kirby (1837), LeConte (1960), Leng (1902) and more recently Leffler (1979).

Notes on synonymy and taxonomic history

There has been much confusion between *C. longilabris* and *C. nebraskana* due to the similarities between individuals of the latter species and less maculate individuals of the nominate form of *C. longilabris*. The fact that populations of the two species can often be found in the same locality where their habitats are immediately adjacent increases the confusion.

I have shown evidence from discriminant analysis, statistical differences in size and proportion of labrum and ratio of head width to pronotal width, differences in qualitative characters such as female labrum colour, colour of ventral abdominal surface, elytral surface and proepisternum, differences in patterns and extent of elytral markings as well as a suggested ecological separation supported by strong differences in distribution relative to major soil types, why two species should be recognized. This view is supported by the observations of Rumpp (pers. comm.) and Leffler and Pearson (1976), that no apparent hybridization occurs where sympatric populations of *C. nebraskana* and *C. longilabris perviridis* exist in California and Washington State.

Kirby's (1837) description of *albilabris* is sufficient to establish its identity as the same as Say's (1824) *longilabris* . Lindroth (1953) examined Kirby's type specimen in the British Museum of Natural History, a male from Nova Scotia, and concluded that it was the same as the nominate form of *C. longilabris*.

Green specimens from the island of Newfoundland were given the subspecific name *novaterrae* by Leng (1902). It is here felt that, due to the discordant pattern of variation between Newfoundland and mainland samples shown by the discriminant analysis (Tests 3 and 4, Tables 5, 9 and 10), and the fact that large numbers of brown and black specimens can be found on the eastern part of the island (Lindroth 1963) and green specimens can be found on the mainland of Quebec and Labrador, the formal naming of the green form is inappropriate.

A single male specimen from Terrace, British Columbia, which Casey (1924) described as *C. oslari terracensis* is black, with the body size, ventral colouration and elytral markings typical of *C. longilabris longilabris* Say.

Horn (1928) incorrectly applied the name *Cicindela* var. *nebraskana* to specimens of *C. longilabris* from Minnesota, with reduced maculations.

The name *laurentii* has historically been applied to olive green, heavily maculated specimens from the Rocky Mountain regions of the United States, and the name *oslari* has been applied to specimens from the same region exhibiting less extensive maculation and dorsal colouration varying from green to bronze to brown.

Leng (1902) described *vestalia* based on immaculate specimens from Maiden, Montana which are, in all other characters, within the range of variation found in *C. l. laurentii* throughout the Rocky Mountain region of the United States.

Specimens described by Casey (1924) as *densissima* and *estesiana* from Colorado were based on slight individual variations in colouration and maculation which are within the range of variation to be found in populations of *C. l. laurentii* in Colorado.

Wallis (1961) confused the relationships between the forms in this group by classifying *laurenti* (sic), *oslari* and *perviridis* under the species name *C. montana*. Wallis applied the names *C. montana oslari* and *C. montana laurenti* (sic) to populations in south central British Columbia which are in a hybrid zone where the Pacific Coast, Rocky Mountain, and boreal forms of *C. longilabris* converge and produce populations with a high degree of individual variation. Specimens from eastern Washington state referred to as *C. longilabris oslari* by Leffler and Pearson (1976) are also from the area of hybridization of the Pacific Coast, Rocky Mountain and boreal forms of *C. longilabris*.

Schaupp (1884) originally described *perviridis* as occurring in California, Oregon, Utah and Newfoundland. Leng (1902) narrowed the type area of this form to Sierra and Placer counties in California, distinguishing *perviridis* from any Rocky Mountain or boreal forms which also exhibit a green colouration.

Notes on designation of a neotype for *C. longilabris* Say

Thomas Say's private collection was entirely destroyed after his death (LeConte 1859 p. VI). It would seem to be in the interest of stability of nomenclature, in light of the confusion that has occurred in the identification and interpretation of the sibling species *C. longilabris* and *C. nebraskana*, to designate a type specimen for the former. Lindroth and Freitag (1969) express the desirability of designating neotypes to stabilize Thomas Say's names, and Leffler (1979) and Huber (pers. comm.) have indicated that a neotype should be designated for *C. longilabris*.

Say had distributed specimens from his own collection to Count P. F. M. A. Dejean in France (Lindroth and Freitag, 1969). Dejean (1826) indicated that he had received specimens from Say and he redescribed many Say species (1825-1831), however, *C. longilabris* was not among them. Dejean (1837) made no mention of *C. longilabris* in the catalogue of his collection. It appears quite definite that none of Say's specimens of *C. longilabris* exist from which to choose a type.

Say (1824) indicated nothing more exact than "Northwest Territory " for a type locality. Wallis (1961) indicated the approximate route of the second expedition of Major Long to the source of the St. Peter's River in 1823, the trip on which Say would have collected this species. It started in Philadelphia from where the party travelled to Chicago, Minneapolis and to Big Stone Lake on the border between Minnesota and the northeast corner of South Dakota. From there the route led down what is now called the Red River (formerly called the St. Peter's River) to Lake Winnipeg, and from Lake Winnipeg east to Lake of the Woods, around the north shore of Lake Superior and southward towards Lake Ontario. Wallis (1961) correctly points out that *C. nebraskana* does not occur throughout most of this area, but *C. longilabris* could be collected anywhere from Lake Winnipeg past the north shore of Lake Superior and southward much of the way towards Lake Ontario.

LeConte (1859) was very familiar with the work of Thomas Say and was probably referring to Say's material when he redescribed *C. longilabris* (1860). LeConte's redescription, though in Latin is very similar to Say's original description including mention of a variant female specimen with reduced or absent maculation from the north shore of Lake Superior. LeConte (1960) also stated the range of the species as "New Hampshire, Canada, Mackinaw, Lake Superior...", mentioning no other areas. If Thomas Say had collected this species farther west than Lake Superior it would probably have been reflected in LeConte's statement of the known range at that time. If Say had collected his specimens very far east and south of Lake Superior, his statement of the range would perhaps have been Canada or Upper Canada, rather than "Northwest Territory". It seems probable that Say's type locality for *C. longilabris* was somewhere along the north shore of Lake Superior. Say's (1824) description of blackish colour, head and thorax tinged with green, white labrum "nearly as long as broad", elytra with rather large, dense punctures, humeral and posthumeral spots, reclivate, nearly transverse middle band and subapical spot are all characters typical of *C. longilabris* in Northwestern Ontario.

A male specimen from Silver Islet, Sibley Provincial Park, Ontario, is designated as neotype and that place as type locality. The neotype specimen's label reads "Ont.: Thunder Bay Distr. Sibley Prov. Pk. 1 km W of Silver Islet on Perry Bay. 48° 20' N 89° 50' W 24 V. 1982. T. Spanton". The neotype and three additional specimens, one male and two females are deposited in the Museum of Comparative Zoology.

Geographic variation and subspecies

Adults of *C. longilabris* are uniform in most characters among populations across the Acadian, Great Lakes-St. Lawrence and Boreal regions and the northern part of the Montana forest region in western Canada (Fig. 79). This form typically exhibits a white labrum (Fig. 12), proepisternum varying between metallic black and green, green, or green and bronze (Fig. 14), ventral abdominal colour of metallic green and blue (Fig. 16), humeral lunule consisting of a humeral and/or posthumeral spot, occasionally connected (Fig. 22), a thin, elbowed middle band (Fig. 24), apical lunule consisting of one subapical spot (Fig. 26), and most specimens have between one and five per cent of the elytral surface covered by these markings (Fig. 20). This is the nominate subspecies *C. longilabris longilabris* Say.

Notable variant populations of this form are those from the island of Newfoundland, and to a lesser extent the adjacent mainland of Quebec and Labrador which contain specimens with a green coloured dorsum (Fig. 18). As shown in the discriminant analysis section, specimens from the island of Newfoundland are, on average, slightly larger in body size than are those from the mainland.

I do not recognize these populations as taxonomically distinct from the nominate subspecies.

As indicated in the discriminant analysis section, there is considerable morphometric variation among populations of the Pacific region from southern British Columbia to Central California and in the Rocky Mountain region from southwest Alberta to Arizona and New Mexico.

In the Pacific coast states of Washington, Oregon and California the majority of specimens have a metallic green proepisternum (Fig. L4) and abdomen (Fig. 16) and higher frequency of green dorsal colouration (Fig. 18) than specimens of the nominal subspecies. A notable exception is the OR2 population which is more variable in all three characters than other populations in the region (Figs. 14, 16, 18). The green elytra surface occurs in all specimens of the Washington state samples (Fig. 18) and becomes slightly less frequent southwards through Oregon to California.

The pattern of markings (pale areas) on the elytra is greater in specimens of the Pacific states than those of the typical *longilabris* (Fig. 20). This is due to an increase in the extent of all three of the lunules (Figs. 22, 24, 26). Notable exceptions are specimens of the Oregon populations, OR1 being more similar to specimens of the other Pacific coast populations in the middle band (Fig. 24) and apical lunule character states (Fig. 26) and OR2 being similar to the nominate form of the species in characters of the elytral markings.

In populations of the Rocky Mountain region of the United States there is a notable increase in bronze colouration of the proepisternum (character states 6 and 7, Fig. 14) and an increase in the frequency of brown, bronze and olive green colouration of the elytral surface (character states 2, 3, and 4, Fig. 18). The maculations on the elytral surface are increased in Rocky Mountain populations as compared to those of the nominate form in the boreal zone (Figs. 20, 22, 24, 26). The bronze proepisternal colour, brown-bronze-olive green elytral colour and development of the pattern of markings of the elytra reach their maximum frequency in CO1, CO2, UT2 and UT3 populations. These characters are variable within this region, possibly due to geographical fragmentation of the montane forest habitat of these beetles. As indicated in the discriminant analysis of morphometric data, and in the pattern of variation in colour (Figs. 14, 16, 18) and pattern of markings on the elytra (Figs. 20, 22, 24, 26), there are a few geographically isolated populations which vary noticeably from the form of the typical *laurentii* of central Colorado. Specimens from the Black Hills of South Dakota (SD1) exhibit somewhat reduced maculation similar to that of specimens of the boreal regions (Figs. 20, 22, 24, 26), but they exhibit variable colouration (Figs. 14, 16, 18) and occur in an isolated area of coniferous forest and dominant soil type similar to that of the Rocky Mountains of Central Colorado and parts of Wyoming and Montana. The populations from Sandoval County (NM1) and Bernallilo Co. (NM2), New Mexico are similarly isolated populations which consist of specimens with reduced maculation (Figs. 20, 22, 24, 26), variable colouration (Figs. 14, 16, 18) and are morphometrically different (discriminant analysis section) from those of neighbouring populations. Samples from Iron Co. Utah (UT3), Kaibab Plateau, Arizona (AZ1) and Apache Co., Arizona (AZ2) represent geographically isolated populations which are morphometrically distinct from each other. UT3 is distinct in exhibiting the most consistently heavily maculated specimens of any population in the species complex (Figs. 20, 22, 24, 26), AZ1 specimens exhibit a pattern of maculation which is reduced noticeably from that of surrounding populations and AZ2 specimens differ only in being slightly more variable in colouration of the peoepisternum and dorsal elytral surface than those of most of the neighbouring populations. Rumpp (unpublished) has proposed subspecific names for these latter three populations. I believe that, although these three populations (AZ1, AZ2, UT3) are zoogeographically interesting, the designating of formal trinomen for each would not improve our understanding of the variation in this species.

Based on the preceding discussion, the morphometric differences between the lumped populations of the Pacific region, Rocky Mountain region and Boreal region presented in the discriminant analysis section, and zoogeographic factors, and despite the fact that the application of subspecific names to morphologically heterogeneous groupings of populations is somewhat controversial, I recognize two subspecies in addition to the nominate form *C. longilabris longilabris* discussed previously.

The subspecies *C. longilabris perviridis* Schaupp here includes the population of the Sierra Nevada and Cascade Mountains from east-central California to southwestern British Columbia (Fig. 79), typified by an increased frequency of green elytral maculation relative to the nominal form, a smaller average body size than *C. longilabris* or *C. l. laurentii* and a proportionally longer narrower pronotum than the nominate form.

The subspecies *C. longilabris laurentii* includes the populations of the Rocky Mountain region from Arizona and New Mexico to Montana, specimens of which are typified by brown to bronze or olive green dorsum (Fig. 18), bronze peoepisternum (Fig. 14), and elytral maculation (in most specimens) increased over that of the nominate subspecies. The arid area of the Great Basin provides a geographic separation between *C. l. laurentii* and *C. l. perviridis* (Fig. 79).

An area of hybridization exists where the ranges of the three subspecies converge geographically in southwestern Alberta, northwestern Montana, northern Idaho, western Washington and southeastern British Columbia (Fig. 79). The population sample AB6 from the Pincher Creek area of Alberta is an example of a hybrid population. The series of specimens was collected the same day at the same local site. Specimens in the series exhibit each of the various colour states of the proepisternum (Fig. 14) all but one of the colour states of the abdomen (Fig. 16), and all of the colour states of the elytra (Fig. 18). The complete range of maculation pattern is represented from completely immaculate specimens to specimens with 20 per cent of their elytral surface covered with white markings. More intensive field collections of large series of specimens from this area are required for a detailed study of the pattern of hybridization between the forms.

Distribution

The geographic range of *C. longilabris* is shown in Figure 79. In eastern North America the southern limit of the distribution of this species approximates the southern limit of Podzols as the dominant soil type, and the southern limit of the ranges of Jack Pine (*Pinus banksiana* Lamb.), White Spruce (*Picea glauca* (Moench) Voss), Balsam Fir (*Abies balsamifera* (L.) Mill) and Balsam Poplar (*Populus balsamifera* Linnaeus) (Little 1971). Across the prairie provinces the southern limit of the distribution of *C. longilabris* corresponds with the southern limit of boreal forest and forest grassland transition, and in the western

United States the range of this species approximates the range of montane forest habitat, or the Canadian life zone of Muesbeck and Krombein (1952). In the north the range of *C. longilabris* appears to be limited by the northern limit of wooded country and the southern limit of continuous permafrost.

In the following distribution records, the number of specimens and the collection where they are housed is indicated in brackets for specimens I have seen. The reference is cited for records from the literature.

Cicindela longilabris longilabris Say

Canada. ALBERTA: Athabasca (2, CAC)

Bentley, Aspen Beach Prov Park (Freitag & Tropea 1971), Bilby (15, CAS) Black Rock Mtn. (1, LU), Castor (1, CNC), Clymont (1, CNC), Drimson Lk (1, WJ), Edmonton (6, CNC), Enoch Indian Reserve nr. Edmonton (1, WJ), Fort Mackay (7, WJ), Garth (1, LU), Grande Prairie (1, CNC), Halfway House (1, CNC), High Prairie (1, CNC), Jasper (1, CU; 4, AMNH), Jasper Park (5, CNC; 1, AMNH), Kootenai Plains (1, SMEK; 4, LU), Lac la Biche (2, LU), Maligne Canyon nr. Jasper (1, UV; 1, CNC), "McMurray", Fort McMurray? (23, CNC), Nordegg (1, CAS; 1, LU), North Sask Crossing, Jasper Park (1, AMNH), Rycroft (1, CNC), Saunders (1, SMEK), Seebe For. Expt. Sta. (w, CNC), Smith Landing, Athabasca Riv., Wabamun (1, CNC), Wm. A. Switzer Prov. Pk. 12 km N. Hinton (18, LU). BRITISH COLUMBIA: no locality given: (1, UIM; 5 CNC; 1, CU; 1, AMNH) Atlin (1, CNC; 3 CAS), East Pine, 10 mi E (1, UAE), Lower Post (1, CNC), McBride (2, UMAA), Rolla (1, CNC), Robinson (1, UBC), Smithers (1, UBC), Terrace (1, type specimen of *C. solari: terracensis* Casey, USNM), Telegraph Crk. (1, labelled 'cotype' *vestalia* Leng, AMNH). MANITOBA: Beaverdam L. (1, CNC), Berens River (4, CNC), Blue Lakes (3, CNC), Brandon (1, CNC), Cowan (3, CNC), Dorn City (1, CNC), Duck Mtns. (6, CNC), Falcon Lake 15 mi E Rennie (1, CNC), Fisher Branch (1, CNC), Flin Flon (1, CNC), Gillam (2, UAE; 83, CNC), Grass River Prov. Pk., Iskwasum Lk. (1, UMW), College, Winnipeg (1, CNC), Myrtle (1, CNC), Norway House (15, CNC), Pikwitonei (1, CNC), Rapid City (1, CNC), Red Rock Lake, Whiteshell Forest (1, CNC), Reynolds (1, CNC), Riding Mtn. Nat. Park (8, CNC), Rounthwaite (1, CNC), Somerset (1, CNC), Telford, 6 mi E. Rennie (2, AMNH), Victoria Beach (2, UAE; 1 UMW; 3, CNC, 3, CU; 5, USNM), Wanless (2, CNC), Waugh (1, CNC). Welliman (6, UOG), Winnipeg (1, CNC). NEW BRUNSWICK: Allardville-Bartibog (3, AMNH), Bathurst (1, CNC), Boisetown (2, CNC, 4, USNM), Dorchester (1, AMNH), Newcastle (1, CNC), Penobsquis (2, CNC; 1, UMAA), Rexton 3.2 mi W (2, LU), Tabusintac (4, CNC). NEWFOUNDLAND AND LABRADOR: Avalon Peninsula; Lot 2 (2, MUN), Avalon Penn. Ocean Pond (1, MUN), Avalon Peninsula, Seal Cove Holyrood (1, MUN), Bay St. George (1, CU; 3 paratypes *C. longilabris novaterrae* Leng 1902, AMNH), Ferryland (7, CMP), Gander (2, UIM; 197, CNC; 130, MUN), Goose Bay (2, CNC), Grande Falls (1, CMP), Harmon Field (4, SMEK; 3, UIM; 30, CNC; 3, CU), Hawk Hills (2, AAM), Lewisport (1, CNC), Mobile, Big Pond nr. St. John's (1, MUN), Northwest River, Hamilton Inlet (Lindroth 1954), Paddy's Pond nr. St. John's (Larson and Langer, 1982), Port aux Port (2, AMNA), Stephenville (2, CAS; MCZ), St. George's (1, UMAA; 1 AMNH), Terra Nova Nat. Park: Salton Pk. (6, MUN), Terra Nova Nat. Pk.: Big Brook Lot 1 (7, MUN), Additional Nfld. records from Lindroth (1955): Badger, Bay of Islands, Cape Bay, Deer Lake, Fogo, Gambo, Great Rattling Brook, Millertown, Millertown Jct. Picadilly, Port aux Basques, Seldom, Springdale, Steady Brook, Tilting, Twillingate Woody Point. NOVA SCOTIA: no further data (2, CAS), Bay St. Lawrence (3, MCZ), Boisdale, Cape Breton (2, AMNH; 2, CAS), Digby (1, CNC; MCZ), Halifax (1, CMA), Kentville (1, CAS; 2, USNM), Newhaven (3, MCZ), N. Sidney Cap Breton Is. (3, CNC), S. Milford (1, CNC), Truro (1, CU), W. Middle River: Baddeck, Cape Breton Is. (2, CNC). NORTHWEST TERRITORIES: no locality data (15, CNC; 1, SMEK; 2, UAE; 1, CAS; 3, UOG), Caribou Lake, Great Slave Lk. Region (1, CNC), Fort Simpson (1, CNC), Fort Smith (119, CNC; 1, CAS). Norman Wells (3, CNC), "Resolution", Ft. Resolution? (1, CNC), Yellowknife (17, CNC; 3 PSU).

ONTARIO: Agawa Bay (6, UMAA), Algonquin Park, Lk. Opeongo (1, UOG), Bear Island, Lk. Temagami (1, AMNH), Black Sturgeon Lake Res. Sta., Thunder Bay District (16, LU), Blue Lk. (3, UMW), Borups Corners (2, CU), Burkis Evis (1, CNC), Caliper Lake Prov. Pk., (1, LU), Camp Otter, Huntsville (1, CU), Chalk River (1, CNC), Charleton (1, AMNH), Crow Lake (4, CNC), Dyers Bay (1, UOG), Eagle River (8, CNC), Rlying Thor (1, CNC), Geraldton (10, AMNH), Gold Rock, Rainy River Distr. (MCZ), Huntsville (Graves 1965), Hensley Bay, Manitoulin Island (1, AAM), Ignace (3, VOG), Ingolf, Kenora District (9, LU; 1, CNC; 1, CU; 1, CAS), Inwood Park, 2 mi SE Upsala (1, AMNH), Kenora, 30 mi E (1, LU), Kirkland Lake (1, AAM), Lake Nipigon, north end Obakika Bay (2, CMP), Lake Nipigon, Orient Bay (2, CMP), Longlac (1, AMNA), Maynooth (6, CNC), Michipicoten Bay, Wawa (1, LU). Moose Factory (1, CNC), Nipigon (1, AMNH; 5, CMA), Nonwatin Lake (2, LU), Ogoki (3, CNC), Old Woman Bay nr. Wawa (2, LU), Orville (1, CU), Ottawa (MCZ), Pancake Bay (1, BGSU), Pass Lake nr. Sibley (5, LU), Petawawa Forest Reserve (Graves 1965), Pickle Lake (1, UOG), Red Lake 20 mi N (1, CNC), Ridgeway (1, CMP), Rushing River Prov. Pk. 15 - 20 km SE Kenora (99, CAS; 20, NDSU), Sand Lake, Kearney (1, CNC), Savant Lake (1, AAM), Sault Ste. Marie (1, UOG), Shaquidandah, Manitoulin Island (1, AAM), Sibley Prov. Pk. (11, BGSU), Silver Islet 1 km W Sibley Prov. Pk. (Neotype 1 male *C. longilabris* Say. plus 3 additional specimens, MCZ; 5, LU), Sioux Lookout (2, CNC), Smoky Falls, Matagami River (1, CNC), Sudbury (3, CNC; 2 CU; 2, UMAA; 2, MPN; 1, AMNH), Thessalon (9, UOG), Thunder Bay (5, LU), Vermillion Bay (1, CNC), Wawa (8, LU), Whitefish Lake Thunder Bay Distr. (3, LU). PRINCE EDWARD ISLAND: Alberton (1, CNC), Brackley Beach (1, CNC), Cavendish Beach Golf Club (Freitag and Tropea 1969). QUEBEC: Abitibi Region (1, CNC), Cascapedia (1, CNC), Covey Hill (1, CNC), Danford Lake (1, CNC), Duchesnay (1, CNC), Duparquet (1, CNC; 57, CAS), Forestville (22, CNC), "Gaspe Co." (2, CNC), Gaspe 25 mi W (10, CNC), Gaspesie Parc Lac St. Anne (1, CNC), Gt. Whale River (2, CNC), Kazabazua (3, CNC), Knoulton (2, CNC), Laniel (2, CNC), Lanoraie (2, LU), Laurentides Parc Lac des Islets (4, AMNH), Matanek (1, AAM), Montreal (MCZ; 2 CMP), Mt Albert (8, CNC), Natashquan (2, CNC), Rupert House (1, CNC), St. Jerome de Matane (1, AMNH), St. Rose (2, CAS), Tadousac (1, UMAA), "Thunder River" Riviere aux Tonneres (18, CNC), Trois Riviere (2, UMAA), Val d'Or (1, CNC), Val Morin (3, UUM; 1, CNC; 7, UMAA; 8, AMNH; 7, CAS), Woburn (1, CNC). Additional Quebec records from Larochelle (1972): Abitibi Co.: Amos, Clova, Senterre. Argenteuil Co.: Riviere Rouge. Berthier Co.: Berthierville. Bonaventure Co.: Grande-Cascapedia. Champlain Co.: Lac Baude. "Charlevoix Co.: Charlevoix-est Co.: Port aux Salmon, Sainte-Fidele, Saint-Simeon. Charlevoix-ouest Co.: Baie-Saint-Paul. Chicoutimi Co.: Baie-des Ha! Ha!, Cap Jaseur, Chicoutimi. Deux-Montagnes Co.: La Trappe, Gaspe-est Co.: Gaspe, Grande-Vallees-des-Monts. Gaspe-ouest Co.: Saint Anne des Monts. Ile-de Montreal: Saint Laurent. Joliette Co.: Saint Beatrix, Saint-Thomas-de-Joliette. Kamouraska Co.: La Pocatiere. Labelle Co.: Nominque. Lac-Saint Jean-Ouest Co.: Lac Saint Jean, Roberval, Saint-Felicien. Levis Co.: Fort Woods, Lauzon, Levis. Islet Co.: Saint-Roches-des Aulnaies. Matane Co.: Matapedia Co., Mistassini Territory: Fort Rupert. Montmorency No. 1 Co.: Saint-Anne-de-Beaupre, Montmorency No. 2 Co.: Sainte-Jean d'Orleans. Parc des Laurentides. Pontiac Co.: Dorval. Portneue Co.: Fossambault-sur-lac, Port Rouge, Portneuf, Sainte-Catharine Station, Sainte Raymond. Quebec Co.: Lac-Beauport, Loretteville, Quebec, Sainte Foy, Val Cartier-Village. Rimouski Co.: Riviere du loup Co.: Lisle Verte. Rouville Co.: Ange-Gardien. Sainte-Maurice Co.: Pointe du Lac. Temiscamingue Co.: Rollet. Terrebonne Co.: Laurentides, Shawbridge. Vaudreuil Co.: Rigaud. SASKATCHEWAN: Big River (9, CNC, 1, VOG), Black Lake (Hooper 1969), Canora, 10 mi NE (4, CNC), Cristopher Lake (2, CNC), Clavet (1, CNC), Deschambault Lk. (Hooper 1969). Goodspirit Lake (2, CNC), H. B. Jct. (1, UAE; 3 CNC; 1 CAS), Madge Lk. (Hooper 1969), McDougal Ck. (2, MUN), Nipawin (4, CNC), Pas Trail (1, CNC), Paynton (1, CNC), Prince Albert (1, UAE; 6, CNC), Redvers (1, UMAA; MCZ), Star City (Hooper 1969), Torch River N of White Fox (1, UAE; 22, CNC), Vonda (1, CNC), Waskesiu Lake (7, CNC), Weekes (Hooper 1969), Yorkton (MCZ). YUKON: Aishihik R. 14 km N of Canyon (2, UBC), Carcross (4, CNC; 5, UBC), Carmacks 27 km E (3, UBC; 1 CAS), Dawson (5, CNC; 16, CAS), Dawson 58 mi E, Gravel Lake (1, CNC), Kluane (1, BC), Klusha Creek (1, UBC), Milepost 30, Klondike Hwy, 30 mi from Stewart Crossing (1, CAS), Rampart House (7, CNC), Stewart Crossing (1, UBC), Tagish (32, UBC), Watson Lake (7, CNC), Whitehorse (35, USNM; 6, CNC; 1, CU; 3, UBC; 15, AMNH; 11, CAS), Yukon Crossing (3, PSU), Yukon River (1, CAS).

United States.
ALASKA: Big Delta (1, CNC), Chitina (4, PSU), "Dawson Alaska"? (9, CMP). MAINE: Franklin Co.: Bigelow (1, AMNH), Rangeley (1, AMNH), Weld (1, CAS). Hancock Co.: Mt Desert Island (various) (3, AMNH; 4, CAS; 4, USNM). Knox Co.: Isle au Haute (MCZ) Penobscot Co.: E. Lincoln (1, CAS), Wissataquoik River (1, CMP). Piscataquis Co.: Mt. Katahdin (2, USNM). Somerset Co.: Mt. Bigelow (1, CAS). Localities of unknown counties: no locality data (3, AMNH), Edmunds (1, SMEK; 1, WJ; 1 REA), Kineo (2, CAS; MCZ), Pleasant Ridge (4, UMAA). MICHIGAN: Alger Co.: Camp Roth (1, UMAA), Munising (3, BGSU). Baraga Co.: (12, NDSU). Berrien Co.: Herbert Dune (1, UMAA; 1, AMNH). Charlevoix Co.: Beaver Island (1, UMAA), Garden Is. (1, UMAA). Cheboygan Co.: No locality data (1, SMEK; 5, CAS; 48, NDSU), Biggsville Rd. (1, UMAA), Cheboygan (2, UMAA), Douglas Lake (1, BGSU; 21, UMAA), Lancaster L. (1, SMEK), Univ. Mich. Bol. Sta. (1, SMEK). Chippewa Co.; Camp Raco (2, WSU), Marquette Nat. For. Bayview Camp (8, BGSU), Strongs Camp (1, WSU), Trout Lake (1, UMAA), Whitefish Pt. (11, UMAA; 3, AMNH). Crawford Co. (1, NDSU). Dickinson Co.: Floodwood (3, UMAA). Emmet Co.: 3 mi N Cross Village (1, UMAA). Gogebic Co.: (2, UMAA), Cisco (1, UMAA), Hughitt-Rawson Preserve (1, UMAA), Watersmeet (1, UMAA). Houghton Co.: (1, SMEK; 7, NDSU), Alston (1, UMAA), Freda (1, PSU; 8, MPM), Houghton (2, PSU), Oskar (1, PSU; 108, MPM). Huron Co.: (1, UMAA). Iosco Co.: Oscoda (1, UMAA). Iron Co.: (1, REA), Michigamme R. (1, BGSU). Keweenaw Co.: (5, NDSU), Isle Royale (2, UMAA; 2, USNM). Luce Co.: McMillan (2, UMAA), NWL Superior Camp (5, BGSU). Mackinac Co.: Brevoort Lake (1, BGSU), Horseshoe Bay (1, UMAA), Naubin Way (6, UMAA), nr. Rexton (1, BGSU), St. Ignace (20, UMAA). Marquette Co.: Huron Mtns. (2, UMAA), Marquette (Graves 1963), Michigamme (Graves 1963). Montmerency Co.: (1, UMAA). Ontanagan Co.: (1, NDSU). Schoolcraft Co.: (3, NDSU), Cooks 4 mi E (4, PSU), Manistique (2, UMAA). MINNESOTA: Aitkin Co.: Solana State Forest (1, PSU; 2, UV; 2, REA). Beltrami Co.: Red Lake Beltrami (1,AMNN). Carlton Co.: F. Exp. Sta. (12, WSU).

Cass Co.: Cass Lake 9 (1, SMEK). Clearwater Co.: Itasca Pk. (2, AMNH; 17, WSU), Lake Itasca (1, UIM), Shevlin (1, SMEK). Cook Co.: Cascade River (Horn 1928), Mt. Lima (1, PSU), Pine Mtn. (2, NDSU), Thomson Lake (1, NDSU). Crow Wing Co.: Pelican Lake, Nisswa (2, CU; 3, UMAA). Lake Co.: Baptisme Creek (Horn 1928), Bengal (Horn 1928), Finland State Forest (1, LU), Green Wood Lake (2, PSU) Isabella 9 mi S. (2, LU), Kawishiwi River (Horn 1928), McNair 1 mi N (14, PSU), Toimi 5 me E (1, REA), Two Harbours 60 mi N. (5, PSU). Roseau Co.: Clear River (Horn 1928). St. Louis Co.: Ash River Trail (2, WJ), Duluth (1, UMAA; 1, NDSU; 7, CMA), Eveleth (3, SMEK), Wolf Lake (1, REA), Wadena Co.: Crow Wing R. (1, NDSU). Localities of unknown counties: Gunflint Trail (2, UV). NEW HAMPSHIRE: No locality data: (1, SMEK; 1, AMNH; 1, CAS), Coos Co.: Glen Whit Mtns (MCZ), Gorham (MCZ), Israel River nr. Jefferson (MCZ), Jefferson (4, UMAA), Randolphe (1, CAS; MCZ), Shelbourne (1, CAS; MCZ), South Branch Rd. nr. Jefferson (4, UMAA), Stag Hollow Rd. nr. Jefferson (MCZ), Twin Mtn. (33, UMAA; 4, AMNH), White Mtns. (1, AMNH). Carroll Co.: Jackson (MCZ). Localities of unknown counties: Franconia (1, AMNH), Martin Location (2, UMAA), Mt. Aggasiz (1, UMAA). Additional Records from Dunn (1978): Coos Co.: Berlin, Carrol, Low and Burbanks Grant, Seargent's Purchase Mt. Washington, Mt. Monroe. Carrol Co.: Conway, Tamworth. Grafton Co.: Benton (Mt. Mooselaukee), Orange (Mt. Cardigan). NEW YORK STATE: No locality data: (2, PUL), Essex Co.: Black Brook (2, CU); Heart Lake (3, CU), Jay Mtns (2, CAS; MCZ), Lake Placid (4, AMNH). Mt. Joe (2, CU), North Elba (3, AMNH; 2, USNM), Whiteface Mtns. (3, CU; 6, USNM). Franklin Co.: Upper Saranac (4, CAS). St. Lawrence Co.: Cranberry Lake (1, CAS). Sullivan Co.: Livington Manor 4 mi E (Freitag and Tropea 1971). VERMONT: Camel's Hump nr Botton (3, UV), Essex Co.: Ferdinand (8, CU; 1, UV). WISCONSIN: Adams Co.: (1, MPM). Ashland Co.: (1, CNC). Bayfield Co.: (Harris 1911). Lake Namekegon (1, UWM). Door Co., (2, UWM). Douglas Co.: Solon Springs 10 mi E 1 mi N (2, SMEK), Solon 11 mi ENE (11, MPM), Solon Springs 12.5 mi ENE (1, MPM). Jackson Co.: City Point 2.9 mi S (1, MPM) Hatfield 9.4 mi SE (1, MPM). Juneau Co.: Mather 5.2 mi SE (5, MPM). Necedah Wildl. Refuge 6 mi NW (3, MPM).

Monroe Co.: Mather 2.2 mi W (6, MPM), Mather, 4.6 mi W (1, WJ). Oconta Co.: Mountain (1, MPM). Oneida Co.: Woodruff (1, MPM). Shawano Co.: Bear Trap Falls (1, MPM). Taylor Co.: Whittlesey (1, MPM). Vilas Co.: Land o' Lakes (5, MPM), Phelps (1, MPM), Presque Isle (1, PSU; 10, MPM), Trout Lake (1, UWM), "T42N-RTE 519" (6, UWM). Wood Co.: Cranmoor (1, UWM).

Doubtful Records

Detroit, Michigan (4, CMP). These are either mislabelled specimens or are old records of a marginal population which has subsequently become extinct, possibly due to habitat destruction by human activities. I have found no other records of *C. longilabris* from the southern half of the lower peninsula of Michigan.

Guelph, Ontario (1 UOG). Assumed mislabelled.

Lincoln, Nebraska. (1, ISU). Assumed mislabelled.

London, Ontario. (3, UOG). Assumed mislabelled.

"Mass". (1, MCZ). This is either a mislabelled specimen or is an old record of a marginal population which is no longer extant.

"Tenn." (3, MPM). Assumed mislabelled.

Cicindela longilabris laurentii Schaupp

United States.
ARIZONA: Apache Co.: Escudilla Mtns 7 mi N. Alpine (11, REA), Sheep's Crossing nr. Bib Lake (13, LU), White Mtns. (1, CU; 2, AMNH), White Mtns, Coulters Ranch (1, CAS), White Mtns. Crescent Lake (1, CU). Coconino Co.: Flagstaff (6, SMEK), Grande Canyon, North Rim (1, CU), Kaibab Forest (9, SMEK), Kaibab Lodge area (30, MPM; 4, PSU; 13, REA), San Francisco Mtns., SW Side (1, SMEK). COLORADO: no locality data: (6, CMP), Adams Co.: South Park (1, SMEK; 2, UMAA; 2, CAS; MCZ). Boulder Co.: Allens Park (1, UMAA; 1, AMNH), Eldora (2, SMEK), Gold Hill (1, SMEK). Lyons (1, REA), Nederland (1, SMEK), Raymond (1, SMEK), Ward (2, SMEK; 1, UMAA). Chaffee Co.: Salida (6, UMAA; 2, AMNH; 1, CMP). Clear Creek Co.: Clear Crk. (1, CU; 3, AMNH), Dolittle Ranch Mt. Evans (1, CNC), Empire (1, CAS), Silver Plume (2, UMAA; 1, CNC; 2, CAS). Conejos Co.: Platoro (1, BGSU), Upper San Juan (1, CAS). Costilla Co.: San Francisco (1, CNC). Dolores Co.: Rico (MCZ), El Paso Co.: Cascade (2, UMAA; 1, AMNH), Colorado Springs, Rock Creek (1, AMNH; 1, CAS), El Paso (1, SMEK), Pike's Peak (1, AMNH). Gilpin Co.: Pine Cliff (1, CMP; 1, UMAA). Grand Co.: Elk Cr. Fraser (3, CU), Granby (1, SMEK), Rabbit Ears Pass hwy 40, 12 km E Steamboat Springs (6, LU), Grande Lake (1, AMNH; 2, CAS), St. Louis Cr. Camp 3 mi SW Fraser (10, AMNH), Tabernash 3 mi W (1, SMEK). Gunnison Co.: Gothic (1, SMEK), Gunnison (5, UMAA). Hinsdale Co.: (1, SMEK). Huerfano Co.: La Veta (2, UMAA), Spanish Peak (2, UMAA). Jefferson Co.: Bear Cr. Morrison (4, UMAA), Chimney Gulch, Golden (6, UMAA; 2, AMNH; MCZ), Golden (4, AMNH), Mother Cabrini Shrine (1, NDSU). La Plata Co.: La Plata (1, AMNH). Larimer Co.: Bennet Creek (2, LU; 1, UV), Estes Park (2, CSU; 1, CAS; 3, AMNH; 1, SMEK; 2, CNC; 1 CU; 1, CMP), Glen Haven (2, AMNH; 3, CSU), Home Morain Roose (1, BGSU), Pingree Park (1, CSU; 1, SMEK; 2, BGSU), Poudre Park 3 mi W (4, LU), Poudre River Canyon (1, CU), Redfeather Lakes (2, AMNH), Rist Canyon Fort Collins (1, UWM; 1, CSU). Mineral Co.: Big Meadows nr. Wolf Creek Pass (18, BGSU), Creede (56, SMEK; 1, UMAA, 2, CAS), Deer Creek Canyon (1, BGSU),

Minerals, Snowball Ranch (1, CU), Wolf Creek (1, CU), Wolf Creek Pass (1, BGSU). Montezuma Co.: Cortez (1, CSU), Montrose Co.: Iron Springs Camp 25 mi SW Montrose (12, AMNH). Park Co.: Bailey (1, SMEK), Fraser (MCZ). Pitkin Co.: Ajax Mtn. nr. Aspen (2, CU), 12 mi W Independence Pass (36, LU). Routt Co.: Steamboat Springs (3, CAS). San Juan Co.: Molas Pass (1, CNC), Silverton (8, UMAA). San Miguel Co.: San Miguel (2, AMNH; 4, CAS; 6, MCZ), San Miguel Mtns. (2, UMAA; MCZ), Trout Lake (1, PUL; 2, CAS). Summit Co.: 52 mi N Climax (7, LU). Rocky Mountain Nat. Park: Glacier Basin (1,CU; 1, AMNH; 1, USU), Loch Vale Trail (2, SMEK; 1, CU; 1, AMNH; 3, CAS, 2, REA), Longs Peak (3, AMNH), Meeker Park (1, PUL; 1, CAS; 1, USU), Science Lodge (1, AMNH), Sprague Hotel (2, CNC; 1, CAS), Wind River (2, CAS). Localities of unknown counties: Arapaho Nat. Forest Willow Creek (1, CMP), Aspen Springs (1, AMNH), Bullion Peak (13, UMAA; 2, AMNH; MCZ), Creede Creek (3, CAS), Halls Valley (17, UMAA; 1, AMNH), Home (1, CAS), Leavenworth Valley (1, UMAA; MCZ), Little Creek (1, UMAA), Mill Creek Rd. (1, CU), Mill Gulch (1, UMAA), Monarch Pass (1, CAS), Muckanawago (1, CAS), Solalis (2, AMNH), Stopps Lake (1, AMNH), Ute Creek (1, AMNH), Wicham (1, AMNH). IDAHO: Bear Lake Co., Bloomington Lake (Leffler 1979). MONTANA: Beaverhead Co.: (1, MSU). Cascade Co.: Neihart 12 mi S (9, AMNH). Fergus Co.: Maiden (2, CAS). Gallatin Co.: (1, CAC; 5, MSU), Marais River (2, CAC), Ste. Captain (1, MSU), Windy Pass Gallatin Range (1, CU). NEVADA: Clark Co.: Charleston Mtns. Kyle Canyon (1, CNC), Washoe Co.: Mt. Rose Summit (1, CAS). SOUTH DAKOTA: no locality data (2, MPM), Custer Co.: Sylvan Lk. Harney Natl. Forest (1, UMAA), Lawrence Co.: Savoy (1, UMAA; 1 cotype *C. l. oslari* Leng 1902, AMNH); Lead 2 mi N (9, AMNH). Meade Co.: Sturgis (10, AMNH). Pennington Co.: 10 mi N Custer (1, LU). Localities of unknown counties; Covered wagon Campground Black Hills, Hill City (1, CAS), Terry Peak (1, CU). UTAH: No locality data (1, CAS) Cache Co.: Logan (3, USU), Providence (1, USU)., Redbanks at Logan Canyon (1, CAS), Tory's Ranger Station Logan Canyon (Tanner 1951), Cache-Rich Co.: Line, hwy. 89E (3, AMNH). Grande Co.: 3 mi W Geyser Pass La Sal Mtns. (2, AMNH), 2.8 mi ESE Moab (3, AMNH). Iron Co.: Cedar Breaks (2, PSU; 1, AMNH), 3.5 mi E Jct hwy 14 & 43 nr.

Cedar Breaks (16, LU). Kane Co.: Long Valley Jct. (1, CAS), Navajo Lake. Salt Lake Co.: Silver Lake (1, CU; 1, CAS; 1, WSU). San Juan Co.: Summit Abajo Mtns. 20 mi N Blanding (11, AMNH). Uintah Co.: 25 mi N Vernal (1, CNC; 2, AMNH). Utah Co.: Timpanagos Aspen Grove Environs (1, CNC). Localities of unknown counties: Alta (1, AMNH), Beaver Rg Mtns. (MCZ), Brighton (4, AMNH), The Mammoth, Top Parowan Mtns. (2, CAS). WYOMING: Albany Co.: 8 mi N Centennial, U of Wyo Science Camp (11, AMNH), Pole Mtn. Medicine Bow (2, SMEK; 4, WJ). Big Horn Co.: (1, AMNH). Crook Co.: 12 mi South Sundance (2, MPM). Sheridan Co.: Big Horn (4, SMEK). Teton Co.: Teton Nat. Park, Cascade Canyon (1, AMNH). Localities of unknown counties: Black Hills, Savoy (2m UMAA), Fox Park (1, AMNH).

Cicindela longilabris perviridis Schaupp

United States.

CALIFORNIA: Alpine Co.: no locality (6, AMNH; 17, CAS), Carson Pass (1, AMNH), Ebbets Pass (1, AMNH; 17, CAS), Lk. Alpine (4, AMNH), Mosquito Lake (1, SMEK), Sonora Pass (34, AMNH). Eldorado Co.: Echo Lk (2, CAS; 1, AMNH), Fallen Leaf Lk. (1, CAS), Keith Dome (2, CAS), Mt. Tallac, Tahoe (1, AMNH; 2, CAS), Wright's Lake (6, CAS). Glenn Co.: Plaskett. Inyo Co.: Inyo Ck. (2, AMNH), nr. More Pass (3, CAS). Lake Co.: Thoms. Isl. Lk. (2, UMAA). Lassen Co.: Facht (10, CAS). Madera Co.: Bass Lk. (1, AMNH), Duck Lake, Duck Pass (2, AMNH), Granite Ck. (2, AMNH). Mono Co.: Rock Ck. 1 mi N Tom's Place (2, CAS), Saddlebag Lake (5, AMNH; 39, CAS), Skelton LK. (1, AMNH), Slate Crk. Valley (1, CAS), Sonora Pass (10, CAS), Tioga Lk. (5, PSU), Tioga Pass (5, AMNH). Nevada Co.: Donner Lk. (1, AMNH), Donner Pass (1, SMEK; 1, AMNH), Norden (2, CAS), Summit (1, AMNH). Placer Co.: no locality data (1, SMEK; 1, UMAA; 1, AMNH; 6, CAS), Cisco (1, AMNH; 16, CAS; 1, CSU), Koebele (2, CAS), Summit (9, CAS). Plumas Co.: Bullfrog Lk., Sierra Nevada Mtns. (2, CAS), Chester (1, BGSU), Lassen Nat. Park Bumpas Hell (1, CAS), Lassen Nat. Pk. Warner Valley Devils Kitchen (1, CAS), Meadow Valley (1, CAS), Mt. Ingals (1, UMAA; 2, AMNH). Shasta Co.: Castella (1, CAS), Kings Ck. Meadow (1, CAS), Manzanita Lk. 5 mi N (1, UWM). Sierra Co.: Gold Lk. (1, AMNH), Sierraville (1, AMNH). Siskiyou Co.: Castle Lake; McCloud (1, CAS), Walker (9, CAS). Tulare Co.: Jennie Ellis Lk. (3, CAS), Milestone Ck. (1, CAS). Tuolumne Co.: No locality data (2, CAS), Sonora Pass (1, SMEK; 1, WJ; 1, PSU), Tioga Pass (33, AMNH). YOSEMITE NAT. PK: Cathedral Lk. (1, AMNH), Gaylor Lk. (2, UV; 1, CAS), Mt. Hoffman (1, AMNH), Mt. Lyell Donahue Pass (1, UV), Tuolumne Meadows (1, AMNH), Yosemite Valley (2, CAS). Localities of unknown counties: Russen River (1, CAS), Sierra Nevada (2, AMNH), Sierra Nevada Mtns. (1, CMP), Summit Lake, Tahoe (1, AMNH), Tallac (3, CAS). OREGON: Benton Co.: Abbott Butte Lookout nr. Corvallis (1, UV), Alpine (1, CAS). Clackamas Co.: Mt. Hood, Govt. Camp (1, UIM; 5, PSU; 1, AMNH; 20, CAS). Deschutes Co.: Bend (MCZ), Cache Mtn. (1, SMEK). Douglas Co.: Diamond Lake (3, CAS)

Klamath Co.: (2, UMAA; 2, CAS), Crater Lake (2, CAS). Lake Co.: Warner Mtns. (1, CAS). Lane Co.: Obsidian Trail (1, CAS). Linne Co.: Lost Prairie Campground 45 mi E Sweethome (1, SMEK; 17, CU; 1, REA). Marion Co.: Olallie Lake (1, CAS). Multnomah Co.: Larch Mountain (1, WSU). Additional Oregon localities from (Leffler 1979): Curry Co.: Red Mtn. Prairie. Deschutes Co.: Bend 10 mi SW, Cache Mtn, Indian Ford Creek. Hood River Co.: Cloud Gap Inn 3 mi NE, Hood River 20 mi S. Jackson Co.: Mount Ashland 7000 ft, Union Creek. Jefferson Co.: Culver. Josephine Co.: 25 mi E Gold Beach. Klamath Co.: Lake of the Woods, Cherry Crk. Upper Klamath Lake, Linne Co.: Iron Mtn., Monument Peak, Summit Santiam Pass, Tombstone Prairie, Wasco Co.: Bear Springs, Flag Point, Maupin. WASHINGTON: Chelan Co.: Holden Village (6, PSU), Stevens Pass (4, SU; 32, CNC; 1, PSU), 5.7 mi N Stevens Pass (6, REA). Clallam Co.: Olympic Nat. Park: Blue Mountain (1, WJ; 36, CNC; 1, PSU), Deer Park (17, CNC). Hurricane Ridge (1, SMEK; 9, PSU; 1, REA). Jefferson Co.: Lake Beauty (1, PSU), Mt. Kimta (1, PSU). Okanagan Co.: Cascade Crest Trail to Windy Pass (5, WSU), Gold Creek (2, CNC). Pierre Co.: Rainier Nat. Park Sunrise Park (1, CAS). San Juan Co.: Orcas Isl. Camp Moran (1, WSU). Additional Washington records from Leffler 1979: Chelan Co.: Holden Village. King Co.: North Fork Skykomish River, W side of Stevens Pass. King-Kittitas Co. Line: Deception Pass. Okanagan Co.: Black Canyon. Skagit Co.: Sauk. Snohomish Co.: Glacier Pk., Miners Ridge E of Glacier Peak. Whatcom Co.: Devil's Pass E of Ross Lake.

C. l. longilabris X *C. l. laurentii* X *C. l. perviridis* Intergrades

Canada.
ALBERTA: Beaver Mines, 20 km W Pincher Creek area (35, LU), Banff (14, CNC; 6, CU; 1, UMAA; 4, AMNH; 102, CAS), 4½ mi N Banff (43, AMNH), Frank (1, CNC), Ft. McLeod "Brit Amer" (1, AMNH), Loggan (20, AMNH; 1, CAS), Waterton Lakes (3, CNC). BRITISH COLUMBIA: Ainsworth (1, CU), Creston (6, CNC; 4, CU; 2, UMAA; 40, UBC; 42, AMNH; 16, CAS), Fernie (5, CAS), Golden (2, AMNH), Hosmer (Leffler 1979), Kaslo (3, CU; 7, UMAA; 19, AMNH; 2, CAS), Loiggan (1, CU), Little Vermillion River (Leffler, 1979), New Denver (Leffler 1979), Sanca (2, UBC), Wynndel (12, CNC; 1, UBC; 7, AMNH; 8, CAS; 1, UAE), Yoho Valley (Leffler 1979).
IDAHO: Benewah Co.: Emerald Creek (Leffler 1979), N. S. Ski Bowl (1, UIM), Potlach 21,5 mi NE (Leffler 1979). Bonner Co.: Clark Fork 8 mi E (3, UIM), Preist Lake (1, UIM), Preist River Exp. For. (1, UIM), Trout Creek 12 mi SE Sandpoint (6, UIM). Boundary Co.: Brush Lake (2, UIM), Caribou Cr. 17 mi W Naples (2, UIM), Ruby Pass 13 mi NW Naples (1, UIM). Clearwater Co.: Elk River 3 mi N (1, UIM). Elmore Co.: Atlanta (Leffler 1979). Idaho Co.: Kooskia 15 mi E (2, REA), Lolo Pass (1, UIM), Moose Creek (15, USU), Moose Creek R. S. Grangeville (5, REA). Kootenai Co.: Coer D'Alene (3, CAS, 1, UIM). Latah Co.: Bovill (1, WSU), Flat Creek (1, REA), Harvard (1, UIM), Harvard 7 mi SE Sand Creek (1, WSU), Little Bear Cr. Helmer (1, UIM), Moscow Mtn. (7, UIM; 1, SMEK; 2, WSU), Moscow 6 mi NE (1, UIM; 3, WSU), Troy (4, IUM). Lemhi Co.: Gibbonsville (1, UIM), Meadow Lake 6 mi N. Gilmore (7, UIM). Shoshone Co.: Pine Creek (3, CMP), Wallace (2, UIM). Valley Co.: Egger's Creek (Leffler 1979), McCall (9, UIM), Yellow Pine (1, UIM). Localities of unknown counties: Spelling (1, WSU), Lk. Waha (1, UIM; 1, CAS).
MONTANA: Deer Lodge Co.: Lost Creek Pass (1, CNC). Flathead Co.: Kila 8 mi S (Leffler 1979). Glacier Co.: St. Mary's (1, UMAA). Jefferson Co.: Homestake Pass (Leffler 1979). Lewis and Clark Co.: Helena (2, CAS), Roger's Pass Summit 20 km W Lincoln (1, LU). Missoula Co.: (2, USU). Blue Mountain (Leffler 1979), Greenhough (Leffler L979), Kitchen Creek (Leffler 1979), Missoula (1, MSU; 1, USNM). Pattee Canyon

(Leffler 1979). Ravalli Co.: Blodgett Mtn. (1, MSU), Blue Nose Peak (2, AMNH: 2, WSU), Camp Creek (1, MSU), Come Lake (2, AMNH), Darby (1, MSU), Darby 19 mi SW (Leffler 1979), East Fork (1, AMNH), Girds Creek (5, MSU; 1, CAS), Hamilton (1, CNC; 2, MSU; 1, AMNH), Hamilton 6 mi NW (Leffler 1979). Sanders Co.: Kaniksu Nat. For. Bull R. Campground (1, SMEK), Thomson Falls (2, CAS), Weeksville (MCZ), White Pine (Leffler 1979). Silver Bow Co.: Butte (1, MSU). Localities of unknown counties: Camp Pleasant (1, CAS), Flathead National Forest Big Creek (1, CMP), Glacier Park (1, CU), Glacier Park, Indian Ridge (2, AMNH), Glacier Pk. McGee Meadow (1, AMNH). OREGON: Umatilla Co.: Athena Wild Horse Mtn. (1, AMNH), Bone Springs Blue Mtn. (12, AMNH), Meacham (2, CAS). Tollgate (11, AMNH; 2, CAS). Union Co.: Oregon Trail Camp (1, SMEK). Localities of unknown counties: Moffat Head Blue Mtns. (1, CAS), Wallows Mtns.: Chimney Lake (2, USU), Minam L. Area (1, WSU), Morcastle Lake (1, WSU). Additional records from Leffler 1979: Baker Co.: Anthony Lake, Baker, Pine Creek nr. Baker, Durkee. Grant Co.: Summit Dixie Pass. Umatilla Co.: Deadman's Pass. Union Co.: Elgin, Phillips Canyon 6.8 km NE Elgin, 8 mi E LaGrande. Wallowa Co.: Hat Point, French Forest Camp, Lost Line River, Wallowa Lk. WASHINGTON: Columbia Co.: Blue Mtns. Tollgate Rd. (1, WSU). Pend Oreille Co.: 7 mi W. Locke (3, PSU). Stevens Co.: Blackwelder (1, UWM). Walla Walla Co.: Walla Walla (1, WSU). Additional Washington records from Leffler 1979: Columbia Co.: Blue Mtns; Goodman Springs, Lewis Peak. Whitman Co.: Pullman.

The species *Cicindela nebraskana* Casey

Cicindela nebraskana Casey 1909, p. 268 (type locality - Nebraska). Casey 1914, p. 18. Leffler 1979, p. 484. Boyd and Associates 1982, p. 6.

Cicindela montana LeConte 1861 (not Charpentier 1825) p. 338 (type area - Valleys of the Rocky Mountains). Casey 1914, p. 17.

Cicindela longilabris montana, LeConte 1875, p. 157. Schaupp 1884 p. 87. Leng 1902, p. 122. Harris 1911, p. 20.

Cicindela longilabris nebraskana, Harris, 1911, p. 20.

Cicindela montana nebraskana, Casey 1913, p. 17.

Cicindela montana canadensis Casey 1913, p. 17 (type locality - Calgary, Alberta).

Cicindela spissitarsis Casey 1913, p. 18 (type locality - Aweme, Manitoba) and 1914, p. 17.

Cicindela canadensis, Casey 1914, p. 17

Cicindela calgaryana Casey 1914, p. 17 (type locality - Lethbridge, Alberta).

Cicindela montana uteana Casey 1924, p. 12 (type locality - Provo, Utah).

Cicindela longilabris chamberlaini, Kanus 1925, p. 182 (type locality - "Stein Mountains", Steens Mountains, Harney Co., Oregon).

Cicindela montana montana, Wallis 1961, p. 49.

Cicindela montana spissitarsis, Wallis 1961, p. 50.

Cicindela montana chamberlaini, Wallis 1961, p. 50.

Cicindela montana montana, Leffler and Pearson 1976, P. 33.

Cicindela nebraskana chamberlaini, Leffler 1979 p. 486. Boyd and Associates 1982, p. 6.

Recognition

Adults of *C. nebraskana* can be distinguished from *C. longilabris* adults by the relatively more smooth elytral surface with punctations occurring in discrete, ordered fashion in some specimens with smooth fields between, normally black abdomen varying to metallic purple or blue or blue and green in a small percentage of specimens, absence of a humeral lunule or apical lunule, and in most specimens, absence of a middle band, black dorsal colouration in the vast majority of specimens, and labrum which is light in colour in 44.8%, intermediate coloured or mottled in 30.6% and black in 24.6% of females, and light in 82.6%, intermediate or mottled in 15.6% and black in 1.8% of male specimens. Descriptions of *C. nebraskana* can be found in LeConte (1961) under the name *montana*, Leng (1902), Casey (1909) and more recently, Leffler (1979).

Notes on synonymy and taxonomic history

LeConte's (1961) name *C. montana* is a junior homonym of *C. montana* Charpentier (1825), itself a synonym of *C. hybrida riparia* Dejean (Huber 1969). *Cicindela nebraskana* Casey 1909 is the oldest available synonymn and therefore becomes the correct name of the taxon.

Casey's names *spissitarsis*, *canadensis* and *calgaryana* are all based on exceedingly minor individual variations.

Casey's (1924) *uteana* was based on one specimen from Provo Utah which exhibited a slightly cupreous brown dorsal colouration and more metallic luster than is typical of the species. A small number of specimens of *C. nebraskana* in that area exhibit some metallic green and blue abdominal colour and a slightly bronze brown dorsal colouration.

Knaus' *chamberlaini* is based on a series of specimens in which a number have a slender middle band which occurs in other specimens of this species.

Geographic variation

Females with a dark coloured labrum vary greatly from locality to locality but a geographical pattern is not evident (Fig. 13). The colour of the proepisternum is black in most specimens of most populations sampled, (Fig. 15) but a significant number of specimens in the Manitoba, Idaho, Wyoming and Utah population samples are metallic green, blue or bronze. The colour of the abdomen is also variable in some populations (Fig. 17). Populations AB2 and MT1 have a large number of specimens with a brown abdomen and MB1, WY1, WY2, and VT1 have a large percentage of specimens exhibiting metallic greens and blues.

Elytral colour varies little in *C. nebraskana*. In most populations a majority of specimens have a black dorsum (Fig. 19). UT1 is a variable population with a larger number of specimens exhibiting some brown or dark olive green elytra.

Most specimens in all populations of *C. nebraskana* are immaculate or very nearly so (Figs. 21, 23, 25, 27). In those populations (ID1, WY2, Fig. 21) where the percentage of the elytral surface covered with maculations is slightly increased it is due to the presence of a thin or incomplete middle band in some of the specimens (Fig. 25). In all of the sampled populations the humeral lunule and apical lunule (Figs. 23, 27) are absent in the majority of specimens.

Leffler (1979), in studying tiger beetles of the northwestern states recognized two subspecies, *C. n. nebraskana* east of the continental divide and *C. n. chamberlaini* west of the divide based on a statistical difference in head width, the eastern form having broader heads, on average. HW was not selected in discriminant tests 27 and 28 as a variable contributing significant variance to the discriminant functions (Table 37). In the discriminant analysis section I reported longer average femur lengths and elytral lengths in populations west of the divide, which suggests that western populations of this species are larger in body size, on average, than eastern populations. These findings are insignificant for justification of subspecific recognition. I treat *C. nebraskana* as a monotypic species.

Distribution

The geographic distribution of *C. nebraskana* is presented in Figure 80. The northern limit of the distribution of this species approximates the northern limit of Chernozemic soils in grassland and grassland-forest transition areas across the prairie provinces of Canada and British Columbia. In the west, its range follows that of the Ponderosa pine-bunchgrass vegetation zone. The range of *C. nebraskana* is limited to the south by arid lands of the great basin. Conditions affecting the eastern limits of the distribution of this species are unclear, but probably involve edaphic factors which do not show up at the order and great group level of soil classification.

In the following list of records, the number of specimens and collection housing them is indicated for specimens I have seen, and the reference is cited for records from the literature.

Canada

ALBERTA: "Alta" no locality stated (1, CMP), "Beavalon" Beauvallon? (2, UAE), Brooks (1, CAS), Calgary (5, CNC; 4, UMAA; 3, CAS), Coronation (2, UAE), Cypress Hills (1, AMNH; 1, CAS; 1, LU), Deer Creek (1, CNC), Elkwater (4, CNC), Empress (Leffler 1979), Foremost (1, CNC), Fort McLeod (1, CAS), Gorge Creek 160 km N. Coleman (Leffler 1979), Hilda (1, UAE), Kananaskis (1, CAS), "L. Caledonia" (1, CNC), Lethbridge (2, UMW; 2, MSU; 17, CNC; 3, CAS; 1, AMNHO, Manyberries Sta. nr. Onefour (1, UAE), Medicine Hat (5, PSU), Millarville (4, CNC), Morley (1, CAS), Onefour (1, CNC), Opal (1, UAE; 1, LU), Paine Lake (Leffler 1979), Patricia (3, UMAA), Patricia 10 mi E (11, LU), Pincher Creek (1, UAE), Steveville (1, CNC), Taber (1, CNC), Tilley (2, CAS), "Turner V." (1, CAS), Waterton Pk. (1, CNC), Welling (1, CAS), 49°04'20"N 110°25'24"W (2, UAE). BRITISH COLUMBIA: no locality (2, SMEK), Aspen Grove (5, AMNH; 2, CAS; 1, CU), Big Bar (1, CAS), Bridesville (2, CAS), Chase (1, CAS), Chilcotin (11, CNC; 27, UBC; 1, AMNH), Clinton (1, CNC), Copper Mtn. (3, UMAA; 1, CNC), Cranbrook (1, AMNH), Creston (1, UAE; 1, AMNH; 1, LU), Douglas Lk. 20 mi E (1, UMW; 3, CAS), Enderby (5, UBC), Forest Grove, 8 mi S (5, PSU), Fort Steele (1, CNC), Goodfellow Cr. Manning Prov. Park (Leffler 1979), Hope Pass nr. Summit (1, UBC), Invermere, 11 mi S (1, UAE), Jesmond (1, CAS) Kamloops (1, CNC; 8, UBC), Kootenay R. 17 mi N Kimberley (1, UAE), Lac La Hache (Leffler 1979), Lansdown (1, CAS), Lillooet (5, CNC), Lorna (2, CAS), Lumby (1, CNC; 1, CAS), Madden Lk. 10 mi N Oliver (1, CNC), Mara (2, CNC), Marysville (2, CU; 8, UBC), Midday Valley (4, CAS; 2, UBC), Nakusp (1, CNC), Nicola (1, CNC; 1, AMNH), Okanagan Falls (1, CNC), Oliver (39, CNC), Osoyoos (1, CNC), Peachland (1, UMAA; 1, CNC), Pillar Lk. (2, UNW; 1, CAS), Riske Ck. (5, UBC), Robson (4, CNC; 2, UBC), Salmon Arm (2, CNC; 5, AMNH), Sheep Cr. nr. Cristina L. (1, CAS), Skookumchuk (1, UBC), Snow Mtn. (1, UBC), "Spious Ck", Spius Ck? (1, CAS), Sugar Lk. (2, CAS), Twin Lakes, Keremeous (4, CNC), Upper Hat Cr. (2, CNC), Voght Ck. (1, CAS), Walhachim (1, UBC), "W. Crescent Valley" Crescent Valley? (1, UBC), Williams Lk. (1, UBC). MANITOBA: Aweme (1, UMAA; 1, SMEK; 4, CNC; MCZ), Erickson (1, NDSU), Glen Souris (1, CNC), Hartney (2, CNC), Husavick (2, CNC), Lyleton (1, CNC), Miami (1, CNC), Minto (2, LU), Ninette (8, CNC), Rosebank (1, CNC), Sandilands (2, UMW), "T. Mountain Mun" (5, NDSU), Westbourne (1, UMAA). SASKATCHEWAN: Attons Lk. (1, CNC) Beverley, 4 mi NW (1, AMNH), Carlyle (2, CNC), Chaplin Lk. (1, UAE; 4, AMNH), Cut Knife (1, CNC), Cypress Hills (2,CNC), Eagle Hill Creek (1, CNC), Elbow (5, CNC), Estevan (4, CNC), Farewell Ck. (1, UTU), Forget (1, CNC), Goodspirit Lake (1, CNC), Gull Lake (3, AMNH), Kennedy (1, CNC). Lancer (1, CNC), Maple Creek, 15 mi W (2, AMNH), Roche Perce (1, CNC), Rock Glen (2, CNC), Saskatoon (9, CNC), Tunstal (2, CNC), Val Marie (2, CNC), Willowbunch (2, CNC), W. of Roblin (1, CNC).

United States.

CALIFORNIA: Lassen Co.: Facht (1, CAS), Mono Co.: Bancroft 1.5 mi S White Mtns (1, PSU), Crooked Cr., White Mtns. (1, UWM; 1, CAS), White Mtns (1, PSU). Mono/Tuolumne Counties: Sonora Pass (6, SMEK; 8, PUL; 3, PSU; 1, AMNH; 27, CAS). COLORADO: Medicine Bow Mtns (1, AMNH). IDAHO: no locality (3, AMNH; 2, WSU; 1, CAS), Ada Co.: Mile High, 8 mi NE Boise (Leffler 1979). Bannock Co.: Giveout 42°24'N 111°10'W (4, AMNH) Lava Hot Springs (2, UMAA), Pocatello (Leffler 1979). Bear Lake Co.: Liberty (4, USU), Montpelier (1, UMAA). Bonner Co.: Preist River Expt. For. (3, UIM), Sagle (1, UIM), Samuels (2, UIM), Sandpoint 8 mi N (1, UIM), Sheepspring (1, UIM). Bonneville Co.: Bluck's Canyon (2, USU), Swan Valley, 11 mi NE (15, UIM). Caribou Co.: Grace (1, USU), Soda Springs (1, UMAA; 3, AMNH; 1, CU; 1, CMP; 1, CAS; 1, UIM), Soda Springs, 11 mi NE (7, UIM; 1, CAS), Wayan, 3 mi E (1, UIM). Cassia Co.: Basin Jct. 1 mi W (1, UIM), Elba, 9 mi W (3, UIM), Elba-Basin Pass (5, UIM), Green Canyon, Elba (1, USU), Hereford, J.S. (1, UIM), Mt. Harrison (1, UIM), Narrow Rock Creek (2, UIM). Clearwater Co.: Greer (1, UIM), Pierce (1, UIM). Franklin Co.: Cub River Canyon (3, USU), Preston 28 mi NE (3, UIM). Fremont Co.: Ashton (3, UIM; 1, USU), Ashton 11 km NE (Leffler 1979), Last Chance 2 mi S (1, UIM), St. Antony (1, UIM), St. Antony 26 mi NW (1, UIM), Targhee Pass (1, UIM). Kootenai Co.: Chilco (4, UIM). Latah Co.: Potlach (6, UIM), Robinson Lk. (4, UIM), Tomer's Butte (1, UIM), Viola (4, UIM; 3, WSU). Lemhi Co.: Bannock Pass (1, UIM). Lewis Co.: Nez

Pierce 10 mi N (4, UIM). Oneida Co.: Black Pine Canyon (1, USU). Owyhee Co.: Silver City (Leffler 1979). Teton Co.: Driggs (2, UIM; 1, UMAA), Rammel Cr. (1, USU). Twin Falls Co.: Magic Mtn. (2, UIM), Roseworth 8 mi N (1, UIM). Localities of unknown counties: Minidoka N.F. (1, USU). MONTANA: Beaverhead Co.: no locality (1, MSU), Alaska Basin, Monida (1, USU), Birch Ck. (1, MSU), Centennial Valley (1, MSU), Lakeview (1, MSU), P & O Ranch (1, MSU). Carbon Co.: Red Lodge (1, MSU). Carter Co.: Pinele (3, MSU). Cascade Co.: Monarch (1, CAS; 2, AMNH; MCZ). Dawson Co.: (1, MSU). Fergus Co.: Denton (1, MSU), Lewiston (1, MSU). Gallatin Co.: no locality given; (3, CNC; 43, MSU), Bozeman (2, CNC; 5, UMAA; 28, MSU), Bridger Mtns. (1, UMAA), Gallatin Mtn. (1, UMAA), Lake Hebgen (Leffler 1979), Logan (1, MSU), Rock Cr. & Madison R., Gallatin Nat. For. (1, CMP), West Yellowstone (1, USU), Glacier Co.: St. Mary's R. (9, CAS). Lake Co.: no locality (1, MSU), Flathead Lake (1, MSU). Lewis & Clarke Co.: no locality (1, CNC), Wolf Creek (1, CNC). McCone Co.: (1, NDSU). Meagher Co.: Ringling (1, MSU). Missoula Co.: Missoula (1, AMNH). Phillips Co.: Beaver Crk. (4, SMEK), Little Rocky Mtns. (1, MSU). Ravalli Co.: Gird Ck. (1, MSU), Hamilton (2, MSU). Roosevelt Co.: no locality (1, NDSU), Scobey, 20 mi S (Leffler 1979). Stillwater Co.: Park City (1, MSU). Rapelje (1, CNC). Sweetgrass Co.: Big Timber, 35 mi N (1, MSU). Teton Co.: Teton Canyon (1, CAS). Wheatland Co.: Harlowtown 15 mi S (Leffler 1979). NEBRASKA: no locality given (1, MCZ; 1, type specimen of *nebraskana* Casey, USNM). Sioux Co.: (4, Meserve, 1936). NEVADA: no locality given: (1, AMNH), Elko Co.: Montello (1, USU). NORTH DAKOTA: Barnes Co.: (1, SMEK; 4, NDSU). Benson Co.: (1, NDSU), York (2, AMNH). Bottineau Co.: (29, NDSU), Turtle Mtns. (1, UMAA). Burleigh Co.: Bismark (1, CMP). Golden Valley, Co.: Beach (1, MSU; 3, NDSU). Grant Co.: (1, NDSU). McHenry Co.: (2, NDSU). Mckenzie Co.: (1, NDSU). McLean Co.: (8, NDSU). Mountrail Co.: (1, NDSU), Stanley (1, AMNH). Pierce Co. (2, NDSU). Rolette Co.: (4, NDSU). Statesman Co.: Buchanan (1, AMNH), Jamestown (1, AMNH). Williams Co.: (1, NDSU). OREGON: Baker Co.: Baker (7, CAS). Crook Co.: Coldsprings (2, UIM), Grizzly Mtn. 13 km NW Prineville (Leffler 1979), N.W. Ochoco Nat. For. (2, CAS), Prineville 23 mi E (Leffler 1979). Harney Co.: "Stein Mtns"

Steens Mtns (1, Paratype *C. chamberlaini* Knaus, CNC; 4, CMP; 28, CAS) Umatilla Co.: Blue Mtns (1, OKS; 1, CAS), Echo (3, UWM), Tollgate (Leffler 1979). Union Co.: North Powder (2, SMEK). Wallowa Co.: (1, CAS). SOUTH DAKOTA: Brookings Co.: Brookings (1, CMP). Hughes Co.: Pierre (3, CMP). Meade Co.: Sturgis (3, AMNH). Localities of unknown counties: Moscoe (2m CMP). UTAH: no locality given (1, AMNH), Box Elder Co.: (2, USU), Park Valley (1, USU), Snowville (1, USU). Cache Co.: Blacksmith Fork Canyon (3, USU), Logan (15, USU), Logan Canyon (2, AMNH; 16, USU), Mendon (6, USU), Poney Grove Lk. Logan Canyon (1, USU), Providence (3, USU), Providence Lk. (1, USU). Daggett Co.: Greendale, Uintah Mtns. (Tanner 1929), Green River Lake (1, USU), Manila (1, USU). Garfield Co.: Escalante, 22 mi N (1, AMNH). Juab Co.: Parley's Canyon (1, UMAA), Trout Creek, Ibapali Mtns. (2, UMAA). Rich Co.: (2, USU). Salt Lake City (1, AMNH). Sanpete Co.: Ephraim (1, USU). Sevier Co.: Fish Lake (1, AMNH). Summit Co.: Kimball's Jctn. (1, AMNH), Park City (1, UMAA). Tooele Co.: Bonneville (1, USU), Loop Camp 13 mi SW Grantsville (1, AMNH), Soldier Canyon, Stockton (MCZ), Stockton (3, UMAA), S. Willow Canyon, Stansbury Mtns. (1, AMNH). Uintah Co.: Gusher (1, USU). Utah Co.: American Fork Canyon (Tanner 1929), Aspen Grove (1, UMAA; 1, OKS; 1, CAS), North Fork Provo Canyon (7, UMAA; 4, AMNH; 1, BGSU), Provo (4, UMAA; 5, CAS). Washington Co.: St. George (1, AMNH), Virgin R. (1, AMNH). Localities of unknown counties: Allen Canyon (1, USU), Card Canyon (1, USU), Conley Canyon (1, USU), Deep Creek Mountains (Tanner 1929), Deer Creek Canyon (Tanner 1929), Green Canyon (6, USU), Monte Cristo (1, USU), Mt. Neb. (1, USU), Pine Valley Mountains (Tanner 1929), Raft River Mountains (Tanner 1929), Sardine Canyon (6, USU), Temple Fork (3, USU), UIntah National Forest (Tanner 1929), Wasatch Mtns. (1, AMNH; MCZ). WASHINGTON: no locality given (1, CU), Asotin Co.: Anatone 4 mi S (1, WSU). Benton Co.: Richland (2, UIM). Chelan Co.: Lake Chelan (Leffler 1979). Leavenworth, 18.7 mi S (Leffler 1979). Columbia Co.: Blue Mtns. (2, CMP), Blue Mtns. Lewis Peak (Leffler 1979), Dayton (Leffler 1979), Cowlitz Co.: Goat Mountain (Leffler 1979). Ferry Co.: Republic 13 mi E (4, PSU), Twin Lakes (1, PSU). Franklin Co.: Pasco (MCZ). King Co.: Red Mtn. (1, AMNH). Kittitas Co.: Cle Elum, 5 mi W (14, PSU), Colockum

Pass (1, SMEK), Easton (3, CAS), Easton 5 mi E (2, CSU), Ellensburg (1, SMEK; 3, PSU), Katchees Lake (2, PSU), Lk Cle Elum (1,AMNH), Robinson Canyon 5 km SW Thorp (Leffler 1979), Rocky Run 1.9 km S Snoqualmie Pass (Leffler 1979), Stampede Pass (Leffler 1979). Lewis Co.: Mt. Rainier Nat. Pk. Box Can. N Fk. Cowlitz River (2, OKS; 2, BGSU), Paradise Valley, Mt. Rainier (2, CAS), Rainier Nat. Forest, Sawmill Flat (3, AMNH). Okanagan Co.: Chesaw, 5 mi E (3, PSU), Gibson Creek 1 km N Conconully (Leffler 1979), Omak 14 mi S (2, PSU). Pend Oreille Co.: 7 mi W Locke (Leffler 1979). Skamania Co.: Goat Mtn Trail 5 mi N Spirit Lake (Leffler 1979), Little Huckleberry Mountain (Leffler 1979), Steamboat Mountain (Leffler 1979), 10 mi N Trout Lake (Leffler 1979). Spokane Co.: Spokane (Leffler 1979). Stevens Co.: Blacktail Mountain (Leffler 1979), Blackwelder (3, UWM), Deer Lake 12 mi SE Chewelah (Leffler 1979), Northport (1, CAS). Whitman Co.: Pullman (2, CU; 1, CAS; 9, WSU). Yakima Co.: 10 mi S Bald Mtn. (1, PSU). localities of unknown counties: Peliman (1, NCSR), Bird Creek (3, CAS). WYOMING: no locality data (1, AMNH; 1, CSU; 1, CMP), Albany Co.: (6, CNC; 2, AMNH), Laramie (1, AMNH). Pole Mtn. Medicine Bow (2, SMEK; 6, CDF). Carbon Co.: Bottle Creek Camp 7 mi SW Encampment (2, AMNH). Fremont Co.: South Pass (1, USU). Hot Springs Co.: Owl Creek Mountains (Leffler 1979). Park Co.: Clay Butte (10, PSU), Lake Cr. Camp 13 mi SE Cooke City (1, AMNH). Sheridan Co.: Big Horn (1, SMEK). Sublette Co.: Bondurant (1, SMEK), Green River Lakes, Wind River Range (38, AMNH), Middle Piney Creek, Sacajawea Camp (23, AMNH). Sweetwater Co.: Green River (Leffler 1979). Teton Co.: Cascade Canyon, Gr. Teton Nat. Pk. (2, UMAA; 2, AMNH). Gr. Teton Nat. Pk. (2, SMEK; 1, LU; 1, CSU), Gr. Teton Nat. Pk. Indian Paintbrush Canyon (1, AMNH), Gr. Teton Nat. Pk. Jackson Hole Res. Sta. (2, CSU), Jackson (4, USU), Jackson 5.4 mi S (1, PSU), Jenny Lake (1, CMP; 5, AMNH), Moran P. O. 4, mi WNW (1, CSU), Teton Pass (1, PSU). Uinta Co.: Fort Bridger (Tanner 1929). Weston Co.: Newcastle (5, UMAA). Yellowstone Nat. Pk.: (1, UMAA; 1, MSU; 6, AMNH; 3, CSU), Canon Camp (1, CU), Mammoth Jct. (1, AMNH), Sylvan Pass (1, AMNH). Locations of unknown counties: Cassell Berry (1, CSU), Firehole Lake (1, CNC).

Doubtful records

Kansas "before 1897" (1, MPM). Assumed mislabelled.

Phylogeny and Zoogeography

The Hennigian method applied here has been thoroughly discussed elsewhere (Hennig 1966; Ball 1975; Freitag 1979). Plesiotypic and apotypic characters in species of the *sylvatica* group are described in Table 41 and Table 42 indicates which of the apotypic characters are found in each of the species in the group. Characters defining the *sylvatica* group have been based on external structures (Horn 1915) and the male genitalia (Rivalier 1950). The main ancestral characters are a long labrum, a short but distinct flagellum (sclerite 4) and a distinct median tooth (sclerite 5) of the internal sac of the male aedeagus, a reduced number of body setae, and pro-and mesotrochanters each with one sensory seta. These among others describe the primitive ancestor of the *sylvatica* group and have changed considerably, giving rise to the following sister groups: *C. soluta-C. gemmata*, *C. sylvatica-C. granulata*, and *C. longilabris-C. nebraskana*, with *C. japana* being most closely related to the *soluta-gemmata* species pair and *C. lacteola* having been derived earlier in the evolution of the whole group.

The group genealogy is expressed in Figure 81. The first separation in the history of the group probably gave rise to the ancestor of those forms retaining the plesiotypic long labrum and the ancestor of those forms in which the labrum has become shortened (*C. japana*, *C. gemmata* and *C. soluta*). Of these three species, *C. gemmata* and *C. soluta* appear to form a species pair because they share the apotypic setose frons, the notched lateral margin of the second gonapophyses of the female

TABLE 41. Character states used in the construction of a geneology of the *Cicindela sylvatica* species group.

CHARACTER	CHARACTER STATE	
	Plesiotypic	Apotypic
1. Body size	Large beetles 14-18 mm	Small 14 mm A
2. Elytra: surface texture	granulate rough	finely granulate appearing smooth B smooth fields between granulate depressions B^1
3. Elytra: colour	dark grey brown to black	gray-green metallic C^1 green, cupreous C^2
4. Elytra: maculations	humeral lunule, or 2 humeral spots; middle band; apical lunule or supapical spot	markings greatly reduced or absent D Markings increased continuous around margin of elytra D^1
5. Frons: setae	Absent	Present E
6. Labrum: shape $\frac{\text{length}}{\text{width}}$	Long	slightly shortened F greatly shortened F^1
7. Labrum: longitudinal ridge	broad & rounded	absent G sharp & distinct Keel G^1
8. Labrum: colour	light tan in both sexes	dark brown or black H dark in many females and some males H^1 dark in only a very few females H^2
Genitalic Characters		
9. 2nd gonapophyses: shaped	curved and pointed See Figs.	notched lateral margin I
10. sternum 8	apex cases to two points with a V-shaped notch	rounded apices J notched apically one seta at each notch (Fig 65) J^1 truncate, setose apices (Fig. 66) J^2
11. oviduct sclerite	shield shaped (Figs.50-61)	large K triangular shaped K^1

TABLE 41 (Cont'd)

12.	apex of aedeagus	roughly arrow shaped (Figs. 28-43)	narrowed prolonged apex	L
			laterally flattened projection at apex	L^1
13.	sclerites of internal sac	sclerites 1-6 distinct (Figs.28-43)	fusion of 1&4 + reduced 5?	M
			sclerite cluster	M^1
			sclerite 2 large & broken in pieces	M^2

TABLE 42. Selected characters and character states of the species of the *Cicindela sylvatica* group. Letters indicate apotypic characters from Table 41, • indicates plesiotypic characters.

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13
C. longilabris	•	•	•C C^1 C^2	•	•	•	•	H^2	•	•	•	•	•
C. nebraskana	•	B^1	•	D	•	•	•	H^1	•	•	•	•	•
C. sylvatica	•	•	•	•	•	•	G^1	H	•	•	•	L	•
C. granulata	•	•	•	•	E	•	•	•	•	•	•	L	
C. japana	•	•	C	•	•	F^1	•	•	•	J	K	•	M
C. gemmata	•	•	C	•	E	F^1	•	•	I	◦	K^1	•	M^1
C. soluta	A	B	C^1	•	E	F	•	•	I	J^1	•	L^1	M^1
C. lacteola	A	B	C^2	D^1	•	•	G	•	•	J^2	◦	•	M^2

genitalia, and the sclerite cluster in the inner sac of the male genitalia. Such a phylogeny requires that the greatly shortened labrum arose independently in *C. japana* and *C. gemmata.* The somewhat shortened labrum exhibited by *C. soluta* was probably the type present in the common ancestor of *japana*, *gemmata* and *soluta.*

Of the remaining five species which exhibit the plesiotypic long labrum, *C. lacteola* probably became a distinct lineage early in the evolution of the group as it is uniquely apotypic in having the maculations increased and continuous around the margins of the elytra, truncate, setose apices on sternum 8 of the female genitalia, and sclerite 2 of the internal sac of the male aedeagus expanded and broken into three pieces, and lacking the broadly rounded longitudinal ridge on the labrum.

The common ancestor of *longilabris*, *nebraskana*, *sylvatica* and *granulata* probably had a holarctic distribution, and possessed a dark coloured labrum in both sexes. The marine transgression of Beringia in the late Pliocene (Matthews 1979) may have been the event which separated the ancestor of the *longilabris-nebraskana* species pair from the ancestor of the *sylvatica-granulata* species pair. The dark labrum colour has remained in *C. sylvatica* had has been lost in *C. granulata. C. longilabris* and *C. nebraskana* appear to be in the process of losing the dark labrum colour, as it occurs in some females of *nebraskana* and rarely in either sex of *longilabris*. *C. sylvatica* and *C. granulata* are similar in possessing a narrowed, prolonged apex of the male aedeagus.

There are some evolutionary inconsistencies in the phylogeny hypothesized in Figure 81. The small body size and finely granulate elytral surface would have to have evolved independently in *lacteola* and *soluta*, and the setose frons would have to have evolved independently in *granulata* and the ancestor of *soluta* and *gemmata*. The metallic green colour would have to have arisen independently in *longilabris* and *soluta* and cupreous colour in *longilabris* and *lacteola* but this is not unlikely, as green and cupreous colours appear in a number of distantly related species of *Cicindela*.

Any consideration of the time scale involved in evolution of the group is necessarily speculative due to the lack of a fossil record. Willis (1967) thought that the cicindelids arose during the Permian and that most of the cicindelid genera arose during the Mesozoic. Estimates of the age of insect species vary. Ross (1965) and Howden (1969) stated that many insect species evolved during the Pleistocene, and Matthews (1980) observed that more recent studies have found fossil remains of many extant species of Coleoptera in late Pliocene deposits. Freitag (1965) thought that the ancestral stock of the *maritima* group of the genus *Cicindela* was in existence in the early Tertiary and that living species may have evolved during the late Tertiary or early Pleistocene. The time scale of the evolution of the *sylvatica* group was probably similar. The *sylvatica* group probably arose in the Palearctic during the early to mid Tertiary. It is possible that the common ancestor of *longilabris*, *nebraskana*, *sylvatica* and *granulata* was a boreal form with a widespread holarctic distribution in the late Miocene or early Pliocene.

Matthews (1980) summarized the recent evidence that boreal forest was holarctic in distribution during the Miocene and that some land connection existed across Beringia until the Beringian Transgression of the Pliocene (approx. 3 ma). It is likely that the ancestor of *longilabris-nebraskana* and the ancestor of *sylvatica-granulata* were separated by approximately 3 ma, and that *longilabris* and *nebraskana* were separated in different refugia during glacial periods at the end of the Pliocene or early in the Pleistocene. It may have taken repeated periods of isolation during glacials and contact and hybridization during interglacials before the two were specifically separate.

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Figs. 1 - 3. Characters of the adult head.

Fig. 1. Head, frontal aspect: hw, head width; ll, labrum length; lw, labrum width.

Fig. 2. Labrum, frontal aspect: ls1, setae at position one; ls2, setae at position two; ls3, setae at position three; ls4, setae at position four.

Fig. 3. Left Antenna, frontal aspect: the scape, sensory setae (ss), other setae (os).

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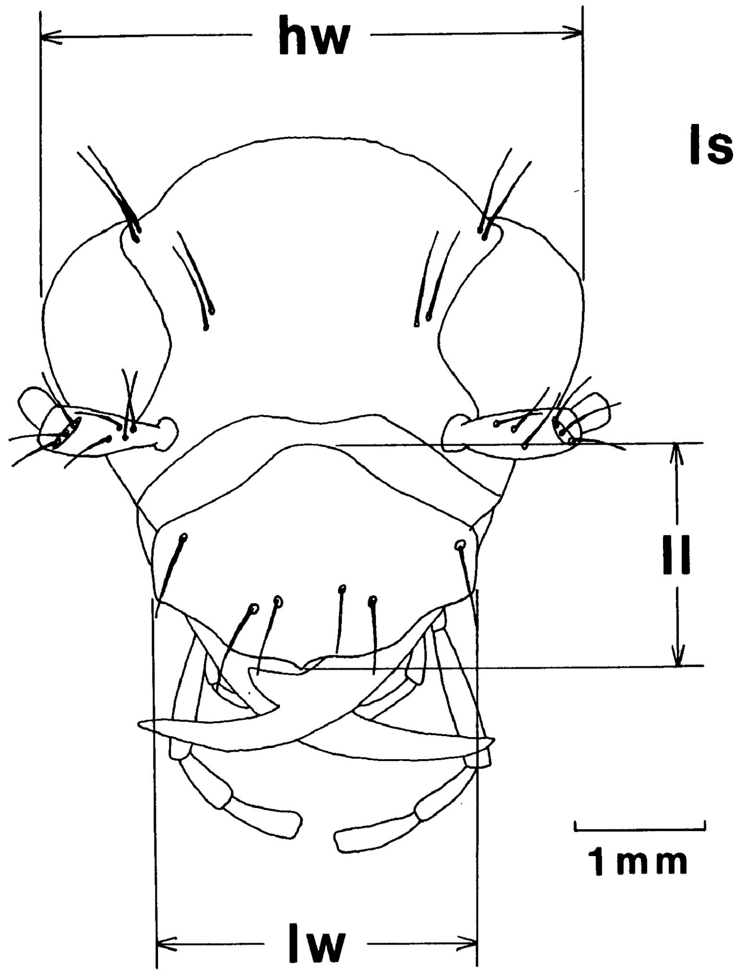

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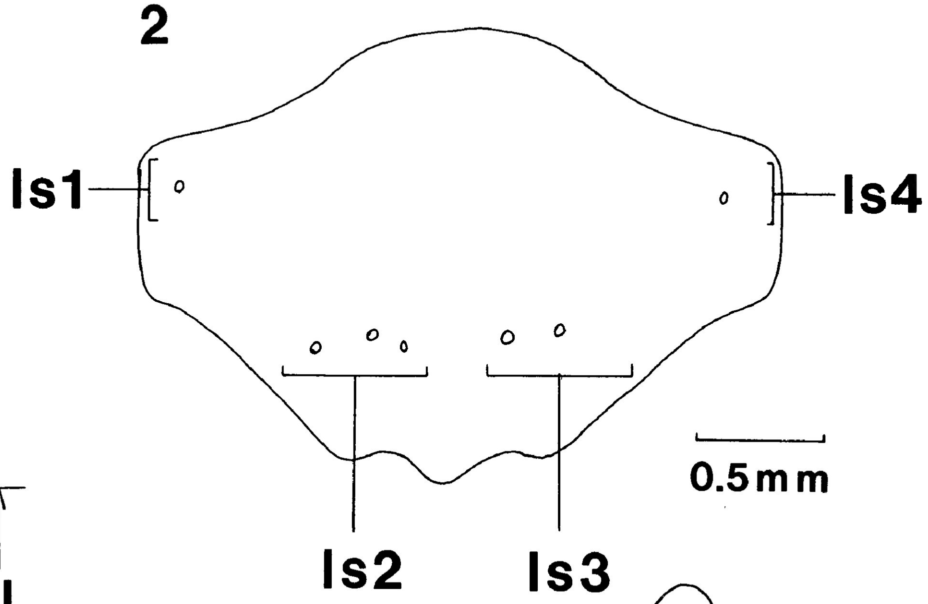

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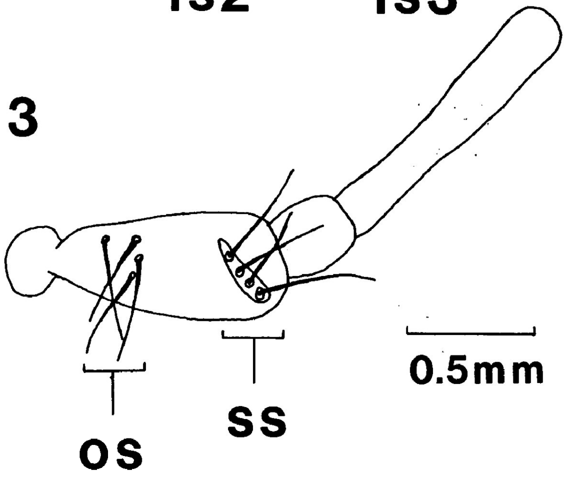
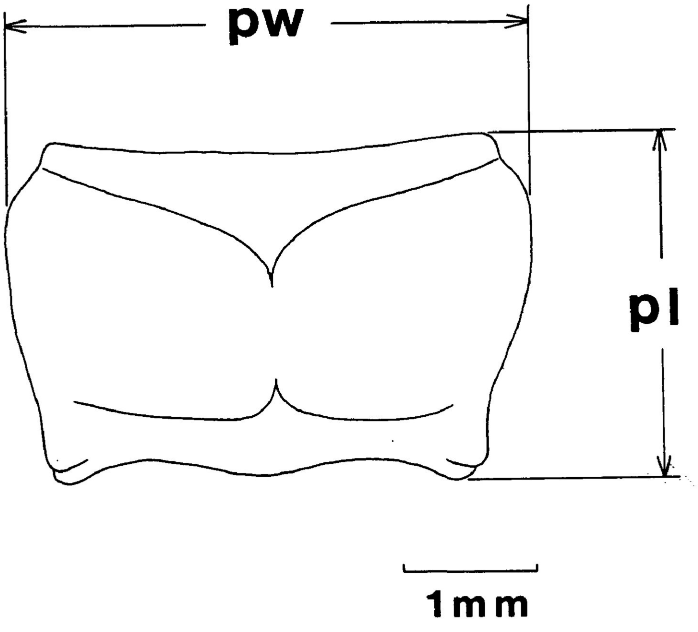


Fig. 4. Adult prothorax, dorsal aspect: pw, pronotal width; pl, pronotal length.

Fig. 5. Mesothoracic leg, lateral aspect: fl, femur length; tl, tibial length.

4



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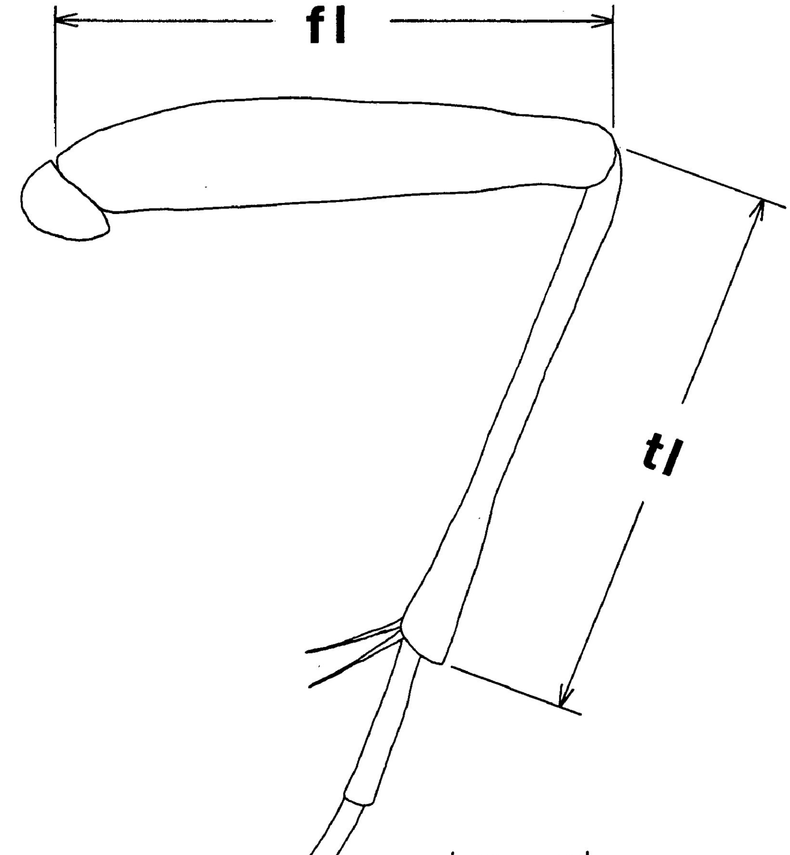

Fig. 6. Adult elytra, dorsal aspect: el, elytral length; ew, elytral width; hl, humeral lunule; mb, middle band; ml, marginal line; al, apical lunule.

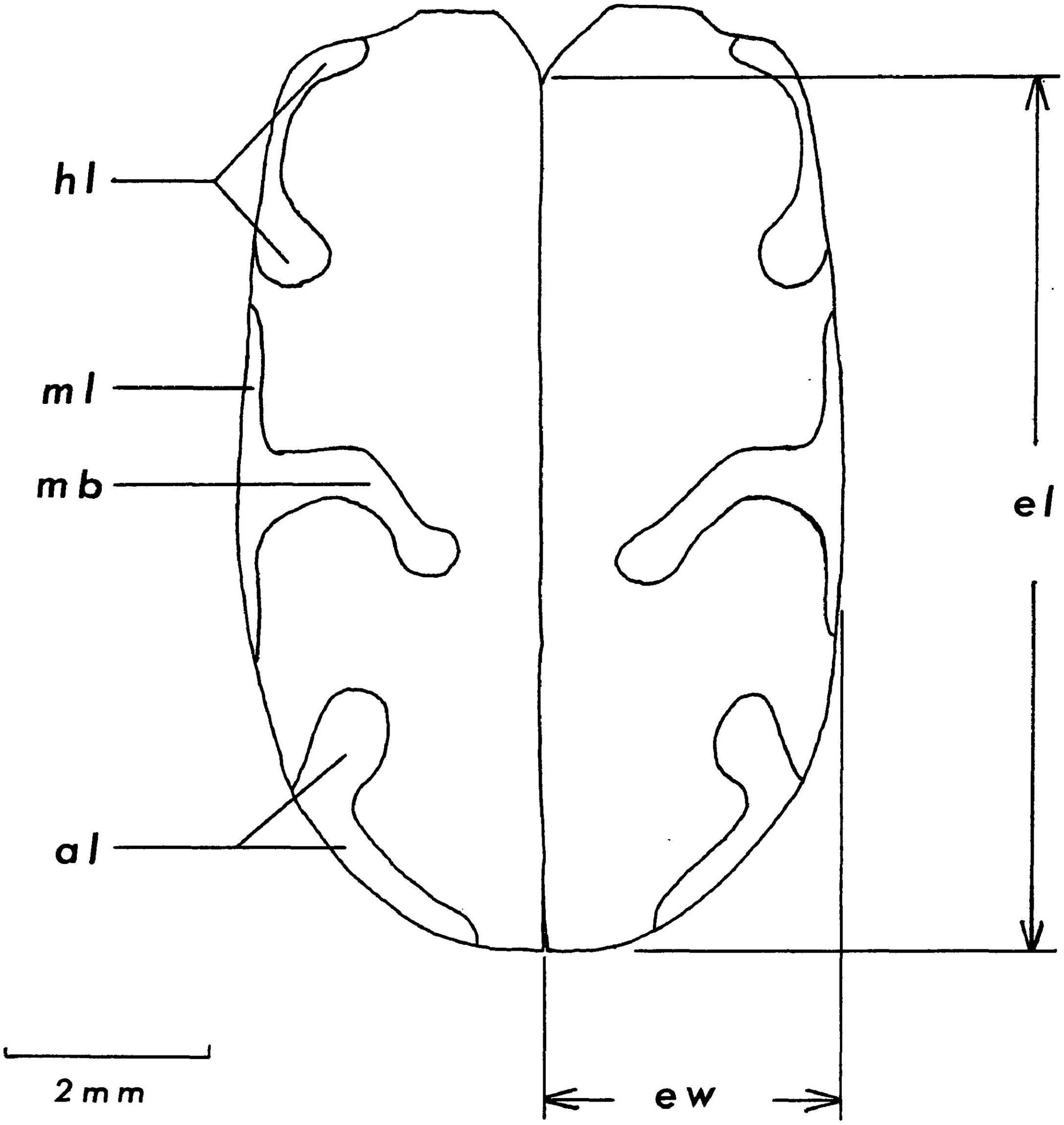
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Fig. 7. Per cent of elytral surface covered by maculations (pale portions).

A	1 per cent
B	2 per cent
C	5 per cent
D	10 per cent
E	20 per cent
F	30 per cent

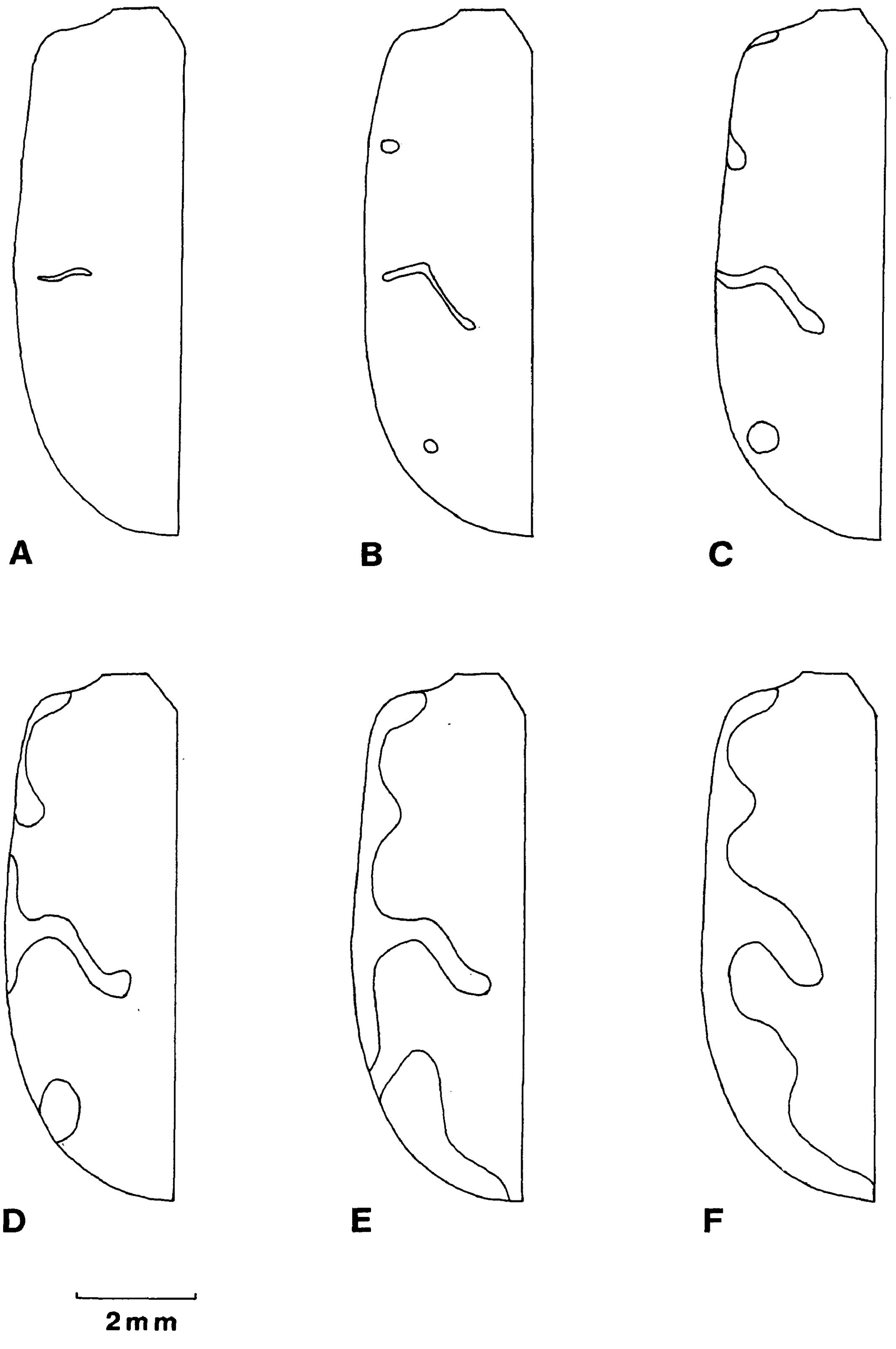
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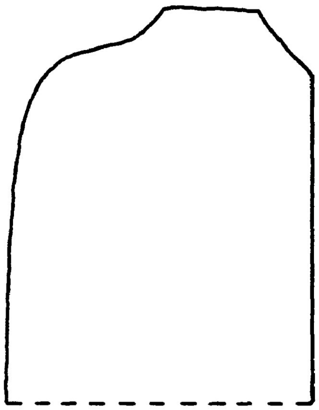
Fig. 8. Humeral lunule character states. The number at the bottom left of each drawing indicates arbitrarily assigned values.



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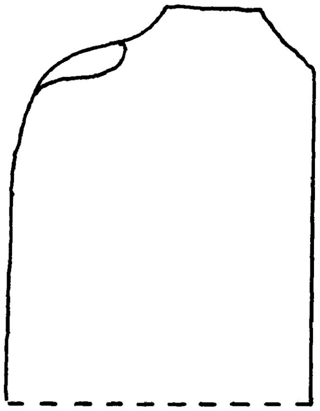

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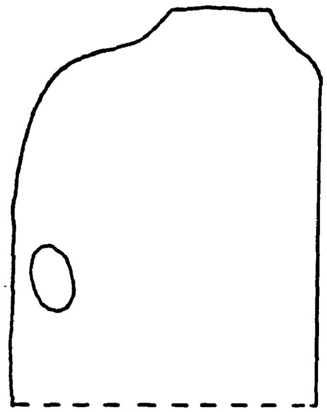

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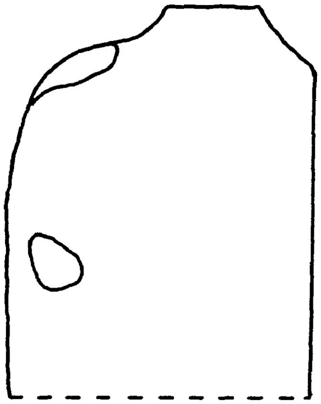

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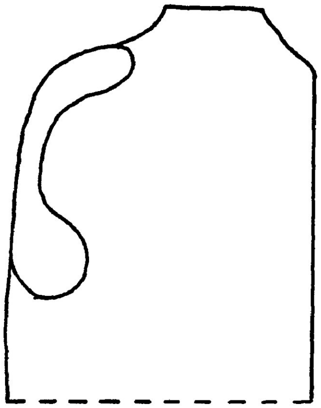

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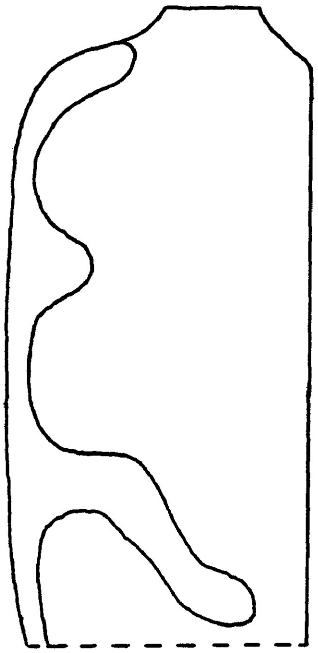

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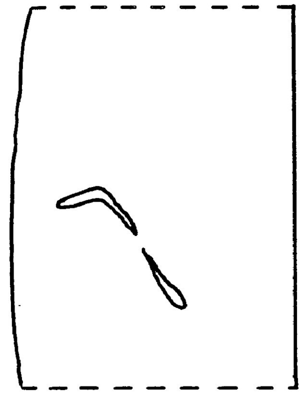
Fig. 9. Middle band character states. The number at the lower left corner of each drawing indicates arbitrarily assigned values. A zero was assigned if the middle band was completely absent.



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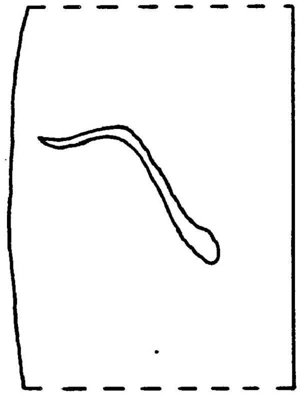

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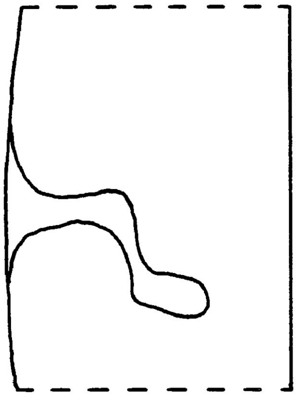

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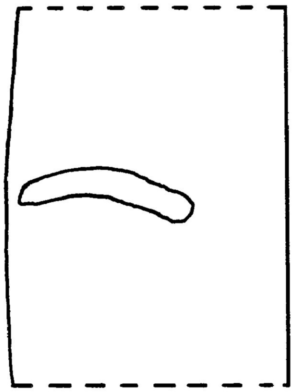

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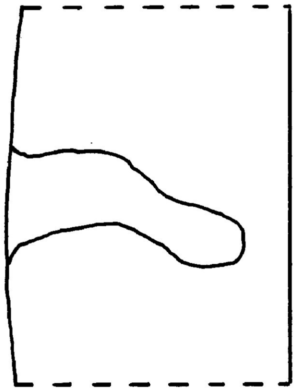

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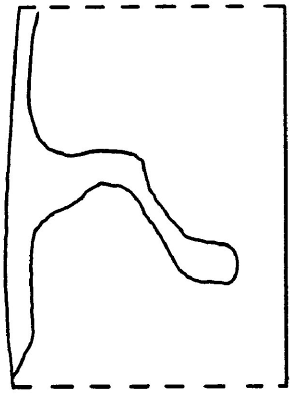

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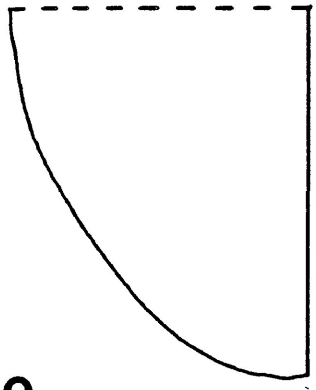
Fig. 10. Apical lunule character states. The number to the lower left of each drawing indicates an arbitrarily assigned value.



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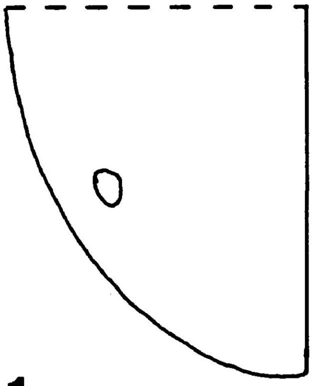

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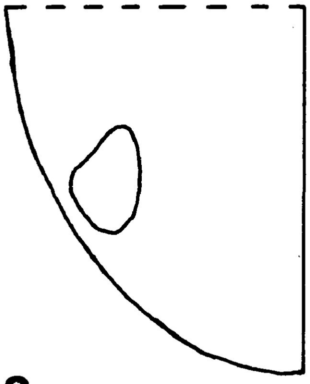

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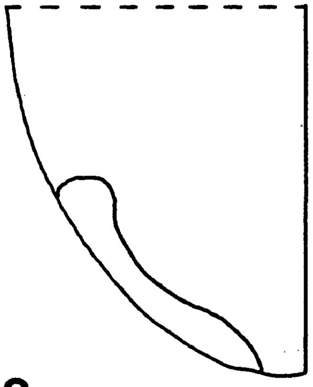

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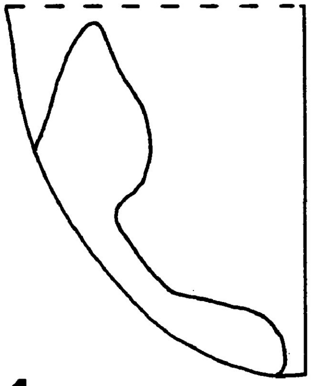

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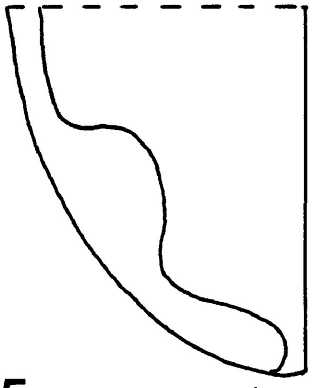

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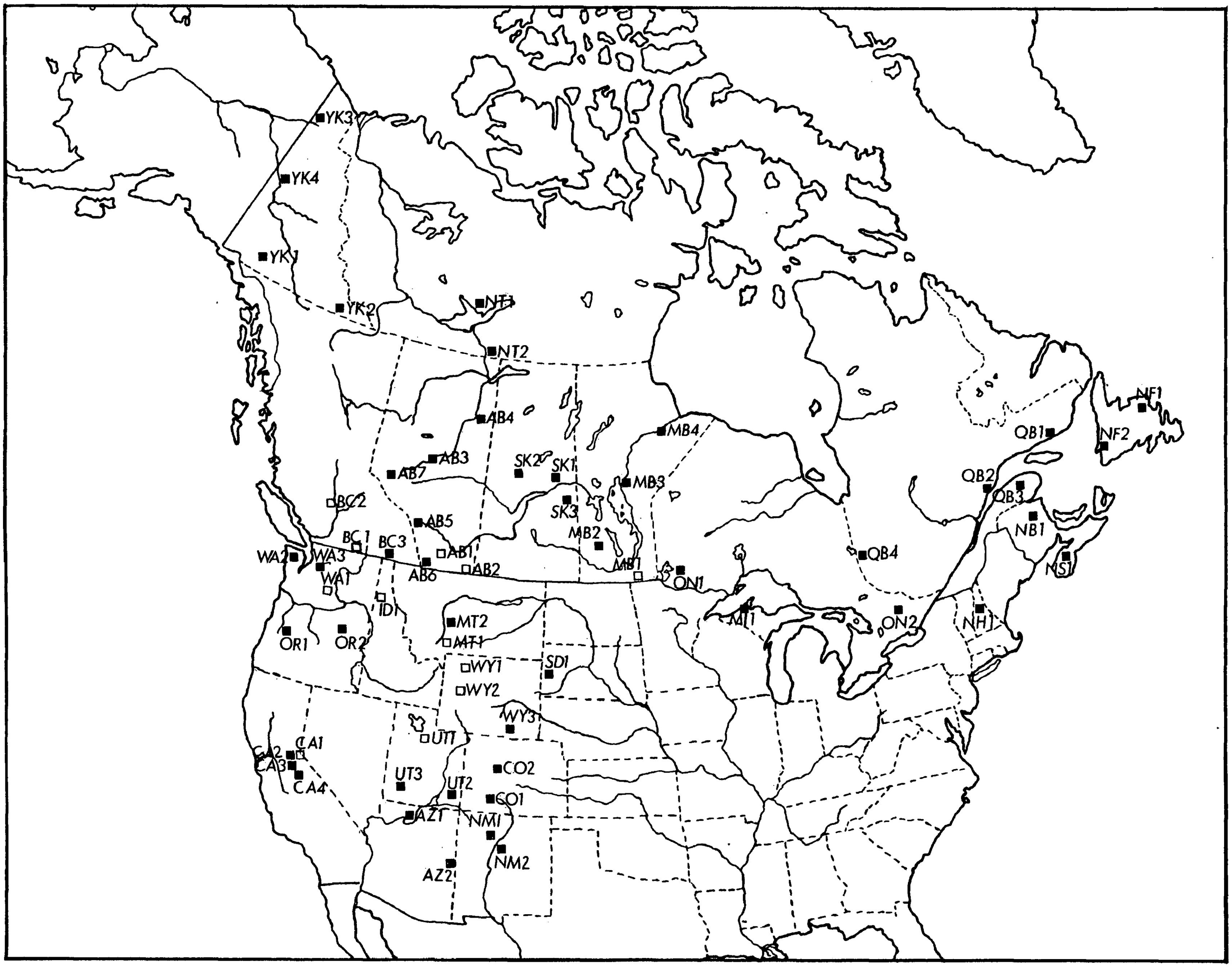
Fig. 11. Population samples used in numerical and colour analysis (Table 4).

■ *Cicindela longilabris* Say

□ *Cicindela nebraskana* Casey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AZ2

Fig. 12. Relative frequency of colour states of the female labrum in population samples of *C. longilabris* Say: white indicates a light coloured labrum; horizontal lines, labrum partly darkened or intermediate in colour; black, labrum black, or nearly so. Population samples are indicated in Table 4 and Figure 11. The four studied Yukon population samples were lumped for this purpose.

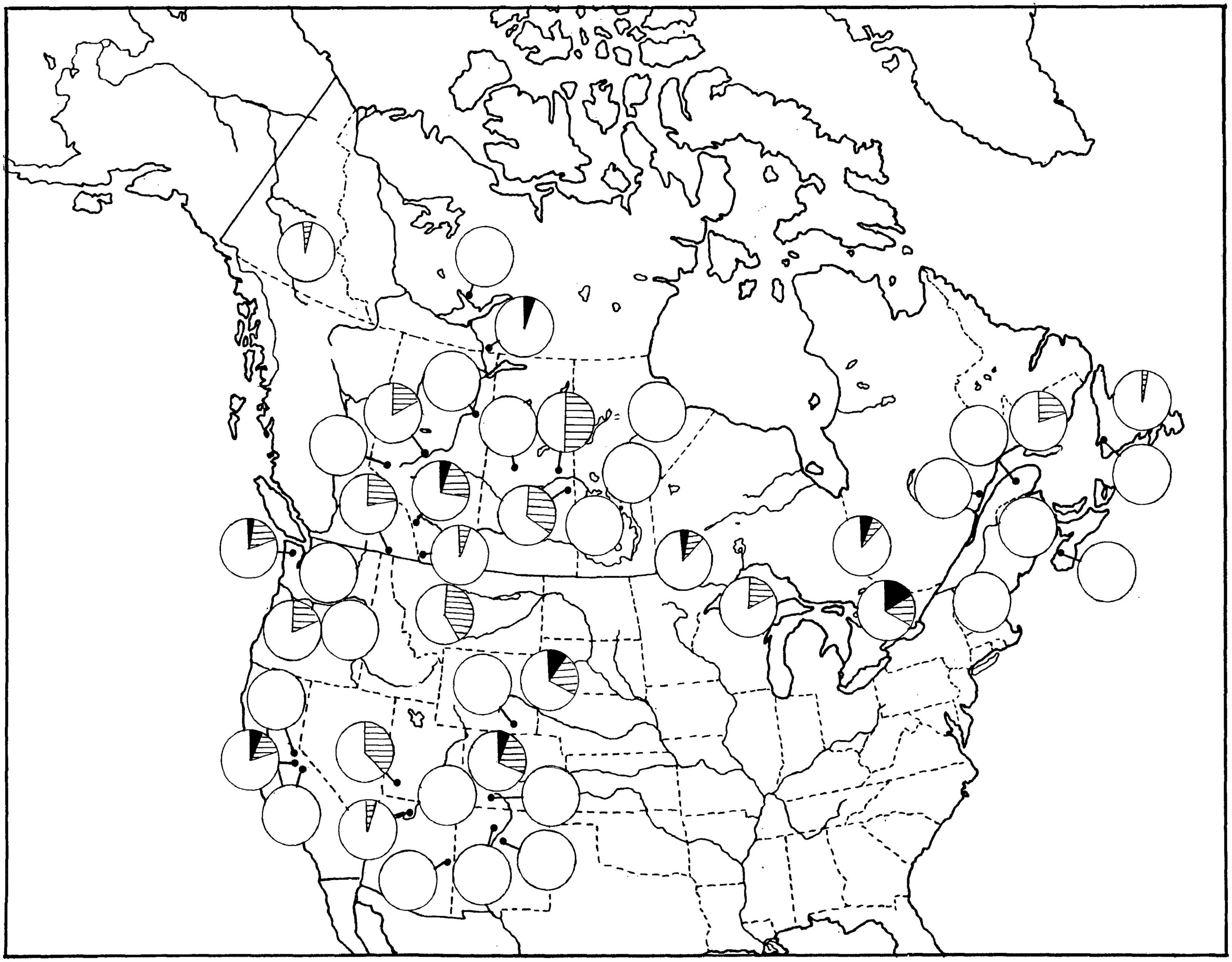


Fig. 13. Relative frequency of colour states of the female labrum in population samples of *C. nebraskana* Casey: white indicates light coloured labrum; horizontal lines, intermediate colour or mottled; black, black or nearly so. Population samples are indicated in Table 4 and Figure 11.

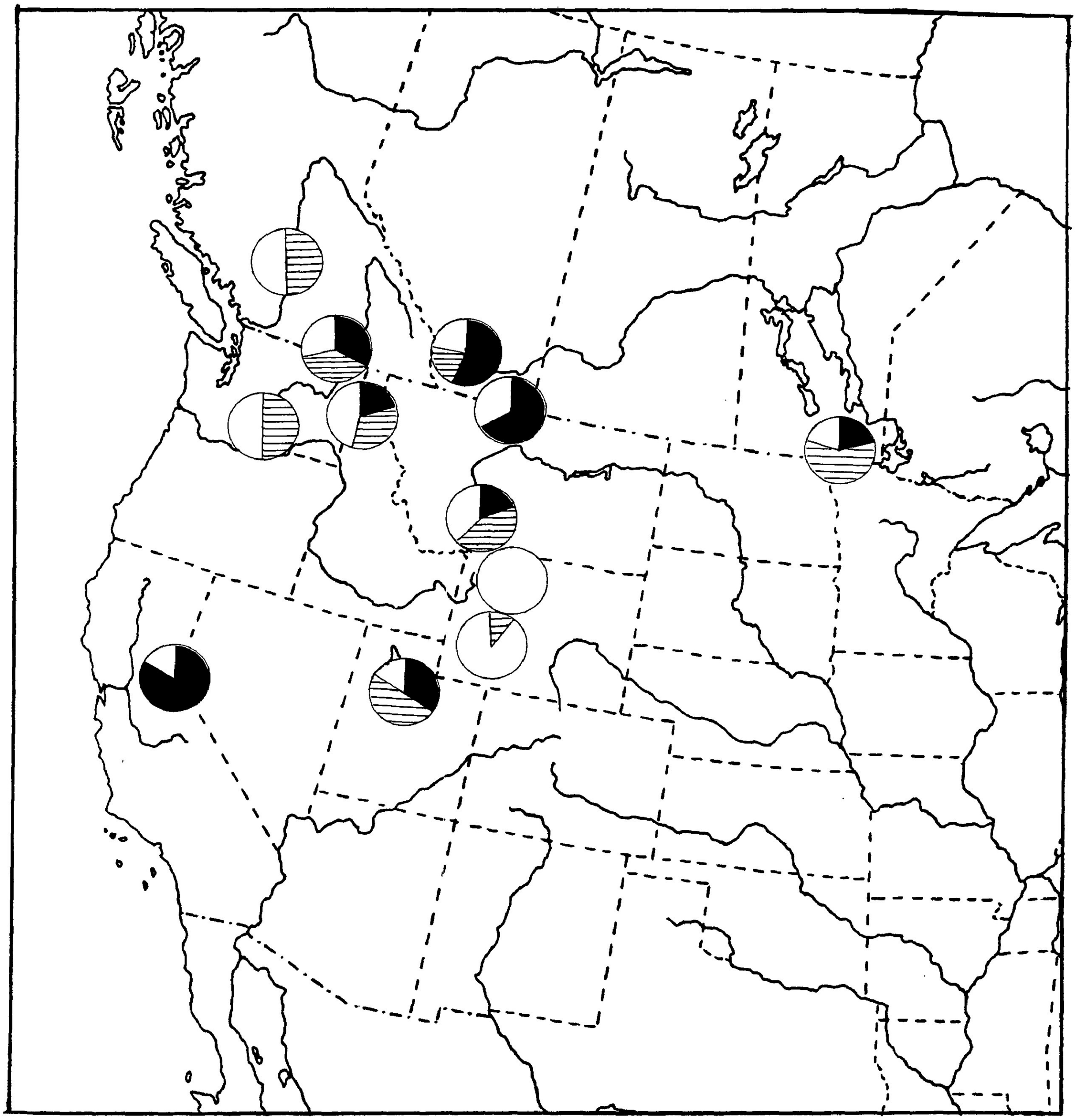


Fig. 14. Relative frequency of colour states of the proepisternum in population samples of *C. longilabris* Say. Colour states are described in Table 2. Population samples are indicated in Table 4 and Figure 11. The four studied Yukon population samples are lumped together.

white	1	black proepisternum
light stipling	2	black and green
heavy stipling	3	metallic green
horizontal lines	4	green and blue
radial lines	5	blue/purple
diagonal cross-hatching	6	bronze/green or bronze/purple
black	7	bronze and/or brown

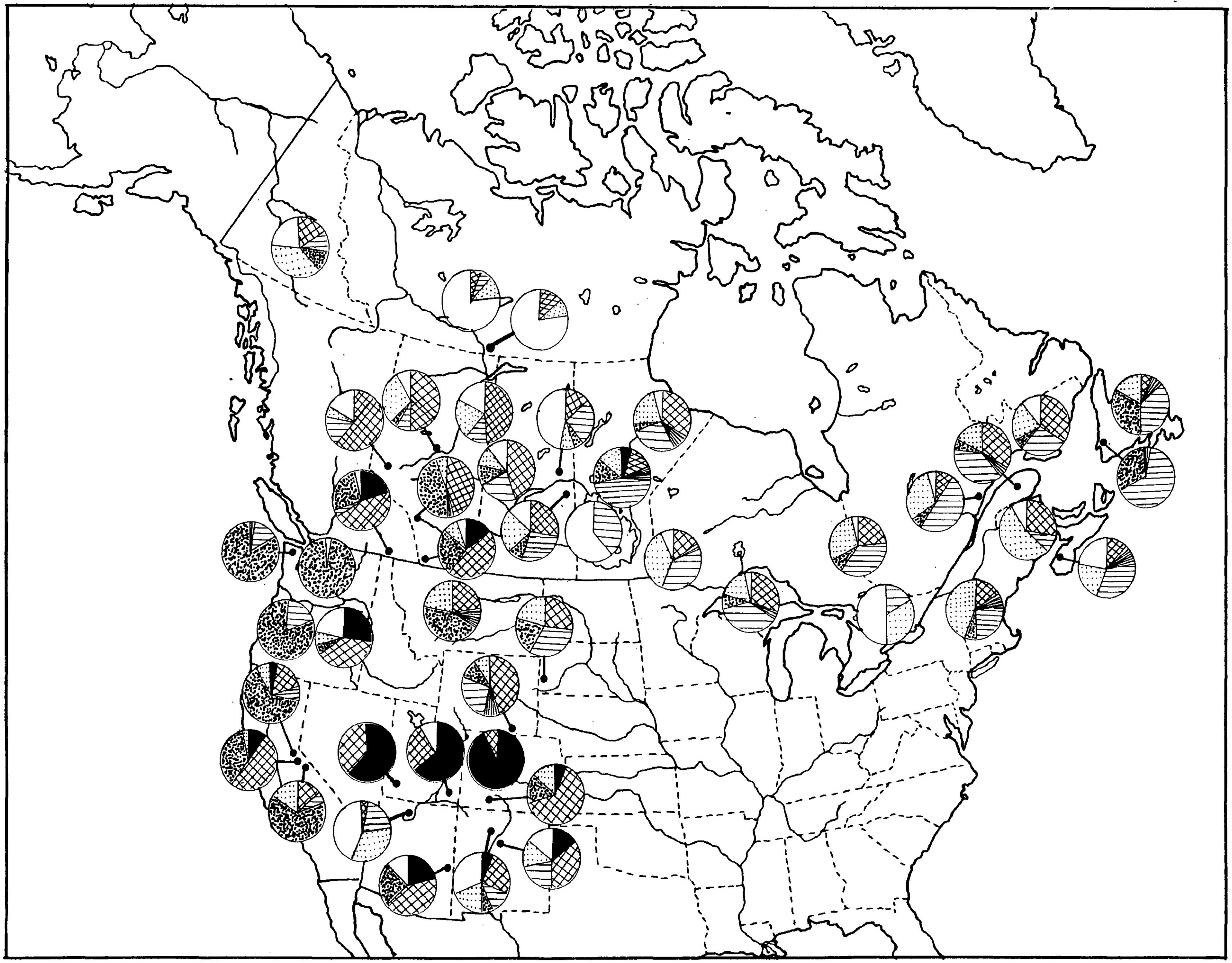


Fig. 15. Relative frequency of colour states of the proepisternum in population samples of *C. nebraskana* Casey. Colour states are described in Table 2. Population samples are indicated in Table 4 and Figure 11.

white	1	black
light stipling	2	black and green
heavy stipling	3	metallic green
horizontal lines	4	green and blue
radial lines	5	blue/purple
diagonal cross-hatching	6	bronze/green or bronze/blue
black	7	bronze and/or brown

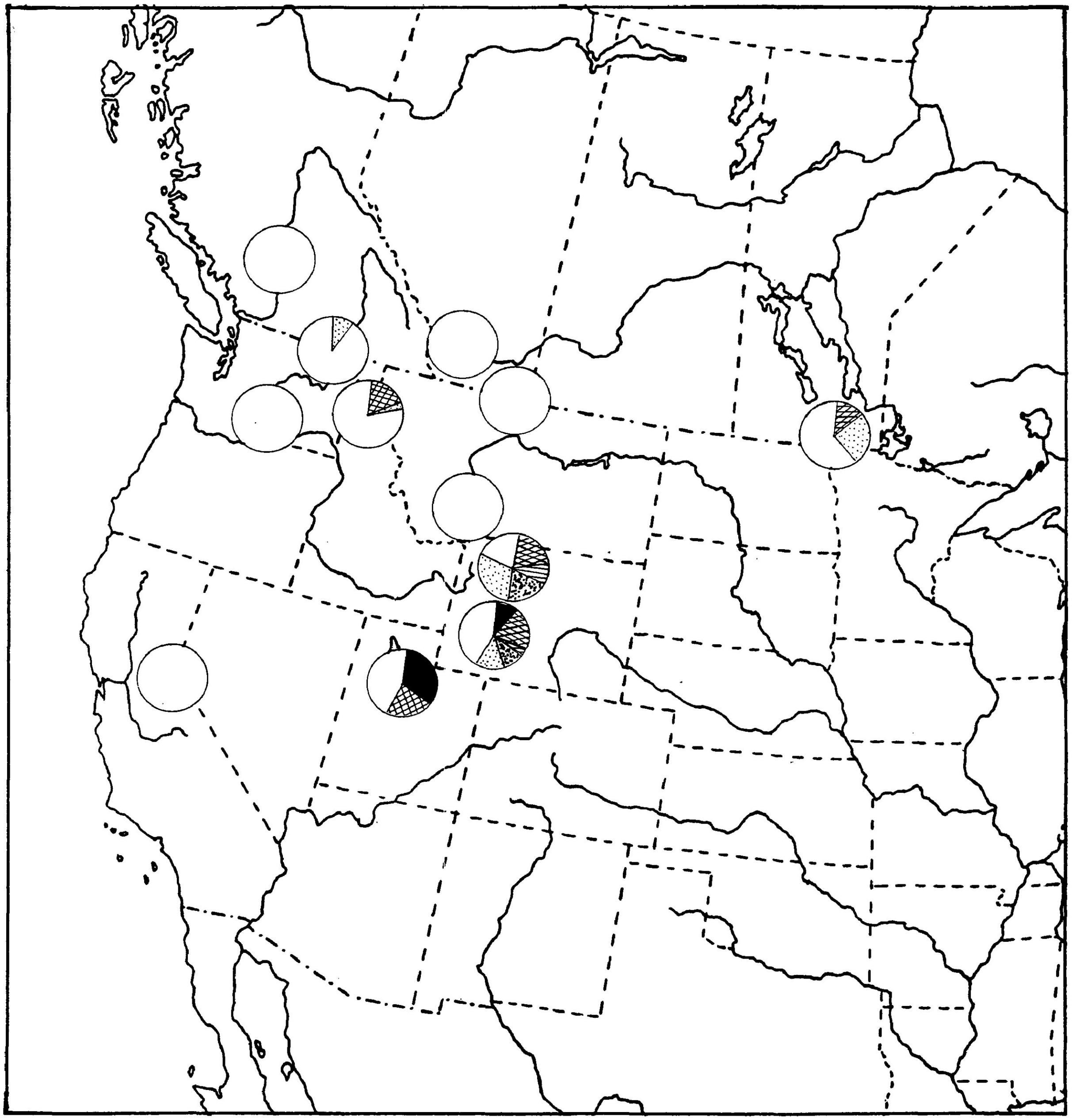


Fig. 16. Relative frequency of colour states of the abdomen in population samples of *C. longilabris* Say. Colour states are described in Table 3. Population samples are indicated in Table 4 and Figure 11, The 4 studied Yukon population samples are lumped together.

white	1	black
light stippling	2	black and green
heavy stipling	3	metallic green
horizontal lines	4	green and blue
radial lines	5	blue/purple
diagonal cross-hatching	6	bronze/green or bronze/blue
black	7	bronze and/or brown

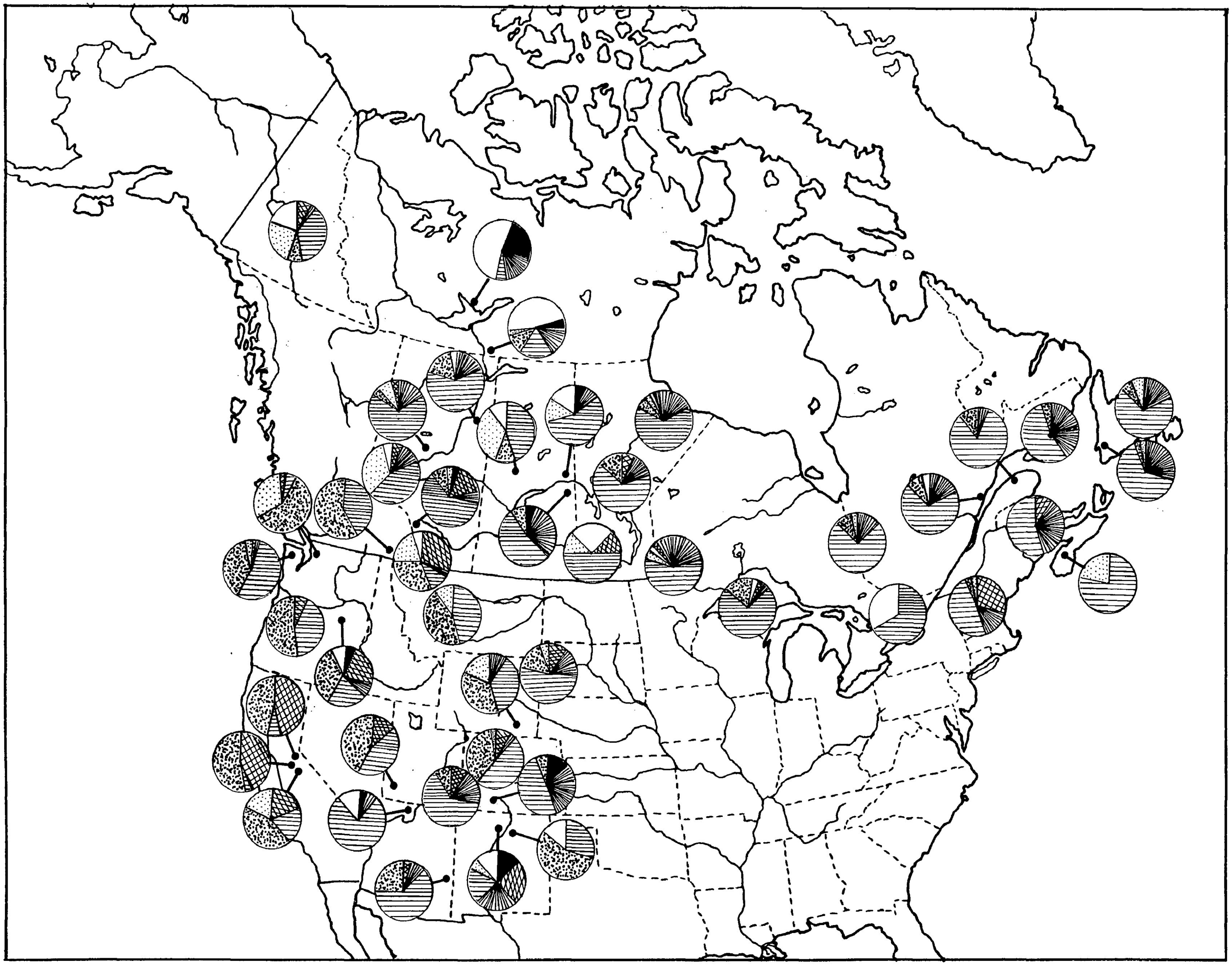


Fig. 17. Relative frequency of colour states of the abdomen in population samples of *C. nebraskana* Casey. Colour states are described in Table 3. Population samples are indicated in Table 4 and Figure 11.

white	1	black
light stipling	2	black and green
heavy stipling	3	metallic green
horizontal lines	4	green and blue
radial lines	5	blue/purple
diagonal cross-hatching	6	bronze/green or bronze/blue
black	7	bronze and/or brown

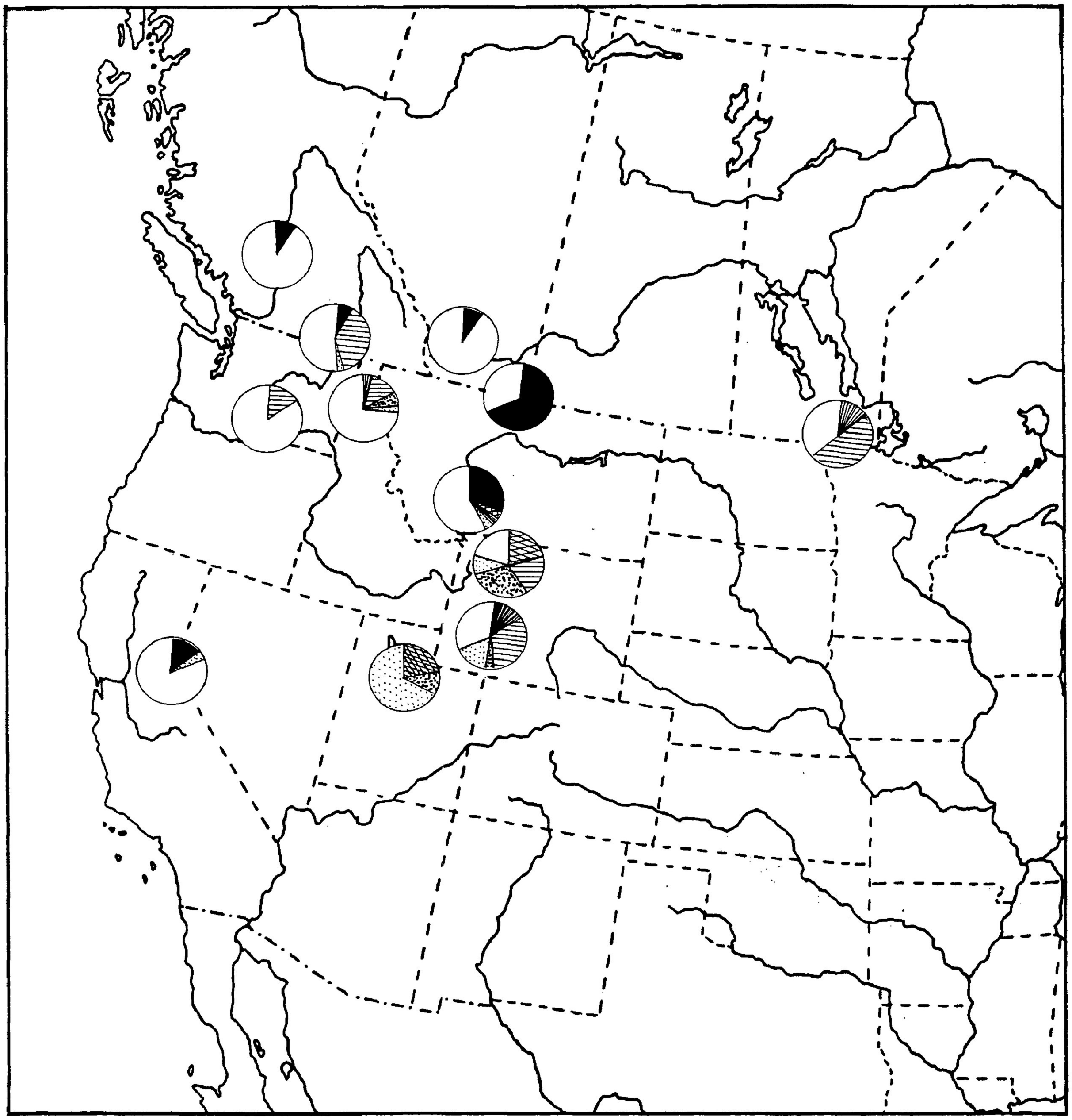


Fig. 18. Relative frequency of colour states of the elytra in population samples of *C. longilabris* Say. Colour states are described in Table 1. Population samples are indicated in Table 4 and Figure 11, The 4 studied Yukon population samples are lumped together.

white	1	black
stipled	2	dark brown
tangential lines	3	mid brown to bronze
radial lines	4	olive green
black	5	green

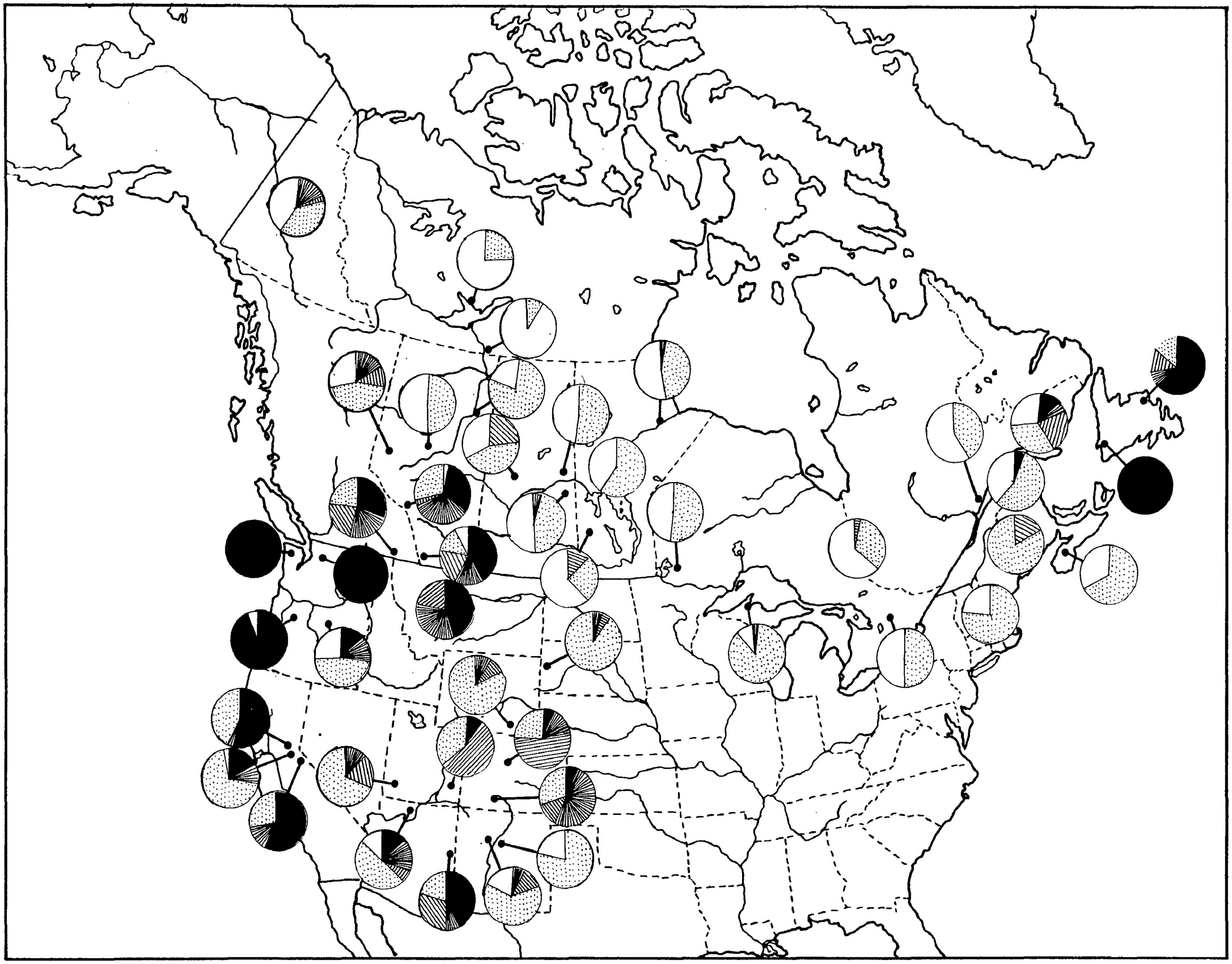


Fig. 19. Relative frequency of colour states of the elytra in population samples of *C. nebraskana* Casey.
Colour states are described in Table 1.
Population samples are indicated in Table 4 and Figure 11.

white	1	black
stipled	2	dark brown
tangential lines	3	mid brown to bronze
radial lines	4	olive green
black	5	green

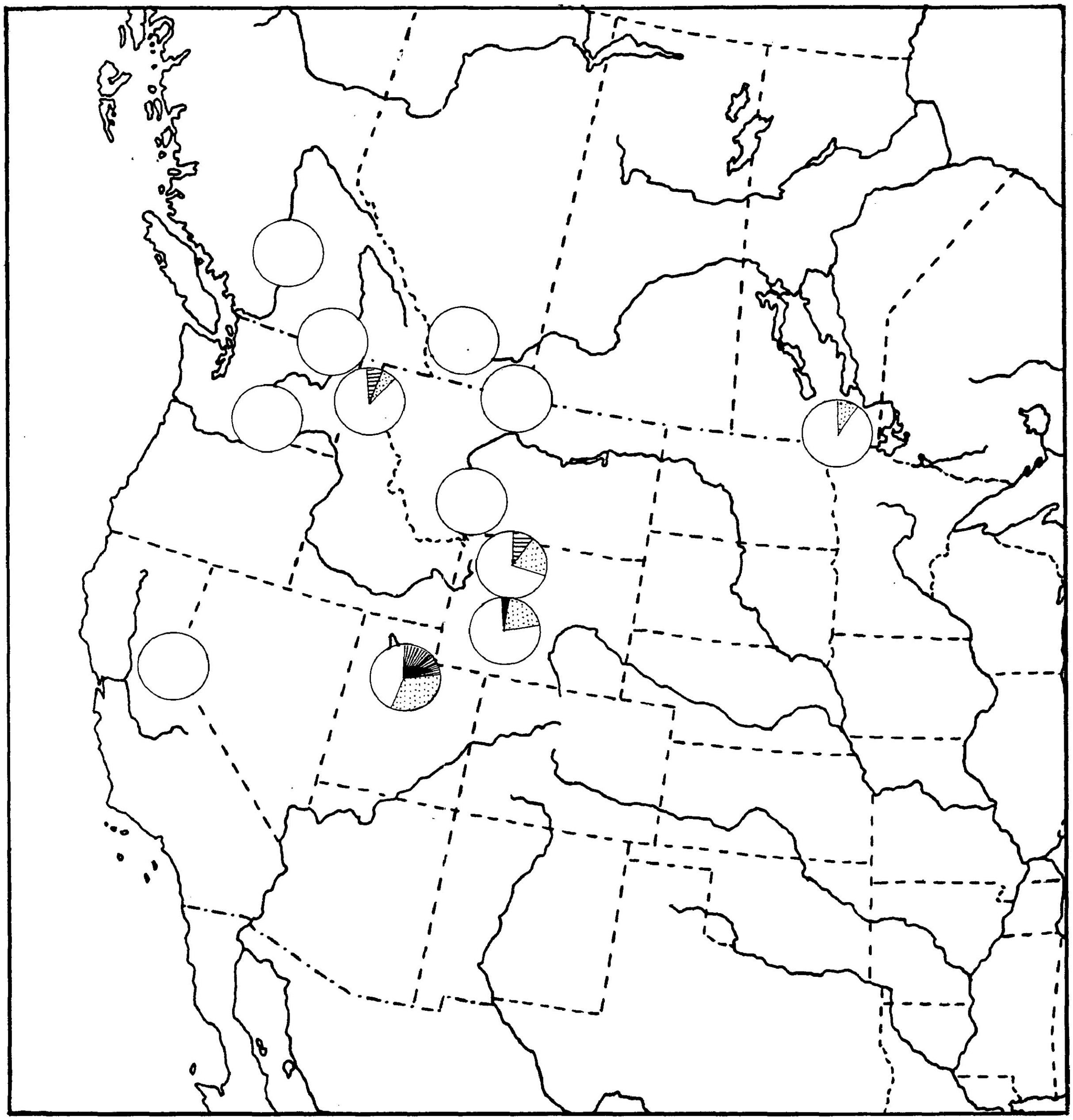


Fig. 20. Weighted mean percentage of surface area of elytra covered with maculations for population samples of *C. longilabris* Say. Data are summarized in Table 38. Population samples are indicated in Table 4 and Figure 11. The 4 studied Yukon population samples are lumped together.

□	0 - 0.99
⊞	1.0 - 4.99
◰	5.0 - 8.99
⬒	9.0 - 12.99
▜	13.0 - 16.99
■	17.0 - 20.99

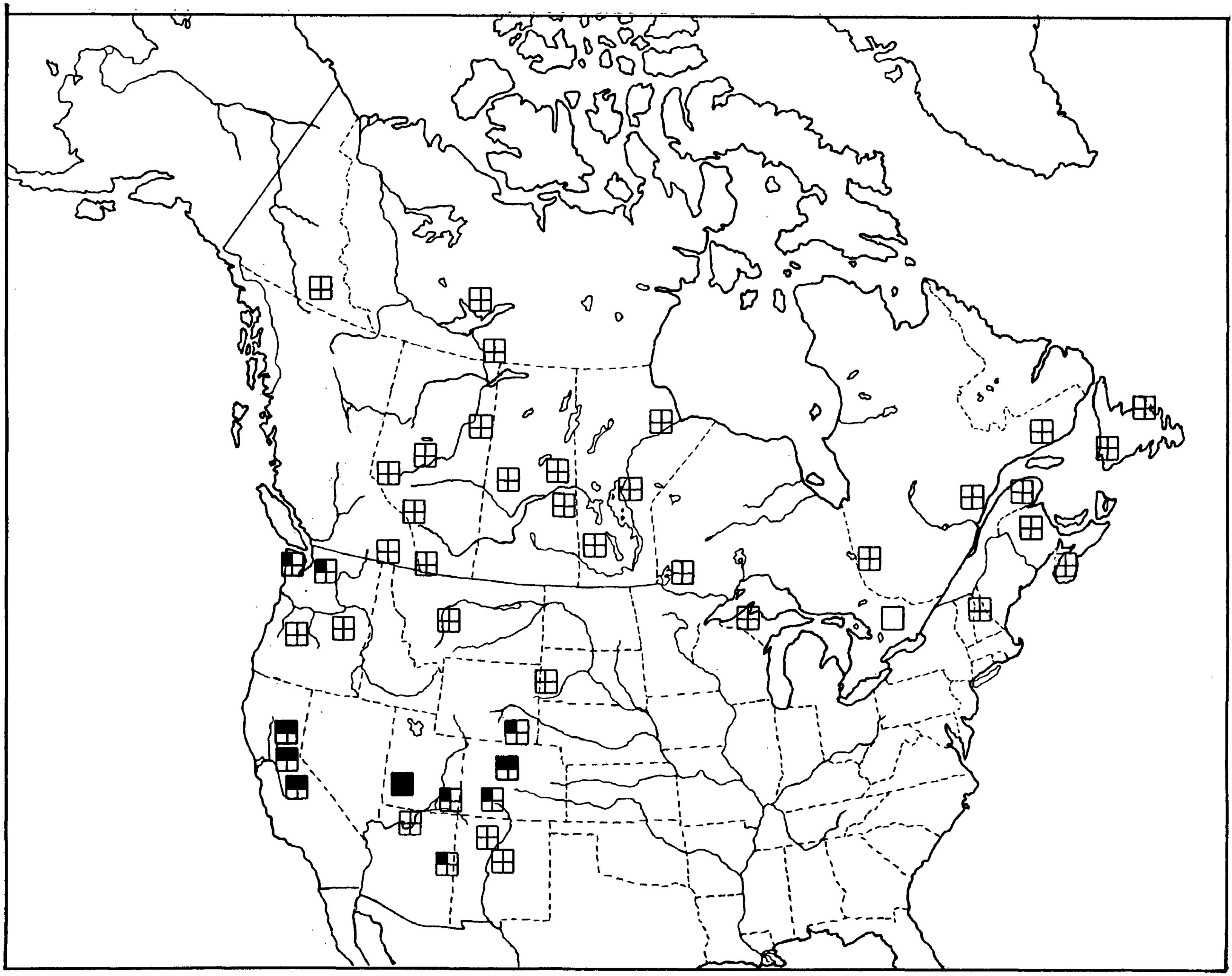


Fig. 21. Weighted mean percentage of surface area of elytra covered with maculation for population samples of *C. nebraskana* Casey. Data are summarized in Table 38. Population samples are indicated in Table 4 and Figure 11.

□	0 - 0.99
⊞	1.0 - 4.99
◰	5.0 - 8.99
⬒	9.0 - 12.99
▜	13.0 - 16.99
■	17.0 - 20.99

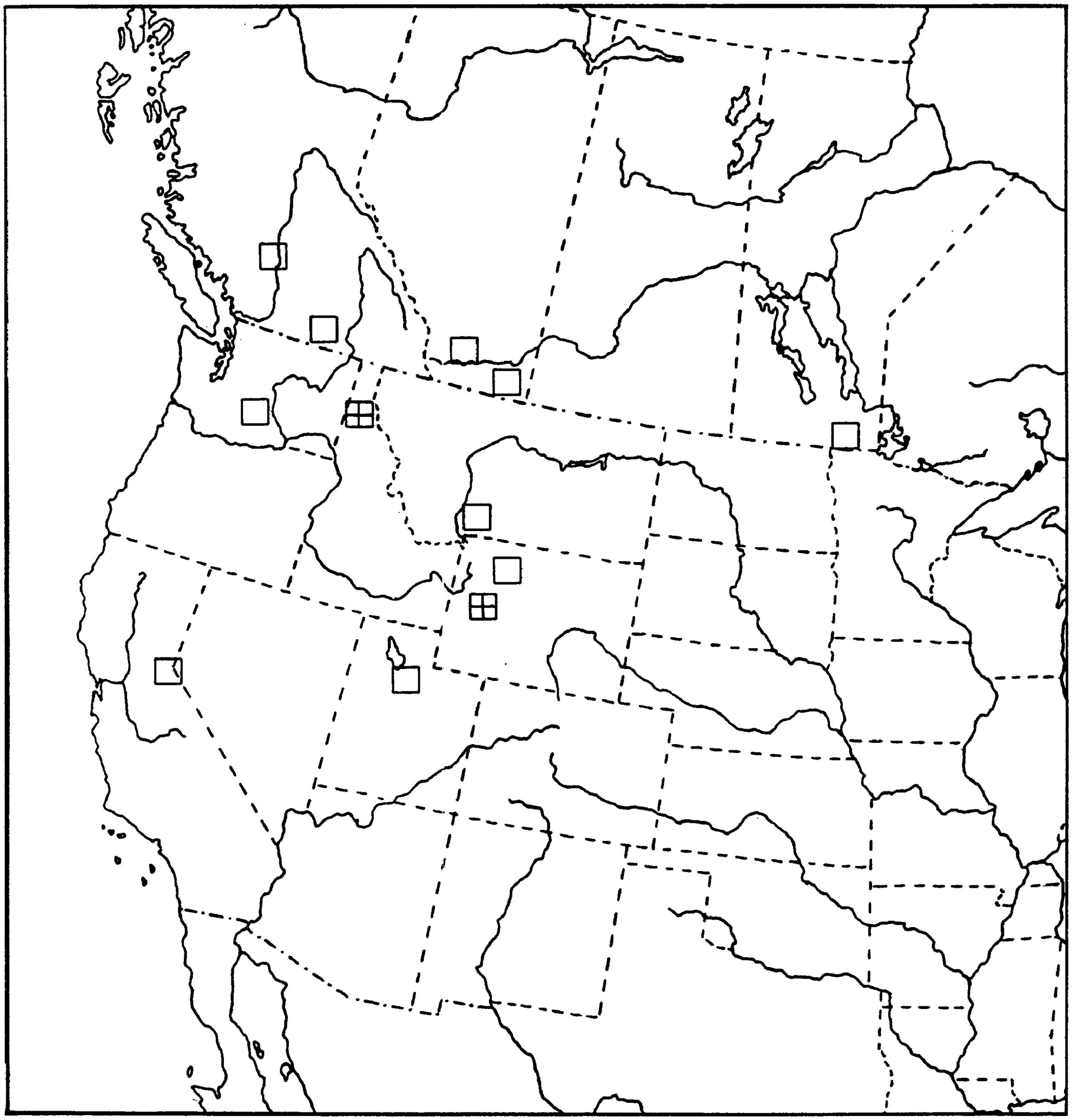


Fig. 22. Weighted mean character value of the humeral lunule (Fig. 8) of population samples of *C. longilabris* Say. Data are summarized in Table 38. Population samples are indicated in Table 4 and Figure 11. The 4 studied Yukon population samples were lumped together.

□	0.0 - 0.99
◳	1.0 - 1.99
⬒	2.0 - 2.99
◪	3.0 - 3.99
■	4.0 - 5.0

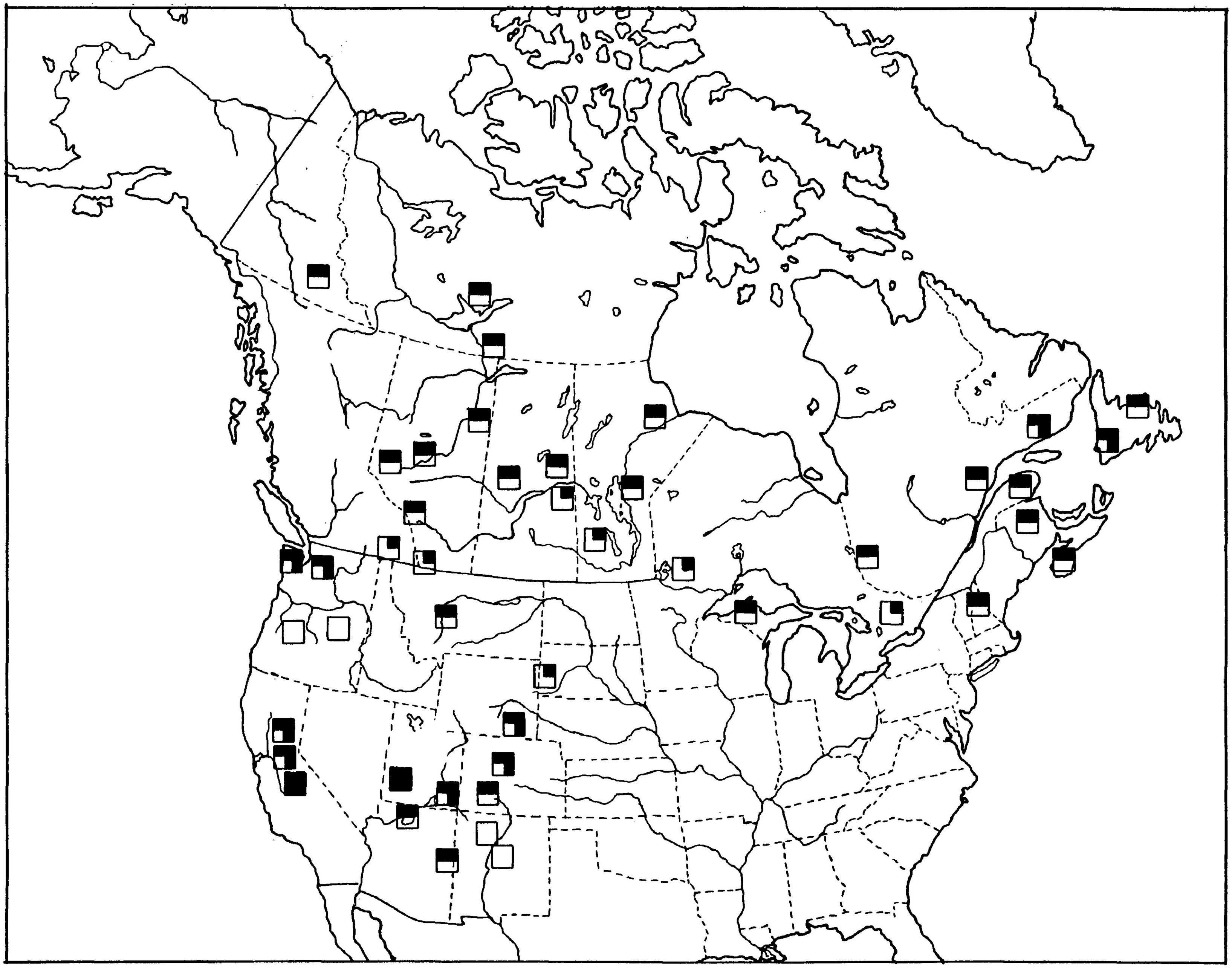


Fig. 23. Weighted mean character values of the humeral lunule (Fig. 8), for population samples of *C. nebraskana* Casey. Data are summarized in Table 38. Population samples are indicated in Table 4 and Figure 11.

□	0.0 - 0.99
◳	1.0 - 1.99
⬒	2.0 - 2.99
▜	3.0 - 3.99
■	4.0 - 4.99

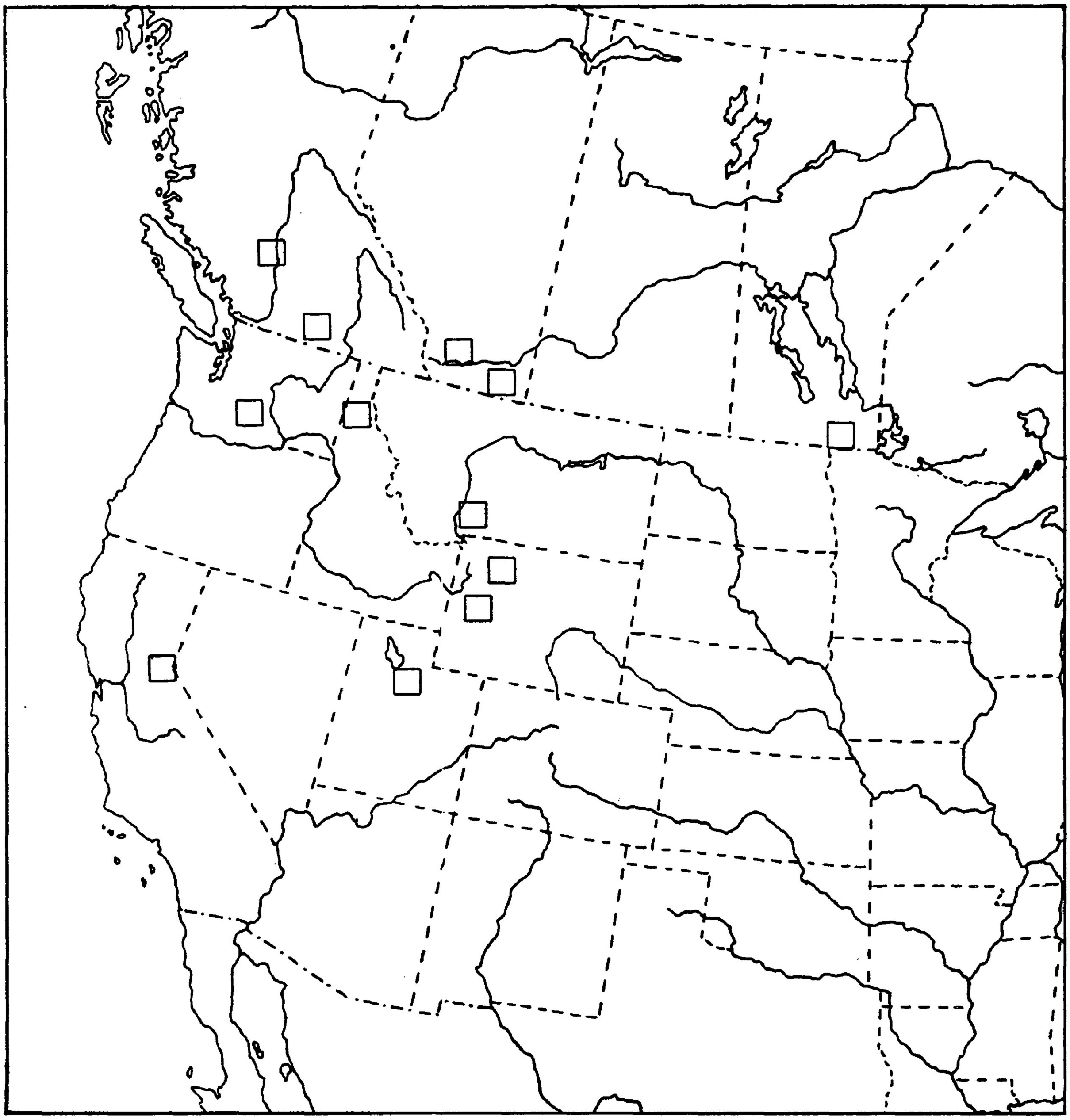


Fig. 24. Weighted mean character values of the middle band (Fig. 9) for population samples of *C. longilabris* Say. Data are summarized in Table 38. Population samples are indicated in Table 4 and Figure 11. The 4 studied Yukon population samples are lumped together.

□	0.0 - 0.99
⊞	1.0 - 1.99
▘	2.0 - 2.99
▀	3.0 - 3.99
▜	4.0 - 4.99
■	5.0 - 6.0

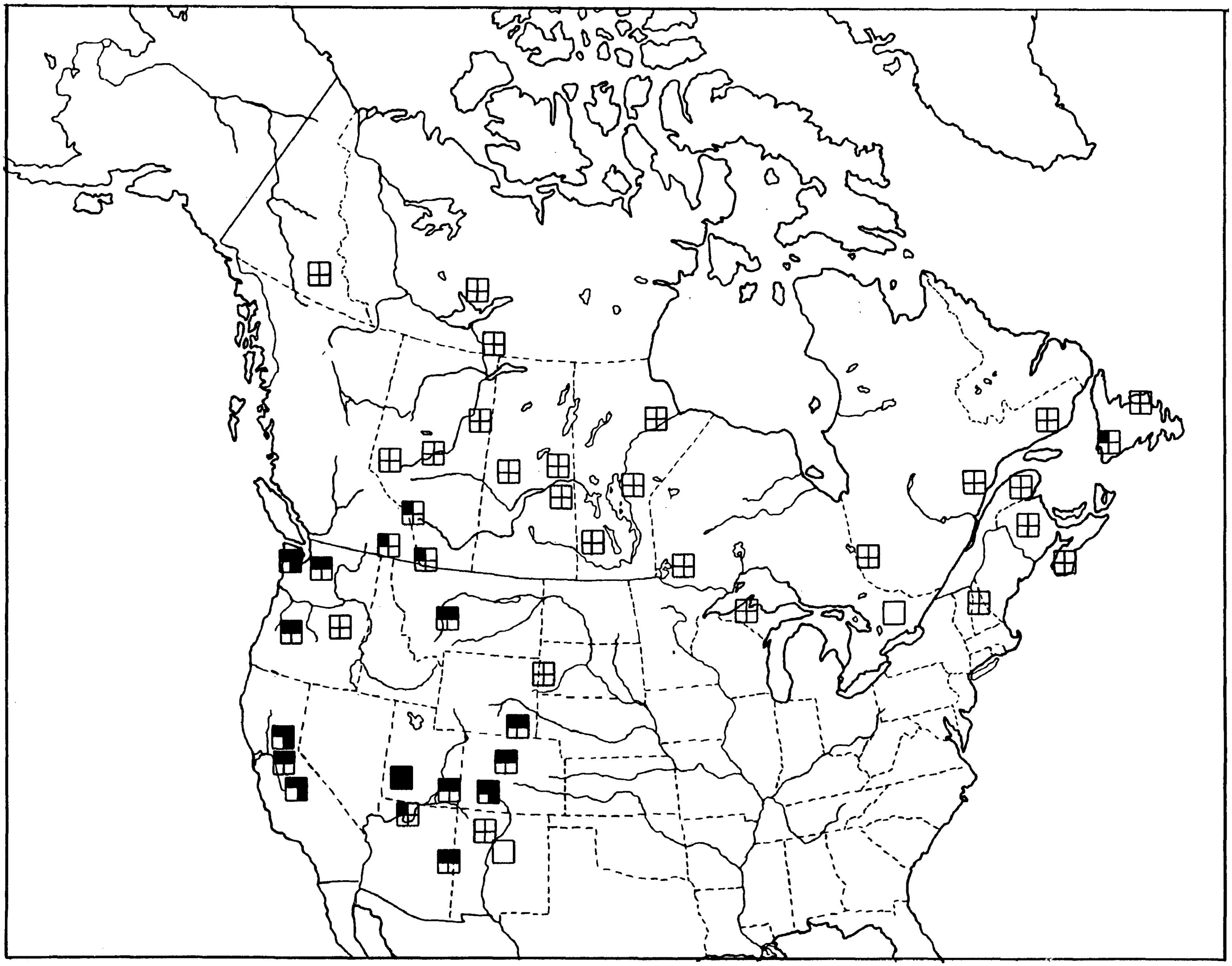


Fig. 25. Weighted mean character values for the middle band (Fig. 9), for population samples of *C. nebraskana* Casey. Data are summarized in Table 38. Population samples are indicated in Table 4 and Figure 11.

□	0.0 - 0.99
⊞	1.0 - 1.99
◰	2.0 - 2.99
⬒	3.0 - 3.99
▣	4.0 - 4.99
■	5.0 - 6.0

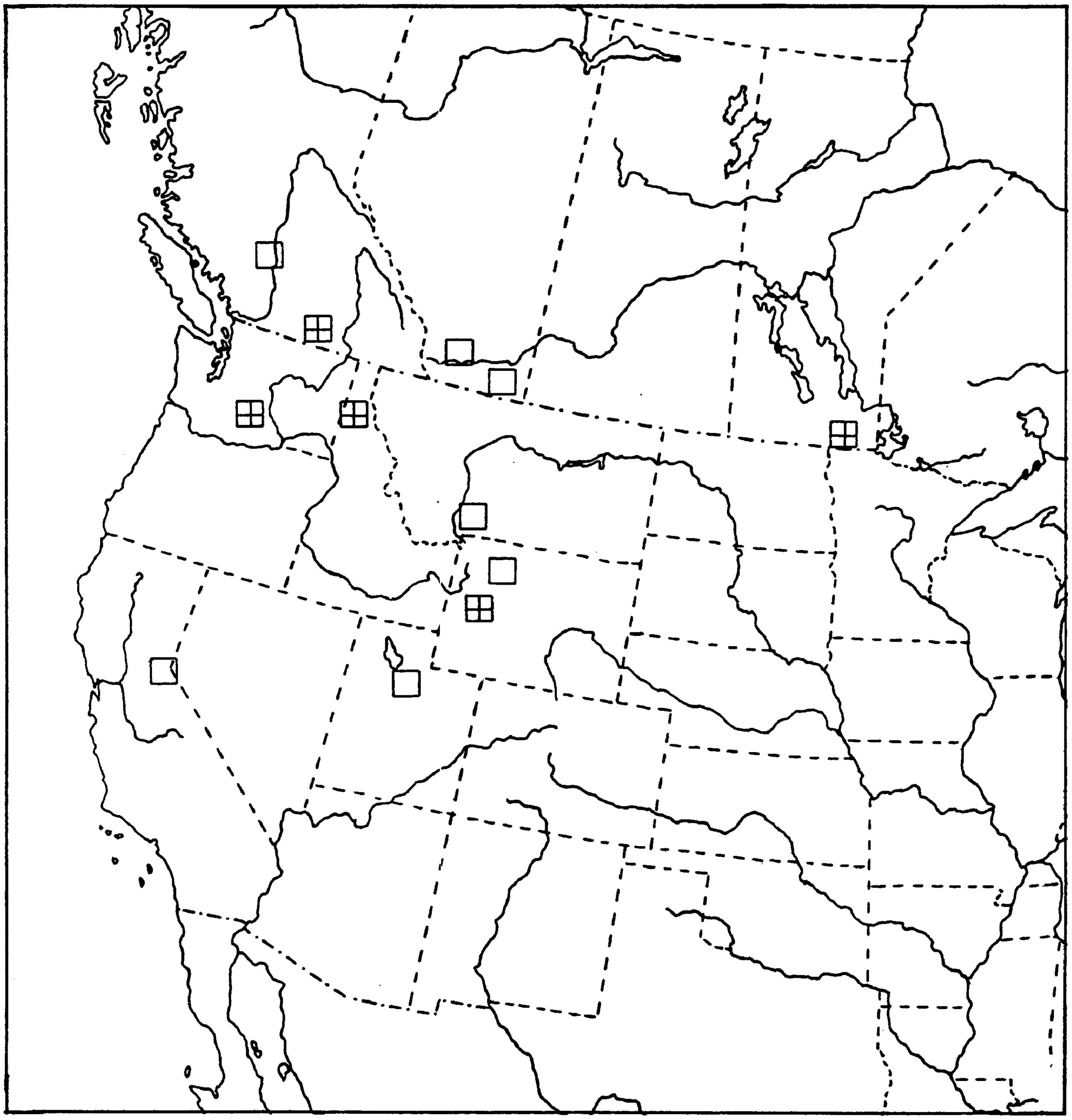


Fig. 26. Weighted mean character values of the apical lunule (Fig. 10) for population samples of *C. longilabris* Say. Data are summarized in Table 38. Population samples are indicated in Table 4 and Figure 11. The 4 studied Yukon population samples were lumped together.

□	0.00 - 0.99
◰	1.0 - 1.99
⬒	2.0 - 2.99
◘	3.0 - 3.99
■	4.0 - 4.99

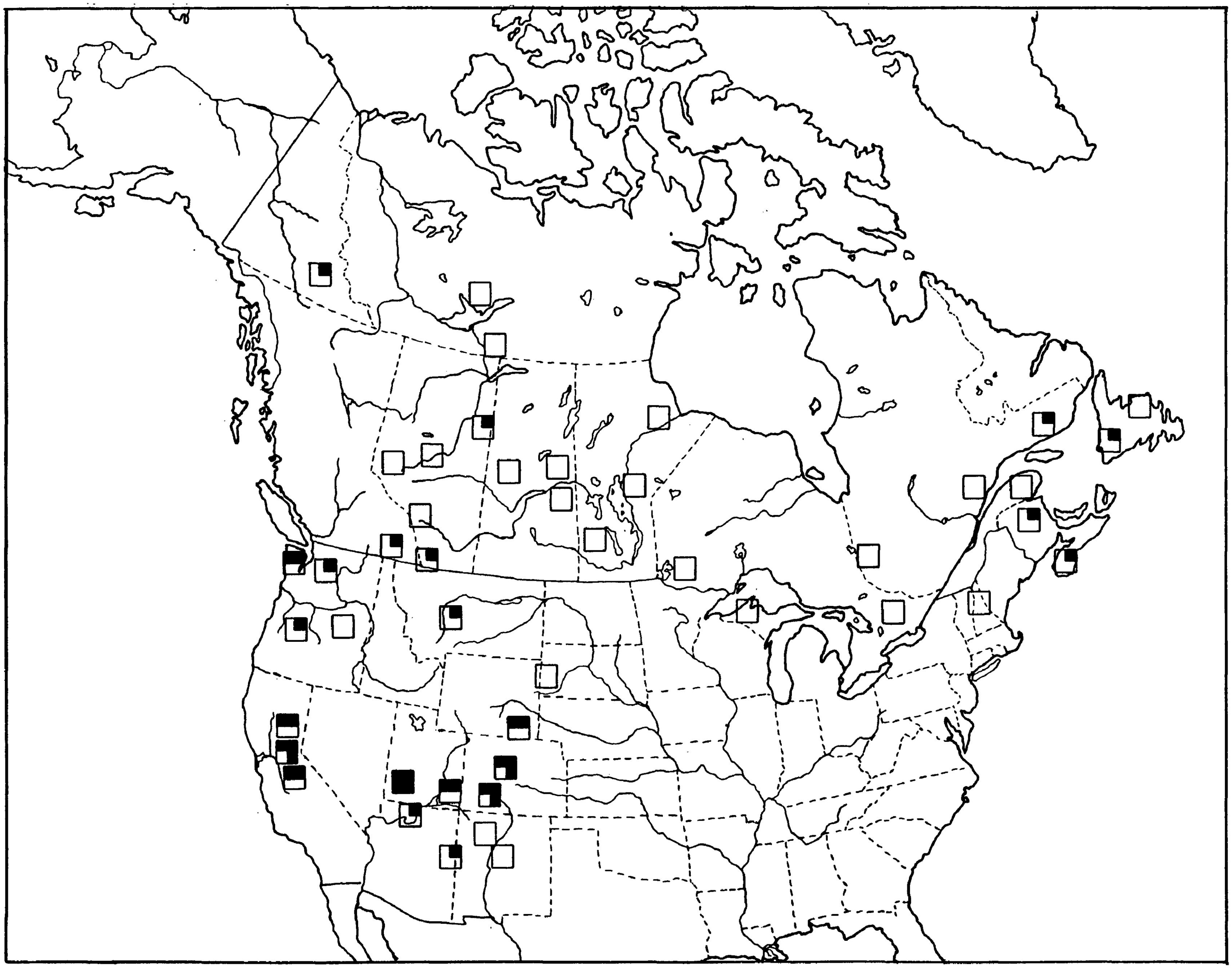


Fig. 27. Weighted mean character values of the apical lunule (Fig. 10) for population samples of *C. nebraskana* Casey. Data are summarized in Table 38. Population samples are indicated in Table 4 and Figure 11.

□	0.00 - 0.99
◳	1.0 - 1.99
⬒	2.0 - 2.99
▜	3.0 - 3.99
■	4.0 - 4.99

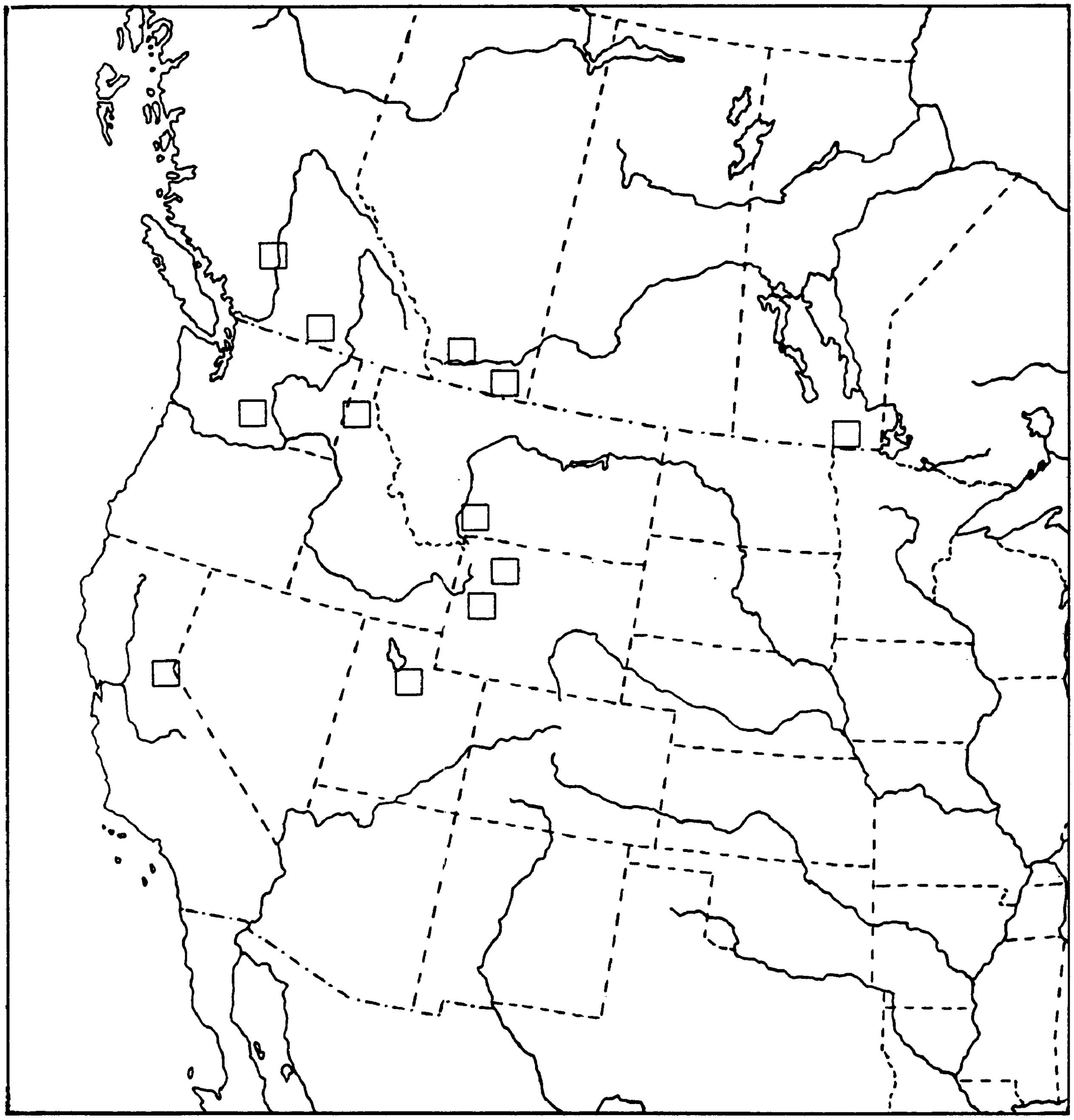
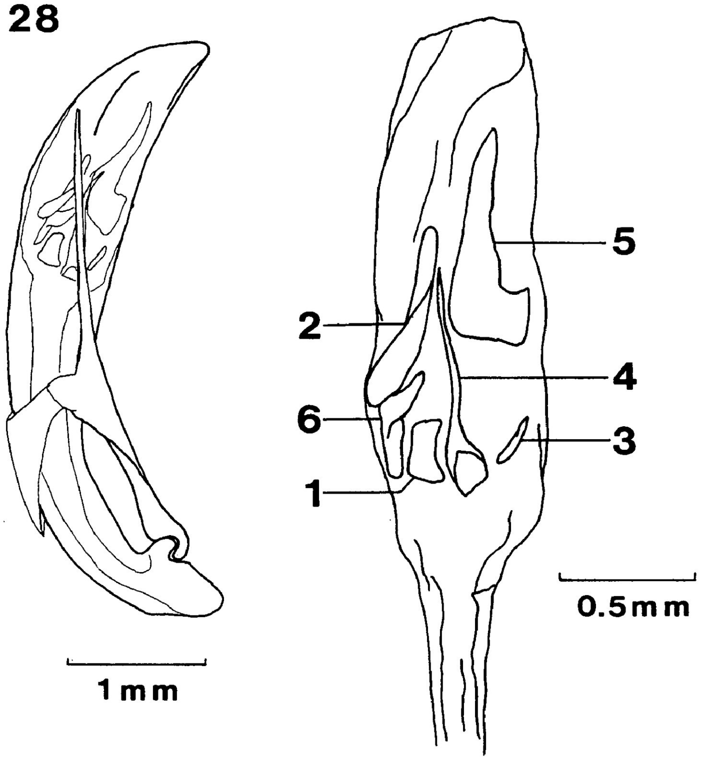


Fig. 28. Aedeagus, left lateral aspect and left lateral aspect of internal sac showing internal sclerites of *C. longilabris* Say from Stanley Hill Cemetery, Thunder Bay District, Ontario.

Fig. 29 - 30. Aedeagus, ventral and left lateral aspects, and sclerites of the internal sac of *C. longilabris* Say from Gander, Nfld. (Fig. 29) and Harmon Field, Nfld. (Fig. 30).

Abbreviations: lf, lateral flange; ml, median lobe; p, paramere; 1, sclerite 1, probably homologous with sclerite 1 of Freitag (1965); 2, sclerite 2 probably homologous with sclerite 2 of Freitag (1965); "la baguette" of Rivalier (1950); 3, sclerite 3, probably homologous with sclerite 3 of Freitag (1965); "le clou" of Rivalier (1950); 4, flagellum, homologous with sclerite 4 of Freitag (1965); "le flagelle" of Rivalier (1950). 5, median tooth "la grande dente" of Rivalier (1950), possibly homologous with sclerite 5 of Freitag (1965); 6, sclerite 6, probably homologous with sclerite 6 of Freitag (1965), "la baguette" of Rivalier (1950).

28



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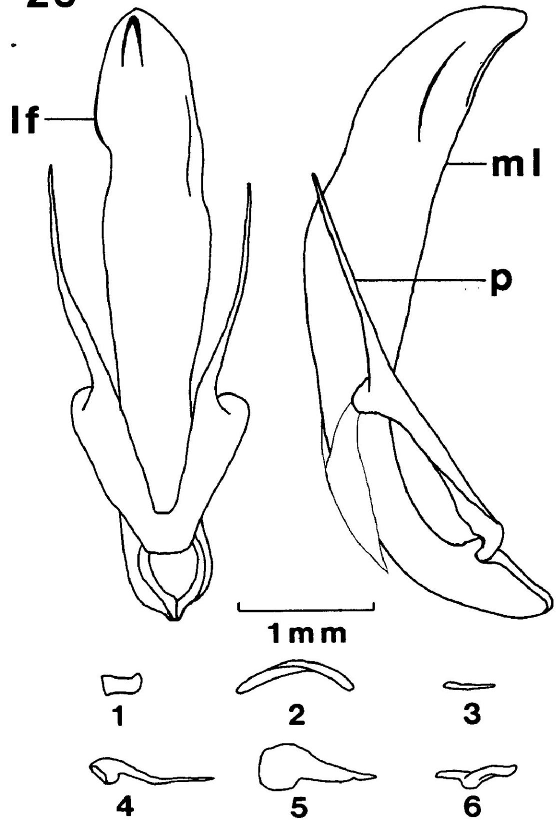

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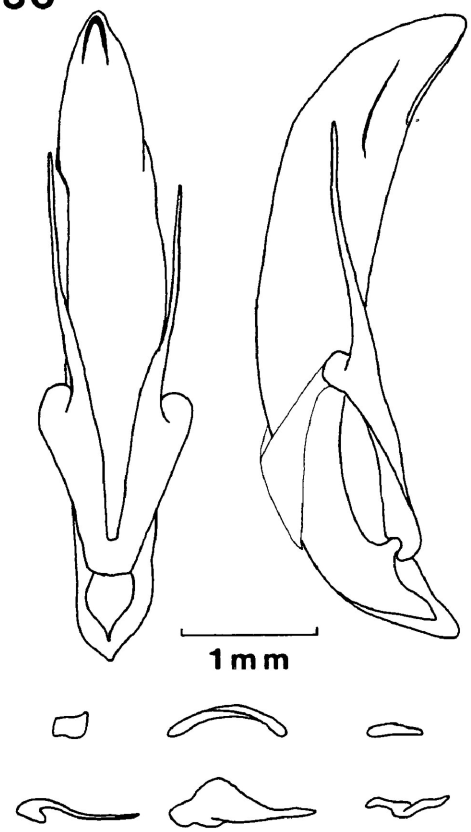
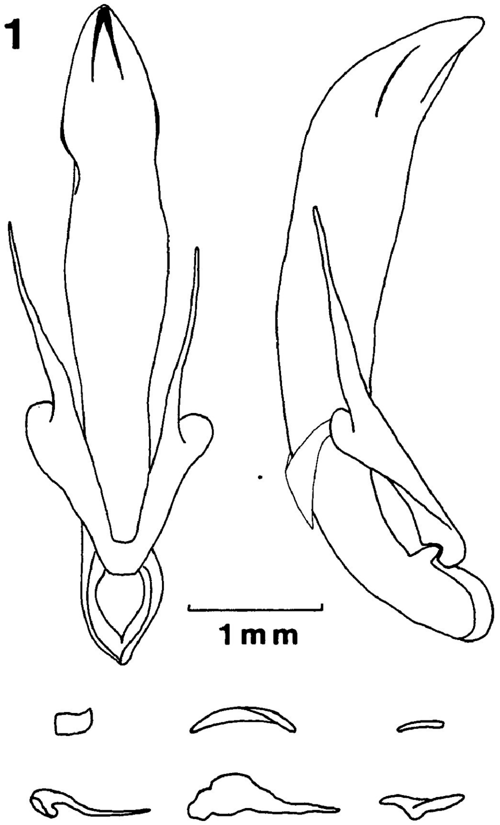


Figs. 31-34. Aedeagus, ventral and left lateral aspects, and sclerites of the internal sac of *C. longilabris* Say from Forestville, Que. (Fig. 31), Whitehorse, Yukon (Fig. 32), Creede, Colorado (Fig. 33), and Sheep's Crossing, Arizona, (Fig. 34).

31



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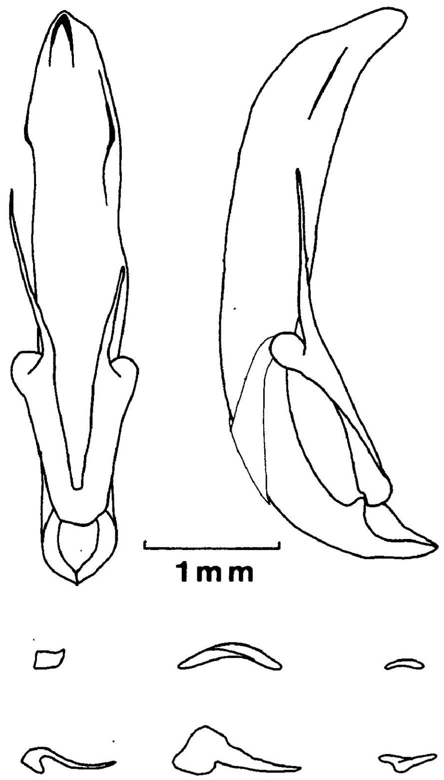

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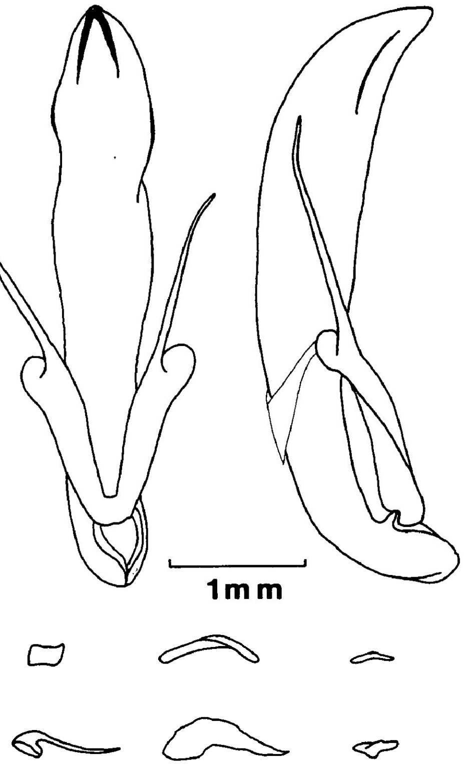

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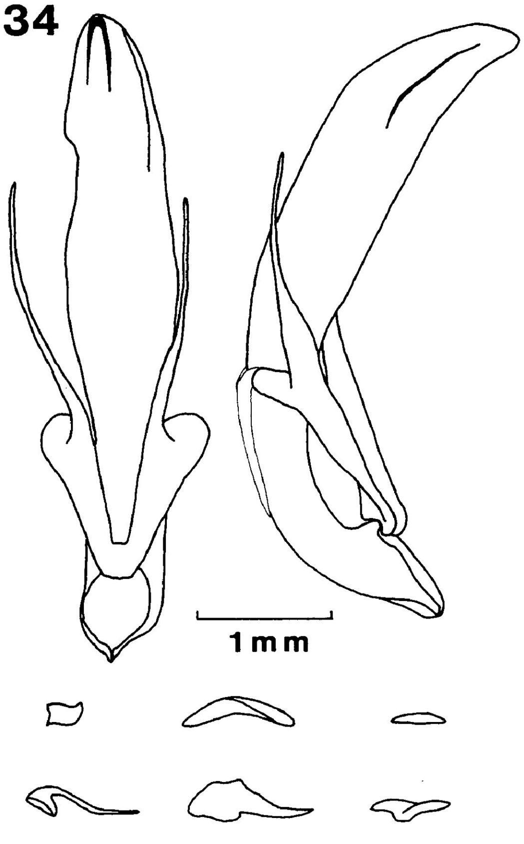
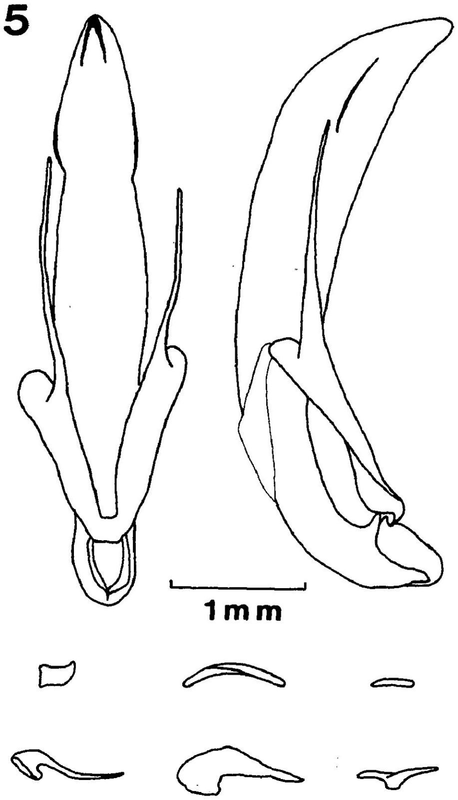


Figs. 35-38. Aedeagus, ventral and left lateral aspects, and sclerites of the internal sac of *C. longilabris* Say from Kaibab Plateau, Arizona (Fig. 35), Cedar Breaks, Utah (Fig. 36), Olympic Nat. Park, Washington (Fig. 37), Lost Prairie Campground, Linne Co., Oregon (Fig. 38).

35



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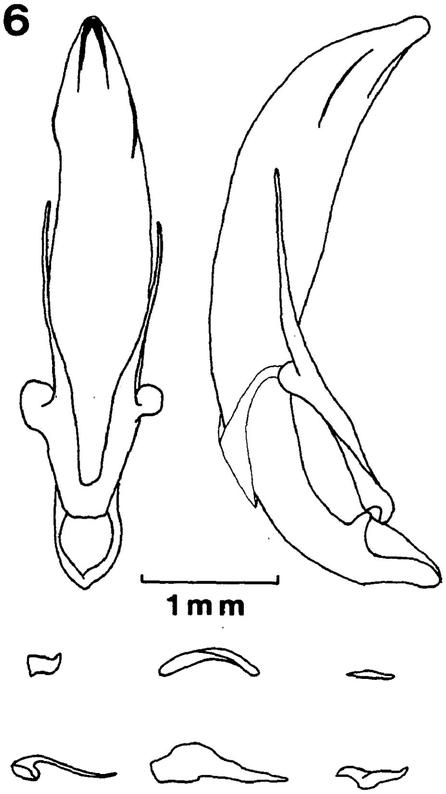

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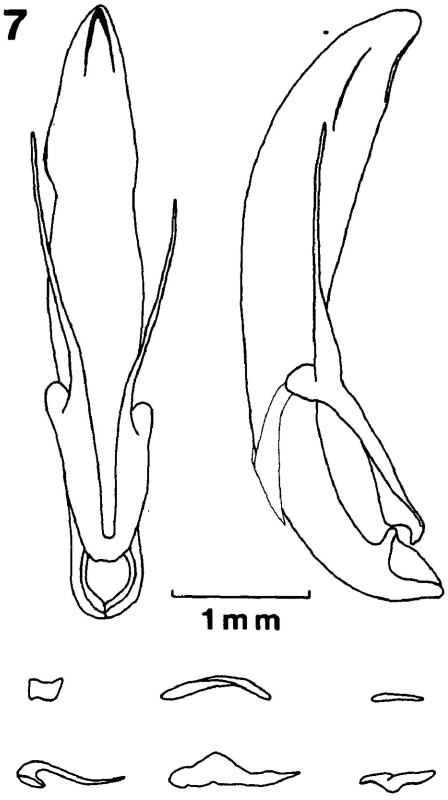

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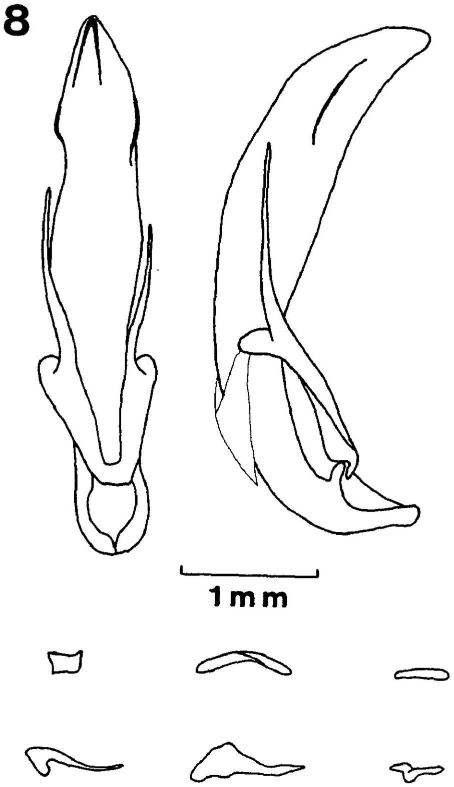
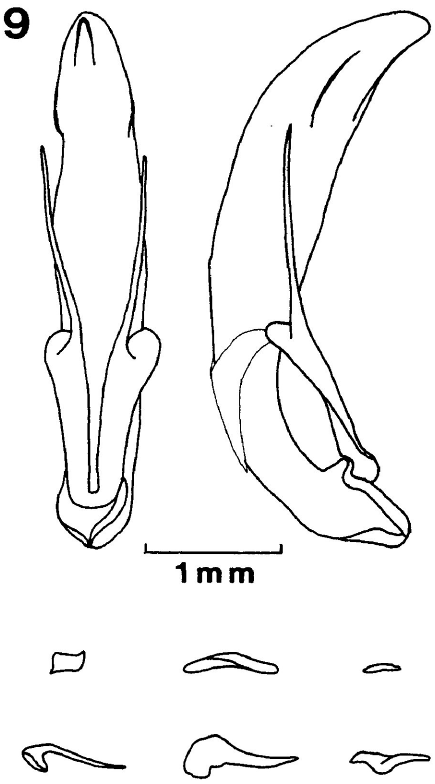


Figs. 39-42. Aedeagus, ventral and left lateral aspects, and sclerites of the internal sac of *C. longilabris* Say from Sonora Pass, California (Fig. 39), and *C. nebraskana* Casey from Mill Creek Canyon, Utah (Fig. 40), Sonora Pass, California (Fig. 41), and Oliver, British Columbia (Fig. 42).

39



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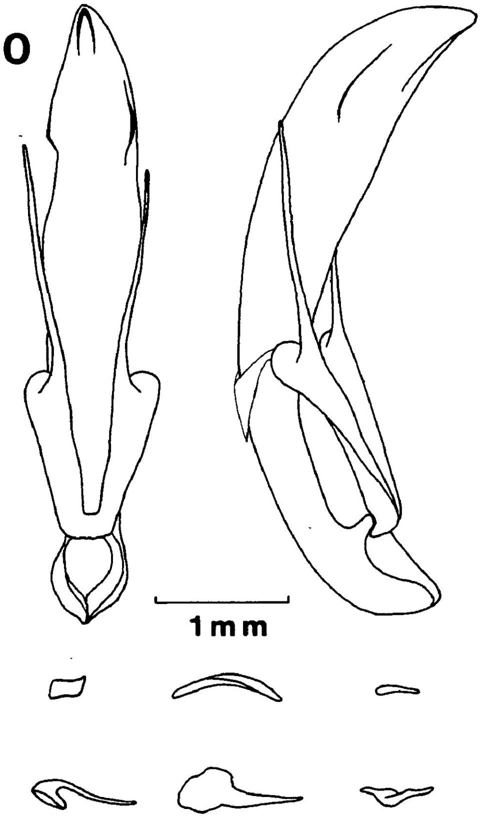

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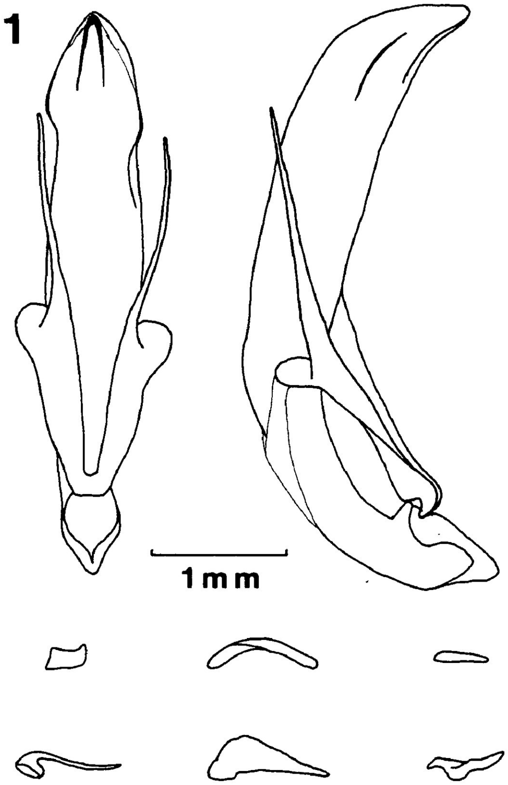

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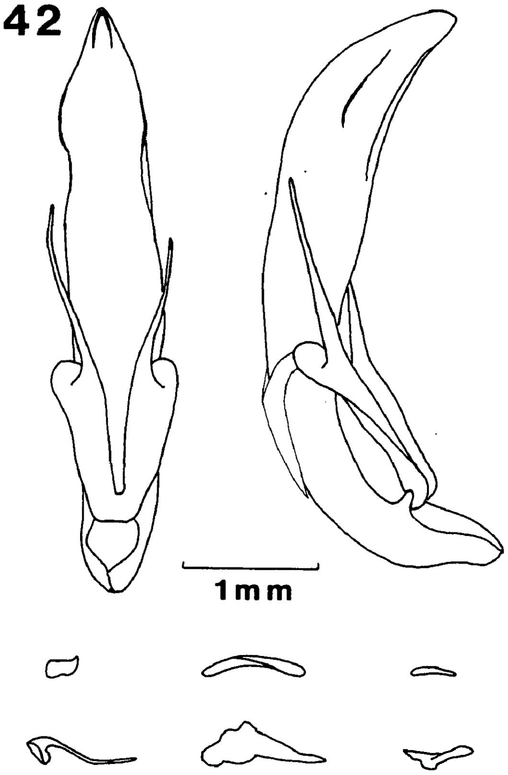
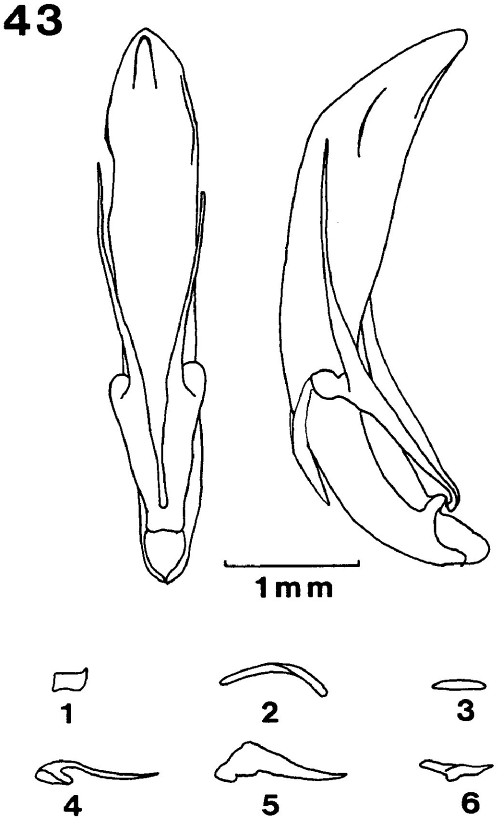


Figs. 43-46. Aedeagus, ventral and left lateral aspects, and sclerites of the internal sac of *C. nebraskana* Casey from 10 mi E of Patricia, Alberta (Fig. 43), *C. sylvatica* Linnaeus from Baikal, Siberia (Fig. 44), *C. granulata* Gebler from Turkestan, USSR (Fig. 45), and *C. japana* Motschulsky from Kanazawa, Japan (Fig. 46).

Sclerites of the internal sac are numbered as in Figures 28 and 29, except in cases where homologies are uncertain: a, possibly a fusion of sclerites 1 and 4; b, sclerite of uncertain homology.

43



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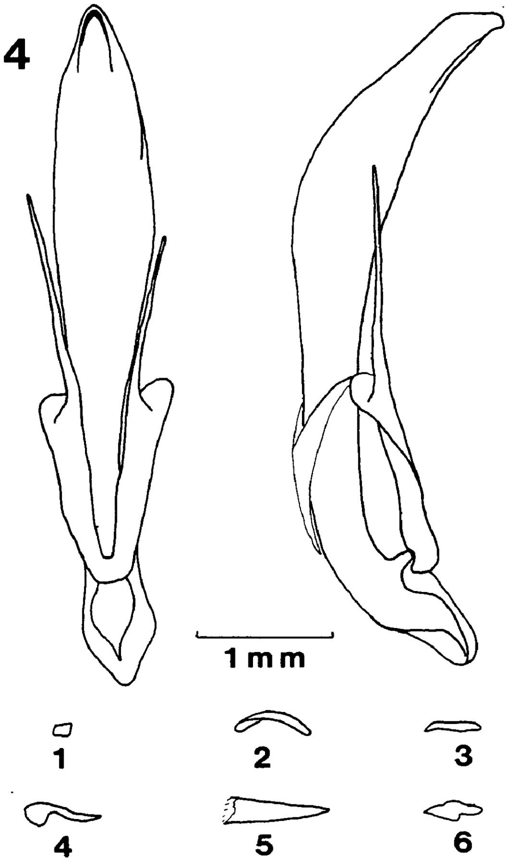

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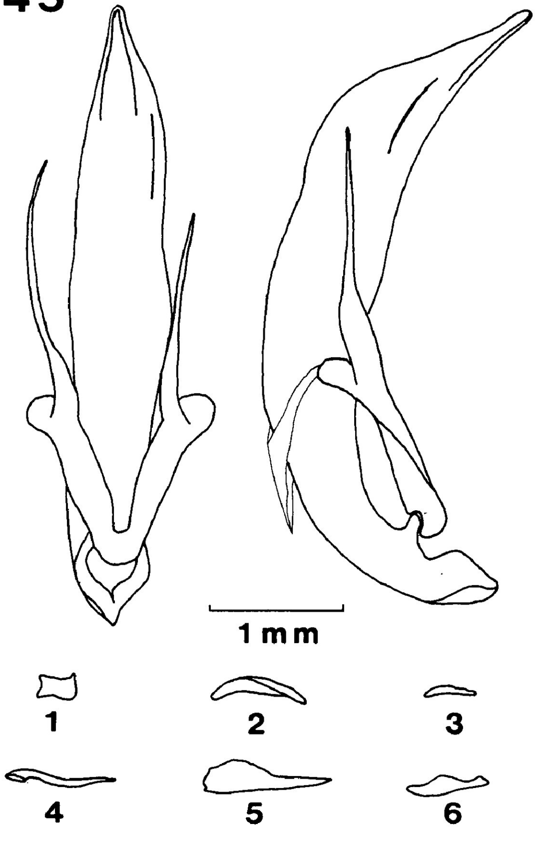

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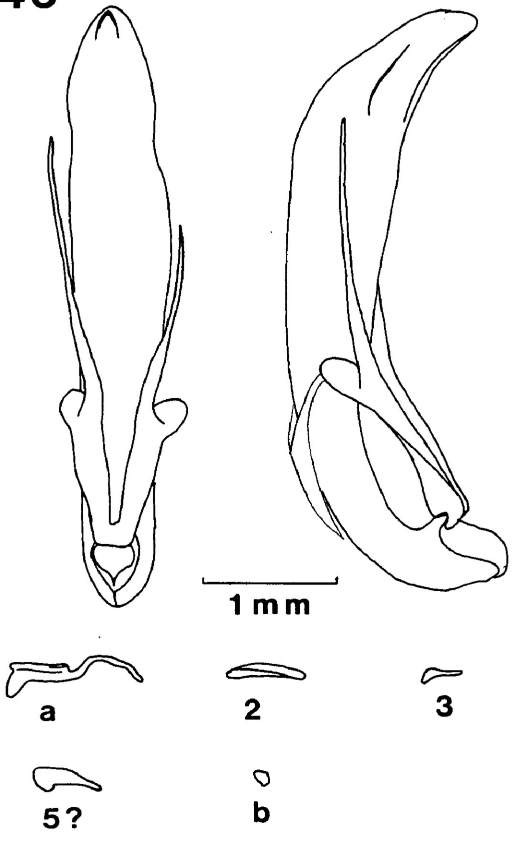
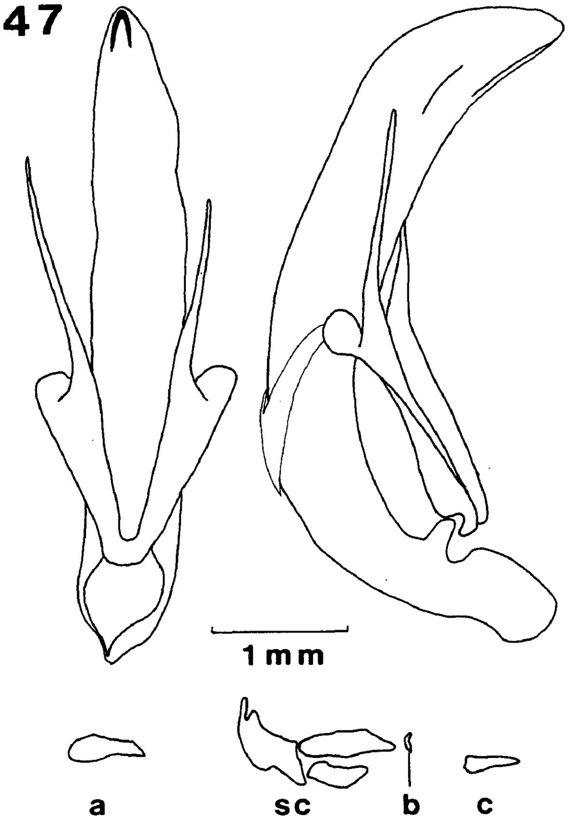


Figs. 47-49. Aedeagus, ventral and left lateral aspects, and sclerites of the internal sac of *C. gemmata* Faldermann from Korea (Fig. 47), *C. soluta* Dejean from Hungary (Fig. 48), and *C. lacteola* Pallas labelled "Turk" (Fig. 49).

Abbreviations: a, b, c, sclerites of unknown homologies;

sc, sclerite cluster.

47



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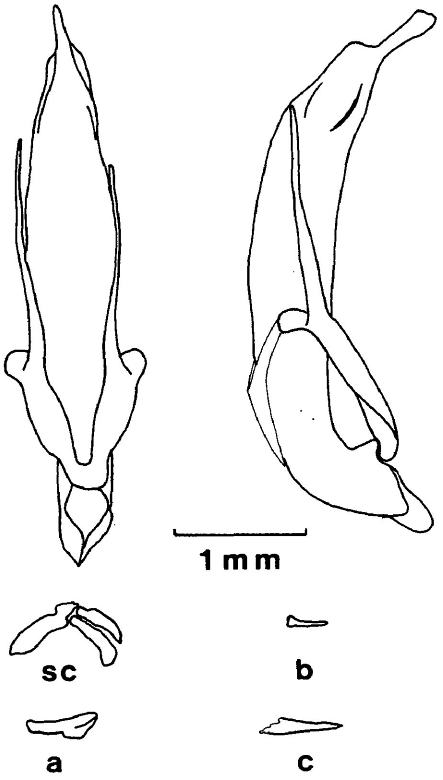

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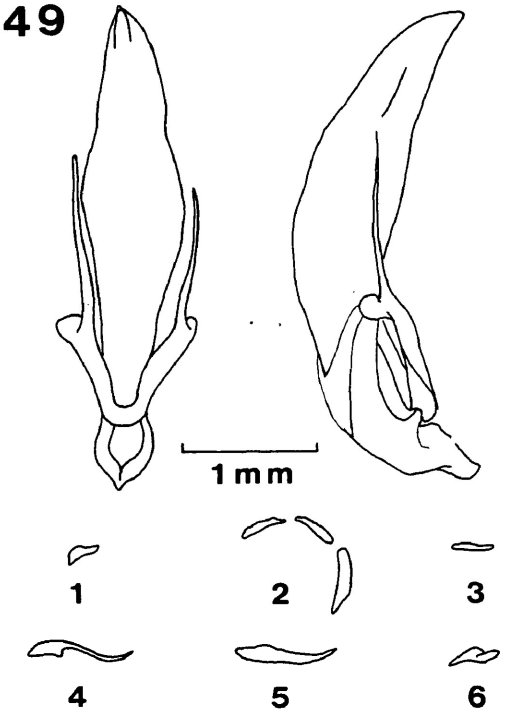
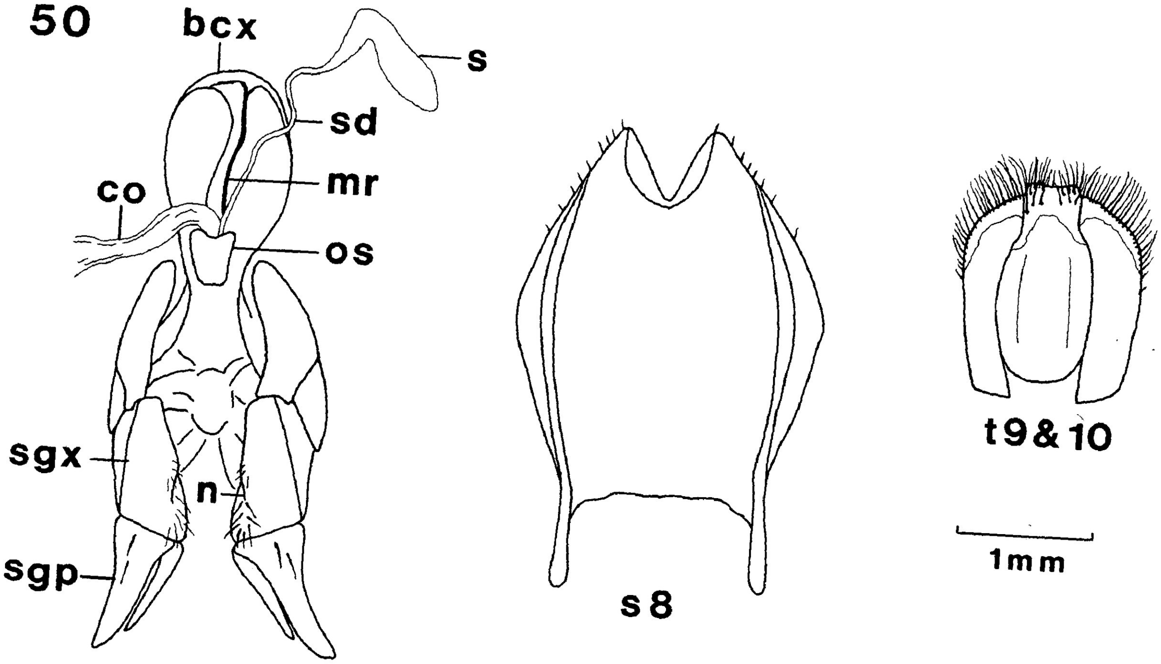


Figs. 50-51. Female genitalia of *C. longilabris* Say from Harmon Field, Nfld. (Fig. 50), and Forestville, Quebec (Fig. 51).

Abbreviations: bcx, bursa copulatrix; co, common oviduct; mr, median ridge of ventral sclerite of bursa copulatrix; n, ventral notch of second gonacoxa, os, oviduct sclerite; s, spermatheca; sd, spermathecal duct; sgp, second gonapophysis; sgx second gonacoxa; s8 sternum eight, ventral aspect; t 9 & 10, syntergum nine and ten, dorsal aspect.

50

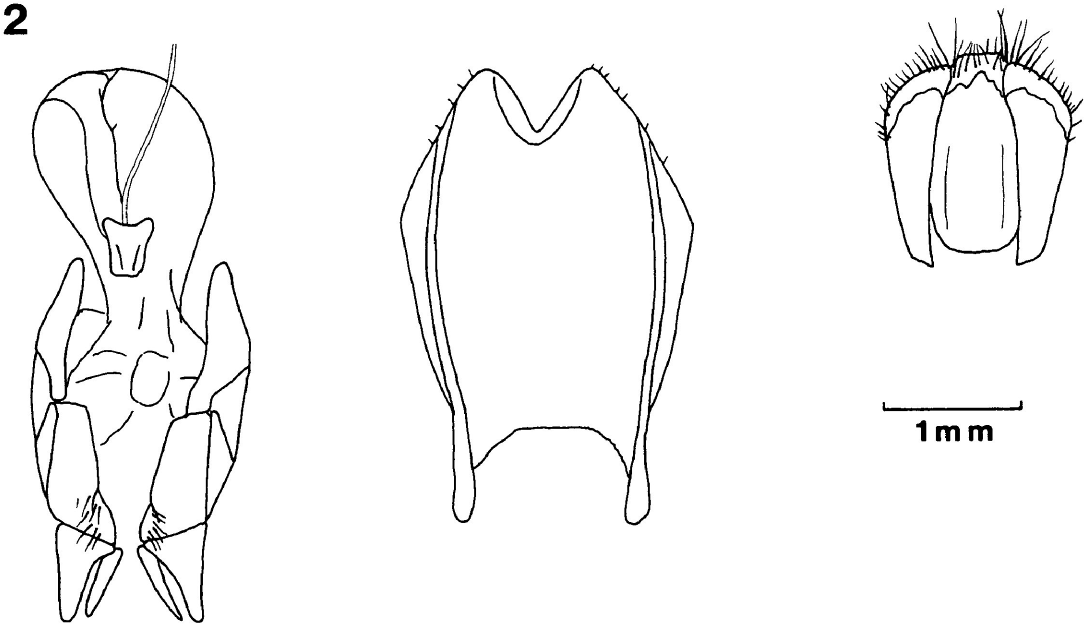


51

Figs. 52-53. Female genitalia of *C. longilabris* Say from Whitehorse, Yukon (Fig. 52), and Creede, Colorado (Fig. 53).

Structures are labelled in Figure 50.

52



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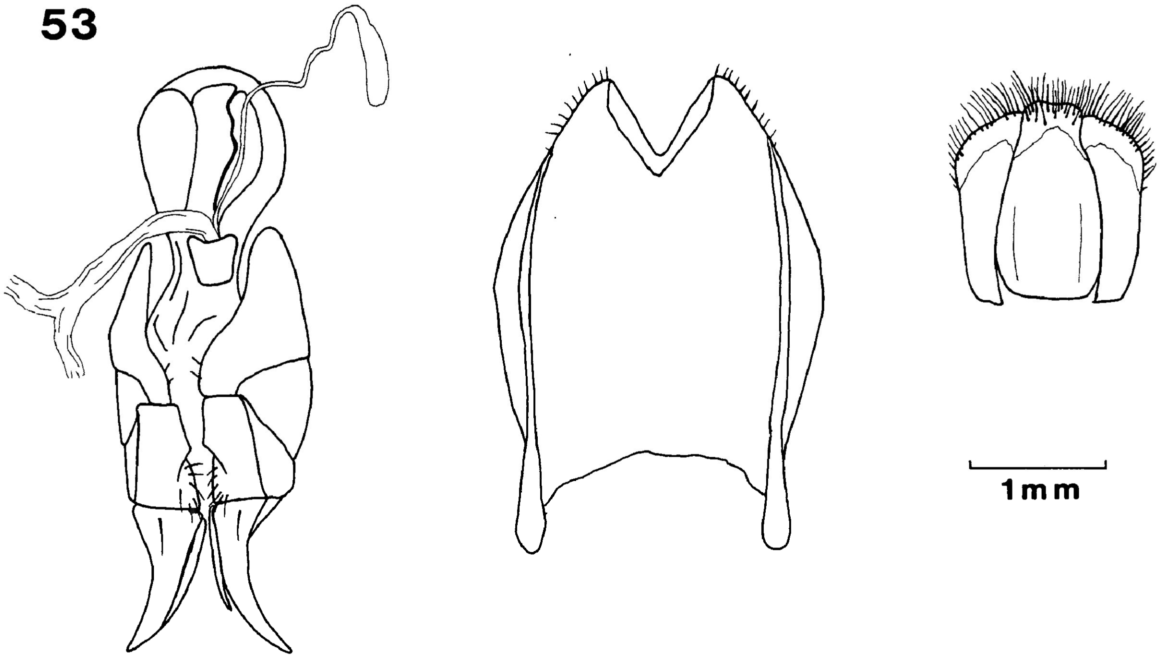
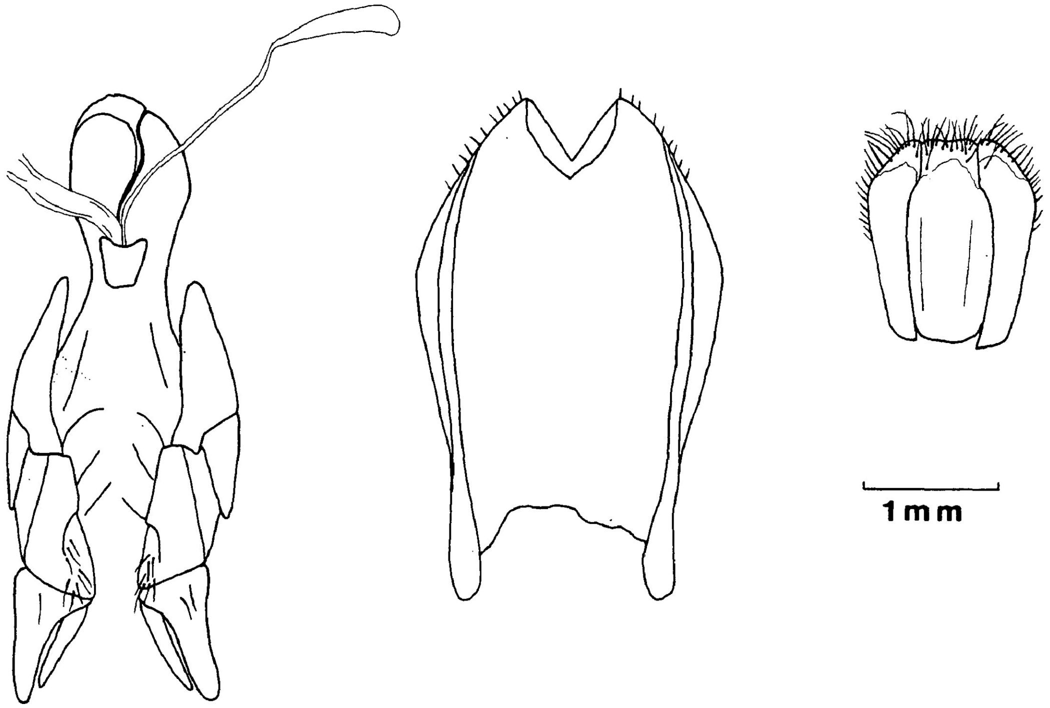


Figs. 54-55. Female genitalia of *C. longilabris* Say from Cedar Breaks, Utah (Fig. 54) and Kaibab Plateau, Arizona (Fig. 55).

Structures are labelled in Figure 50.

54



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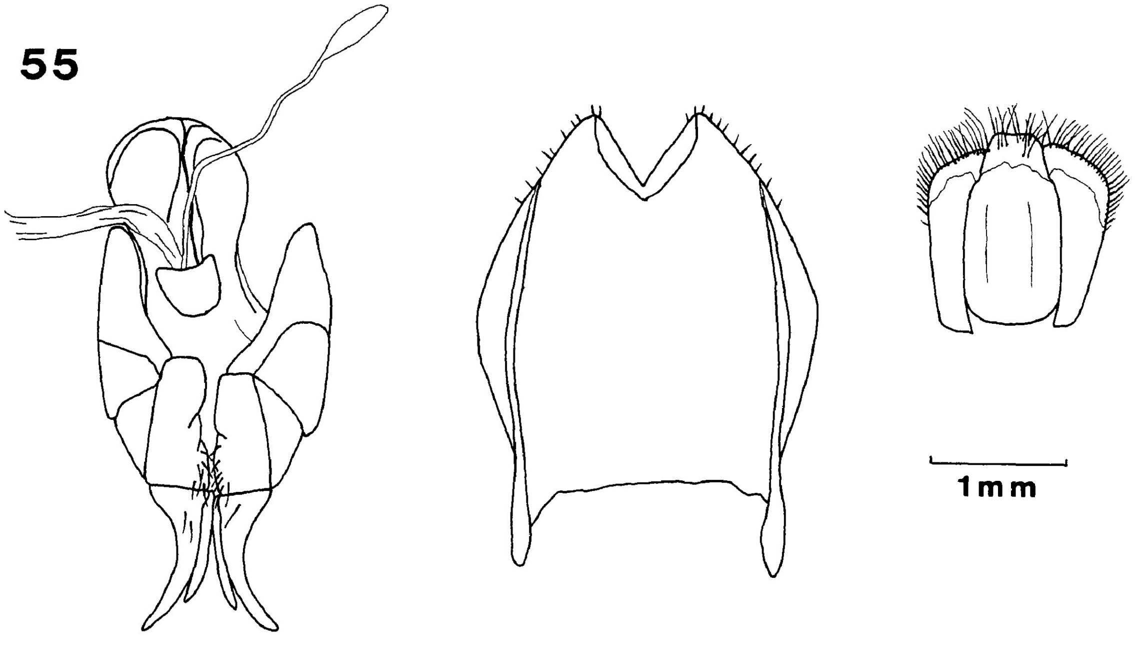
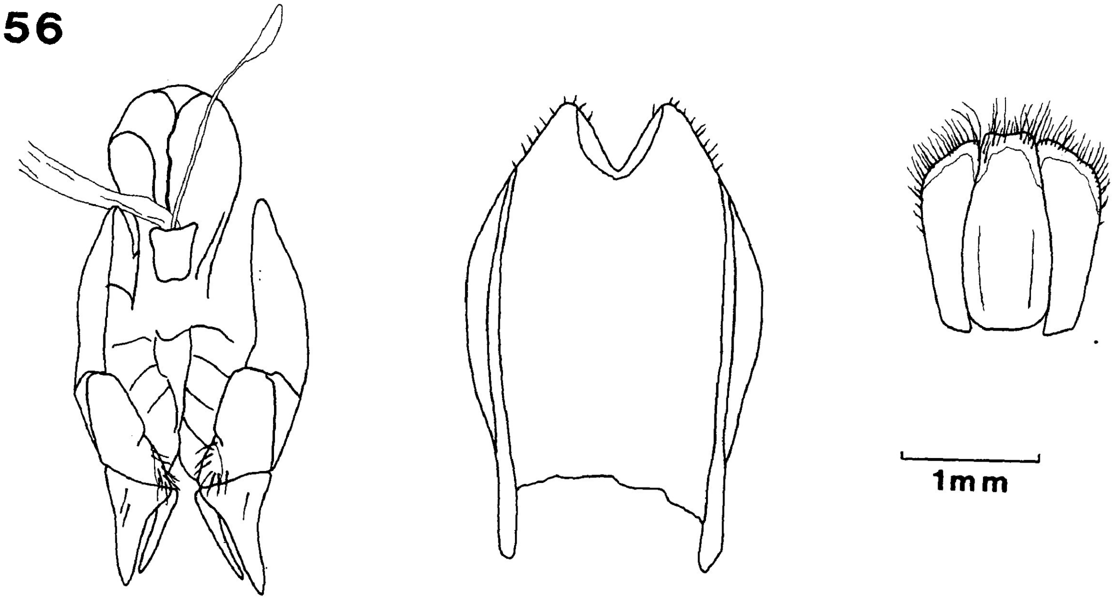


Figs. 56-57. Female genitalia of *C. longilabris* Say from Sheeps Crossing Apache Co., Arizona (Fig. 56), and Lost Prairie Campground, near Sweethome, Oregon (Fig. 57),

Structures are labelled in Figure 50.

56



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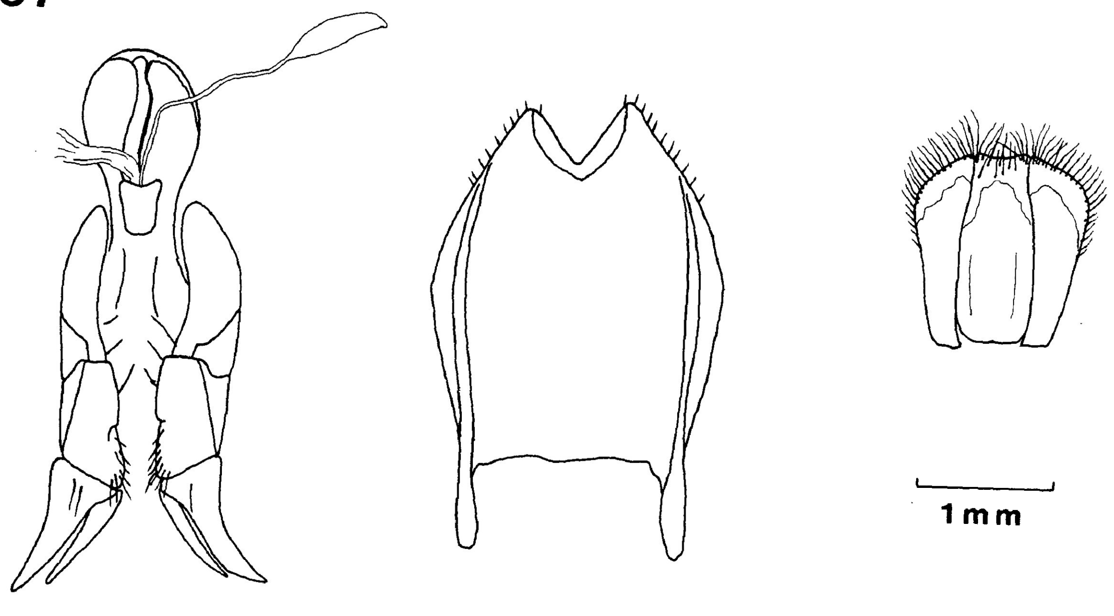
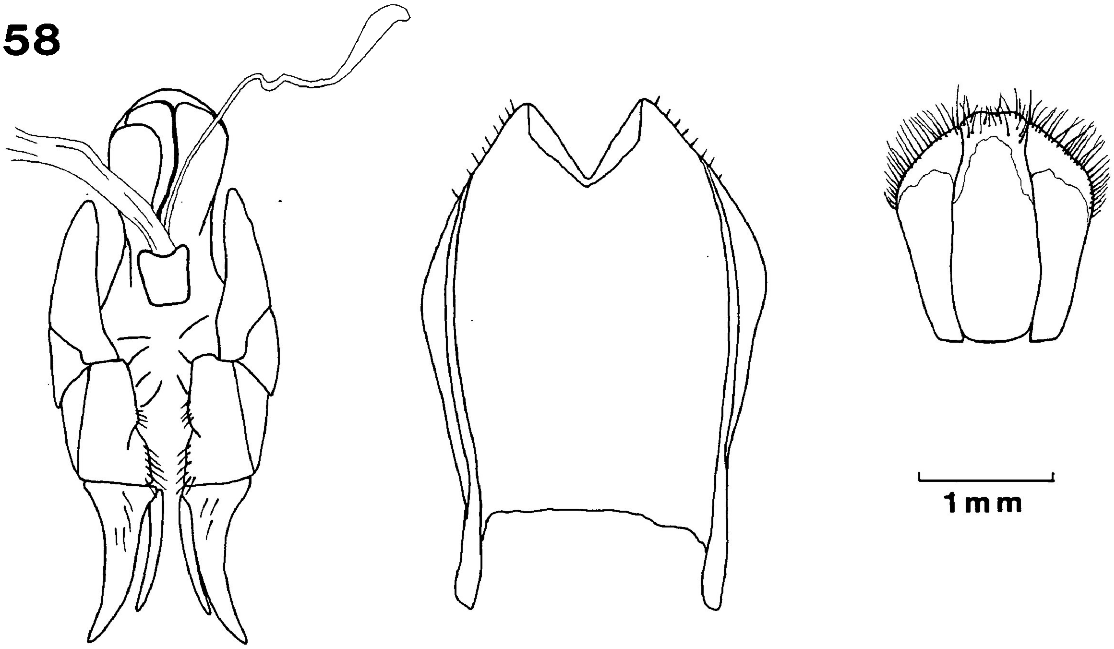


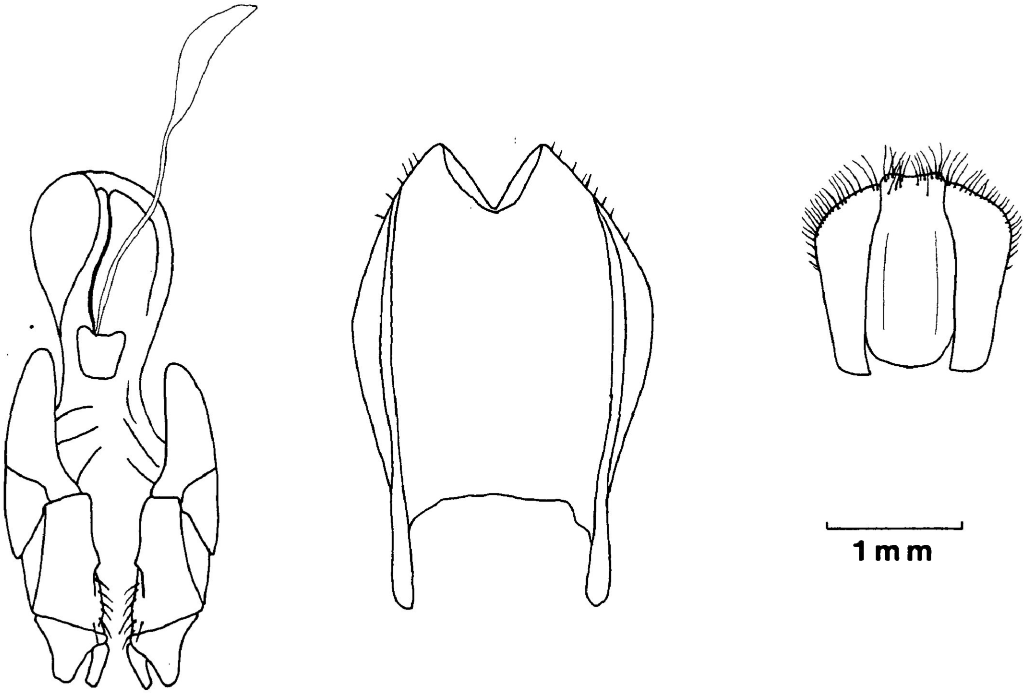
Figs. 58-59. Female genitalia of *C. nebraskana* Casey from Sonora Pass, California (Fig. 58), and Fairview Rd., Oliver, British Columbia (Fig. 59).

Structures are labelled in Figure 50.

58



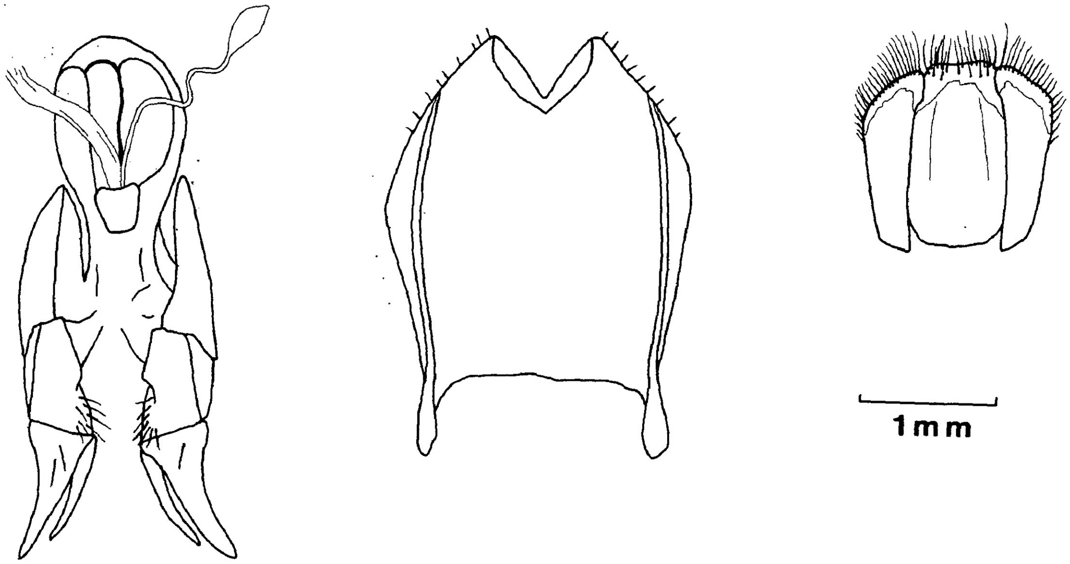
59



Figs. 60-61. Female genitalia of *C. nebraskana* Casey from 10 mi E of Patricia, Alberta (Fig. 60), and *C. sylvatica* Linnaeus from Baikal, Siberia (Fig. 61).

Structures are labelled in Figure 50.

60



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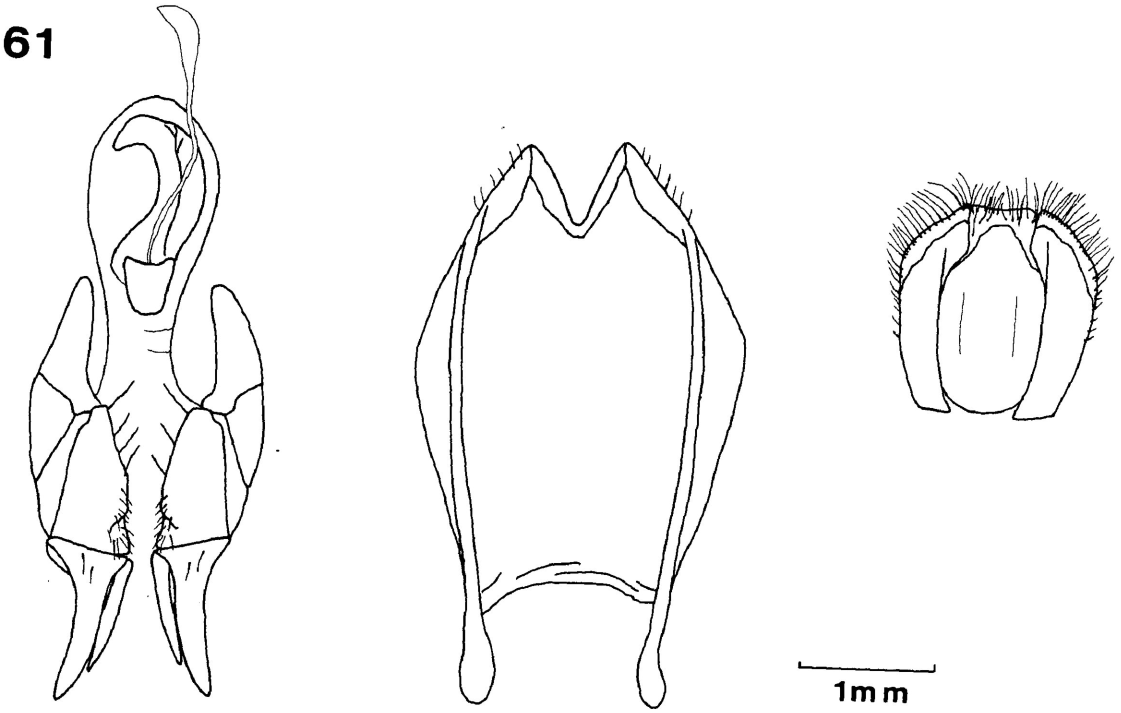
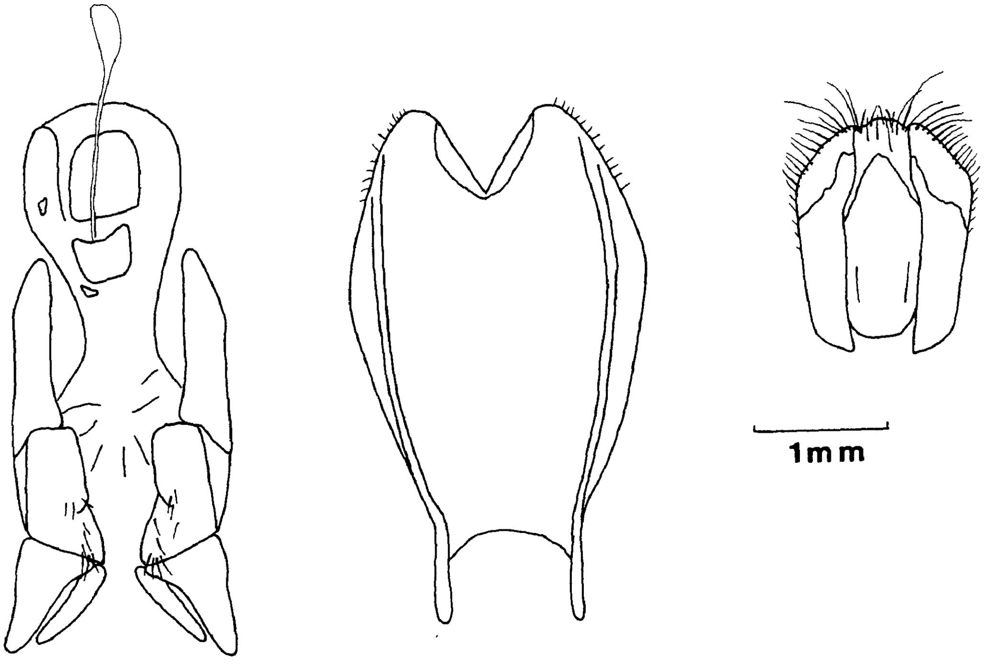


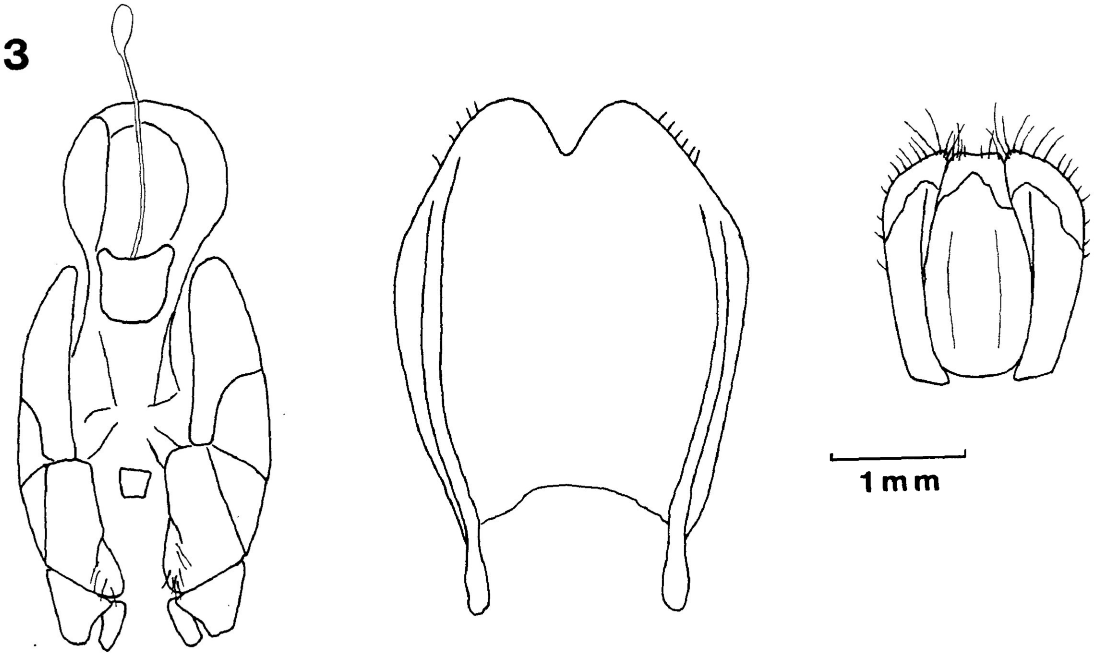
Figs. 62-63. Female genitalia of *C. granulata* Gebler from Turkestan, USSR(Fig. 62), and *C. japana* Motschulsky from Kanazawa, Japan (Fig. 63).

Structures are labelled in Figure 50.

62



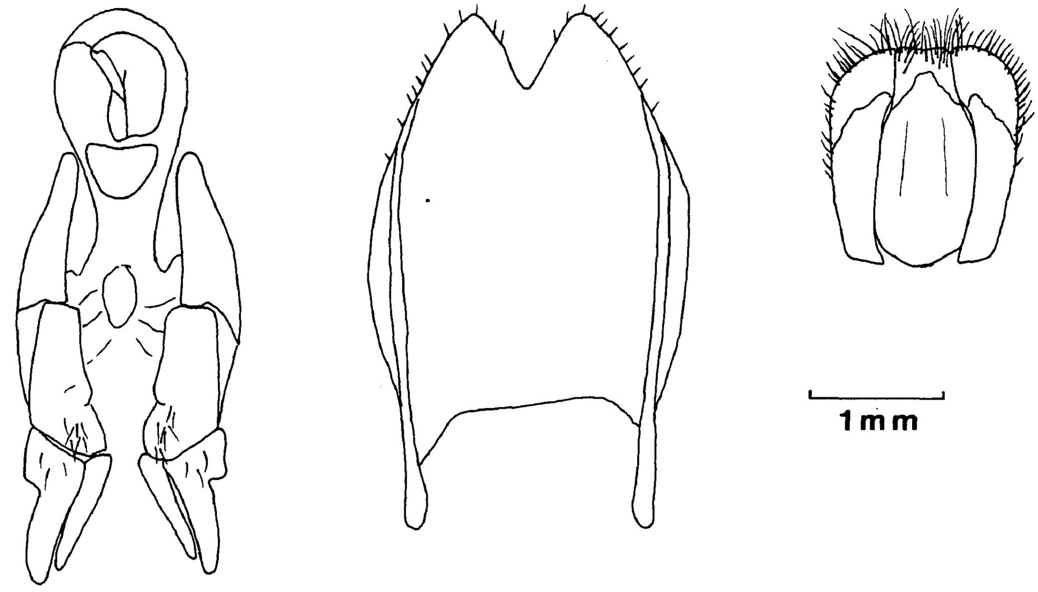
63



Figs. 64-65. Female genitalia of *C. gemmata* Faldermann from Kanazawa, Japan (Fig. 64), and *C. soluta* Dejean from Hungary (Fig. 65).

Structures are labelled in Figure 50.

64



65

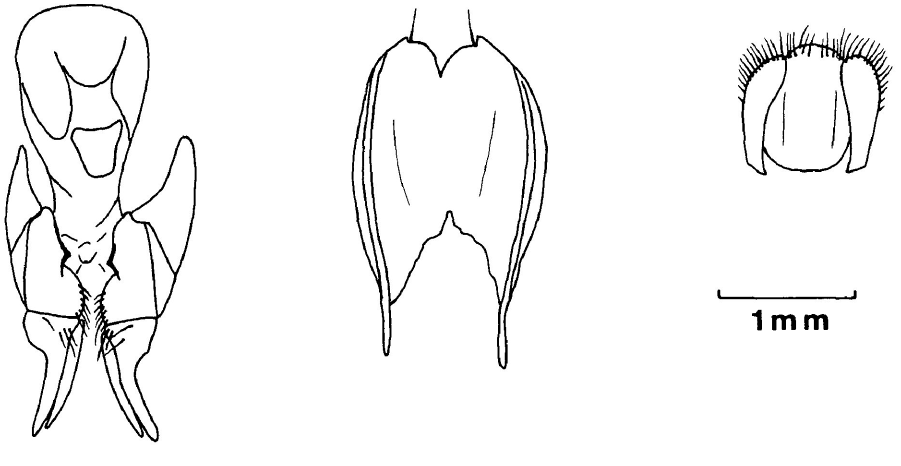
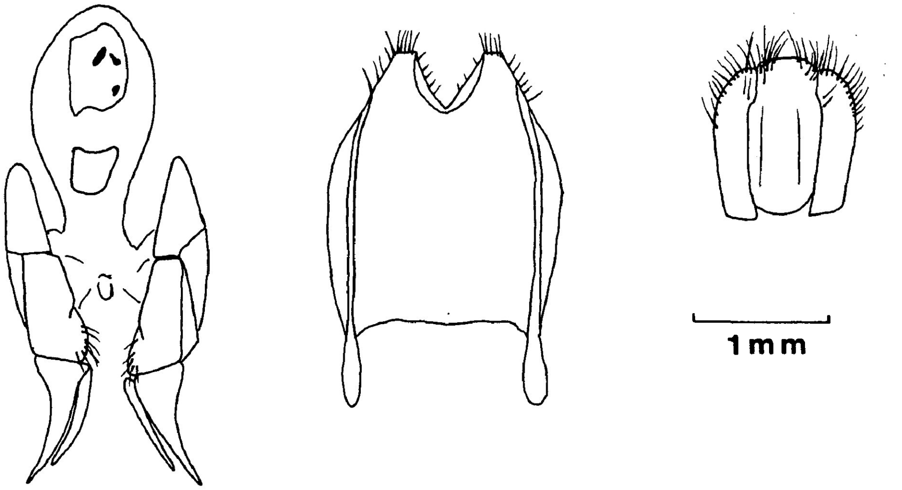


Fig. 66. Female genitalia of *C. lacteola* Pallas from Aulic Ata.

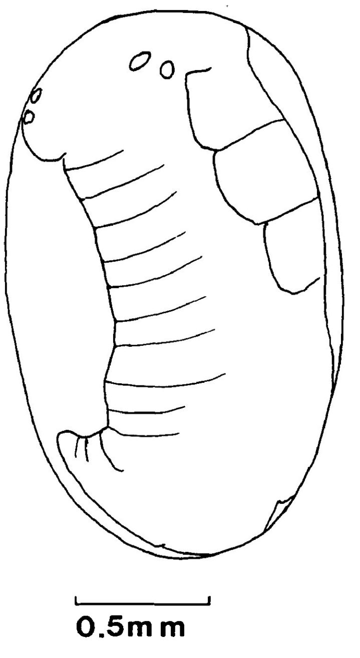
Structures are labelled in Figure 50.

Fig. 67. Egg of *C. longilabris* Say.

66



67



Figs. 68-72. Third instar larva of *C. longilabris longilabris* Say.

Fig. 68. Head and pronotum, dorsal aspect

Fig. 69. Head, ventral aspect

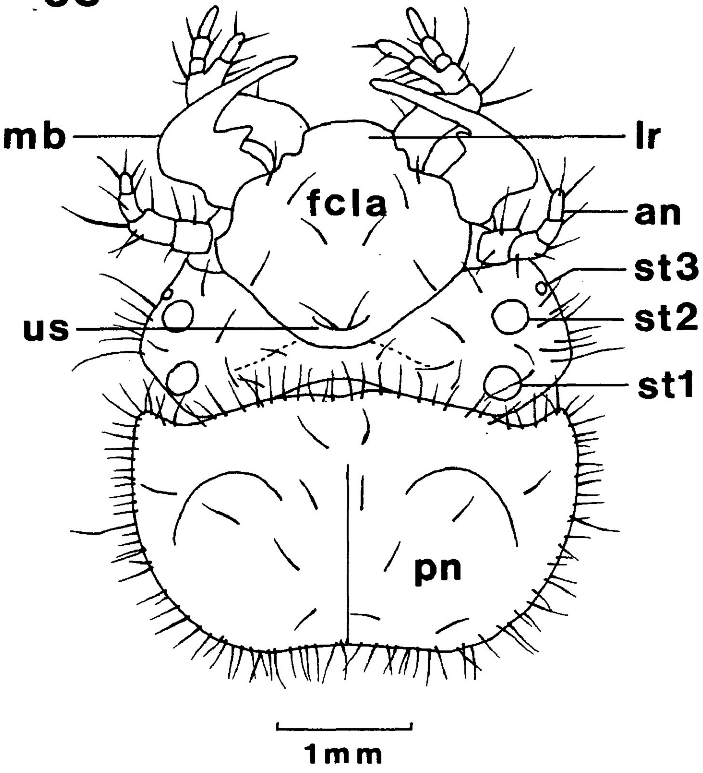
Fig. 70. Ninth abdominal sternum

Fig. 71. Pygopod, dorsal aspect

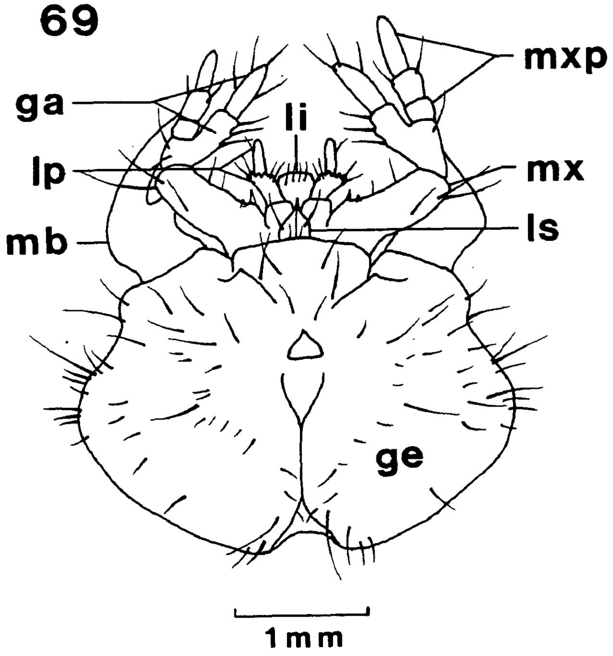
Fig. 72. Dorsum of fifth abdominal segment.

Abbreviations: an, antenna; fcla; frontoclypeolabral area; ga, galea; ge, genae; ih, inner hook; li, ligula; lp, labial palpus; lr, labrum; ls, labio-stipites; mb, mandible; mh, median hook; mx, maxilla; mxp, maxillary palpus; pn, pronotum; st1, stemma one; st2, stemma two; st3, stemma three.

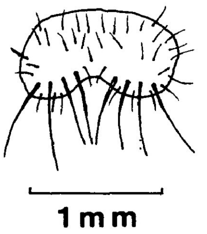
68


mb
lr
fcla
an
st3
us
st2
st1
pn
1mm

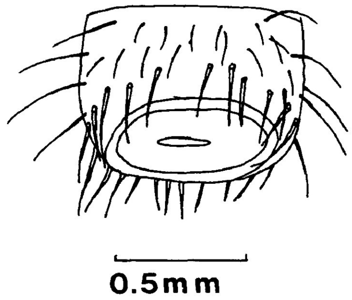
69


mxp
ga
li
lp
mx
mb
ls
ge
1mm

70


1mm

71


0.5mm

72

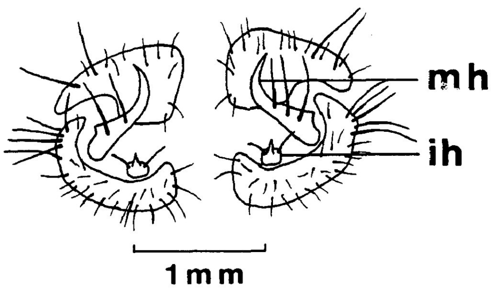

mh
ih
1mm

Fig. 73. Life cycle of *C. longilabris* Say compared with those of other species of *Cicindela* studied by Shelford (1908), Huie, (1915).

The exact time of appearance and duration of larval stages varies geographically and from year to year.

○○○○○○○○ egg

——— 1st instar larva

▭ 2nd instar larva

☰ 3rd instar larva

▥ pupa

□ adult

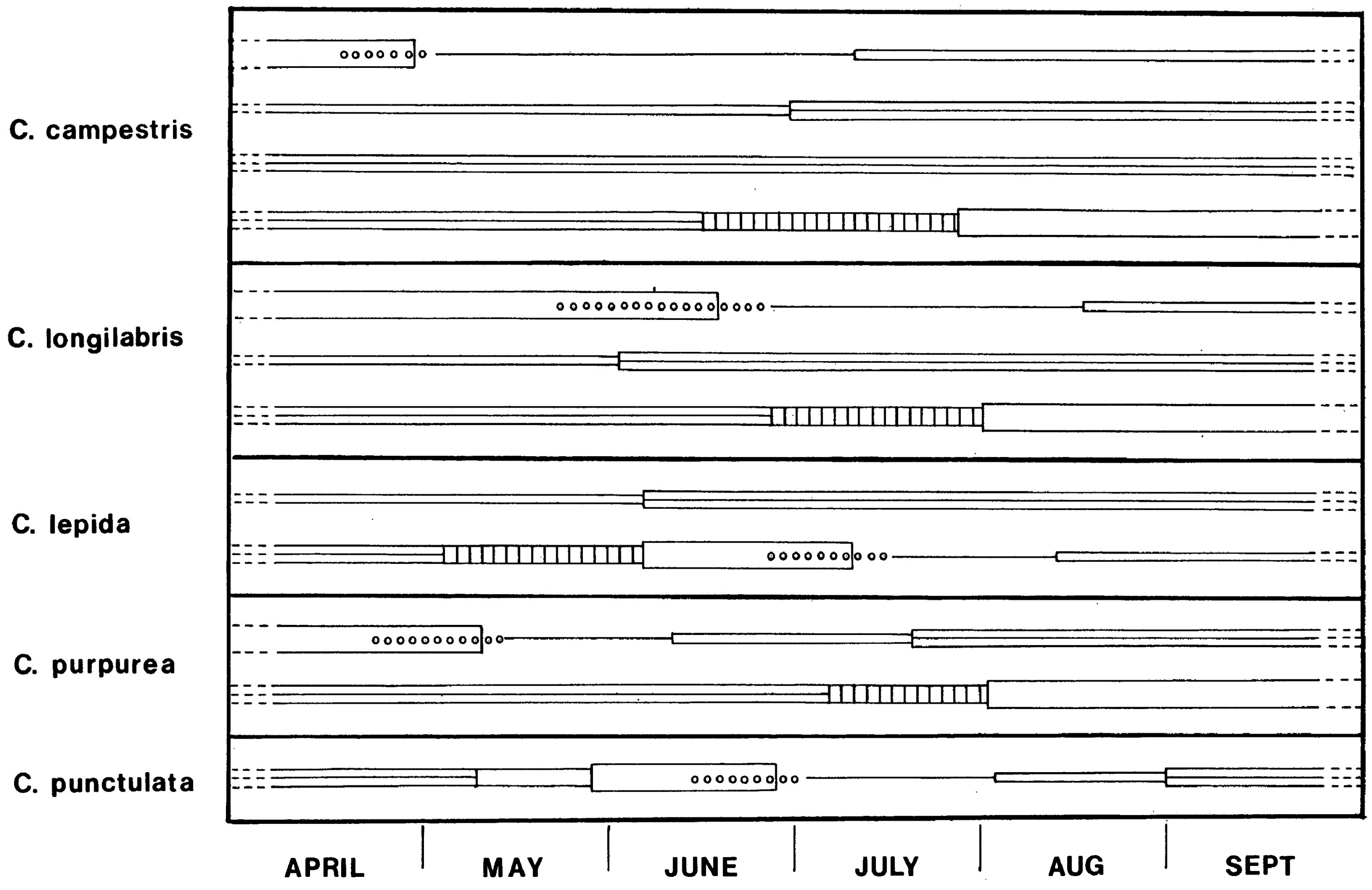

C. campestris
C. longilabris
C. lepida
C. purpurea
C. punctulata
APRIL
MAY
JUNE
JULY
AUG
SEPT

Fig. 74. Total catch of adults of *Cicindela longilabris* Say Stanley Hill study site, Thunder Bay District, Ontario in the summer of 1982.

A. males

B. females

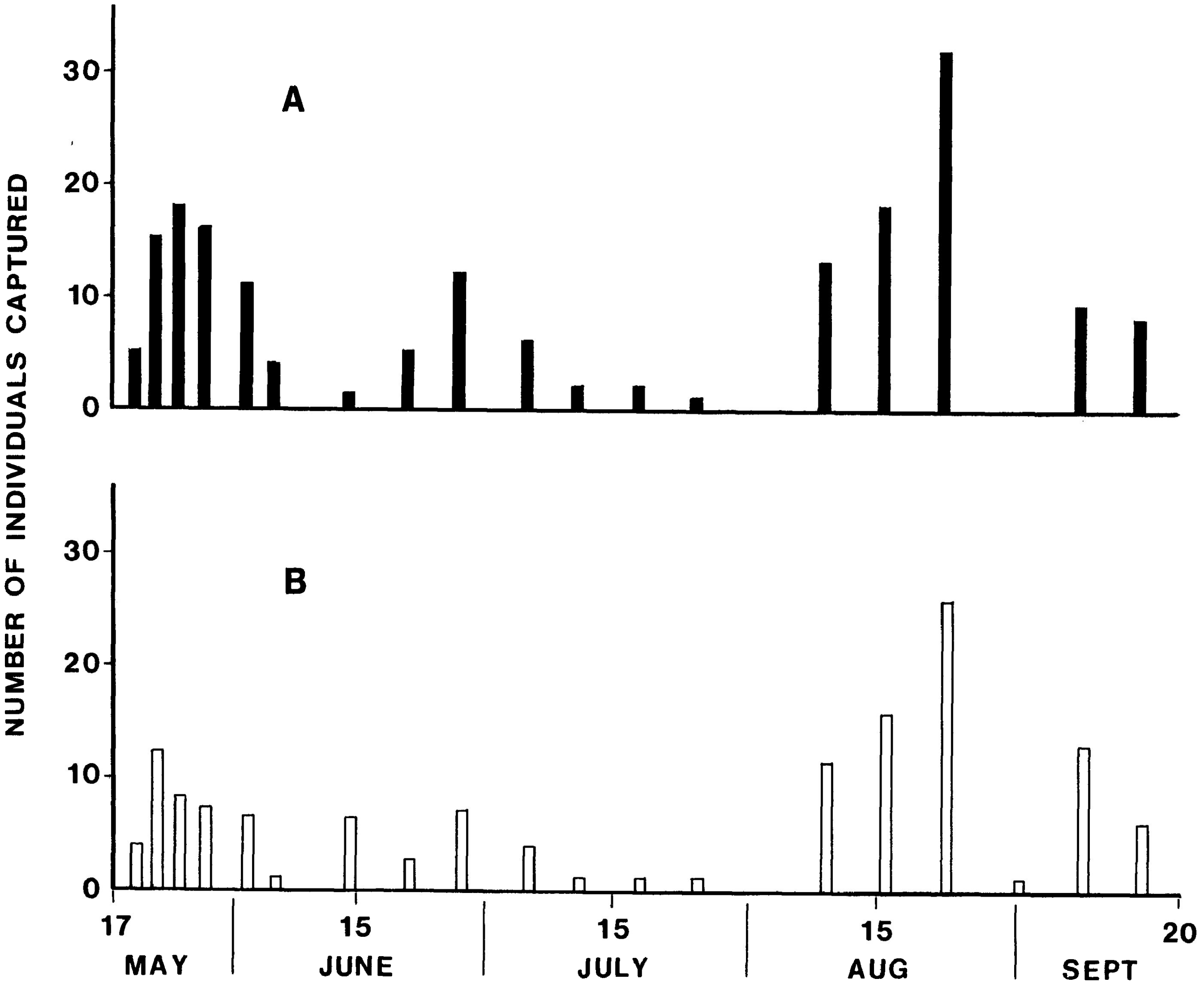

A
B
NUMBER OF INDIVIDUALS CAPTURED
0
10
20
30
0
10
20
30
17
15
15
15
20
MAY
JUNE
JULY
AUG
SEPT

Fig. 75. Collection dates of borrowed adult specimens of *Cicindela longilabris* Say collected in Canada.

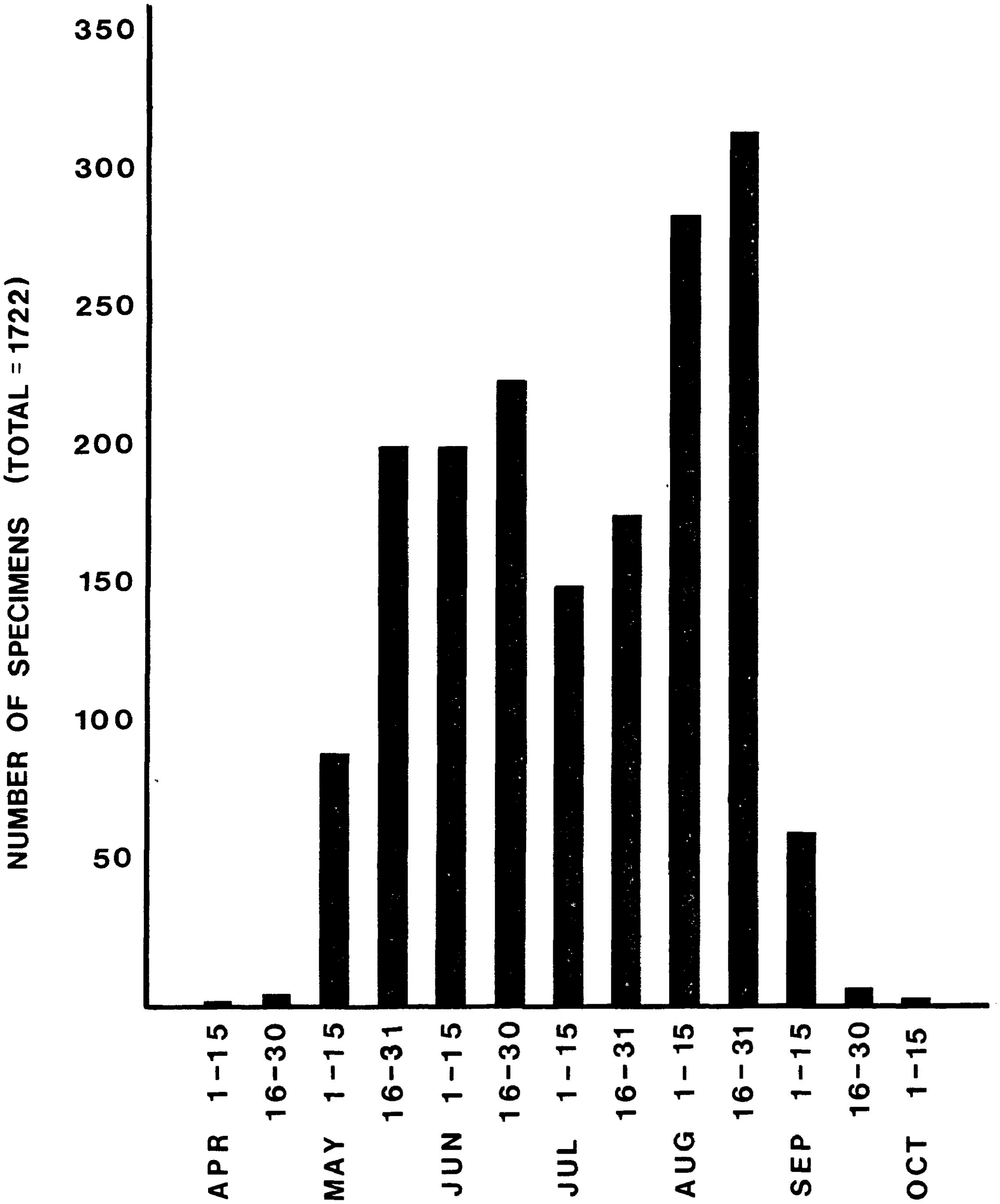

NUMBER OF SPECIMENS (TOTAL = 1722)
350
300
250
200
150
100
50
APR 1-15
16-30
MAY 1-15
16-31
JUN 1-15
16-30
JUL 1-15
16-31
AUG 1-15
16-31
SEP 1-15
16-30
OCT 1-15

Fig. 76. Collection dates of borrowed adult specimens of *Cicindela longilabris* Say collected in Washington, Oregon and California.

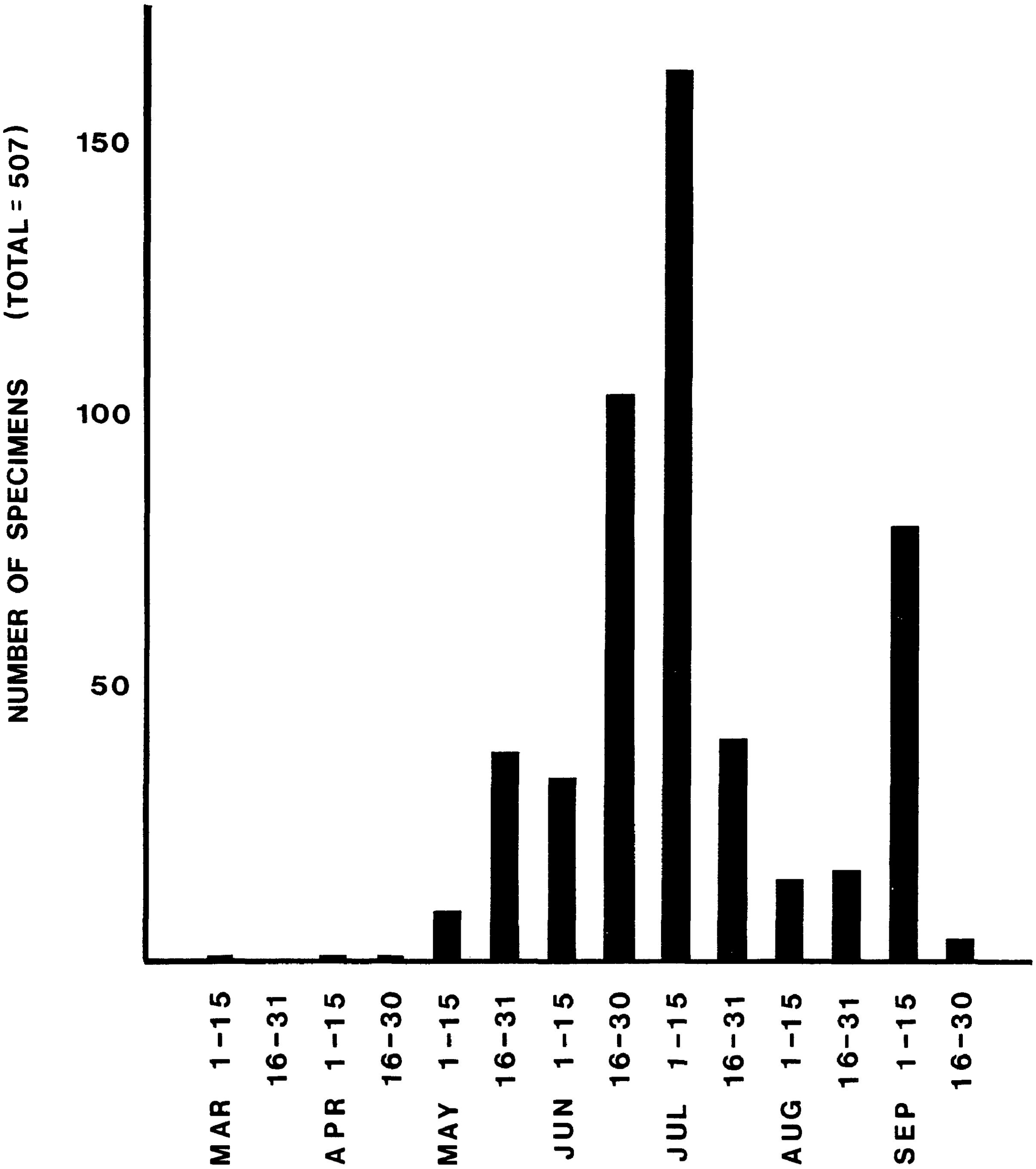

NUMBER OF SPECIMENS (TOTAL = 507)
150
100
50
MAR 1-15
16-31
APR 1-15
16-30
MAY 1-15
16-31
JUN 1-15
16-30
JUL 1-15
16-31
AUG 1-15
16-31
SEP 1-15
16-30

Fig. 77. Collection dates of borrowed adult specimens
of *Cicindela longilabris* Say collected
in Colorado, Utah, Arizona and New Mexico.

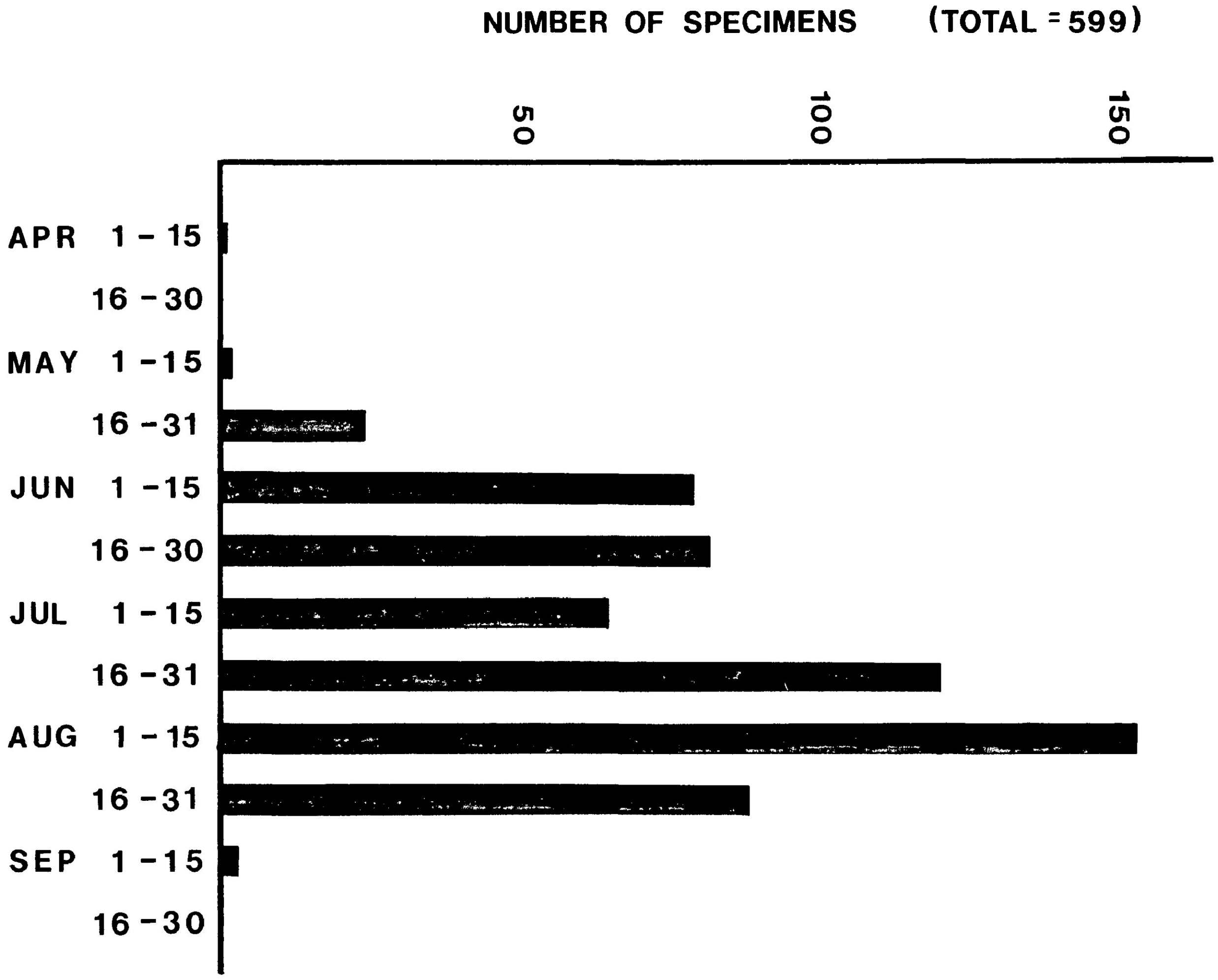

NUMBER OF SPECIMENS (TOTAL = 599)
50
100
150
APR 1 - 15
16 - 30
MAY 1 - 15
16 - 31
JUN 1 - 15
16 - 30
JUL 1 - 15
16 - 31
AUG 1 - 15
16 - 31
SEP 1 - 15
16 - 30

Fig. 78. Collection dates of borrowed adult specimens of *Cicindela nebraskana* Casey.

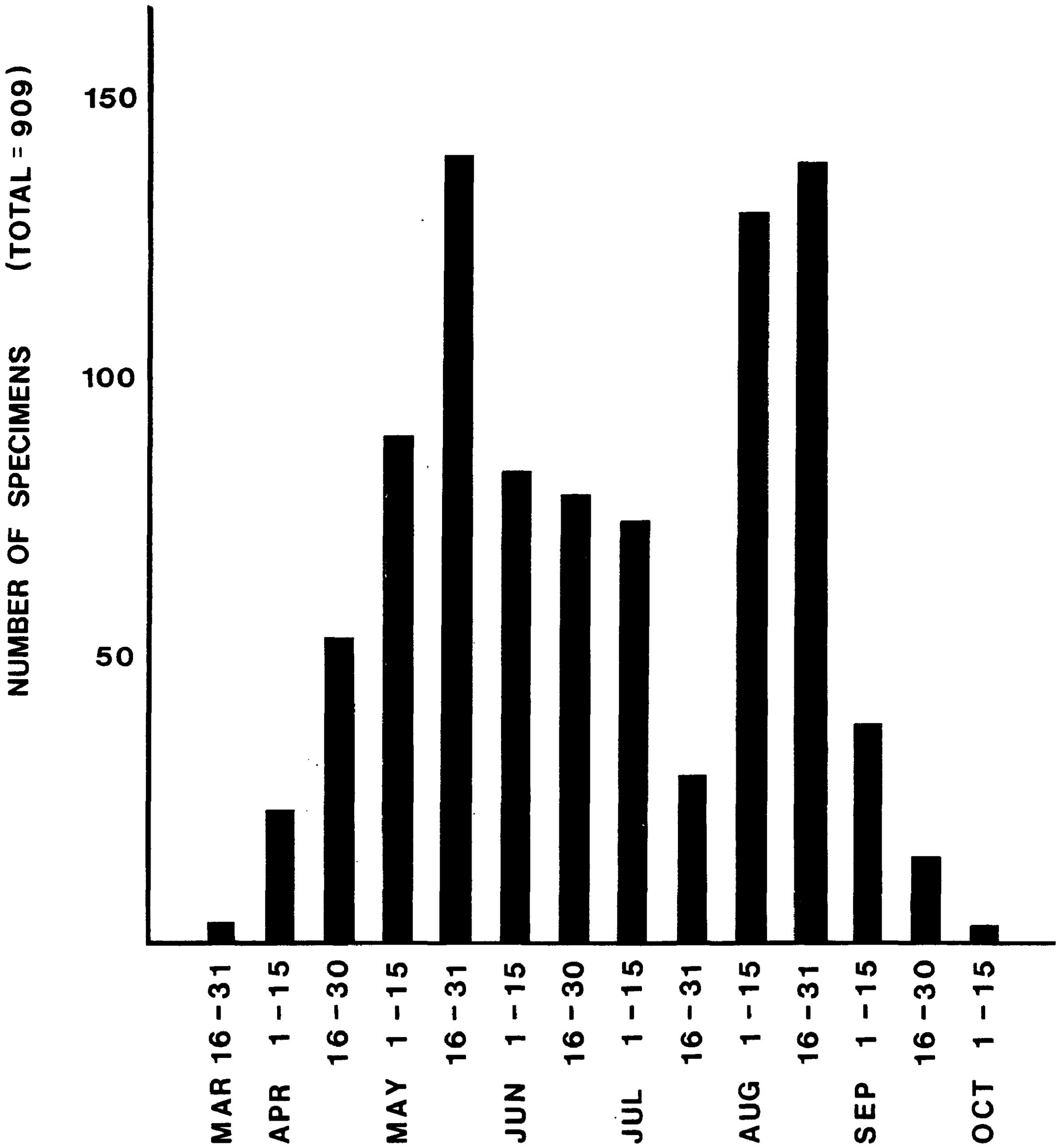

NUMBER OF SPECIMENS (TOTAL = 909)
150
100
50
MAR 16 – 31
APR 1 – 15
16 – 30
MAY 1 – 15
16 – 31
JUN 1 – 15
16 – 30
JUL 1 – 15
16 – 31
AUG 1 – 15
16 – 31
SEP 1 – 15
16 – 30
OCT 1 – 15

Fig. 79. Distribution of *Cicindela longilabris* Say.

● *C. longilabris longilabris* Say

▲ *C. longilabris laurentii* Schaupp

■ *C. longilabris perviridis* Schaupp

○ *C. l. longilabris* x *laurentii* x *perviridis* intergrades

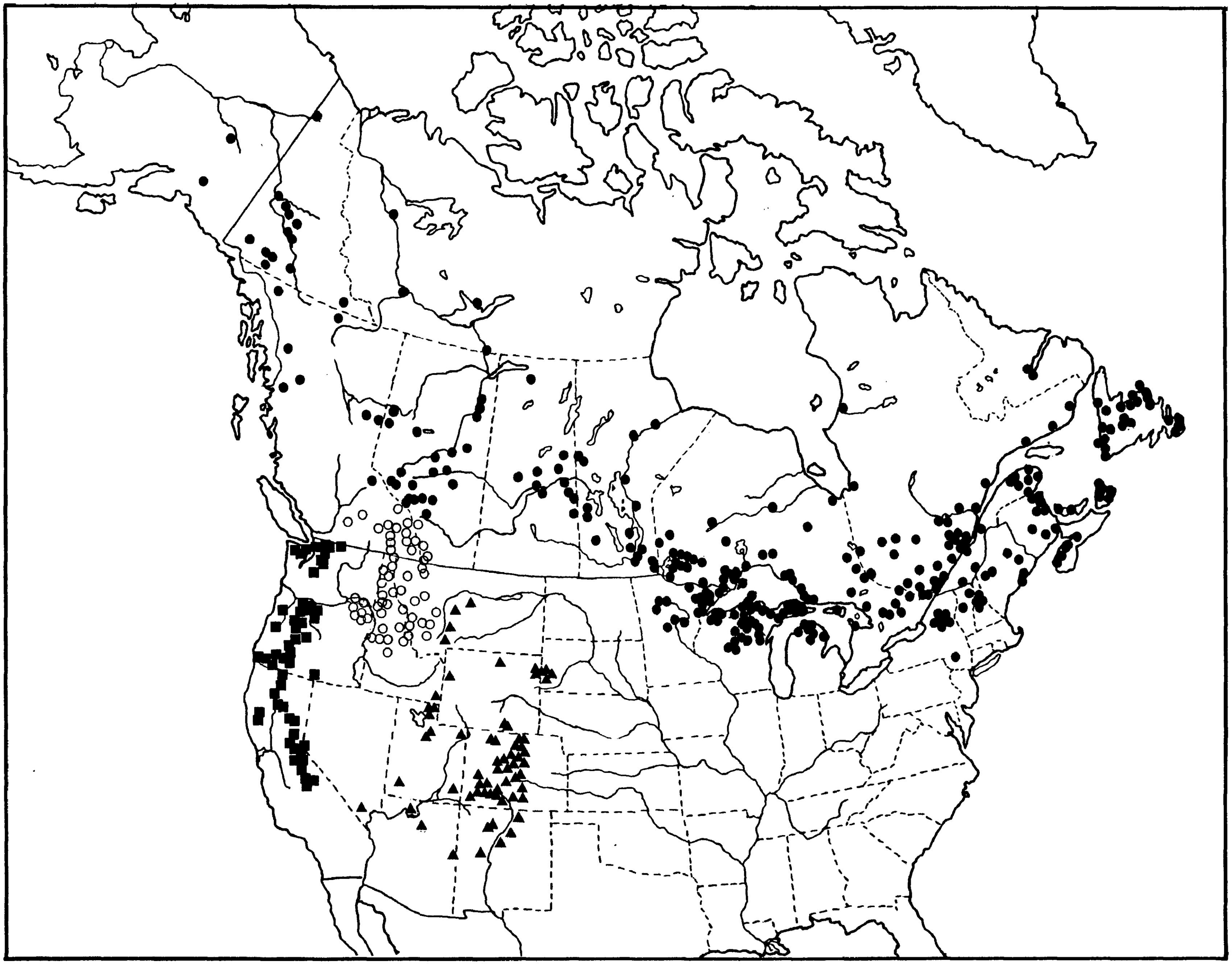


Fig. 80. Distribution of *Cicindela nebraskana* Casey

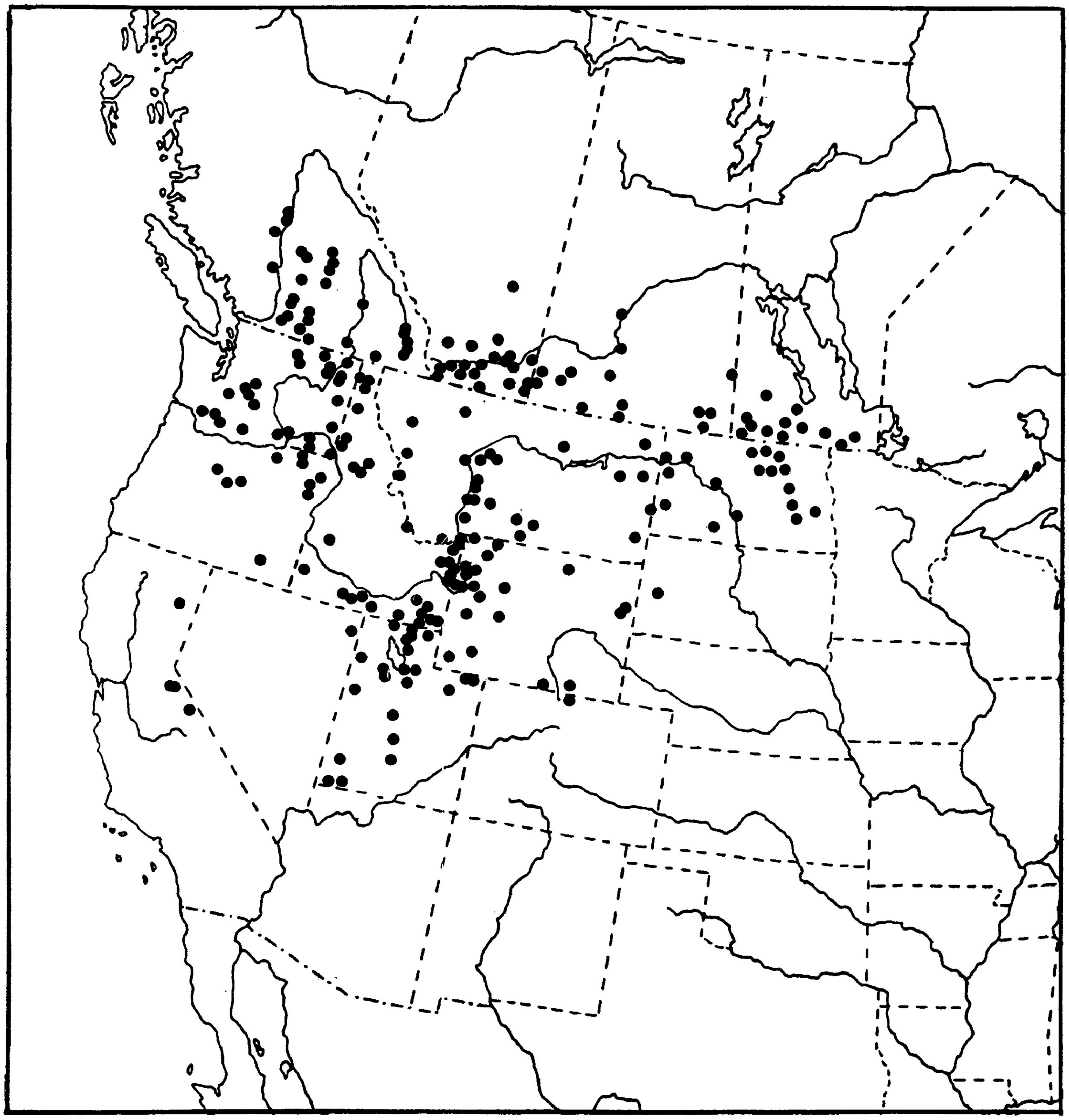
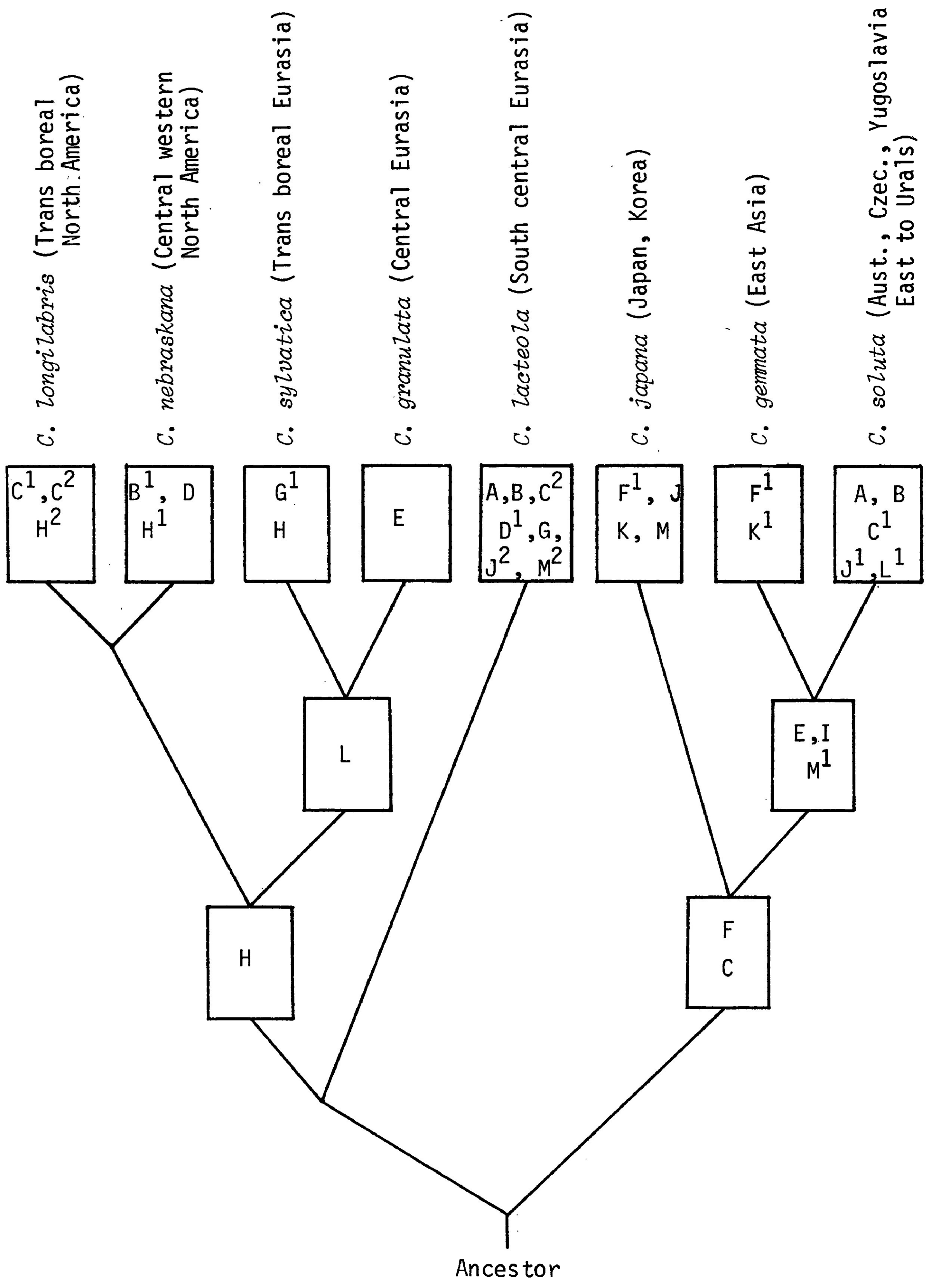


Fig. 81. Reconstructed phylogeny of the *Cicindela sylvatica* group. Letter coded character states are defined in Table 41.


C. longilabris (Trans boreal North America)
C. nebraskana (Central western North America)
C. sylvatica (Trans boreal Eurasia)
C. granulata (Central Eurasia)
C. lacteola (South central Eurasia)
C. japana (Japan, Korea)
C. gemmata (East Asia)
C. soluta (Aust., Czec., Yugoslavia East to Urals)
C1, C2 H2
B1, D H1
G1 H
E
A, B, C2 D1, G, J2, M2
F1, J K, M
F1 K1
A, B C1 J1, L1
L
E, I M1
H
F C
Ancestor