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TIGER BEETLES OF THE PACIFIC NORTHWEST
(COLEPTERA: CICINDELIDAE).

UNIVERSITY OF WASHINGTON, PH.D., 1979

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Tiger Beetles of the Pacific Northwest

(Coleptera: Cicindelidae)

by

Sanford Ross Leffler

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1979

Approved by Robert L. Jaca

Program Authorized
to Offer Degree College of Forest Resources

Date 23 May 1979

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To the memory

of my Brother,

Dr. Lynn Leffler

INTRODUCTION

Tiger beetles are popular with collectors because of their often brilliant colors and "the excitement of the chase" generated by attempts at capturing these agile animals. Also, a large quantity of literature has accumulated since Linnaeus (1758) first brought his "tigrides veloces" into the realm of modern scientific nomenclature. However, development of a gamma taxonomic approach to the study of cicindelid biology is in its infancy. Although adults are fairly well known taxonomically, immature stages are undescribed for most species, and there have been few attempts at correlation of anatomy, behavior, zoogeography, and adaptations. The large number of species, 1,400 - 1,500 worldwide, makes an all-encompassing faunal study cumbersome. Walther Horn (1908 - 1915) presented a worldwide treatment for the *Genera Insectorum*. He listed available literature as it pertained to aspects of cicindelid biology and summarized characteristics, ranges, and synonymies of the world fauna. The classification in use today is based on Horn's work.

Our knowledge has greatly increased and methods of assessing knowledge have changed since 1915. Thus, a study of the scope of Horn's monograph is unfeasible. Another approach is to treat cicindelid biology on a regional basis. To this end, I have chosen the Pacific Northwest fauna. My goal is to present information

concerning systematics, life histories, zoogeography, and adaptations of the 24 species of Cicindelidae from the region consisting of the southern third of British Columbia, Montana west of the Continental Divide, and the entire states of Washington, Oregon and Idaho.

HISTORICAL REVIEW

World Fauna

The majority of the literature on Cicindelidae is taxonomic. Linnaeus (1758) named the genus *Cicindela* and included in it five Palearctic species. Linnaeus did not use any intermediate hierarchical ranks between his "Ordo" and "Genus," but his genera are approximately equivalent to the modern family rank. Latreille (1804) first used the "Family" rank in Coleoptera, placing *Cicindela* in his Cicindélètae, in the identical sense of the present Cicindelidae (Watt, 1974). W. Horn (1908 - 1915) reviewed the worldwide fauna, recognizing 1,299 species in 35 genera. He summarized all available literature, presented synonymies, and included lengthy discussions of interrelationships and bionomic aspects. His classification is basically the one in use today. Excluding additions or synonymy of species and subspecies and elevation of a few former subgenera to generic rank, there was little change from Horn's concepts until Rivalier (1950, 1954, 1958, 1961, 1963) divided the genus *Cicindela sensu* Horn into 55 genera. Rivalier (1969) similarly divided the pantropical genus *Odontochila*, although not to so great an extent as he did *Cicindela*. Finally, Rivalier (1971) attempted to redefine subtribes within the tribe Cicindelini.

species of the subgenus *Ellipsoptera* Dokhturow. Willis (1968) published the most recent key to the Nearctic species of *Cicindela*. Rivalier (1954) arranged the new world species of *Cicindela* among 12 genera and subgenera, which I accept; however, for all 12, I use the subgeneric rank.

Details of distributions of the Nearctic fauna are known for few species. W. Horn, Leng and Schaupp gave brief, telegraphic range outlines but with no specific localities. A number of state lists have been published, and Cazier (1954) and Wallis (1961) presented maps for all the species of Mexico (*Cicindela* only) and Canada, respectively. Complete distribution maps exist for *Omus* (Cazier, 1942), *Amblycheila* (Vaurie, 1955), and 12 species of *Cicindela* (Freitag, 1965 [3]; Leffler and Pearson, 1976, and Maser, 1973 [1]; Willis, 1967 [8]).

Hamilton (1925), Shelford (1908) and Willis (1967) are responsible for most of our knowledge of larval cicindelids, but unquestionably correctly identified larvae of only 31 species have been described. Pupae have been described (Balduf, 1935; Shelford, 1908; Willis, 1967) but have never been studied systematically.

Bionomic studies are few in number, most of the literature having been devoted to taxonomy and little to interrelationships, morphological adaptations, or habitat preferences. Freitag (1965, 1974), Shelford (1908, 1917) and Willis (1967) have presented the most extensive bionomic studies.

Pacific Northwest Fauna

Four authors described 13 (or 54.2%) of the 24 species found in the Pacific Northwest: T. L. Casey - 4 (16.7%); J. L. LeConte - 4 (16.7%); T. Say - 3 (12.5%) and L.-J. Reiche - 2 (8.3%). Eleven other authors each described one species. Thirty-one species and subspecies are here recorded for the Pacific Northwest, the names or descriptions of four of which are either in press or in preparation. Of these taxa, 13 are based on specimens from the Northwest. Typological details are presented in Appendix II.

Literature particularly devoted to the Pacific Northwest cicindelid fauna, other than those papers in which new taxa are described, is limited. Hatch (1938) presented the first list and key to Washington species. Leffler and Pearson (1976) updated Hatch's list. Wallis (1961) included British Columbia species in his survey of the Canadian fauna. No published state lists are available for Idaho, Montana or Oregon. Hatch (1953) published a key and gave a brief outline of the distribution for the entire geographic region treated in the present report. Bionomical studies of Northwest fauna are limited to short statements in papers of scopes not emphasizing the Northwest. Details for *Omus* spp. were written by Cazier (1942), for *Cicindela arenicola* (Rumpp, 1967), for species of the *maritima*-group of *Cicindela* (Freitag, 1965, 1972) and for *Cicindela bellissima* (Leffler, in press) and Maser (1973). Willis (1967) revised *C. willistoni* and included Oregon specimens in his statistical samples.

OBJECTIVES

General Objective

The overall objective of this study is to clarify systematics and habitat parameters of the 24 species of Cicindelidae in the Pacific Northwest.

Specific Objectives

1. Present outlines of diagnostic characters, ranges, subspeciation and relationships of suprageneric taxa in the Cicindelidae, and particularly of the three species of *Omus* and 21 species of *Cicindela* inhabiting the Pacific Northwest.
2. Describe larvae and pupae of available species, their morphological adaptations and systematic implications.
3. Correlate distributions with physiographic provinces and historical geology.
4. Delineate soil parameters, habitat preferences, and correlate 2nd gonapophysis proportions with soil particle size distribution.

METHODS AND MATERIALS

Methods

Rearing Larvae

Materials

1. Plastic vials
2. Soft-bodied live food: wax moth larvae, young cricket nymphs, fly maggots, termites, etc.
3. Tissue-lined petri dishes

Procedure

1. One larva (they are highly cannibalistic) is placed in an uncovered vial filled with tamped-down (not compacted), damp (but not wet) soil. I find a 40-dram vial ideal for rearing all but the very smallest species. Ideally, the soil used should be that in which the larva originally lived, but I have successfully reared several species in other soils. The soil level should be no closer to the vial's mouth than a distance greater than the total extended length of the larva, as the larva may leave its burrow and escape. Covering the vial or placing it in a second deep container will prevent escape.

2. The larva should be allowed to become acclimatized for 24 hours following the digging of its burrow. Live food of appropriate size is placed carefully on the larva's head or down its burrow (head first is preferred, as then the food item will crawl down the burrow). Feedings once every day or two will insure the health of the larva.

3. The soil surface should be checked every few days for mites and fungal hyphae, as these may kill the larva. If they are present, the soil should be changed and the larva washed with lukewarm water.

4. If the larva closes its burrow, it is often ready to molt or pupate, although a well-fed larva may close its burrow for a few days, presumably to digest its latest meal. Burrow closure is also a sign of ill-health or inadaptability to captivity. If, after two weeks, the burrow has not yet been reopened, the condition of the larva should be checked. A prepupa or pupa will develop normally if removed from its burrow. A well-fed or unhealthy larva will make a new burrow, the former often leaving the new burrow, but the latter usually closing it. *Omus* spp. and *C. purpurea* proved difficult to rear and would repeatedly close their burrows and refuse all food. In such cases, nothing can be done.

5. Frequently, the burrow will be located along the wall of the vial so direct observation of the larva is possible. If the burrow is not in such a position, the larva may be dug up repeatedly until it does construct such a burrow. Light shining on such an exposed burrow will eventually cause the larva to plaster soil over

the exposed burrow side, cutting off the light and, unfortunately, the observer's view. A sleeve around the vial will offset this problem and it can be removed temporarily for observation.

6. If such a view is possible, the larva's behavior may be observed. When the larva prepares for pupation, it greatly enlarges the bottom of the burrow into a pupal chamber and then closes the burrow. After a few days, it assumes a suppine position, head uphill. It may be left in the burrow until the adult eclodes or it may be removed.

7. The prepupa may be placed in a petri dish lined with lightly-dampened tissue. The tissue must be wrinkled to give the prepupa and the ecloding adult a sufficiently rough surface to push against during ecdysis. A smoothed substrate may not offer enough purchase against which the insect can push. Thus, ecdysis cannot be completed and the insect will die. Removal of the prepupa or pupa to a petri dish is desirable because color changes may be observed in unhampered view.

Techniques for Cleaning Specimens

Rationale

It was quickly apparent upon microscopic examination of specimens at 30X magnification, that some structures were often obscured by secretions, sand-grains, dust and other unwanted materials. Preservation in alcohol of adults followed by air-drying

resulted in matting of setae. Fat of adults might ooze onto the surface of the cuticle, staining maculation and holding dust. Larval pronota might be covered with a secretion (autochthonous or from body fluids of prey) to which soil particles were glued. Thus, I had to devise cleaning techniques to be used for some specimens before study.

Larvae and Pupae

Materials

1. Commercial liquid dishwashing detergent
2. 50% ethanol
3. Appropriate containers for soaking and permanent storage
4. Tap water
5. 70% ethanol

Procedure

1. Fix a specimen in 70% ethanol or some other suitable preservative. Soak it for about 24 hours (a period of convenience, rather than necessity) with occasional vigorous shaking in a solution consisting of several drops of detergent in 50% ethanol.

2. Rinse the specimen with tap water a few times to remove all traces of detergent.

3. Soak the specimen in tap water three hours (longer than three hours might result in the onset of disintegration and loss of setae).

4. Place the specimen in 70% ethanol or other suitable preservative for permanent preservation.

Adults

Materials and equipment

1. Fresh, dried or fluid-preserved specimen
2. Commercial liquid dishwashing detergent
3. 50% ethanol
4. Appropriate containers for soaking
5. Tap water
6. Containers with 30, 50, 70, 95 and 100% ethanol
7. Toluene
8. Insect pins appropriate for size of specimen

Procedure

1. Soak a specimen (fresh, dried and pinned, or fluid-preserved) for about 24 hours (a period of convenience, rather than necessity), with occasional shaking only after several hours to prevent breakage of appendages, in a solution of several drops of detergent in 50% ethanol.

2. Rinse the specimen with tap water a few times to remove all traces of detergent.

3. Place the specimen successively through a dehydration series of 30, 50, 70, 95 and 100% ethanol, 30 minutes in each.

4. Place the specimen in toluene for 12 hours.

5. Remove the specimen from the toluene and air-dry until the cuticular surface is no longer "wet" with toluene. The breath or a gentle flow from an air hose can be used to speed up air-drying.

6. Pin the specimen on a pinning board and neatly arrange legs and antennae.

Upon subsequent microscopic examination, I found that this process results in a specimen that is lipid-free and with unmatted setae. It is important that the specimen is arranged properly on the pinning board. Legs and antennae in slovenly disarray often result in breakage and can obscure sutures and waste time during measurements.

Burrow Casting Techniques

Materials

Note: I used a sterno stove, tin can and candles, and found such primitive materials cheap and completely suitable. More elegant equipment may be used, of course, but probably would not improve results.

1. Portable stove
2. Wax (paraffin, household candles, etc.)
3. Container for melting wax modified for pouring
4. Suitable digging tools (ice pick, knife, etc.)

5. Tissue paper

6. Small, sturdy box

Procedure

1. Care should be taken in choosing the burrow to be cast. Most *Cicindela* burrows are in exposed situations on fairly flat ground. Burrows on steep slopes or those in or surrounded by vegetation were chosen only when there was no other choice, as with *Omus*. The reason is that it is difficult to pour wax down a burrow located on a steep slope, and vegetation may have roots which complicate excavation efforts.

2. Melt wax over the stove in a container until near the ignition point. Extremely hot wax is absolutely essential so that it pours easily down the burrow and does not congeal quickly upon contact with cold or wet soil (moisture in the soil often boiled when the hot wax hit it).

3. While the wax is melting, clear debris away from the area around the mouth of the burrow, taking care not to damage the burrow mouth itself or drop materials into it. In the case of a burrow on a slope, a downslope retaining wall can be built to insure that as much wax as possible will enter the burrow.

4. Pour hot wax down the burrow as quickly as possible until it overflows. Several burrows can be filled, as long as there is

sufficient wax which is hot enough. Pour sufficient wax to cover the area around the burrow mouth for a radius of at least one centimeter.

5. Allow at least 15 minutes for the wax to congeal completely.

6. Evacuate the wax cast slowly and carefully with appropriate digging tools, keeping in mind that, depending on the quality of the wax, the cast can be fragile. Being broken into pieces, so long as all pieces are recovered, will not reduce the utility of the cast, but may make it more difficult to handle. A one-half hour excavation period is common.

7. Make a label and carefully wrap it and the cast in tissue and place in a sturdy box for transport or storage.

8. Remove adhering soil particles in the laboratory by soaking the cast in cold water. Hot water softens and warps the cast, or, worse, melts it.

As the larva occupying the burrow becomes imbedded in the wax of the cast, usually at the bottom end, it becomes unavailable for identification or study, although its location can be discerned. Should it be necessary to extract the larva, a mold must be made of the entire burrow, using an appropriate latex or resin. This must be done quickly after the wax cast is made, as the larva is cooked by the wax and begins to deteriorate within a few hours (after 48 hours, only heavily chitinized portions and a brown "soup" remained of an L3 *Omus audouini*). After a mold is made, the larva can be

dissolved from the wax with some suitable organic solvent such as toluene. This, of course, destroys the cast.

Technique for Clearing Aedeagi and Elytra

I have attempted several of the techniques presented in the literature for clearing aedeagi for study, but without success. Dr. J. M. Kingsolver, National Museum of Natural History (pers. comm., 1976) gave me his method for clearing whole beetles, a technique I have adapted with excellent results. Initial relaxing of a specimen from which an elytron or aedeagus is to be removed can be the same (the same specimen can be utilized for both extractions). If an elytron only is required, it can be detached from a fresh, fluid-preserved or dried specimen with forceps.

Procedure for Extraction of Aedeagus

1. A dry specimen must be relaxed. A fresh or fluid-preserved specimen requires no initial preparation.

2. Pull the aedeagus through the genital opening or dissect it out through the dorsal surface of the abdomen.

Procedure for Clearing

Materials and equipment

1. Water bath at 100°C
2. 5% NH_4OH (household ammonia will suffice)
3. 2% H_2O_2
4. Forceps
5. Appropriate glass containers and storage vials
6. 70% E+OH

Procedure

1. Set up a water bath heated to 100°C.

2. Place a vessel with two parts NH_4OH and one part H_2O_2 on the water bath and bring to boiling. Replenish both chemicals periodically to make up for losses caused by evaporation and heat destruction.

3. Place the aedeagus or elytron into this liquid and leave until cleared, about five minutes.

4. Rinse the specimen in cold water and store in a stoppered vial of 70% E+OH cross-labelled with the pinned specimen from which it was extracted.

5. Immediately after clearing, evert the inner sac by squeezing it through the aedeagal orifice with forceps. Often, boiling in the clearing fluid everted the inner sac.

Soil Testing Techniques

Preparation and testing of soil samples follows the procedure given by Ugolini (unpubl. class syllabus), in turn following Black (1965).

Collection and Storage of Soil Samples

Materials and equipment

1. "Sharp-shooter" shovel
2. 4-liter plastic bags
3. 2-liter, doubled paper bags

Procedure

Place soil samples collected in the field by means of an elongate shovel in plastic bags temporarily until they can be transported to the laboratory. In the laboratory, remove each sample from the temporary container and air-dry at room temperature. Then place each sample in a doubled paper bag labelled with the locality and a list of associated tiger beetle species, and store until time for testing.

Initial Preparation of Samples for Testing

Materials and equipment

1. Rolling pin
2. Balance
3. Assembly of U.S. Standard Sieves, one each of 4.76 mm^2 and 2 mm^2 mesh, cover and collecting tray
4. 3 4-liter plastic bags with ties for each sample

Procedure

1. Most samples, particularly those with a high percentage of sand, require no initial preparation. Some clayey samples form massive aggregates upon drying and require breaking up with a rolling pin.

2. Weigh each entire sample, this weight to be used as the base against which particle-size percentages are determined.

3. Separate a sample into three fractions by sieving through an assembly of two U.S. Standard Sieves, one each of 4.76 mm^2 and 2 mm^2 diameter mesh screen. This separates the sample into a fraction of particles greater than 4.76 mm diameter, between 2 and 4.76 mm, and less than 2 mm.

4. Weigh the two larger diameter fractions and record the ratio of each weight to the total sample weight.

5. Retain the smallest diameter fraction for further analyses.

pH

Samples are treated differently, depending on the result of gross examination of sand content. If a sample is perceived as being mainly sand (i.e., from a sand bar or dune), procedure A is followed; otherwise, procedure B is used. Samples are drawn from the fraction of particles less than 2 mm diameter obtained by sieving.

Materials and equipment

1. 250 ml beaker
2. Glass stirring rod
3. Distilled water
4. 0.01 M $CaCl_2$ solution (0.1 gm $CaCl_2$/100 ml H_2O)
5. Corning Model 12 research glass electrode Ph meter

Procedure A

1. Stir 5 gm of soil thoroughly with 20 ml distilled water in a beaker with a glass stirring rod.
2. Allow the mixture to stand 30 min to come to equilibrium.
3. Stir the mixture thoroughly and allow to settle for 20 sec.
4. Take a reading with a pH meter and record it.

Procedure B

1. Stir 5 gm of soil with 20 ml 0.01 M $CaCl_2$ solution.

2 - 4. Same as Procedure A.

Electroconductivity

Materials and equipment

1. Distilled water
2. 250 ml plastic centrifuge bottle
3. Centrifuge
4. Yellow Springs Instrument Model 31 Conductivity Bridge

Procedure

Samples were drawn from the fraction of particles less than 2 mm diameter obtained by sieving.

1. Mix 5 gm soil and 25 ml distilled water thoroughly in a centrifuge bottle.
2. Allow the mixture to stand 30 min to come to equilibrium.
3. Centrifuge the sample at 2,750 RPM for 4 min.
4. Pour the supernate into the conductivity cell of a conductivity bridge; note and record the reading in micromhos/cm.

Particle Size Distribution

Samples are drawn from the fraction of particles less than 2 mm in diameter obtained by sieving. Before the actual analysis is performed, it is necessary to remove organic material and free iron from each sample because their presence aggregates some small particles, giving incorrect determination of silt and clay fractions.

Organic matter removal

Materials and equipment

1. Liquid laundry bleach (5% NaOCl solution) buffered to pH of 9.0 with HCl
2. Antifoam B reagent or 95% E+OH
3. 250 ml plastic centrifuge bottle
4. 100 ml graduated cylinder
5. Thermometer
6. Glass stirring rod
7. Balance
8. Water bath at 70°C
9. Centrifuge
10. Saturated NaCl solution

Procedure

1. Place 100 gm of soil in a centrifuge bottle.
2. Add 200 ml of buffered bleach slowly to minimize any violent chemical reaction. The bleach is buffered because the high alkalinity of unbuffered bleach may degrade some clay minerals. A few drops of antifoam B reagent or 95% E+OH is added if foaming is particularly vigorous.
3. Allow the bottle to stand until foaming ceases.
4. Place the bottle on a water bath at a temperature near 80°C (the exact temperature is unimportant), stir, and allow to settle for 15 min.

5. Centrifuge the bottle at 2,500 RPM for 15 min.

6. If the supernate is cloudy, indicating that dispersion of clay has occurred, 30 ml saturated NaCl solution is added. If no such cloudiness is present, this step is omitted.

7. Thoroughly stir the bottle's contents and add a small amount of bleach. If no foaming occurs, the sample is ready for iron removal. If foaming does occur, steps 2 through 7 are repeated. The samples can be stored in covered containers until time for further treatment is convenient, or iron removal may be performed immediately.

Removal of iron

Iron has to be removed from every sample because it could otherwise aggregate some particles. A sample from which organic matter has been removed is used directly for iron removal.

Materials and equipment

1. 300 ml prepared citrate-buffer solution (consisting of 225 gm sodium citrate, 25 gm sodium bicarbonate, and 3.5 l distilled water), divided into two portions, 200 ml and 100 ml
2. Water bath at 75-80°C
3. 8 gm of sodium dithionate powder
4. Stirring rod
5. Thermometer
6. Centrifuge
7. Evaporating dish

Procedure

1. Centrifuge the sample at 2,500 RPM for 15 min, pour off the supernate, stir with distilled water, recentrifuge and pour off the supernate.

2. Stir the sample with 200 ml citrate-buffer solution.

3. Place the sample on a water bath until the temperature reaches 75-80°C.

4. Stir in 8 gm of sodium dithionate powder, slowly to prevent vigorous foaming; leave the sample on the water bath for an additional 10 min.

5. Centrifuge the sample at 2,500 RPM for 15 min.

6. If the supernate is dark brownish-red in color, indicating a high iron content, repeat steps 2 through 5. If the color is only yellowish, pour off the supernate and stir the soil with 100 ml citrate-buffer.

7. Centrifuge the sample at 2,000 RPM for 2 min.

8. Pour off the supernate and stir the sample with a small quantity of distilled water.

9. Transfer the sample to an evaporating dish and allow to air-dry at heat in an oven no hotter than 60°C for 24 hours.

Particle-size analysis

Materials and equipment

1. Drying oven at 105°C

2. Covered metal can

3. Liter graduated cylinder

4. Plunger

5. Standard hydrometer, ASTM No. 152H, with Bouyoucos scale in gm/l.

6. Semilogarithmic paper

7. Thermometer

Procedure

1. Fill a graduated cylinder with one liter of distilled water.

2. Calibrate the hydrometer in the cylinder and record the reading of the calibrated hydrometer in distilled water as R_L.

3. Take and record ambient air temperature.

4. Place 5 gm of soil from which organic matter and iron have been removed in a covered metal can and place in a drying oven at 105°C for 24 hours. After drying, reweigh it and multiply the weight by 8 (to give a weight equivalent to 40 gm of soil). Record the adjusted weight as C_o.

5. Place 40 gm of soil from which organic matter and iron have been removed in the water-filled liter cylinder and thoroughly mix with a plunger.

6. Carefully lower the hydrometer into the suspension and after 30 sec, record the reading as R_1.

7. Leave the hydrometer in the suspension 30 sec more (total elapsed time from T_0 = 60 sec) and record the reading (R_2). Remove the hydrometer.

8. Take readings (R_{3-9}) respectively at 3, 5, 10, 30, 90, 270 and 480 min, without stirring the suspension, and record, recording temperatures (T_{3-9}) as well.

Calculations

1. Calculate for each reading (R_{1-9})

$$C = R - R_L$$

where C = concentration of suspension

$R = R_{1-9}$

R_L = reading at T_o

2. Calculate

$$P = 100\ (C/C_o)$$

where P = summation percentage

C is derived from equation 1: $C = R - R_L$

C_o = oven-dried corrected weight of soil (procedure step 4)

3. Calculate

$X = \sqrt{t}$ for each variable R_{0-9}

where X = particle size diameters

t = cumulative sedimentation time at each reading R_{0-9}

= sedimentation parameter from published tables corrected when t = 30°C by multiplying by $\overline{t}/30$

where t = temperature for each variable R_{0-9}

4. Plot on semilogarithmic paper P vs X using the semilog scale for X. Interpolate from the curve the summation percentages at the values of X:0.002, 0.05, and 2.0 mm.

5. Read the percentages of sand, silt and clay from the X-axis of the graph (P):

Sand = 0.05-2.0 mm

Silt = 0.002-0.05 mm

Clay = 0.002 mm

6. Determine the soil class from the soil texture triangle in Brady (1974:49).

Computer Analysis

Characters of most Pacific Northwest species are easily enough studied that statistical procedures were unnecessary. I analyzed statistically series of 120 *Cicindela bellissima*, 280 *C. longilabris*, and 167 *C. nebraskana*. Characters and localities are listed in the respective species accounts.

I took all measurements used in the statistical analysis using a calibrated ocular micrometer. In addition, some qualitative characters were coded appropriately for analysis by the computer used. Measurements were used for discriminant analysis using SPSS (Statistical Package for the Social Sciences) procedures as described by Nie (1975). Discriminant analysis was performed using SPSS version 7.0 as maintained on the University of Washington Academic Computer Center Operating System. Programs were written and character coding done with the aid and direction of Mr. Charles M. Fornia, College of Forest Resources, University of Washington.

Scanning Electron Microscopy

Elytral fragments of eight species of *Cicindela* were examined using the scanning electron microscope. I cut out triangular pieces from the left elytron near the suture at a point about halfway along the total length of the elytron. The pieces were cleaned in a 1:1 solution of ethanol-ether, mounted on Cambridge specimen mounts using silver conductive paint, and coated with palladium in a Varian Micros model VE-10 vacuum evaporator.

The coating and scanning electron microscopy were done by Mr. Warren Lindholm at the University of Washington Department of Mining, Metallurgical and Ceramic Engineering Materials Analysis Center on a Cambridge Stereoscan Electron Microscope, Model Mark 2A

using an accelerating voltage of 20 kv. Micrographs were taken on Polaroid 12.7 x 10.2 cm black-and-white Land Film type 55/positive-negative.

Species photographed were: *C. cinctipennis, longilabris, nebraskana, plutonica, pugetana, purpurea, terricola* and *tranquebarica*.

Materials

List of Abbreviations

Specimens in the collections of the following institutions and persons have been examined. The abbreviations are those used in the text and in Appendix I to indicate these collections. Certain publications have been used frequently in the locality compilation of Appendix I and abbreviations for these are included in their respective positions in the following alphabetized listing:

AM	American Museum of Natural History, New York City
BCP	British Columbia Provincial Museum, Victoria
CM	Chris Maser collection
CN	Canadian National Museum, Ottawa
DF	Donald R. Frechin collection
DP	David L. Pearson collection
DS	D. H. Smith collection

FMB	Frank M. Beer collection
F65	Publication: Freitag (1965)
HLW	Harold L. Willis collection
H38	Publication: Hatch (1938)
JS	John Stamatov collection
L-P	Publication: Leffler and Pearson (1976)
NM	National Museum of Natural History, Washington, D.C.
ODA	Oregon State Department of Agriculture, Salem
OSU	Oregon State University (includes Hatch and former University of Washington collections)
RB	Russell Biggam collection
RW	Richard C. Wescott collection
SL	Sanford R. Leffler collection
UALTA	University of Alberta, Edmonton
UBC	University of British Columbia, Vancouver
UC	University of California, Berkeley
UCD	University of California at Davis
UI	University of Idaho, Moscow
UMT	University of Montana, Missoula
VC	Vernon G. Clifford collection
WSU	Washington State University, Pullman

RESULTS AND DISCUSSION

Classification and Checklist of Cicindelidae of the Pacific Northwest

Family Cicindelidae Latreille

Subfamily Cicindelinae Latreille

Tribe Megacephalini

Subtribe Omina Castelnau

Omus Eschscholtz

O. dejeani Reiche

O. californicus Eschscholtz

O. c. californicus Eschscholtz

O. audouini Reiche

Tribe Cicindelini Latreille

Subtribe Cicindelina Latreille

Cicindela Linnaeus

C. (*Cicindela*) Linnaeus

maritima - group

repanda - subgroup

C. (*C.*) *repanda* Dejean

C. (*C.*) *r. repanda* Dejean

C. (*C.*) *oregona* LeConte

C. o. oregona LeConte

C. o. oregona x *guttifera*

C. (*C.*) *depressula* Casey

C. d. depressula Casey

C. d. eureka Fall

C. d. depressula x *eureka*

limbata - subgroup

C. (*C.*) *columbica* Hatch

C. (*C.*) *bellissima* Leng

C. b. bellissima Leng

C. b. n. ssp. Leffler

C. (*C.*) *arenicola* Rumpp

C. a. arenicola Rumpp

C. a. n. ssp. Clifford

formosa - group

decemnotata - subgroup

C. (*C.*) *decemnotata* Say

C. d. decemnotata Say

C. d. n. ssp. Clifford

purpurea - subgroup

C. (*C.*) *purpurea* Olivier

purpurea - section

C. p. auduboni LeConte

lauta - section

C. p. lauta Casey

C. p. new name Leffler

C. p. lauta x new name Leffler

C. (*C.*) *plutonica* Casey

C. (*C.*) *pugetana* Casey

sylvatica - group

C. (*C.*) *longilabris* Say

C. l. laurenti Schaupp

C. l. perviridis Schaupp

C. l. laurenti x *perviridis*

C. (*C.*) *nebraskana* Casey

C. n. chamberlaini Knaus

C. n. chamberlaini x *nebraskana*

pulchra - group

C. (*C.*) *parowana* Wickham

C. p. parowana Wickham

C. p. platti Cazier

C. p. parowana x *platti*

C. p. wallisi Calder

C. (*Cicindelidia*) Rivalier

willistoni - group

C. (*C.*) *amargosae* Dahl

C. a. nyensis Rumpp

C. (*C.*) *willistoni* LeConte

C. w. echo Casey

carthagena - group

C. (*C.*) *haemorrhagica*

C. h. nigroides Hatch

C. (*Tribonia*) Rivalier

lengi - group

C. (*T.*) *tenuicincta* Schaupp

C. (*T.*) *lengi* W. Horn

C. l. versuta Casey

tranquebarica - group

C. (*T.*) *tranquebarica* Herbst

tranquebarica - section

C. t. "kirbyi" auct.

vibex - section

C. t. vibex G. Horn

C. t. "kirbyi" x vibex

C. (*Cylindera*) Westwood

C. (*C.*) *cinctipennis* LeConte

C. c. imperfecta LeConte

Hypothetical, Accidental, Doubtful and Erroneous Records

Eleven species and subspecies of *Cicindela* have status in one or another of these four categories in the Pacific Northwest.

Hypothetical

1. *C. duodecomguttata* Dejean. Freitag (1965:110) reported this species from MT. Cascade Co., Ulm. This locality is 117 km east of the Continental Divide. The species is riparian and could follow rivers westward to some of the lower mountain passes. However, there it would contact *C. oregona*, a species with which it hybridizes northward.

2. *C. limbalis* Klug. Hatch (1953:38) recorded this species from northern Idaho. I have been unable to locate such specimens. However, Dr. D. L. Pearson has collected the species at MT. Glacier Co., 11.7 km N. St. Marys, just east of Glacier National Park. In view of the species' preference for steep clay banks, it could follow road cuts westward.

3. *C. nevadica* LeConte. This inhabitant of saline situations was collected by Johnson (1975:22) from NV. Humboldt Co., Valmy, 142 km south of the Oregon border. The locality is in the Humboldt River drainage and the species may either be a recent invasion or of a remnant of a circum-Pluvial Lake Lahontan distribution. In either case, it could follow river courses northward into Oregon and Idaho.

Accidental

1. *C. macra macra* LeConte. Willis (1971:8) determined a specimen originally reported by Fender (1945:66) as *C. cuprascens* LeConte as being this species. It was found dead in a mail sack sent from Council Bluffs, Iowa, to McMinnville, Oregon. Perhaps individuals so dispersed could escape and become established. The specimen is preserved in the Hatch Collection, OSU.

2. *C. punctulata* Olivier. As in the case of *C. macra*, this species was reported by Fender (1945) in mail sacks sent from Council Bluffs, Iowa, to McMinnville, Oregon. Some of the specimens were still alive. I have a specimen from UT. Uinta Co., Ashley Natl. For., 16 July 1966. This region and northwestern Colorado, where the species is abundant along road cuts, form a source from which this eurytopic species might extend its range into southeastern Idaho.

Doubtful

1. *C. purpurea cimarrona* LeConte. Wallis (1961:39-40) reported this distinctive subspecies from BC. Canal Flats and Victoria. Dr. A. Smetana, Canadian National Museum, was unable to verify the former record; neither was I in either the BCP or UBC collections. As this subspecies is found in southeastern Colorado and parts of adjacent states, I doubt its presence in British Columbia, insofar as the different *C. p. auduboni* is found

throughout the intervening area. A specimen in the BCP from BC. Victoria is an aberrantly-marked *C. p.* new name Leffler and certainly unlike *C. p. cimarrona*. It is, however, possible that this is the specimen to which Wallis alluded.

2. *C. splendida* Hentz. G. Horn (1872) recorded this species from southeastern Idaho. As it is ordinarily found east of the Rocky Mountains, I question this record. Either the material is misidentified, or perhaps what was then called "Idaho" was actually part of Montana or Wyoming. The record needs verification.

Erroneous

1. *C. denverensis* Casey. Hatch (1953:38) listed this western Great Plains species from eastern Washington and southern Idaho. I have examined the specimens (OSU), finding that the former are *C. pugetana* and the latter, *C. plutonica*.

2. *C. propinqua* Knaus *nec* Chaudoir. Specimens in the Hatch Collection, OSU, under this name are actually *C. pugetana*. *C. propinqua* is a preoccupied synonym of the extralimital and unrelated *C. arida* Davis.

3. *C. p. purpurea* Olivier. This is an eastern subspecies. Reddish-violet coloration occurs to varying degrees in *C. p. audubboni*, and it is the most extreme of these which Hatch (1953:37) erroneously referred to the nominate race.

4. *C. tranquebarica horiconensis* Leng. After examination of the lectotype, I consider this form indistinguishable from

C. t. tranquebarica Herbst. At any rate, Hatch (1953:39) reported it from several places in the northwest. Specimens from southeastern Idaho and eastern Oregon with complete humeral lunules are *C. t. "kirbyi"* x *vibex*. This character-state occurs in low frequency in western Washington *C. t. vibex* and nearly so in eastern Washington and British Columbia. The specimens are not the northeastern Nearctic nominate race.

Life History

General biological information on Cicindelidae is widely scattered through the literature. The most comprehensive reviews of *Cicindela* life histories are by Balduf (1935), Criddle (1907, 1910), Hamilton (1925), Shelford (1908), Willis (1967) and Zikan (1929). Cazier (1942) summarized the limited information on *Omus*. Other genera were treated to varying degrees by Hamilton and Zikan, and there is an excellent presentation on the megacephaline *Pseudoxychila* by Palmer (1976). Known life histories of all Cicindelidae are similar. Major departures are in the arboreal adaptations of the Collyrinae and *Therates* and in the time of the year when the various events occur. The sequence of events is identical, however.

Life History Patterns

Life histories of several species of Nearctic cicindelids were described in detail by Shelford (1908) and Willis (1967), among others. Life history patterns are ordinarily described in terms of the number of years required for the larva to go through complete development, whether it be one, two, or more years. Whereas this is often applicable, it is possible, in wide-ranging species, for the larval stadium to require variable lengths of time. Criddle (1907, 1910) stated that several species required longer development periods in Manitoba than did the same species further south. Also, a species in the southern part of its range requires less time than in the northern part. Likewise, there may be elevational differences, lowland populations requiring less time than high altitude populations.

Criddle (1907:105-106) divided Manitoba species into two groups based on habits. He stated that the ". . . difference in habit has not . . . received any marked attention (in the literature), though (it may be) . . . a factor of some importance . . . ." I agree with Criddle. In order to eliminate any possible latitudinal or elevational discrepancies in describing life histories in terms of possibly variable larval stadia, I propose to base my life history patterns on whether or not there is a winter diapause in the adult stage.

I recognize two patterns. I shall refer to them as Pattern A and Pattern B. I intend them to apply only to the Nearctic fauna (they may prove applicable to Palaerctic species, also).

Pattern A: Adults eclode in middle to late summer and feed until the onset of cold weather. Diapause lasts until the following spring and, after emergence, the adults feed, reproduce, and die. Among the 24 Pacific Northwest species, this is the pattern of all but four. The character is of taxonomic value because, among the 12 subgenera of *Cicindela* of North America north of Mexico, three are Pattern A: *Cicindela* (except for two species), *Pachydela* and *Tribonia*. Of the 17 northwest Pattern A *Cicindela* (s.l.) species, 14 belong to subgenus *Cicindela*, and three to *Tribonia*. *Omus* spp. also are Pattern A. There is, unfortunately, no relevant published information on *Megacephala* or *Amblycheila*, but, based on adult dates, the former, at least, appears to be Pattern A in the Nearctic Region.

Pattern B: Adults eclode in late spring or summer, feed, reproduce, and then die without ever entering winter diapause. The remaining nine Nearctic subgenera of *Cicindela* and, probably, *Amblycheila* are Pattern B. *C. amargosae*, *haemorrhagica* and *willistoni* (*Cicindelidia*) and *C. cinctipennis* (*Cylindera*) are the northwest species showing this pattern.

Significance of the Patterns

Pattern A: These species have generally northern distributions. Three subgenera have this type: *Cicindela*, *Pachydela* and *Tribonia*. Unfortunately, ranges of very few species have been mapped. However, if the pooled ranges of all the included species could be plotted on a map, it would be seen that the main part of the pooled distribution lies north of 35° north latitude, exceptions being southern extensions of typically northern species or distinctly southern subspecies.

Except in the extreme north or at high elevations, and excluding the Great Plains, this area has a moderate climate. The majority of species are western and the west receives most of its non-winter precipitation (tiger beetles are in diapause during the winter) in the spring and fall. Thus, in spring and fall, soil is friable enough for oviposition and food is plentiful. Summers are dry, so food is scarce and soil often very hard and dry. Summer is when most species pupate, the prepupal and pupal stadia requiring 5-6 weeks, usually the period coinciding (at least in the Pacific Northwest) with the most inhospitable summer climate. Exceptions are those species or populations or high montane or extreme northern areas where the growing season is so short that it is limited to the summer months.

The distribution of *C.* (*T.*) *tenuicincta* is anomalous for Pattern A species. It and some Great Basin subspecies of *C.* (*T.*)

tranquebarica retain a presumably ancestral Pattern A in an area where most species are Pattern B. Two *pulchra*-group species, subgenus *Cicindela* (*pulchra* and *pimeriana*), both with southern ranges, are Pattern B. The other two, *fulgida* and *parowana*, retain Pattern A, regardless of their anomalous ranges. Being Pattern A, these species do not compete with the numerous sympatric Pattern B species by being active at a different time of the year.

Pattern B: Pattern B species have primarily Great Plains, Great Basin or southern distributions, most associated with alkaline areas, grasslands, or the hot and humid southeastern United States. Few species range north of 35° north latitude and, outside of the southeast, all of these are in the Great Basin and Great Plains. None are entirely northern.

Most of this area receives its non-winter precipitation in the summer, usually after mid-July. Adult activity begins after this time. Springtime is often dry and the prepupal and pupal stadia occur between the times that the spring sun has dried out the soil following winter precipitation and the onset of the summer rainy season.

Excluding the three Neotropical ones which barely enter the Nearctic Region, six Nearctic subgenera are Pattern B: *Cicindelidia*, *Cylindera*, *Dromochorus*, *Ellipsoptera*, *Eunota* and *Habroscelimorpha*. Only the first two have Pacific Northwest representatives and these survive the more northerly dry summers by being active principally in early summer or living around bodies of water.

Outline of Life History

The plan of the cicindelid life cycle is well-documented in the literature. I shall limit my treatment to a summary, including original observations on oviposition, burrow morphology, and pupal stadia at the appropriate places.

Oviposition

The female adult chooses the oviposition site, often digging several egg burrows before ovipositing in any given one. The 2nd gonapophyses serve as chelicerae in moving soil particles during excavation of the egg burrow. The 2nd gonapophyses consist of a fixed lobe and an opposable, movable lobe. There is a correlation between the proportions, length and breadth of the fixed lobe and the proportions of sand, silt and clay in the soil. I shall discuss this correlation at length in "Soil Analysis." The essential point is that ability of excavation of an egg burrow is related to both the proportions and size of the 2nd gonapophyses and the soil particle size. The Collyrinae and *Therates* differ from other Cicindelidae in that the egg burrow is excavated in wood and, correspondingly, the 2nd gonapophyses are strongly dentate. Zikan (1929) discussed oviposition in Collyrinae at length.

Fecundity

Published information on cicindelid fecundity is sparse. I am summarizing the limited information on New World species in hope that it will serve as a starting point for future work.

Family Carabidae. Rivard (1964:1082) counted the maximum number of mature eggs in 30 species of Carabidae from eastern Ontario representing eight tribes. The range was 5 - 40, $\bar{X}$ = 14.8.

Family Cicindelidae.

Omus californicus: Cazier (1942:21-22) dissected "about 30 gravid females" of *O. c. angustocylindricus* and *O. c. californicus*. He found an average of 9 ova, of which an average of 7 were full-sized.

Pseudoxychila tarsalis: Palmer (1976:82, 85) determined fecundity by recovering eggs laid under laboratory conditions and by dissecting field-collected specimens. She found that fecundity ranged from $\bar{X}$ = 0.47 eggs/day (field) to $\bar{X}$ = 2.03 (laboratory); totals, assuming an adult stadium of 56 days, of 26 and 114, respectively.

Cicindela purpurea: Shelford (1908:161) stated for laboratory conditions: "About fifty eggs are laid . . . by one female. Whether or not more than one lot of eggs is laid by one female has not been definitely determined, but it is quite improbable from all evidence at hand."

The Ovum

Willis (1967) discussed ovum sizes, embryological development and stadia in detail. I have seen ova of *Omus dejeani* and *Cicindela purpurea* only. In both cases, the ova are elongate-elliptical and pale yellowish in color. Measurements are: *O. dejeani* - 1.2 x 1.0 mm (N = 1); *O. purpurea* - 2.4 x 1.6 mm (N = 1). Ova of both species were covered with a sticky substance to which soil particles adhered, and neither was stalked as in Willis' (1967: Fig. 13) illustration of *C. togata*. Willis (1967:161) gave the stadia for four individuals of *C. togata* as 10.5 - 11.24 days under laboratory conditions at 24.5°C.

The Larva

I am presenting detailed descriptions of larvae of 19 species of Pacific Northwest Cicindelidae in my section "Larval Stage." There are three larval instars, abbreviated L1 (1st instar), L2 (2nd instar), and L3 (3rd instar) following VanEnden (1943). The instars may be distinguished by the number of setae on the mesial side of the basal segment of the maxillary galea: L1-1, L2-2, and L3-3.

The larva lengthens its egg burrow following eclosion and remains in the same burrow throughout its larval and pupal life, leaving the burrow only under adverse microclimatic conditions. The larva plugs the mouth of the burrow preceding each moult and prior to pupation. Otherwise, the burrow is kept open except

during diapause and, in captivity at least, following particularly large meals. Maser (1973) stated that burrow mouths of *C. bellissima* become filled with drifted sand, and I have seen those of *C. hirticollis* in similar conditions. Thus, the larva must periodically clean its burrow of extraneous debris.

The larva is well-adapted for maintaining a position in the burrow during its wait for the approach of suitable prey. The head and pronotum form a lid to the burrow, and the legs, dorsal abdominal hooks and pygopod provide points of contact with the burrow wall. By straightening its body, a larva can drop to the bottom of its burrow, although it can move backwards quite rapidly by alternately flexing and extending its body while running in reverse. Larvae eat any suitable prey item they are capable of subduing. Larochelle (1977) and Willis (1967) have summarized some of the prey species utilized. Dow (1916) described traps constructed at the mouths of burrows by some species that aid in prey capture. Burrows of *C. cinctipennis*, *nebraskana* and *purpurea* that I have examined have funnel-like openings that may hinder escape of prey. I shall describe the burrows of *Omus* spp. in more detail beyond. The larva may further hinder escape of prey by assuming an upside-down position at the bottom of the burrow, thus imprisoning the prey between the burrow floor and the larva itself. I have observed this behavior repeatedly in larvae of *Omus dejeani* and *Cicindela bellissima* and *cinctipennis*. Fecal and uneaten material is ejected from the

burrow, although some species may retain cuticular remnants at the bottom of the burrow (see Willis, 1967:179).

Stadia of larval instars probably depends on the amount of food available and meteorological conditions, resulting in individual, latitudinal and elevational variation. Under laboratory conditions with fairly uniform temperatures and humidity and ample food, larvae may pupate and eclode in winter. Undoubtedly, climate and seasons under natural conditions insure that the life cycle is optimally regulated.

The Pupa

Upon attainment of full growth, the larva enlarges the bottom of the burrow, using at least some of the displaced soil to plug the burrow entrance. The larva then assumes a sigmoid position on its back with the head directed uphill at the bottom of the pupal chamber. The actual prepupal stadium is difficult to determine because the prepupa retains full locomotory faculties until within a day or so of actual pupation. A freshly-ecloded pupa can be distinguished from one that pupated more than 24 hours previously because the eyes are devoid of pigment. The pupa is supported, still with the head directed uphill at the bottom of the burrow, by the abdominal tergal spines.

Pupal Stadium

Pupal stadia of Nearctic Cicindelidae is another topic that has received almost no attention in the literature. Only indefinite statements have been made: by Criddle (1910:9), ". . . two to four weeks . . .;" by Shelford (1908:160) for *C. purpurea*, ". . . two to three weeks." Cazier (1942:23) erred in stating: "The pupal stage in *Omus* is probably of brief duration, possibly two to three days . . . ." Only Willis (1967)189) presented definitive data, recording for *Cicindela circumpicta* ". . . 18 to 21 days at a temperature of 24.5°C."

I have reared seven species through the pupal stage and present my data in Table 1 as a starting point for future research. Specimens were maintained under uncontrolled temperatures averaging from 18-25°C, and kept on a damp substrate to prevent dessication. Dates presented represent captive specimens and must not be construed to correspond to actual pupation dates under natural conditions. It is possible, however, that pupal stadia are under more stringent genetic control than larval instar stadia which are more than likely regulated by nutrition (see Willis, 1967:180-183). Thus, stadia I have observed perhaps approximate those under natural conditions.

Table 1. Pupal stadia of seven species of Pacific Northwest Cicindelidae under laboratory conditions (ambient temperature, 18-25°C).

Species	Source of Specimens	No.	Observed Dates	Stadium (in days)
Omus dejeani	WA. King Co., Seattle, Univ. WA campus	1	15 June-13 July, 1974	28
Cicindela oregona	WA. King Co., Carnation, Tolt River campground	1	2 July-20 July, 1974	18
C. repanda	WA. Whitman Co., 2.8 km W. Lewiston	2	2 Oct.-19 Oct., 20 Oct. - 6 Nov., 1972	17, 17
C. nebraskana	WA. Kittitas Co., 2.5 km S. S. end Lk. Katchees	1	30 July-19 Aug., 1974	21
C. tranquebarica	BC. 6.7 km N. Canal Flats	1	27 July-15 Aug., 1976	18
	OR. Grant Co., Dixie Pass	1	27 July-15 Aug., 1976	18
	UT. Salt Lake Co., 15.9 km W. Salt Lake Int. Airport	1	22 Sept.-16 Oct., 1976	24
C. haemorrhagica	WA. Grant Co., 15.2 km S. Electric City	1	31 Dec., 1972-17 Jan., 1973	17
	WA. Walla Walla Co., 4 km E. Wallula Jct.	1	14 June-4 July, 1974	19
C. cinctipennis	WA. Douglas Co., 9.9 km NW Leahy Jct.	1	26 Feb.-9 Mar., 1977	11

The Adult

Shelford (1908, 1917) and Willis (1967) described pupal and post-eclosional changes for several species in detail. I have observed additional species and have noted no deviations from previously reported patterns. The imago requires about three or four days before the cuticle is adequately tanned to permit terrestrial activities. At this point, the imago digs its way to the surface, although as Willis (1967) has stated, not necessarily through the original, now-plugged course of the larval burrow.

The imagines of Pattern A species feed following eclosion, but are not yet sexually mature, their genitalia not being fully sclerotized until well after the somal cuticle has tanned thoroughly. (I dissected a *C. parowana* whose aedeagus was unsclerotized and largely transparent, even though the somal cuticle had tanned beyond the teneral condition.) Following winter diapause, Pattern A species have sclerotized genitalia and are sexually mature and are, thus, capable of reproduction. Correspondingly, Pattern B species (based on my observations on *C. cinctipennis* and *haemorrhagica*) undergo genitalic sclerotizion concurrently with somal cuticular tanning.

Mating activities have been summarized by Willis (1967). Freitag (1972) studied the morphology of the female mesepisternal coupling sulcus. This is a depression into which the mandibles of

the male fit during copulation and permit him to maintain his position. The sulcus morphology shows an evolutionary sequence so that generalized forms have either no sulcus (Mantichorini and Megacephalini), a groove (generalized Cicindelini), or a deep cavity (apomorphic species of *Cicindela*).

I have seen no literature on post-reproductive survival. Presumably, reproductive activity depletes energy reserves and imposes great stress on the adults, hastening death. In addition, senescent individuals have worn mandibles and tarsal claws and abraded somal cuticles. The abraded cuticle probably has lost much of its ability to regulate water loss. Worn mandibles would hinder prey capture and worn tarsal claws would reduct substrate purchase during prey-capture or predator-evasion. Also, extremely scenescent females have the 2nd gonapophyses so worn as to be practically absent, so that further oviposition might be impossible, even if fecundity permitted it.

Burrow Structure and Adaptations

Important information on the structure of the cicindelid larval burrow was summarized or written by Criddle (1907, 1910), Dow (1916), W. Horn (1908-1915), Shelford (1908, 1911), Willis (1967) and Zikan (1929). As most of an individual's life is spent in its larval burrow, adaptation to and use of the burrow is crucial to its existence. The larval burrow serves initially as the place of oviposition and incubation of the egg; the location of day-to-day

living, shelter and food capture for the larva; the locality during the entire pupal stadium; and the place where imaginal eclosion and cuticular tanning occur.

The larva is anatomically adapted for life in its burrow. The mandibles, so well-formed for capturing, piercing and holding prey, also serve in loosening soil during actual burrow construction. The head and pronotum together form a circular lid to the burrow and their slightly concave surface acts like a mason's hod for lifting loosened soil to the surface. Willis (1967:173-177) gave a detailed description of burrow construction. The legs, abdominal hooks and pygopod all serve to maintain the larva's position in its burrow, and, frequently, the neck of the burrow is oriented diagonally, rather than perpendicularly to the axis of the ground surface. Coloration or adhering soil help to camouflage the head and pronotum. Wigglesworth (1929) found through experimentation that stimulation of tactile setae on the head and pronotum by the prey is required to trigger closure of the mandibles. Such closure is so powerful that audible "clicks" can be heard.

Location and structure (course, length and orientation) of the burrow depends on topography, vegetation, soil structure and moisture and soil particle size distribution at the burrow site. There are several ways in which a burrow is kept from collapsing in upon itself (maintenance of burrow integrity): suitable soil friability or moisture, appropriate density and diameter or roots, or the larva's own ability to secrete burrow wall coatings that hold

particles in place. Willis (1967:174-176) listed species that adapt the courses of their burrows around obstacles such as rocks or roots that are encountered. Burrow depth depends on several factors: location of the water table, type of soil, and friability. I have excavated *Cicindela haemorrhagica* burrows to a depth of 22 cm in uniformly silty soil. On the other hand, burrows of *C. nebraskana*, *C. purpurea* and *Omus dejeani* in shallow, stony soil were less than 5 cm deep. One *C. nebraskana* burrow was so short that the larva was visible even though it was at the bottom of the burrow. Inhabitants of riparian sand bars, such as *C. repanda*, locate their burrows near enough to water so that the soil is damp. Aeolian dune dwellers, e.g., *C. bellissima* or *hirticollis*, extend their burrows through the dry surface sand deeply enough that the bottom is near the water table but not so close as to allow flooding. The walls of the part of the burrow in dry sand are shored up by larval secretions, perhaps saliva or other digestive tract fluids, which prevent collapse of the burrow neck. I have actually picked up sections of this part of burrows that I have excavated without their disintegration through handling.

Adult Burrows and Their Purposes

There is little published information on burrowing by adults. Sleep and diapause in many species occur in burrows. Adults are, remarkably, able to dig, although only the mandibles, used for loosening the soil by means of biting motions, seem anatomically

suitable. The long, slender, cursorially-adapted legs work alternately and rapidly like brooms to push loosened soil backwards. In particularly loose soil, a beetle can bury itself by wriggling. Lecordier (1969) and Leffler (1975) described prestorm burrowing activities by adults. I made a wax cast of an adult night burrow of *C. repanda* (Figure 1F). It is about twice as long and wide as the beetle. The beetle is oriented with its head toward the surface. The same orientation is true for *C. theatina* under natural conditions, and *C. bellissima*, *oregona* and *repanda* in captivity. These three species all belong to the same species-group. There are many references (e.g., Lawton, 1972b) to adults having been found beneath stones, leaves or dried dung. I have kept *C. decemnotata*, *parowana*, *purpurea* and *tranquebarica* in captivity and never observed them digging burrows, sleep occurring on the surface of the soil of the terrarium.

Blaisdell (1912) described "hibernation" burrows of *C. senilis* and Criddle (1907) excavated burrows in Manitoba 10-25 cm in depth. I have found *Omus audouini* in diapause in an otherwise empty larval burrow in the midst of an aggregation of larva-containing burrows of its own species.

Differences Between Larval Burrows in *Cicindela* and *Omus*

Cicindela. I have examined burrows of 12 species in the field. In general, there is no enlarged chamber at the bottom of the burrow. Burrows vary in their course, being straight, curved, or irregular, but never regularly sinuate. At least six species (summarized by Willis, 1967:176) construct a chimneylike structure (turret) at the burrow entrance; I have never seen such a structure, although I have examined some of the species discussed by Willis.

Except for funnel-like depressions around the burrow mouth, I never observed any of the elaborately-constructed traps illustrated by Dow (1916). Shelford (1908) stated that *C. lepida* has a funnel formed by the action of gravity. I have observed *C. nebraskana*, *pugetana* and *purpurea* using the dorsum of the head and pronotum to tamp down the soil around the burrow mouth, thus actually constructing the funnel. The remaining nine species I observed construct no such funnel; the burrow mouth is flush with the ground surface.

I consistently found burrows of *C. cinctipennis* (N = 4) and *purpurea* (N = 9) oriented diagonally into the ground (30-40° from vertical), whereas those of other species entered approximately perpendicular to the ground surface. Most species are found on more-or-less level ground. *C. tranquebarica* burrows into embankments exceeding 45° of slope curved to align with a gravitationally-oriented vertical direction.

Table 2 summarizes observations on larval burrows of 12 species of *Cicindela* and occurrences of turrets are from Willis (1967). Explanations of the headings of each of the five data columns in the tables are as follows:

Vertical - the burrow is approximately perpendicular to the ground surface.

Diagonal - the burrow is oriented 30-40° from a perpendicular direction.

Flush - the mouth of the burrow is flush with the surface of the ground.

Funnel - there is a shallow, funnel-like depression around the mouth of the burrow.

Turret - there is an elevated chimney-like construction at one side of the burrow entrance.

Figures 1D and E, respectively, illustrate diagonal burrows with entrance funnels of *C. purpurea* and *cinctipennis* LL3, drawn from wax casts.

Omus. Larval burrows of *Omus* spp. differ from those of *Cicindela* spp. in being distinctly sinuate and in having an enlarged terminal chamber. The *O. dejeani* burrow is more generalized than that of *O. audouini* in having the terminal chamber gradually rather than abruptly enlarged. Also, in *O. audouini*, there is a constriction before the terminal chamber which *O. dejeani* burrows back

Table 2. Summary of burrow characteristics of 12 species of *Cicindela* from the Pacific Northwest. (See text for explanation of headings of each column.)

Burrow Characteristic				
Vertical	Diagonal	Flush	Funnel	Turret
C. oregona	*C. purpurea*	*C. oregona*	*C. purpurea*	*C. tranquebarica* (after Macnamara, 1922)
C. depressula	*C. cinctipennis*	*C. depressula*	*C. pugetana*	
C. repanda		*C. repanda*	*C. nebraskana*	*C. willistoni* (after Willis, 1967)
C. hirticollis		*C. hirticollis*	*C. cinctipennis*	
C. bellissima		*C. bellissima*		
C. pugetana		*C. haemorrhagica*		
C. nebraskana		*C. lengi*		
C. haemorrhagica		*C. tranquebarica*		
C. lengi				
C. tranquebarica				

(Figures 1A and C). As seen, L1 and L3 burrows of *O. dejeani* differ only in diameter and length (Figures 1A and B).

Omus burrows are usually located on steep or even vertical embankments where it is unlikely that potential prey would be walking about on the ground surface. Additionally, burrow entrances may be covered by fallen leaves or fern fronds, so that access by potential prey may be difficult. Burrowing invertebrates such as earthworms, centipedes, campodeids and larvae of several beetle families may be found in the soil in which *Omus* burrows have been dug. I have *Omus* burrow casts with indications of small side burrows where, presumably, soil animals encountered the *Omus* burrow, followed its course to the bottom, and were captured by the larva. Burrow investigators, animals which enter burrows or crevices in search of food or shelter, may enter *Omus* burrows from the surface and be captured.

The *Omus dejeani* burrow shows little specialization, but that of *O. audouini* appears to be modified as a trap. The terminal chamber is greatly enlarged and the constriction immediately before it may hamper escape of prey.

Fig. 1. Drawings (XI) of wax casts of cicindelid burrows.

A. L3 burrow of *Omus dejeani*.
Source: WA. King Co., Seattle, Univ. WA. campus.

B. L1 burrow of *Omus dejeani*.
Source: same as A.

C. L3 burrow of *Omus audouini*.
Source: same as A.

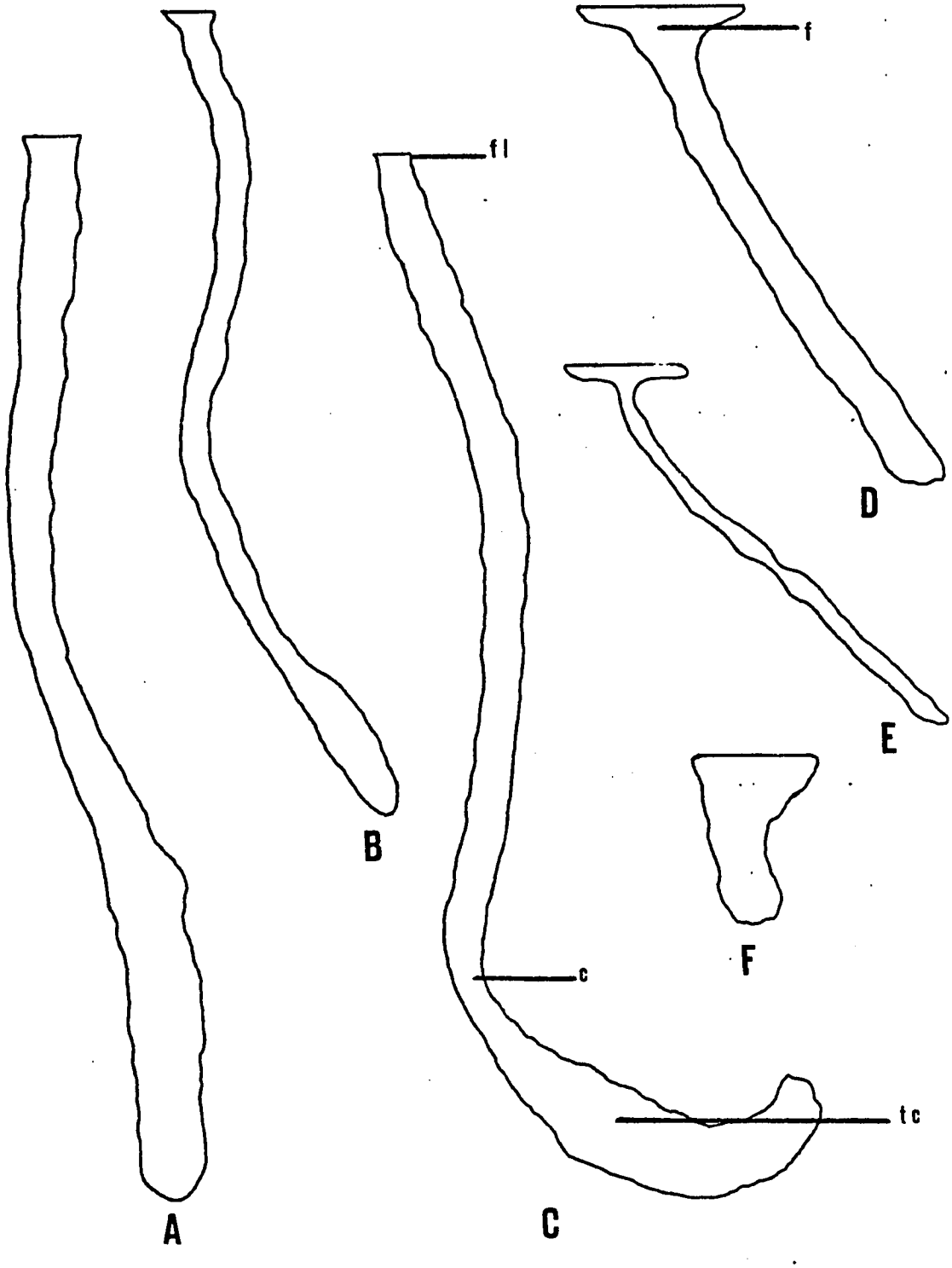
D. L3 burrow of *Cicindela purpurea* new name Leffler.
Source: WA. Thurston Co., Rocky Prairie, 4.8 Km. W. Tenino.

E. L3 burrow of *Cicindela cinctipennis imperfecta*.
Source: WA. Douglas Co., 9.5 Km. NW Leahy Junction.

F. Adult night burrow of *Cicindela repanda repanda*.
Source: WA. Grant Co., Lower Crab Creek WRA, 6.4 Km. E. Beverly.

Abbreviations:

c - constriction
f - funnel-like burrow entrance
fl - burrow entrance flush with ground surface
tc - enlarged terminal chamber


A
B
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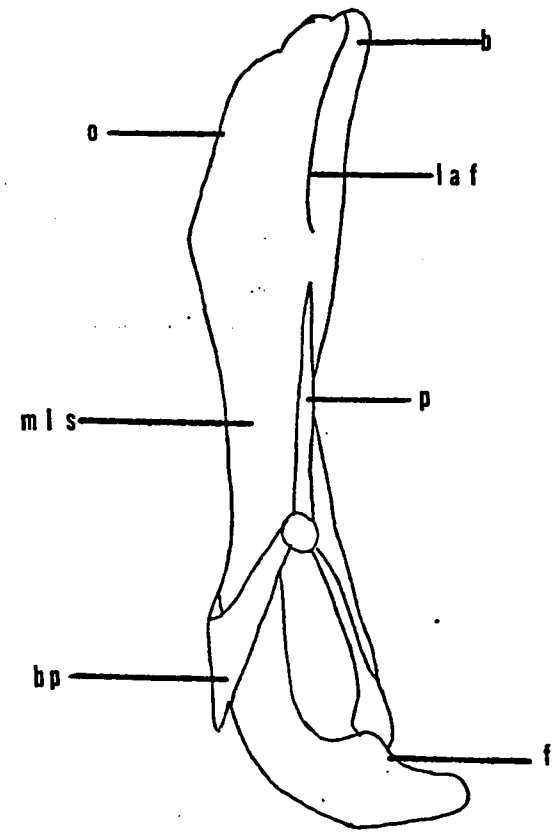

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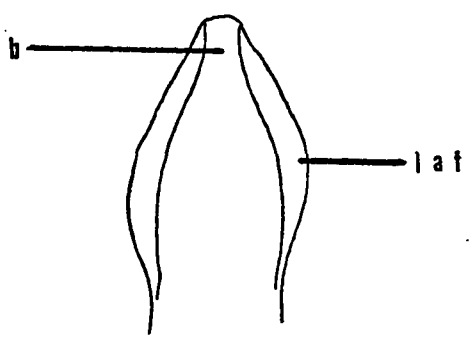


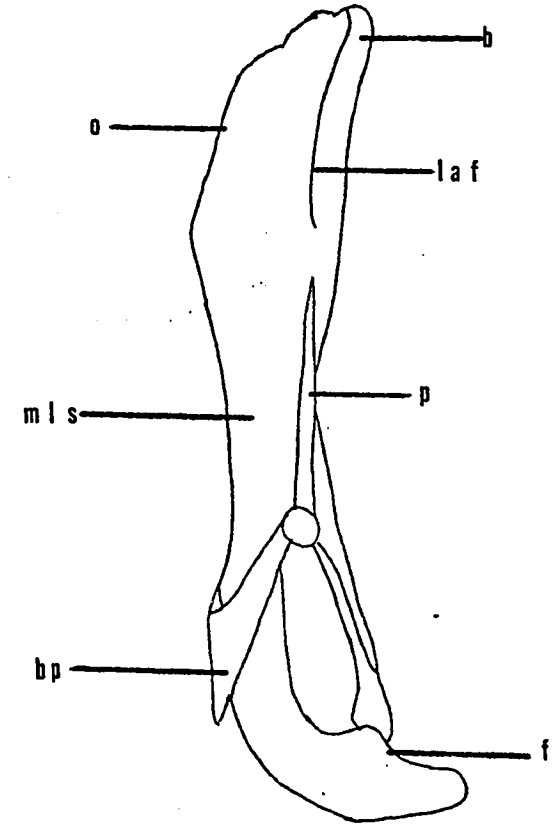
B

Fig. 2. Idealized external view of aedeagus of *Cicindela*. X 16.

A. Lateral view, left side
B. Ventral view, apex

Legend:

b - beak
bp - basal piece
f - foramen for ejaculating duct
laf - lateral apical flange
mls - shaft of middle lobe
o - orifice
p - paramere



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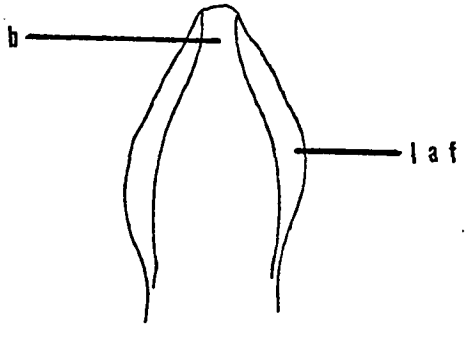


B

Fig. 3. Idealized external female genitalia of *Cicindela*. X 20.

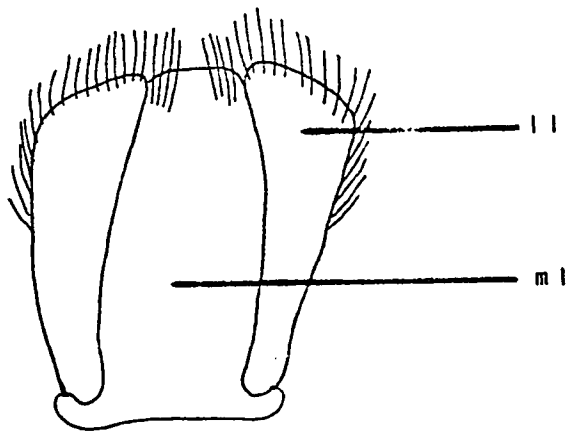
A. Syntergum IX + X, dorsal view

B 2nd gonocoxa and 2nd gonapophysis, ventral view

C. Sternite VIII, ventral view

Legend:

a - apex
ae - apical emargination
bs - basal seta
fl - fixed lobe
ga - 2nd gonapophysis
gc - 2nd gonocoxa
ll - lateral lobe
ml - median lobe
mvl - movable lobe
vn - ventral notch



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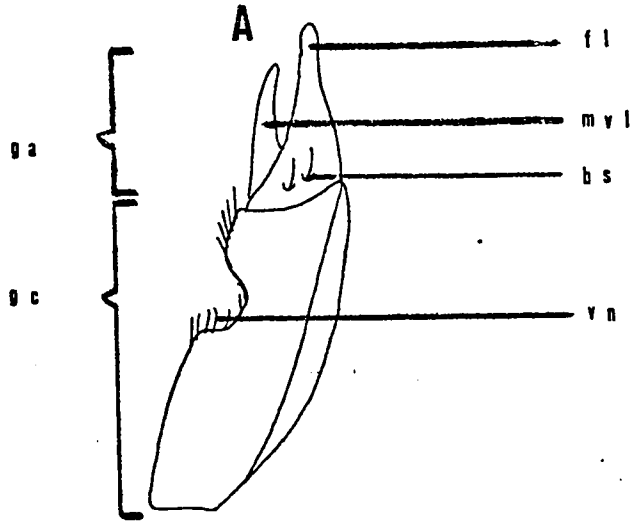

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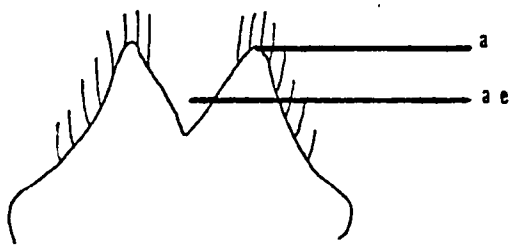


C

Larval Stage

Previous authors made no use of larval characteristics in the study of interrelationships of Nearctic Cicindelidae. By my count, detailed descriptions have been published for only 31 definitely identified species. Of these, larvae of only seven Pacific Northwest species are known. Of these, *Omus californicus* and *Cicindela hirticollis*, *oregona*, *repanda*, *purpurea* and *tranquebarica* were described by Hamilton (1925), and *C. willistoni* was treated by Willis (1967). These descriptions are detailed and well-illustrated, but no attempts were made to delineate character-states either unique to each species or common to more than one species, except for purposes of constructing dichotomous keys for identification. Nor were there any attempts at determining possible adaptive functions of the character-states.

I have personally collected, have on loan from various institutions, or have received as gifts larvae of 19 of the 24 species found in the Pacific Northwest. I lack only *Omus californicus* (described by Hamilton, 1925), *Cicindela arenicola* (superficially treated by Rumpp, 1967), *C. columbica*, *C. plutonica* and *C. tenuicincta*. Of the 20 species included, either by specimens and/or published descriptions, 13 are described here for the first time (*O. dejeani* was superficially described by G. Horn [1878], but only to serve as an example of the genus).

General Considerations

A detailed description of a "typical" cicindelid larva will not be given here because such descriptions have been presented already by Hamilton (1925), W. Horn (1908-1915), Shelford (1908) and Zikan (1929). Figures 4 - 7 illustrate the basic anatomy with important structures labelled.

Comprehensive Larval Descriptions

The detailed descriptions presented here follow the plans of Hamilton (1925) and Willis (1967) with slight modifications in terminology and order only for purposes of clarity. I realize that many of the character-states are common to more than one species and, in some cases, to most of the species. Such detailed descriptions are given in the interest of uniformity of presentation. For purposes of brevity, instars are called L1, L2 and L3, for 1st, 2nd and 3rd instars, respectively. Descriptions are of LL3 only because LL1 and LL2 were available for only a few species. The key is based on LL3 only and may not work for earlier instars because these have fewer setae on the pronotum, the hooks of abdominal tergum V, and surrounding the pygopod. Instars are quickly recognized by the number of setae on the mesial edge of the basal segment of the maxillary galea: L1-1, L2-2 and L3-3.

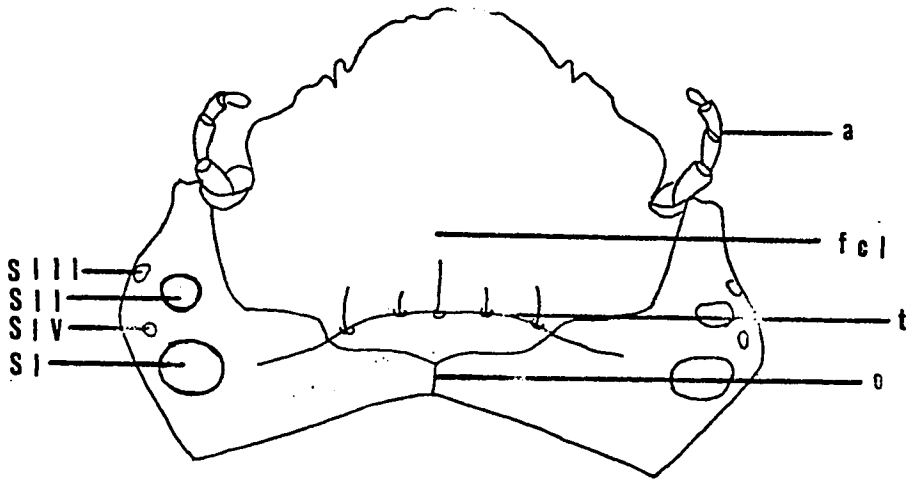
Fig. 4. Dorsal view of larval head showing form of frontal caudal ridge and relative sizes of stemmata (mouthparts and most setae are omitted). X 16.

A. *Omus californicus*

B. Idealized *Cicindela* sp.

Legend:

a - antenna
fcl - frontoclypeolabral area (horizontally-oriented surface)
o - occiput (vertically-oriented surface)
SI - stemma I
SII - stemma II
SIII - stemma III
SIV - stemma IV
t - transverse-type caudal frontal ridge
U - U-shaped caudal frontal ridge



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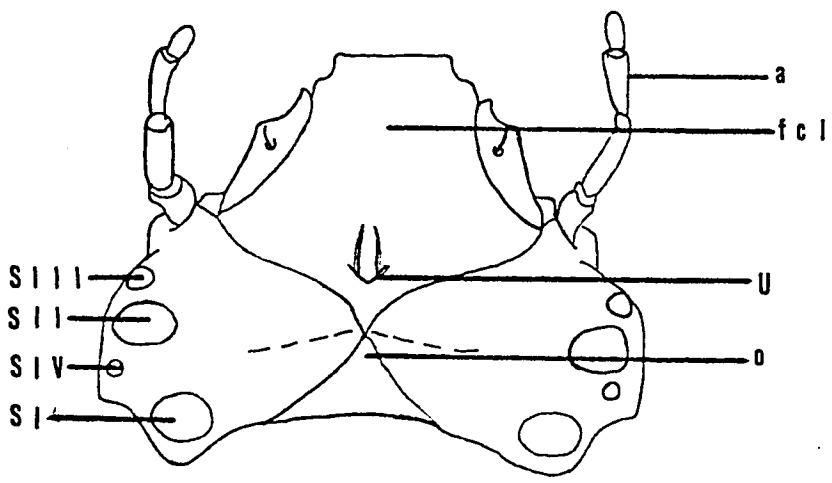


B

Fig. 5. Larval pronotal form and chaetotaxy in specie of
A-D, X 10; E-F, X 60.

A. *C. repanda*, showing full compliment of 7 primary discal setae

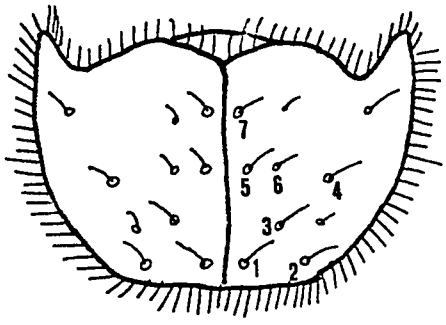
B. *C. oregona*, showing longitudinal rows of supernumary setae

C. *C. purpurea*, showing lack of primary discal seta 6 and 7

D. *C. (Ellipsoptera) nevadica*, showing extent of anterior margin anterior to anterior level of anterolateral angles

E. *C. bellissima*: seta showing terete and pointed form

F. *C. hirticollis*: seta showing flattened, blunt-ended form



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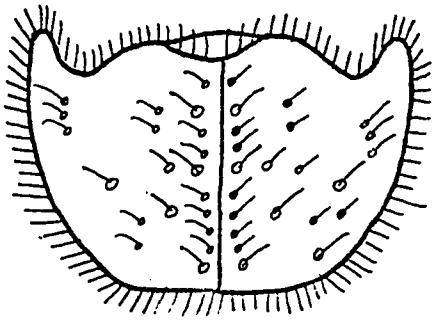

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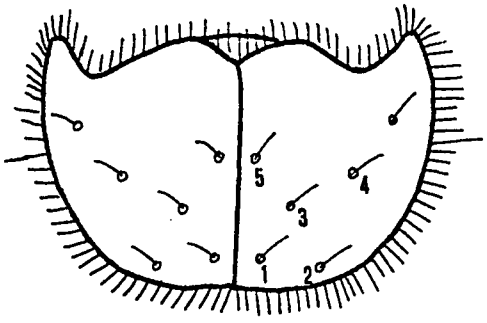

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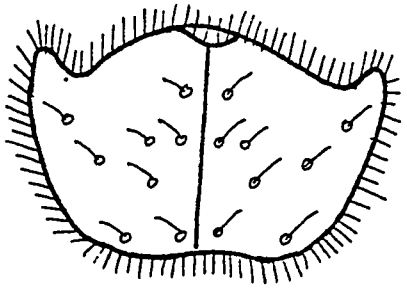

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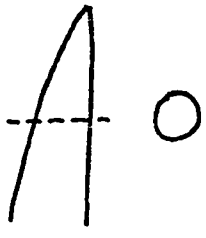

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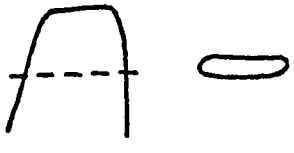


F

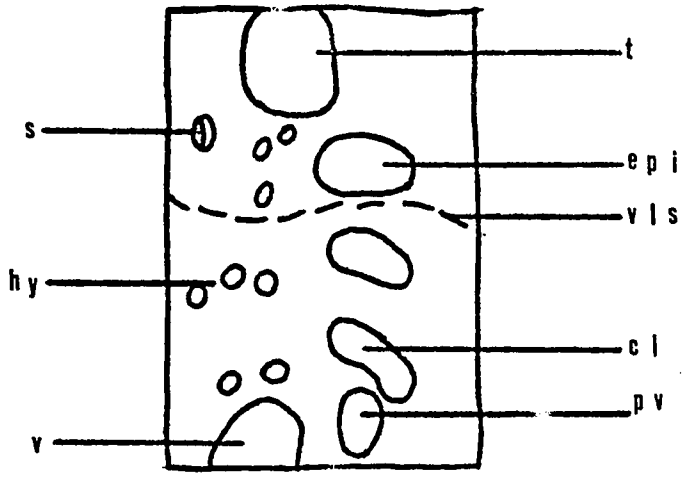
Fig. 6. Idealized lateral views of larval abdominal segment III to illustrate arrangement of sclerites and hypopleural types.

A. Type I hypopleuron.

B. Type II hypopleuron.

Abbreviations:

cl - coxal lobe
epi - epipleurite
hy - hypopleurite
pv - postventrite
s - spiracle
t - tergite
v - ventrite
vls - ventrolateral suture



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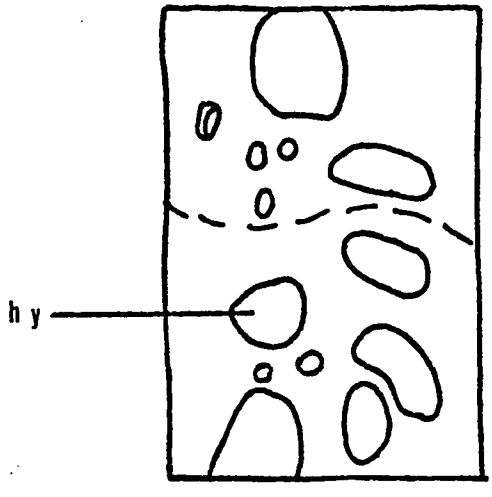


B

Fig. 7. Larval structures in *Omus* and *Cicindela*. X 12.

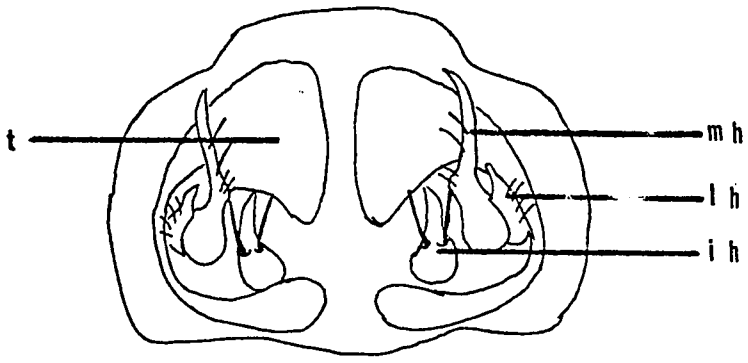
A. *Omus audouini:* abdominal tergum V, doral view.

B. *Cicindela oregona:* abdominal tergum V, dorsal view.

C. *Cicindela oregona:* abdominal segments IX and X, ventral view.

Legend:

ih - inner hook
lh - lateral hook
ls - lateral sternal elevation
mh - middle hook
p - pygopod
S9 - sternum IX
S10 - sternum X
t - tergite



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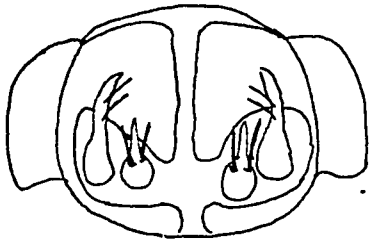

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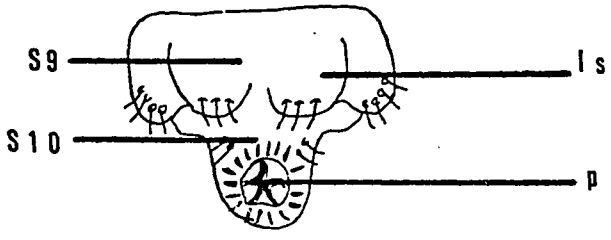

C

Omus dejeani Reiche

Material available. WA King Co., Seattle, Univ. WA campus, 5 March 1974: L1-2 (SL), L2-1 (SL), L3-1 + 1 exuvium (SL); WA. King Co., 10 km W. Carnation, 28 April 1975: L1-1 (SL), L2-1 exuvium (SL); WA. Thurston Co., 5.8 km N. Tenino, 29 Sept. 1976: L3-1 (SL); WA. Lewis Co., 8.4 km E. Mossyrock, 10 May 1974: L1-1 (SL), L2-2 (SL), L3-3 (SL); OR. Douglas Co., 5.8 km S. Curtin, 20 March 1977: L1-1 (SL), L2-3 (SL).

Color. Head black with light blue and brassy metallic reflections; clypeus brown with irregular lateral light patches; labrum black; antennae, palps, basal third of mandibles excluding teeth, and ventral surface of head rufous, remainder of mandibles black; pronotum light rufous with irregular dark brown discal spots, one on either side of midline; mesonotum, metanotum, legs, and sclerotized areas of abdomen yellowish-brown; all setae dark brown.

Head. Setae on dorsum long; diameter of stemma II less than that of stemma I and wider than interstemmatal distance; length of frontoclypeolabral area 62-75% of breadth; transverse ridge continuous with caudal edge of frons shallowly sinuate and bearing five setae, the lateralmost one-third as long as mesial three; antennal segments 1 and 2 equal, 3 slightly longer but half as thick, and 4 one-third as long as 3, 1 with five setae, 2 with five, 3 with three, 4 with three; maxilla with three setae on mesial margin of

basal segment of galea, four on distal; maxillary palp three-segmented, segment 1 with one seta, 2 with two, 3 with zero; basal segment of labial palp with one short ventrodistal spine flanked laterally by one seta, and distal segment with one ventral seta; ligula with four setae.

Pronotum. Anterolateral angles not extending as far anterior as mesial edge; margin continuously carinate except anterior edge; primary discal setae long, 8 per half.

Abdomen. Type I hypopleuron; median hooks of tergite V with one seta, inner hooks with fixed spine twice as long as three setae on shoulder; ventral elevations of sternum IX with four main setae each; pygopod with 20 setae.

Age variation. L1: Two setae on transverse caudal frontal ridge; tergite V with inner hook with only two setae and fixed spine only as long as setae; ventral elevations of sternum IX with three main setae; pygopod with 10 setae. L2: Five setae on transverse caudal frontal ridge; tergite V with inner hook with only two setae and fixed spine 1.5 times longer than setae; ventral elevations of sternum IX with four main setae; pygopod with 18-20 setae.

Omus californicus Eschscholtz (Figure 4A)

This species has been described in detail by Hamilton (1925). I have had no material to examine personally.

Omus audouini Reiche (Figure 7A)

Materials available. WA. King Co., Seattle, Univ. WA. campus, 7 June 1975: L3-4 + 3 exuvia (SL); 19 Dec. 1975: L3-1 exuvium (SL).

Color. Head including clypeus and labrum black and shining but without colored reflections; antennae, palps, basal third of mandibles excluding teeth, and ventral surface of head rufous, remainder of mandibles black; pronotum black with anterolateral angles fading to rufous; mesonotum, metanotum, legs and sclerotized areas of abdomen yellowish-brown; setae of head and pronotum dark brown, other setae yellowish-brown.

Head. Setae on dorsum long; diameter of stemma II 66-77% that of stemma I and wider than interstellatal distance; length of frontoclypeolabral area 59-75% of breadth; transverse ridge continuous with caudal edge of frons shallowly sinuate and bearing three long setae of equal length; antennal segment, 1 slightly shorter than 2, 3 slightly shorter than 2 and half as thick, 4 half as long as 3, 1 with three to five setae, 2 with four to sex, 3 with three, and 4 with two to three; maxilla with three setae on mesial margin

of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with three, and 3 with zero; basal segment of labial palp with one short ventrodistal spine flanked laterally with one seta, and distal segment with one ventral seta; ligula with four setae.

Pronotum. Anterolateral angles averaging about as far anterior as mesial edge; margin continuously carinate except anterior edge; primary discal setae long, 14 per half.

Abdomen. Type I hypopleuron; median hooks of tergite V with zero setae, inner hooks with fixed spine equal in length to three setae on shoulder; ventral elevations of sternum IX with four main setae each; pygopod with 14 setae.

Cicindela repanda Say (Figure 5A)

Materials available. *C. r. repanda* - WA. Whitman Co., 2.8 km W. Lewiston (Idaho), 5 Sept. 1972: L2-1 (SL), L3-6 + 3 exuvia (SL).

This species was described in detail by Hamilton (1925). He did not mention four characters I am including in my analyses: antennal segment 3 with two setae, and segment 4 with three; stemmata I and II equal in diameter; Type I hypopleuron; and pygopod with 16-18 setae.

Age variation. L2 differs in the smaller number of secondary setae.

Individual variation. Of five specimens, four have the median hooks with two setae, and the other has one on the right and two on the left. Three specimens have 18 pygopodal setae and two have 16.

Cicindela oregona LeConte (Figures 5B, 7B and C)

Materials available. *C. o. oregona* - WA. King Co., Carnation, Tolt River Cpgd., 28IV 1974: L3-1 (SL); WA. Benton Co., Plymouth, 15 July 1974: L2-1 (SL), L3-1 (SL). *C. o. oregona* x *guttifera* - ID. Lemhi Co., 30.2 km S. Salmon, 11 July 1974: L3-2 + 1 exuvium (SL).

This species has been described in detail by Hamilton (1925). He stated that the setae of the head and pronotum are only moderate in length and non-conspicuous; in the several specimens available to me, the setae are long and well-developed. Hamilton did not mention four characters that I am including in my analyses: antennal segment 3 with two setae, and segment 4 with three setae; stemmata I and II equal in diameter; Type I hypopleuron; and pygopod with 18 setae.

Age variation. L2 lacks the midline rows of secondary setae on the pronotum, and has the median hooks with two, rather than three, setae.

Individual variation. The lateral pronotal margin and anterolateral angles are paler than the disc in three out of four specimens.

Cicindela depressula Casey

Materials available. *C. d. depressula* - WA. Skagit Co., Granite Mtn., 22 July 1973: L3-1 (SL); WA. Yakima Co., Chinook Pass, 22 Sept. 1974: L1-3 (SL), L2-2 (SL), L3-4 (SL). *C. d. eureka* - WA. King Co., Carnation, Tolt River Cpgd., 28 April 1974: L3-2 (SL).

Color. Head including clypeus and labrum metallic cupreous with brassy-green reflections; antennae, mandibles and ventral surface of head dark brown; palps yellowish-brown; pronotum metallic cupreous with bluish-green longitudinal stripes on mesial half of disc and greenish suffusion on anterolateral angles, angles not lighter than disc; anterior edge and center of disc of mesonotum and metanotum brown; remainder of mesonotum and metanotum, legs and sclerotized areas of abdomen yellowish-brown; setae of head and pronotum white, other setae yellowish.

Head. Setae on dorsum long; diameters of stemmata I and II equal and equalling interstemmatal distance; length of fronto-clypeolabral area 66-78% of breadth; U-shaped ridge on caudal part of frons bearing two setae; antennal segment 1 shorter than 2, 2

and 3 of equal length but 3 half as thick, and 4 less than half as long as 3, 1 with nine setae, 2 with ten, 3 with two, and 4 with three; maxilla with three setae on mesial margin of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with one, and 3 with zero; basal segment of labial palp with two short ventrodistal spines flanked laterally and medially with one short and one long seta per side; ligula with four setae.

Pronotum. Anterolateral angles averaging about as far anterior as mesial edge; posterior and lateral margins continuously carinate up to but not including anterolateral angles; primary discal setae of moderate length and slender, seven per half; secondary setae forming longitudinal row on either side of midline incorporating primary setae 1, 3, 5 and 7.

Abdomen. Type I hypopleuron; median hooks of tergite V with three to four setae, inner hooks with fixed spine one-third of length of entire hook and shorter than two setae on shoulder; ventral elevations of sternum IX with three main setae; pygopod with 20 setae.

Age variation. Younger larvae lack the secondary setae forming the longitudinal rows on either side of the midline of the pronotal disc and have only one or two setae on the median hooks of tergite V.

Individual variation. Pronotal stripes are variable in intensity.

Cicindela hirticollis Say (Figure 5F)

Materials available. *C. h.* ssp. A - WA. Whitman Co., 2.8 km W. Lewiston (Idaho), 5 Sept. 1972: L2-1 exuvium (SL), L3 (same individual as L2 exuvium) - 1 (SL).

This species was described in detail by Hamilton (1925). He did not mention four characters I am including in my analyses: antennal segment 3 with two setae, and segment 4 with three; stemmata I and II equal in diameter; Type I hypopleuron; and pygopod with 16 setae.

Age variation. The one available L2 exuvium has about half as many secondary pronotal setae as L3.

Individual variation. Hamilton stated that the U-shaped ridge has three setae; my specimen (both instars) has but two. Hamilton also listed only two setae on the tergite V median hooks; my specimen has three but the proximal one is half as long as the others.

Cicindela bellissima Leng (Figure 5E)

Materials available. *C. b. bellissima* - WA. Grays Harbor Co., Ocean Shores, 29 June 1975: L2-1 (SL). *C. b.* n. ssp. Leffler - WA.

Clallam Co., Mukkah Bay, 10 Sept. 1976: L2-1 (SL), L3-1 (SL); 13 Sept. 1977: L3-1 (SL).

Color. Head including clypeus and labrum and pronotum metallic cupreous with green, blue and violet reflections; antennae, lateral surface and distal third of mandibles, distal segment of maxilla and maxillary palp, and ventral surface of head dark brown, remainder of maxillae and mandibles yellowish; mesonotum light brown; metanotum, legs and sclerotized areas of abdomen yellowish-brown; setae of head and pronotum white, other setae brown.

Head. Setae on dorsum of varying lengths and numerous; diameter of stemma I greater than II and equal to or greater than stemmatal distance; length of frontoclypeolabral area 74-79% of breadth; U-shaped ridge on caudal part of frons bearing four setae; antennal segment 1 shorter than 2, 3 slightly shorter than 1 and half as thick, 4 slightly more than half as long as 3, 1 with fifteen setae, 2 with twelve to fourteen, 3 with two and 4 with three; maxilla with three setae on mesial margin of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with two, and 3 with zero; basal segment of labial palp with two short ventrodistal spines flanked laterally and medially with two setae; ligula with four setae.

Pronotum. Anterolateral angles averaging about as far anterior as mesial edge; posterior and lateral margins continuously carinate

up to but not including anterolateral angles; setae short, thick, pointed, not flattened, and very numerous, primary and secondary setae largely indistinguishable.

Abdomen. Type I hypopleuron; median hooks of tergite V with three to four setae, inner hooks with fixed spine less than one-quarter length of entire hook and much shorter than two setae on shoulder; ventral elevations of sternum IX with three main setae; pygopod with 20-24 setae.

Age variation. Younger larvae have fewer antennal and pronotal setae.

Individual variation. There is variation in the number of setae on the median hooks of tergite V and surrounding the pygopod.

Cicindela purpurea Olivier (Figure 5C)

Material available. *C. p. audubonі* - WA. Whitman Co., Kamiak Butte St. Pk., 12 May 1972: L3-1 (SL). *C. p.* new name Leffler - WA. Thurston Co., Rocky Prairie, 5 km N. Tenino, 19 April 1975: L3-2 (SL); 4 May 1974: L3-1 + 1 exuvium (SL); 16 Sept. 1976: L3-2 (SL).

This species has been described in detail by Hamilton (1925). He did not mention four characters that I am including in my analyses: antennal segment with three setae, and segment 4 with three

setae; stemmata I and II equal in diameter; Type I hypopleuron; and pygopod with 18 setae. Also, pronotal primary setae 6 and 7 are absent.

Individual variation. Setae of the head and pronotum vary from glassy to white. The blue reflections on the pronotum vary in intensity. One specimen has four setae on the mesial edge of the basal segment of the right galea and the normal three on the left.

Subspecific variation. *C. p.* new name Leffler averages smaller than *auduboni* but is otherwise identical. Hamilton (1925) suggested that his species B might be *C. p. cimarrona*. However, the presence of primary pronotal setae 6 and 7 and the numerous secondary discal setae disprove this.

Cicindela pugetana Casey

Materials available. WA. Kittitas Co., 23.4 km E. Ellensburg, 16 Sept. 1976: L3-2 (SL).

Color. Head black with metallic cupreous gloss, clypeus and labrum black; antennae, mandibles, palps and ventral surface of head brown; pronotum metallic reddish-violet with blue reflections; mesonotum, metanotum, legs and sclerotized areas of abdomen yellowish-brown; setae of head and pronotum glassy, other setae light-brown.

Head. Setae on dorsum of moderate length; diameters of stemmata I and II equal and shorter than interstemmatal distance; length of frontoclypeolabral area 69-74% of breadth; U-shaped ridge on caudal part of frons bearing two setae; antennal segment 1 shorter than 2, 3 and 4 equal and half as long and in thickness as 2, 1 with six setae, 2 with nine, 3 with two, and 4 with three; maxilla with three setae on mesial margin of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with two, and 3 with zero; basal segment of labial palp with two short ventrodistal spines flanked laterally and medially by two setae; ligula with four setae.

Pronotum. Anterolateral angles ending at same level as mesial edge; posterior margin carinate becoming obsolescent anteriorly; primary discal setae short and thick, five per half, numbers 6 and 7 absent.

Abdomen. Type I hypopleuron; median hooks of tergite V with two to three setae, distal one-half as long in specimen with three, inner hooks with fixed spine one-half of length of entire hook and slightly shorter than two setae on shoulder; ventral elevations of sternum IX with four to five main setae; pygopod with 22-24 setae.

Individual variation. One specimen has two setae on the median hooks of tergite V; the other has three. One specimen has 22 pygopodal setae; the other has 24.

Cicindela decemnotata Say

Material available. *C. d.* n. ssp. - WA. Walla Walla Co., 4 km E. Wallula Jct., 15 April 1974: L3-2 + 2 exuvia (SL).

Color. Head, clypeus and labrum black with cupreous reflections; antennae, palps and ventral surface of head yellowish-brown; mandibles and distalmost segment of antennae and palps dark brown; pronotum dark metallic cupreous; anterior half of mesonotum and disc of metanotum brown; remainder of mesonotum and metanotum, legs and sclerotized areas of abdomen yellowish-brown; all setae yellow.

Head. Setae on dorsum of moderate length; diameters of stemmata I and II equal and equalling interstemmatal distance; length of frontoclypeolabral area 68-70% of breadth; U-shaped ridge on caudal part of frons bearing two setae; antennal segments 1 and 2 equal, 3 half as long and half as thick, 4 shorter than 3, 1 with six setae, 2 with seven, 3 with two and 4 with three; maxilla with three setae on mesial margin of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with two and 3 with zero; basal segment of labial palp with two short ventrodistal spines flanked laterally and medially by two setae; ligula with four setae.

Pronotum. Anterolateral angles ending slightly posterior of mesial edge; posterior margin carinate becoming obsolescent anteriorly; primary discal setae short and thick, seven per half.

Abdomen. Type I hypopleuron; median hooks of tergite V with two setae, inner hooks with fixed spine one-half of length of hook and equal in length to two setae on shoulder; ventral elevations of sternum IX with four to five main setae; pygopod with 20-22 setae.

Individual variation. One specimen has four setae on either of the ventral elevations of sternum IX, the other three have five. Three have 20 pygopodal setae, one has 22.

Cicindela longilabris Say

Material available. *C. l. laurenti* x *perviridis* - ID. Latah Co., Moscow Mtn., 15 May 1965: L2-1 (UI).

Insofar as only L2 was available, some of the characters described below reflect the age differences from LL3 described for other species. I have placed them in brackets.

Color. Head and clypeus rufous with strong brassy and bluish-green metallic reflections; labrum rufous with brassy reflections only at base; antennae, basal half of mandibles, maxillae and ventral surface of head light brown, remainder of mandibles dark brown; pronotum rufous with strong cupreous, violet, brassy, and bluish-green reflections; anterior edge and disc of mesonotum dark

brown; remainder of mesonotum, metanotum, legs and sclerotized areas of abdomen yellowish-brown; setae of head and pronotum white, other setae brown.

Head. Setae of dorsum short and thick; diameters of stemmata I and II equal and equalling interstemmatal distance; length of frontoclypeolabral area 80% of breadth; U-shaped ridge on caudal part of frons bearing two setae; antennal segment 1 shorter than 2, 3 and 4 equal and slightly shorter and half as thick as 1, [1 with five setae, 2 with six], 3 with three, and 4 with three; [maxilla with two setae on mesial margin of basal segment of galea], five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with two, and 3 with zero; basal segment of labial palp with two short ventrodistal spines flanked laterally and medially with two setae; ligula with four setae.

Pronotum. Anterolateral angles extending slightly anterior to level of mesial edge; posterior margin carinate, ending laterally in point midway between posterior edge and anterolateral angle; primary discal setae of moderate length, [six per half].

Abdomen. Type I hypopleuron; [median hooks of tergite V with two setae], inner hooks with fixed spine one-third length of hook and slightly shorter than two setae on shoulder; ventral elevations of sternum IX with three main setae; [pygopod with 16 setae].

Cicindela nebraskana Casey

Material available. *C. n. chamberlaini* - WA. Kittitas Co., 2.8 km S. end Lk. Kachees, 17 June 1974: L3-1 + 3 exuvia (SL).

Color. Head black with uniform brassy-green metallic reflections; clypeus and labrum black; antennae, palps and ventral surface of head brown; mandibles completely black; pronotum uniformly dark metallic maroon with brassy green and blue reflections; mesonotum, metanotum, legs and sclerotized areas of abdomen light yellowish-brown; all setae light brown.

Head. Setae on dorsum long; diameters of stemmata I and II equal and less than interstemmatal distance; length of frontoclypeolabral area about 76% of breadth; U-shaped ridge on caudal part of frons bearing two setae; antennal segments 1 and 2 equal, 3 slightly shorter but half as thick, 4 half as long., 1 with six setae, 2 with nine, 3 with three, and 4 with three; maxilla with three setae on mesial margin of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with one, and 3 with zero; basal segment of labial palp with three short ventrodistal spines flanked laterally and medially with two setae; ligula with four setae.

Pronotum. Anterolateral angles ending slightly posterior to level of mesial edge; posterior and lateral margins continuously and broadly carinate; primary setae long, seven per half.

Abdomen. Type I hypopleuron; median hooks of tergite V with two to three setae; inner hooks with fixed spine one-third length of entire hook and equal in length to two setae on shoulder; ventral elevations of sternum IX with four to five main setae; pygopod with 20 setae.

Individual variation. Pronotal highlights vary in intensity. One specimen has two setae on the median hooks of tergite V, three have 3, and two have 4 on the right and 5 on the left.

Cicindela parowana Wickham

Material available. *C. p. parowana* - ID. Canyon Co., 23 May 1962: L3-3 (UI). *C. p. wallisi* - WA. Grant Co., Quincy, 12 May 1959: L3-1 (WSU).

Color. Head, clypeus and labrum metallic cupreous with brassy-green reflections; antennae, basal quarter of mandibles, palps and ventral surface of head rufous, remainder of mandibles black; pronotum reddish-brown with cupreous, violet, brassy and green reflections fading toward posterior margin and anterolateral angles to dull brown; remainder of mesonotum, metanotum, legs and sclerotized areas of abdomen yellowish-brown; setae of head and pronotum white, remainder of setae yellowish-brown.

Head. Setae of dosrum long; diameter of stemma I greater than stemma II and about equal to interstemmatal distance; length of

frontoclypeolabral area 65-71% of breadth; U-shaped ridge on caudal part of frons bearing two setae; antennal segments 1, 3 and 4 of equal length and shorter than 2, 3 and 4 half as thick as 1 and 2, segment 1 with five setae, 2 with nine, 3 with three, and 4 with four; maxilla with three setae on mesial margin of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero, 2 with two and 3 with zero; basal segment of labial palp with three short ventrodistal spines flanked laterally and medially by two setae; ligula with four setae.

Pronotum. Anterolateral angles averaging very slightly posterior to level of mesial edge; posterior margin carinate becoming obsolescent halfway to anterolateral angles; primary discal setae moderate in length, seven per half.

Abdomen. Type II hypopleuron; median hooks of tergite V with three setae, inner hooks with fixed spine less than one-quarter of length of entire hook shorter than two long setae on shoulder; ventral elevations of sternum IX with three to four main setae; pygopod with 20 setae.

Individual variation. Two specimens have three setae on the ventral elevations of sternum IX and two have four.

Cicindela amargosae Dahl

Material available. *C. a. amargosae* - CA. Inyo Co., Tecopa Hot Springs, 16 April 1965: L2-1 (UI); L3-8 (UI).

Color. Head, clypeus and labrum black with brassy and green metallic reflections; antennae, basal one-third of mandibles, palps, and ventral surface of head rufous, remainder of mandibles black; pronotum reddish-violet with blue and green reflections, becoming browner toward anterolateral angles; anterior two-thirds of mesonotum and metanotum, legs and sclerotized areas of abdomen yellowish-brown; setae of head and pronotum glassy, remainder of setae brown.

Head. Setae of dorsum long; diameters of stemmata I and II equal and greater than interstemmatal distance; length of frontoclypeolabral area 54-72% of breadth; U-shaped ridge on caudal part of frons bearing two setae; antennal segments 1 and 2 equal, 3 and 4 equal and half as long and as thick as 1 and 2, segment 1 with five setae, 2 with eight, 3 with two, and 4 with three; maxilla with three setae on mesial margin of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with two, and 3 with zero; basal segment of labial palp with two short ventrodistal spines flanked laterally and medially with two setae; ligula with four setae.

Pronotum. Anterolateral angles not extending as far anteriorly as level of mesial edge; margin along posterior and lateral edges

continuously carinate to and including anterolateral angles; primary setae of moderate length, seven per half.

Abdomen. Type I hypopleuron; median hooks of tergite V with three setae, distalmost one directed dorsally, others directed anteriorly, inner hooks with fixed spine less than one-quarter of length of hook and shorter than two long setae on shoulder; ventral elevations of sternum IX with three main setae; pygopod with 18 setae.

Cicindela willistoni LeConte

Material available. *C. w. sulfontis* - AZ. Cochise Co., Willcox Playa, 10 July 1976: L3-1 (SL).

This species has been described in detail by Willis (1967). In my one available specimen, the setae of the head and pronotum are glassy rather than white as stated by Willis. The lateral part of the pronotal carina ends at the midpoint along the lateral edge. The distalmost seta on the median hook of tergite V is directed dorsally, whereas the two proximal ones are directed anteriorly. The hypopleuron is Type II.

Cicindela haemorrhagica LeConte

Material available. *C. h. nigroides* - WA. Grant Co., 15.2 km S., 0.5 km W. Electric City, 30 Sept. 1972: L2-1 (SL), L3-2

exuvia (SL); WA. Grant Co., 1.8 km E. Beverly, 10 May 1975: L3-3 (SL); WA. Benton Co., Prosser, 27 June 1967: L3-1 (WSU); WA. Walla Walla Co., 4 km E. Wallula Jct., 16 Apr. 1974: L3-2 (SL).

Color. Head black with violet and blue reflections; clypeus and labrum black; antennae, basal third of mandibles and ventral surface of head dark brown, remainder of mandibles and palps yellowish-brown; pronotum violet with blue reflections; mesonotum dark brown with posterior edge yellowish-brown; metanotum, legs and sclerotized areas of abdomen light brown; setae of head and pronotum glassy, remainder of setae brown.

Head. Setae on dorsum of moderate length; diameters of stemmata I and II equal and equalling interstemmatal distance; length of frontoclypeolabral area 61-65% of breadth; U-shaped ridge on caudal part of frons bearing two setae; antennal segments 1 and 2 equal, 3 and 4 equal to one another and shorter than and half as thick as 1 and 2, segment 1 with six setae, 2 with seven, 3 with three, and 4 with three; maxilla with three setae on mesial margin of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with two, and 3 with zero; basal segment of labial palp with two short ventrodistal spines flanked laterally and medially with two setae; ligula with four setae.

Pronotum. Anterolateral angles not extending as far anteriorly as level of mesial edge; margin along posterior and lateral edges carinate, carina ending in point halfway to anterolateral angle along lateral margin; primary setae of moderate length, seven per half.

Abdomen. Type I hypopleuron; median hooks of tergite V with three setae, distalmost one directed dorsally, others directed anteriorly, inner hooks with fixed spine less than one-quarter of length of hook and shorter than two long setae on shoulder; ventral elevations of sternum IX with three main setae; pygopod with 16 setae.

Cicindela lengi W. Horn

Material available. *C. l. versuta* - CO. Moffat Co., 15.9 km W. Craig, 21 June 1976: L3-1 (SL).

Color. Head black with violet reflections; clypeus and labrum black; antennae, distalmost segments of palps, mandibles and ventral surface of head dark brown, remainder of palps rufous; pronotum black with slight violet reflections fading at anterolateral angles to yellowish; anterior two-thirds of mesonotum and all of netanotum dark brown; remainder of mesonotum, legs and sclerotized areas of abdomen yellowish-brown; setae of head and pronotum glassy, remainder light brown.

Head. Setae on dorsum of moderate length; diameters of stemmata I and II equal and slightly less than interstemmatal distance; length of frontoclypeolabral area 68% of breadth; U-shaped ridge on caudal part of frons bearing two setae; antellan segment 1 longer than 2, 3 shorter than 2 and half as thick, and 4 shorter than 3, 1 with seven setae, 2 with eight, 3 with three and 4 with three; maxilla with three setae on mesial margin of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with two, and 3 with zero; basal segment of labial palp with two short ventrodistal spines flanked laterally and medially by two setae; ligula with four setae.

Pronotum. Anterolateral angles ending slightly anterior to level of mesial portion; posterior margin carinate becoming obsolescent anteriorly; primary setae short and thick, seven per half.

Abdomen. Type I hypopleuron; median hooks of tergite V with three setae, inner hooks too damaged on sole available specimen for description; ventral elevations of sternum IX with four main setae; pygopod with 18 setae.

Cicindela tranquebarica Herbst

Material available. *C. t. admiscens* - CO. Moffat Co., 16.2 km W. Maybell, 21 June 1976: L3-1 (SL). *C. t. moapana* - UT. Salt Lake Co., 15.9 km W. Salt Lake Intl. Airport, 22 June 1976: L2-2

exuvia (SL), L3-1 + 2 exuvia (SL). *C. t. vibex* - BC. 6.8 km N. Canal Flats, 16 June 1976: L3-1 exuvium (SL); WA. Whitman Co., S. end Rock Lake, 7 May 1972: L3-5 (SL); OR. Marion Co., 3.5 km W. Mill City, 8 May 1974: L3-1 exuvium (SL): OR. Grant Co., Dixie Pass, 24 June 1976: L3-1 exuvium (SL).

This species has been described in detail by Hamilton (1925). He did not mention four characters that I am included in my analyses: antennal segment 3 with three setae, and segment 4 with three setae; diameters of stemmata I and II equal, Type I hypopleuron; and pygopod with 22 setae.

Cicindela cinctipennis LeConte

Material available. *C. c. imperfecta* - WA. Douglas Co., 9.9 km NW Leahy Jct., 24 April 1976: L3-2 + 1 exuvium (SL); WA. Grant Co., 1.75 km E. Beverly, 15 April 1974: L3-1 (SL): WA. Grant Co., 6.7 km E. Beverly, 8 July 1974: L2-1 (SL).

Color. Head black with violet reflections; clypeus and labrum black; antennae, distalmost segment of palps, and ventral surface of head rufous, anterior and lateral portions of ventral surface of head blue-washed, remainder of palps light brown; mandibles black; pronotum dark brown with blue and violet reflections and fading toward anterolateral angles to rufous; anterior and lateral edges of mesonotum brown, remainder of mesonotum, metanotum, legs and

sclerotized areas of abdomen yellowish-brown; setae of head and pronotum glassy, remainder of setae brown.

Head. Setae on dorsum sparse and of moderate length; diameters of stemmata I and II equal and averaging greater than interstemmatal distance; length of frontoclypeolabral area 58-67% of breadth; U-shaped ridge on caudal part of frons bearing two setae; antennal segment 1 shorter than 2, 2 and 3 equal, 3 half as thick as 2, and 4 shorter than 3, 1 with seven setae, 2 with eight, 3 with three, and 4 with four; maxilla with three setae on mesial margin of basal segment of galea, five on distal; maxillary palp three-segmented, segment 1 with zero setae, 2 with two, and 3 with zero; basal segment of labial palp with two short ventrodistal spines flanked laterally and medially by two setae; ligula with four setae.

Pronotum. Anterolateral angles ending anterior to level of mesial edge; posterior and lateral margins continuously carinate, carina ending in point immediately posterior to anterolateral angles; primary setae of moderate length, seven per half.

Abdomen. Type I hypopleuron; median hooks of tergite V with three setae, distalmost directed dorsally, others directed anteriorly, inner hooks with fixed spine rudimentary and with two short stout spines on shoulder; ventral elevations of sternum IX with three main setae; pygopod with 16 setae.

Table 3 presents six ratios and measurements of third instar larvae only. The numbers given are the range with the arithmetic mean in parentheses. Item 6 refers to *Omus* spp. only, and is not presented for *Cicindela* spp.

1. Ratio: length frontoclypeolabral area/posterior breadth head
2. Ratio: diameter stemma II/diameter stemma I
3. Ratio: diameter stemma II/interstemmatal distance
4. Ratio: lateral length pronotum/mesial length pronotum
5. Greatest breadth pronotum
6. *Omus* only - ratio: length setae on shoulder inner spine/length fixed spine.

Table 3. Measurements and proportions of LL3 *Cicindela* spp. and *Omus* spp. Note that No. 6 does not apply to *Omus* spp. Numbers are the range with the mean in parentheses.

Species	N	Measurements & Proportions 1	2	3	4	5	6
O. dejeani	4	62.20-75.10 (66.52)	87.04-93.62 (90.27)	72.34-93.18 (82.23)	93.25-102.41 (98.17)	5.00-5.54 (5.30)	50.0-62.59 (57.88)
O. audouini	5	58.55-74.68 (64.29)	65.85-77.27 (72.49)	74.07-100.0 (86.59)	82.17-102.41 (95.83)	3.92-4.49 (4.26)	67.50-84.50 (79.10)
C. oregona	4	52.82-67.24 (60.66)	100.0	100.0	88.67-95.88 (91.89)	2.87-3.20 (3.01)	x x x
C. depressula	7	66.01-78.39 (72.48)	100.0	100.0	96.11-106.60 (100.13)	2.93-3.30 (3.12)	x x x
C. repanda	5	73.87-76.16 (75.07)	100.0	100.0	94.37-105.46 (100.33)	2.77-3.43 (3.19)	x x x
C. hirticollis	1	70.87	100.0	81.82	84.55	3.33	x x x
C. bellissima	2	73.64-78.67 (76.16)	81.74-89.00 (85.37)	72.75-90.00 (81.49)	94.55-105.00 (99.75)	3.33-3.47 (3.40)	x x x
C. nebraskana	1	76.26	100.0	90.00	95.07	3.23	x x x
C. purpurea	5	67.10-78.22 (70.46)	100.0	106.67-117.39 (110.59)	98.16-109.66 (103.41)	3.20-4.00 (3.63)	x x x
C. pugetana	2	68.61-73.67 (71.14)	100.0	83.33-93.33 (88.33)	100.0	3.43-3.47 (3.45)	x x x
C. decemnotata	2	67.99-69.97 (68.98)	100.0	110.0	92.27-98.24 (95.26)	3.20-3.43 (3.32)	x x x
C. parowana	4	65.52-71.38 (68.88)	90.91-93.75 (92.23)	106.67-116.67 (112.05)	94.54-100.0 (96.88)	2.80-3.07 (2.89)	x x x
C. amargosae	8	54.31-72.13 (62.54)	93.75-100.0 (99.22)	88.33-100.0 (92.04)	89.85-100.0 (94.65)	2.83-3.20 (3.01)	x x x
C. willistoni	1	60.40	100.0	90.91	92.51	2.93	x x x
C. haemorrhagica	3	61.17-64.64 (62.49)	100.0	100.0	85.89-89.85 (88.37)	2.70-2.87 (2.80)	x x x
C. lengi	1	67.58	100.0	96.43	104.93	3.33	x x x
C. tranquebarica	6	62.79-69.23 (65.33)	100.0	100.0-107.14 (102.20)	82.17-100.0 (93.22)	3.65-3.93 (3.77)	x x x
C. cinctipennis	3	58.21-66.54 (62.34)	100.0	100.0-110.0 (103.33)	106.13-106.54 (106.31)	2.73-2.93 (2.83)	x x x

Analysis of Larval Characteristics

A survey of the descriptions just presented shows great uniformity among the several species. This is to be expected, in that 16 of the 19 species are of the same genus. However, the limited literature shows that uniformity extends throughout the family, in contrast to the diversity of larval types in the Carabidae. Although larvae of major groups of carabids may be recognized upon cursory examination by body form alone, only minor structural details can be employed for cicindelids.

Of the 35 cicindelid genera recognized by W. Horn (1908-1915), descriptions exist for only 14. Fortunately, excellent and well-illustrated treatments of 12 of these were presented by Böving and Craighead (1930), Hamilton (1925), and Zikan (1929). The 14 genera described represent both subfamilies and all three tribes of the Cicindelinae. However, only Hamilton and, to a lesser degree, Böving and Craighead presented generic keys; none exists for taxa above the generic level, although Zikan (1929:286-287) gave 17 characters for distinguishing the two subfamilies.

In the Collyrinae, larval structure of *Collyris* and *Ctenostoma* shows a high degree of specialization. Larvae of the tribes of Cicindelinae may be distinguished only by minor proportions of stemmata and setae and hooks of abdominal tergum V. At least one genus of each of the three tribes of Cicindelinae is known in the larval stage, but some subtribes are unknown. A key

to the larvae of the two subfamilies and the tribes of Cicindelinae is presented below, followed by a discussion of characters I consider important. Data are from Böving and Craighead (1930), Hamilton (1925), W. Horn (1908-1915), Shelford (1908) and Zikan (1929).

1A. Leg with tibia and tarsus fused and tarsus lacking distinct, movable claws; lateral hooks of abdominal tergum V present.....*Sf. Collyrinae*
(genera known: *Collyris Ctenostoma*)

B. Leg with tibia and tarsus not fused and tarsus bearing distinct, movable claws; lateral hooks of abdominal tergum V present or absent (Sf. Cicindelinae).....2

2A. Antennal segments 2-4 much more slender than scape.....*T. Mantichorini*
(genus known: *Mantichora*)

B. Antennal segments 1 and 2 of equal thickness and much thicker than segments 3-4.....3

3A. Caudal frontal ridge continuous with posterior edge of frons, and transverse, not U-shaped.....*T. Megacephalini*
(genera known: *Amblycheila*, *Eucallia*, *Megacephala*, *Omus*, *Oxychila*)

B. Caudal frontal ridge separated from posterior edge of frons and U-shaped, not transverse.....*T. Cicindelini*
(genera known: *Cicindela*, *Eurosopus*, *Iresia*, *Odontochila*, *Prepusa*, *Therates*)

Subfamily Collyrinae. The two genera for which larvae are known, *Collyris* and *Ctenostoma*, agree in adaptations to living in galleries dug into wood of living trees: reduction of the segments of the legs and particularly the lack of movable tarsal claws, and the reduction of the hump on abdominal tergite V and the relative size of its hooks. The two genera differ widely in that *Collyris* has the caudal frontal ridge U-shaped and separate from the posterior margin of the frons, whereas *Ctenostoma* has the ridge sinuate and continuous with the posterior margin; also, the pronotal setae are arranged in distinct fields in *Collyris*, but setae are undifferentiated in size and generally distributed in *Ctenostoma*. These differences suggest that the two lineages have been distinct for a long time during their geological history. This is reflected in their distribution and the classification into separate tribes.

Subfamily Cicindelinae. The 12 known cicindeline larvae differ from the Collyrinae in having unreduced legs with movable claws

(except *Therates*) and have the hump and hooks of abdominal tergite V well-developed.

Distinguishing subfamilial larval characters are negative ones: cicindelines (except *Therates*) lack collyrine specializations for living in galleries in wood. The several cicindeline tribes and genera show a mosaic pattern of characters: some of the most important features are present in one genus within a tribe but absent in another. The presences or absences do not coincide exactly with the degree of plesiomorphy or apomorphy of the adult. Thus, it is often difficult to determine which expression of a character-state is plesimorphic or apomorphic. Characters most useful are the proportions of the antennal segments, size relations of the stemmata, and number of hooks on abdominal tergite V.

T. Mantichorini: Péringuey (1896:5) stated: "However dissimilar the facies of a full-grown (*Mantichora*) is to that of a *Cicindela*, the larval state is almost identical." Of greatest importance in his brief description are that antennal segment 1 is thicker than the others and that the lateral hooks of abdominal tergite V are lacking. In other genera, antennal segments 1 and 2 are of equal thickness, the thicker first segment thus being unique to *Mantichora*. *Collyris*, *Ctenostoma*, *Euprosopus*, *Omus*, *Oxychilla* and *Therates* all have the lateral hooks present, whereas they are lacking in other genera. With three pairs present in at least one genus each of both subfamilies and two cicindeline tribes, the

character is difficult to interpret. Either three pairs is the plesiomorphic state, retained by only a few genera, or it is the apomorphic state which has developed in parallel fashion in at least five lineages. I favor the former explanation as being more in line with the law of parsimony and also in that both known genera of Collyrinae bear three pairs, a group otherwise highly specialized. The distribution of two versus three pairs emphasizes the mosaic pattern of plesiomorphic and apomorphic characters in larvae.

T. Megacephalini: Larvae of five genera are known, representing two of the three subtribes, although lack of knowledge of too many of the remaining genera precludes development of a meaningful subtribal key. They agree in the form of the caudal frontal ridge: transverse, sinuate and confluent with the edge of the frons, as opposed to U-shaped and not confluent in the Cicindelini (unfortunately, the condition in the Mantichorini has not been described). *Omus* and *Oxychila* have three pairs of hooks; two pairs in the other genera. I have been unable to obtain a description of *Eucallia*.

The subtribe Omina differs from the Megacephalina in that stemma II is much smaller than I, as opposed to subequal. *Amblycheila* agrees with most (but not all) Cicindelidae in having fields of pronotal setae, rather than a small number of primary ones as in *Omus*. Reduction in number is probably apomorphic. Thus, the

genera of Omina have mosaics of plesiomorphic and apomorphic characters, making it difficult to call one or the other more primitive.

The three known *Omus* species larvae differ in a number of important characters (data for *O. californicus* are from Hamilton, 1925):

1. Pronotal color:
   O. audouini - black with pale margin
   O. californicus - uniformly light brown
   O. dejeani - light rufous with irregular brown spots
2. Primary pronotal discal setae:
   O. audouini and *californicus* - numerous
   O. dejeani - 8 per half
3. Caudal frontal ridge setae:
   O. audouini - 3
   O. californicus and *dejeani* - 5
4. Comparative lengths of spine and setae of inner hook:
   O. audouini and *californicus* - about equal
   O. dejeani - spine twice length of setae

The reduced number of pronotal setae and long inner hook spine of *O. dejeani* are apomorphic, but many setae on the caudal frontal ridge is, as in *Amblycheila* and several other genera, plesiomorphic (only three in *O. audouini* is apomorphic). The characters indicate three lineages, with *O. audouini* and *californicus* most closely allied.

T. Cicindelini: Larvae of all four of the subtribes I recognize of Cicindelini are known: Cicindelina, Odontochilina, Prothymina and Theratina. Cicindeline larvae differ from those of the Megacephalini in the U-shaped caudal frontal ridge which is also separate from the caudal edge of the frons. Zikan (1929) did not describe the condition in the prothymines and I cannot determine it from his figures. The prothymine *Euprosopus* appears to have a transverse ridge and, certainly, has three pairs of hooks on abdominal tergite V. Adult pronotal structure is cicindeline, not megacephaline. The pronotal setal pattern is identical with that of *Iresia*. Either *Euprosopus* is not a cicindeline, Zikan's figure is incorrect, or the genus is extremely primitive.

Zikan gave no characters by which the Odontochilina (*Odontochila* and *Prepusa*) may be distinguished from the Cicindelina.

Therates (St. Theratina) has the legs reduced as in the Collyrinae, but the tibia and tarsus are not fused (Böving and Craighead, 1930).

Of the Cicindelina, only *Cicindela* larvae are known. The larva is chacterized by a combination of the U-shaped caudal frontal ridge separate from the caudal edge of the frons, two pairs of hooks and seven primary pronotal discal setae per half, except in specialized species. Too little information is available on larvae of most of Rivalier's "genera" on a worldwide basis, and I must regretfully limit my discussion to the Nearctic groups. Of the

eight Nearctic subgenera with known larvae, only two may be recognized by larval characters. Neither, *Habroscelimorpha* or *Ellipsoptera*, is found in the Pacific Northwest. Four of the remaining subgenera, *Cicindela*, *Tribonia*, *Cicindelidia* and *Cylindera*, have northwest species. None has characters suitable for defining it at the subgeneric level. For instance, *C.* (*Cylindera*) *cincti-pennis* has a rudimentary spine on the inner hook, but the other known larvae of *Cylindera* (*germanica* and *unipunctata*) have well-developed spines. Thus, subgeneric diagnoses will not be given.

Phylogenetic and Adaptive Characters

The following characters are considered plesiomorphic because they are expressly identical in most of the species:

1. Caudal frontal ridge with two setae. Only *C. bellissima* has more than two, a reflection of its extreme pilosity. Hamilton (1925) listed nine Nearctic species with more than two setae, although my specimen of *C. hirticollis* has only two. Of the remaining eight, two only are pilose, and several pilose species have only two setae.

2. Pronotal disc with seven primary setae per half. The primary setae cannot be distinguished as such in very pilose species in L3, although Hamilton's figures 55-56 of L1 and L2 *C. hirticollis* show them to be readily distinguishable. Setae 6 and 7 are absent in *C. f. formosa* (Hamilton, 1925), *C. purpurea,* and *C. pugetana*, and seta 6 is absent in *C. f. generosa* (Hamilton, 1925).

3. First antennal segment with nine or more setae. This is the number found in species of the *maritima*-group of subgenus *Cicindela*, species considered the most generalized.

4. Setae of head and pronotum long and white. This is the condition in most species. A few have the setae glassy, yellow or brown. They are short and modified in some of the arenicolous species.

5. Number of setae on shoulder of inner hook. There are two setae in all of the northwest species, the most typical number. At least one species in each of five subgenera has more than two, but there is no uniformity among all the species in any subgenus except *Pachydela*, of course, in which there is but one species.

Hypopleural Form

There are two main forms taken by the larval abdominal hypopleuron which I am designating Type I and Type II. They are illustrated in Figure 6.

Type I. The hypopleuron consists of several, usually four or more, small, setiferous tubercle-like sclerites. Variations of this type are seen in *Amblycheila cylindriformis* and *Cicindela abdominalis* in which the sclerites are absent, the setae only being present. A type I hypopleuron is characteristic of most of the known species and is undoubtedly the plesiomorphic state.

Type II. The hypopleuron consists of a single (two in *Cicindela circumpicta*) large setiferous sclerite. A Type II hypopleuron is seen in only 9 of the 43 known larvae (20.9%) and is certainly the apomorphic state.

In addition to the 13 species described for the first time in the present report, I have been able to examine specimens of *C. nigrocoerulea* and certainly-identified *C. obsoleta*. Of Hamilton's four species identified as A, B, C and D, species A can be identified by process of elimination as *C. trifasciata*. I have eliminated from my list Hamilton's species B - D, *C. macra*, *obsoleta* and *pulchra*, because the identifications are unknown or suspect. Distribution of the two types is tabulated in Table 4.

Trends

I have not been able to determine any trends in coloration or chaetotaxy. These afford useful characters for distinguishing species, but do not correlate with any edaphic factors of phylogenetic lineages.

One character shows convergent evolution. Several species have supernumerary setae on the head and pronotum. Freitag (1965:161) wrongly considered this to be a primitive character. It is found in seven Nearctic species, some not particularly primitive, representing four subgenera: *C. bellissima*, *hirticollis* and *limbata* in *Cicindela*; *C. abdominalis* in *Cicindelidia*; *C. saulcyi* in

Table 4. Distribution of Type I and Type II hypopleura in known Nearctic Cicindelidae. Data from Hamilton (1925), Willis (1967) and personal observations (*).

Species	Type I	Type II
Amblycheila cylindriformis	X	
**Omus dejeani*	X	
O. californicus	X	
**O. audouini*	X	
Cicindela duodecimguttata	X	
C. oregona	X	
**C. depressula*	X	
C. repanda	X	
C. hirticollis	X	
**C. bellissima*	X	
C. limbata	X	
**C. decemnotata*	X	
C. sexguttata		X
C. formosa		X
C. limbalis	X	
C. purpurea	X	
**C. pugetana*	X	
**C. nebraskana*	X	
**C. longilabris*	X	
C. fulgida		X
**C. parowana*		X
C. scutellaris	X	
**C. lengi*	X	
C. tranquebarica	X	
C. latesignata	X	
**C. amargosae*	X	
C. willistoni		X
C. trifasciata		X
C. punctulata	X	
**C. nigrocoerulea*	X	
**C. obsoleta*	X	
C. ocellata	X	
**C. haemorrhagica*	X	
C. abdominalis	X	
C. circumpicta		X
C. saulcyi	X	
C. togata	X	
**C. cinctipennis*	X	
C. unipunctata	X	
C. nevadica		X
C. marginata	X	
C. gratiosa	X	
C. lepida		X

Habroscelimorpha; and *C. gratiosa* and *lepida* in *Ellipsoptera*. All are characteristic of dune habitats. My theory as to the function of this character is that, as these species are found in areas of dry sand, sand grains drift into the opening of the larval burrow. They may cover or damage some of the setae. With supernumerary setae, some are always exposed and functional. Other species, lacking supernumerary setae, live in wet, clayey, or otherwise stabilized soil in which there is little chance of loose grains entering the burrow mouth. I predict that when larvae of other arenicolous species are found, they too will be found to have supernumerary setae.

Important Species Characteristics

The following analyses are intended to point out characters diagnostic of the 19 known northwest species and to emphasize whatever features of indicative of relationships. As I have already stated, none of the subgenera and only a few species-groups can be defined on the basis of larval characters. However, some characters may be used to differentiate individual species and even to show relationship of two or more species.

Omus dejeani. The small number of primary pronotal discal setae and the elongate inner hook spine readily distinguish this species from the other two. Minor differences between the three

species in nearly every character of color and chaetotaxy indicate lengthy separate evolution.

Omus californicus. The pronotal setal number and short inner hook spine indicate relationship to *O. audouini*, but differences in chaetotaxy and color show separation of the two species.

O. audouini. See remarks under *O. californicus*. Presence of only three setae on the caudal frontal ridge is probably apomorphic.

Cicindela oregona. This species, as well as the others of the *maritima*-group of the subgenus *Cicindela*, share nine or more setae on antennal segment 1. It shares with *C. depressula* a longitudinal row of secondary and primary setae on either side of the midline of the pronotum. *C. duodecimguttata*, a species so closely related to *C. oregona* that they are able to hybridize, does not show this character. It is thus primitive, and the other two show the apomorphic condition. They differ primarily in pronotal coloration: blue in *oregona*, green in *depressula*.

C. depressula. See remarks under *C. oregona*.

C. repanda. *C. repanda* and *duodecimguttata* are the only two of the eight known *maritima*-group larvae without notable modifications in chaetotaxy, indicating plesimorphy. These two species differ in minor details of number of setae and coloration.

C. hirticollis. *C. hirticollis*, *bellissima*, *limbata* and the Palearctic *maritima* all have supernumerary head and pronotal setae. All are arenicolous. Those of *C. hirticollis* are truncate and scale-like. Hamilton (1925) describes those of *C. limbata* and

maritima as but slightly flattened. Those of *C. bellissima* are terete and pointed. The different expression of the character indicates convergence, rather than relationship. This is further reflected in the structure of the male genitalia and the lineages determinable therein (Freitag, 1965; Rumpp, 1967).

C. bellissima. See remarks under *C. hirticollis*. *C. bellissima* and *limbata* are closely related, as substantiated by the unmodified form of the supernumerary setae.

C. decemnotata. Larvae of six species of the *formosa*-group are known. All have less than nine setae on antennal segment 1, inner hood spine one-third or more of the length of the entire hook, and four to five setae on the ventral elevations of sternum IX. *C. formosa*, *pugetana* and *purpurea* all have lost at least one of the primary pronotal discal setae. Head and pronotal setae of all three species tend to glassiness. *C. formosa* has a non-metallic, patterned pronotum, thus differing from the other species. *C. formosa* and *sexguttata* have Type II hypopleura; all other known *formosa*-group species have Type I hypopleura.

C. decemnotata shares the combination of characters of the *formosa*-group. It has the full compliment (seven) of primary pronotal discal setae, thus agreeing with *C. sexguttata* and *limbalis*. It and *sexguttata* are peculiar in the non-white or glassy head and pronotal setae; these are yellow in *decemnotata* and brown in *sexguttata*.

C. purpurea. *C. purpurea* and *pugetana* lack primary pronotal discal setae 6 and 7, and may be distinguished only by differences in pronotal coloration and abdominal chaetotaxy. The differences are minor but definitive enough to emphasize that the two are separate species.

C. pugetana. See remarks under *C. decemnotata* and *purpurea*.

C. longilabris. There are no special larval characters diagnostic of a *silvatica*-group. Numerous differences between *C. longilabris* and *nebraskana* larvae indicate long phylogenetic separation. White head and pronotal setal coloration is plesiomorphic.

C. nebraskana. This species has brown head and pronotal setae, only four setae on antennal segment 1, and four to five setae on the ventral elevations of sternum IX, all atypical and, thus, certainly apomorphic.

C. parowana. Of the *pulchra*-group, only the *pimeriana* larva remains unknown, although there is some question as to the correct identity of *C. pulchra* (Hamilton, 1925:51-53). His *pulchra* may be *obsoleta* and vice-versa, or, perhaps from their great similarity, both may be the same species. Larvae of *C. parowana* and *fulgida* (Willis, 1967) are more like one another than to the alleged *pulchra*, casting further doubt in my mind of Hamilton's material. Both *fulgida* and *parowana* have Type II hypopleura; the alleged *C. pulchra* has Type I.

C. fulgida and *parowana* differ from one another primarily in the much shorter inner hook of *parowana*.

C. amargosae. Of the 57 species of the subgenus *Cicindelidia*, larvae of only six or possibly seven are known. Hamilton's alleged *C. obsoleta* contrasts strikingly with the other species in the number of caudal frontal ridge setae (as opposed to two), the long inner hook spine, and four rather than three setae per group on sternum IX. The other six species are similar, except that the arenicolous *C. abdominalis* has supernumerary setae on the pronotum as well as on antennal segment 1 (seven to eight, rather than five to six), and has three setae on the shoulder of the inner hook (two is typical). The remaining six species (*amargosae*, *haemorrhagica*, *ocellata*, *punctulata*, *trifasciata* and *willistoni*) are all similar, *trifasciata* and *willistoni* differing in having Type II hypopleura.

C. amargosae differs from *willistoni* and *haemorrhagica* in the long rather than short to moderately long setae on the dorsum of the head.

C. willistoni. See remarks under *C. amargosae*. Dorsal head setae are short to moderate in length as in *C. haemorrhagica*. *C. willistoni* differs from both *C. amargosae* and *C. haemorrhagica* in that the spine on the inner hook is greater than one-third the length of the hook rather than less than one-quarter and in the Type II hypopleuron.

C. haemorrhagica. See remarks under *C. amargosae* and *willistoni*.

C. lengi. Three species of the subgenus *Tribonia* are known as larvae, although *C. latesignata* was identified by Hamilton (1925:29) with some doubt. The characters agree with those of *C. lengi* and *tranquebarica* except for the smaller average number of setae on antennal segment 1 (five to seven rather than seven to eight) and group of thre rather than four on sternite IX. The large size of Hamilton's larvae rules out *C. trifasciata*, *haemorrhagica* or *gabbi*. *C. lengi* differs from *C. tranquebarica* mainly only in pronotal coloration.

C. tranquebarica. See remarks under *C. lengi*.

C. cinctipennis. Only three species of *Cylindera* (*cinctipennis*, *germanica* and *unipunctata*) are known as larvae. All differ strongly from one another. Their pronotal outlines have no resemblance to those of species of *Ellipsoptera* (excluding Hamilton's *macra*, which I believe to be misdetermined), casting doubt in addition to that derived from adult chaetotaxy on the contention by Rumpp (1977) that *Ellipsoptera* should be synonymized with *Cylindera*. Diversity in characters of the three known species suggests either that *Cylindera* is not a natural group or that it includes long separate lineages. Both possibilities are likely. *C. cinctipennis* is unique among northwestern species in the rudimentary spine on the inner hook. This is not true of *C. germanica* of *unipunctata* and it is also rudimentary

in *C.* (*Cicindelidia*) *abdominalis* and very short in *C.* (*Cicindela*) *repanda* and *C.* (*Ellipsoptera*) *gratiosa* and *lepida*.

Summary

Cicindelid larvae are similar in their characteristics. Generic and supergeneric taxa are readily definable, and species can be distinguished. However, at the present level of knowledge, few subgeneric or species groups can be characterized. Although there are few positive definitions, there are also no extreme anomalies.

Pupal Stage

Pupal characteristics have been among the most ignored aspects of cicindelid biology. There have been only three substantive treatments of the pupal stage: Shelford (1908), Willis (1967) and Zikan (1929). Unfortunately, workers may have taken Shelford (1908: 171) too literally when he stated: "No generally practicable way of distinguishing the pupae has been found." I have found characters distinguishing *Omus* and *Cicindela*, as well as subgenera, species-groups, and some species of *Cicindela*. I have studied two species of *Omus* and nine of *Cicindela*.

General Considerations

Willis (1967) and Zikan (1929) have given detailed descriptions of two "typical" cicindelid pupae and such an account will not be repeated here. Figures 8-10 illustrate the basic anatomy with important structures labelled.

Four characters readily distinguished the sexes of cicindelid pupae:

1. Females have a greater ocular index because of the somewhat smaller eyes.

2. The proximal four protarsal articles are dilated in the male, but are no wider than the fifth article in the female. Presumably, this character is not true of genera in which male adults lack protarsal dilation (e.g., *Amblycheila*).

3. The ratio, length abdominal segments VI-X/I-V, is greater in the female because of the longer VI-X component.

4. Females have gonocoxae readily visible as ventrolateral spurs.

Six measurements and ratios were taken to aid in species descriptions and identifications. Because of the small numbers of available specimens, these measurements and ratios must be used with extreme caution. They are summarized in Table 5.

Fig. 8. Lateral view of pupa of *Omus dejeani* Reiche (X 6).

Legend:

as - abdominal tergal spines
c - clypeus
ds - dorsal spines of tergum V
g - female genitalia
l - labrum
msw - mesothoracic wing

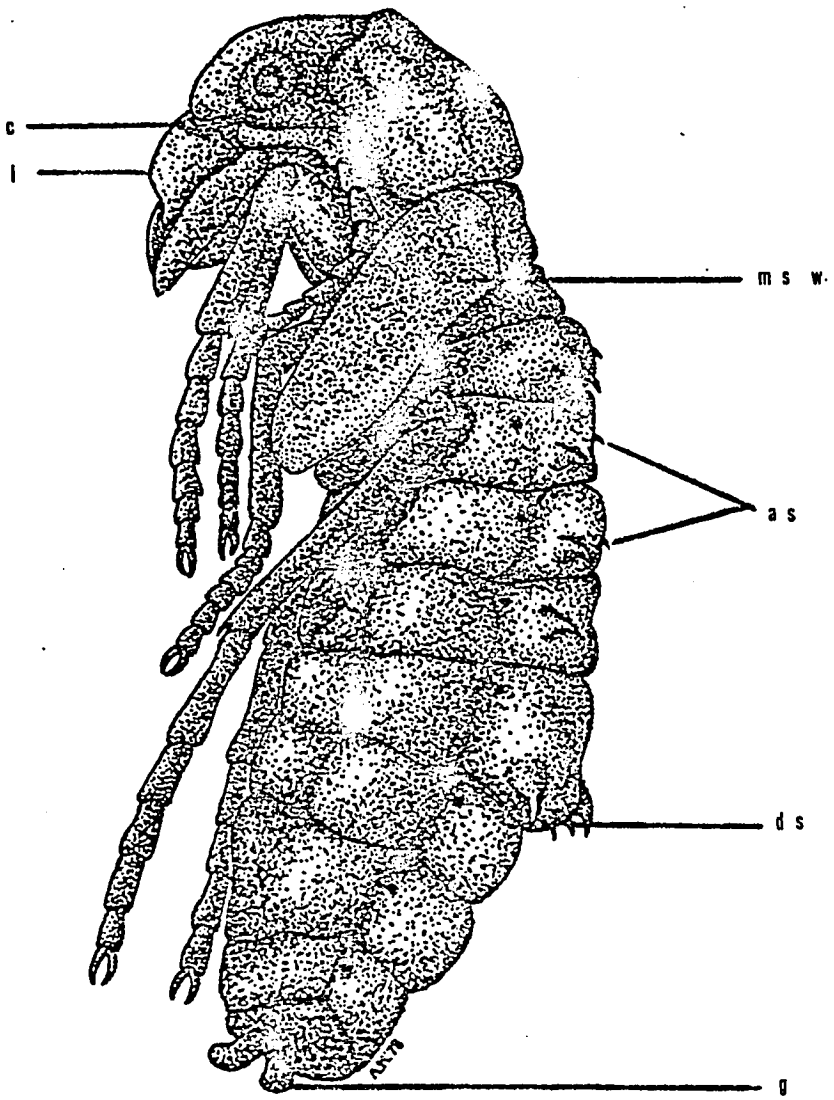
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Fig. 9. Lateral view of pupa of *Cicindela oregona* Le Conte (XII).

Legend:

as - abdominal tergal spines
c - clypeus
g - female genitalia
l - labrum
msw - mesothoracic wing
mtw - metathoracic wing

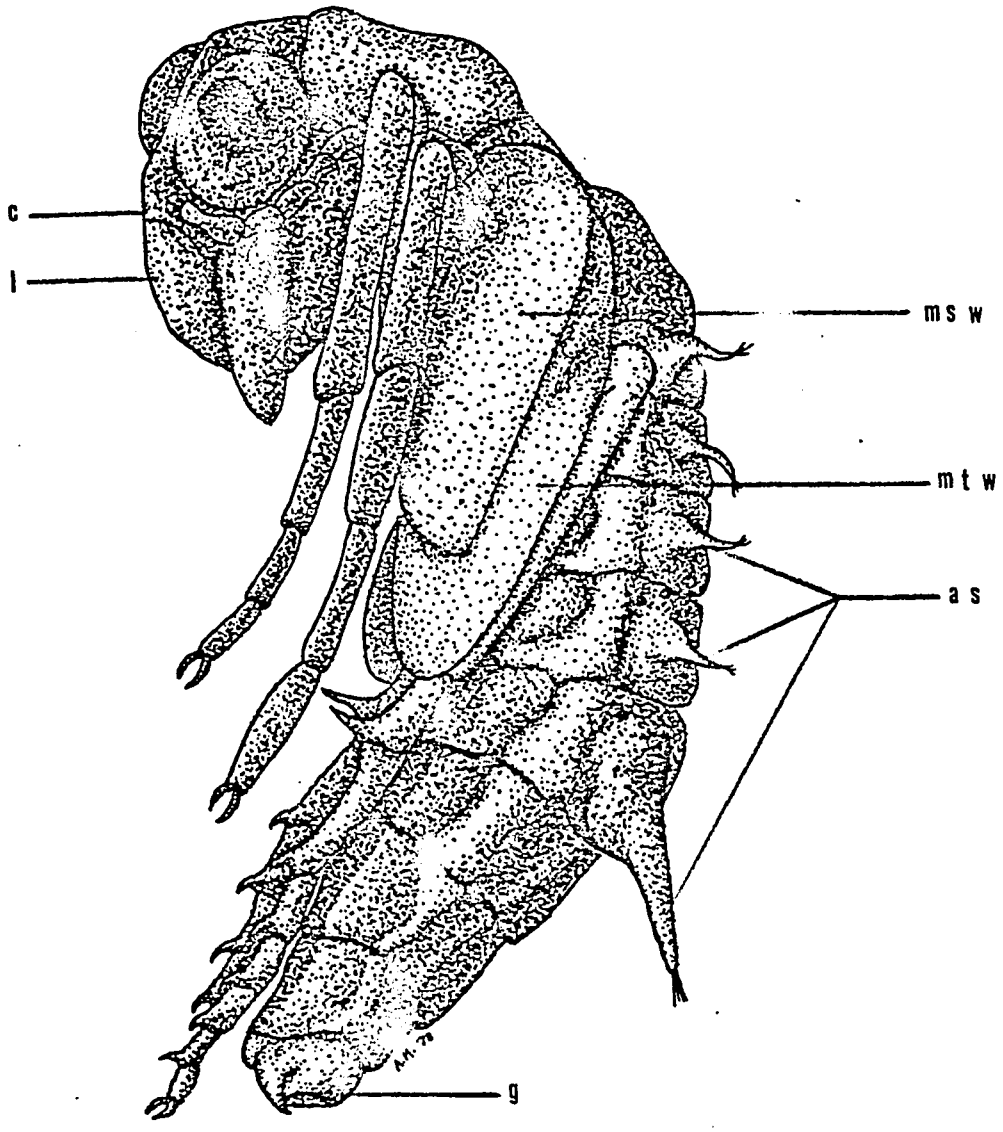
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Fig. 10. Pupal structures in *Omus* and *Cicindela*.
A - M, X 12; N - O, X 35; P, X 50.

A. *Omus dejeani*, head: dorsal view.

B. *Omus audouini*, head: dorsal view.

C. *Cicindela oregona*, head: dorsal view.

D. *Cicindela tranquebarica*, head: dorsal view.

E. *Cicindela haemorrhagica*, head: dorsal view.

F. *Cicindela cintipennis*, head: dorsal view.

G. *Omus dejeani*, pronotum: dorsal view.

H. *Cicindela oregona*, pronotum: dorsal view.

I. *Cicindela tranquebarica*, pronotum: dorsal view.

J. *Cicindela haemorrhagica*, pronotum: dorsal view.

K. *Cicindela cinctipennis*, pronotum: dorsal view.

L. *Omus dejeani*, abdominal tergum V: dorsal view.

M. *Cicindela oregona*, abdominal tergum V: dorsal view.

N. *Omus dejeani*, apex of lateral spine of abdominal tergum V.
i - lateral view showing apical setae
ii - apical view, showing I-pattern of setae

O. *Cicindela tranquebarica*, apex of lateral spine of abdominal tergum V.
i - lateral view showing apical setae and isolated seta on posterior face of spine
ii - apical view showing randomly arranged setae

P. *Cicindela cinctipennis*, apex of lateral spine of abdominal tergum V.
i - lateral view showing patch of setae on anterior face of spine
ii - apical view showing setae shifted toward anterior face

Legend:
a - antenna
e - eye
f - frons
l - labrum
ls - lateral spine
m - mandible

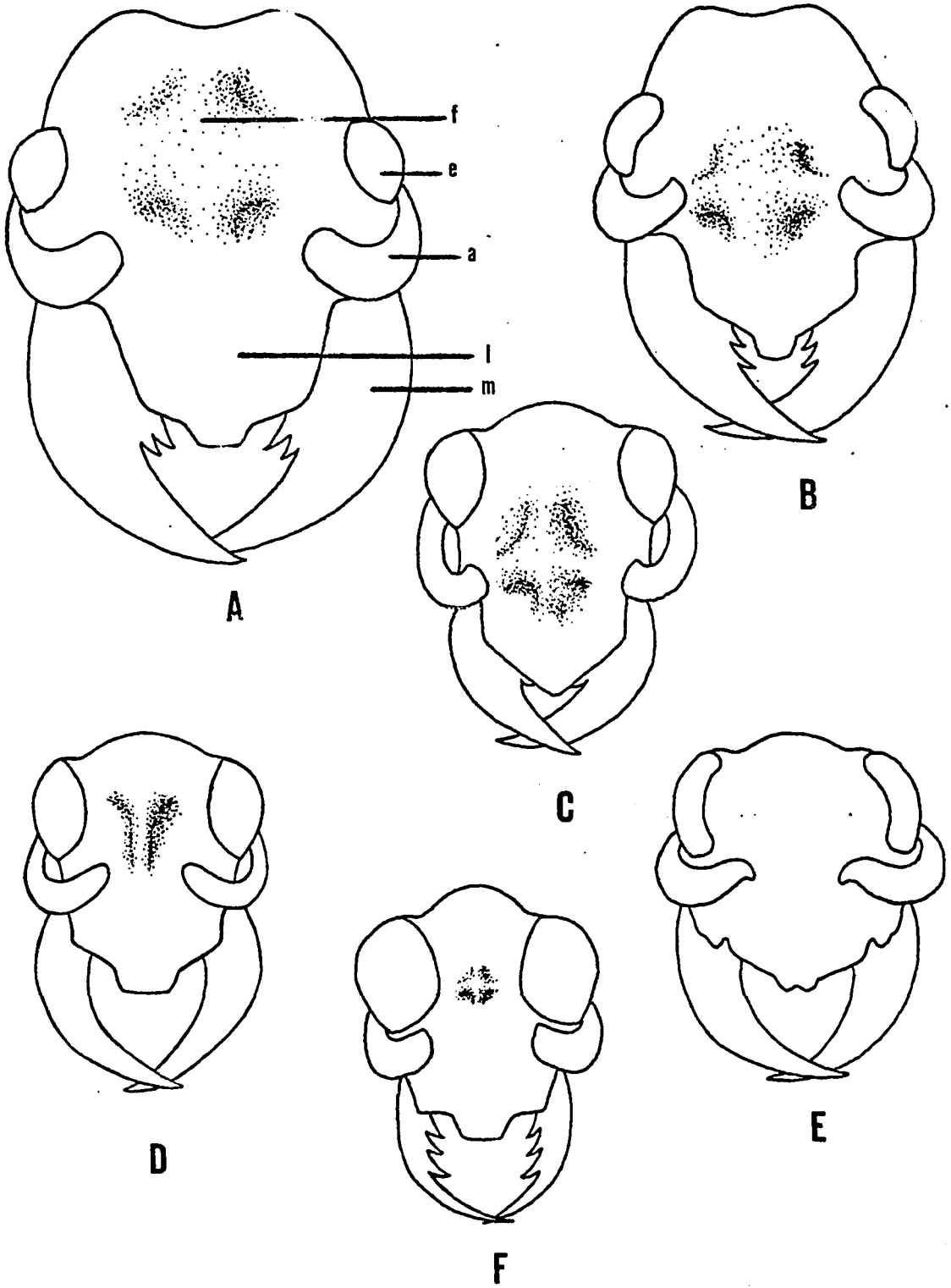
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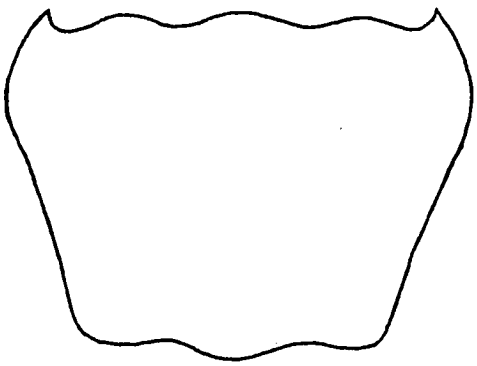
Figure 10 (continued)



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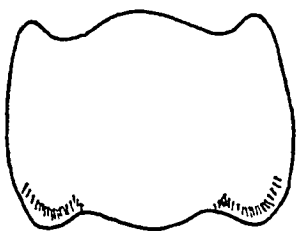

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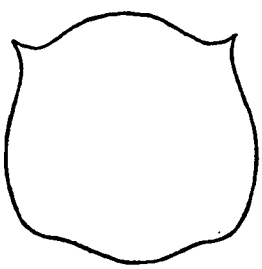

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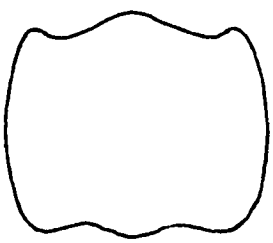

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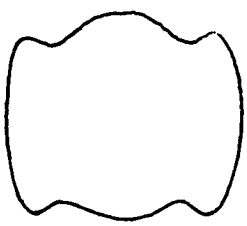

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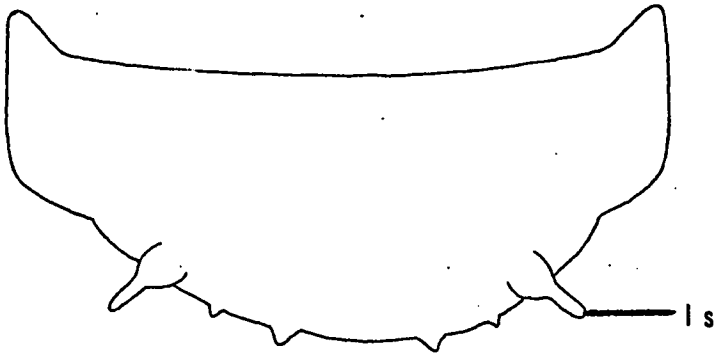

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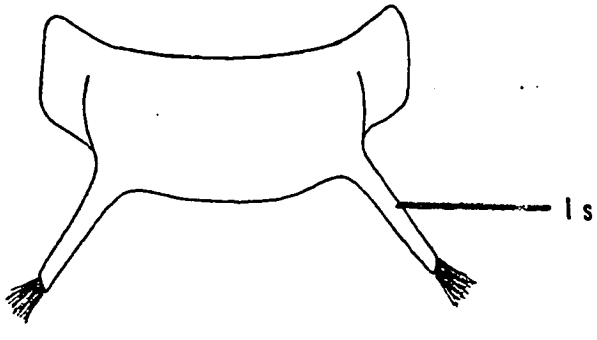

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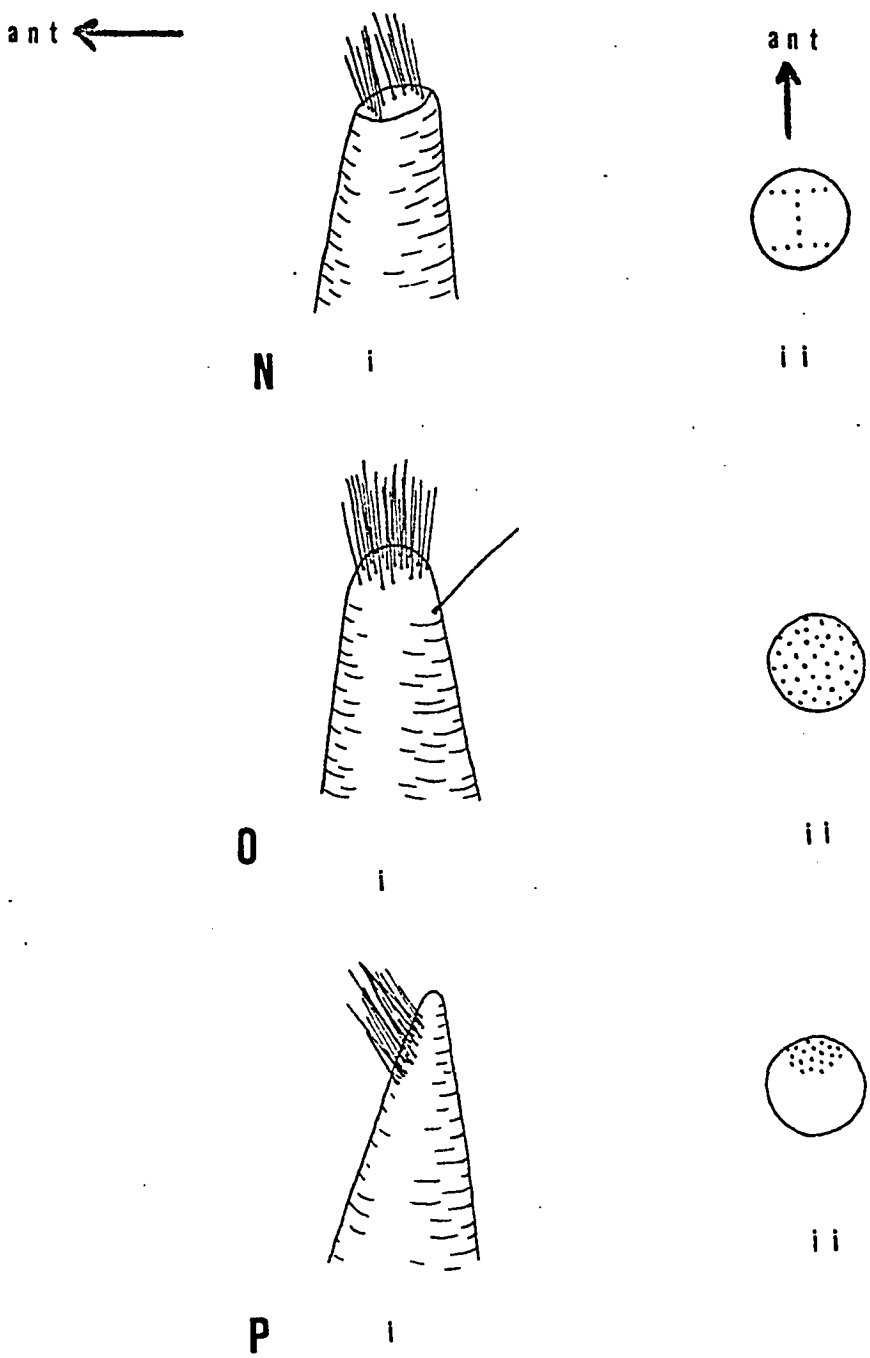


Table 5. Measurements and proportions of pupae of *Omus* spp. and *Cicindela* spp. Values when more than one is given represent the range with the arithmetic mean in parentheses. Character numbers are explained in the text.

Species/Sex	N	1	2	3	4	5	6
O. dejeani M	1	17.55	80.67	56.48	67.76	24.68	84.16
O. audouini M	2	12.29-13.64 (12.97)	57.83	50.00-68.75 (59.38)	55.62-87.87 (71.75)	21.70-27.27 (24.49)	84.38-85.71 (85.09)
F	1	13.37	73.41	63.91	84.65	33.27	92.50
C. oregona M	1	10.13	63.64	56.25	84.05	45.83	75.84
F	1	11.61	77.44	57.14	83.33	48.08	90.21
C. depressula M	1	9.86	76.30	42.86	81.48	50.00	76.67
F	1	12.69	84.70	45.00	87.50	43.55	83.25
C. repanda M	1	7.83	68.75	50.00	86.70	52.67	75.89
F	1	9.86	65.00	46.55	77.78	50.00	90.00
C. nebraskana F	1	14.31	69.83	85.91	70.43	44.14	93.54
C. decemnotata M	1	17.82	76.66	71.88	79.31	44.90	74.07
F	1	13.77	88.69	62.50	84.05	44.08	79.41
C. purpurea F	1	14.51	76.53	63.57	79.32	46.43	91.38
C. tranquebarica M	1	12.56	72.73	44.75	63.91	42.45	85.62
F	2	12.69-14.45 (13.57)	76.52-81.07 (78.80)	49.31-69.32 (59.57)	81.37-81.82 (81.60)	41.33-42.01 (41.67)	87.10-91.80 (89.45)
C. haemorrhagica M	1	11.48	84.96	70.99	88.89	40.00	56.25
F	2	10.26-10.53 (10.40)	62.50-83.05 (72.78)	52.07-54.32 (53.20)	76.52-93.10 (84.10)	40.00-45.45 (42.73)	72.65-76.92 (74.79)
C. cinctipennis M	1	11.07	80.00	66.67	75.00	47.54	52.21

1. Length of pupa in natural position. A cicindelid pupa reposes with its head deflexed onto its thorax. It is more convenient to measure the length between the anterior end of the pronotum to the posterior end of the abdomen, which this measurement represents.

2. Ocular index. Use of this character follows Campbell and Marshall (1964), permitting a measurement of the distance separating the eyes. It is calculated as follows:

$$\text{Ocular index} = 100\left(\frac{\text{minimum distance between medial edges of eyes}}{\text{maximum dorsal breadth of head across eyes}}\right)$$

The ocular index differs between the sexes, reflecting the larger eyes of the males.

3. Labral proportions. The pupal labrum is longer than that of the adult. As the adult labrum develops within, the distal edge of the pupal labrum degenerates to only the cuticular layers and becomes transparent. Thus, in measuring the pupal labrum, it is necessary to choose a specimen in which the entire structure is opaque. The components of the ratio are: greatest length, measured along the midline, divided by the greatest breadth, measured along the clypeal margin.

4. Pronotal proportions. The following ratio is calculated:

$$100\left(\frac{\text{greatest length measured along the midline}}{\text{greatest breadth}}\right)$$

5. Metanotal proportions. This ratio has potential as an index of hindwing development. A lower ratio reflected in the

shorter anteroposterior length correlates with lesser muscular development and, hence, smaller wings. The ratio is calculated:

$$100\left(\frac{\text{greatest length measured along the midline}}{\text{greatest breadth excluding the wings}}\right)$$

6. Ratio: $100\left(\frac{\text{length abdominal segments VI-X}}{\text{length abdominal segments I-V}}\right)$

The measurements are self-explanatory. The ratio reflects sexual dimorphism. The smaller ratio of the male correlates with the proportionally shorter combined length of segments VI-X.

Systematic Pupal Descriptions

All specimens are in my personal collection. All specimens were reared from captive larvae so dates are not given, except for one field-obtained *Cicindela repanda* pupa whose collection date I have stated in the appropriate place.

Omus dejeani

Material available. WA. King Co., 10 km W. Carnation: one male.

Head. Median frontal boss distinct, as inflated as tempora, and separated from tempora by defined frontal sulci; ocular index 84% (male); medial edge of eye evenly rounded; clypeus lateral lobes equilaterally triangular, with apices directed anteriorly; labrum with squared median lobe; distal end of mandibles, with head in

completely deflexed position, extending posteriorly nearly to level of meso-metathoracic boundary.

Thorax. Pronotum: trapezoidal in outline, with short base posterior; apical and basal margins shallowly sinuate; lateral margins very slightly arcuate, slightly sinuate immediately anterior to basal angles; anterolateral angles completely visible in dorsal view; rounded discal depression, one on either side of midline; longitudinal sulcus shallow. Mesonotum: trapezoidal in outline with long base posterior; apical margin arcuate; basal margin sinuate; rounded discal depression, one on either side of midline; longitudinal sulcus absent. Metanotum: trapezoidal in outline, with long base posterior; apical margin weakly arcuate; basal margin convex; discal depression, one on either side of midline, extending from middle of disc anteriorly to apical margin; longitudinal sulcus absent. Wings: hindwings approximately two-thirds as long and half as broad as forewings.

Abdomen. Ratio segments VI-X/I-V: 84% (male); basal breadths of tergal spines about 40% of lengths; spines of segments I-IV with five apical setae; lateral spines of segment V with "I" pattern of setae, bases anterior and posterior; tergite of segment V with three spines arranged transversely, in addition to long lateral ones.

Omus audouini

Material available. WA. King Co., Seattle, Univ. Washington campus: three (two male, one female).

Head. Median frontal boss distinct, as inflated as tempora, and separated from tempora by defined frontal sulci; ocular index: 58% (male), 73% (female); medial edge of eye evenly rounded; clypeus with lateral lobes directed laterally; labrum with margin forming rounded, equilaterally triangular median lobe; distal end of mandibles, with head in completely deflexed position, extending posteriorly to posterior edge of abdominal segment I.

Thorax. Pronotum: trapezoidal in outline, with short base posterior; apical and basal margins shallowly sinuate; lateral margins very slightly arcuate, slightly sinuate immediately anterior to basal angles; anterolateral angles deflexed with tips not visible in dorsal view; rounded discal depression, one on either side of midline; longitudinal sulcus shallow. Mesonotum: trapezoidal in outline with long base posterior; apical margin arcuate; basal margin strongly sinuate; discal depression, one on either side of midline, transversely ovoid; longitudinal sulcus shallow. Metanotum: trapezoidal in outline with long base posterior; apical margin weakly arcuate; basal margin convex; discal depressions absent; longitudinal sulcus absent. Wings: hindwings approximately two-thirds as long and one-third as broad as forewings.

Abdomen. Ratio segments VI-X/I-V: 84-86% (male), 93% (female); basal breadths of tergal spines about 53% of lengths; spines of segments I-IV with five apical setae; spines of segment V with "I" pattern of setae, bases anterior and posterior; tergite of segment V with lateral spines only.

Cicindela oregona

Material available. *C. o. oregona* - WA. King Co., Tolt River Cpgd., Carnation: one (female); *C. o. oregona* x *guttifera* - ID. Lemhi Co., 30.2 km S. Salmon, 1,219 m: 1 (male).

Head. Median frontal boss restricted to portion of frons anterior to eyes, separated from tempora by broad, shallow frontal sulci; vertex 77% (female); medial edge of eye evenly rounded; clypeus with lateral lobes directed laterally; labrum with distally notched, short, squared median tooth; distal end of mandibles, with head in completely deflexed position, extending posteriorly to level of posterior edge of metathorax.

Thorax. Pronotum: rectangular in outline; apical and basal margins sinuate with median lobe of base pronounced; lateral margins straight; basal depressions shallow with medial elevations, and connected by low, transverse ridge within groove; longitudinal sulcus broad and shallow. Mesonotum: transversely ovoid; anterior margin shallowly sinuate; posterior margin arcuate; longitudinal

sulcus faintly indicated. Metanotum: trapezoidal in outline with short base anterior; anterior margin concave; posterior margin arcuate; longitudinal sulcus faintly indicated. Wings: hindwings slightly longer than and as broad as forewings.

Abdomen. Ratio segments VI-X/I-V: 76% (male), 90% (female); basal breadths of tergal spines about 75% of lengths; spines of segments I-IV with five apical setae arranged in circle; lateral spines of segment V with random pattern of apical setae; tergite of segment V with lateral spines only.

Cicindela depressula

Material available. *C. d. depressula* - WA. Yakima Co., 1 km E. Chinook Pass, 1,584.9 m: two (one male, one female).

Head. Median frontal boss restricted to portion of frons anterior to eyes, separated from tempora by broad, shallow frontal sulci; vertex broadly U-shaped in transverse cross-section; ocular index: 76% (male), 85% (female); medial edge of eye evenly rounded; clypeus with lateral lobes directed laterally; labrum with distally notched, short, squared median tooth; distal end of mandibles, with head in completely deflexed position, extending posteriorly to level of posterior edge of metathorax.

Thorax. Pronotum: rectangular in outline; apical and basal margins sinuate with median lobe of base pronounced; lateral margins straight; basal depressions shallow with median elevations, and connected by low, transverse ridge within groove; longitudinal sulcus broad and shallow. Mesonotum: transversely ovoid; anterior margin shallowly sinuate; posterior margin arcuate; longitudinal sulcus faintly indicated. Metanotum: trapezoidal in outline with short base anterior; anterior margin concave; posterior margin arcuate; longitudinal sulcus faintly indicated. Wings: hindwings slightly longer than and as broad as forewings.

Abdomen. Ratio segments VI-X/I-V: 77% (male), 83% (female): basal breadths of tergal spines about 75% of lengths; spines of segments I-IV with five apical setae arranged in circle; lateral spines of segment V with random pattern of apical setae; tergite of segment V with lateral spines only.

Cicindela repanda

Material available. *C. r. repanda* - WA. Whitman Co., 2.8 km W. Lewiston, 255 m: two (one male, one female; male coll. 5 Sept. 1972).

Head. Median frontal boss restricted to portion of frons anterior to eyes, separated from tempora by broad, shallow frontal sulci; vertex broadly U-shaped in transverse cross-section; ocular

index: 69% (male), 65% (female); medial edge of eye evenly rounded; clypeus with lateral lobes directed laterally; labrum with distally notched, short, squared median tooth; distal end of mandibles, with head in completely deflexed position, extending posteriorly to level of posterior edge of metathorax.

Thorax. Pronotum: rectangular in outline; apical and basal margins sinuate with median lobe of base pronounced; lateral margins straight; basal depressions shallow with median elevations, and connected by low, transverse ridge within groove; longitudinal sulcus broad and shallow. Mesonotum: transversely ovoid; anterior margin shallowly sinuate; posterior margin arcuate; longitudinal sulcus faintly indicated. Metanotum: trapezoidal in outline with short base anterior; anterior margin concave; posterior margin arcuate; longitudinal sulcus faintly indicated. Wings: hindwings slightly longer than and as broad as forewings.

Abdomen. Ratio segments VI-X/I-V: 76% (male), 90% (female); basal breadths of tergal spines about 75% of lengths; spines of segments I-IV with five apical setae arranged in circle; lateral spines of segment V with random pattern of apical setae; tergite of segment V with lateral spines only.

Cicindela nebraskana

Material available. *C. n. chamberlaini* - WA. Kittitas Co., 2.8 km S. S. end Lk. Kachees, 762 m: one female.

Head. Median frontal boss extending between eyes to occiput, separated from tempora by broad, shallow frontal sulci; ocular index: 70% (female); medial edge of eye evenly rounded; clypeus with lateral lobes directed laterally; labrum with distal edge broadly arcuate but with defined distolateral angles; distal end of mandibles, with head in completely deflexed position, extending posteriorly to mid-point level of mesothorax.

Thorax. Pronotum: rectangular in outline; apical and basal margins sinuate with median lobe of base pronounced; lateral margins straight; basal depressions circular and connected by deep transverse groove; longitudinal sulcus absent. Mesonotum: transversely ovoid; anterior margin shallowly sinuate; posterior margin arcuate; longitudinal sulcus absent. Metanotum: trapezoidal in outline with short base anterior; anterior margin concave; posterior margin arcuate; longitudinal sulcus absent. Wings: hindwings slightly longer than and as broad as forewings.

Abdomen. Ratio segments VI-X/I-V: 94% (female); basal breadths of tergal spines about 88% of lengths; spines of segments I-IV with five apical setae arranged in circle; lateral spines of segment V with random pattern of apical setae; tergite of segment V with lateral spines only.

Cicindela decemnotata

Material available. *C. d.* n. ssp. Clifford - WA. Walla Walla Co., 4 km E. Wallula Jct.: two (one male, one female).

Head. Median frontal boss restricted to portion of frons anterior to eyes, separated from tempora by broad, shallow frontal sulci; vertex broadly U-shaped in transverse cross-section; ocular index: 77% (male), 89% (female); medial edge of eye evenly rounded; clypeus with lateral lobes directed laterally; labrum with distally notched, short, squared median tooth; distal end of mandibles, with head in completely deflexed position, extending posteriorly to mid-point level of mesothorax.

Thorax. Pronotum: rectangular in outline; apical and basal margins sinuate with median lobe of base pronounced; lateral margins straight; basal depressions shallow with median elevations, and connected by low, transverse groove; longitudinal sulcus broad and shallow. Mesonotum: transversely ovoid; anterior margin shallowly sinuate; posterior margin arcuate; longitudinal sulcus faintly indicated. Metanotum: trapezoidal in outline with short base anterior; anterior margin concave; posterior margin arcuate; longitudinal sulcus faintly indicated. Wings: hindwings slightly longer than and as broad as forewings.

Abdomen. Ratio segments VI-X/I-V: 74% (male), 79% (female); basal breadths of tergal spines about 75% of lengths; spines of

segments I-IV with five apical setae arranged in circle; lateral spines of segment V with random pattern of apical setae; tergite of segment V with lateral spines only.

Cicindela purpurea

Material available. *C. p.* new name Leffler - WA. Thurston Co., Rocky Prairie, 5 km N. Tenino, 61 m: one female

Head. Median frontal boss restricted to portion of frons anterior to eyes, separated from tempora by broad, shallow frontal sulci; vertex broadly U-shaped in transverse cross-section; ocular index: 77% (female); medial edge of eye evenly rounded; clypeus with lateral lobes directed laterally; labrum with distally notched, short, squared median tooth; distal end of mandibles, with head in completely deflexed position, extending posteriorly to level of suture between prothorax and mesothorax.

Thorax. Pronotum: rectangular in outline; apical and basal margins sinuate with median lobe of base pronounced; lateral margins straight; basal depressions shallow with medial elevations, and connected by low, transverse ridge within groove; longitudinal sulcus broad and shallow. Mesonotum: transversely ovoid; anterior margin shallowly sinuate; posterior margin arcuate; longitudinal sulcus faintly indicated. Metanotum: trapezoidal in outline with short base anterior; anterior margin concave; posterior margin

arcuate; longitudinal sulcus faintly indicated. Wings: hindwings slightly longer than and as broad as forewings.

Abdomen. Ratio segments VI-X/I-V: 91% (female); basal breadths of tergal spines about 75% of lengths; spines of segments I-IV with five apical setae arranged in circle; lateral spines of segment V with random pattern of apical setae; tergite of segment V with lateral spines only.

Cicindela tranquebarica

Material available. *C. t. moapana* - UT. Salt Lake Co., 15.9 km W. Salt Lake City Intern. Airport: two (one male, one female); *C. t. vibex* - OR. Marion Co., 3.5 km W. Mill City, 222 m: one female.

Head. Median frontal boss well-developed on portion of frons anterior to eyes, but with narrow extension extending posteriorly onto occiput, and separated from ocular peduncles by triangular depressions, apex anterior, located medial to posterior part of eyes; boss separated from tempora by broad, shallow frontal sulci; ocular index: 73% (male), 77-81% (female); medial edge of eye evenly concave except for evenly rounded anteromedial angle; clypeus with lateral lobes directed laterally; labrum with distal edge evenly arcuate; distal end of mandibles, with head in completely

deflexed position, extending posteriorly to level of posterior edge of metathorax.

Thorax. Pronotum: rectangular in outline; apical and basal margins sinuate with median lobe of base pronounced; lateral margins strongly arcuate, sinuate immediately anterior to basal angles, and edge thickened; basal depressions shallow and not connected by any transverse groove; longitudinal sulcus faintly indicated. Mesonotum: trapezoidal in outline with short base anterior; anterior margin shallowly sinuate; posterior margin arcuate; longitudinal sulcus faintly indicated. Metanotum: transversely ovoid in outline; paired elongate, low bosses, one on either side of midline, located near anterior edge of disc; anterior margin concave; posterior margin arcuate; longitudinal sulcus broad and shallow. Wings: hindwings one-third longer, slightly broader, and more pointed than forewings.

Abdomen. Ratio segments VI-X/I-V: 86-87% (male), 92% (female); basal breadths of tergal spines about 50% of lengths; spines of segments I-IV with five apical setae arranged in circle; lateral spines of segment V with random pattern of apical setae and one long, isolated seta on posterolateral face about one-quarter of distance basal of apex; tergite of segment V with lateral spines only.

Cicindela haemorrhagica

Material available. *C. h. nigroides* - WA Grant Co., 2.5 km E. Beverly: three (one male, two females).

Head. Median frontal boss restricted to portion of frons anterior to eyes, separated from tempora by broad, shallow frontal sulci; vertex very shallowly concave in transverse cross-section; ocular index: 85% (male), 64-83% (female); medial edge of eye evenly rounded; clypeus with lateral lobes directed laterally; labrum with distally notched, short, squared median tooth; distal end of mandibles, with head in completely deflexed position, extending posteriorly to level of suture between mesothorax and metathorax.

Thorax. Pronotum: rectangular in outline; apical and basal margins sinuate with median lobe of base pronounced; lateral margins gently arcuate, with portions immediately anterior to basal angles straight; basal depressions rounded, shallow, with anteromedial elevations, and without interconnecting groove; longitudinal sulcus faintly indicated. Mesonotum: transversely ovoid; anterior margin ovoid; anterior margin shallowly sinuate; posterior margin arcuate; basomedian area elevated and bounded laterally by concavities; longitudinal sulcus faintly indicated. Metanotum: trapezoidal in outline with short base anterior; anterior margin concave; posterior margin arcuate; longitudinal sulcus faintly indicated. Wings: hindwings about one-third longer, one-third broader, and more pointed than forewings.

Abdomen. Ratio segment VI-X/I-V: 56% (male), 73-77% (female); basal breadths of tergal spines about 20% of lengths; spines of segments I-IV with five apical setae arranged in circle; lateral spines of segment V with random pattern of apical setae; tergite of segment V with lateral spines only.

Cicindela cinctipennis

Material available. *C. c. imperfecta* - WA. Douglas Co., 9.9 km N.W. Leahy Jct., St. 17, 609.6 m: one male.

Head. Median frontal boss very weakly developed and restricted to portion of frons anterior to eyes, separated from tempora by very shallow, broad frontal sulci; vertex very broadly U-shaped in transverse cross-section; ocular index: 80% (male); medial edge of eye straight; clypeus with lateral lobes directed laterally; labrum evenly rounded along apical margin; distal ends of mandibles, with head in completely deflexed position, extending posteriorly to midpoint level of mesothorax.

Thorax. Pronotum: rectangular in outline; apical margin arcuate; basal margin sinuate; lateral margins slightly arcuate anterior to midpoint, then shallowly concave; basal depressions very shallow and not connected by any transverse groove; longitudinal sulcus faintly indicated. Mesonotum: transversely ovoid, and very narrow anteroposteriorly; anterior margin shallowly

sinuate; posterior margin arcuate; longitudinal sulcus absent. Metanotum: transversely ovoid in outline; anterior margin concave; posterior margin very broadly arcuate; longitudinal sulcus absent. Wings: hindwings one-third longer than and as broad as forewings; both hindwings and forewings lanceolate.

Abdomen. Ratio segments VI-X/I-V: 52% (male); basal breadths of tergal spines about 50% of lengths, spines laterally compressed; spines of segments I-IV with five setae arranged in anteroposteriorly oriented oval; lateral spines of segment V with setae arranged in patch on anterior face of distal quarter of spines; tergite of segment V with lateral spines only.

Analysis of Pupal Characteristics

Zikan (1929:287-288, 322, 336) presented virtually the only information about pupal anatomy of cicindelid genera other than *Cicindela*, briefly describing or illustrating pupae of *Ctenostoma* and *Odontochila*, as well as *Cicindela*. He (op. cit.: 288) differentiated the pupae of the two subfamilies:

> The (Collyrinae) possess cylindrically-formed pupae with subdorsal hooks on abdominal segments 1 to 5 reduced to low tubercles with short apical setae. The prothorax likewise shows a pair of such tubercles which the (Cicindelinae) lack.

The abdominal tubercles serve for purchase to aid in freeing the pupae from the larval exuvium during ecdysis (Shelford, 1908;

Willis, 1967) and in elevating the pupa off the substrate in its pupal chamber. Carabidae also possess setiferous tubercles on abdominal terga I-V (Balduf, 1935: Figure 17); these are presumably homologous to those of the Cicindelinae. Reduction of the tubercles in the Collyrinae is a specialization perhaps related to the characteristic of the wood in which the gallery is constructed, making substrate purchase easier during ecdysis and not requiring elevation.

Zikan's illustration of the *Odontochila* pupa (op. cit.: Figure 98) lacks detail necessary for me to distinguish it from other cicindeline pupae. Therefore, I can depend only on my own examinations of pupae of two species of *Omus* and nine species of *Cicindela* for characteristics of the subfamily Cicindelinae. These two genera at least represent separate tribes. I doubt that other genera, when described, will present any radical departure in form.

In general facies, pupae of *Omus* and *Cicindela* are similar (Figures 8 and 9). They differ primarily in the form of the head, the shape of the pronotum, and in the apical setal pattern on the spines of abdominal tergite V. The head of *Omus* has the eyes smaller in area, more rounded, and located laterally, with the frons in frontal section broad and convex. In *Cicindela*, the eyes are larger and located more dorsally so that the frons is shallowly excavated between the eyes, like a broad U in frontal section. The *Omus* pronotum is trapezoidal in outline, rectangular (broader than long) in *Cicindela*. *Omus* has an I-shaped setal pattern on the

apex of the spines of tergite V. In *Cicindela*, the setae are arranged randomly in a patch.

The following analyses are intended to point out characters of the pupae of the 11 known northwest species, emphasizing features unique or indicative of relationships.

Omus. The two species agree in the generic characters outlined above, but differ in several minor features. These differences in so structurally conservative a stage as the pupa suggest a long independent evolutionary history for the two species, a conclusion also reached through study of the larvae.

O. dejeani: Important characters are that the labrum has a squared median apical lobe, the pronotal basal depressions are rounded and not extended to the basal margin, and there are three short spines in addition to the long lateral ones on abdominal tergite V. The rounded basal depressions may be related to weaker prothoracic musculature, requiring a less extensive insertion area. I cannot propose any functional significance for the other features: the labrum is of doubtful use to a pupa and, because of the greater length of the lateral spines, the short median ones of tergite V do not touch the pupal chamber substrate. The high ocular index, 84% for a male pupa compared with 58% for *O. audouini*, indicates comparatively smaller eyes in *O. dejeani*.

O. audouini: Important characters are that the labrum has an equilaterally triangular apical lobe, the pronotal basal depressions extend to the basal margin, and only lateral spines are present on abdominal tergite V. I have commented on these features in the account of *O. dejeani* previously. The elongate pronotal basal depressions suggest stronger prothoracic musculature than in *O. dejeani*, a feature also reflected in the declivous-sided, deep prothorax of the adult.

Cicindela. The nine species are similar, the four subgenera represented presenting the greatest structural departures from a common plan.

Subgenus *Cicindela*: Six species are represented in my collection. Except for minor differences in size and proportions, five are indistinguishable: *C. oregona*, *depressula*, *repanda*, *decemnotata* and *purpurea*. *C. nebraskana* differs in the extension onto the occiput of the median frontal boss and the elongate labrum. The domed frons thus produced is, oddly, the exact opposite of the condition in the adult in which the frons is excavated. An elongate labrum is expected in the pupa of a species whose adults are characterized by elongate labra.

C. (*Cicindela*) pupae agree with those of subgenera *Cicindelidia* and *Tribonia* in the chaetotaxy of the spines of abdominal tergite V. *Cicindela* differs from *Tribonia* in lacking depressions medial

to the eyes, lacking a narrow interocular extension of the median frontal boss (any extension at all is absent in all species of *Cicindela* except *C. nebraskana*), having a convex rather than concave medial edge of the eye, and having unmodified lateral pronotal margins. From *Cicindelidia*, *Cicindela* differs in the deeper interocular outline as seen in frontal section and straight rather than arcuate lateral pronotal margins.

Subgenus *Tribonia*: This subgenus, represented in my collections by *C.* (*T.*) *tranquebarica*, is unique in having triangular depressions between the medial edges of the eyes and a narrow, posteriorly-directed interocular extension of the median frontal boss, a concave rather than convex medial edge of the eye, pronounced thickening of the lateral pronotal margins, and an isolated seta on the posterolateral face of the lateral spines of tergite V.

Subgenus *Cicindelidia*: This subgenus, represented in my collections by *C.* (*C.*) *haemorrhagica*, is unique in the broad, nearly interocular outline as seen in frontal section, and in the arcuate lateral pronotal margins. The pupa of *Cicindelidia* is more like that of *Cicindela* than *Tribonia*.

Subgenus *Cylindera*: This subgenus, represented in my collections by *C.* (*C.*) *cinctipennis*, differs greatly from other subgenera indicating a much more distant relationship. The medial edge of the eye is distinctly straight in outline, as opposed to concave or convex in other subgenera, the rather narrow lanceolate

wings and, particularly, in the chaetotaxy of the lateral spines of tergite V. In other subgenera, the setae are located apically, but in *Cylindera*, they are arranged in a patch on the anterior face of the distal quarter of the spine.

Summary

Cicindelid pupae are similar in structure. The two subfamilies differ in the presence or absence of abdominal tergal spines. *Omus* and *Cicindela* pupae are readily distinguishable, but on characters of a far lesser magnitude than those at the subfamilial level. The four subgenera of *Cicindela* have distinctive characters. *Cicindela* species are largely indistinguishable and most closely resemble *Cicindelidia*. *Tribonia* more closely resembles *Cicindela* and *Cicindelidia* than *Cylindera*.

Systematic Zoology

Introductory Remarks and Conventions

Most of the present study is devoted to systematics of the Cicindelidae with special emphasis on the 24 species found in the Pacific Northwest. Data concerning extralimital taxa are given in detail when relevant to the Pacific Northwest fauna. Systematic problems in the study of Cicindelidae are not governed by political geographic boundaries. Hence, it is often difficult to limit my discussions to systematics of some species and species-groups at the boundaries I have drawn to delineate the Pacific Northwest. Systematic problems within the Pacific Northwest. Systematic problems within the Pacific Northwest are often part of the picture of a more extensive geographic area. Thus, it is with regret that I have often had to exclude some areas adjacent to the northwest because of their lack of direct relevance.

The reader will note that I have not been consistent in my review methods for all of the species. Some species, such as those of the *maritima*-group (*Cicindela*) among others, have already been systematically revised. Others such as in the *formosa*-group (*Cicindela*) and *Omus* spp. have required only the delineation of heretofore unused diagnostic features. Some species (e.g., *C. tranquebarica*) need systematic review over their entire range; in these cases, I have pointed out problems requiring study and have

presented tentative conclusions. Finally, I have presented results of statistical analyses of *C. bellissima*, *C. longilabris* and *C. nebraskana* because only in this way could the variation in these species be interpreted.

Larval, pupal and adult keys to genera and species in the Pacific Northwest are presented in Appendix IV.

Use of Group, Subgroup and Section

These terms have no status in the taxonomic hierarchy (see Simpson, 1945:14-15). I am using them as noncommittal terms for groups of categorical rank.

Group: This category is used for a level between subgenus and species; that is, the species-group. Example, *maritima*-group of subgenus *Cicindela*.

Subgroup: A group may be divided into two or more subgroups. The term is more-or-less equivalent to "superspecies (see Mayr, 1969: 52-53, 412)," but I am not using it as a synonym or substitute for that term. Example, I divide the *maritima*-group into three subgroups.

Section: This category is used for a level between species and subspecies; that is, for a group of related subspecies. Example, *vibex*-section of *Cicindela tranquebarica*.

Use of Terms of Phylogenetic Antiquity

A number of terms have come into general usage to denote extremes of phylogenic antiquity. I use some terms synonymously and reject others because of personal preference or inappropriatness.

Primitive, generalized, plesiomorphic: I use these three terms interchangeably for organisms or character-states most like an ancestral form.

Advanced, derived, apomorphic: "Advanced" has a teleologic connotation and I reject its usage for that reason. "Derived" can serve as an antonym for primitive, but I personally prefer "apomorphic" denoting morphology distant from the original condition.

Anatomical Conventions

I have defined a number of anatomical systems in the appropriate places in the following sections and have given sources for terminology used. In addition, because differences in terminology for male and female genitalia exist, I have used that of Freitag (1965 for male; 1972 for female) with additions from Rivalier (1950, 1954). Female genitalia pose no difficulty in orientation. However, because the aedeagus differs in orientation when retracted within the body or extruded as during copulation, it is necessary to employ one set of positional directions. Thus, following Freitag (1965), the aedeagus is described as if retracted within the body cavity,

with the orifice dorsal. Figures 2 and 3 illustrate basic male and female genitalia with parts labelled.

The Subspecies Concept

The validity of the subspecies rank in the taxonomic hierarchy has been argued at length in the literature without resolution. Classical arguments concerning the concept are contained in the often-quoted papers by Edwards (1954) in favor and Wilson and Brown (1953) against. The arguments are largely philosophical and, to some degree, semantic. I support the subspecies as a valid category with the full realization that the concept can be misused unless care is taken (cicindelid taxonomy has particularly suffered from inappropriate and often overzealous creation of large numbers of ill-founded subspecific names). The following criteria for definition of a subspecies are adapted from Willis (1967:233-234):

1. Occupation of a defined geographic area separate from or adjacent to that of other subspecies of the same species (zones of intergradation may occur between neighboring subspecies).

2. Exhibition of relatively uniform expression of characters within populations referrable to one subspecies.

3. Expression of one or more characters readily separating each subspecies from others within the species.

The subspecies is also useful in zoogeography. Four species of Nearctic Cicindelidae have nearly continent-wide distributions.

To speak of one of these species strictly as a whole and make attempts at determining dispersal routes and zoogeographic relations is futile. However, these species can be separated into discrete divisions (subspecies) consisting of individuals structurally more like one another than to individuals of other divisions (subspecies) of the same species. Such subspecies can be used in determining possible dispersal routes and direction of evolution from an ancestral form. The alternatives to use of subspecies are to label these populations A and B, etc., or to outline their geographic ranges. Populations A and B must be characterized in order that individuals may be placed in one or the other, and they must be distinguished so that their ranges can be defined. In either case, the subspecies is implied in spirit.

Family Cicindelidae Latreille, [1802]

Cicindélètae Latreille, [180]. Hist. Nat., Paris, 3:77

Diagnosis. Adult: Characters of order Coleoptera, suborder Adephaga and infraorder Geadephaga; clypeus extended lateral to level of antennal insertion; antenna inserted on frons anteromedial to eye, not directly anterior to eye; gena dorsoventrally deeper than anteroposteriorly long (except in *Pycnochila*); procoxa closed, separated and unbridged, mesocoxa and metacoxa disjunct and confluent (terminology and concepts following Bell, 1967); isochaetous (criteria of Hlavac, 1971, not Bell, 1967, or Jeannel, 1941); oblongum of hindwing absent (except in *Ctenostoma* and *Pogonostoma*). Male genitalia: middle lobe only slightly arcuate if at all; parameres slender, terete, and joined by dorsal basal piece. Female genitalia: 2nd gonapophysis chelicerate with two styli. Larva: four stemmata present, I and II much larger than others; maxilla

with basal segment of galea and palpiger ankylosed; head and pronotum together forming circular shield; abdominal tergum V with enlarged hump bearing 2-3 pairs of hooks; urogomphi absent.

Pupa: clypeus extended lateral to level of antennal insertion; antenna inserted on frons anteromedial to eye, not directly anterior to eye; abdominal terga I-V with dorsolateral spines, spines of tergum V comparatively greatly enlarged.

Relationships

In the previous section, I have argued for familiar status for the Cicindelidae, while emphasizing relationship with the Carabidae. Research by Bell (1966, 1967), Bell and Bell (1962), Hlavac (1971), and Lindroth (1960, 1960-1969) suggested that familial limits in the Adephaga may eventually be reorganized. All of these studies showed that the Carabidae, as presently formulated, are the basal stock of the suborder, and other groups of Adephaga can be derived from one carabid group or another, Rhysodidae from tribe Scaritini (Bell and Bell, 1962) and Hydradephaga from subfamily Trachypachinae (Bell, 1966).

Crowson (1967:7) stated that if the difference in the position of the antennal insertion is ignored, Cicindelidae would key to his

Carabinae. The important common character is the separation of the mesepisternum and mesosternum by the mesepimeron. Using criteria of Hlavac (1971), Cicindelidae have a Grade A antennal cleaner on the protibia (generalized isochaetous type) also seen in all Carabinae except *Pamborus*, Cychrini, Opisthiini and Enceladini. Although the combination of ventral thoracic characters of Cicindelidae is unique (Bell, 1967), the Carabinae differ uniformly only in having the metacoxa separated rather than confluent.

Of the tribes of Carabinae (*sensu* Ball, 1960, and Hatch, 1953, not Lindroth, 1969-1969), only the Carabini have the proper combination of characters to place them in contention as probable ancestors for the Cicindelidae. Indeed, some generalized carabines such as *Carabus* and *Callistenes* closely resemble in general facies *Mantica* or *Omus*.

Familial Status of the Cicindelidae

Some authors have merely followed other authorities in considering the tiger beetles to be a subfamily or tribe of Carabidae, whereas others have employed a familial rank. Few authors have discussed reasons behind their use of one taxonomic rank or another. Hierarchical rank for tiger beetles is partly a question of philosophy. Should similarities or differences be emphasized: should a group be included in the same taxon as its presumed ancestor, thus emphasizing similarities (e.g., inclusion by Bell

and Bell, 1962, of the Rhysodidae in the Carabidae); or placed in a separate taxon, thus emphasizing differences (e.g., division of Carabidae into numerous families by Jeannel, 1941)?

In a discussion of the familial rank, Mayr (1969:91-96 *passim*) stated:

> . . . nonarbitrary definitions for the supraspecific categories are not available . . . . Higher taxa are often, if not usually, well delimited and separated from other taxa of the same rank by a pronounced gap . . . . the family is usually distinguished by certain adaptive characters which fit it for a particular niche or adaptive zone . . . . each family usually presents a general facies which is recognizable at a glance, and all its species occupy a similar niche in their particular community . . . ."

Cicindelid specializations appear to fall into at least seven seemingly independent categories. Mayr's (1969:225) warning, however, must be heeded: "Just exactly what 'independent' is, and how this can be determined, is still controversial." It is possible that some characters in the seven adaptive categories may represent expressions of pleiotropic influences. However, the state of our knowledge of pleiotropy does not permit use of this phenomenon in determining whether characters in the adaptive categories are independent or not.

Adaptive Categories

1. Adult feeding. Lateral broadening of the clypeus over the bases of the mandibles is a universal feature of Cicindelidae and has been used as a major key character for the family. The

clypeus serves as the point of cibarial muscle insertions and for attachment of the labrum (Chapman, 1971). The mechanics of clypeal action are undescribed (Evans, 1965), but, presumably, the function of the broad clypeus and labrum is for holding and manipulating prey. The carabid clypeus does not extend laterally to completely cover the bases of the mandibles.

II. Antennal insertion. Another universal feature of Cicindelidae is the position of the antennal insertion. In Carabidae, the antennae are located directly anterior to the eyes, but in Cicindelidae, they are displaced slightly dorsally onto the frons so as to occupy a point anterodorsal to the eyes. I theorize that the shift allows uninterrupted anterior vision, useful to a diurnal predator largely dependent on vision for finding prey. Perhaps the small eyes of some primitive cicindelids (tribe Mantichorini and subtribe Omina) are a secondary, possibly neotenic, modification for nocturnal activity, expressed in size and not antennal insertion change which might involve too great a genetic change to permit return to the ancestral lateral position.

The position of the cicindelid antennal insertion is perhaps another way in beetles of achieving uninterrupted anterior vision. Other families have evolved analogous arrangements for the same purpose by shifting the insertion to the dorsum of the frons (Chrysomelidae, Staphylinidae); ventrally below or posterior to the eyes (Coccinellidae, Histeridae, Scarabaeidae); arranged on a prolonged

beak (Curculionoidea); and by having the eye partially surrounding the antennal base (Cerambycidae, Scolytidae, Tenebrionidae).

III. Oblongum. The oblongum is a cell in the hind wing formed between M_2, M_{3+4} and m cross vein. Its presence is a primitive feature of Megaloptera and Coleoptera. It is absent in all Cicindelidae except *Pogonostoma* (I have found it present in a specimen of *Ctenostoma ichneumonium* Dejean, although W. Horn (1908-1915) listed the cell only in *Pogonostoma*). Its loss in most Cicindelidae is apomorphic, and the functional anatomy and its possible relationship to some aspect of wing folding or strengthening is a topic that is worthy of study. Whether loss of the oblongum represents loss of the base of either M_2 or M_{3+4} or a fusion of these to form M_{2+3+4} as Wallace and Fox (1975:Figure 18) showed requires histological sectioning through the area in question. It is possible that the vein in Cicindelidae consists of veins making up the basal and apical sides of the original oblongum that have collapsed together. If so, presence of the oblongum in *Ctenostoma* and *Pogonostoma* is secondary, rather than primitive.

IV. Aedeagal form. Jeannel (1941) pointed out that the cicindelid aedeagus most closely resembles those of the carabine tribes Carabini and Nebriini, but is unique in having a sclerotized basal dorsal piece articulating with the parameres. The cicindelid middle lobe is more-or-less straight compared with arcuate in Carabidae, and the parameres are slender and terete,

rather than platelike or of some other form. I do not want to speculate on possible reasons for the anatomical differences.

V. Female genitalia. Survey of descriptions and illustrations by Pomeroy (1932) and Tanner (1927) of the 2nd gonapophyses of carabid tribes (some tribes were not treated) reveals no group showing the chelicerate cicindelid form. The 2nd gonapophyses of the oviposition aid in excavation of the egg burrow. Oviposition habits of Carabidae are more varied than in Cicindelidae, and carabid larvae are not dependent on a burrow, constructed by enlarging the egg burrow, to trap prey. Digging of an egg burrow by Cicindelidae may improve survival of the egg and the non-hunting yet predaceous larva, so that an effective digging organ has evolved.

VI. Larva. Four larval characters, and perhaps a fifth indirectly, are adaptations for life in a burrow. Excluding anomalous specialized groups, carabid larvae are generally active predators that do not use burrows in trapping food. On the other hand, Cicindelidae use the larval burrow as a food trap. The head and pronotum are modified to form a lid for the burrow mouth. Presumably the enlarged stemmata I and II are also an adaptation for burrow-dwelling, their form directed toward vision upward, since the burrow prevents vision in any other direction. The hooks on abdominal tergum V are an obvious adaptation to life in a burrow because they are used as a dorsal brace for maintaining the larva's position in its burrow. Lack of urogomphi in the cicindelid larvae is expected in a relatively sedentary organism in which posterior

sensory organs would be useless. Active wandering predators such as most carabid larvae would find great value for such sensory structures, particularly in leaf litter, crevices or beneath bark where vision is limited.

A fifth larval feature has a less obvious adaptation. In Cicindelidae, the palpiger and the basal segment of the galea of the maxilla are enlarged and ankylosed (whether they are actually fused requires study through histological sectioning, although the sutures are clearly visible), forming a segment referred to as "forked" by Mandl (1971:508). Also, the galea is two-segmented. In Carabidae, the segments are not enlarged and are either completely separated or basely touch basally; also, the galea is four-segmented. Stability produced by ankylosis and reduction in number of segments may serve in improving manipulation of prey in a limited space (the burrow), whereas Carabidae which are not so confined may not require such stability.

VII. Pupal abdominal spines. Elongated spines on abdominal terga I-V and enlargement of those of tergum V are unique to Cicindelidae, although reduced in Collyrinae (Zikan, 1929). Setae alone are present at the homologous positions in Carabidae. The cicindelid pupa is elevated off the substrate within the pupal chamber, whereas, presumably, the dorsum of the carabid pupa would directly contact the substrate. Pupation in members of both families is passed in a pupal chamber. Perhaps the spines reduce the possibility of fungal infection in cicindelid pupae, but unless the

spines serve some special function, the identification of which requires additional research, spines and spinelessness may both be successful anatomical arrangements.

In summary, I believe that the unique characteristics of the Cicindelidae are sufficient to argue for their separation from the Carabidae. Use of familial or subfamilial ranking is a matter of opinion. There is a distinct gap in habits and their associated anatomical adaptations between Cicindelidae and Carabidae, and this fulfills the general requirements in the definition of the familial rank presented by Mayr (1969:95-96).

Validity of Cicindelid Subfamilies

Classification within the Cicindelidae has traditionally followed W. Horn (1908-1915). He divided the family into two subfamilies, largely based on the arrangement of the ventral mesothoracic sclerites. Horn's "Alocosternales" and "Platysternales" respectively correspond in modern usage to subfamilies Collyrinae and Cicindelinae. The naturalness of these subfamilies has not been systematically scrutinized. The Collyrinae are characterized by their alocosternalean thoracic structure and by degenerate larval structures suited for life in galleries in trees. Similar but not so pronounced degeneracy is shown by the larva of *Therates*, a cicindeline whose larva also lives in galleries in trees. The Cicindelinae are characterized by platysternalean structure and

non-degenerate larvae (except for *Therates*). The Collyrinae are traditionally divided into two tribes (Collyrini and Ctenostomatini) and the Cicindelinae into three tribes (Cicindelini, Mantichorini and Megacephalini).

The Collyrinae are listed first in a vertical classification, apparently because of the presence in the Ctenostomatini of an oblongum in the hindwing, a primitive coleopteran feature (of the Collyrini, *Collyris* lacks the oblongum and the nature of the character cannot be ascertained in the brachypterous *Tricondyla*). Both tribes agree in the following characters:

1. Prothorax cylindrical with continuous, circumferential basal and apical grooves; anterolateral angles of pronotum extended no further anterior than anterior edge of prosternum. This character is identical with the condition in the Cicindelini and decidedly unlike the cordate form of Mantichorini, Megacephalini, and most other Adephaga.

2. Alocosternalean (see W. Horn, 1908-1915, and Willis, 1969, for a definition and illustration). This feature is unique to the Collyrinae.

3. Larval degeneration: legs with femur, tibia and tarsus ankylosed; tarsus one-segmented and with single tarsal claw fused to tarsus. Zikan (1929:286-287) listed this character and 16 others of larvae, many such as the absence of circumpygopodal setae probably being degenerate in nature and being adaptations for life in a

gallery in a tree where the walls of the gallery are not subject to crushing or micrometeorological fluctuations.

4. Hooks of abdominal tergum V: larvae of both *Collyris* and *Ctenostoma* have three pairs of hooks.

5. Pupal abdominal spines: only the pupa of *Ctenostoma* has been described (Zikan, 1929), and it has the dorsolateral spines of abdominal segments I-V present but reduced in size compared with pupae of Cicindelinae. The reduced size is probably the result of degeneracy through adaptation for life in a gallery in a tree.

Larval and pupal similarities of the two tribes could be the result of convergence because of similar habitats, and, indeed, *Therates* larvae anatomically approach those of Collyrinae closely. However, prothoracic and mesothoracic anatomy cannot be explained in terms of convergence and argues that the Collyrinae are a natural group. However, the two tribes have undergone a long independent evolutionary history, resulting in many striking differences:

1. Digitus of maxillary lacinia: present in Collyrini, absent in Ctenostomatini.

2. Proportions of labial palp segments: apical article about 60% of length of second article in Collyrini, about 30% or less in Ctenostomatini.

3. Oblongum: absent in Collyrini, present in Ctenostomatini.

4. Posterior frontal ridge of larva: U-shaped in Collyrini, transverse in Ctenostomatini.

5. Arrangement of larval pronotal setae: arranged in distinct patches in Collyrini, uniformly distributed in Ctenostomatini.

Two lineages are present in the Cicindelinae: one consists of the tribes Mantichorini and Megacephalini, and the other of the tribe Cicindelini. The two differ strongly in the form of the prothorax. That of the first group has the pronotum cordate in form with the anterolateral angles extending anteriorly to a level anterior to the anterior edge of the prosternum, precisely the form typical of Carabidae. Known larvae all have a transverse posterior frontal ridge. In the Cicindelini, the pronotum is cylindrical (although not as strongly as in the Collyrinae) with the anterolateral angles at about the same level anteriorly as the anterior edge of the prosternum. Known larvae have a U-shaped posterior frontal ridge (it may be transverse in *Euprosopus* but Zikan's [1929:Figure 82] is difficult to interpret). In those characters in which Collyrini differ from Ctenostomatini, Collyrini agree with Cicindelini and only in part with Mantichorini and Megacephalini. Table 6 presents comparison pairing of the several groups.

The following is a classification which probably best reflects the relationships of the groups. It is presented for consideration as a possible result of future research and is not intended to replace the current classification.

Table 6. Comparison pairing of character-states in tribes or tribal-groups of Cicindelidae. Symbols: (+) = common to both; (-) = differ in both; gen = most members show the same character-state; Ci = Cicindelini; Co = Collyrini; Ct = Ctenostomatini; M = Mantichorini + Megacephalini.

Character-state	Co vs. Ct	Ct vs. M	Ct vs. Ci	Co vs. M	Co vs. Ci
1. digitus of maxillary lacinia	(-)	(-)	(-)	(-)	(+)
2. proportions of labial palp segments	(-)	(-)	(-)	(+)	(+)
3. oblongum	(-)	(-)	(-)	(-)	(+)
4. larval posterior frontal ridge	(-)	(+)	(-)	(+)	(+)
5. arrangement of larval pronotal setae	(-)	gen (+)	(-)	gen (-)	gen (+)

Family Cicindelidae

Subfamily Megacephalinae

Tribe Megacephalini

Tribe Mantichorini

Subfamily Cicindelinae

Subfamily Collyrinae

Tribe Collyrini

Tribe Ctenostomatini

The classification of the Cicindelidae I have adopted is as follows. Genera are not included, except for *Cicindela* and *Omus*.

Family Cicindelidae Latreille

Subfamily Cicindelinae Latreille

Tribe Mantichorini

Tribe Megacephalini

Subtribe Omina Castelnau

Omus Eschscholtz

Subtribe Megacephalini

Subtribe Platychilina

Tribe Cicindelini Latreille

Subtribe Dromicina

Subtribe Prothymina

Subtribe Theratina

Subtribe Cicindelina Latreille

Cicindela Linnaeus

Subfamily Collyrinae

Tribe Ctenostomatini

Tribe Collyrini

Figure 11 presents my concept of the relationships of suprageneric groups of Cicindelidae.

Subfamily Cicindelinae Latreille, 1804

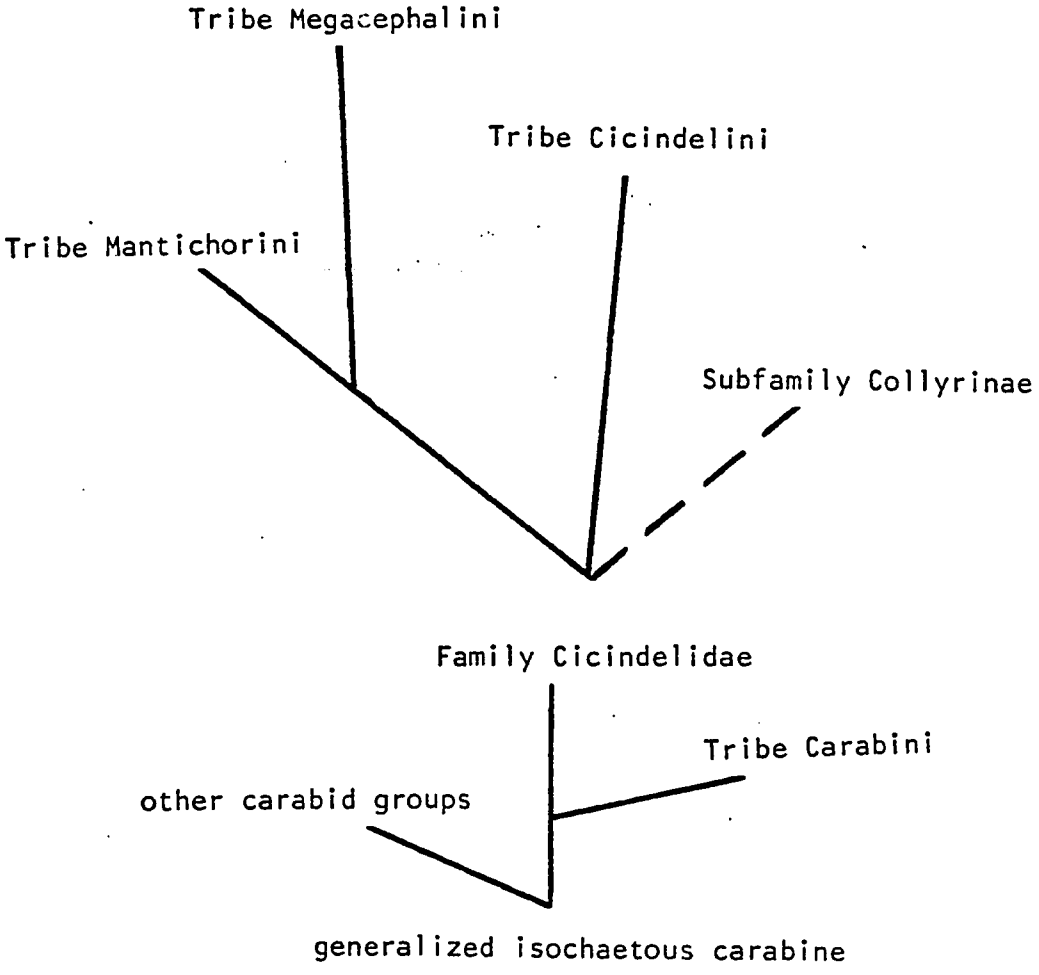
Diagnosis. Cicindelidae with digitus of maxillary lacinia always present; mesepisternum not extending medially to mescoxa, resulting in contact of mesosternum and mesepimeron.

There are three tribes: Cicindelini, Mantichorini and Megacephalini. I consider the following characters significant in distinguishing the tribes, indicating their interrelationships and plesiomorphy or apomorphy. This information is based on study of genera of all tribes and extracts from W. Horn (1908-1915) and Shelford (1915).

1. Setae at base of mandible. If a general setoseness is plesiomorphic, then the Mantichorini are primitive in this regard, and the condition extends to the presence of setae on the mandibles.

2. Proportions of maxillary palp segments. Excluding anomalous genera, the Mantichorini, some Megacephalini and

Fig. 11. Proposed phylogeny of Family Cicindelidae based on morphological characters. (Note that "Subfamily Cicindelinae" has been purposely omitted because of the doubt that all of the included tribes should actually be included in the same subfamily.)


Tribe Megacephalini
Tribe Cicindelini
Tribe Mantichorini
Subfamily Collyrinae
Family Cicindelidae
Tribe Carabini
other carabid groups
generalized isochaetous carabine

Cicindelini have the basal segment short. It is elongated in some Megacephalini. A short basal segment is also characteristic of most Carabidae and is thus plesiomorphic. The Mantichorini and Cicindelini differ from the Megacephalini in having the fourth segment shorter than the third, also here considered plesiomorphic.

3. Setoseness of apical segment of palpi. The comments about mandibular setae also apply here. Only the Mantichorini have the apical segments setose.

4. Form of pronotum. Pronota of the Mantichorini and Megacephalini are trapezoidal in outline, the long base anterior (the shape called "cordate" by Hatch, 1953), with the anterolateral angles produced anteriorly to a level anterior to the anterior margin of the prosternum. Also, the anterior pronotal sulcus is not continuous with the anterior prosternal sulcus but lies anterior to it. In the Cicindelini, the pronotum approaches a cylindrical shape without produced anterolateral angles, and with the anterior sulcus continuous with the anterior prosternal sulcus. The cordate shape characterizes many carabines (Carabini, Cychrini and Nebriini), whereas the cylindrical form of the Cicindelini is unique (it also characterizes the Collyrinae).

5. Elytral form. Midline fusion of the elytra occurs in flightless species in many unrelated families and no taxonomic significance should be attached to the character. The Mantichorini are unique in having the entire basal margin depressed, with a declivous

slope leading to the flattened and elevated disc. Elytra of the Megacephalini and Cicindelini are usually unmodified, being gently convex both in transverse and longitudinal sections.

6. Elytral tracheation. The generalized pterygote forewing has six equally developed tracheal trunks (Shelford, 1915). This is characteristic of the Mantichorini and some Omina. Other Megacephalini have the media the most prominent and the anal reduced or absent. The subtribes of Cicindelini agree only in the reduced or absent anal; other veins are reduced, fused or branched, depending on the group.

7. Elytral setae. The generalized pterygote forewing has the setae generally distributed (Shelford, 1915). This is characteristic only of the Mantichorini and some Megacephalini. In Cicindelini and other Megacephalini, setae are reduced to certain regions, reduced in number, modified or absent altogether.

8. Aedeagus. In the Mantichorini and Megacephalini, the apex of the middle lobe is gradually tapered distally and bears a keeled apical process on the left surface. The apex of the cicindeline aedeagus is broad dorsoventrally with dorsal and ventral flanges on the left surface. Neither form particularly resembles the aedeagus of any carabid.

9. Larval caudal frontal ridge. This ridge is transverse and contiguous with the posterior edge of the frons in the Mantichorini, Megacephalini and *Euprosopus* of the known Cicindelini. The ridge

is U-shaped and separated from the posterior edge of the frons in remaining Cicindelini. I do not know which expression is plesiomorphic, but I would intuitively consider a transverse, contiguous ridge as primitive.

10. Larval pronotal setal pattern. I shall discuss this character is more detail beyond under Megacephalini. To summarize, I consider an arrangement of undifferentiated rows of setae to be plesiomorphic. There are lineages among genera of both the Megacephalini and Cicindelini from this undifferentiated condition to derived expressions.

11. Hooks on larval abdominal tergite V. This character is discussed in detail in the larval section. I do not know whether two or three pairs of hooks if primitive. *Mantichora* of the Mantichorini (the *Mantica* larva is unknown) has two pairs and some genera of both the Megacephalini and Cicindelini have three pairs and some only two pairs. As another example, in *Euprosopus* (Cicindelini), the lateral hooks are small, whereas in *Omus*, they are well-developed. Perhaps, three pairs is primitive.

Table 7 summarizes these 11 character-states for the three tribes. This table shows that the Mantichorini are generalized in all characters except the peculiar depression of the elytral basal margins. As I shall show beyond in my discussion of the Megacephalini, the Omina are generalized and Megacephalina and Platychilina are variable in many characters, resulting in the high frequency of characters rated V (variable) in the table. In

Table 7. Analysis of tribes of subfamily Cicindelinae regarding plesiomorphic and apomorphic states of 11 characters presented in text. Symbols: P = plesiomorphic, A = apomorphic, V = variable, ? = unknown.

Character No.	Mantichorini		Megacephalini		Cicindelini	
1	setose	P	glabrous except *Amblycheila*	A	glabrous	A
2	basal segment short; 4th segment shorter than 3rd	P	length of basal segment variable; 3rd segment shorter than 4th	A	same as Mantichorini	P
3	setose	P	glabrous	A	glabrous	A
4	cordate	P	cordate	P	rectangular	A
5	depressed basal margin, elevated flattened disc	A	unmodified	P	unmodified	P
6	6 equally prominent trunks	P	variable	V	anal reduced; other trunks modified	A
7	generally distributed	P	variable	V	located regionally, modified, or absent	A
8	gradually tapered; keeled apical process on left side	?	same as Mantichorini	?	dorsoventrally broad with dorsal and ventral flanges on left surface	?
9	transverse; contiguous with posterior edge of frons	P	transverse; contiguous with posterior edge of frons	P	variable	V
10	irregularly arranged, numerous	P	variable	V	variable	V
11	2 pairs	?	variable	V	variable, but mainly 2 pairs	V
	ΣP=8; ΣA=1; unanalyzed=2		ΣP=3; ΣA=3; ΣV=4; unanalyzed=1		ΣP=2; ΣA=5; ΣV=3; unanalyzed=1	

general body facies and the form of the aedagus, the Mantichorini and Megacephalini are more closely related to one another than is either to the Cicindelini. The Cicindelini are modified in nearly all characters being plesiomorphic only in those two characters in which the other tribes show unique expressions, namely, the modified elytra of the Mantichorini and the comparative lengths of the maxillary palp segments in the Megacephalini.

In summary, I consider the Mantichorini the most generalized tribe, specialized mainly in flightlessness. I have already commented on a derivation of the Cicindelini independent of the other two tribes. Certainly, none of the Mantichorini or Megacephalini closely resembles any of the Cicindelini.

Tribe Megacephalini W. Horn, 1907

Diagnosis (from Willis, 1969, after W. Horn, 1908-1915). Cicindelinae with mandibular scrobe largely glabrous (only small numbers of scrobal setae present in *Amblycheila*); distal segment (fourth) of maxillary palp shorter than paenultimate (in *Eucallia*, reverse is true); apical segment of palpi

glabrous; dorsal margin of epipleuron lacking stridulatory file (except in *Chiloxia* and *Oxychila*); and antero-lateral angles of pronotum extended to level farther anterior than anterior margin of prosternum.

There are three subtribes: Megacephalina with six or more genera, Omina with three genera, and Platychilina with one genus. Literature is limited and the following information has been extracted from W. Horn (1908-1915), Shelford (1915), Willis (1969), and specimens of six genera. I consider the following characters significant in distinguishing the subtribes, indicating their interrelationships, and plesiomorphy or apomorphy:

1. General body facies. The figures by W. Horn (1908-1915: Plates 9, 10 and 12) show striking similarity in general body form among the genera of Megacephalina and Omina. *Platychila* is strongly aberrant in its flatness and translucency and in the shape of the pronotum (treated beyond). The facies of *Mantica* of the Mantichorini is like that of the Megacephalina and Omina. Such a facies is decidedly carabid-like and I consider it plesiomorphic.

2. Length of basal labial palp segment. The Omina agree with the Mantichorini and Cicindelini in that the basal segment is shorter than the depth of the notch between the paraglossa and the mental tooth. In the Megacephalina, the segment greatly surpasses

the notch depth. The Platychilina are intermediate in that the segment only very slightly surpasses the notch depth. The short segment of the Omina is probably plesiomorphic.

3. Form of pronotum. The Omina and Megacephalina have the pronotum trapezoidal in outline, the long base anterior, with the anterolateral angles produced anteriorly to a level anterior to the anterior margin of the prosternum. In these two subtribes, the base of the pronotum is unmodified, but, in the Platychilina, the basal angles are produced and the basal margin developed as a shelf over the basal end of the elytra. In this regard, the Platychilina are clearly aberrant and thus apomorphic.

4. Elytral setae. Shelford (1915:242) stated that different species of the same genus may differ in pilosity: *Megacephala aequinoctalis* has the elytra uniformly covered with fine setae, whereas *M. klugi* and *limata* have setae only at the elytral bases, for instance. Thus, lineages may be delineated based on degrees of setal covering, a general distribution being plesiomorphic.

The Omina, except for the nearly glabrous *Pycnochila*, and the Megacephalina agree in having the elytra setose to varying degrees. *Platychila* is nearly completely glabrous and are thus apomorphic.

5. Elytral tracheation. Six is the number of tracheal trunks basic to the forewings of pterygotes (Shelford, 1915). In the Mantichorini and Omina (except *Omus*), all six trunks are present and equally developed. *Platychila* has the anal trunk reduced to

a basal rudiment, but the other five are equally developed. In the Megacephalina, the anal trunk is reduced (*Oxychila* and some species of *Megacephala*) or absent (*Pseudoxychila* and some species of *Megacephala* [the condition in the other three genera is undescribed]), and the media is the most prominent trunk. In this character, the Omina are plesiomorphic (even in *Omus*, in which the radius and media are rudimentary, the anal is well-developed).

6. Larval pronotal setae. I consider an arrangement of undifferentiated rows of setae to be the generalized condition, seen in *Ctenostoma*, *Euprosopus*, *Iresia*, *Mantichora* and *Oxychila*. The rows are modified somewhat in *Megacephala* by development of primary setae. *Amblycheila* has fields of undifferentiated setae, an arrangement in turn modified in *Omus* by development of primary setae and great reduction in total number of setae. This shows at least two lineages among known larvae of megacephalini: one from *Oxychila* to *Megacephala* and the other from *Amblycheila* to *Omus*.

7. Hooks on abdominal tergite V. I have already commented on this character in my section on larval characters. In summary, I do not know whether two or three pairs of hooks is plesiomorphic. Both character-states occur in the Megacephalini and, indeed, both states occur in each of the two subtribes in which larvae are known.

Table 8 summarizes these seven character-states for the three subtribes. As is seen, Omina are generalized in all character-states except in the arrangement of larval pronotal setae.

Table 8. Analysis of subtribes of tribe Megacephalini regarding plesiomorphic. intermediate, and apomorphic states of seven characters present in text. Symbols: P = plesiomorphic, I = intermediate, A = apomorphic, ? = unknown.

Character No.	Megacephalina		Omina		Platychilina	
1	generalized	P	generalized	P	very flattened and translucent	A
2	very elongate	A	short	P	intermediate	I
3	trapezoidal	P	trapezoidal	P	produced basal angles and posterior margin developed as shelf over elytral bases	A
4	variable but some genera and species with setae generally distributed	P	same as Megacephalina	P	glabrous	A
5	M most prominent trunk, A reduced or absent	A	all trunks equally prominent, R and M reduced in *Omus* only, A well developed	P	all trunks but A equally prominent, A reduced	I
6	arranged in rows	P	arranged in fields	A	———	?
7	2 or 3	?	2 or 3	?	———	?
	ΣP=4; ΣA=2; unanalyzed=1		ΣP=5; ΣA=1; unanalyzed=1		ΣP=0; ΣA=3; ΣI=2; unanalyzed=2	

The Megacephalina are apomorphic in their elongate labial palpi and modified elytral tracheation. Anatomy and interrelationships of the Megacephalina are beyond the scope of the present study. However, from comparison of specimens of *Megacephala* and *Pseudoxychila* and descriptions in W. Horn (1908-1915), Shelford (1915) and Willis' (1969) adaptation of Horn's work, I believe *Megacephala* to be the most generalized of the living genera, the others having specializations of sculpture, stridulatory organs, or tarsi. Enough variation occurs among the species of *Megacephala* to suggest to me that the genus might best be divided into several genera.

The Platychilina are clearly aberrant, but the intermediate condition of the labial palps and elytral tracheation suggests that it split from a proto-Megacephalina stock before the specializations of that subtribe had fully developed. Its aberrancies may be related to its life style as a nocturnal fossorial arenicole.

In summary, I consider the Omina most generalized, having retained an ancestral form and having become specialized only in flightlessness. An ancestor to the Megacephalini probably resembled one of the Omina but with fully-developed hind wings. Platychilina are highly apomorphic in body form but are more primitive than the Megacephalina to which they are more closely related than to the Omina.

Subtribe Omina Castelnau, 1832

Diagnosis (from Willis, 1969, after W. Horn, 1908-1915). Megacephalini with palpiger of labial palp reaching no farther distad than mental notch; pronotum constricted basally and without basal angles extended posteriorly to cover base of elytra; elytra lacking humeri.

The subtribe contains three distinct, allopatric genera: *Amblycheila* Say, *Omus* Eschscholtz and *Pycnochila* Motschulzky. Generic limits are well-defined. The monotypic *Pycnochila* was described and figured by Peña (1969, 1973) and W. Horn (1908-1915) who also listed pertinent literature. *Amblycheila*, with four species, was revised by Vaurie (1955). I will discuss *Omus*, the only Pacific Northwest genus of the subtribe, in detail further on in the present paper.

I consider the following character-states to be plesiomorphic in the Omina (since larvae and pupae of *Pycnochila* and pupae of *Amblycheila* are undescribed, I cannot include larval and pupal characters):

1. Setae present in mandibular scrobe. It is difficult to assess this character. Scrobal setae are absent in mostCicindelidae

and number one or none in Carabidae. One or none is probably plesiomorphic.

2. Dorsoventral depth of gena equalling or less than dorsoventral diameter of eye. The gena is shallow in Carabidae, regardless of the size of the eye.

3. Elytra costate. This is characteristic of most Carabidae. However, the either sparse (*Amblycheila*) or greatly thickened (*Pycnochila*) striae of what few Cicindelidae have striae do not resemble those of Carabidae at all and represent modifications.

4. Presence of six elytral tracheal trunks. This is the number of tracheal trunks basic to the forewings of pterygotes (Shelford, 1915).

5. Inflexed portions of lateral margin of elytra narrow. Excluding the epipleura, most Carabidae and Cicindelidae do not have the lateral margins of the elytra inflexed, so even a narrow inflection is a modification.

6. Inflexed lateral edge of elytra punctate. Shelford (1915) pointed out that hairs cover the entire wing of a primitive insect, so that development of glabrous areas is apomorphic.

7. Thickening of anterior portion of intermetacoxal process. Most Cicindelidae, including *Cicindela*, *Mantichora* and *Pycnochila*, are unmodified.

8. Deeply emarginate abdominal sternite VI in male. This is typical of Cicindelidae (G. Horn, 1876).

9. Dilated basal 3-4 protarsal articles in male. This is typical of Cicindelidae (G. Horn, 1876) and, indeed, of most Adephaga.

10. Lack of sexual dimorphism in hind trochanters. This is characteristic of most Cicindelidae and, indeed, of most insects.

Table 9 shows that *Pycnochila* is plesiomorphic in all but two of the ten character-states, being apomorphic only in the peculiarly thickened elytral costae and in the absence of setae on the inflexed lateral margins of the elytra. Indeed, *Pycnochila* is glabrous over nearly the entire body, with setae only on the head, limbs, a few on the elytral disc, and around the genital opening. *Omus* and *Amblycheila* have different combinations of plesiomorphic and apomorphic states, and it is not possible to choose which could be considered more generalized as a whole. The more general distribution of pronotal setae of the larval *Amblycheila* is more like the condition in most cicindelid genera, as opposed to the development of primary setae and a reduction in number of secondary ones in *Omus*. The *Omus* larvae has three pairs of hooks on abdominal tergite V, the probable plesiomorphic state, whereas *Amblycheila* lacks the lateral hooks, leaving only two pairs.

Cazier (1942) distinguished *Pycnochila* partly on the basis of its narrower gena compared with the eye, but anatomical direction is unclear in his statement. I interpret the direction he meant as the dorsoventral depth of the gena and the dorsoventral diameter of

Table 9. Analysis of genera of subtribe Omina regarding plesiomorphic vs. apomorphic states of 10 characters listed in text. Symbols: P = plesiomorphic, A = apomorphic.

Character No.	*Amblycheila*		*Omus*		*Pycnochila*	
1	3 or more	A	absent	P	absent	P
2	greater than	A	greater than	A	less than	P
3	2 or 3 but slender and widely spaced	A	absent	A	4 but greatly thickened	A
4	all 6 fully developed	P	R and M very short	A	all 6 fully developed	P
5	about 2/3 of breadth of elytron	A	less than 1/3 of breadth of elytron	P	less than 1/3 of breadth of elytron	P
6	punctate	P	impunctate	A	impunctate	A
7	present	A	present	A	absent	P
8	absent	A	present	P	present	P
9	absent	A	present	P	present	P
10	absent	A	present	P	present	P
	ΣP=2; ΣA=8		ΣP=5; ΣA=5		ΣP=8; ΣA=2	

the eye, the only direction that fits the distinguishing criteria. *Pycnochila* has larger eyes compared with both *Omus* and *Amblycheila*, and this greater diameter might be construed as taking up part of the depth of the gena. *Omus* and *Amblycheila*, both with small eyes, have deep genae. However, several diverse genera of Cicindelidae, all with large eyes, have deep genae. Conversely, randomly chosen genera of Carabidae of several tribes all have narrow genae, regardless of the diameter of the eyes. The depth of the genae is certainly related to the volume of jaw muscles. Carabidae have smaller mandibles than Cicindelidae and, thus, have a smaller muscle volume requiring less space in the head capsule. *Pycnochila* has typically cicindeliform, large mandibles, but carabiform, narrow genae. A volumetric study would probably show weak musculature, probably a primitive character although possibly representing a secondary reduction.

It is difficult to choose between *Amblycheila* and *Omus* as more generalized. Some species of *Amblycheila* have elytral striae, six equally long elytral tracheal trunks, and larvae with fields of undifferentiated pronotal setae. But, most of the characters are apomorphic. *Omus*, on the other hand, lacks elytral striae, has the radius and media atrophied, and larvae with pronotal setae differentiated into primaries and secondaries. Otherwise, *Omus* is more generalized. The pronota of *O. dejeani* and *Pycnochila* are superficially similar in their flatness and almost explanate

anterolateral portions of the margins, different from the condition in *Amblycheila* and other species of *Omus*.

In summary, I consider *Pycnochila* to be the most primitive genus within the subtribe Omina, although it is too modified to indicate how the earliest omines may have looked. *Omus* and *Amblycheila* show mosaics of plesiomorphic and apomorphic character-states, indicating a long independent evolution.

Genus *Omus* Eschscholtz, 1829

Omus Eschscholtz, 1829, Zoologischer Atlas, 1:3-5.

Megomus (as subgenus) Casey, 1914, Mem. Col., 5:1.

Leptomus (as subgenus) Casey, 1914, Mem. Col., 5:1.

Diagnosis (modified from Cazier, 1942; and Willis, 1969, after W. Horn, 1908-1915): Omina with genae deeper dorsoventrally than dorsoventral diameter of eye; elytra not striate; inflexed lateral elytral margin comprising less than 30% of total elytral breadth; margins of intermetacoxal process of abdominal sternite II thickened; and male with protarsal articles 1-3 dilated

and with palmar surfaces

setose.

Among Cicindelidae, the genus *Omus* has suffered particularly hard taxonomically, mainly through the descriptions by Casey (1897, 1909, 1913, 1914, 1916, 1924). Casey (1914) divided the genus into three subgenera. Of the 117 specific and subspecific taxa referred to the genus, 93 were named Casey. It is perhaps ironic, although certainly not on purpose, that, in the present treatment of *Omus*, not a single one of Casey's names has escaped synonymy.

Subgenera of *Omus*. Casey (1914:1) recognized three subgenera which were, in his own words, ". . . passably well defined . . . ." The characters of *Megomus* coincide with those of the single included species *O.* (*M.*) *dejeani* Reiche, namely: numerous, irregularly-arranged, very large elytral foveae, and pronotum with lateral margins acute. *O. dejeani* certainly stands apart from other species of *Omus* in larval, pupal and adult characters, and I am greatly tempted to recognize *Megomus* for it. However, monotypic subgenera in a genus which, by my criteria, only contains four species add no more to our understanding of interrelationships between the species than would a phylogenetic tree. Thus, I follow Cazier (1942:45) in denying recognition to *Megomus* as a distinct subgenus.

The characters of *Leptomus* coincide with those of its single included species *O.* (*L.*) *submetallicus* G. Horn. Casey (1914:1) characterized *Leptomus* mainly on the basis of "generally submetallic"

coloration, not present in subgenus *Omus*. The submetallic nature of *O. submetallicus* is not the same as the truly metallic condition of the ventral surface of most *Cicindela*. It represents a lack of fine microsculpture rather than a diffraction gradient, and might better be termed shiny than submetallic. Such shininess appears often in populations of *O. audouini* and *californicus* near the California-Oregon border. The brassy appearance of occasional specimens of *O. dejeani* also results in a weak sheen. Thus, although Casey's character is typical of the *O. submetallicus* population as a whole, the character is neither unique nor even particularly striking. The holotype of *O. submetallicus*, now apparently lost (R. D. Ward, pers. comm.), was described by G. Horn (1868:129) as being aeneous-black. Cazier (1937, 1942) found no such aeneous sheen in a series of 29 *O. submetallicus*, some of which I have examined. Apparently, then, the aeneous coloration is of only sporadic occurrence, perhaps like that seen in *O. dejeani*, *O. c. californicus* ("*cupreonitens*" Blaisdall and Reynolds), and *O. audouini* ("*vandykei*" W. Horn), and should be afforded no more importance than any individual variation. G. Horn (1868), Schaupp (1883), Leng (1902) and Casey (1914) all apparently missed the presence of the stout lateral pronotal setae so characteristic of *O. submetallicus* and, indeed, unique among Cicindelidae. However, as in the case of *Megomus*, *Leptomus* includes only a single species with whose diagnosis it coincides. I again follow Cazier (1942:45) in not recognizing *Leptomus* as a distinct subgenus.

Note on *Omus submetallicus* G. Horn

This species is not known from the Pacific Northwest, but, for the sake of completeness in my review of *Omus*, a statement as to its characteristics and range is valuable in order that an assessment of its relationships with other species of *Omus* can be made. It was described by G. Horn (1868) in a brief note. Mr. R. D. Ward (pers. comm., 1976) is currently reviewing the status of holotype which may no longer exist. Statements by Schaupp (1883-1884) and Leng (1902) as to the type of locality are questionable, as is the supposed metallic brassy coloration of the holotype which I have already discussed.

A type locality was not stated by Horn and has been given by other authors variably as Eldorado (Schaupp) or Plumas (Leng) Counties, California. F. W. Nunenmacher searched unsuccessfully for the species in the northern Sierra Nevada Mountains, finding only *O. californicus*. The species was rediscovered by R. S. Wagner at CA. Fresno Co., Warthan Canyon, and Cazier (1937) described a new subspecies, *O. s. niger*, which is entirely black. Cazier (1942: 341-345) synomized *niger*, stating that the supposed color difference is unimportant, and, in view of the abundance of the species in western Fresno County, localities in the Sierra Nevada Mountains are unlikely.

Cazier (1942) used a diagnostic character for this species which had been missed by all previous authors. There is an anteroposterior linear row of stout setae, each placed in its own setigerous

puncture, along the lateral pronotal margins, irregular in number and arrangement (even on either side of the same individual), and ranging in number from 8 to 42 (males, $\overline{X}$ = 24, females, $\overline{X}$ = 26). This character is unique and readily observable under low magnification (X7). Other species of *Omus* may have a few fine setae, but these are not positioned in punctures and are quickly lost through abrasion. *Amblycheila* and many other genera of cicindelids, including *Cicindela*, have lateral pronotal setae but they are neither stout nor positioned in punctures. Ascertainment of function of such setae of *O. submetallicus* will require behavioral and histological studies. The soil in which it burrows is hard, abrasive, dry much of the year and compact, and may require some special sensory adaptations by the beetles. However, other species of cicindelids inhabit soils of similar characteristics and have no comparable adaptations.

Species of *Omus*

The following chronology summarizes some of the major events in the history of *Omus* taxonomy. I do not intend this outline to be an exhaustive review, as that would entail a tedious listing of all of the many named species and subspecies. Cazier (1942) presented a complete bibliography of the genus through 1940. Since 1940, *Omus* literature has been sparse, important papers being Hatch (1953), Leffler and Pearson (1976), and Maser (1976, 1977).

1829. Eschscholtz named the genus *Omus* and its genotype *O. californicus*.

1838. Reiche named *O. audouini* and *O. dejeani*.

1868. G. Horn named *O. submetallicus*. He did not give a complete type locality.

1883-1884. Schaupp recognized nine species and presented a key, characteristics, ranges and bibliography. He initiated the confusion surrounding *O. submetallicus* by emphasizing a supposed bronzy coloration never stated by G. Horn (1868), gave an improper type locality, and listed an incorrected citation for Horn's original reference. He arranged his species in two groups on the basis of a character shown by Leng (1902) to vary too much to be of value.

1902. Leng recognized 10 species and reduced several taxa to varietal rank or complete synonymy. He presented a key, characteristics, ranges and bibliography, and pointed out the extreme variability of some of the species. He (p. 100) used elytral and thoracic characters ". . . very sparingly, and only when supported by geographical distribution." He recognized two species-groups, one composed of *O. dejeani* alone, and the other containing all remaining species, and, thus, his groupings did not coincide at all with those of Schaupp (1883). He characterized

O. audouini on the basis of its unique pronotal form, but gave a locality for *O. submetallicus* that has not been substantiated by further collecting.

1914. Casey named *Megomus* and *Leptomus* as new monotypic subgenera. He divided *Omus* spp. into seven species-groups. He presented extensive keys but some of the couplets, under careful scrutiny, do not completely separate the included taxa. His groups coincide essentially with Leng's species, the differences being that Leng's *ambiguus* and *auduouini* are both in Casey's Group I and that Casey's Group IV includes species not yet described when Leng's paper was published. However, Casey (1916) showed that his Group IV species (*parvicollis*) was related to Leng's previously named *int rmedius* (Leng, 1902) and took this change into account in renaming his Group IV the *intermedius*-group.

1930. W. Horn recognized three species-groups, Groups 1 and 2 (*dejeani* and *submetallicus*, respectively) being monotypic, and 3 (*californicus*) composed of 10 species. His work was based on aedeagal form, which Cazier (1942) showed to be too variable for such taxonomic use. Horn's I-IV correspond to Casey's Group I (*audouini*), V to Casey's Group II (*californicus*), VI to Casey's Group V (*lecontei*),

VII to Casey's Group IV (*intermedius*), and Horn's VIII-X and Casey's VI and VII correspond but do not coincide. Horn gave ranges (including some elevational data) but gave no reasons in print for his extensive synonymies.

1942. Cazier did a statistical study and recognized three species, *dejeani*, *submetallicus* and *californicus*, with four subspecies of the last. His work is invaluable in fixing the type localities of many of Casey's taxa. He showed how much individual variation there is even within a series taken on the same date at the same locality.

This paper. I follow Cazier (1942) but recognize four species, according specific rank to *O. audouini* considered by Cazier synonymous with *O. c. californicus*.

There has never been any dissent as to the recognition of *Omus dejeani* and *O. submetallicus*. Synonymy concerning these two species involves only five of the 117 names. I shall treat the remaining synonymy and the number of species in detail beyond in my accounts of *O. audouini* and *californicus*. Suffice it to say here that I recognize four species of *Omus*, one of which, *O. californicus*, has four subspecies. Of the four species, only *O. submetallicus* is not found in the Pacific Northwest, and *O. c. californicus* is known from but a single locality. The four species of *Omus* may be distinguished as follows:

1A. Elytral punctures large, foveate, irregularly arranged, and each with seta; size large: greatest thoracic breadth of males >5.8mm, of females >6.6 mm; range: S.W. B.C., W. WA., W. OR.....*O. dejeani*

B. Elytral punctures variable in shape and arrangement but never foveate or setigerous; size variable: greatest thoracic breadth of males <5.2 mm, of females <5.9 mm.....2

2A. Lateral pronotal margins steeply declivous and with corners of anterolateral pronotal angles not completely visible in dorsal view; elytral punctures irregularly arranged and wider than smooth area between punctures; range: S.W. B.C., WA. and OR. generally west of Cascade Range, N.W. CA.....*O. audouini*

B. Pronotum in transverse section evenly arcuate to flattened and with corners of anterolateral pronotal angles completely visible in dorsal view; elytral punctures variable but, when developed, regularly arranged and equalling or narrower than smooth area between punctures.....3

3A. Lateral margins of pronotum with linearly-arranged row of stout setae, each positioned in setigerous puncture; range: CA. Fresno-Monterey Co. line, Warthan Canyon, Priest Valley.....*O. submetallicus*

B. Row of stout setae and setigerous punctures not developed; range not as above: S.W. OR., Coast, Siskiyou and Sierra Nevada Mtns., CA.....*O. californicus*

Omus dejeani Reiche, 1838

(Figures 13-15)

Omus dejeani Reiche, 1838, Ann. Soc. Ent. France, 7:299-300.

Omus d. robustus Casey, 1916, Mem. Col., 7:7-8.

Omus d. foveatus Casey, 1916, Mem. Col., 7:8.

Diagnosis. Adult: size large; pronotum with lateral positions of disc declivous at only slight angle from horizontal, anterolateral angles completely visible in dorsal view, glabrous except for short, fine lateral setae; elytra with 30-45 large, irregularly-placed setigerous

Fig. 12. Proposed phylogeny of *Omus* based on morphological characters.

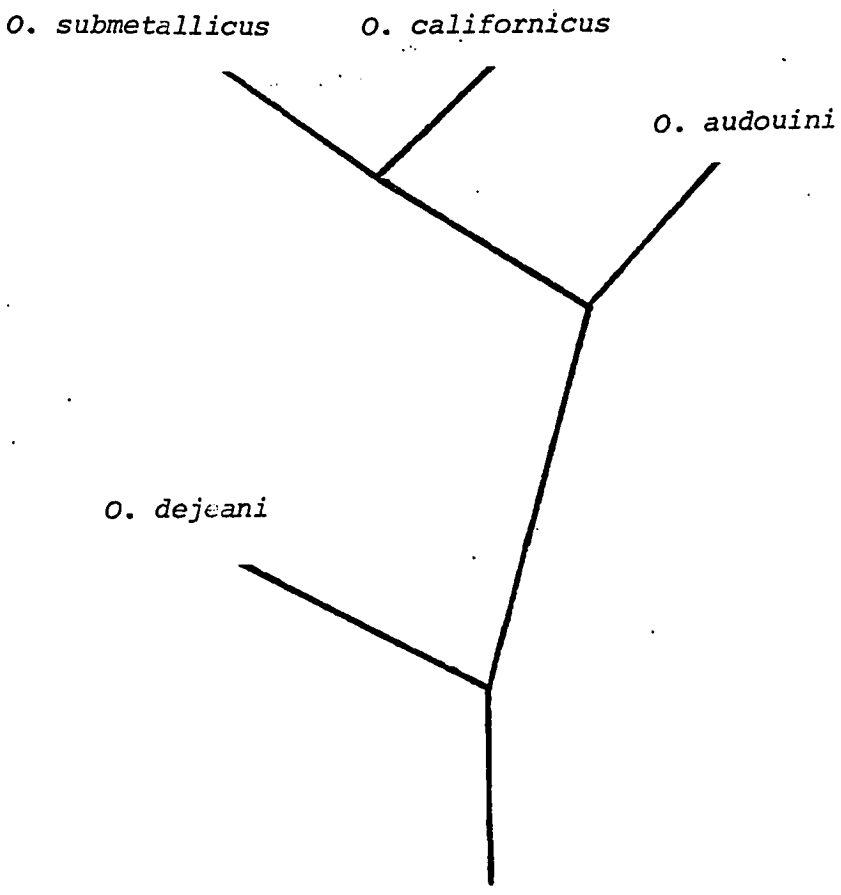
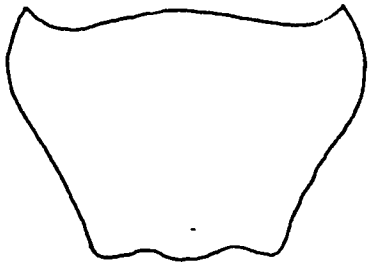

O. submetallicus
O. californicus
O. audouini
O. dejeani

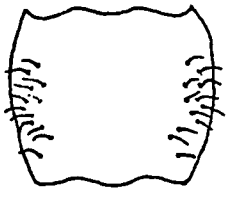
Fig. 13. Pronotal structure of *Omus* and *Cicindela* adults. X 6.

Legend:

A. *O. dejeani*, dorsal view showing trapezoidal shape
B. *C. bellissima*, dorsal view showing rectangular shape
C. *O. californicus*, dorsal view showing completely visible anterolateral angles
D. *O. californicus*, transverse section showing arcuate sides
E. *O. audouini*, dorsal view showing incompletely visible anterolateral angles
F. *O. audouini*, transverse section showing declivous sides



A



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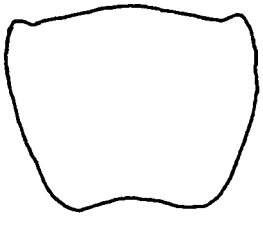

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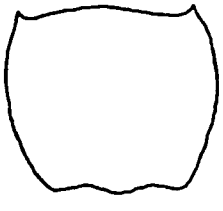


E

F

foveae. Pupa: abdominal tergum V with two pairs of short, dorsal tubercles arranged transversely in addition to large dorsolateral tubercles. Larva: caudal frontal ridge with five setae; pronotum light rufous with irregular brown mottling; inner hook of abdominal tergum V with fixed spine about twice as long as movable setae on shoulder.

Synonymic notes. Three names have been applied to *Omus dejeani* Reiche. Reiche (1838:299-300) based the species on specimens from "Oregon." Casey (1916:7-8) based *O. d. robustus* on a large black female from WA. King Co., Seattle, differentiating it from *O. d. dejeani* by its black rather than subcupreous coloration. Subcupreous coloration is a rare variation, and such specimens occur throughout the species' range. Thus, this coloration is not a valid subspecific character. Casey (1916:8) based *O. d. foveatus* on material from OR. Clackamas Co., Bull Run. It is of average size and sculpture, and it is certainly unworthy of subspecific recognition.

Characteristics. *O. dejeani* is readily distinguishable from other species of *Omus* by adult features and, also, larval and pupal characteristics, as far as these can be compared with those of other species. Some features indicate a primitive form. The elytra are setose, each seta located in an irregularly-shaped, shallow

fovea. Other species lack the setae, and their foveae are not enlarged, but rather in the form of punctae. The more regular arrangement indicates greater organization and thus apomorphy. A subjective feature of the adult *O. dejeani* is its less compact facies compared with the other species.

The mottled pronotal color pattern of the larval *O. dejeani* differs from the unicolored or zoned patterns of other known *Omus* species. Also unique is the comparatively much greater length of the fixed spine of the inner hook of abdominal tergite V. The small tubercles in addition to the large lateral ones on pupal abdominal tergite V are unique among cicindelid pupae known to me. Because immature stages are so poorly known in related genera and species, it is impossible to assess larval and pupal features as indicators of relationships.

The larval burrow, although sinuate as in *O. audouini*, lacks the constriction before the terminal chamber, and thus is simpler in structure (see Figures 1A and B).

In summary, *O. dejeani* appears to be more generalized than other *Omus* species. It bears a striking resemblance to the African *Mantica*, differing, however, in characters of tribal value. The resemblance is perhaps one of true relationship, although the stocks have been separate for millions of years. The resemblance suggests how a common ancestor may have looked. *O. dejeani* is the most distinct species of *Omus*, but placement in a separate subgenus,

definition of which coincides with that of the species itself, only obscures its relationships.

Omus audouini Reiche, 1838

Omus audouini Reiche, 1838, Ann. Soc. Ent. de France, 7:300-301.

Omus ambiguus Schaupp, 1884, Bull. Brooklyn Ent. Soc., 6:121.

Omus vandykei W. Horn, 1903, Deutsche Ent. Zeitsch., 1903:185.

Omus californicus humeroplanatus W. Horn, 1910, Ann. Soc. Ent. de Belgique, 54:293-295.

Omus borealis Casey, 1909, Canadian Ent., 41:256.

Omus audouini parvulus Casey, 1913, Mem. Col., 4:2.

Omus oregonensis Casey, 1913, Mem. Col., 4:2-3.

Omus rugipennis Casey, 1914, Mem. Col., 5:3.

Omus solidulus Casey, 1914, Mem. Col., 5:3.

Omus audouini brevicornis Casey, 1916, Mem. Col., 7:8-9.

Omus audouini aequicornis Casey, 1916, Mem. Col., 7:9.

Omus audouini tacomae Casey, 1916, Mem. Col., 7:9.

Omus audouini delicatulus Casey, 1916, Mem. Col., 7:9-10.

Omus audouini distans Casey, 1916, Mem. Col., 7:10.

Omus ambiguus humeralis Casey, 1916, Mem. Col., 7:10.

Omus thoracicus Casey, 1916, Mem. Col., 7:11.

Omus cephalicus audens Casey, 1924, 11:3-4.

Omus ambiguus socius Casey, 1924, 11:4.

Fig. 14. Dorsal view of *Omus dejeani* Reiche (X 6).

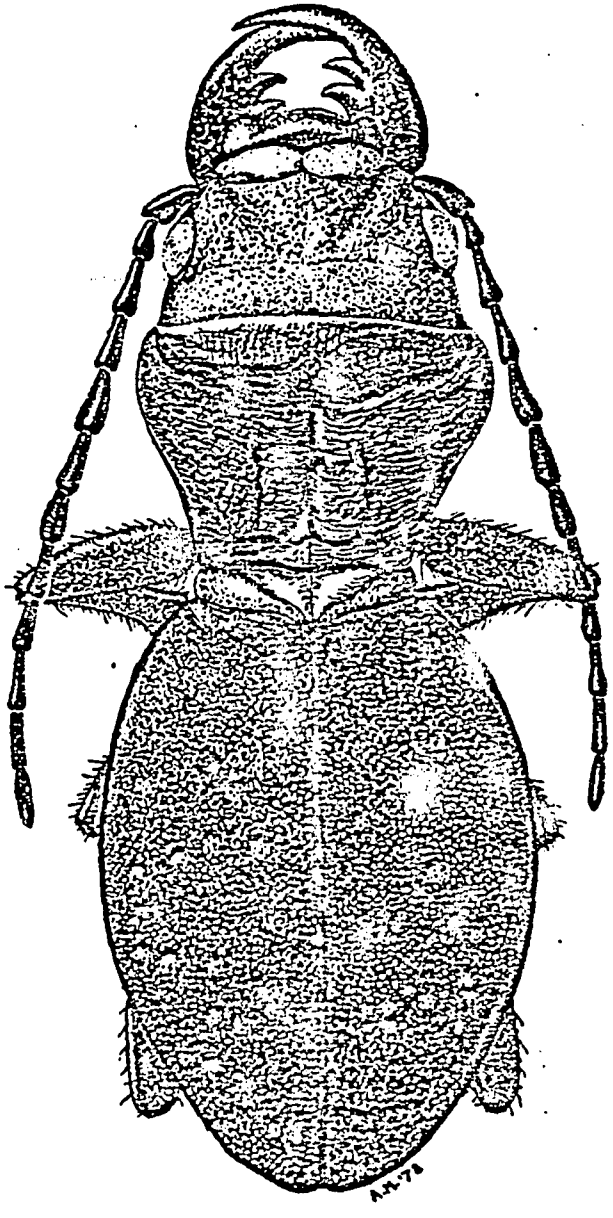
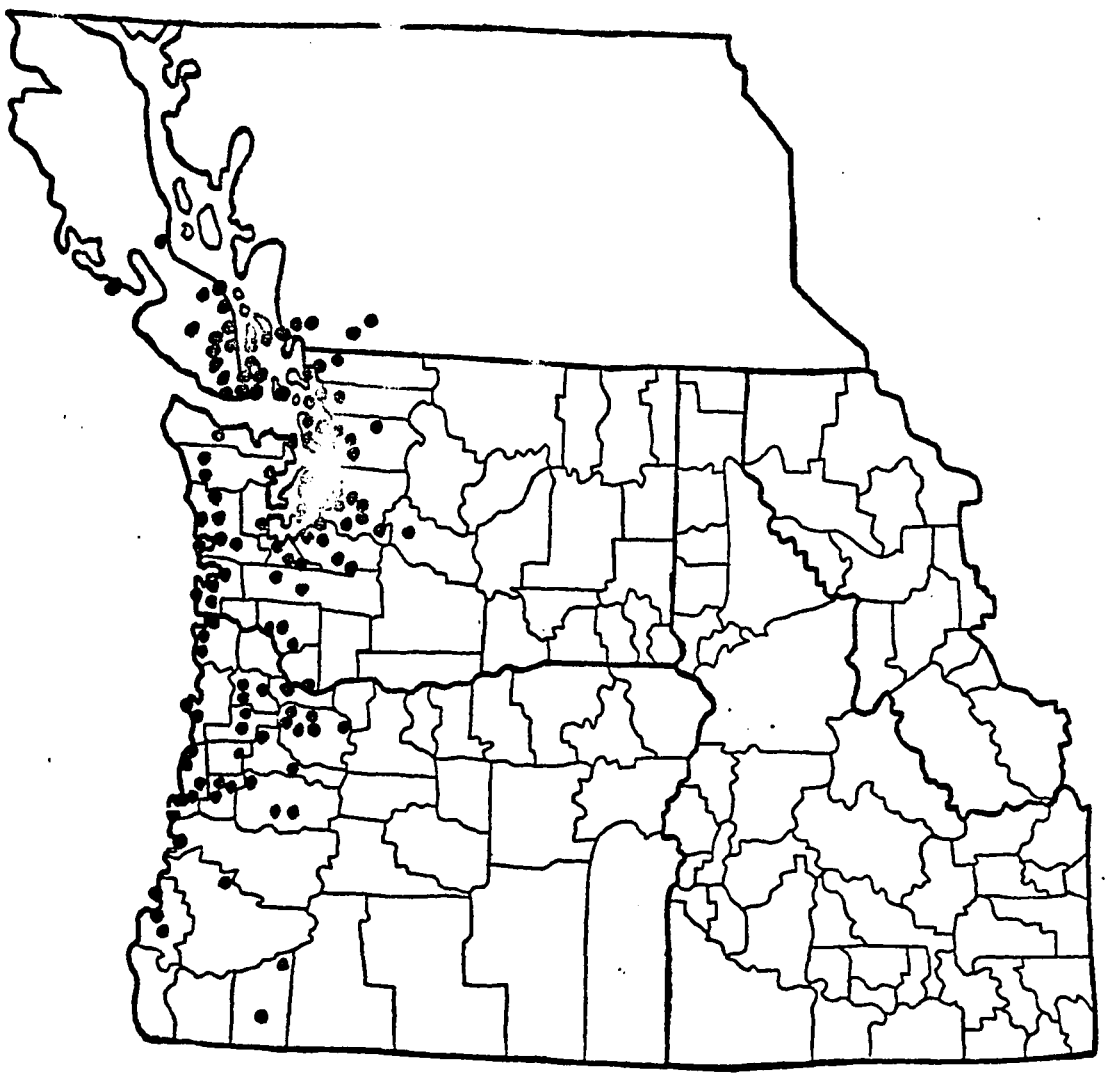


Fig. 15. Pacific Northwets distribution of *Omus dejeani*. See Appendix I for tabulation of localities.



Diagnosis. Adult: size small to medium; pronotum with lateral portions of disc steeply declivous, median portion of disc flattened, with apices of anterolateral angles not visible in dorsal view, and glabrous except for short, fine lateral setae; sculpture of head and pronotum consisting of irregular, shallow, vermiculate grooves (best-developed in northern populations and nearly obsolescent in southern populations), nearly smooth in central portion of pronotal disc; elytral sculpture variable, but, when developed, punctures shallow, irregular in shape and size but never large and foveate and always more than 50 in number, and with ridges between punctures narrower than breadth of punctures. Pupa: abdominal tergum V with large dorsolateral tubercles, one on either side, only. Larva: caudal frontal ridge with three setae; pronotum uniformly dark brown; inner hook of abdominal tergum V with fixed

spine and movable setae on shoulder of approximately same length.

Synonymic notes. Difficulties caused by Casey's splitting within the genus *Omus* have greatly hindered reviews of the species. I examined the holotypes of all but three (*audouini*, *humeroplanatus* and *vandykei*) of the 17 taxa I am synonymizing under the species *Omus audouini*. I have been greatly aided by the unpublished Ph.D. thesis of Dr. M. A. Cazier (1942) from which Dr. Cazier has graciously permitted me to quote liberally. Some of the taxa were collected in California but, even though the geographic scope of the present study stops at the Oregon-California state line, the seven California taxa are essential to the total understanding of the species.

The following accounts are based on examinations of types, original descriptions, treatments in publications other than the original descriptions, and Cazier's study. I must emphasize that Cazier did not recognize *O. audouini* as an entity distinct from *O. californicus*. An invaluable contribution from Cazier's study is his summary of locality data from the field notes of and conversations with F. W. Nunenmacher who collected many of the holotypes of taxa named by Casey, information permanently pinning down type localities for seven of the 18 taxa.

O. audouini Reiche, 1838. The holotype appears to be a female from Reiche's (1838:Plate 10, Figure 2) illustration. Cazier

stated that the type is a female (1942:350), but (op. cit.: 386) wrote: ". . . *audouini* . . . proposed for small male . . . . ." Casey (1909, 1913, 1914, 1916), Leng (1909) and Schaupp (1883-1884, 1884) referred clearly to the steeply declivous lateral portions of the pronotum, but this diagnostic character was disregarded by Cazier. Reiche (1838:300-301) stated that the type was collected in 1836 ". . . on the west side of the Rocky Mountains, in the district of Oregon . . . ." In 1836, "Oregon Territory" included both the present states of Oregon and Washington.

O. ambiguus Schaupp, 1884. Schaupp (1884) placed his new species in his group II (delineated by Schaupp, 1883-1884) which includes *O. californicus* and characterized by "lateral margin of the (pronotum) attaining the basal margin." His group I, including *O. audouini*, *dejeani* and *submetallicus*, has the lateral pronotal margin ". . . obliterated posteriorly, not attaining basal margin." Leng (1902) pointed out the extreme variability of this character. A series from CA. Trinity Co., Coffee Creek, University of California at Berkeley collection, have seven with a complete margin and one obliterated posteriorly.

The holotype of *O. ambiguus* (NM) has the characteristic pronotal form of *O. audouini* but is strongly sculptured compared with *O. audouini* at the southern end of its range, although weakly compared with northern California *O. californicus*. Such slight difference in sculpture is no more than individual variation.

The type locality is CA. Siskiyou Co., Mt. Shasta District. Leng (1902) added, "probably upper Soda Springs."

O. vandykei W. Horn, 1903. W. Horn (1903:185) named this as a new species based on a specimen from "Mittel-Oregon" with the declivous lateral part of the pronotum as in *O. audouini*, but differing in that the lateral part is even steeper, particularly posteriorly, and the disc flatter compared with *audouini*. Both features are variable for *audouini*. The shininess of the elytra led the holotype's original owner to refer it to *O. submetallicus*. This apparently led W. Horn (1930) later to synonymize *O. cupreonitens* and *O. reynoldsi* under *vandykei*, but these are *O. californicus*.

O. borealis Casey, 1909. Casey (1909:256) based this taxon on a female from Oregon with no further data. He (1913) placed it along with *O. humeroplanatus*, *mimus* and *oregonensis* in a group related to but distinct from *O. audouini*. He (1914) dismantled this group, placing *humeroplanatus* in Group I (*audouini*), *mimus* and *oregonensis* in Group II (*californicus*), and *borealis* in Group V (mainly coastal Californian *californicus*). The holotype is peculiar for *audouini* in that the anterolateral pronotal angles are visible (barely) in dorsal view, but the lateral portions of the pronotum are declivous, and the sculpture, although rather regular, is weak compared with northern populations of *O. c. californicus sensu mihi*. I consider *O. borealis* aberrant but, nontheless, an absolute synonym of *O. audouini*.

O. humeroplanatus W. Horn, 1910. W. Horn (1910:293-295) originally named this taxon *O. californicus humeroplanatus*. Cazier (1943) recorded that F. W. Nunenmacher collected the holotype at CA. Del Norte Co., Crescent City during a trip in May and June, 1910. Its characteristics are typical of *O. audouini*, and its weak sculpture is in keeping with the general southward clinal reduction in sculpture of the species.

O. parvulus Casey, 1913. Casey (1913:2) described this taxon as *O. audouini parvulus*, basing it on a small male from Oregon (no further data were given). He (1916:8) considered it a full species based on its smaller, shorter scape than in allied "species" of his *audouini*-group (Group I). My examination of the holotype indicates a specimen indistinguishable from typical *O. audouini*. The shallow sculpture suggests that the specimen may have come from the southern portion of the species' range.

O. oregonensis Casey, 1913. Casey (1913:2-3) described this taxon as a full species, later (1914) including it in his Group II. F. W. Nunenmacher collected the holotype, a male, in June, 1910, at OR. Josephine Co., Selma and Waldo (Waldo is an abandoned townsite 5 km E.S.E. of O'Brien). Although the pronotum is deeply vermiculatorugose for so southerly a locality, the specimen does not differ from *O. audouini* in structure.

O. rugipennis Casey, 1914. Casey (1914:3) included this taxon as a full species, including it in his Group I. The holotype, a female, was collected by F. W. Nunenmacher at CA. Siskiyou Co., Mud Lake, 7 mi N.W. Cottage Grove, perhaps in May, 1911, when he obtained the holotype of *O. brevicornis* at the same locality, although this information is not given by Cazier (1942). The specimen is large, peculiar in view of the southward cline in size decrease of *O. audouini*.

O. solidulus Casey, 1914. The holotype, a male, was collected at CA. Siskiyou Co., Shasta Retreat, Bucks Lake (*fide* Cazier, 1942: 220). Casey (1914) included it in his Group I (*audouini*). W. Horn (1930) synonymized it with *O. ambiguus* based on the aedeagus, a structure too variable to be of value. Cazier considered it merely an individual variant of his expanded *O. c. californicus* concept, and twice, pp. 220 and 388, in what is certainly a *lapsus calumni*, referred to it as *O. solidus*. He used the correct name on p. 378. The holotype has conspicuous elytral microgranulation. Casey's (1914:3) couplet 6 is based in part on the presence of elytral punctures, and these are obliterated in *O. solidulus* by the microgranulation; thus, the couplet does not work.

O. brevicornis Casey, 1916. This taxon was named by Casey (1916:8-9) *O. audouini brevicornis*, basing it on a male from CA. Siskiyou Co., Mud Lake, 7 mi N.W. Cottage Grove, collected by F. W. Nunenmacher, May, 1911, not from CA. Humboldt Co. as stated by Casey (*fide* Cazier). The holotype was described as being rather

Shiny and with less pronounced rugosity than in *O. audouini*. W. Horn (1930) synonymized it with *O. borealis*.

O. aequicornis Casey, 1916. F. W. Nunenmacher collected the holotype, a male, and other specimens, in May or June, 1910, from OR. Josephine Co., Selma and Waldo. Casey (1916:9) considered the peculiar aedeagal structure to be of specific value, but I consider it perhaps as the result of a developmental aberration or eclosional injury.

O. tacomae Casey, 1916. Casey (1916:9) based this taxon on a teneral female from WA. Pierce Co., Tacoma as *O. audouini tacomae*. The sculpture is strong, reflecting both the northward clinal increase in rugosity and the unworn teneral nature of the holotype.

O. delicatulus Casey, 1916. The holotype, a small male from Oregon (no further locality data), was called by Casey (1916:9-10) *O. audouini delicatulus*. Casey referred to its ". . . somewhat metallic elytra, which are less deeply sculptured." This is correlated with a lack of fine punctulation and suggests that the holotype may have come from the southern portion of the species' range.

O. distans Casey, 1916. Casey (1916:10) based *O. audouini distans* on a female collected May, 1907, by M. Blasse from WA. King Co., Seattle.

O. humeralis Casey, 1916. Casey (1916:10) originally named this taxon *O. ambiguus humeralis*. The type locality is given as CA. Humboldt Co. Cazier (1942:104) stated that F. W. Nunenmacher

collected the holotype, a female, at CA. Humboldt Co., 10 mi E. Orick. It was defined on the basis of the well-developed elytral humeri and reduced sculpture. Blaisdell and Reynolds (1917) found the former character to be extremely variable and the reduction in sculpture follows the southward cline of *O. audouini*. Pronotal structure is typical of *O. audouini*.

O. thoracicus Casey, 1916. Casey (1916:11) based this taxon on a male from OR. Klamath Co., Upper Klamath Lake, collected 20 May, 1913, by F. W. Nunenmacher. Sculpture is peculiar in resembling diagonally-directed, shallow ripples. The locality, east of the Cascades, may represent a post-glacial migration at a time when the Klamath and Rogue River drainages were connected by headwater stream capture (Hubbs and Miller, 1948). Structure, except for the peculiar (but not extremely so) sculpture, is identical with that of *O. audouini*.

O. audens Casey, 1924. Casey (1924:3-4) based his *O. cephalicus audens* on a large female collected by O. B. Johnson at WA. King Co., Seattle. *O. cephalicus* was considered as a species, with *audens*, *rugipennis* and *tacomae* as subspecies. *O. cephalicus cephalicus* is, in my estimation, synonymous with *O. californicus californicus*, but its proposed subspecies are indistinguishable from *O. audouini*. *O. cephalicus* was distinguished by Casey (1916) on the basis of its more contiguous elytral punctures than *O. shastanicus*, a form with a characteristic *californicus*-type pronotum. The pronotum of the holotype of *O. cephalicus* is indeed like that of *O. californicus*,

but those of *audens*, *rugipennis* and *tacomae* agree with *O. audouini*. The large size of the holotype of *audens* and its slight middiscal pronotal sculpture confluence are characteristic of the northward clines toward larger size and stronger sculpture of *O. audouini*.

O. socius Casey, 1924. F. W. Nunenmacher collected the holotype, a male, of what Casey (1924:4) named *O. ambiguus socius* in 1913 at CA. Shasta Co., Round Mountain, considering it shorter and stouter than *O. a. ambiguus*. It has the pronotum nearly smooth discally with feeble sculpture, a trend correlating with a southward clinal reduction in reduced sculpture in *O. audouini*.

Relationships. The identity of *Omus audouini* as a distinct species has been obscured by Casey's splitting within the genus. The characteristic pronotal form of *O. audouini* was recognized by Reiche (1838) as well as by Casey (op. cit), Leng (1902), and Schaupp (1883-1884), but appears to have been disregarded by Cazier (1942) who considered the species a synonym of *O. c. californicus*. *O. audouini* is certainly more closely related to *O. californicus* and *submetallicus* than to *O. dejeani*, but I believe that its morphology, pattern of variation, and zoogeography argue for specific rank.

Morphology. *O. audouini* is characterized by the steeply declivous lateral portions of the pronotum. Elytral sculpture is extremely variable, but, when well-developed, tends to consist of irregularly-arranged, shallow punctures, with the areas between the punctures narrower than the breadth of an individual puncture.

Elytral sculpture of *O. californicus*, by comparison, when well-developed, is more regular, with deeper, rounded punctures separated by smooth areas as wide or wider than the breadth of an individual puncture. The compact facies of the adult *O. audouini* agrees with *O. californicus* and *submetallicus*, differing from *O. dejeani*.

The larva of *O. submetallicus* is still unknown, but those of the other three species differ in pronotal coloration. Chaetotaxy of *O. audouini* and *californicus* is nearly identical, indicating closer relationship to one another than to *O. dejeani*.

Pupae of *O. californicus* and *submetallicus* are unknown. That of *O. dejeani* is distinct from those of *O. audouini* and, indeed, all other known cicindelid pupae in having additional tubercles on abdominal tergite V (Figures 8 and 10).

The enlarged terminal chamber and the constriction before it of the larval burrow (Figure 1C) in *O. audouini* show greater organization than the unmodified gallery of *O. dejeani* (Figures 1A and 1B). Burrows of the other species are unknown to me.

Variation. Although *O. audouini* shows less individual variation than *O. californicus*, there is sufficient variation to have misled Casey into describing several "species" and "subspecies." Most of the supposed taxa here synonymized under *O. audouini* were based on one specimen or, at best, a very few. They are not distinct enough from one another to warrant formal recognition but do indicate several clinal trends:

1. Size. There is a north to south decrease in size except for the population from OR. Klamath Co., Upper Klamath Lake (*O. thoracicus*). However, Cazier (1942:150-151) showed that only 3% of males and 51% of females of this population could always be distinguished from those from western Oregon. Cazier based his differentiation on greatest labral length, the only measurement he found significant. He found that the Klamath County population diverged slightly in mean value toward lower ratio values compared with western populations, but not significantly. Apparently, the geographic isolation of this population has allowed some slight differentiation but not enough to warrant taxonomic recognition. Cazier showed that remaining populations of *O. audouini* vary gradually, with overlaps in measurement of geographically adjacent samples.

2. Sculpture. There is a north to south clinal decrease in sculpture of the head and pronotum. Northern populations (British Columbia, Washington and northern Oregon) have shallow, often parallel striae on the head and all but the discal portion of the pronotum. The stronger sculpture of the northern populations led Casey to recognize taxa such as *audens* and *tacomae*. In more southern populations, sculpture becomes increasingly finer and shallower, often obsolescent, and resulting in a nearly smooth central discal portion of the pronotum. This trend is reflected in such taxa as *brevicornis*, *delicatulus*, *humeralis*, *humeroplanatus* and *socius*.

Casey also used fine microgranulation of the elytra in his descriptions. Extensively developed microgranulation results in an opaque appearance of the elytra. Conversely, reduced microgranulation results in shininess or a metallic quality. *O. solidulus* was based (Casey, 1914:3) partly on its conspicuous microgranulation which largely obliterates the elytral punctures. On the other hand, *O. delicatulus*, *brevicornis* and *vandykei* were all characterized by their elytral shininess. As I have already pointed out, this metallic appearance led W. Horn (1930) to refer variants of *O. californicus* to *O. vandykei*.

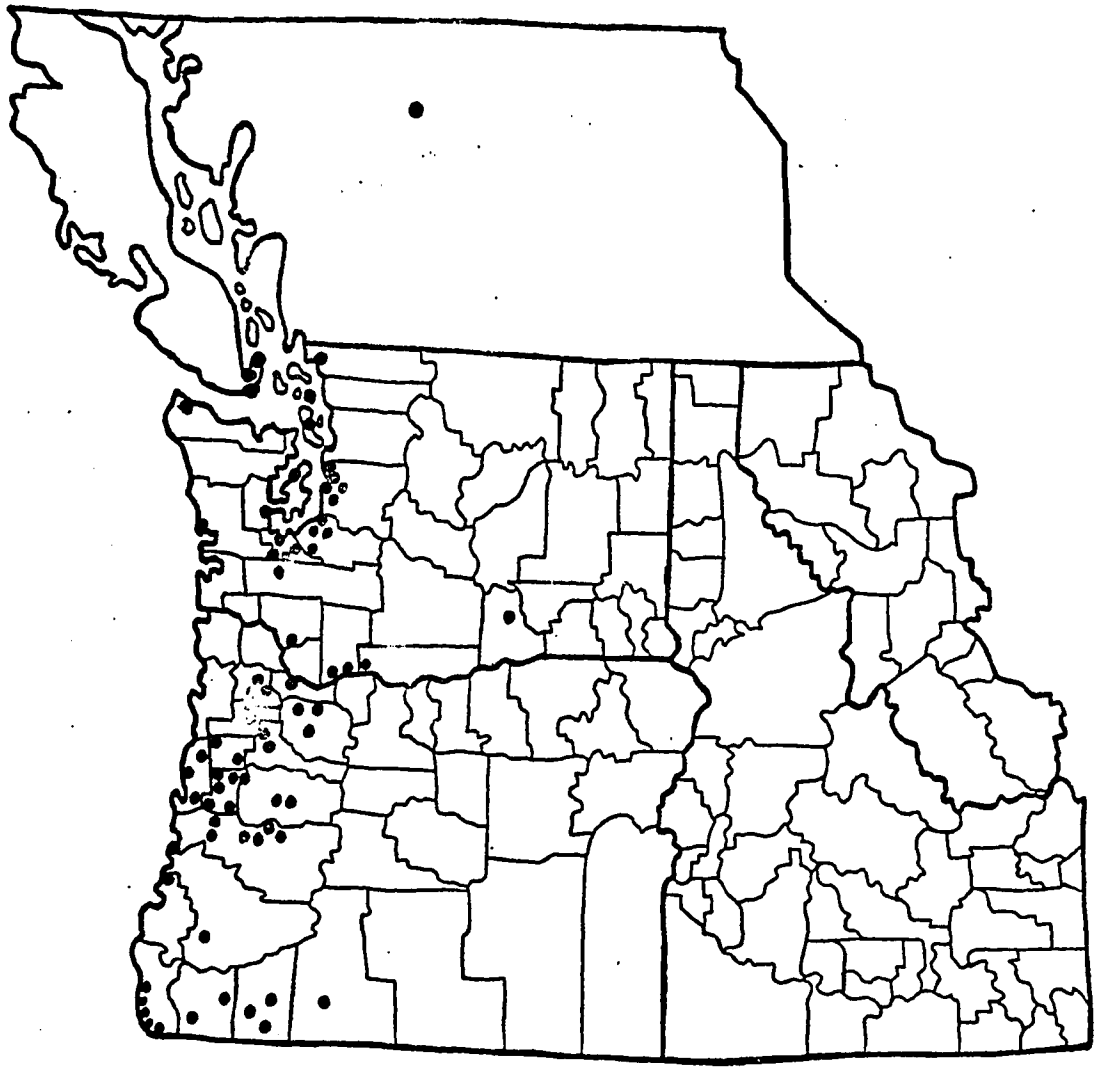
3. Coloration of scape. Casey (1916:8) made use of the fact that northern populations have the ventral surface of the antennal scape bearing a ". . . large and nebulously defined bright testaceous area . . . ." Cazier (1942:151-152) showed this character to be clinal. Table 10 is based on his observations. With the exception of the population from Klamath County, Oregon, Casey's *Omus thoracicus* (aberrant in other ways as well), this feature shows a well-defined character-gradient from north to south. I cannot offer any explanation for such a character, nor reasons for its clinal nature. It is, perhaps, a localized neotenic lack of tanning. Perhaps histological sections would reveal structural differences.

Other characters were used by Casey and other workers including aedeagal form, lengths of antennae and legs, and form of labrum.

Table 10. Percentages of occurrence of a rufous area on the ventral surface of the antennal scape in populations of *Omus audouini* (adapted from Cazier, 1942:151).

Locality	% Rufous	% Black
S.W. British Columbia	100	0
W. Washington	100	0
N.W. and W.C. Oregon	100	0
Klamath Co., Oregon	18	82
S.W. Oregon	57	43
Del Norte Co., California	37	63
Siskiyou Co., California	21	79
Humboldt Co., California	19	81

Fig. 16. Pacific Northwest distribution of *Omus audouini*. See Appendix I for tabulation of localities.



Many of the variations were based on single specimens and merely underline the extreme variability of *O. audouini*.

In summary, the deep, declivous-sided pronotum of *O. audouini* is the most distinctive of the four species of *Omus*. Characteristics of the species ally it more closely with *O. californicus* and *O. submetallicus* than with *O. dejeani*. The relationship with *O. californicus* is also seen in larval characters.

Omus californicus Eschscholtz, 1829

(Classification and synonymy is modified from Cazier, 1942, by the exclusion of taxa here referred to *O. audouini*.)

Omus californicus californicus Eschscholtz, 1829.

Omus californicus Eschscholtz, 1829: Zool. Atlas, 1:3-5.

Omus xanti LeConte, 1859, Proc. Acad. Nat. Sci. Philadelphia, 11:69.

Omus laevis G. Horn, 1866, Proc. Acad. Nat. Sci. Philadelphia, 18:394-395.

Omus lecontei G. Horn, 1872, Trans. American Ent. Soc., 4:143.

Omus sequoiarum Crotch, 1874, Trans. American Ent. Soc., 5:73.

Omus edwardsii Crotch, 1874, Trans. American Ent. Soc., 5:73.

Omus hornii LeConte, 1875, Trans. American Ent. Soc., 6:157.

Omus hornianus W. Horn, 1892, Deutsche Ent. Zeitsch., 1892: 91-92.

Omus montanus Casey, 1897, An. New York Ac. Sci., 9:290.

Omus punctifrons Casey, 1897, An. New York Ac. Sci., 9:291.

Omus confluens Casey, 1897, An. New York Ac. Sci., 9:291-292.

Omus sculptilis Casey, 1897, An. New York Ac. Sci., 9:292.

Omus elongatus Casey, 1897, An. New York Ac. Sci., 9:293.

Omus fuchsi W. Horn, 1903, Deutsche Ent. Zeitsch., 1903:188-189.

Omus mimus Casey, 1909, Canadian Ent., 41(8):256.

Omus dunni Casey, 1909, Canadian Ent., 41(8):258.

Omus dunni regularis Casey, 1909, Canadian Ent., 41(8):258.

Omus dunni maritimus Casey, 1909, Canadian Ent., 41(8):259-260.

Omus cribripennis Casey, 1909, Canadian Ent., 41(8):260-261.

Omus edwardsi lobatus Casey, 1909, Canadian Ent., 41(8):261.

Omus montanus ludicollis Casey, 1909, Canadian Ent., 41(8):262.

Omus montanus brunnescens Casey, 1909, Canadian Ent., 41(8):262.

Omus punctifrons degener Casey, 1909, Canadian Ent., 41(8):263.

Omus fraterculus Casey, 1909, Canadian Ent., 41(8):263.

Omus collaris Casey, 1909, Canadian Ent., 41(8):265.

Omus compositus Casey, 1909, Canadian Ent., 41(8):265.

Omus tularensis Casey, 1909, Canadian Ent., 41(8):265.

Omus tularensis gracilior Casey, 1909, Canadian Ent., 41(8):266.

Omus lugubris sierricola Casey, 1913, Mem. Col., 4:3.

Omus californicus intermediopronotalis W. Horn, 1913, Ent. Mitteilungen, 2(1):347-348.

Omus californicus nunenmacheri W. Horn, 1913, Ent. Mitteilungen, 2(11):347-348.

Omus californicus pronotalis Casey, 1914, Mem. Col., 5:4.

Omus californicus vermiculatus Casey, 1914, Mem. Col., 5:5.

Omus sequoiarum longitarsis Casey, 1914, Mem. Col., 5:12.

Omus laevis temperatus Casey, 1914, Mem. Col., 5:15.

Omus laevis opacellus Casey, 1914, Mem. Col., 5:16.

Omus shastanicus Casey, 1916, Mem. Col., 7:11.

Omus shastanicus cephalicus Casey, 1916, Mem. Col., 7:11-12.

Omus shastanicus tenuiculus Casey, 1916, Mem. Col., 7:12.

Omus semilucens Casey, 1916, Mem. Col., 7:12-13.

Omus semilucens diminuens Casey, 1916, Mem. Col., 7:13.

Omus californicus latipennis Casey, 1916, Mem. Col., 7:13.

Omus sculptilis opacipennis Casey, 1916, Mem. Col., 7:13-14.

Omus lacertus Casey, 1916, Mem. Col., 7:15.

Omus laticollis Casey, 1916, Mem. Col., 7:16.

Omus temperatus difficilis Casey, 1916, Mem. Col., 7:17.

Omus temperatus mariposae Casey, 1916, Mem. Col., 7:17.

Omus temperatus sparsellus Casey, 1916, Mem. Col., 7:18.

Omus subsericens Casey, 1916, Mem. Col., 7:18.

Omus collaris antennalis Casey, 1916, Mem. Col., 7:19.

Omus collaris trapezicollis Casey, 1916, Mem. Col., 7:19-20.

Omus collaris erraticus Casey, 1916, Mem. Col., 7:20.

Omus horni brevis Casey, 1916, Mem. Col., 7:21.

Omus horni propinquus Casey, 1916, Mem. Col., 7:21.

Omus horni asperatus Casey, 1916, Mem. Col., 7:21-22.

Omus horni granosus Casey, 1916, Mem. Col., 7:22.

Omus horni sinuosus Casey, 1916, Mem. Col., 7:22-23.

Omus horni punctatus Casey, 1916, Mem. Col., 7:23.

Omus horni farctus Casey, 1916, Mem. Col., 7:23.

Omus marginalis Casey, 1916, Mem. Col., 7:24.

Omus tularensis remissus Casey, 1916, Mem. Col., 7:25.

Omus laevis peropacus Casey, 1916, Mem. Col., 7:25.

Omus cupreonitens Blaisdell and Reynolds, 1917, Ent. News, 28:49-54.

Omus cupreonitens reynoldsi Casey, 1924, Mem. Col., 11:5.

Omus sculptilis densicollis Casey, 1924, Mem. Col., 11:5.

Omus sculptilis argutus Casey, 1924, Mem. Col., 11:6.

Omus mimus debliceps Casey, 1924, Mem. Col., 11:6.

Omus mimus insulsus Casey, 1924, Mem. Col., 11:6-7.

Omus mimus modicus Casey, 1924, Mem. Col., 11:7.

Omus mimus stolidus Casey, 1924, Mem. Col., 11:7.

Omus mimus subparallelus Casey, 1924, Mem. Col., 11:7-8.

Omus ventricosus Casey, 1924, Mem. Col., 11:8.

Omus ventricosus leachi Casey, 1924, Mem. Col., 11:8.

Omus pullatus Casey, 1924, Mem. Col., 11:9.

Omus edwardsi pollens Casey, 1924, Mem. Col., 11:9.

Omus californicus turbulentus Casey, 1924, Mem. Col., 11:10

Omus californicus aethiops Casey, 1924, Mem. Col., 11:10.

Omus californicus sparsus Casey, 1924, Mem. Col., 11:10-11.

Omus horni callosus Casey, 1924, Mem. Col., 11:12.

Omus vanlooi Nunenmacher, 1940, Pan-Pacific Ent., 16(3):144.

Omus californicus angustocylindricus W. Horn, 1913.

Omus californicus angusto-cylindricus W. Horn, 1913, Ent. Mitteilungen, 2(11):348-349.

Omus cylindricus Casey, 1914, Mem. Col., 5:4.

Omus californicus intermedius Leng, 1902.

Omus intermedius Leng, 1902, Trans. American Ent. Soc., 28: 104-105.

Omus procenus 1909, Canadian Ent., 41(8):259.

Omus blaisdelli Casey, 1909, Canadian Ent., 41(8):260.

Omus procenus parvicollis Casey, 1909, Canadian Ent., 41(8):260.

Omus spissipes Casey, 1913, Mem. Col., 4:3-4.

Omus parvicollis ovipennis Casey, 1916, Mem. Col., 7:14-15.

Omus torvus Casey, 1924, Mem. Col., 11:11.

Omus maurus Casey, 1924, Mem. Col., 11:11-12.

Omus californicus subcylindricus Nunenmacher, 1940.

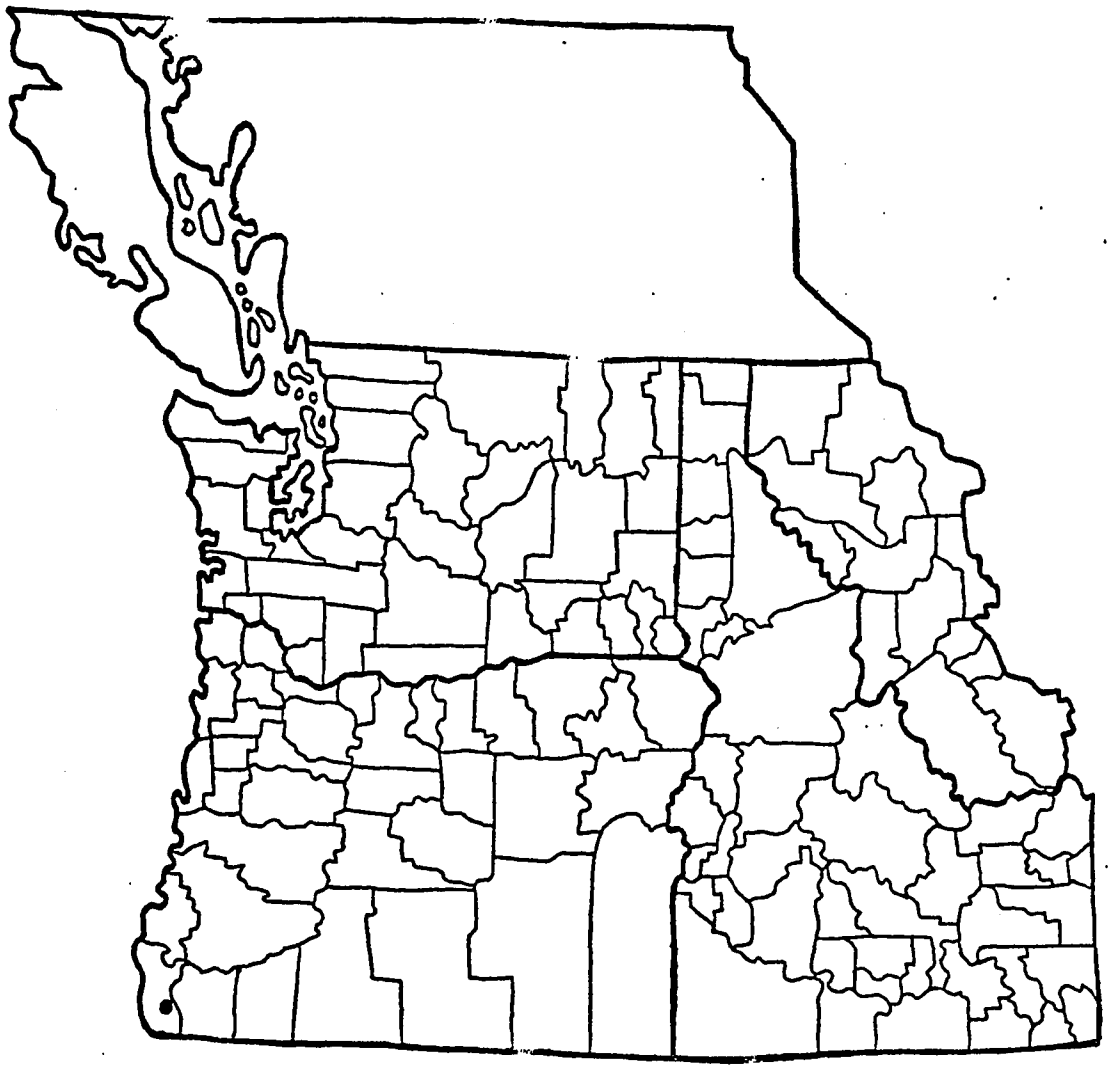
Omus subcylindricus Nunenmacher, 1940, Pan-Pacific Ent., 16(3):143-144.

Diagnosis. Adult: size medium to large; pronotum variable but never with lateral portions of disc declivous, pronotum either gently arcuate or flattened in transverse section, with apices of anterolateral angles fully visible in dorsal view, and glabrous except for short, fine lateral setae; sculpture

of head and pronotum variable, ranging from deep, regular vermiculations covering all portions including middle of disc (northern populations), to shallow vermiculations covering all portions (western and most of eastern populations), to smooth (high montane southeastern populations); elytral sculpture variable, but, when developed, punctures deep, rounded and regular in shape and size but never large and foveate and more than 50 in number, and with ridges between punctures as wide or wider than breadth of punctures (high montane southeastern populations without elytral punctures). Pupa: unknown. Larva: caudal frontal ridge with three setae; pronotum dark brown with pale margins; inner hook of abdominal tergum V with fixed spine slightly longer than movable setae on shoulder.

Synonymic notes. Because *O. californicus* barely enters the geographic area treated in the present study, detailed accounts of the reasons for synonymizing the many names is irrelevant, as all

Fig. 17. Pacific Northwest distribution of *Omus californicus californicus*. See Appendix I for tabulation of localities.



apply to California populations. I have followed Cazier (1942), differing only in my recognition of *O. audouini* as a separate species and the resultant removal of the applicable names from Cazier's list. I have personally examined the types of all but nine of the 94 included taxa. Two names, *cylindricus* and *pronotalis*, are merely Casey's (1914) invalid emendations, respectively, of *angustocylindricus* W. Horn and *intermediopronotalis* W. Horn, emendations made because Casey objected to Horn's unwieldy names. Some of the Sierra Nevada populations (*edwardsi*, *sequoiarum* and *laevis* and their many "species" and "subspecies" *sensu* Casey) appear distinct when compared with, for instance, specimens from northern and western California. If it were not for the facts that many intermediate populations exist and that many of the names are based on single aberrant variants found with more normal appearing individuals or from completely recorded localities, I might be inclined to consider some of the taxa as valid.

Subspecies of *O. californicus*. Cazier (1942) recognized four subspecies based on his studies of holotypes of most of the named taxa and statistical analyses of over 2,000 specimens. I am in general agreement with his results, although I believe further study of the lower elevation southern Sierra Nevada populations might yet be profitably undertaken. Cazier's subspecies key (op. cit.:389-390) makes too much use of geographic range and not enough of anatomical features. The apparent reason is the difficulty in

constructing a key that differentiates all the subspecies while still accounting for the extreme variability in the species over its entire geographic range. Figure 18 shows the ranges of the four subspecies which may be distinguished by the following key, modified from Cazier (1942):

Key to Subspecies of *Omus californicus*

1A. Elytral length: males, 11.39-16.19 mm, females, 13.74-16.90 mm; ventral surface of scape rufous in 72% of population; pronotal sculpture deeply vermiculate; range: restricted to vicinity of CA. Santa Clara Co., San Martin.....*O. c. subcylindricus*

B. Elytral length: variable, but in part of range geographically closest to that of *subcylindricus*, males, less than 12.88 mm, females, less than 15.22 mm (over 75% separation); ventral surface of scape black in over 93% of population; pronotal sculpture shallow in populations in part of range near that of *subcylindricus*; range: widespread, but not sympatric with *subcylindricus*.....2

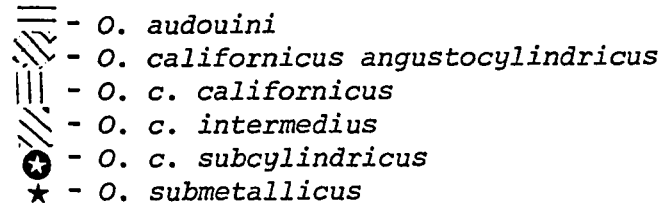
2A. Elytral breadth: males, 5.17-6.70 mm, females, 4.97-7.40 mm; range: above 1500 m elevation in CA. Plumas and Lassen Cos.....*O. c. angustocylindricus*

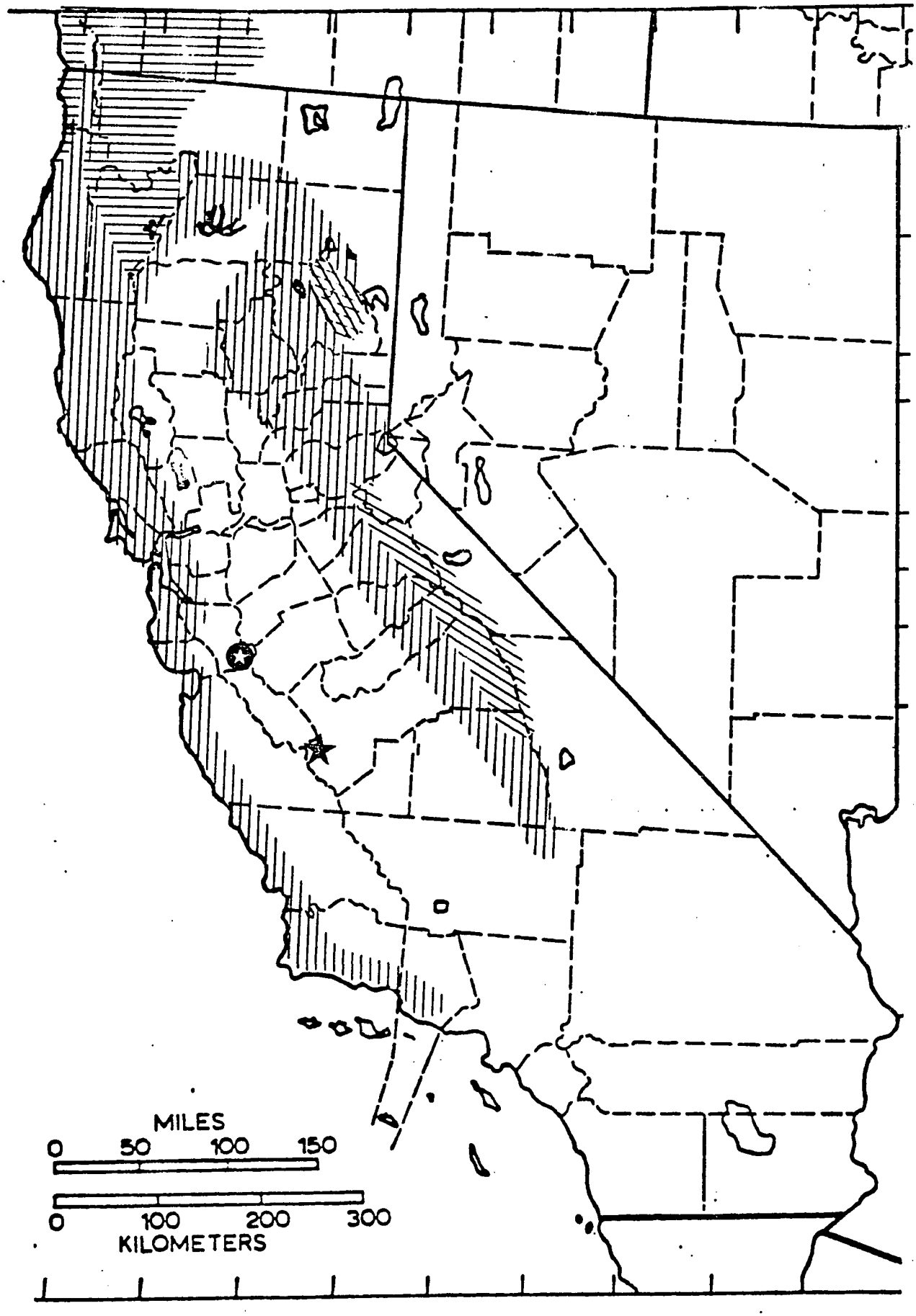
B. Elytral breadth: males, greater than 6.40 mm, females, greater than 6.98 mm; range: widespread, but below 1500 m in part of range near that of *angusto-cylindricus*.....3

3A. Ratio elytral length/posterior pronotal breadth: males, 21.0-27.5%, females, 21.2-28.5%; ratio elytral length/ greatest labral length: males 5.6-8.0%, females, 6.0-8.6%; range: above 900 m between CA. El Dorado and Kern Cos.....*O. c. intermedius*

B. Ratio elytral length/posterior pronotal breadth: males, 27.5-40.2%, females, 27.8-40.7%; ratio elytral length/ greatest labral length: males, 7.7-10.8%, females, 7.8-11.1%; range: widespread, but below 900 m elevation in part of range near that of *intermedius* .....*O. c. californicus*

Fig. 18. Distribution of *Omus* in California and southwestern Oregon (modifed from Cazier, 1942).

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O. c. californicus. This variable subspecies occupies most of the range of the species, and is the one which barely enters southwestern Oregon. I shall discuss the clinal variation of this subspecies in more detail below. It is difficult to characterize it other than in that it lacks the modifications of the other three subspecies. This is admittedly unsatisfactory. From geographically approximate populations of *O. c. subcylindricus*, *californicus* differs in smaller size and much weaker pronotal sculpture. *O. c. californicus* has wider elytral than *angustocylindricus* (90% separation). *O. c. intermedius* differs in the proportionally (and actually) broader and longer elytra, resulting in a different ratio of elytral length/posterior pronotal breadth:

	male	female
californicus	27.5-40.2%	27.8-40.7%
intermedius	21.0-27.5%	21.2-28.5%

O. c. californicus ranges from the Oregon-California border to CA. Ventura Co., Ojai in the southwest and to CA. Kern Co., Greenhorn Mtns., Shirley Meadows in the southeast. It is absent from the Sacrament and San Joaquin Valleys and the inner coastal valleys and ranges of the California coastal area south of San Francisco. Its range coincides with the distribution of moist conifer forest. It is parapatric with *O. audouini* in northwestern California, the two species having been taken together only at

CA. Tehama Co., Round Mountain, 1772 m. Details of this parapatry are presented beyond.

O. c. angustocylindricus. This subspecies is well-characterized by the small size and narrow elytra. Cazier's data give a 90% separation from geographically adjacent populations of *O. c. californicus* based on elytral breadth and these two subspecies are parapatric.

O. c. angustocylindricus is relatively uniform compared with *O. c. californicus*. It is known from localities in only two adjacent California counties (Lassen and Plumas) at elevations from 1500-2100 m, on both east and west slopes of the Sierra Nevada Mountains. The Lassen County populations average smaller in size, indicating clinal variation. The larger Plumas County population approaches Plumas County populations of *O. c. californicus* from lower elevations in size and may indicate both a relationship and perhaps the origin and evolutionary trends of the ancestral stock.

O. c. angustocylindricus has been recorded from the following localities (from Cazier, 1942):

CA. Lassen Co.: Lassen Co. (type locality); Westwood. Plumas Co.: Mount Hough, Mount Ingalls, Quincy.

O. c. intermedius. This subspecies is well-characterized by a combination of large size, weak sculpture, no trend toward dorsoventral flattening of the prothorax, and long and wide elytra. Geographically adjacent populations of *O. c. californicus* approach

it in size but tend to show less sculpture, narrower elytra and pronounced dorsoventral flattening of the prothorax. It is similar in general facies to *O. c. subcylindricus*, differing mainly in the weak sculpture, but it is geographically remote from that subspecies. The small, narrow-bodied *O. c. angustocylindricus* shows no resemblance.

Cazier found little variation in the subspecies over its rather extensive range. It extends along the western side of the Sierra Nevada Mountains at elevations between 900 and 2100 m, from El Dorado County in the north to Tulare County in the south. *O. c. californicus* is found generally at elevations lower than 900 m, and the two subspecies have not been found at the same localities.

O. c. intermedius has been recorded from the following localities (from Cazier, 1942):

CA. El Dorado Co., El Dorado Co.; Calaveras Co.: Mokelumne Hill; Mariposa Co.: Coulterville (type locality); Madera Co.: Northfork; Fresno Co.: Kings Canyon Nat. Park; Tulare Co.: Kaweah, Sequoia Nat. Park.

O. c. subcylindricus. This well-characterized subspecies is allopatric from other subspecies. It differs from geographically approximate populations of *O. c. californicus* in its elongate elytra and deep, vermiculate pronotal sculpturing. It approaches the shape and size of *californicus* populations to the west and south and sculpture of those to the north. Cazier (1942:391) showed that the coefficient of variability of *subcylindricus* males is nearly twice

that of adjacent populations of *californicus* males, but that of females is only half as great compared with *californicus* females.

O. c. subcylindricus is known only from CA. Santa Clara Co., vicinity of San Martin. This locality is in the eastern portion of the Santa Clara Valley and isolated from the range of *O. c. californicus* by the western portion of the Santa Clara Valley and the east slope of the Santa Cruz Mountains, approximately 30 km.

The *Omus c. californicus* Cline

As can be seen from Figure 18, the range of *O. c. californicus* roughly resembles an inverted U, the free ends directed southward. The free ends of the U are marked by CA. Ventura Co., Ojai and CA. Kern Co., Greenhorn Mountains, a distance of about 140 air km. No specimens have been reported from the intervening area, approximately equivalent to the Tehachapi Mountains, a largely roadless and generally inaccessible region, although it is possible that the beetle may eventually be found there. The populations at the southern free ends of the U are very distinct from one another. The Kern County beetles are large, heavily punctate, and rather flattened, particularly the pronotum. They superficially resemble *O. dejeani*, but the elytral sculpture is of an entirely different type. The southwestern coastal populations ("*lecontei*") are large and weakly sculptured, have narrow, rather elongate elytra, and have the pronotum unmodified. Conversely, northern Californian populations are small and heavily sculptured and punctate, and have neither the

elytra nor pronotum particularly modified. If specimens from intervening areas were unknown, the southwestern, southeastern and northern populations would unquestionably be considered separate subspecies or species. However, there is ample material from the intervening regions. Cazier's (1942) study of *Omus* showed that, although there are clinal trends in size, shape and sculpture, and, often, even rather distant populations cannot be distinguished statistically. Cazier's statement (1942:209), in reference to coastal California populations, in slightly modified form applies well to the entire situation: "The distribution of *Omus* (*c. californicus*) . . . is continuous and there appears to be no climatic barrier or abrupt divergence in any of the characters studied."

Several terms have been created to designate a series of intergrading populations. Certain of these refer to complexes clearly involving more than one species or subspecies:

1. Artenkreis (Rensch, 1929:15). ". . . a complex of interfertile and morphologically similar forms . . . not divided into geographical races." Mayr (1931) substituted the term "superspecies" as a convenient equivalent because the literal translation of Artenkreis was frequently misunderstood. Mayr (op. cit.) stated that the largely obsolete terms Artengruppe and Formengruppe are synonymous.

2. Formenkreis (Kleinschmidt, 1901). This term was proposed because of problems in correspondence between "Art" and "Rasse."

Rensch (1929) criticized Kleinschmidt's improper use of rules of priority and urged abandonment of the term.

3. Rassenkette (Sarasin and Sarasin, 1899). This term applies to subspecies arranged geographically in a circle, a chain of races (Rensch, 1929:13).

4. Rassenkreis (Rensch, 1926). "A Rassenkreis is a complex of . . . races . . . geographically substituing for one another and in which at times the neighboring forms are interfertile (Rensch, 1929)." As this term was intended for a complex of more than one subspecies, it is inapplicable to *O. c. californicus*.

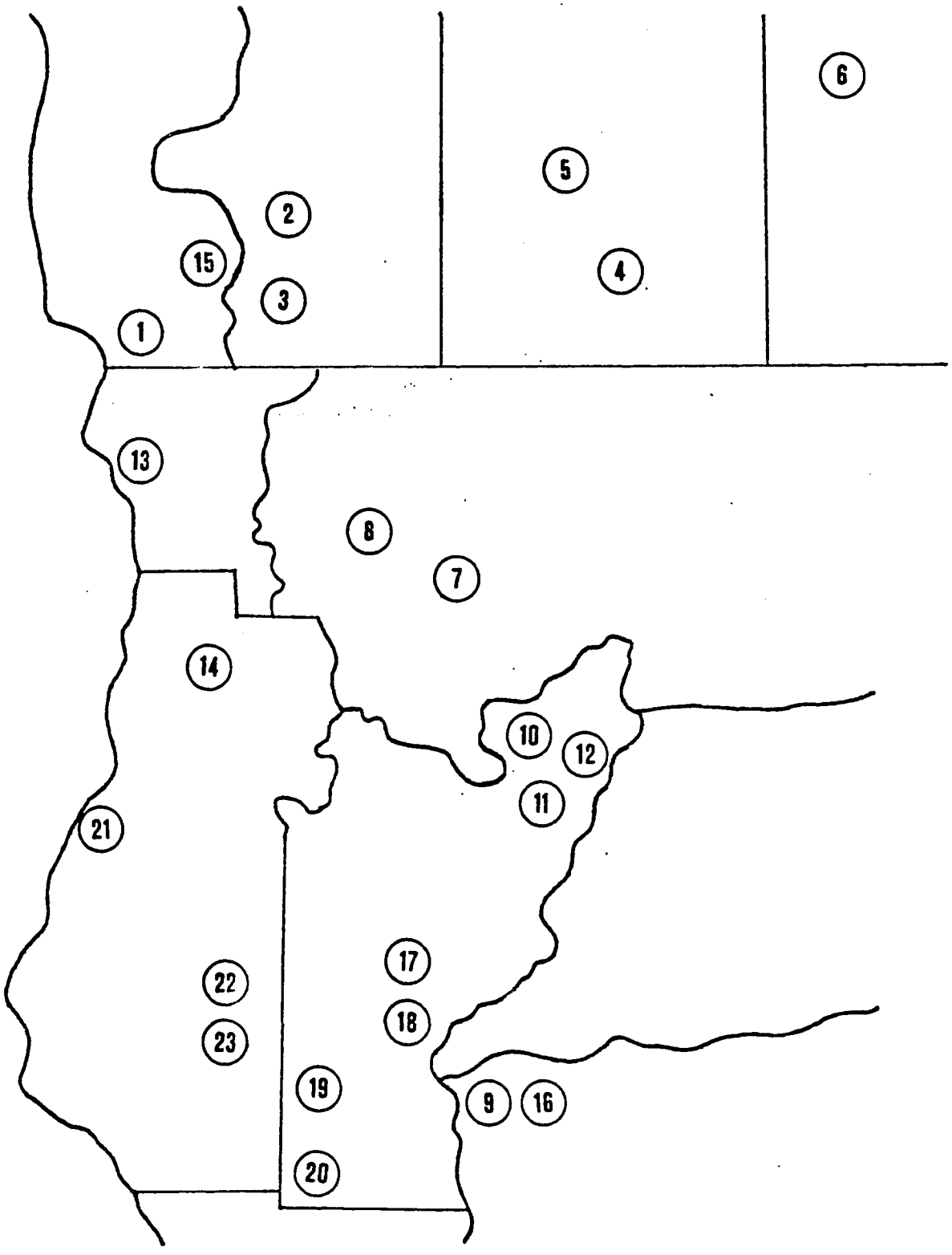
5. Cline (Huxley, 1938). "A cline is formed by a series of contiguous populations in which a given character changes gradually (Mayr, 1969:44-50)."

Of these several terms, only one, the cline, applies to the situation in *O. c. californicus*. The other terms apply only to members of a polytypic species or, for one reason or another, are unsatisfactory. In proposing his term "cline," Huxley (1938) intended it to serve both within a species or between species. Variation within a group ("intra-group clines") concerns continuous variation within a population. Simpson (1961:178-180) qualified Huxley's term by stating that ". . . the gradation of a cline is within a single species (or subspecies), that it is unidirectional, and that it is more or less uniform rather than distinctly steplike." This definition applies perfectly to *O. c. californicus*, based on Cazier's study. Casier showed the variation in his concept of

O. c. californicus to be gradual and not steplike. Only those segregates referred to by distinct subspecific names (*angusto-cylindricus*, *intermedius* and *subcylindricus*) are not part of the cline; they may be distinguished statistically from geographically adjacent samples of *O. c. californicus*. Because there are no morphological breaks in the cline throughout its range, I agree with Cazier (1942) in referred the entire series of clinally intergrading populations to a single, highly variable subspecies, *O. c. californicus*. It is perhaps useful to speculate on how populations at the southeastern and southwestern ends of the cline might interact biologically if and when they actually were found to be in contact in the Tehachapi Mountains. Would such overlapping populations be able to interbreed or would they react like separate biological species, infertile or even competitive?

The status of *O. californicus* in the Pacific Northwest. *O. californicus* is known from a single locality in Oregon: OR. Curry Co., Red Mountain Prairie, 53 km (by road) N.E. Brookings, 998 m (specimen in ODA collection). My determinations of types and other specimens and evaluation of literature records reveal that *O. audouini* and *californicus* are largely parapatric in northwestern California and southwestern Oregon. They have both been taken at only one locality, CA. Tehama Co., Round Mountain, 1777 m. Figure 19 is a map of the nine counties under consideration showing localities for the two species. Elevations are added wherever possible in the following legend.

Fig. 19. Distribution of *Omus audouini* (1-14) and *Omus californicus* (15-23) in southwestern Oregon and northwestern California. See text for tabulation of localities.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O. audouini. OR. Curry Co.: 1. Winchuck River (SL). Josephine CO.: 2. Selma, 404 m (Cazier, 1942; type locality of *aequicornis* and *oregonensis*); 3. Waldo 5 km E.S.E. O'Brien, 430 m (Cazier, 1942; type locality of *aequicornis* and *oregonensis*). Jackson CO.: 4. Ashland, 578 m (UC); 5. Medford, 421 m (UC). Klamath CO.: 6. Upper Klamath Lake, 1260 m (Cazier, 1942; type locality of *thoracicus*). CA. Siskiyou CO.: 7. Shasta Retreat, Bucks Lake (Cazier, 1942; type locality of *solidulus*); 8. Mud Lake, 7 mi N.W. Cottage Grove (Cazier, 1942; type locality of *brevicornis* and *rugipennis*). Tehama Co.: 9. Round Mountain, 1772 m (Casey, 1924, type locality of *socius*; Casey placed this locality incorrectly in Shasta County). Trinity Co.: 10. Preacher's Meadow (UC); 11. Stuart's Fork, 704 m (UC); 12. Coffee Creek, 902 m (UC). Del Norte Co.: 13. Crescent City, near sea level (W. Horn, 1910; type locality of *humeroplanatus*). Humboldt Co.: 14. 10 mi E. Orick (Cazier, 1942; type locality of *humeralis*). Locality not found. CA. Siskiyou Co., Mt. Shasta District (Schaupp, 1884; type locality of *ambiguus*; according to late 19th century maps, Mt. Shasta District was applied to most of Siskiyou County).

O. californicus. OR. Curry Co.: 15. Red Mountain Prairie, 53 km N.E. (by road) Brookings, 998 m (ODA). CA. Tehama Co.: 16. Round Mountain, 1772 m (Cazier, 1942; type locality of *aethiops*, *cephalicus*, *shastanicus* and *tenuiculus*). Trinity Co.: 17.4 mi S. Hayfork, 731 m (UC); 18. 5 mi S.E. Peanut, 762 m (UC); 19. Zenia, 994 m (Cazier, 1942); 20. Island Mountain (Cazier,

1942; type locality of *leachi*, *mimus* and *sculptilis*; this locality refers to the town, as the nearby mountain of the same name is in Humboldt County). Humboldt Co.: 21. Arcata Beach, near sea level (Cazier, 1942; type locality of *cupreonitens* and *reynoldsi*); 22. Blocksburg, 486 m (UC); 23. Ft. Seward, 114 m (UC).

Examination of the map shows that the Siskiyou and Salmon Mountains are largely occupied by *O. audouini* and it is replaced in the Yolla Bolly, Trinity and California Cascade Mountains by *O. californicus*. The boundary along the coast coincides largely with the region where *Sequoia sempervirens* is dominant, although I do not wish to draw any more than coincidental association. Further collecting in the western Siskiyou (Del Norte-Siskiyou County line) and Trinity (Trinity-Shasta County line) Mountains will probably delineate the boundaries between the ranges of the two species.

Character-gradients in *O. audouini* and *O. californicus* run in opposite direction. *O. audouini* decreases in size from north to south and pronotal and elytral sculpture becomes progressively shallower, even becoming obliterated along the midline of the pronotum, from north to south. Conversely, *O. californicus* decreases in size from south to north and sculpture becomes stronger from south to north. Thus, where the ranges of the two species meet, specimens are small for their species but *O. audouini* has very little sculpture and *O. californicus* is heavily sculptured. I take this directional difference in character-gradients to be a further reason for recognizing the two species as distinct. Pronotal and larval characters

and lack of evidence of intergradation where the ranges meet argue for specific rather than subspecific rank.

Interrelationships of Species of *Omus*

My interpretation of the interrelationships of the four species of *Omus* is presented in Figure 12. *O. dejeani* stands apart from the remaining species by reason of its unique setigerous elytral foveae. It differs also in its general facies, a character readily observable but difficult to describe; that is, it is not so compactly built. The less compact facies and regularly-distributed elytral setae are primitive features if such a conclusion can be drawn from comparisons with the Mantichorini which *O. dejeani* resembles more closely than any other genus or species of Omina. The similarity may be convergence but, in view of the differences in ecological requirements, this is unlikely. I believe that the *Omus* ancestor looked much like *O. dejeani*.

The remaining three species are more closely related to one another than any to *O. dejeani*. The unique pronotal structure of *O. audouini* is apomorphic, and it has diverged the most from an ancestral form. *O. californicus* and *submetallicus* are closely related and differ mainly only in the unique lateral pronotal setae. Populations of *O. c. californicus* from the southern Sierra Nevada Mountains approach the large size and pronotal flatness of *O. dejeani* although retaining the characters diagnostic of their

species. They may be closest to an ancestral stock of the species, or their features may merely reflect the effects of local geographical environmental conditions.

Tribe Cicindelini Fischer, 1821

Diagnosis. Cicindelinae with fourth segment of maxillary palp longer than third, except in *Prothyma* (*Vata*); prothorax cylindrical, apex and base of approximately equal breadth, and with anterolateral angles not extending to level anterior edge of prosternum.

W. Horn (1908-1915) recognized five subtribes: Dromicina (one genus), Prothymina (10 genera), Theratina (one genus), Odontochilina (four genera) and Cicindelina (three genera). Rivalier (1971) rearranged some of Horn's subtribes, and (1969, 1971) erected a new genus and some previous subgenera to generic rank. Under his arrangement, only the subtribe Theratina remains identical with Horn's concept. Rivalier grouped Horn's Dromicina, Prothymina (part), and Odontochilina into a subtribe Prothymina; he erected a new subtribe Iresiina (improperly spelled Iresina) for the remaining genera of Horn's Prothymina; and divided Horn's Cicindelina into

the Cicindelina *ss.* and Apteroessina, newly erected for the genus *Apteroessa*. Rivalier based his groups on chaetotaxy, pilosity and structure of the aedeagus and its internal sac.

I am inclined to compromise between the two arrangements, but my conclusions are based on personal examination of only a few genera and a review of the limited literature, notably W. Horn (1908-1915), Rivalier (1971), Shelford (1915), Tanner (1927) and Zikan (1929).

For the purpose of this discussion, I recognize four subtribes: Dromicina, Promythina (including Iresiina and Odontochilina), Theratina and Cicindelina (including Apteroessina). I shall discuss my reasons for this arrangement farther on in the present section.

I consider the following characters significant in distinguishing the subtribes, indicating their interrelationships, and plesiomorphy and apomorphy:

1. Labrum. Labral elongation has occurred independently in several lineages, often within the same genus. All four subtribes have species or species-groups with elongate labra. All Theratina have long labra.

2. Labral sensory setae. Sensory setae are orginarily submarginal, but, in the Theratina and some genera of Prothymina, they are marginal. Four well-developed setae are characteristic of the Dromicina, most Prothymina (*sensu mihi*: the genera in Rivalier's Iresiina are hexachaetous or polychaetous), and some Theratina. Variation between species and often even between

individuals of the same species of *Cicindela* make generalization for the Cicindelina impossible. A submarginal poaition is characteristic of most Cicindelidae and Carabidae and I consider it to be plesiomorphic. I cannot generalize as to the plesiomorphic seta number: *Mantichora*, *Megacephala* and *Omus* are hexachaetous; other genera examined range from tetrachaetous to decachaetous. In Table II, only position of the setae is assessed.

3. Maxillary galea. The Theratina are characterized by a reduced, one-segmented galea. In other subtribes, the galea is well-developed and two-segmented.

4. Elytral tracheation. The following information is based on descriptions and illustrations by Shelford (1915).

Dromicina. Five trunks, anal absent; costa unbranched, sometimes reduced; radius and media sometimes connected distally. Except for the lack of the anal trunk, an unmodified dromicine arrangement is closest to a primitive condition (but see Theratina).

Theratina. Six trunks, anal reduced; costa branched near three-quarters of distance to apex; radius and media connected distally between subcosta and radius, and between medial distal costal branch and radiomedia fusion point. The Theratina have a combination of plesiomorphic (retention of the anal trunk, albeit reduced) and apomorphic (crossveins and connectives between trunks) characters.

Prothymina. Five trunks, anal absent; costa unbranched or branched near apex; medial distal costal branch and cubitus

connected in some species but usually unconnected; subcosta and media sometimes connected distally; media shortened in some species; crossveins few or absent. A distally-branched costa is characteristic of all subtribes except the Dromicina and most Prothymina, but in those Prothymina that are branched, the branch is located the most distally.

Cicindelin. Five to six trunks present, anal reduced or absent; costa branched near three-quarters of distance to apex; crossveins variable (even between left and right sides of same individual) but numerous; media shortened. The position of the costal branch and the shortened media are characteristic.

5. Proportions of metepimeron. Correlated with a fully-developed hindwing is an elongate metepimeron, the sclerite into which the subalar muscles insert. In forms with reduced hindwings, the metepimeron is correspondingly reduced in size and, thus, must not be used to indicate anything beyond flight ability. Ordinarily, a reduced metepimeron is squared in outline, rather than having the elongate-rectangular form of volant species. The small, triangular form of the dromicine metepimeron is unique.

6. Tarsal structure. The Theratina are unique in the shortened, apically-dilated fourth tarsal segment and a subapical insertion of the fifth segment dorsally into the fourth. *Oxygonia* (Prothymina) has this anteapical dorsal insertion also, but on the hind tarsi only. Other genera have a normal apical insertion.

7. Ovipositor. The Theratina are convergent with the Collyrinae in the toothed 2nd gonapophyses (Tanner, 1927, with terminology after Freitag, 1966). Larvae of both live in galleries in wood (Böving and Craighead, 1931; Zikan, 1929). The ovipository is used in excavating the egg burrow. Other genera have untoothed 2nd gonapophyses.

8. Pilosity. Rivalier (1971) attempted to use pilosity, particularly that of the ventral surface, as a subtribal character. His couplet 2 does not separate completely the groups for which it was intended. The Theratina, Dromicina and Promythina are all ventrally glabrous. *Apteroessa* is completely pubescent. Some species of *Cicindela* are quite pubescent and others nearly glabrous. I personally doubt that pilosity should have much weight above the species level. As most of the primitive cicindelids are at least setose, this is probably the plesiomorphic state. Complete glabrousness is certainly apomorphic.

Table 11 summarizes these eight character states in the four subtribes.

Horn's (1908-1915) definitions were based mainly on negative or very minor features. I am not satisfied, however, with Rivalier's rearrangement, either. His characters such as pilosity and number of labral setae are too variable to be useful at the subtribal level. Similarly, the variability between genera in Horn's Odontochilina makes a comprehensive diagnosis of that subtribe impossible, and diagnosis is hampered by Rivalier's recognition of additional

Table 11. Analysis of subtribes of tribe Cicindelini regarding plesiomorphic and apomorphic states of 8 characters presented in text. Symbols: P = plesiomorphic, A = apomorphic, V = variable. Note: for character no. 2, only setal position is assessed.

Character No.	Dromicina		Prothymina		Theratina		Cicindelina	
1	variable	V	variable	V	long	A	variable	V
2	position sub-marginal tetrachaetous	P	most submarginal number variable	V	marginal tetrachaetous	A	submarginal number variable	P
3	normal	P	normal	P	one-segmented; size reduced	A	normal	P
4	most generalized when unmodified	P	variable	V	6 trunks but with many crossveins	A	variable; media usually shortened; many crossveins	A
5	small and triangular	A	normal or normally reduced	P	normally reduced	P	normal or normally reduced	P
6	normal	P	normal (except *Oxygonia*)	P	highly modified	A	normal	P
7	normal	P	normal	P	2nd gonapophyses toothed	A	normal	P
8	glabrous	A	glabrous	A	glabrous	A	variable	V
	$\Sigma P=5$; $\Sigma A=2$; $\Sigma V=1$		$\Sigma P=4$; $\Sigma A=1$; $\Sigma V=3$		$\Sigma P=1$; $\Sigma A=7$; $\Sigma V=0$		$\Sigma P=5$; $\Sigma A=1$; $\Sigma V=2$	

genera. Based on my personal conclusions, I tentatively recognize four subtribes:

1. Dromicina. This group contains a single African genus with several species, all of which are flightless. The small, triangular metepimeron is unique. The subtribe shows the least modified elytral tracheation of all the Cicindelini except in lacking the anal trunk. W. Horn (1908-1915:159) pointed to the presence of apical metatrochanteric setae as substantiating ". . . the theory of the primitive position of the Dromicina." Unfortunately, he only mentioned the character again for the Theratina in which these setae are absent. The setae are absent in specimens of *Cicindela* (Cicindelina) and *Distipsidera* and *Odontochila* (Promythina) which I have examined, but I do not know if this is true of all members of these groups.

2. Prothymina. As here constituted, this subtribe includes the Prothymina and Odontochilina (*sensu* Horn), and using Horn's classification, contains 14 genera (many more are recognized by Rivalier), together having a pan-tropical distribution. The wide range of variation makes a comprehensive subtribal diagnosis difficult, as seen in the high number of "variable" scores in my Table 11. The costa is unbranched and crossveins are few or absent in most Prothymina. When the costa is branched, the fork is located at the distal end, a unique position. Most of the genera have labra with four submarginal setae. Unmodified elytral tracheation and labral chaetotaxy agree with the Dromicina. Rivalier's

arrangement employed the latter feature in grouping Horn's Odontochilina and Prothymina (tetrachaetous) and recognizing the Iresiina (hexachaetous or polychaetous) as separate. It would be useful to attempt to find any correlation between elytral tracheal patterns and labral chaetotaxy among the named genera of Prothymina. Further study of the genera should result in a better arrangement. However, for the time being, I am including within the bounds of this subtribe an assemblage that l[illegible]s the triangular form of the dromicine metepimeron, lacks the theratine maxillary and tarsal modifications, and lacks the characteristic cicindeline elytral tracheation.

3. Theratina. This subtribe contains a single genus, *Therates*, with several species of Oriental and Australian distribution. It was afforded recognition by both Horn and Rivalier without question. Its maxillary, tarsal and gonocoxal characteristics are unique in the subfamily Cicindelinae. In addition, its elytral tracheation shows a peculiar combination of plesiomorphic and apomorphic features that I have already discussed. W. Horn (1908-1915) derived the Theratina from the Dromicina, but gave little evidence for doing so. The marginal position of the labral setae in *Therates* and some Prothymina may indicate relationship. The labrum of some species of *Dromica* (e.g., *D. gigantea*) closely resembles the peculiarly-shaped *Therates* labrum, but that of others (e.g., *D. laticollis*) shows no such similarity. Facies, habits, and distribution of the two subtribes do not support relationships.

4. Cicindelina. I shall discuss the limits of this subtribe in more detail beyond. The position of the elytral costal fork appears to be diagnostic. The shortened media is characteristic but is also seen in some Prothymina. Presence of a remnant of the anal trunk in some species is plesiomorphic and is also seen in the Theratina. The two subtribes also agree in having numerous crossveins and connectives, but this is more likely to be convergent as the two groups have no other close similarities.

In summary, subtribal limits require more detailed study than I am able to give. I recognize four subtribes, only one of which, the Theratina, is well-marked. The remaining three are so variable that their definitions require combinations of characters.

Subtribe Cicindelina Fischer, 1821

Diagnosis. Cicindelini with elytral tracheation as follows: costa branched at level near three-quarters of distance to apex, media shortened, crossveins variable but numerous; head, pronotum, prosternum, mesosternum, base of abdominal venter, or base of elytra setose OR posterior third of elytra with pale sutural or discal markings.

There are three genera: *Apteroessa* Hope (one species), *Cicindela* Linnaeus (about 700 species), and *Eurymorpha* Hope (one species). I consider the following characters important in distinguishing the genera. The information is based on study of about 75 species of *Cicindela* and extracts from Fairmaire (1856), W. Horn (1908-1915) and Rivalier (1971).

1. Antennal chaetotaxy. *Eurymorpha* is unique in having two divergent groups of setae each on articles 3 and 4. Some species of *Cicindela* have at least one such tuft on antennal article 4 (Rivalier, 1950).

2. Head and pronotal sculpture. *Apteroessa* has the frons, genae and anterior pronotal margin finely punctate rather than variably rugose as in *Cicindela*, *Eurymorpha* and many other cicindelids. Neither punctate nor rugose sculpture is plesiomorphic (smooth is) and neither is derivable from the other.

3. Pronotal shape. The flattened, transversely-elongate pronotum of *Eurymorpha* with its compressed lateral margins and produced anterolateral and posterolateral angles is unique. Only that of *Platychila* even remotely resembles it, but the similarity is not great. Pronota of *Cicindela* (except for some peculiarly modified species) and *Apteroessa* are of the typical cylindrical form of the tribe Cicindelini.

4. Relationships of mesepisternum and mesepimeron. *Apteroessa* differs from all other cicindelid genera in that the posterior edge of the mesepisternum is swollen and overlaps the lateral part of

the anterior margin of the mesepimeron. Also, the posterolateral margin of the mesepimeron overlaps the anterolateral portion of the metepisternum. Other genera lack such swollen and overlapping portions. These modifications apparently strengthen the articulations between the sclerites, but for what purpose I cannot venture a guess. The function must be determined from behavioral studies, but, as yet, *Apteroessa* is known only from fragments of three specimens!

5. Pilosity. Rivalier (1971) grouped those genera of Cicindelini whose thoracic and abdominal sternites are ". . . more or less clothed with pubescence. The definition of the subtribe would appear rather mediocre and one might like to be able to find at least one additional common character." Species of *Cicindela* range from extremely pilose to completely glabrous, thus obliterating the value of the character. *Eurymorpha* has much of the ventral portion of the thorax and at least the posterolateral part of the abdomen thickly pilose. *Apteroessa* is peculiar in being completely covered dorsally and ventrally with thick pubescence.

I have not constructed a table for the Cicindelina because *Eurymorpha* and *Apteroessa* are so clearly apomorphic in most of their characteristics. *Eurymorpha*, by reason of its unique antennal chaetotaxy and pronotal form, and *Apteroessa*, particularly because of its sculpture, pubescence and ventral thoracic structure, stand far apart from *Cicindela*. Rivalier (1971) placed *Apteroessa* in its own subtribe. *Eurymorpha* is certainly as deserving of separate

subtribal status as *Apteroessa*, but Rivalier left it in the Cicindelina *ss*. As no survey of the over 700 species of *Cicindela* has ever been made to determine any approaches toward the characters of *Apteroessa* and *Eurymorpha*, it is impossible to trace the interrelationships of the three. Division of the three-genus Cicindelina (*sensu* W. Horn) into more than one subtribe, particularly subtribes with only one species, adds nothing to our understanding of the Cicindelina. Rivalier's recognition of a separate subtribe for *Apteroessa* and not *Eurymorpha* is not consistent in my opinion, and I synonymize Rivalier's Apteroessina under the Cicindelina.

It is probable that some of the 55 genera into which Rivalier has divided *Cicindela* are worthy of recognition. I am in no position, nor is this study the proper place, to assess this problem, and I retain the admittedly ponderous genus *Cicindela sensu* W. Horn.

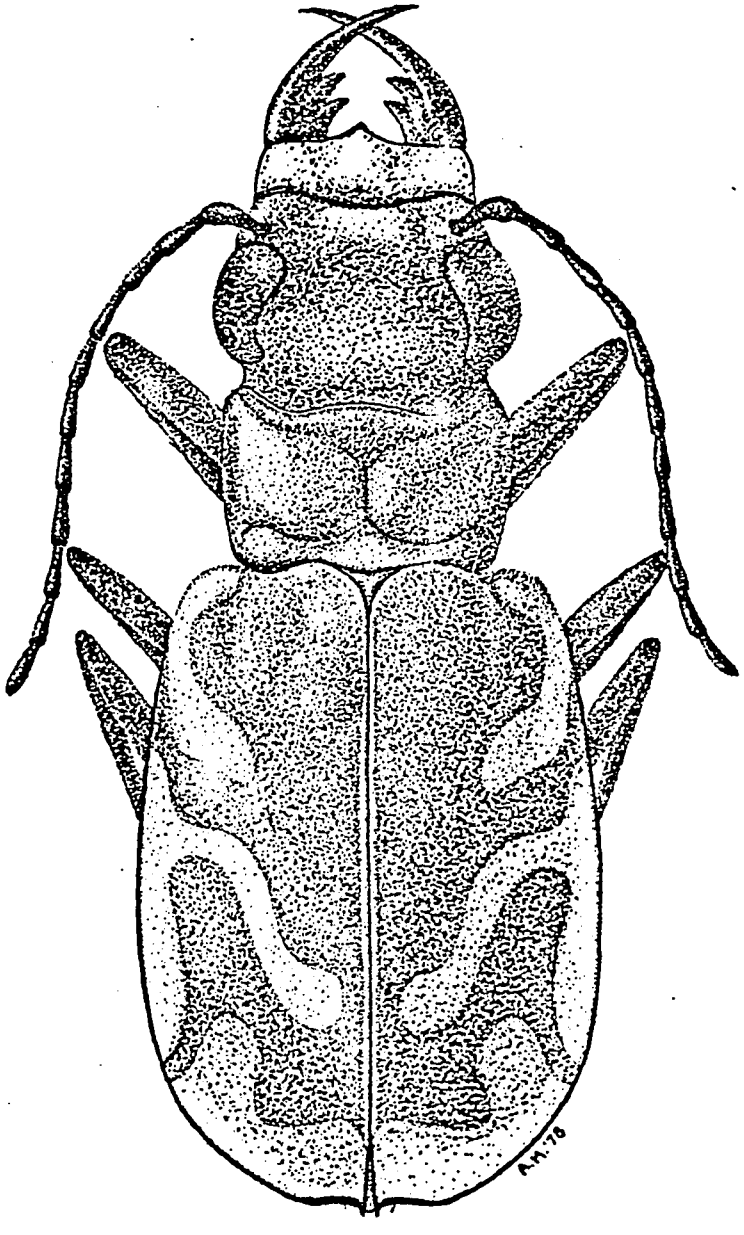
Genus *Cicindela* Linnaeus, 1758

(Genotype: *C.* (*C.*) *campestris* Linnaeus, 1758)

Cicindela Linnaeus, 1758. Syst. Nat., 407.

Diagnosis. Characters of subtribe Cicindelina; antennal articles 3 and 4 without two diverging groups of setae; pronotum without dorsoventrally

Fig. 20. Dorsal view of *Cicindela columbica* Hatch (X 11).



compressed margins or produced anterolateral and posterolateral angles; mesepisternum and mesepimeron unmodified.

Determination of the validity of all subgenera of the genus *Cicindela* is beyond the scope of this study. Rivalier (1963) divided the genus *Cicindela auct.* into 55 "genera," further dividing some of these "genera" into "subgenera." Undoubtedly, some of these "taxa" are valid, but, at the same time, some should probably be synonymized. This problem can be solved only by revisions of the over 700 species involved. Until validity of each Rivalier taxon is proven or disproven, I recommend continued use of his names in a subgeneric sense.

Nearctic subgenera. Rivalier (1954) recognized 12 "genera" and "subgenera" of *Cicindela* with species found north of the Mexican border. I am using the subgenus rank for all 12, although some perhaps should fall into synonymy. Only Rivalier (1954), Rumpp (1967, 1977) and Willis (1967) have attempted to determine relationships between these groups. I shall argue against some of Rumpp's conclusions beyond in my accounts of subgenera *Cicindelidia*, *Cylindera* and *Tribonia*.

Since only four subgenera, *Cicindela*, *Cicindelidia*, *Cylindera* and *Tribonia*, are found in the Pacific Northwest, a detailed discussion of interrelationships of the Nearctic subgenera is

inappropriate here because it should involve treatment of all Nearctic subgenera and Palearctic ones as well.

I have concluded, after surveying specimens and descriptions of species from all 12 Nearctic subgenera, that two broad lineages, one further divided into two groups, are represented. My conclusion resembles the phylogeny presented by Willis (1967). My interpretation of the phylogeny of the Nearctic subgenera is presented in Figure 21.

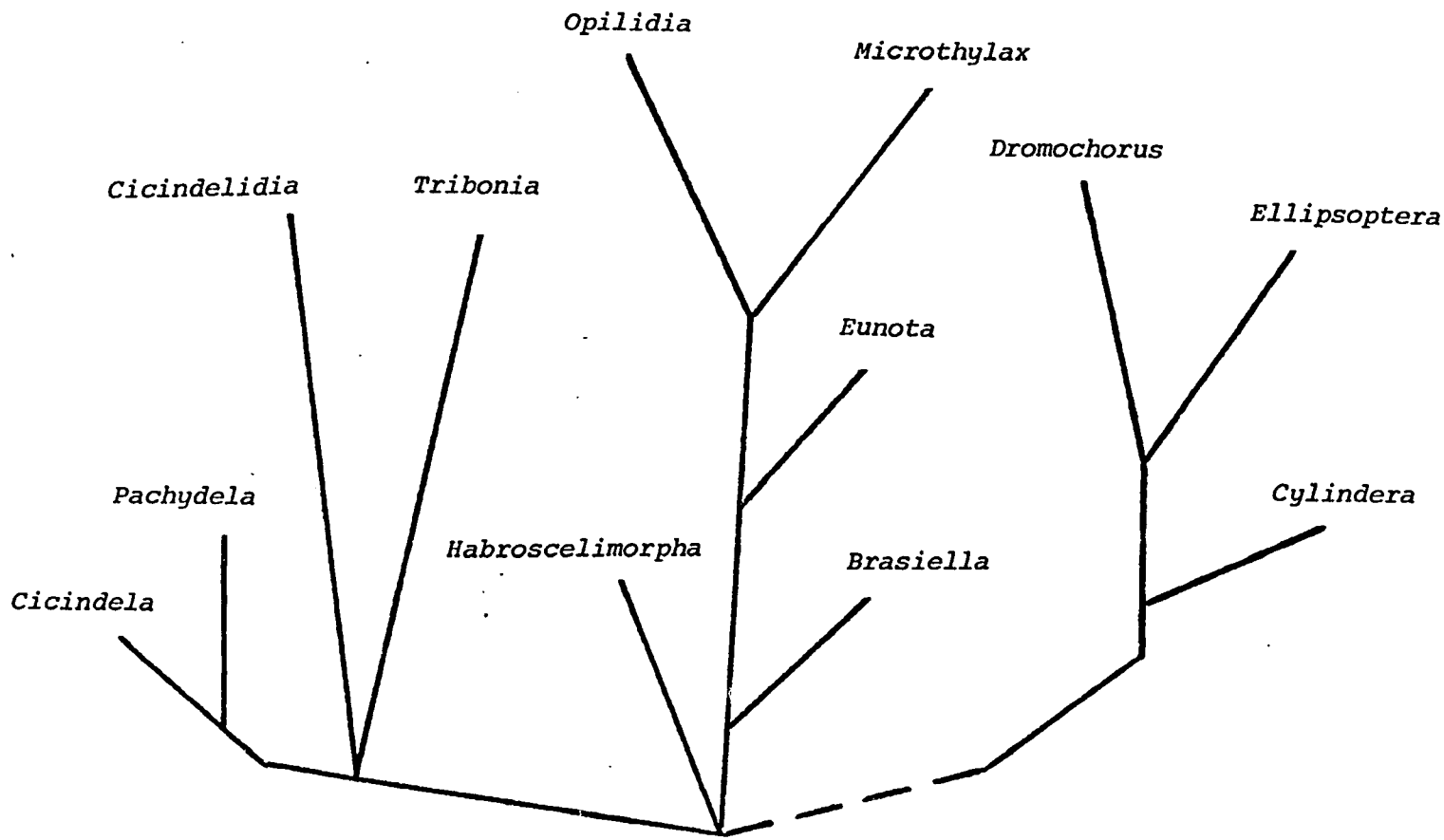
Lineage I. Angle between longitudinal axis of middle lobe of aedeagus and extruded inner sac about 25°.

Group A: Flagellum simple, or, if circumvolutory, not concentric. Included subgenera - *Cicindela*, *Cicindelidia* *Habroscelimorpha*, *Pachydela* and *Tribonia*. *Habroscelimorpha* is intermediate between Groups A and B in having a well-developed flagellum but also fusion of sclerites.

Group B: Tendency toward fusion of inner sac sclerites; flagellum sometimes reduced or even absent. Included subgenera - *Brasiella*, *Eunota*, *Microthylax* and *Opilidia*.

Lineage II. Angle between longitudinal axis of middle lobe of aedeagus and extruded inner sac 10° or less; flagellum with concentric loops. Included subgenera - *Cylindera*, *Dromochorus* and *Ellipsoptera*.

Fig. 21. Suggested phylogeny of Nearctic subenera of *Cicindela*.


Opilidia
Microthylax
Dromochorus
Cicindelidia
Tribonia
Ellipsoptera
Eunota
Pachydela
Cylindera
Habroscelimorpha
Brasiella
Cicindela

Characters of a Hypothetical Ancestral Species of *Cicindela*

Cain and Harrison (1960) outlined a method of reconstructing the characteristics of a hypothetical ancestral form when no fossil record is available. The method consists of surveying living species and choosing the least variable or most commonly occurring expressions of various character-states. This technique has been used by Freitag (1972, 1979) and Willis (1971b) within the genus *Cicindela*.

I. Adult

A. Chaetotaxy

1. antennal scape glabrous except for 3-5 apical sensory setae
2. frons and vertex setose
3. genae at least partly setose
4. clypeus glabrous
5. propleuron, proepisternum and abdominal sternites with abundant erect setae
6. gula, prosternum and mesosternum glabrous
7. apical seta present on pro- and mesotrochanters

B. Color

1. propleuron cupreous
2. elytron dull dark brown, dull, or lightly bronzed
3. venter uniformly metallic green, blue-green, or blue, including all abdominal sternites

4. all setae white

C. Mesepisternal coupling sulcus

1. distinct, thin groove (type N of Freitag, 1974)

D. Maculation

1. humeral lunule complete and evenly C-shaped
2. marginal line contiguous with humeral and apical lunules
3. maculation of average breadth, no tendency toward confluence.

E. Elytron

1. normally sclerotized, not brittle or soft
2. evenly arched in transverse section, not depressed
3. microserrate
4. sutural spine short, not recessed
5. sculpture uniformly shallowly punctate, no punctal confluence, non-granulate or foveate

F. Labrum

1. short (ratio, length/breadth <50%)
2. unidentate
3. glabrous except for 6-10 submarginal setae
4. color whitish to pale yellow in both sexes
5. no sexual dimorphism

G. Male genitalia

1. shaft of middle lobe symmetrical
2. beak present but neither produced nor constricted

3. lateral apical flanges narrow, evenly rounded, not confluent apically
4. dorsal face of apex with short distance between beak and orifice
5. ventral face of apex smooth, unkeeled
6. inner sac confined to apical 40% of middle lobe
7. flagellum short, <50% of length of inner sac
8. sclerite 6 moderate in size, not sclerotized or tooth-like

H. Female genitalia

1. syntergum IX + X ovoid with broadest portion apical
2. sternum VIII with shallow apical emargination; apices glabrous or with only occasional fine setae
3. ventral notch of 2nd gonocoxa present, with setae on proximal and distal lips; lip not raised; short, shallow excavation distal to notch
4. 2nd gonapophysis glabrous

II. Larva

1. U-shaped ridge of head bisetose
2. antennal scape with nine or more setae
3. setae of head and pronotum long and white
4. anterolateral angles of pronotum extended little if at all anterior to anterior level of median portion of pronotum

5. seven primary setae on either half of pronotal disc; no supernumerary secondary setae
6. abdominal hypopleuron consisting of four small setiferous tubercles
7. two setae on shoulder of inner hook of abdominal tergum V

III. Pupa

1. median frontal boss low and simple
2. lateral pronotal margin unthickened
3. setae arranged in random patch on apex of lateral spine of tergum V; no isolated seta on anterior face

Subgenus *Cicindela* Linnaeus, 1758

Cicindela (*Cicindela*) Linnaeus. Rivalier, E., 1950, Rév. Française d'Ent., 17:223-224.

Diagnosis. Adult: Characters of genus *Cicindela*; eyes not greatly enlarged; proepisternum setose. Aedeagus: angle between longitudinal axis of middle lobe and extruded inner sac about 25°; flagellum less than entire length of inner sac, often <50%, at most gently sinuate; no fusion of inner sac sclerites. Pupa:

Fig. 22. Elytral macular patterns of Pacific Northwest Cicindelidae.

A. *C. o. oregona*

B. *C. d. depressula*

C. *C. r. repanda*

D. *C. hirticollis* ssp. A

E. *C. h.* ssp. B

F. *C. a. arenicola*

G. *C. a.* n. ssp. Clifford

H. *C. columbica*

I. *C. b. bellissima*

J. *C. b.* n. ssp. Leffler

K. *C. decemnotata* n. ssp. Clifford

L. *C. purpurea auduboni*

M. *C. p.* new name Leffler

N. *C. pugetana*

O. *C. plutonica*

P. *C. tenuicincta*

Q. *C. lengi versuta*

R. *C. tranquebarica vibex*

S. *C. t. "kirbyi" x vibex*

T. *C. willistoni echo*

U. *C. amargosae nyensis*

V. *C. haemorrhagica nigroides*

W. *C. cinctipennis imperfecta*

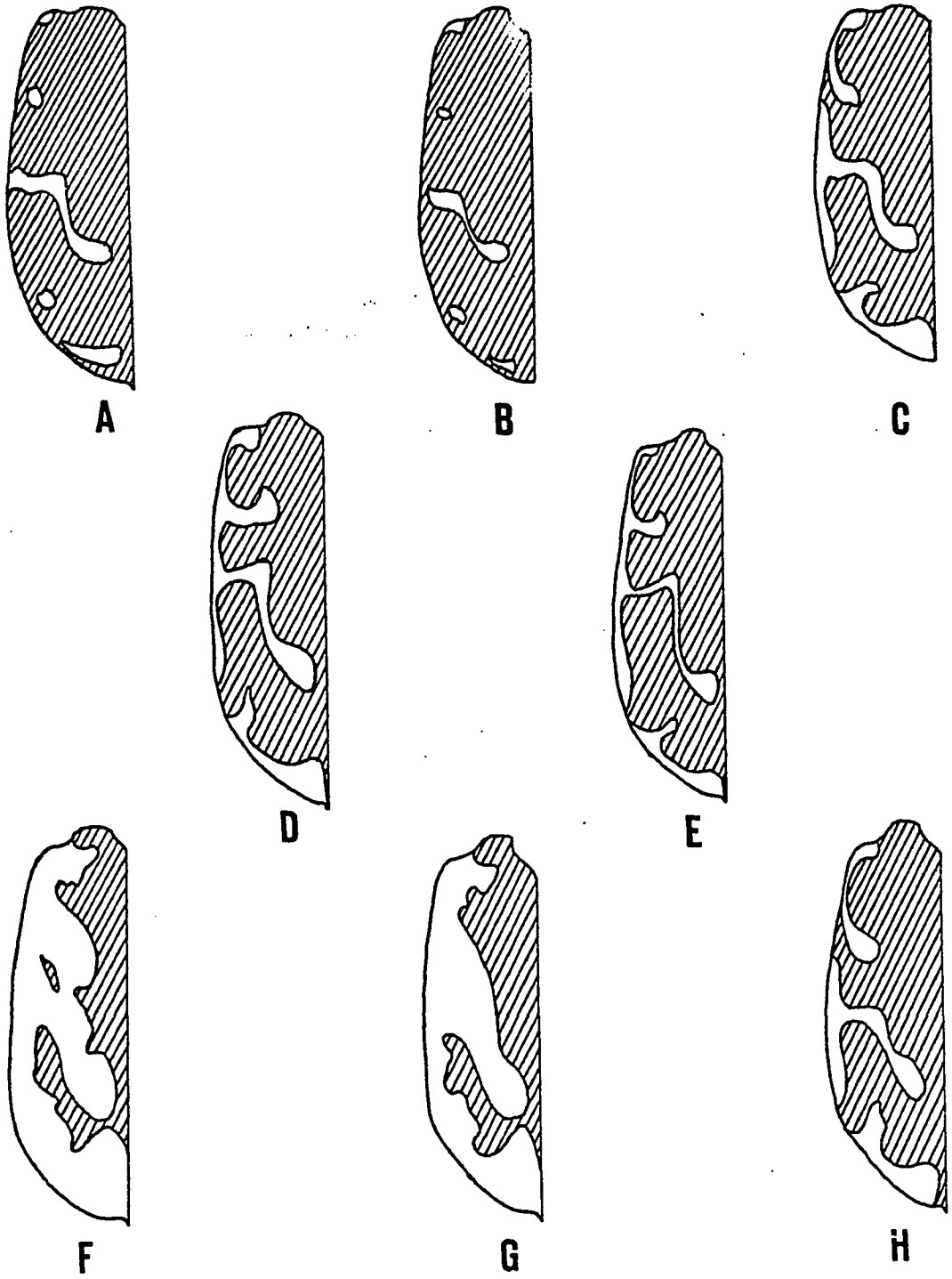

A
B
C
D
E
F
G
H

Figure 22 (continued)

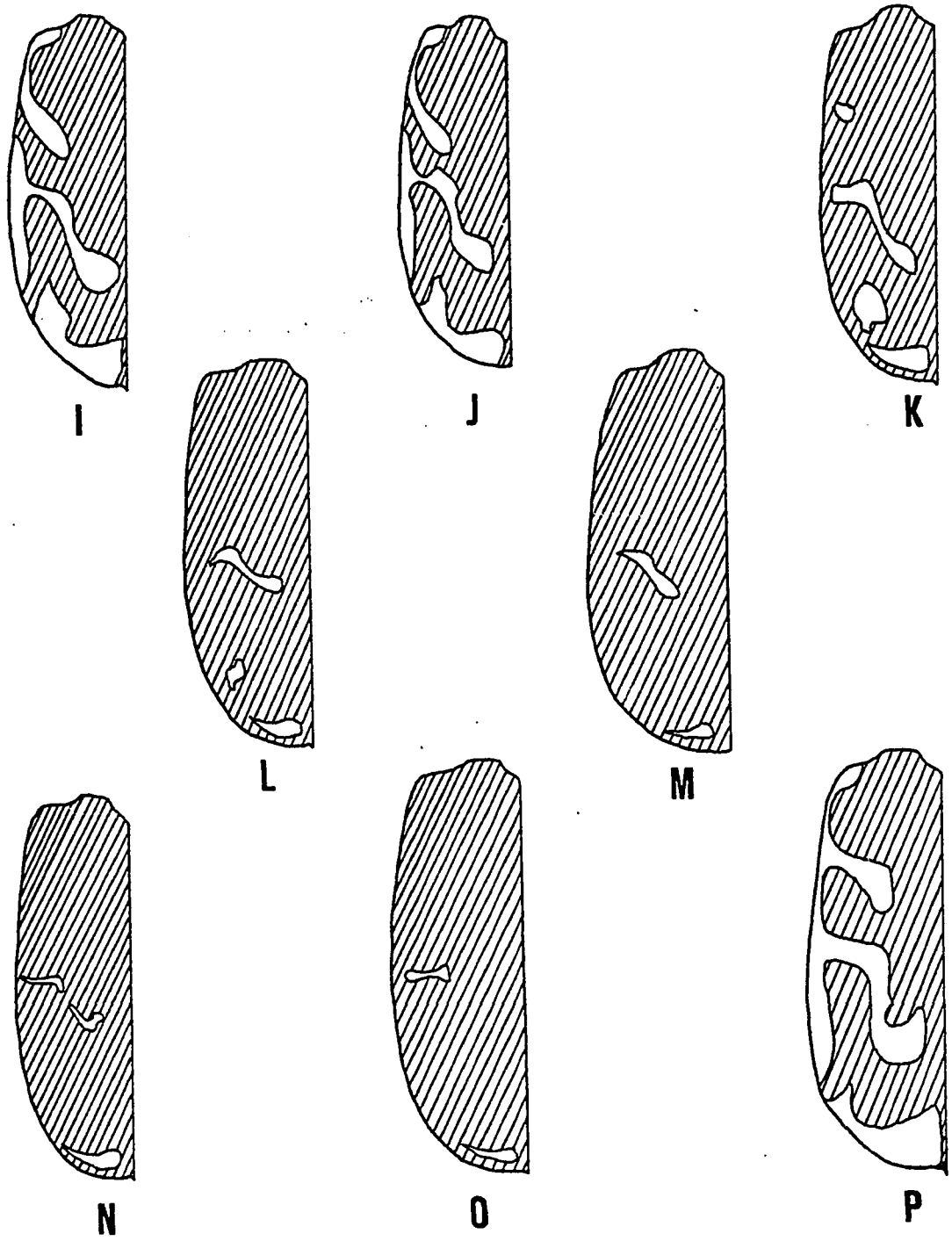


Figure 22 (continued)

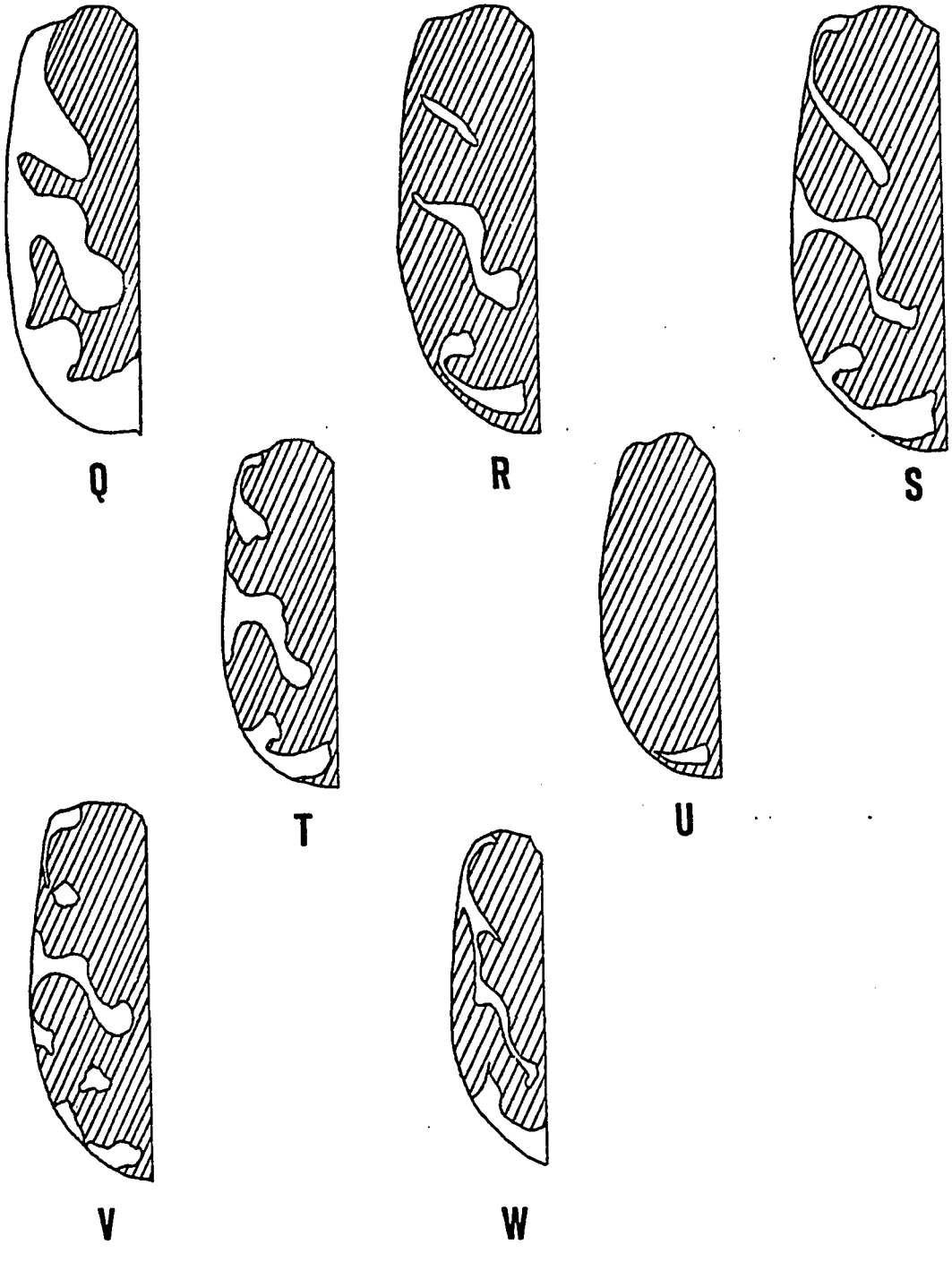


Fig. 23. Labra of *Cicindela* ssp. X 25.

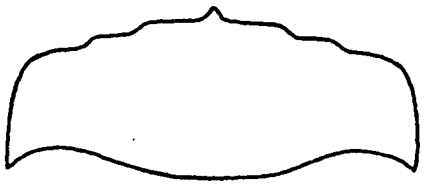
A. Unidentate: *C. oregona*

B. Tridentate: *C. purpurea*

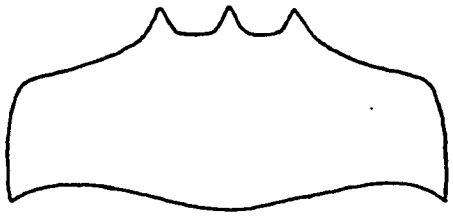
C. Long: *C. longilabris*

D. Long, tridentate: *C. parowana*

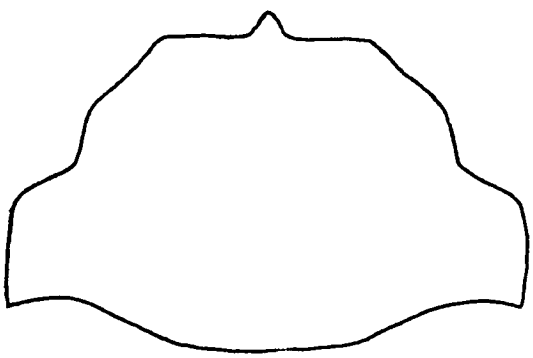
E. Unidentate: *C. tenuicincta*



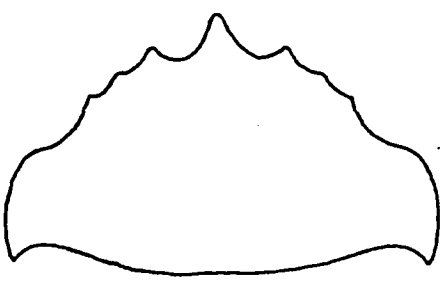
A



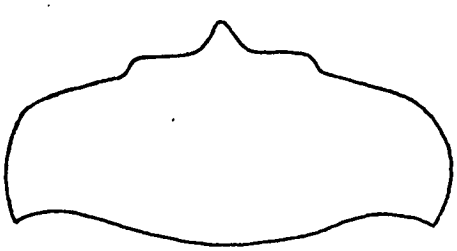
B



C



D



E

Table 12. Comparison of species-groups of subgenus *Cicindela* as adapted in part from Rivalier (1950, 1954, 1957).

Character	Group *maritima*	*formosa*	*hybrida*	*campestris*	*pudibunda*
1. Zoogeographic Region	Nearctic, Palearctic	Nearctic	Palearctic	Palearctic	Ethiopian
2. Flagellum, form and length	slender, >75% of length of inner sac	slender, 50-100% of length of inner sac	small, slender	well-developed, 100% of length of inner sac	slender, 75% of length of inner sac
3. Lateral apical flanges	winglike, well-developed	variable in form, usually present	small, not winglike	long and linear	absent
4. Sclerite 6	not sclerotized	not sclerotized	elongate, well-sclerotized	sclerotized apically	sclerotized apically
5. Special aedeagal features	Nearctic species with middle lobe assymetrical with decided left skew	shaft of middle lobe arcuate, assy-metrical with slight left skew	none	middle lobe arcuate and proportionally elongate	shaft of middle lobe arcuate, beak produced
6. Other notable features	none	labrum tridentate	none	none	none

Table 12 (cont.)

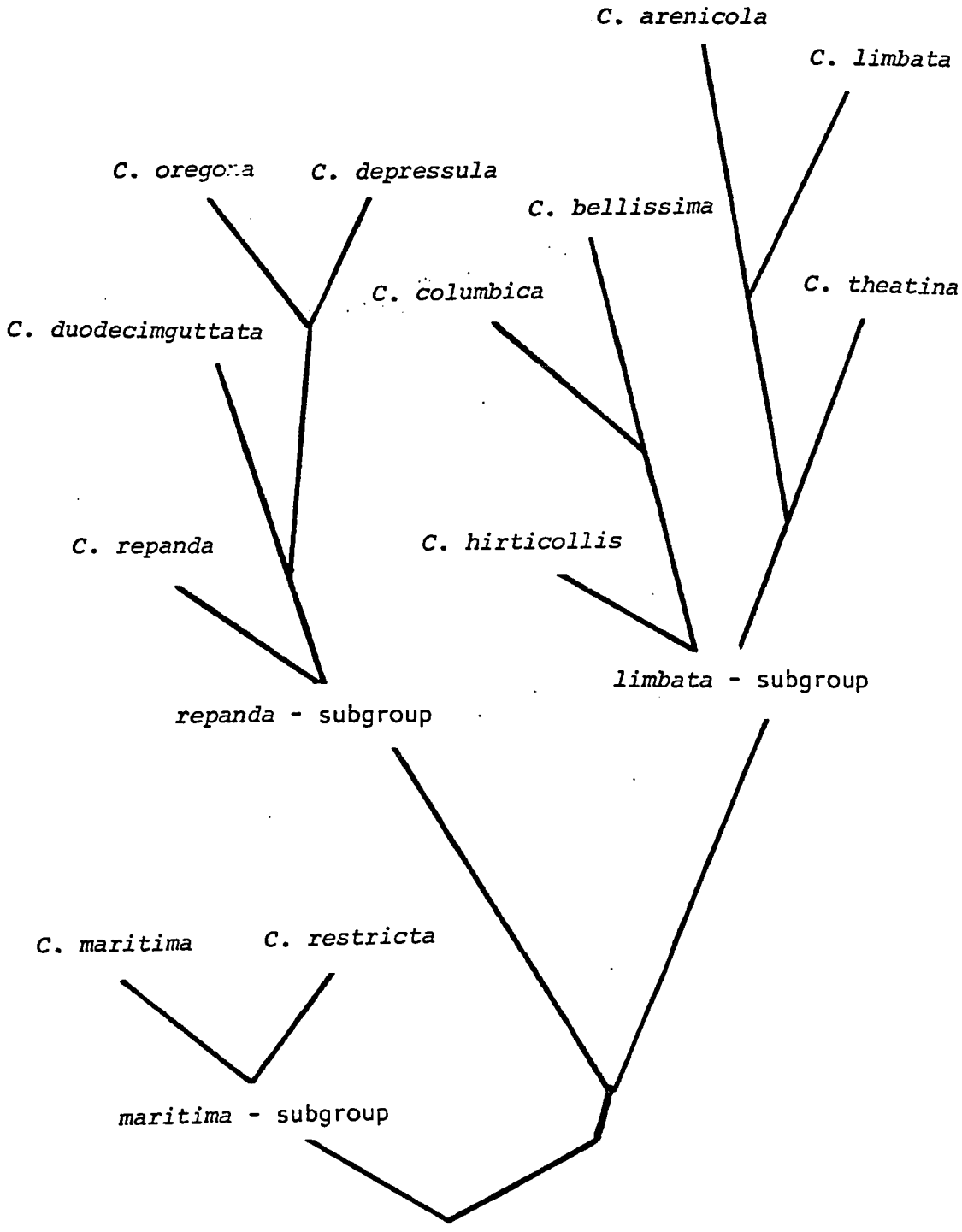
Character	Group *transbaicalica*	*silvatica*	*chinensis*	*pulchra*
1. Zoogeographic Region	Palearctic	Nearctic, Palearctic	Oriental, Palearctic	Nearctic
2. Flagellum, form and length	slender	short, thick, almost unrecognizable	well-developed, 100% of length of inner sac	long, 100% of length of inner sac
3. Lateral apical flanges	absent	small and winglike	long and linear	narrow and winglike or absent
4. Sclerite 6	incompletely sclerotized	well-sclerotized and located on right flank of sac	sclerotized apically	well-sclerotized and located on right flank of sac
5. Special aedeagal features	middle lobe proportionally small	beak with tendency to be produced	voluminous, semi-sclerotized wedge on left flank of sac	none
6. Other notable features	none	labrum long, frons excavated	labrum pentadentate	none

The *maritima*-group

Diagnosis. Adult: labrum short (ratio, length/breadth <50%), unidentate; mesepisternal coupling sulcus Type N; sculpture with shallow, irregularly-arranged punctae, occasionally confluent, non-granulate. Aedeagus: flagellum less than 50% of length of inner sac; sclerite 6 not sclerotized. Female genitalia: no unique external genitalic characters. Larva: seven pairs of primary pronotal setae (may be indistinguishable in species with supernumerary setae); antennal chaetotaxy, 1:9-15 (usually 9-11), 2:7-14 (usually 9-11), 3:2, 4:3; Type I hypopleuron. Pupa: no unique characters.

Rivalier (1950, 1954) united a number of species as his Group IV, with *C. maritima* as its "type." Research by Freitag (1965, 1972), Mandl (1935-1936), and Rumpp (1967) has defined the included species and this group is now the best known taxonomically of any in the genus. However, it is a difficult group to define because its characters are essentially negative; that is, the

Fig. 24. Phylogeny of *maritima* - group of subgenus *Cicindela* based on morphological characteristics.


C. arenicola
C. limbata
C. oregona
C. depressula
C. bellissima
C. columbica
C. theatina
C. duodecimguttata
C. repanda
C. hirticollis
limbata - subgroup
repanda - subgroup
C. maritima
C. restricta
maritima - subgroup

character-states show only plesiomorphic expressions. Some of the species such as *C. duodecimguttata*, *maritima* and *repanda* have most of the characters I presented for a hypothetical ancestral species of *Cicindela*.

Rivalier (1950) based his group IV on the form of sclerite 6 of the aedeagal inner sac. In the *maritima*-group, sclerite 6 is not developed into an elongated tooth and is not chitinized. Only groups III and VII have a similarly poorly developed sclerite 6. In the remaining six species-groups (including the Ethiopian *C. pudibunda* and its allies as an additional species-group [Rivalier, 1958]), sclerite 6 is produced as a strongly-chitinized tooth, or some other aberrant aedeagal feature is developed.

The Palearctic species differ from the Nearctic group in lacking an assymetrical bulge on the left side of the shaft of the middle lobe of the aedeagus. Since such a bulge is not ordinarily, if at all, found in any other species group of *Cicindela*, except group VII, it is certainly an apomorphic character. Since such a peculiar character is common to all 10 Nearctic species, it is most likely that the Nearctic group is monophyletic. My theoretical phylogeny of the *maritima*-group is presented in Figure 24. Relationships with group VII are discussed under "The *formosa*-group."

I divide the *maritima*-group into three species-subgroups which are defined as follows:

maritima-subgroup: Palearctic distribution; shaft of aedeagus symmetrical, lacking bulge on left side. Included species: *C. maritima*, *C. restricta*.

repanda-subgroup: Nearctic distribution; shaft of aedeagus asymmetrical, with bulge on left side; apices of female sternum VIII largely glabrous; larval pronotum lacking supernumerary secondary setae. Included species: *C. depressula*, *C. duodecimguttata*, *C. oregona*, *C. repanda*.

limbata-subgroup: Nearctic distribution; shaft of aedeagus asymmetrical, with bulge on left side; apices of female sternum VIII with fine (*theatina* only) or stout setae (other species); larval pronotum with abundant supernumerary secondary setae (larvae known for three of the six species).

Notes on the *maritima*-subgroup

The Palearctic members of the *maritima*-group were revised by Mandl (1935-1936) who recognized one species, *C. maritima* Dejean, with six subspecies. Rivalier (1950) stated that *C. reitteri* W. Horn, from the Kamchatka Peninsula of Siberia (see Mandl, 1935-1936: Figure X, No. 5), considered a subspecies of *maritima* by Mandl, has an aedeagus identical with that of *maritima* but differs in size and maculation. W. Horn (1897) gave the length of *reitteri* as 13 mm, Csiki (1946:88) stated that *maritima* measures 13-14 mm. Also, only

the complete post-middle band-portion of the marginal line is at all distinctive, compared with subspecies of *maritima* (Mandl, 1935-1936: Figure VI), and is not a character of greater than subspecific value. I follow Mandl in calling the form *C. maritima reitteri*.

Mandl (op. cit.) called the Siberian *C. restricta* Fischer a subspecies of *C. maritima*. Rivalier (1950:Figure 2C) showed that the stouter aedeagus with its proximally truncate, produced lateral apical flanges is distinct from that of *C. maritima* in which the flanges are evenly arcuate.

The larva of *C. maritima* (Hamilton, 1925) has a pronotum with supernumerary setae, as in members of the Nearctic *limbata*-subgroup. *C. maritima* inhabits ocean dunes. As I have stated in my larval section, a setose pronotum is characteristic of larvae of a number of unrelated dune-dwelling species, and I believe that the expression of this character is more-than-likely convergence rather than indication of a particularly close relationship of the *maritima*- and *limbata*-subgroups.

In summary, as I see them, the Palearctic *maritima*-subgroup consists of two species: *C. maritima*, with five subspecies (*finnmarkica*, *kirgisica*, *maritima*, *reitteri* and *spinigera*), and the monotypic *C. restricta*.

Accounts of the Pacific Northwest Species of the *maritima*-group

C. repanda-subgroup

Cicindela (*Cicindela*) *repanda* Dejean, 1825

(Figures 22C and 25)

Cicindela repanda Dejean, 1825. Spécies général des coleóptères, chez Crevot, Paris, 1:74-75.

Cicindela hirticollis Say, *pars*. Gould, A. A., 1834. Boston J. Nat. Hist., 1:49.

Cicindela duodecimguttata repanda Dejean. Horn, W., 1930. Trans. American Ent. Soc., 56:81.

Cicindela (*Cicindela*) *duodecimguttata repanda* Dejean. Rivalier, E., 1954. Rév. Française d'Ent., 21:252.

Cicindela (*Cicindela*) *repanda* Dejean. Freitag, R., 1965. Quaest. Ent., 1:87-170.

Diagnosis. Adult: Characters of *repanda*-subgroup of *maritima*-group of *Cicindela*; antennal scape glabrous except for 3 apical sensory setae; frons thickly setose; genae setose; pronotal length 80% of breadth; pronotum with anterolateral angles rounded and not produced; propleural coloration cupreous; humeral lunule normally complete and evenly

C-shaped; when maculation complete, marginal line complete or connection to humeral and apical lunules only narrowly broken. Aedeagus: lateral apical flanges narrow; beak short, not produced; dorsal notch between beak and orifice not developed; inner sac confined to apical 30% of middle lobe; sclerite 5 of inner sac large, heavily sclerotized. Female genitalia: lateral portion of syntergum IX + X prominent and evenly apically rounded; sternite VIII with apical emargination broad and apices narrowly rounded; ventral notch of 2nd gonocoxa with produced basal margin and almost completely encircles by setae. Larva: pronotum cupreous with green reflections; no supernumerary or special supplemental pronotal setae; spine of inner hook of abdominal tergite V <1/6 of total length of hook; pygopod surrounded by 16-18 setae; Pupa: no diagnostic specific characters.

Synonymic notes. *C. repanda* has always been associated with species to which it is now considered related, except that Casey (1913, 1916) included *C. ancocisconensis* in his *repanda*-group. Gould (1834) synonymized *repanda* with *hirticollis* without stating reasons. W. Horn (1930) treated it as a subspecies of *duodecim-guttata*, also without giving reasons, and was followed by Hatch (1938) and more reticently by Rivalier (1954). Research by Freitag (1965, 1972) has delineated its specific identity.

Relationships. Freitag (1965, 1972) placed *C. repanda* as a slightly isolated member of a group also including *C. depressula*, *duodecimguttata* and *oregona*. The fully setose frons, unbroadened pronotum, complete maculation and unmodified larval pronotal chaetotaxy are plesiomorphic character-states. The enlarged inner sac sclerite 5 and the raised basal margin of the ventral notch of the 2nd gonocoxa are apomorphic.

Subspecies. Currently, three subspecies are recognized, although this might change if a review of the species over its entire extensive range were undertaken. The species shows limited variation and this has been reflected in the small number of proposed subspecific names.

C. r. repanda Dejean. Elytral coloration usually dark brown; maculation usually complete for species and of average breadth; range: most of distribution of species. Details will be presented in the subspecific account.

C.r. novascotiae Vaurie. Elytral coloration bronze-brown to reddish or with green tinge; maculation usually reduced or broken (24% have complete markings); range: restricted to Nova Scotia, Prince Edward Island, Magdalen Islands and Cape Breton Island.

Reduced maculation is rare in *C. r. repanda* but characterizes 76% of Vaurie's (1951) sample. *C. r. novascotiae* also shows a lighter, more bronzy elytral coloration rather than the normally dull, dark chocolate brown of *C. r. repanda*.

C. r. tanneri Knaus. Elytral coloration reddish-brown; maculation complete for species and broad, but with no tendency toward confluence; range: E. and S. UT.

C. r. tanneri was considered by Knaus (1929) to be related to *C. willistoni* which it superficially resembles in maculation. It appears to be restricted to the drainage system of the Green and San Juan Rivers in southeastern Utah and some of the tributaries to the west (Leffler, 1975). I have specimens from western Colorado which may be intergrades with *C. r. repanda*: dark coloration but moderately wide maculation. Casey's (1909) *unijuncta*, from TX. El Paso Co., El Paso, is similar to *tanneri*, although typical *repanda* inhabit the intervening geographic area. Such an occurrence emphasizes the need for analysis of the species *C. repanda* over its entire range to determine if these localized populations are actually worthy of separate taxonomic rank, or if they are merely individual variants. *C. r. tanneri* is distinctive and uniform over its limited

range and should probably be retained. If *C. r. repanda* proves not to be subdivisible, the species will show the commonly-occurring pattern of one widespread and two restricted peripheral subspecies.

C. r. repanda Dejean, 1825

Cicindela repanda Dejean, 1825, Spécies générales Coleop., Paris, 1:74.

Cicindela baltimorensis Le Conte, 1857, Trans. American Phil. Soc., n.s., 11:43.

Cicindela repanda unijuncta Casey, 1897, An. New York Acad. Sci., 9:29.

Cicindela repanda var. *hoosieri* Mares, 1921, Ent. News, 32:310.

Cicindela repanda-unijuncta var. *duncani* Knaus, 1924, J. New York Ent. Soc., 32(3):126.

Cicindela repanda var. *maehleri* Robinson, 1948, An. Ent. Soc. America, 41:27.

Diagnosis. Elytral coloration usually dull, dark chocolate brown, but occasionally green, blue, black or bronzed-brown; maculation usually complete for species and of average breadth.

Synonymic notes. The rare tendency for *C. r. repanda* to have coloration other than dull, dark chocolate brown has led to the creation of five synonyms. Casey (1897) used *unijuncta* for a bronze-colored specimen with broader than average maculation from TX. El Paso Co., El Paso. Mares (1921) and Knaus (1924) named green forms *hoosieri* (type locality: IN. Lake Co., Cedar Lake) and *duncani* (type locality: AZ. Pima Co., Phoenix), respectively. Robinson (1948) used *maehleri* for a dull black morph from TX. Brazos Co. Finally, Le Conte (1857) named *C. baltimorensis* for a form Casey (1913) stated has the posterior oblique arm of the middle band shorter than usual. Only a review of the subspecies over its entire extensive range will show if any of these names deserve recognition.

Typology. Dejean (1825) gave the range as "America septentrionale," western America. When the subspecies is taxonomically reviewed, it would be worthwhile to restrict the type locality. I do not know the present location of a type specimen, if one exists.

Variation. Graves (1969) studied a population from MG. Alger Co., Grand Sable Sand Dunes, in which 73.9% (51 of 69 specimens) have the maculae divided or reduced to spots. Vaurie (1951) found only 27 specimens out of 400 (6.75%) from many localities with partly obliterated markings. None of over 60 specimens from Washington that I have examined have broken markings, although maculae may be occasionally narrow.

I have seen specimens from 11 states and one Canadian province and have seen only two (brownish-black specimens from WA. Clark Co.,

Washougal, Reed Island [OSU]) that were not dull, dark chocolate brown. Apparently, occasional specimens of other colors do occur. I have mentioned some examples in "Synonymic notes." Tenerals tend to have a slightly greener tinge than fully tanned specimens (also mentioned by Shelford, 1918) but two specimens I reared lost the tinge within two days.

Probably availability of food to the larvae affects the size of the adult. Elytral lengths of the extremes of a series of males from WA. Whitman Co., vicinity of Wawawai are 5.2 and 6.2 mm, an 8.4% difference.

Dates of occurrence. 16 March-3 July, 13 August-3 October. Leffler and Pearson (1976:37) discussed larval dates.

Cicindela (*Cicindela*) *oregona* Le Conte, 1857

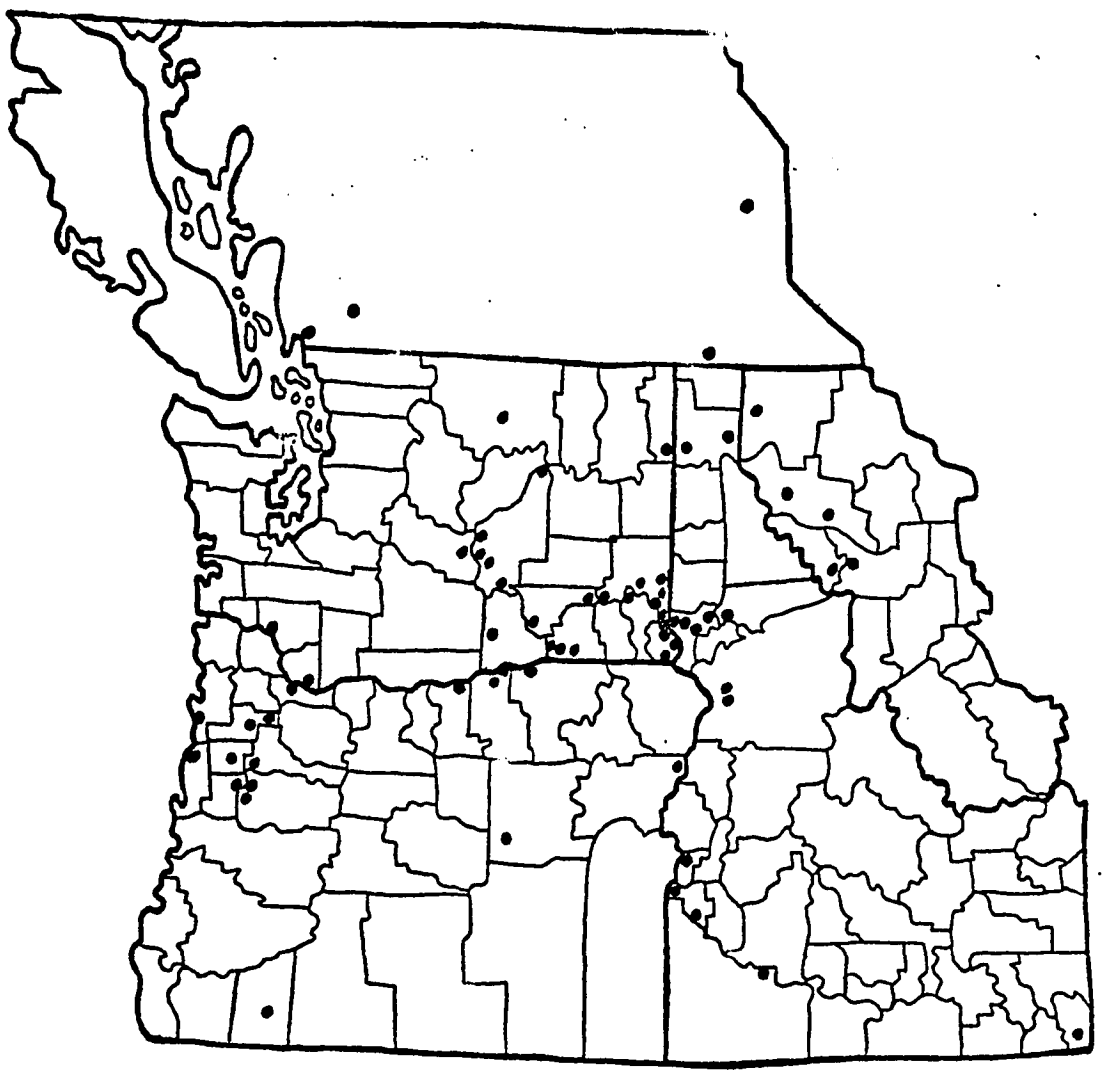
(Figures 22A, 23, 26)

Cicindela oregona Le Conte, 1857. Trans. American Phil. Soc., n.s., 11:41.

Cicindela (*Cicindela*) *oregona* Le Conte. Rivalier, E. 1954. Rév. Française d'Ent., 21:252.

Diagnosis. Adult: characters of *repanda*-subgroup of *maritima*-group of *Cicindela*; antennal scape sparsely setose in addition to 3-4 apical sensory setae; frons glabrous except for

Fig. 25. Pacific Northwest distribution of *Cicindela repanda repanda*. See Appendix I for tabulation of localities.



clusters of 8-11 anterior supraorbital setae; genae glabrous; pronotal length <70% of breadth; pronotum with antero-lateral angles angular and produced; propleural coloration variable according to subspecies; humeral lunule divided into humeral and posterior dots; transverse portion of middle band concave anteriorly; marginal line absent. Aedeagus: lateral apical flanges narrow; beak produced; dorsal notch between beak and orifice long; inner sac confined to apical 40% of middle lobe; sclerite 5 of inner sac of moderate size. Female genitalia: lateral portions of syntergum IX + X not produced, resulting in shortened, circular outline; sternum VIII moderately deep, V-shaped emargination, apices narrowly rounded and glabrous; 2nd gonocoxa with ventral notch defined but without produced basal margin, and with setae confined to proximal and distal portions of notch. Larva: pronotum with strong blue reflections; distinct longitudinal row

or pronotal setae on either side of midline consisting of secondary setae and incorporating primary setae 1, 3, 5 and 7; spine of inner hook of abdominal tergite V 1/3 of total length of hook; pygopod surrounded by 18 setae. Pupa: no diagnostic specific characters.

Synonymic notes. *C. oregona* was revised by Freitag (1965) who presented details of synonymy. Like *C. repanda*, *C. oregona* has always been associated with species to which it is now considered related and has never included extraneous species.

Relationships. Freitag (1965, 1972) considered *C. oregona* to be most closely related to *C. depressula* and *C. duodecimguttata*. He (1965) described a zone of hybridization between *oregona* and *duodecimguttata* in Alberta and Saskatchewan. There is no evidence of hybridization between *oregona* and *depressula*. Table 13 presents a comparison of the three species. The table shows that in five character-states (Nos. 2, 5, 8-10), *oregona* is intermediate and *depressula* strongly modified. I consider *C. duodecimguttata* to be nearest the ancestral form for this complex and *oregona* and *depressula* more closely related than Freitag allowed.

Subspecies. Freitag (1965) revised *C. oregona* and recognized four subspecies. He presented a complete synonymy which also

Table 13. Comparisons of *C. depressula*, *C. duodecimguttata* and *C. oregona*.

Character-state	*C. duodecimguttata*	*C. depressula*	*C. oregona*
1. Hybridization	with *oregona*	none	with *duodecim-guttata*
2. Frons	strongly setose	2-4 anterior supraorbital setae	cluster of 8-11 anterior supraorbital setae
3. Genae	setae	glabrous	glabrous
4. Propleural coloration	cupreous	cupreous	variable depending on subspecies
5. Aedeagal beak	produced and with marked ventral curve	short and rounded	produced but without ventral curve
6. Aedeagal lateral apical flanges	moderately broad, not confluent apically	very broad, confluent apically	narrow, not confluent apically
7. Shape of syntergum IX+ X of female	lateral portions tapered medially and narrowed basally	rectangular	circular
8. Apical emargination of sternum VIII of female	deep, narrow	moderate, wide	moderate, narrow
9. Apices of sternum VIII of female	sharp, pointed	narrowly rounded	not sharp, narrow
10. Ventral notch of 2nd gonocoxa of female	open, shallow	deep, strong basal lip	moderate, weak basal lip
11. Dorsolateral curve of lateral face of 2nd gonapophysis of female	strong	not strongly curved	not strongly curved
12. Submedian longitudinal row of setae on larval pronotum	not developed	distinct	distinct

involves names proposed for intergrade populations. The four subspecies are characterized as follows:

C. o. guttifera Le Conte, 1857. Propleural coloration cupreous; pronotal and elytral coloration dark brown with metallic lustre; elytral maculation narrow.

C. o. maricopa Leng, 1902. Propleural coloration violet; pronotal coloration brown to metallic green; elytral coloration violet; elytral maculation broad.

C. o. navajoensis Van Dyke, 1947. Propleural coloration cupreous; pronotal and elytral coloration light brown; elytral maculation broad.

C. o. oregona Le Conte, 1857. Propleural coloration blue, green, or violet; pronotal and elytral coloration green, blue, dark brown or black; elytral maculation narrow.

C. o. oregona Le Conte, 1857

Cicindela oregona Le Conte, 1857. Trans. American Phil. Soc., n.s., 11:41.

Cicindela guttifera Le Conte, *pars*. Fall, H. C., 1901, Ent. News, 12:308

Cicindela depressula scapularis Casey, 1909. Canadian Ent., 41:272.

Cicindela guttifera sonoma Casey, 1913. Mem. Coleop., 4:29.

Cicindela quadripennis Casey, 1913. Mem. Coleop., 4:30.

Cicindela ovalipennis Casey, 1913. Mem. Coleop., 4:30

Cicindela oregona scapularis Casey. W. Horn, 1915, Gen. Insect., 82C:378.

Diagnosis. Propleural coloration blue, green or violet; elytral coloration green, blue, dark brown, or black.

Synonymic notes. The variability in this subspecies misled Casey (1909, 1913) into creating four names now considered as synonyms of *C. o. oregona*. Casey (1909:272) proposed *scapularis* as a subspecies of *C. depressula* from CA. (no further locality data), but it is only the randomly occurring dark green morph of *C. o. oregona*. *C. guttifera sonomae* was compared by Casey (1913:29) only with *C. o. guttifera* and not *C. o. oregona* of which it is a typical example of the brown morph. *C. quadripennis* and *ovalipennis* are, respectively, male and female specimens named by Casey (1913:30) and are indistinguishable from black morph *C. o. oregona*.

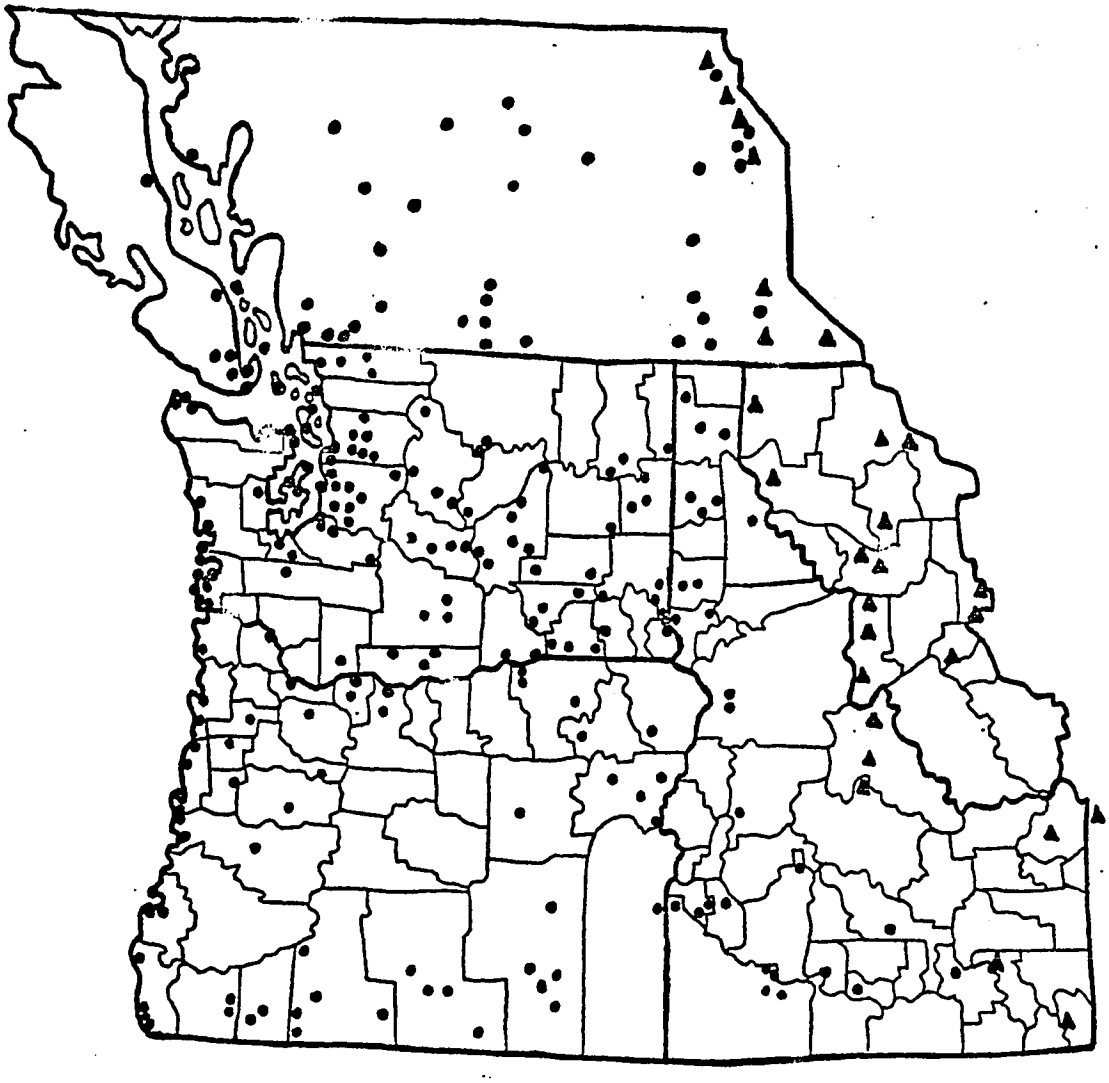
Typology. The type locality of *C. o. oregona* is "Oregon Territory and northern California as far as San Francisco (Le Conte, 1857:41)." I do not know if the holotype is still extant. Holotypes of the four synonyms are all in the Casey Collection, National Museum of Natural History, and have been examined by me.

Variation. This was analyzed statistically by Freitag (1965).

Fig. 26. Pacific Northwest Distribution of *Cicindela oregona*. See Appendix I for tabulation of localities.

Symbols:

● - *C. o. oregona*
▲ - *C. o. oregona* x *guttifera*



Dates of occurrence. I have dates from 8 March-15 October, although the species is most abundant from late April through June and August to early September. I have collected teneral adults in early August. Both LL2 and LL3 were collected in mid-April, suggesting that the species overwinters as LL2 or young LL3.

Intergrades. Freitag (1965) delineated a broad zone of intergradation between *C. o. oregona* and *C. o. guttifera*. Included in this zone are localities in southeastern Idaho and western Montana, enumerated in Appendix I and mapped in Figure 26. These populations contain individuals with cupreous or blue propleura, as well as some with green or even dorsally cupreous and ventrally blue or green propleura. In Freitag's Figure 19, samples I, J, K and O are intergrade populations and are represented graphically.

Cicindela (*Cicindela*) *depressula* Casey, 1897

(Figures 22B, 27)

Cicindela depressula Casey, 1897. An. New York Acad. Sci., 9:297.

Cicindela (*Cicindela*) *depressula* Casey. Rivalier, E., 1954. Rév. Française d'Ent., 21:253.

Diagnosis. Adult: characters of *repanda*-subgroup of *maritima*-group of *Cicindela*; antennal scape sparsely setose in addition to 3-4 apical sensory setae; frons glabrous except for

clusters of 2-4 anterior supraorbital setae; genae glabrous; pronotal length <70% of breadth; pronotum with anterolateral angles angulate and produced; propleural coloration cupreous; humeral lunule divided into humeral and posterior dots; transverse portion of middle band with anterior edge straight; marginal line absent. Aedeagus: lateral margins broad and confluent across beak; beak not developed; dorsal notch between beak and orifice short; inner sac confined to apical 40% of middle lobe; sclerite 5 of inner sac of moderate size. Female genitalia: syntergum IX + X rectangular in outline; sternum VIII with shallow, broadly V-shaped emargination, apices narrowly rounded and glabrous; 2nd gonocoxa with ventral notch defined, with produced basal margin, and with setae confined to proximal and distal portions of notch. Larva: pronotum with strong green reflections; distinct longitudinal row of pronotal

setae on either side of midline consisting of secondary setae and incorporating primary setae 1, 3, 5 and 7; spine of inner hook of abdominal tergite V 1/3 of total length of hook; pygopod surrounded by 20 setae. Pupa: no diagnostic specific characters.

Synonymic notes. *C. depressula* was revised by Freitag (1965) who also presented details of synonymy. Like *C. repanda* and *oregona*, *depressula* has always been associated with species to which it is now considered related and has never included extraneous species. Until Freitag's revision, *C. d. eureka* was usually given full specific rank.

Relationships. I have treated these under *C. oregona*.

Subspecies. Freitag (1965) revised *C. depressula*, recognizing two subspecies. As both are found in the Pacific Northwest, I shall treat them in their respective subspecies accounts.

C. d. depressula Casey, 1897

Cicindela depressula Casey, 1897. Ann. New York Acad. Sci., 9:297.

Cicindela oregona depressula Casey. Horn, W., 1930. Trans. American Ent. Soc., 56:82.

Diagnosis. Trend to smaller size and green or blue elytral coloration.

Synonymic notes. There are no synonyms.

Typology. The holotype, a male, No. 45987, is preserved in the Casey Collection, National Museum of Natural History. It was collected CA. Placer Co. Holotype examined.

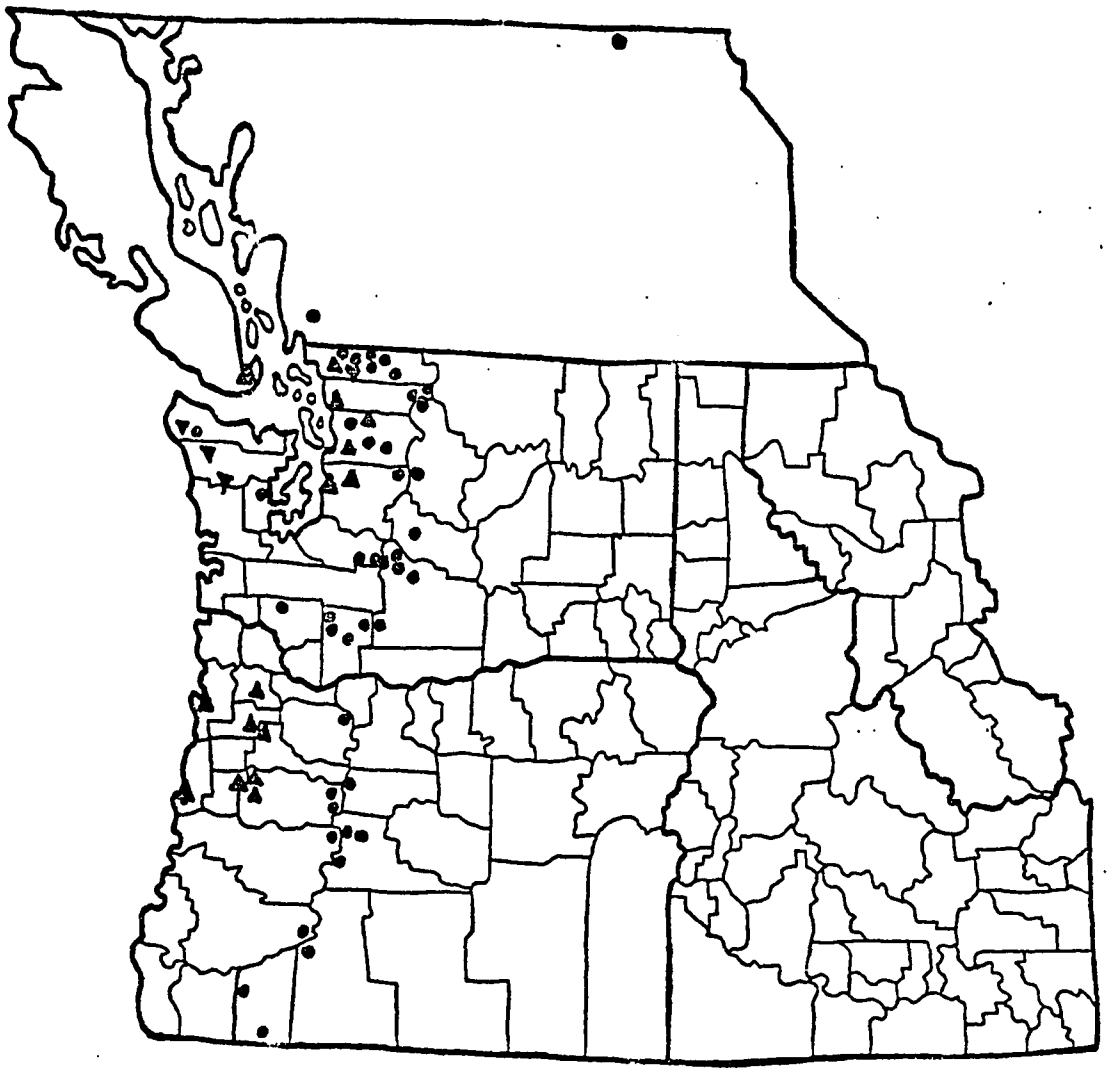
Variation. Freitag (1965) treated variation in this subspecies in detail. It shows north to south clinal variation in size, percentage of individuals with brown rather than blue or green elytra, and breadth of maculation. Alaskan specimens are largest, mainly brown, and have maculation complete for the species. They average smaller than but are otherwise indistinguishable from *C. d. eureka*. Specimens from the Washington and northern Oregon Cascades are variable in all characters but tend to be green or blue with complete maculation. Southern Oregon Cascades and Sierran populations are mainly green and with reduced markings. Freitag (1965) suggested that *C. d. depressula* as we know it today represents an amalgamation of a brown, maculate northern stock and a green southern stock with reduced maculation. The extreme variability of the Washington and northern Oregon population represents the zone of intergradation between the parental stocks.

Dates of occurrence. Snowfall and melting regulate the activity period of this subspecies, restricting it to the summer. Washington dates are 1 May-5 October. Freitag (1965) remarked about the difference in activity periods of *C. d. depressula* and *eureka*.

Fig. 27. Pacific Northwest distribution of *Cicindela depressula*. See Appendix I for tabulation of localities.

Symbols:

● - *C. d. depressula*
▲ - *C. d. eureka*
▼ - *C. d. depressula* x *eureka*



I have collected LL1 and LL3 on 28 August, 1974, suggesting that larvae overwinter as LL1 or LL2 and LL3 and that more than one year is required for the larval stage.

Intergrades. See account of *C. d. eureka*.

C. d. eureka Fall, 1901

Cicindela eureka Fall, 1901. Ent. News, 12:307-308.

Cicindela depressula eureka Fall. Freitag, R., 1965. Quaest. Ent., 1:138.

Diagnosis. Trend to larger size and nearly uniform in dark brown elytral coloration and maculation complete for species.

Synonymic notes. Fall (1901) described *eureka* as a distinct species. Freitag (1965) presented evidence as to why it should be considered a subspecies of *C. depressula*.

Typology. I do not know the present location of the holotype. Fall (1901) gave the type locality only as CA. Humboldt Co.

Variation. This subspecies is uniform in its characteristics. Freitag (1965) and Freitag and Pearson (1973) treated variation at length. The limited variability suggests a geologically old and stable form.

Dates of occurrence. Dates known to me are 4 April-21 July. This shows a seasonal difference between *C. d. eureka* and *C. d. depressula*. The dates of intergrade populations in Washington overlap those of the parent subspecies: 4 April-2 July.

Intergrades. These have been reported on by Freitag and Pearson (1973). Additional records are presented in Appendix I and Figure 27.

C. limbata-subgroup

Cicindela (*Cicindela*) *hirticollis* Say

(Figure 22D and E, 28)

Cicindela hirticollis Say, 1817. J. Acad. Nat. Sci. Philadelphia, 1:20.

Cicindela (*Cicindela*) *hirticollis* Say. Rivalier, E. 1954. Rév. Française d'Ent., 21:252.

Diagnosis. Adult: characters of *limbata*-subgroup of *maritima*-group of *Cicindela*; antennal scape with 2 setae in addition to 4 apical sensory setae; frons thickly setose; genae glabrous; propleura cupreous; posterior tip of humeral lunule oriented transversely and with slight anteriorly-directed

hook; marginal band usually complete. Aedeagus: median lobe with lateral apical flanges narrow, not contiguous at beak, and not constricted basally; beak small; dorsal notch between beak and orifice obliterated by apical extension of inner sac; inner sac with field 6 not bulged and sclerite 5 large. Female genitalia: syntergum IX + X rectangular; apices of sternite VIII with 2-3 stout setae; elongate, shallow ventral notch of 2nd gonocoxa with sparse setae. Larva: head and pronotum with supernumerary flattened, squared-ended setae; pygopod surrounded by 16 setae. Pupa: unknown.

Synonymic notes. *C. hirticollis* has usually been associated with the species with which it is now associated. It is currently under study by R. C. Graves whose study should summarize all synonymic information.

Relationships. This species was considered to be an isolated member of the *maritima*-group by Freitag (1965), but he later (1972) placed it as an aberrant relative of the *limbata*-subgroup. The strongly setose frons and large inner sac sclerite 5 are

plesiomorphic characters, but maculation, the rectangular shape of the female syntergum IX + X, and the flattened, squared-ended form of the larval head and pronotal supernumerary setae are decidedly aberrant. I agree with Freitag (1972) that *C. hirticollis* is a primitive but aberrant member of the *limbata*-subgroup.

Subspecies. Delineation of subspecies of *C. hirticollis* must await Graves' revision. Two are found in the Pacific Northwest. Leffler and Pearson (1976) referred to these as ssp. A and ssp. B for convenience. Ssp. A is the larger, dark brown inland form with broader maculation and a complete marginal band. Ssp. B is a smaller, dull greenish coastal form with narrow, often broken maculation, and an interrupted marginal band. Ssp. B was called *C. h. gravida* by Hatch (1953), but that subspecies has maculation complete for the species and an allopatric geographical range about 1400 km to the south.

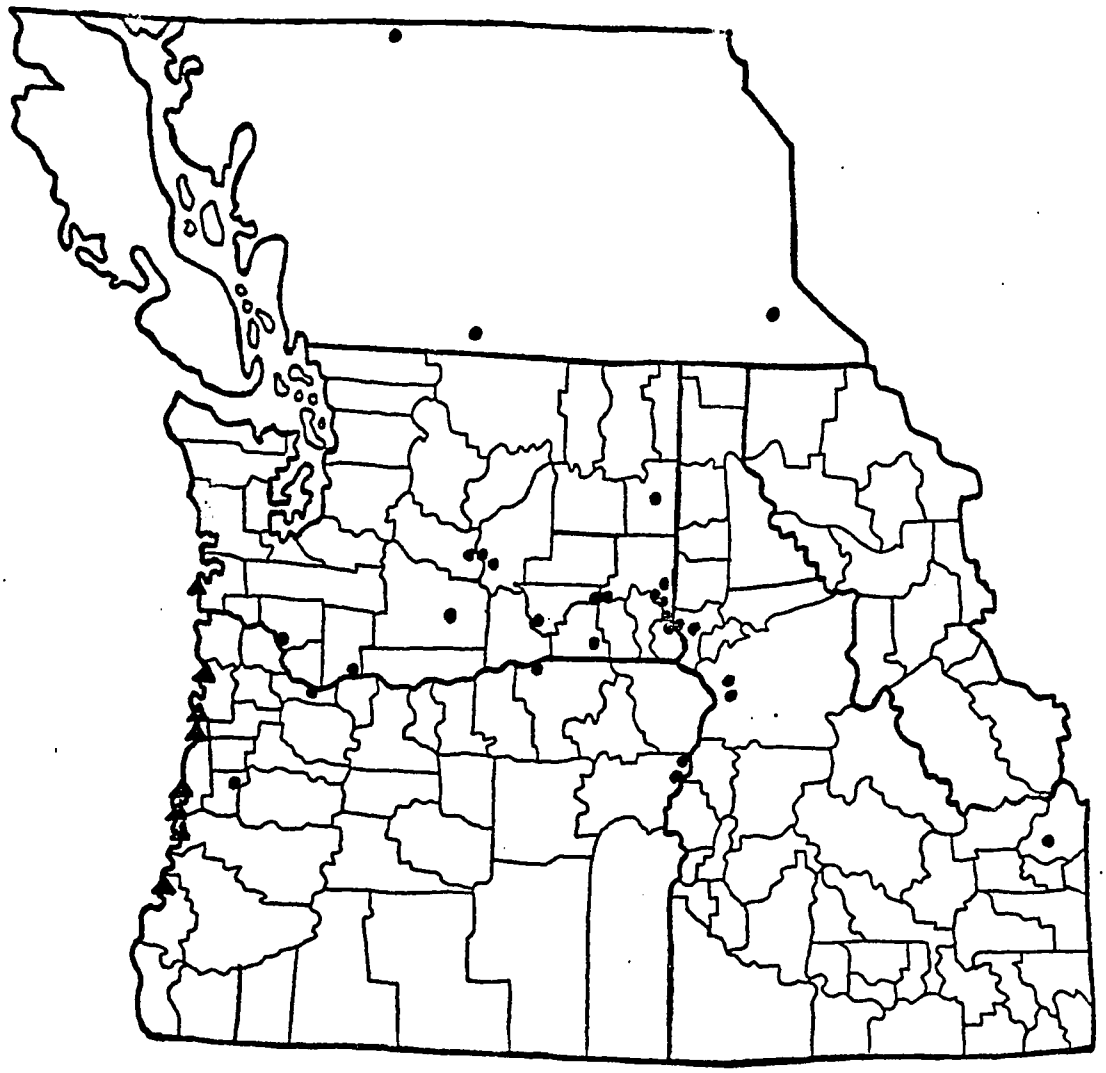
Variation. Shelford (1918) stated that *C. hirticollis* shows little variation and was largely unaffected by his temperature and humidity experiments, probable signs of a geologically old and stable species. The two subspecies in the Pacific Northwest are almost invariate. A population from WA. Cowlitz Co., Kalama is intermediate in color between the two subspecies but has the complete maculation of the inland form.

Dates of occurrence. Leffler and Pearson (1976) gave dates of occurrence for ssp. A as 10 April-26 June and 1 August-5 September. Dates for ssp. B, mainly from Oregon, are 2 April

Fig. 28. Pacific Northwest distribution of *Cicindela hirticollis*. See Appendix I for tabulation of localities.

Symbols:

● - *C. h.* ssp. A
▲ - *C. h.* ssp. B



to 12 September. A 2nd-instar larva was collected 5 September, 1972, and moulted in captivity shortly therafter. I have seen 3rd-instar larval burrows 12 May, 1974. These observations suggest that larvae overwinter as 2nd or young 3rd instar.

Cicindela (*Cicindela*) *bellissima* Leng, 1902

(Figures 22 I and J, 30)

Cicindela bellissima Leng, 1902. Trans. American Ent. Soc., 28: 142-143.

Cicindela (*Cicindela*) *bellissima* Leng. Rivalier, E. 1954. Rév. Française d'Ent., 21:253.

Diagnosis. Adult: characters of *limbata*-subgroup of *maritima*-group of *Cicindela*; antennal scape with 0-2 setae in addition to 4-5 apical sensory setae; frons sparsely setose; genae glabrous; propleura cupreous; humeral lunule obliquely elongate and apex only narrowly separated from middle band; elongate marginal extensions of middle band not connected to humeral or apical lunule. Aedeagus: median lobe with lateral apical flanges moderately broad,

not contiguous at beak, and only slightly constricted basally; ventral surface of apex without midline keel; beak produced; dorsal notch between beak and orifice short and shallow; inner sac with field b moderately bulged and sclerite 5 absent. Female genitalia: syntergum IX + X short, not reaching bases of gonapophyses; apices of sternite VIII with 4-5 stout setae; elongate, shallow, glabrous excavation distal to notch of 2nd gonocoxa. Larva: setae of head and pronotum short, terete, and pointed, and supernumerary; pygopod surrounded by 20-24 setae. Pupa: unknown.

Synonymic notes. Hatch (1938) originally described *C. columbica* as a subspecies of *C. bellissima* but later (1949) raised it to full specific rank. *C. bellissima* has not, with that exception, ever included or been included in any other species.

Relationships. Previous references of this species to the *tranquebarica*-group by Casey (1913, 1916) are without merit in view of researches by Freitag (1965, 1972) Rivalier (1954) and Rumpp (1967). Freitag and Rumpp have shown the closest relative to be *C. columbica*. They agree in having a moderately bulged field b of the inner sac, broad lateral apical flanges of the aedeagus that are

slightly constricted basally, lacking a ventral midline aedeagal keel, and the elongate, shallow, glabrous excavation distal to the ventral notch of the second gonapophysis, in addition to the characters common to the *limbata*-subgroup.

The two species show different combinations of plesiomorphic and apomorphic characters so that neither can actually be considered more generalized than the other. Table 14 compares the two species as to this mosaic of traits. The result of enumeration of 10 traits is that each species has five plesiomorphic and five apomorphic character-expressions. A common ancestor probably inhabited the lower Columbia River Valley and its mouth and the stocks were separated during the late uplife of the Cascade Range and have diverged since that time.

Subspecies. Subspecies had not been recognized in *C. bellissima* until I statistically analyzed measurements of a large series, finding that the Clallam County, Washington, population was proportionally smaller and had statistically narrower humeral lunules than southern populations. I (Leffler, in press) have described this northern population as a new subspecies, here referred to as *C. b.* n. ssp. Leffler, as opposed to *C. b. bellissima* Leng. As both are restricted to the Pacific Northwest, detailed discussions are presented in the subspecies accounts.

Table 14. Enumeration of plesiomorphic and apomorphic character-states in *Cicindela bellissima* and *C. columbica*. P = plesiomorphic, A = apomorphic.

Item Character	Plesiomorphic-state	Apomorphic-state	*C. bellissima*	*C. columbica*
1. Habitat	riparian	otherwise	A	P
2. Frontal setae	generally distributed anterior, between and posterior to eyes; density unimportant	very sparse, restricted, or absent	P	A
3. Propleural coloration	completely cupreous	not completely cupreous or color otherwise	P	A
4. Elytral coloration	dark brown	otherwise	A	P
5. Humeral lunule	C-shaped; posterior end distant from middle band	obliquely elongate; posteriorly proximate to middle band	A	P
6. Aedeagal beak	not produced	produced and laterally excavated	A	P
7. Dorsal aedeagal notch between beak and orifice	short	long	P	A
8. Aedeagal apical lateral flanges	narrower, not contiguous across beak	broader, contiguous in beak area	P	A
9. Inner sac sclerite 5	present, may be small	absent	A	P
10. Setae on apices of female sternite VIII	several	two	P	A
			ΣP=5 ΣA=5	ΣP=5 ΣA=5

Table 15. Pooled within groups covariance matrix for both subspecies of *Cicindela bellissima*.

A. Males

B. Females

	C1	C2	C3	C4	C5	C6	C7
C1	.15125						
C2	.04304	.03882					
C3	.05635	.02005	.03769				
C4	.01365	.00396	.00463	.00382			
C5	.03291	.01295	.01302	.00478	.01566		
C6	.00664	.00492	.00027	-.00011	.00205	.00880	
C7	.01441	.00670	.00336	.00137	.00568	-.00126	.01509

A

	C1	C2	C3	C4	C5	C6	C7
C1	.16674						
C2	.04722	.04007					
C3	.06203	.02156	.03987				
C4	.01764	.00545	.00979	.00753			
C5	.03872	.01204	.01762	.00796	.01800		
C6	.01260	.00533	.00365	.00111	.00361	.00737	
C7	.01638	.00926	.00830	.00409	.00806	-.00026	.02086

B

Table 16. Statistical information from discirminant analysis of males of subspecies of *Cicindela bellissima*. See Leffler (in press) for explanation of characters represented by C 1-7.

Group 1 = *C. b.* new ssp. Leffler;

Group 2 = *C. b. bellissima*.

STEP NUMBER	VARIABLE ENTERED	VARIABLE REMOVED	F TO ENTER OR REMOVE
1	C6		28.31671
2	C4		9.07494
3	C2		2.43975
4	C3		2.11442
5	C7		.14267
6	C1		.15235
7	C5		.12213

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	-.16427
C2	-.55154
C3	.44649
C4	-.61959
C5	.09529
C6	-.86159
C7	-.10595

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	-.407907
C2	-2.44315
C3	3.57577
C4	-8.11269
C5	.820315
C6	-6.93989
C7	-.731904
CONSTANT	7.33077

CENTROIDS OF GROUPS IN REDUCED SPACE

	1
GROUP 1	-.60758
GROUP 2	1.46534

PREDICTION RESULTS -

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2
GROUP 1	1	41	40. 97.6 PCT	1. 2.4 PCT
GROUP 2	2	17	5. 29.4 PCT	12. 70.6 PCT

89.7 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

Table 17. Statistical information from discriminant analysis of females of subspecies of *Cicindela bellissima*. See Leffler (in press) for explanation of characters represented by C 1-7.

Group 1 = *C. b.* new ssp. Leffler;

Group 2 = *C. b. bellissima*.

STEP NUMBER	VARIABLE ENTERED	VARIABLE REMOVED	F TO ENTER OR REMOVE
1	C6		50.25424
2	C5		2.96668
3	C1		2.14100
4	C7		.42075
5	C4		.38846
6	C2		.23710
7	C3		.09524

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	.53682
C2	-.11171
C3	-.10891
C4	-.15890
C5	-.61337
C6	-1.15091
C7	.16420

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	1.24948
C2	-.525301
C3	-.517676
C4	-1.68316
C5	-3.90666
C6	-9.65220
C7	1.14761
CONSTANT	7.96515

CENTROIDS OF GROUPS IN REDUCED SPACE

	1
GROUP 1	-.79924
GROUP 2	1.47229

PREDICTION RESULTS -

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2
GROUP 1	1	35	32. 91.4 PCT	3. 8.6 PCT
GROUP 2	2	19	2. 10.5 PCT	17. 89.5 PCT

90.7 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

Table 18. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) for males of *Cicindela bellissima* n. ssp. Leffler (1) and *C. b. bellissima* (2). * shows a group centroid. The table shows nearly complete separability of the two subspecies.

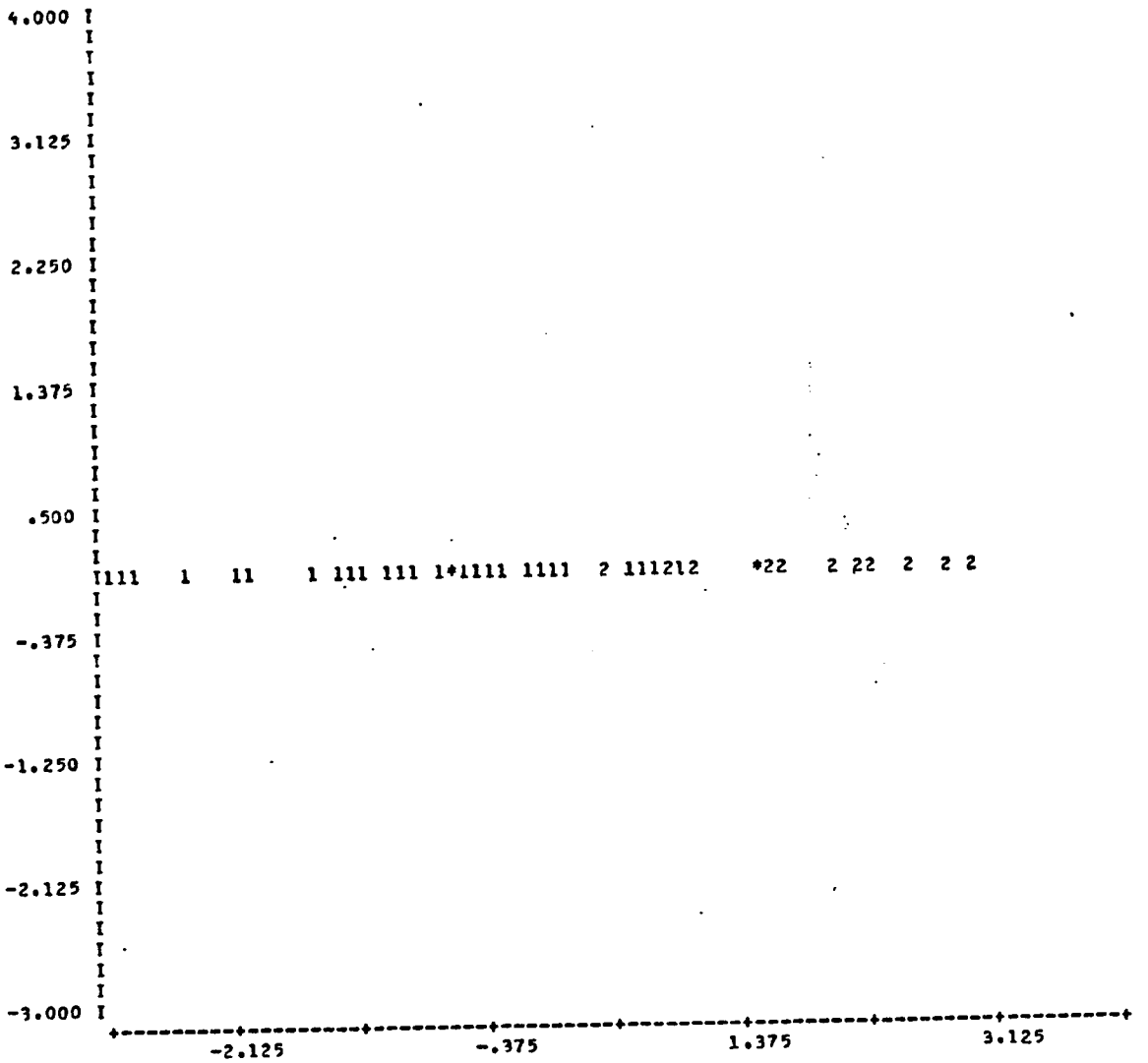

4.000
3.125
2.250
1.375
.500
-.375
-1.250
-2.125
-3.000
-2.125
-.375
1.375
3.125

Table 19. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) for females of *Cicindela bellissima* n. ssp. Leffler (1) and *C. b. bellissima* (2). * shows a group centroid. The table shows nearly complete separability of the two subspecies.

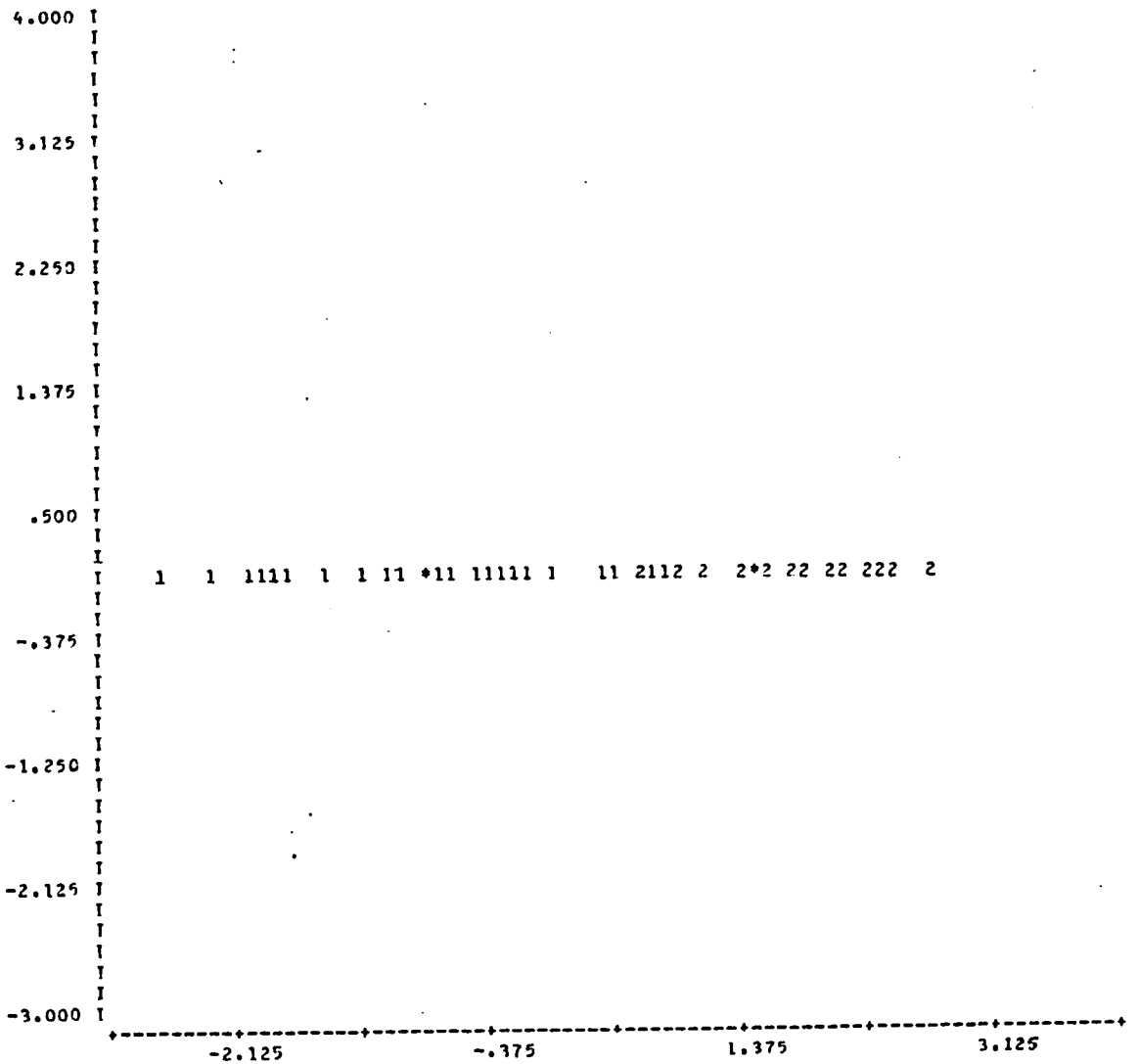

4.000
3.125
2.250
1.375
.500
-.375
-1.250
-2.125
-3.000
1 1 1111 1 1 11 *11 11111 1 11 2112 2 2*2 22 22 222 2
-2.125
-.375
1.375
3.125

Table 20. Pooled within groups covariance matrix for *Cicindela b. bellissima*.

A. Males

B. Females

	C1	C2	C3	C4	C5	C6	C7
C1	.13954						
C2	.03104	.03916					
C3	.03201	.01188	.01486				
C4	.01138	.00152	.00252	.00480			
C5	.02271	.00849	.00633	.00321	.01231		
C6	.01144	.00721	.00402	-.00012	.00228	.01073	
C7	-.00519	-.00424	.00200	.00037	.00060	-.00241	.02102

A

	C1	C2	C3	C4	C5	C6	C7
C1	.16444						
C2	.02599	.03489					
C3	.03111	.00940	.01273				
C4	.01183	.00201	.00237	.00466			
C5	.02708	.00558	.00589	.00394	.01363		
C6	.01182	.00780	.00377	-.00003	.00223	.01252	
C7	-.01521	-.01068	-.00010	-.00008	-.00114	-.00590	.02287

B

Table 21. Statistical information from discriminant analysis of males of *Cicindela b. bellissima*. See Leffler (in press) for explanation characters represented by C1-7.

STEP NUMBER	VARIABLE ENTERED	REMOVED	F TO ENTER OR REMOVE
1	C2		4.05931
2	C7		4.34990
3	C4		1.84627
4	C1		1.36213
5	C5		.76551
6	C3		.50954
7	C6		.36381

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2
C1	-.48452	.21491
C2	-.76566	-.62878
C3	.05911	.73070
C4	.52149	.47458
C5	.12419	-.67862
C6	-.27394	.01180
C7	-.86525	.29087

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2
C1	-1.19663	.530762
C2	-3.81722	-3.13480
C3	.497516	6.15056
C4	7.56435	6.89406
C5	1.08724	-5.94104
C6	-2.41725	.104110
C7	-5.53592	1.85984
CONSTANT	11.3342	-9.07533

CENTROIDS OF GROUPS IN REDUCED SPACE

	1	2
GROUP 1	1.03770	.01536
GROUP 2	-.55541	-.76550
GROUP 3	-.61781	.32787

PREDICTION RESULTS -

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3
GROUP 1	0	15	9. 60.0 PCT	2. 13.3 PCT	4. 26.7 PCT
GROUP 2	1	8	2. 25.0 PCT	2. 25.0 PCT	4. 50.0 PCT
GROUP 3	2	18	3. 16.7 PCT	1. 5.6 PCT	14. 77.8 PCT

61.0 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

Table 22. Statistical information from discriminant analysis of females of *Cicindela b. bellissima*. See Leffler (in press) for explanation of characters represented by C 1-7 and localities represented by Groups 1-3.

STEP NUMBER	VARIABLE ENTERED	VARIABLE REMOVED	F TO ENTER OR REMOVE
1	C7		11.41235
2	C1		5.54063
3	C4		3.44400
4	C3		2.35615
5	C6		1.73271
6	C5		.64431
7	C2		.27511

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2
C1	-1.10858	-1.13914
C2	-.18684	-.26682
C3	1.01298	.37780
C4	.98719	.20019
C5	-.37871	-.30048
C6	.51753	-.14442
C7	1.10330	.32658

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2
C1	-2.45607	-2.52376
C2	-.861395	-1.23015
C3	4.59345	1.71319
C4	13.2260	2.69207
C5	-2.63162	-2.08800
C6	5.37171	-1.49898
C7	7.07223	2.09338
CONSTANT	-6.45541	19.2192

CENTROIDS OF GROUPS IN REDUCED SPACE

	1	2
GROUP 1	-1.12573	.74752
GROUP 2	-1.41409	-1.05036
GROUP 3	1.31068	-.05119

PREDICTION RESULTS -

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3
GROUP 1	0	11	7. 63.6 PCT	1. 9.1 PCT	3. 27.3 PCT
GROUP 2	1	7	2. 28.6 PCT	5. 71.4 PCT	0 0 PCT
GROUP 3	2	17	0 0 PCT	0 0 PCT	17. 100.0 PCT

82.9 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

Table 23. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) for male *Cicindela b. bellissima* from three localities (1-3). * indicates a group centroid. The table shows that discriminant analysis does not permit systematic separation of the populations.

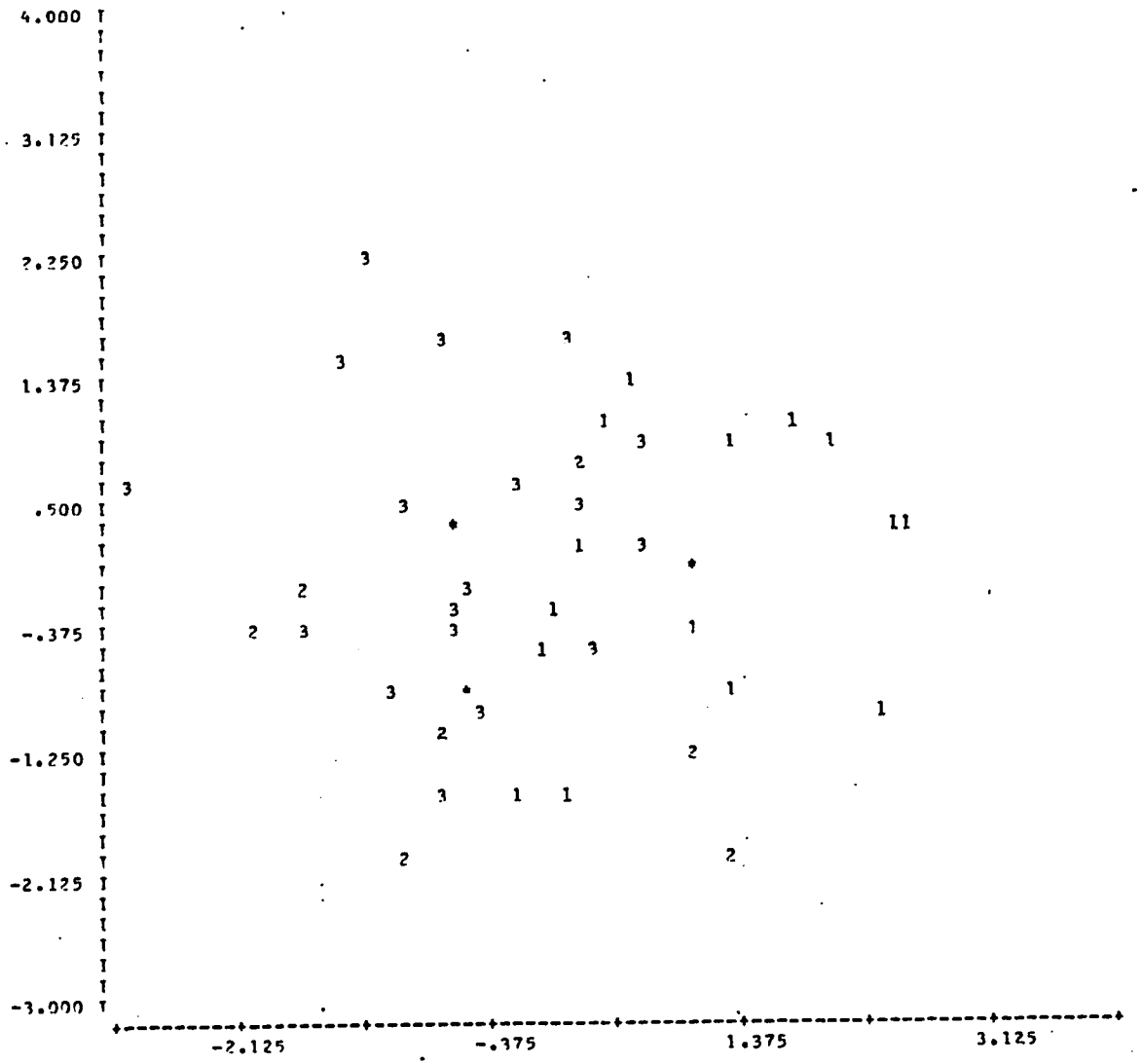
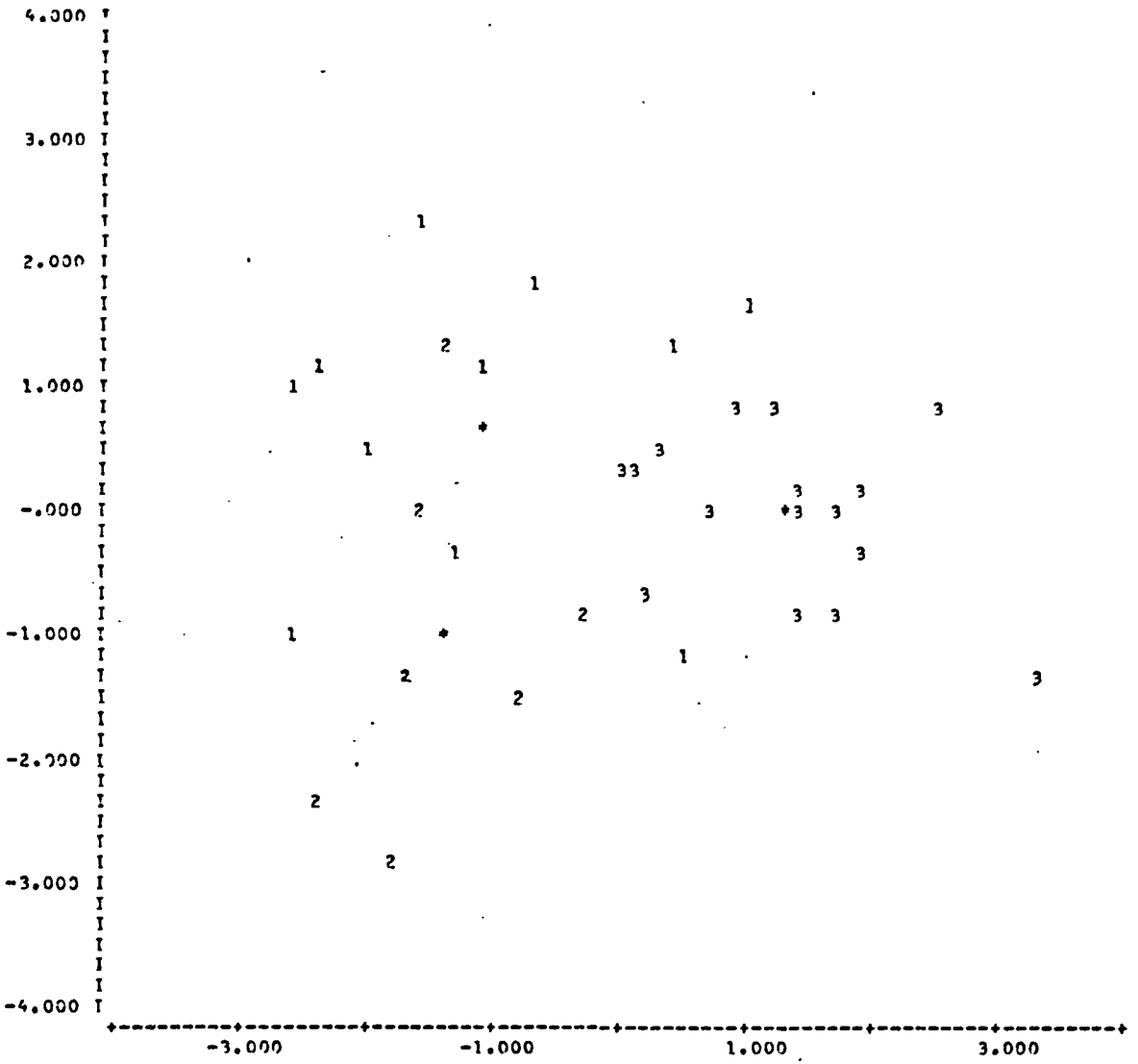

4.000
3.125
2.250
1.375
.500
-.375
-1.250
-2.125
-3.000
-2.125
-.375
1.375
3.125

Table 24. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) for female *Cicindela b. bellissima* from three localities (1-3). * indicates a group centroid. The table shows that discriminant analysis does not permit systematic separation of the populations.


4.000
3.000
2.000
1.000
-.000
-1.000
-2.000
-3.000
-4.000
-3.000
-1.000
1.000
3.000

C. b. bellissima Leng, 1902

Cicindela bellissima Leng, 1902. Trans. American Ent. Soc., 28: 142-143.

Diagnosis. Posterior breadth of humeral lunule averaging greater than 0.50 mm; 70.4% of sample greenish dorsally.

Synonymic notes. There are no synonyms.

Typology. The lectotype, a male, AM No. 1218, was collected at OR. Lincoln Co., Yaquina Bay, Newport. It is representative of the greenish-brown morph. Lectotype examined.

Variation. Maser (1973) and I (Leffler, in press) have treated variation of this subspecies in detail. There is an ill-defined north-to-south clinal size increase but one which is not statistically significant. Color varies from brown to brownish-green to green to blue. Analysis was presented by Leffler (in press). I have not seen any of the black individuals mentioned by Cazier (1939).

Dates of occurrence. Leffler and Pearson (1976) gave the dates as 3 April-5 September, with most records from May through August. Presumably the moderating littoral temperatures permit this Life History Pattern A subspecies to live longer in the spring and eclode earlier in the summer so that generations overlap. LL2 of *C. b. bellissima* collected 5 May, 1975, and both LL2 and LL3 of

C. b. new ssp. Leffler collected 10 September, 1976, and 13 September, 1977, suggest that either larvae overwinter as both L2 and L3 or that larvae require two years for development.

C. b. new ssp. Leffler, in press

Cicindela bellissima n. ssp. Leffler, in press. Coleop. Bull.

Diagnosis. Posterior breadth of humeral lunule averaging less than 0.42 mm; 36.8% of sample greenish dorsally.

Synonymic notes. This subspecies was not yet recognized by Leffler and Pearson (1976) was was included in their treatment of *C. bellissima*.

Typology. The holotype, a male, has been deposited at the AM, the same institution that owns the lectotype of *C. b. bellissima*. I collected the holotype 13 September, 1977, at WA. Clallam Co., Mukkah Bay.

Variation. I (Leffler, in press) have treated variation of this subspecies in detail. This subspecies shows more variation in color than *C. b. bellissima*. Of the series of 19 studied as to color variation, 78.9% are brownish-green or green dorsally, as opposed to 21.1% brown (sexes pooled).

Dates of occurrence. My only dates of collection are 10 September, 1976 and 13 September, 1977. The subspecies was not found 26 June, 1977, a day with optimal climate. It is possible that the adults had already died off following breeding. Many individuals from my September observations were teneral. Both LL2 and LL3 were collected in September. One mound had eight larval burrows of which, judging from their diameters, five were L2 and three were L3. Two LL2 collected from this mound moulted within two weeks. See also comments for *C. b. bellissima*.

Cicindela (*Cicindela*) *columbica* Hatch, 1938

(Figures 20, 22H, 29)

Cicindela bellissima columbica Hatch, 1938. Univ. Washington Publ. Biol., 9(5):234.

Cicindela columbica Hatch. Hatch, 1949, Pan-Pacific Ent., 25(3):113.

Cicindela (*Cicindela*) *columbica* Hatch. Freitag, R., 1965. Quaest. Ent., 1(3):87-170.

Diagnosis. Adult: characters of *limbata*-subgroup of *maritima*-group of *Cicindela*; antennal scape glabrous except for 3-4 apical sensory setae; frons with sparse setae only posterior to eyes; genae glabrous; propleura cupreous with green ventral portion;

proepisternal setae erect; humeral lunule intermediate between C-shaped and posteriorly oblique and apex widely separated from middle band; elongate marginal extensions of middle band not connected to humeral and narrowly separated from or connected with apical lunule. Aedeagus: median lobe with apical lateral flanges broad, contiguous at beak, and slightly constricted basally; ventral surface of apex without midline keel; beak not developed; dorsal notch between beak and orifice long but shallow; inner sac with field b moderately bulged and sclerite 5 small. Female genitalia: syntergum IX + X short, only slightly overlapping bases of gonapophyses; apices of sternite VIII with 2 stout setae; elongate shallow, glabrous excavation distal to notch of 2nd gonocoxa. Larva and pupa: unknown.

Synonymic notes. Hatch (1938) originally described *C. columbica* as a subspecies of *C. bellissima*, later (1949) raising it to full specific rank.

Relationships. Hatch (1949) considered *C. columbica* most closely related to *C. repanda*. Freitag (1965, 1972) and Rumpp (1967) showed it to be a member of the *limbata*-subgroup. Of these species, *C. bellissima* is its closest relative. See the account of *C. bellissima* for further remarks.

Subspecies. No subspecies have ever been proposed and the limited variation warrants none.

Typology. The holotype, a female, was collected 14 April, 1937, at WA. Franklin Co., Perry, a small town no longer in existence but which was located on the west side of the mouth of the Palouse River. The holotype is part of the Hatch Collection, now at OSU.

Variation. This species shows no significant individual variation.

Dates of occurrence. Leffler and Pearson (1976:41) gave the dates as 14 April-26 June and 1 August-30 September. My examination of specimens since that paper was written (1973) produced no changes. Tenerals were collected in mid-August.

Remarks. Dam building on the Snake and Columbia Rivers has flooded most of the habitat suitable for this species. Until a locality was found in 1977, I had considered the species as possibly extinct. It is unfortunately necessary to keep the location of the locality secret to protect the species from unscrupulous collectors until a program can be developed to reintroduce the species to other areas.

Fig. 29. Pacific Northwest distribution of *Cicindela columbica*. See Appendix I for tabulation of localities.

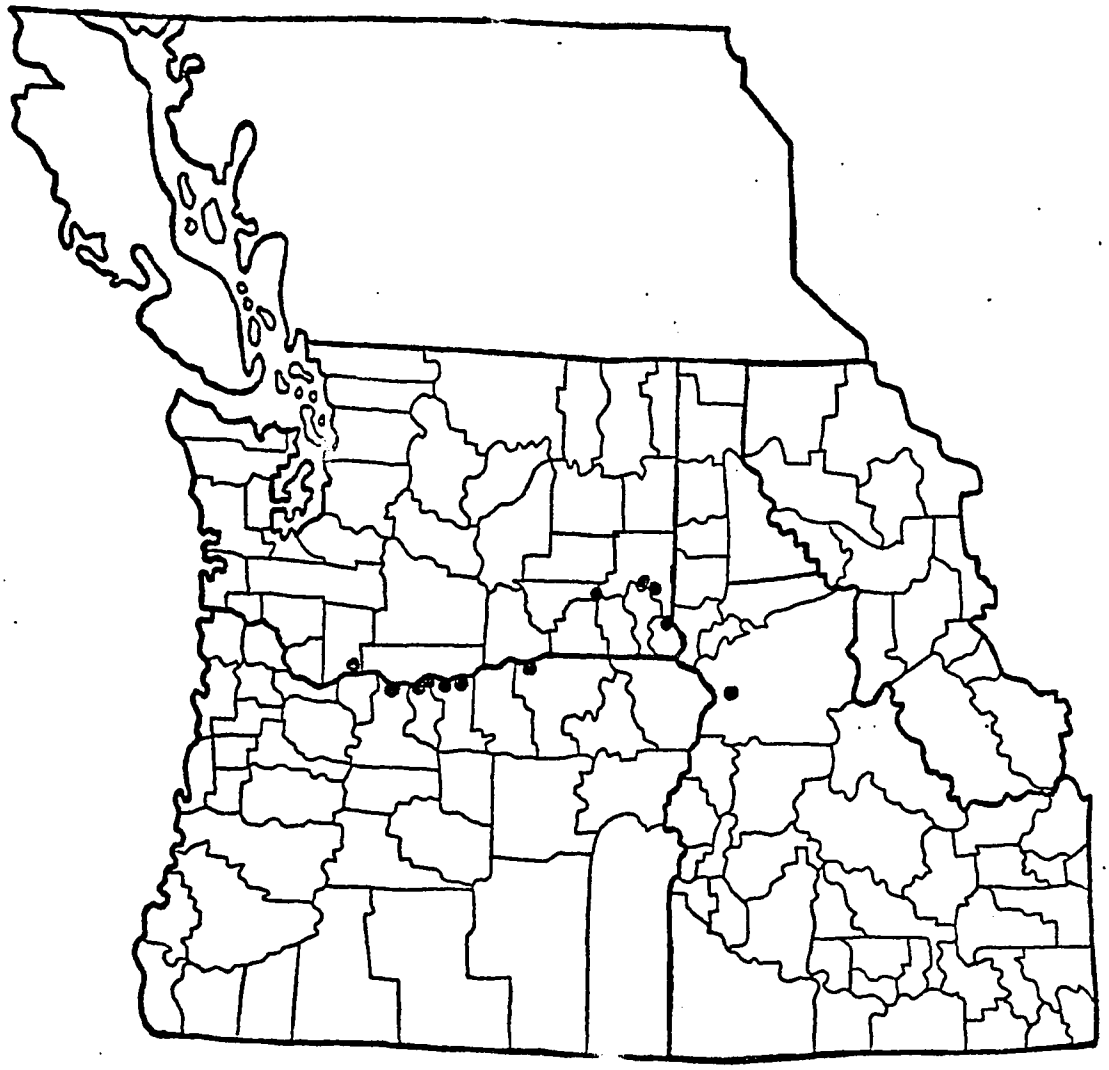
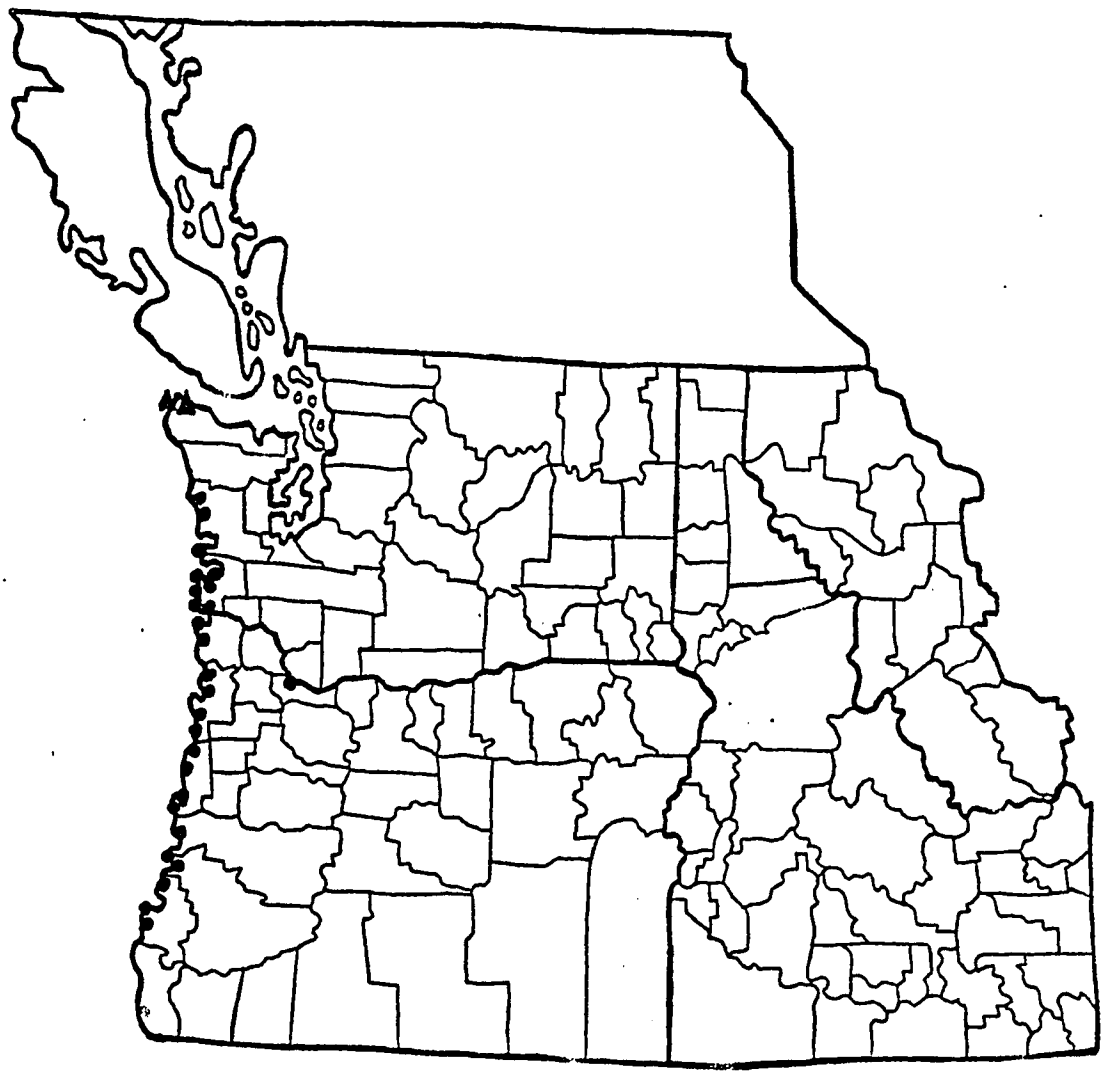


Fig. 30. Pacific Northwest distribution of *Cicindela bellissima*. See Appendix I for tabulation of localities.

Symbols:

● - *C. b. bellissima*
▲ - *C. b.* n. ssp. Leffler



Cicindela (*Cicindela*) *arenicola* Rumpp, 1967

(Figures 22 F and G, 31)

Cicindela (*Cicindela*) *arenicola* Rumpp, 1967. Proc. California Acad. Sci., Ser. 4, 35(7):129-140.

Diagnosis. Adult: characters of *limbata*-subgroup of *subgroup*-group of *Cicindela*; antennal scape sparsely setose in addition to 4-5 apical sensory setae; frons setose; genae setose; propleural color variable according to subspecies; humeral lunule with basal extension present although often incorporated into confluent maculation; maculation very broad to confluent, with posterior arm of humeral lunule directed diagonally when not incorporated into confluent maculation. Aedeagus: median lobe with apical lateral flanges broad, not constricted basally, and not contiguous at beak; ventral surface of apex with midline keel; beak developed but not produced; dorsal notch between beak and orifice short; inner sac with field b strongly bulged and sclerite 5 absent. Female genitalia: syntergum IX + X long, reaching

posteriorly to midpoint of gonapophyses; apices of sternite VIII with 5-6 stout setae, emargination deep; excavation distal to notch of 2nd gonocoxa absent; 2nd gonapophysis with ventral basal setae.

Immature stages: unknown.

Synonymic notes. Rumpp (1967) placed *C. arenicola* with the "'*limbata*' stem species" of the "'*repanda*' group (= *limbata*-subgroup of the *maritima*-group)."

Relationships. Rumpp (1967) considered *C. arenicola* to be most closely related to *C. theatina* Rotger, but unfortunately he did not compare it with *C. limbata* Say. Freitag (1972) stated that *limbata* is the closest relative of *arenicola*. Table 25 is a comparison of eight character-states of *arenicola*, *limbata* and *theatina*. Four character-states are shared by *arenicola* and *limbata* but not *theatina*, and two each are shared by *arenicola* and *theatina* but not *limbata* or *limbata* and *theatina* but not *arenicola*. Thus, I agree with Freitag (1972) that these three species are closely related and that *C. arenicola* and *limbata* are closer to one another than is either to *theatina*. It is difficult to determine which of the three species is the most generalized. *C. limbata* has the largest geographical range, extending from Manitoba southwest to Utah, whereas *theatina* and *arenicola* are restricted to southcentral Colorado and southern Idaho, respectively. A common ancestor perhaps inhabited

Table 25. Comparisons of *C. arenicola*, *C. limbata* and *C. theatina*.

Character-state	*arenicola*	*limbata*	*theatina*
1. Basal dot of humeral lunule	present	present	absent
2. Ventral midline keel on aedeagal middle lobe	present	absent	present
3. Length of notch between aedeagal beak and orifice	short	long	long
4. Bulge of field b of aedeagal inner sac	large	large	moderate
5. Emargination of female sternite VIII	deep	shallow	shallow
6. Setae on apices of female sternite VIII	stout	stout	fine
7. Setae on female 2nd gonapophysis	present	absent	present
8. Lateral flanges on oviduct sclerite	present	present	absent

a contiguous range which was fragmented by development of the Rocky Mountains. *C. theatina* fits the hypothetical progenitor of the *maritima*-group outlined in Freitag's Table I best, but has developed aberrant features as well. *C. arenicola* and *C. limbata* are best considered as divergent stocks from a common ancestor, neither being more generalized than the other but, rather, having a mosaic of plesiomorphic and apomorphic traits.

Subspecies. I shall treat the two subspecies, both geographically restricted to southern Idaho, in their respective subspecies accounts.

Cicindela arenicola arenicola Rumpp, 1967

Cicindela (*Cicindela*) *arenicola* Rumpp, 1967. Proc. California Acad. Sci., Ser. 4, 35(7):129-140.

Diagnosis. Total length, male: >11.7 mm, female: >12.0 mm (measurements adapted from Rumpp, 1967, and representing mean minus one standard deviation); male mandible with anteapical tooth in same plane as remaining teeth; pigmented portion of elytra dull bronzed reddish-brown in 96% of population sample (N=78), green-tinged reddish-brown

in remaining 4%; propleural coloration cupreous.

Synonymic notes. The species was unknown to science prior to its 1967 description. Rumpp (1967) did not differentiate the subspecies now known as *C. a.* n. ssp. Clifford, known to him by only a single specimen.

Typology. The holotype, a male, California Academy of Sciences Type No. 9374, is from ID. Fremont Co., St. Anthony Dunes, 11 km N.E. St. Anthony, 1525 m. Holotype not seen.

Variation. Color variation is treated in the diagnosis. Rumpp (1967:232) stated that 5% of his sample of 78 specimens have clearly defined lunules and middle bands, and an additional nearly 15% have indentations in the otherwise confluent maculation. The remaining 80% have completely confluent maculation. The male is smaller than the female but less variable in total length.

Dates of occurrence. Available dates do not accurately reflect the complete activity period of this subspecies but are presented to summarize known information: 3-4 June-11 July, 5 September. Rumpp (1967) collected 3rd-instar larvae 21 April, 1965. Adults I collected 11 July, 1974, were abraded and had worn mandibles, denoting near senescence; one specimen was found dead.

C. a. n. ssp. Clifford

Diagnosis. Total length, male: <11 mm, female: <12 mm; male mandible with anteapical tooth directed more anterodorsally and, hence, not in same plane as remaining teeth; pigmented portion of elytra green to greenish-blue; propleural coloration greenish-blue.

Synonymic notes. None.

Typology. Subspecies not yet published.

Variation. The small number of specimens I have seen show some variation in the degree of macular confluence.

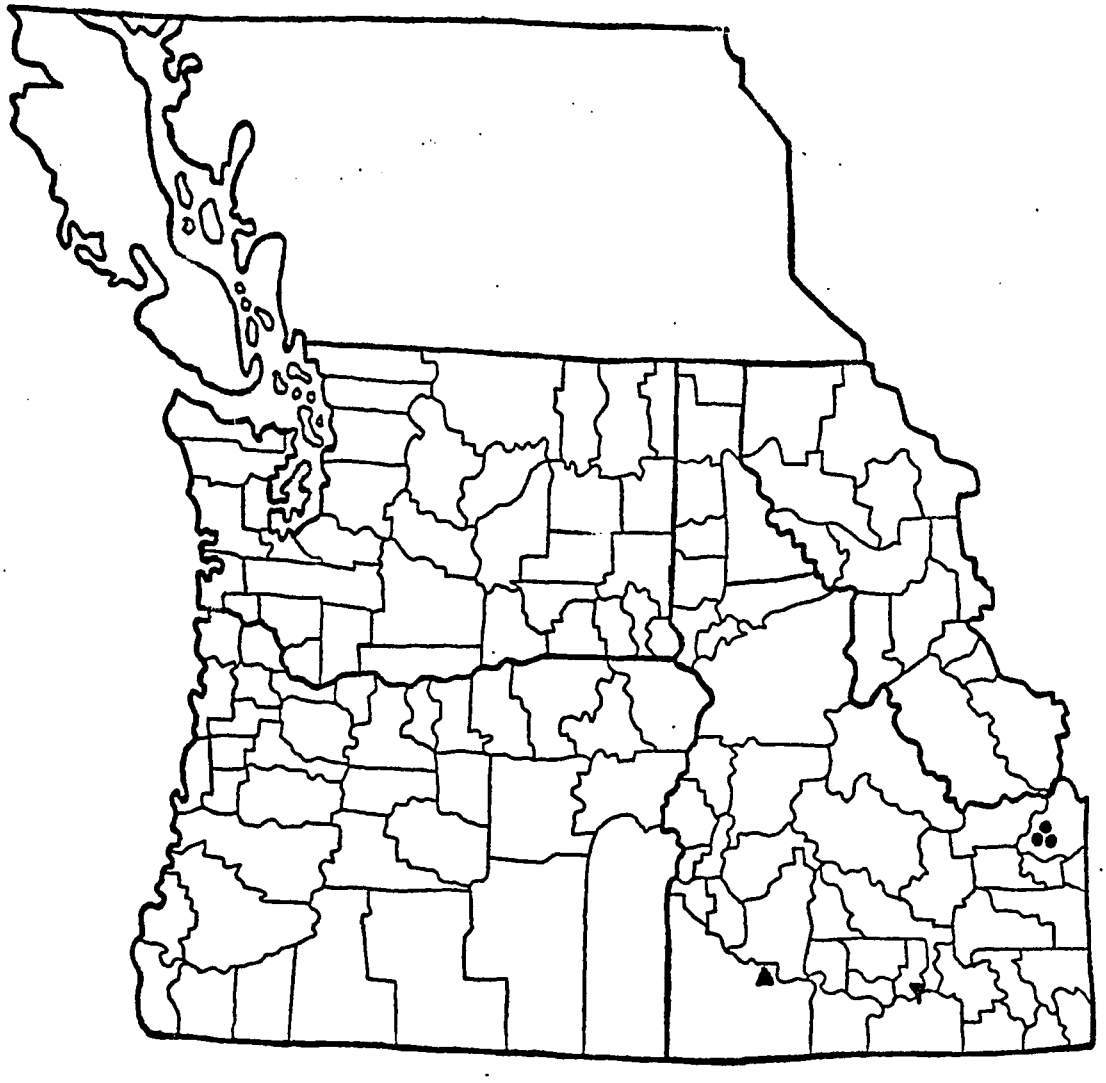
Dates of occurrence. I have spring records only: 9 April-10 May.

Intergrades. At ID. Minidoka Co., Jackson Dunes Area, Snake River, V. G. Clifford has found an intergrade population. If it were not for this population, he would have considered the Owyhee County population as a species distinct from *C. arenicola*. The intergrades show combinations of the characters of the parent subspecies and the locality is approximately halfway between those of the parent forms. The intermediates are the size of n. ssp. Clifford, have the orientation of the mandibular teeth as in *arenicola*, and are intermediate (greenish-cupreous) in color.

Fig. 31. Pacific Northwest distribution of *Cicindela arenicola*. See Appendix I for tabulation of localities

Symbols:

● - *C. a. arenicola*
▲ - *C. a.* n. ssp. Clifford
▼ - *C. a. arenicola* x n. ssp. Clifford



Remarks. The range and habitat of this subspecies are limited and it is particularly vulnerable to overexploitation by unscrupulous collectors. Until 1975, it was abundant, but, in 1976, it was collected nearly to extinction. Its future status depends on how much the population is allowed to recover. *C. a. arenicola* inhabits dunes that could be threatened by off-road vehicles, although they are geographically extensive.

The *formosa*-group

(Figures 32-34)

Diagnosis. Adult: labrum usually short to medium (ratio, length/breadth <60%); tridentate. Aedeagus: shaft of middle lobe slightly assymetrical, with weak left-skewed bulge; flagellum 50-100% length of inner sac; sclerite 6 not sclerotized. Female genitalia: no unique external genitalic characters, similar to generalized members of *maritima*-group. Larva: antennal chaetotaxy, 1:5-7, 2:7-10, 3:2, 4:3; spine of inner hook 1/3-1/2 or more of length of entire hook; ventral elevations

of sternum IX with 4-5 main setae.

Pupa: no unique characters.

Rivalier's (1954) Group VII of the subgenus *Cicindela* was based on *C. formosa* Say, and characterized by the arcuate aedeagus with an unsclerotized sclerite 6. The number of species included in the group depends on the rank, specific or subspecific, given to some of its members. Rivalier listed five species, Willis (1968) recognized 10 species and Freitag's group IC (equivalent to Rivalier's *formosa*-group) contains 10 species. Species limits in these three lists are not always equivalent, although the same taxa are involved. After examination of external anatomy, male and female genitalia, and specimens or descriptions of larvae of six species, I tentatively recognize 11 species in this species-group, four of which are found in the Pacific Northwest. Work remains to be done to delineate species boundaries in the complex and I must emphasize that my conclusions as to the number of species I recognize may change. Subspecies validities are, in many cases, even more uncertain. My studies have shown me that the species involved are closely related and difficult to arrange phylogenetically.

Characters and interrelationships of *formosa*-group species

Table 26 compares some of the character-states of 10 of the 11 species I recognize as belonging to the *formosa*-group (I lack

Table 26. Comparison of external features of species of *formosa*-group of *Cicindela*.

	Character	*C. formosa*	*C. decemnotata*	*C. denverenix*	*C. sexguttata*
1.	antennal scape setae (besides apical sensory setae	present	present	present	absent
2.	frons	setose	setose	setose	glabrous
3.	gena	setose	setose	setose	glabrous
4.	mesepisternal coupling sulcus type	D	N	N	B
5.	elytral sculpture	deeply punctuate-granulate	punctuate-granulate	punctuate-granulate	deeply punctate-granulate
6.	larval primary pronotal discal setae	6th absent, 7th sometimes absent	all 7 present	?	all 7 present

	Species					
ata	*C. denverenix*	*C. sexguttata*	*C. denikei*	*C. patruela*	*C. limbalis*	*C. spendida*
	present	absent	absent	absent	present	present
	setose	glabrous	glabrous	glabrous	setose	setose
	setose	glabrous	glabrous	glabrous	setose	setose
	N	B	B	B	N	N
	punctuate-granulate	deeply punctate-granulate	deeply punctuate-granulate	obsoletely punctate, strongly granulate	punctuate-granulate	punctuate granulate
sent	?	all 7 present	?	?	all 7 present	?

Species					
i *C. patruela*	*C. limbalis*	*C. spendida*	*C. purpurea*	*C. plutonica*	*C. pugetana*
absent	present	present	present	present	present
glabrous	setose	setose	setose	setose	setose
glabrous	setose	setose	setose	setose	setose
B	N	N	B	B	B
obsoletely punctate, strongly granulate	punctuate-granulate	punctuate-granulate	punctuate-granulate	granulate	punctate
?	all 7 present	?	6 and 7 absent	?	6 and 7 absent

Fig. 32. Male genitalia in species of *formosa*-group of subgenus *Cicindela*. X 24.

A. *C. formosa*: apex, ventral view

B. *C. formosa*: apical half, left view

C. *C. decemnotata*: apex, ventral view

D. *C. decemnotata*: apical half, left view

E. *C. sexguttata*: apex, ventral view

F. *C. patruela*: apex, ventral view

G. *C. limbalis*: apex, ventral view

H. *C. limbalis*: apex, left view

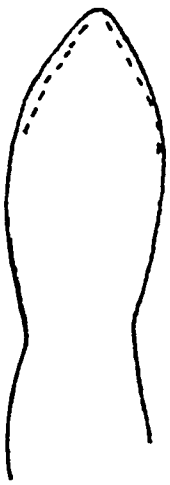
I. *C. splendida*: apex, left view

J. *C. purpurea*: apex, ventral view

K. *C. purpurea*: apical half, left view

L. *C. plutonica*: apex, ventral view

M. *C. pugetana*: apex, ventral view



A

B

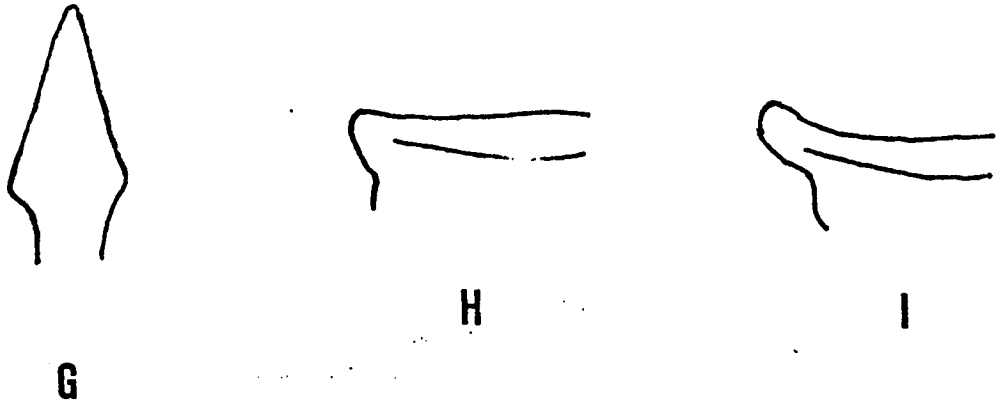
C

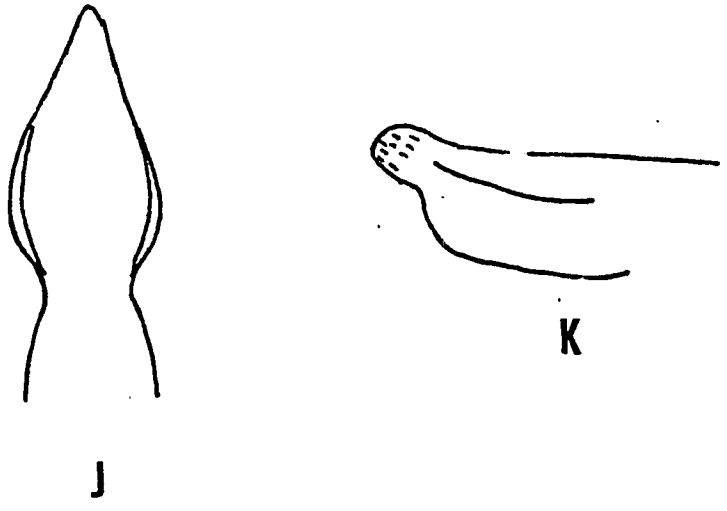
D

E

F

Figure 32 (continued)





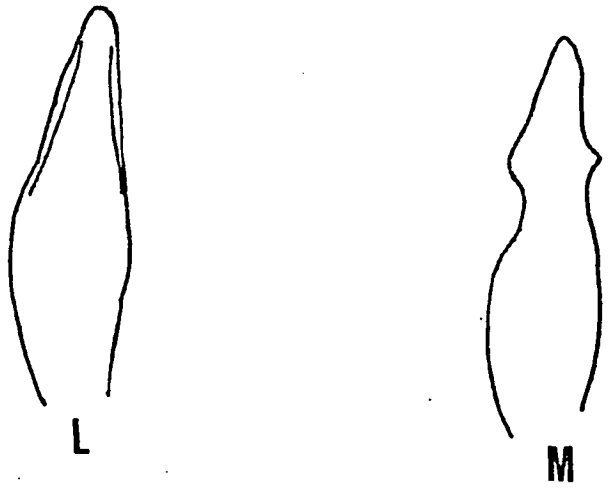


Fig. 33. Female genitalia in species of *formosa*-group of subgenus *Cicindela*. X 24.

A. *C. formosa*: syntergum IX + X, dorsal view

B. *C. formosa*: left 2nd gonocoxa, ventral view

C. *C. formosa*: sternite VIII, ventral view

D. *C. d. decemnotata*: syntergum IX + X, dorsal view

E. *C. d.* n ssp. Rumpp: syntergum IX + X, dorsal view

F. *C. d. decemnotata*: left 2nd gonocoxa, ventral view

G. *C. d. decemnotata*: sternite VIII, ventral view

H. *C. d.* n. ssp. Clifford: sternite VIII, ventral view

I. *C. d.* n ssp. Rumpp: sternite VIII, ventral view

J. *C. sexguttata*: syntergum IX + X, dorsal view

K. *C. sexguttata*: sternite VIII, ventral view

L. *C. patruela*: sternite VIII, ventral view

M. *C. purpurea*: syntergum IX + X, dorsal view

N. *C. purpurea*: left 2nd gonocoxa, ventral view

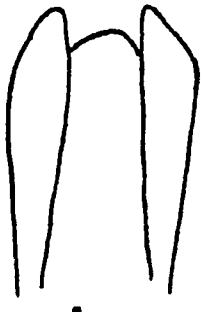
O. *C. purpurea audubonii*: sternite VIII, ventral view

P. *C. pugetana*: syntergum IX + X, dorsal view

Q. *C. pugetana*: left 2nd gonocoxa, ventral view

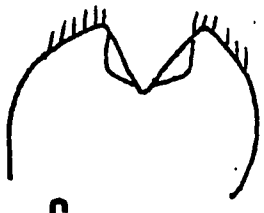
R. *C. pugetana*: sternite VIII, ventral view

S. *C. plutonica*: syntergum IX + X, dorsal view

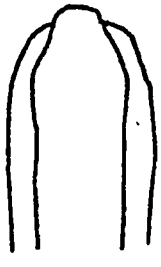


A

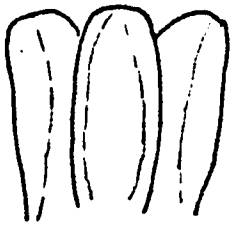
B



C



D



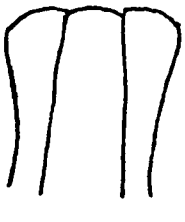
E

F

G

H

I

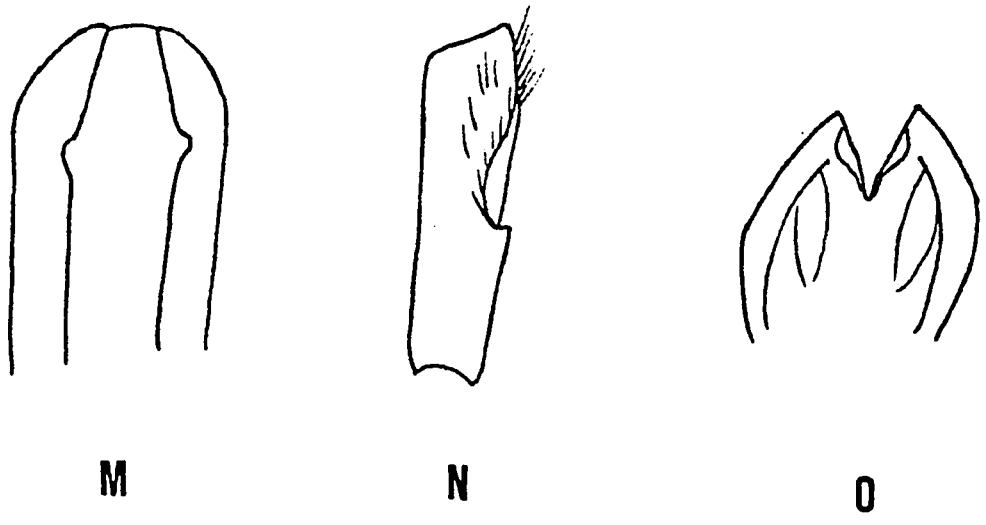


J

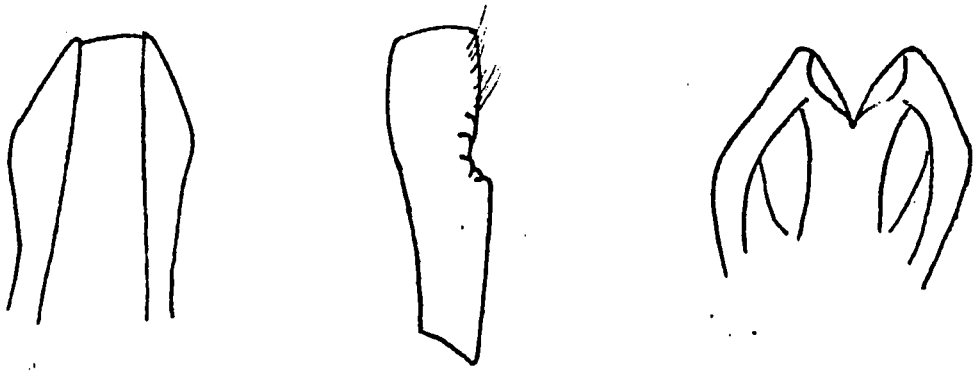
K

L

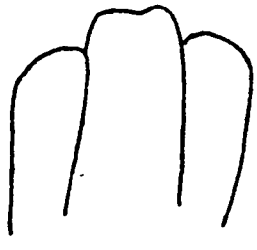
Figure 33 (continued)



M N O

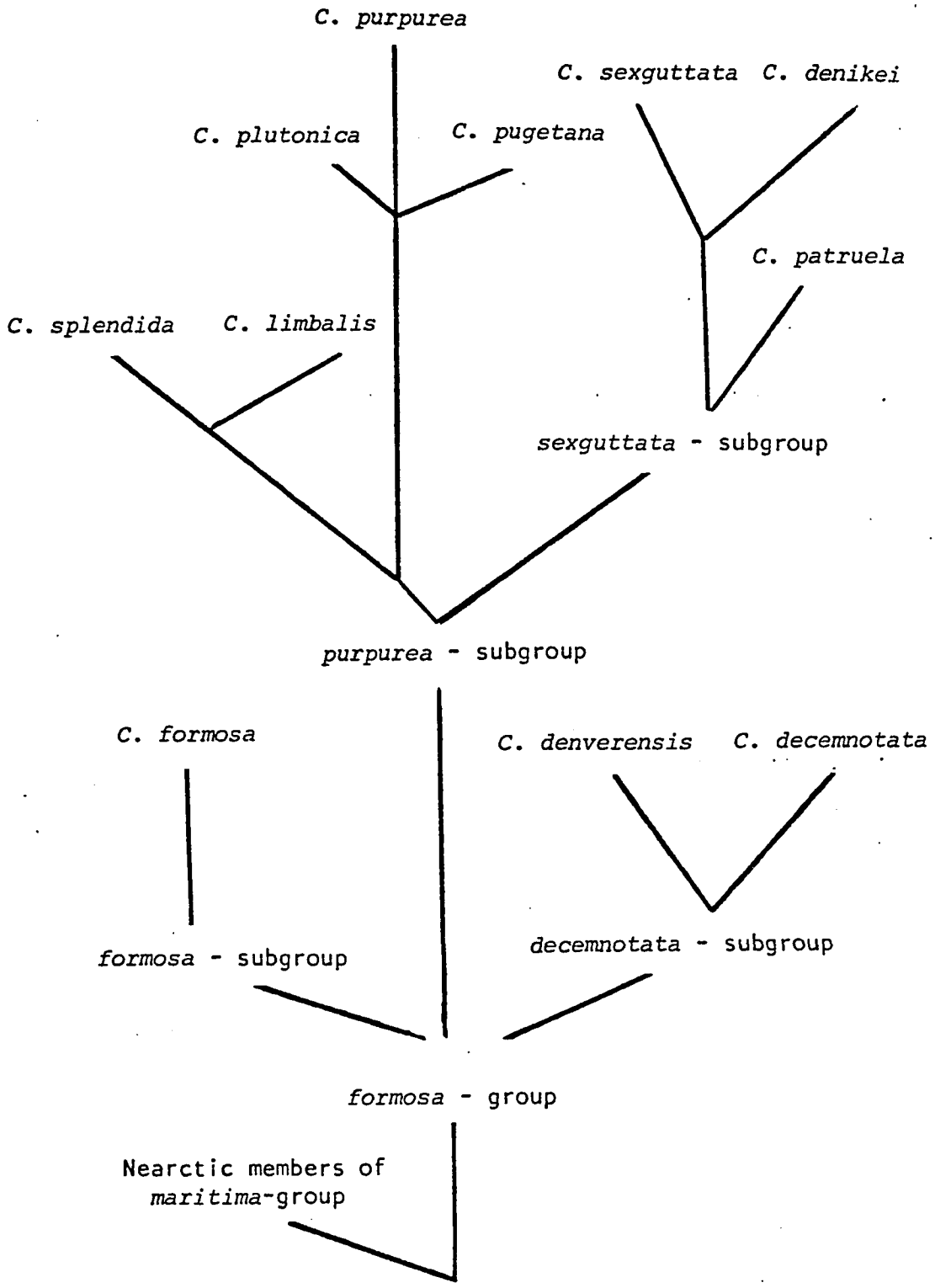


P Q R



S

Fig. 34. Proposed phylogeny of species of *formosa*-group of *Cicindela* based on morphological characters.


C. purpurea
C. sexguttata
C. denikei
C. plutonica
C. pugetana
C. patruela
C. splendida
C. limbalis
sexguttata - subgroup
purpurea - subgroup
C. formosa
C. denverensis
C. decemnotata
formosa - subgroup
decemnotata - subgroup
formosa - group
Nearctic members of
maritima-group

specimens of *C. denikei* Brown and have been able to study *C. denverensis* Casey only superficially).

It is difficult to assess the character-states in terms of the weight that should be given to them in determining relationships. The following are summaries of the important features and statements of affinities of the several species.

C. formosa Say. This eastern species has deeply punctate-granulate slytra, a type otherwise found only in *C. sexguttata* (in most of the *formosa*-group species, punctae are shallow). *C. formosa* is unique in the species-group in the deep, narrow mesepisternal coupling sulcus. The aedeagus has a broadly-ovoid apex as seen in ventral view, with very narrow, non-earlike lateral apical flanges. This form is similar to that of *C. patruela* and less like that of *sexguttata*. Details of the female genitalia are not as in any other species. The larva (described and figured by Hamilton, 1925) agrees with *C. purpurea* and *pugetana* in lacking primary pronotal seta 6 at least (6 only in *C. f. generosa*, 6 and 7 in *C. f. formosa*). Pronotal coloration of *formosa* differs from *purpurea* and other larval characters are too generalized to be of systematic use. *C. formosa* is thus not particularly closely related to any of the other members of the species-group and, in my estimation, comprises its own subgroup, the *formosa*-subgroup, diagnosed as follows:

Frons and genae setose; antennal scape with setae in addition to apical sensory setae (see note below); mesepisternal coupling sulcus Type D; elytral sculpture deeply punctate-granulate; aedeagus with lateral apical flanges not earlike, shape of ventral surface of apex broadly ovoid; female sternum VIII without ridges or depressions except along margins of median emargination; larva lacking at least primary pronotal seta 6.

Note. Willis (1968) intended couplet 76 to define *C. formosa*. The antennal scape is setose in at least three subspecies, so the couplet does not work.

C. decemnotata Say and *denverensis* Casey. These species mainly differ in the pale color of the second segment of the labial palp in the male *denverensis* (black in female *denverensis* and both sexes of *decemnotata*). With the discovery of an as yet unnamed species of *C. decemnotata* from Utah (H. L. Willis, in litt., 1973), the macular differences do not always hold. A series of *decemnotata* (AM) from UT. Rich Co., Summit Logan Canyon, 7800 ft, are indistinguishable in color and maculation from specimens of *C. d. denverensis* with reddish elytra (except for the presence of traces of the posterior arm of the

middle band). *C. denverensis* tends to be smaller than *decemnotata*. *C. denverensis conquista* Casey, if it is indeed a valid subspecies, is intermediate in maculation between *C. d. denverensis* and *C. decemnotata* from west of Great Salt Lake, Utah. However, *conquista*, being from western Nebraska, is not geographically intermediate. Where ranges of *decemnotata* and *denverensis* overlap, *decemnotata* is heavily maculated. Also, *denverensis* prefers steep embankments and *decemnotata* is found on flatter terrain (Lawton, 1972b).

C. decemnotata and *denverensis* agree in sculpture (shallowly punctate-granulate), mesepisternal coupling sulcus (Type N), female genitalia, and at least in the external form of the aedeagus (I have not had a cleared aedeagus of *denverensis* available for study). Sculpture and coupling sulcus anatomy are generalized. Aedeagal form is most like those of *limbalis* and *splendida*, primitive in other characters, and perhaps the aedeagus is also generalized for the *formosa*-group. Female genitalia are unique in the extreme narrowness of the lateral lobes of syntergum IX + X. The 2nd gonocoxa resembles that of *C. formosa* in notch morphology but, otherwise, the genitalia of these species is not particularly similar. The *decemnotata* larva (that of *denverensis* is still unknown) is generalized in all characters except for the yellow color of head and pronotal setae.

In summary, I consider these two species to be closely related, probably sibling species, generalized in their characteristics,

and not more losely related to any other division of the *formosa*-group than to another. Together, they comprise the *decemnotata*-subgroup which is diagnosed as follows:

> Frons and genae setose; antennal scape with setae in addition to apical sensory setae; mesepisternal coupling sulcus Type N; elytral sculpture shallowly punctate-granulate; aedeagus with beak very short, ventral outline of apex lanceolate, and lateral apical flanges small but angulate; lateral lobe of female syntergum IX + X very narrowed, sternum VIII with submarginal lateral ridge and constricted vertex of emargination angle; larva with head and pronotal setae yellow.

C. denikei Brown, *patruela* Dejean and *sexguttata* Fabricus. These are three eastern species. The status of *C. denikei* is uncertain. Brown (1934) described it as a subspecies of *sexguttata*. Graves (1965) and Wallis (1961) both retained the subspecific status but suggested sibling species status. Willis (1968) also mentioned the probability that *denikei* is a sibling of *sexguttata* and gave it specific rank, although not ignoring a possible subspecific rank. *C. denikei* is allopatric from *sexguttata* and lives in a different

habitat (rocky knolls in coniferous forest rather than open areas in deciduous forest). I have only been able to examine specimens superficially, and genitalia not at all, but, in view of the geographical and ecological differences, I believe *C. denikei* should be accorded specific rank.

C. patruela and *sexguttata* are superficially similar, *patruela* being more maculate and more robust, and agree in most structural characters, differing sufficiently in labral form, sculpture and genitalia to make separate specific ranking unquestionable. They agree in the glabrous frons, genae and antennal scape (unique in the *formosa*-group), the Type B mesepisternal coupling sulcus and the female genitalia. *C. sexguttata* has deeply punctate-granulate elytral sculpture (as in *C. formosa*). In *C. patruela*, sculpture consists of nearly obsolete punctures and distinct granules. The labrum of *C. patruela* has shallow notches between the teeth ($\bar{X}$ ratio, length excluding median tooth/basal breadth: >52%; N=2) compared with *sexguttata* ($\bar{X}$ ratio: < 48.2%; N=5), an 8% difference between the means. The *sexguttata* aedeagal apex is lanceolate in ventral view, with narrow untriangular lateral apical flanges. That of *patruela* resembles *formosa* more than *sexguttata*, but lacks flanges and is not constricted basal to the apical area. Female genitalia differ only in the blunter apices and stronger ventral ridge of sternum VIII of *patruela*.

Characters of these species are sufficient to place them in their own subgroup. Sculpture, at least of *sexguttata*, is most like that of *formosa*. Female genitalia agree with the *purpurea*-subgroup in the apically-flared lateral lobes of syntergum IX + X and in details of the 2nd gonocoxa. The aedeagus of *sexguttata* is more as in *purpurea* than in any other species, but the apex is more lanceolate, the lateral flanges broader, and the beak shorter. The larva of *sexguttata* is of a generalized form. I consider the *sexguttata*-subgroup to be an aberrant yet generalized offshoot closest to the stock that gave rise to the *purpurea*-subgroup. It is diagnosed as follows:

> Frons, genae, and antennal scape (except for apical sensory setae) glabrous; mesepisternal coupling sulcus narrow; female genitalia with lateral lobes of syntergum IX + X apically flared, sternum VIII with submedial longitudinal ridges; larva with combination of chestnut pronotal coloration and 7 pairs of primary pronotal setae (in *sexguttata*).

C. limbalis Klug, *C. plutonica* Casey, *C. pugetana* Casey, *C. purpurea* Olivier and *C. splendida* Hentz. A series of paper (in sequence: Nicolay and Weiss, 1932; Smyth, 1933; Nicolay, 1934; Smyth, 1935) involved their respective authors in taxonomic

controversy. Differences in taxonomic philosophy and species concepts of these authors interfered with clarification of the systematics of these species. No subsequent authors have attempted to resolve the problems. My lack of adequate material and the fact that two of the species and most of the ranges of two others are extralimital to the Pacific Northwest prevent me from making a complete taxonomic review of all of the species of this subgroup. However, I shall outline the results of my limited personal observations and present tentative conclusions in the hope that they will form a basis for future study.

C. limbalis and *splendida* are closely related. They are largely parapatric but with a broad zone of sympatry from Kansas to the mid-Atlantic coast (Willis, 1970). Morphological differences are slight, minor details of color and maculation having been used by Eckhoff (1939) and Willis (1968). I have found the two species identical in sculpture, mesepisternal coupling sulcus form and characters of the female genitalia. The aedeagi differ only in the longer beak of *splendida* but I have only had two aedeagi of *limbalis* and one of *splendida* for examination. The best evidence that the two species are distinct is that they maintain differences in coloration even when collected at the same locality (Lawton, 1972b: 36-37). Study of the ecological requirements of the two taxa where they occur together is needed to show that two species are involved and that the differences are not merely a Mendelian or other genetic effect.

Confusion also exists in attempts at differentiating *C. purpurea* from *limbalis* and *splendida*. Again, differences in color and maculation are minor, and individual and subspecific variation make it impossible to find constant specific characters. *C. purpurea* is identical in sculpture to *limbalis* and *splendida* but differs in having a broad rather than narrow mesepisternal coupling sulcus. The aedeagus of *purpurea* has a long beak and evenly rounded rather than triangularly angulate lateral apical flanges. *C. splendida* has the beak as long as in *purpurea* but the flanges are like those of *limbalis*, not *purpurea*. The female genitalia of the three species are identical except that the lateral lobes of syntergum IX + X are proportionally narrower in *purpurea* and the median lobe does not extend beyond them apically. The larva of *purpurea* differs from that of *limbalis* primarily in lacking primary pronotal setae 6 and 7 (the *splendida* larva is unknown). The nearly glabrous genae, Type B coupling sulcus and incomplete larval pronotal seta compliment of *purpurea* are apomorphic. *C. purpurea* is sympatric with *limbalis* and *splendida* but is usually ecologically separate. Eckhoff (1939), Lawton (1971, 1972b) and Willis (1970) all described the propensity of *limbalis* and *splendida* for steep gullies and embankments and flat ground for *purpurea*. In broad regions of sympatry, *purpurea* inhabits lower elevations and the others at higher elevations (see Lawton, 1971:62; Smyth, 1933:203).

C. plutonica and *C. pugetana* have usually been considered subspecies of *C. purpurea* (Wallis, 1961; Willis, 1968), but they

differ in sculpture and aedeagal form. Also, Beer and Maser (1973) and Leffler and Pearson (1976) mentioned areas of sympatry of *purpurea* with *plutonica* in Oregon and *pugetana* in Washington, respectively. The three species agree in the Type B mesepisternal coupling sulcus. The elongate beak gives a similar slender apical outline to the aedeagus of all three species, although the different form of the lateral apical flanges make them superficially dissimilar. Female genitalia of all three species agree in the details of the syntergum IX + X (the apex of the lateral lobe of *purpurea* is more flared) and sternum VIII, but the 2nd gonocoxa of *plutonica* and *pugetana* lack the excavation distal to the ventral notch in *purpurea*. The larvae of *purpurea* and *pugetana* agree in lacking primary pronotal setae 6 and 7 (the *plutonica* larva is unknown) and differ only in pronotal coloration.

C. purpurea has the shallowly punctate-granulate sculpture of most of the other species of the *formosa*-group, showing this to be the plesiomorphic state for the group. *C. plutonica* and *pugetana* have diverged in separate directions in sculpture, *plutonica* lacking granules and *pugetana* lacking punctures. The aedeagus of *purpurea* has evenly rounded lateral apical flanges. Flanges of *plutonica* are extremely narrow and those of *pugetana* are triangularly angulate, although the "ears" thus produced are very tiny. The shaft in *pugetana* is more decidedly assymetrical than in the other species. Although the species may be found at the same general locality (there is sympatry in Washington and Oregon), they are ecologically

separated: *C. purpurea* prefers sparsely grassy, flat ground; *C. plutonica* inhabits scabrock situations; and *C. pugetana* is found in tracts of sagebrush (*Artemisia* spp.).

The five species comprise what I call the *purpurea*-subgroup which is diagnosed as follows:

> Frons and antennal scape setose; aedeagal beak elongate; female genitalia with sternum VIII with each lobe bearing sublateral ridge and median rugose depression; larva lacking primary pronotal setae 6 and 7.

As the key by Willis (1968) does not properly separate members of the *formosa*-group, I am here presenting a new key which should serve for identifications based on external characters. I do not personally like the inclusion of range in a systematic key, but, in the case of distinguishing *decemnotata* from *denverensis* and *denikei* from *sexguttata*, range presents an important differentiating character.

1A. Frons glabrous except for supraorbital setae (*sexguttata*-subgroup).....2

B. Frons setose.....4

2A. Elytra punctate-granulate.....3

B. Elytra granulate with punctae obsolescent.....*C. patruela*

3A. Range restricted to S.E. Manitoba, S.W. Ontario and extreme N. Minnesota; habitat: summit of rocky knolls in conifer stands.....*C. denikei*

B. Range eastern United States and southeastern Canada except portions in 3A; habitat: shaded paths in deciduous forests.....*C. sexguttata*

4A. Mesepisternal coupling sulcus Type D; elytral sculpture deeply punctate-gradulate (*formosa*-subgroup).....*C. formosa*

B. Mesepisternal coupling sulcus Type N or B, not D; sculpture shallowly punctate-granulate or otherwise.....5

5A. Elytra punctate-granulate; genae setose or nearly glabrous.....7

B. Elytra punctate or granulate; genae nearly glabrous.....6

6A. Elytra punctate, no granules, giving shiny lustre.....*C. plutonica*

B. Elytra granulate, no punctae, giving dull lustre.....*C. pugetana*

7A. Genae with 5 or more setae.....8

B. Genae with less than 5 setae, usually only one; mesepisternal coupling sulcus Type B.....*C. purpurea* (part)

8A. Mesepisternal coupling sulcus Type N.....9

B. Mesepisternal coupling sulcus Type N or B.....10

9A. Head, pronotum and elytra of same color.....*C. limbalis*

B. Head and pronotum of different color than elytra.....*C. splendida*

10A. Range east of Mississippi River; mesepisternal coupling sulcus Type B.....*C. p. purpurea*

B. Range from Great Plains westward; mesepisternal coupling sulcus Type N.....11

11A. Middle band complete or at least with traces of posterior arm present; 2nd segment of labial palpi dark in both sexes; range widespread.....*C. decemnotata*

B. Middle band consisting of transverse arm only or absent; 2nd segment of labial palpi pale in male, dark in female; range restricted to western edge of Great Plains.....*C. denverensis*

Accounts of the Pacific Northwest Species of the *formosa*-group

C. decemnotata-subgroup

Cicindela (*Cicindela*) *decemnotata* Say, 1817

(Figures 22K, 35)

Cicindela decemnotata Say, 1817. J. Acad. Nat. Sci., Philadelphia, 1:19.

Cicindela purpurea decemnotata Say. Schaupp, F., 1883-1884, Bull. Brooklyn Ent. Soc., 6:90.

Cicindela limbalis decemnotata Say. Rivalier, E., 1954. Rév. Française d'Ent., 21:253.

Diagnosis. Adult: characters of *decemnotata*-subgroup of *formosa*-group of *Cicindela*; at least traces of posterior arm of middle band present.

Synonymic notes. Although Rivalier (1954:253) called this a species of *C. limbalis* and Schaupp (1883-1884:90) considered it a variety of *C. purpurea*, most authors have given it full specific standing.

Relationships. See discussion of *decemnotata*-subgroup.

Subspecies. A review of the species over its entire extensive range is needed. I tentatively recognize three subspecies, two of

which have not yet been formally described. However, the geographic limits cannot be delineated until populations from the northern Great Plains and northern Great Basin have been examined with regard to their subspecific identities. I have examined female genitalia of a limited number of specimens following conversation with Mr. V. G. Clifford, and consider the differences worthy as subspecific characters. My conclusions and assignments must remain tentative, however, because I have not been able to study specimens in sufficient number or from geographically crucial localities.

C. d. decemnotata: Dorsal coloration most commonly green with strong cupreous wash; maculation complete for species; female genitalia with outer half of lateral lobe of syntergum IX + X >18% of entire apical breadth of syntergum, with ventral ridges on either half of sternum VIII located at midline of each half and with apices of sternum VIII narrowly rounded. Range: Alberta, S.W. Saskatchewan, S.W. Yukon Territory, CO., S. ID., E. MT., W., N.E., WY. Includes *C. d. albertina* and *C. lantzi* as synonyms.

C. d. n. ssp. Clifford: Dorsal coloration bright green, no specimens with cupreous wash seen; maculation complete for species; female genitalia with outer half of lateral lobe of syntergum IX + X <18% of entire apical breadth of syntergum, with ventral ridges on either half of sternum VIII located lateral to midline of each half, and with apices of sternum VIII acute. Range: BC, WA.

C. d. n. ssp. Rumpp: Dorsal coloration blue-green; maculation ranging from complete for subspecies but narrowed, to immaculate except for apical portion of apical lunule; female genitalia as in *C. d. decemnotata*. Range: UT.

C. d. decemnotata Say, 1817 (1818)

Cicindela decemnotata Say, 1817 (1818). J. Acad. Nat. Sci. Philadelphia, 1:19.

Cicindela decemnotata decemnotata Say. Casey, T. L., 1913, Mem. Coleop., 4(1):24.

Cicindela decemnotata albertina Casey, 1913. Mem. Coleop., 4(1):24.

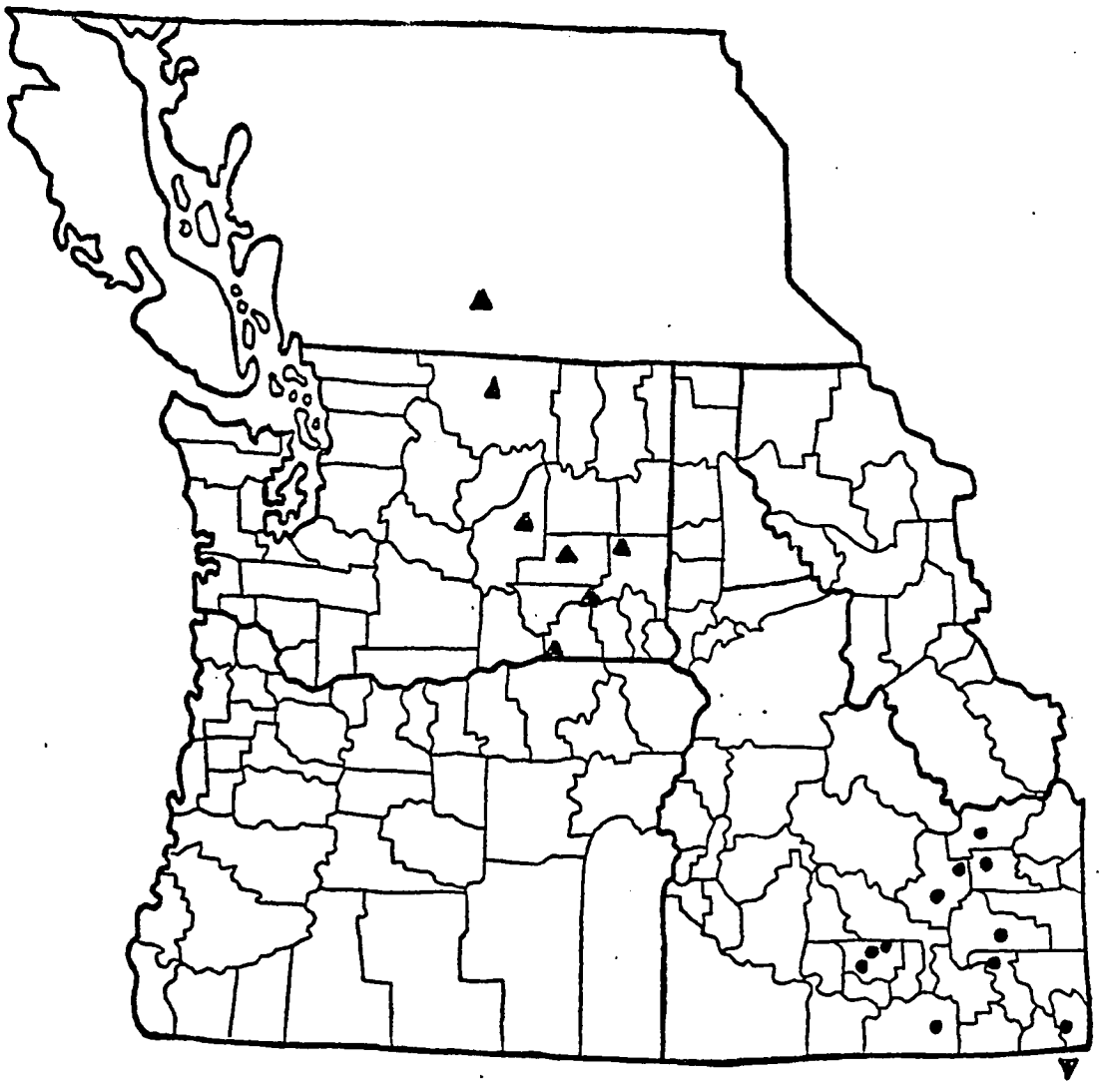
Cicindela lantzi E. D. Harris, 1913. J. New York, Ent. Soc., 21: 68-69.

Diagnosis. Dorsal coloration usually green with strong cupreous wash, but occasionally uniformly green, blue-green, or cupreous; maculation of average breadth: consisting of complete middle band, with large apical spot connected or not connected to apical lunule, and with humeral lunule usually absent but occasionally present in part or completely; female genitalia with outer half of lateral lobe of syntergum

Fig. 35. Pacific Northwets distribution of *Cicindela decemnotata*. See Appendix I for tabulation of localities.

Symbols:

● - *C. d. decemnotata*
▲ - *C. d.* new ssp. Clifford
▼ - *C. d. decemnotata* x new ssp. Rumpp



IX + X >18% of entire apical breadth of syntergum, with ventral ridges on either half of sternum VIII located at midline of each half, and with apices of sternum VIII narrowly rounded.

Synonymic notes. Casey (1913:24) based *C. d. albertina* partly on the ". . . apical lunule, which is . . . strongly divided, the outer part forming a rounded discal spot." Wallis (1961:40) stated that ". . . this is a characteristic not possessed even by the majority of Alberta specimens, and it was from this province that the [subspecies] was described." I surveyed 15 specimens in the AM collection from Alberta, CO., ID., and WY., finding the apical spot separated in 11. Localities of the four *decemnotata* morphs are: Alberta. Medicine Hat (1); CO. Larimer Co., South Park (2); CO. Routt Co., 10 mi S. Steamboat Springs (1). This random distribution of the *decemnotata* morph and Wallis' statement convince me that *albertina* should be synonymized with *C. d. decemnotata*.

E. D. Harris (1913 (68-69) described *C. lentzi* on a specimen from CO. Jefferson Co., Jefferson City (given by Harris as Jefferson). E. D. Harris and Leng (1916) synonymized it with *decemnotata*. I have not seen the holotype, but, after studying Harris' description and illustration, I tentatively concur with Harris and Leng. A complete humeral lunule is unusual for *C. decemnotata*, occasional occurrence of a humeral dot being the only

remnant, but the form of the middle band and the large apical spot exclude other possible species.

Typology. Say (1817 [1818]:19) stated that his specimen was collected by Thomas Nuttall on the "sandy alluvions of the Missouri, above the confluence of the river Platte." R. L. Huber (in litt., 1976) is currently attempting to work out Nuttall's itinerary and suggests that the type locality is in Montana. Many of Say's types are no longer extant and his collection should be surveyed to determine if the holotype of *C. d. decemnotata* still exists; if not, a neotype should be designated.

The holotype of *C. d. albertina*, a male, NM No. 45937, is from Alberta. Lethbridge. Holotype examined.

E. D. Harris (1913) did not state the sex or provenance of his holotype of *C. lantzi*. His collection is now at the Museum of Comparative Zoology, Harvard University, and presumably includes the holotype of *lantzi*.

Variation. I have already discussed variation in the form of the humeral and apical lunules. Dorsal coloration ranges from green, blue-green, green washed with cupreous, or cupreous. Willis and Stamatov (1971) summarized the variability in color of their series. I studied 42 specimens in the AM and UI collections, finding the variation presented in Table 27.

Range. A summary of the range of this subspecies has been presented in the species account. Several papers have delineated

Table 27. Variation in dorsal coloration of *Cicindela decemnotata decemnotata* (N = 42).

Dorsal Coloration	Number	Percent of Total
Green	4	9.52
Blue-green	1	2.38
Green with cupreous wash	28	66.67
Mainly cupreous	8	19.04
Green with apical third of elytra cupreous	1	2.38

the northern and eastern margins of the subspecies' range. It is now known from NV. (LaRivers, 1946), OK. (Drew and Bartholemew, 1962), or TX. (Gaumer and Murry, 1971). Willis (1970) questioned the one KS. record. Unfortunately, no published data exist for NM, although I have examined specimens from S.W. CO. None of the several collections I have surveyed has specimens from S.E. OR. or N.W. UT., areas where I would expect the subspecies to occur. The records by W. Horn (1930) for AK. and Schaupp (1883-1883) for CA. are probably in error.

Dates of occurrence. Data for specimens from CO., ID., and WY. (AM, UI) give the following chronology: 19 May - 13 July (most dates from March to June) and 24 August-6 September. The summer dates are for elevations above 1900 m. Lawton and Willis (1974:49) reported that their specimen collected 9 July was senescent.

Intergrade population. Five specimens from UT. Rich Co., summit Logan Canyon, 7800 ft (AM), are labelled as intergrades between *C. d. decemnotata* and an undescribed new subspecies. They have the cupreous color of *decemnotata* and the reduced maculation of the undescribed form. The locality is only 6 km south of the Idaho border and further collecting may reveal additional records including some from Idaho.

C. d. n. ssp. Clifford

Diagnosis. Dorsal coloration bright green; maculation as in *C. d. decemnotata*; female genitalia with outer half of lateral lobe of syntergum IX + X <18% of entire apical breadth of syntergum, with ventral ridges on either half of sternum VIII located lateral to midline of each half and with apices of sternum VIII acute.

Synonymic notes. This subspecies has not been previously recognized.

Typology. A typological statement cannot be made until the subspecies has been formally described.

Variation. The limited series available to me for detailed study (five specimens) shows minor differences in the length of the posterior arm of the middle band. One specimen has a small humeral dot, the other four lack all traces of the humeral lunule. The apical spot is confluent with the apical lunule in only one of the five. No Washington specimen I have seen is any other color dorsally than green.

Range. The entire range of the subspecies if presented in Figure 35 and Appendix I. A specimen from BC. Quesnel (OSU) is probably referrable to this subspecies on geographical grounds.

I have seen no Oregon specimens but expect the species in the Umatilla Basin as I have collected it at WA. Walla Walla Co., 3.9 km E. Wallula Junction, only 6 km north of the Oregon border.

Dates of occurrence. Leffler and Pearson (1976) gave the dates as: 17 March - 24 June, and 10 September - 10 October. I have collected mature 3rd instar larvae 16 April, 1974.

Cicindela (*Cicindela*) *purpurea* Olivier, 1790

(Figures 22 L and M, 23B, 36-41)

Cicindela purpurea Olivier, 1790. Entomologie, 2:14.

Cicindela marginalis Fabricius, 1801. Syst. Eleutheratorum, Kiliae, 1801:240.

Cicindela ramosa Gistl, 1837. Syst. Insectorum, Munich, 1:31.

Cicindela superba Dahl, in litt. (*fide* E. D. Harris and Leng, 1916). NOMEN NUDUM.

Cicindela (*Cicindela*) *purpurea* Olivier. Rivalier, E., 1954. Rév. Française d'Ent., 21:253.

Diagnosis. Adult: characters of *purpurea*-subgroup of *formosa*-group of *Cicindela*; labrum pale in both sexes; mesepisternal coupling sulcus Type B; elytral sculpture shallowly punctate-granulate; maculation variable according

Fig. 36. Scanning electronmicrographs of elytral sculpture of species of *purpurea*-group of *Cicindela* (anterior is toward the top of the page and median is toward the right-hand margin).

A. *Cicindela purpurea auduboni* (X 174)

B. *Cicindela plutonica* (X 172)

C. *Cicindela pugetana* (X 174)

to subspecies, but with angle, measured posteriorly, formed by bend of middle band, slightly greater than 135°. Aedeagus: beak elongate; lateral apical flanges evenly rounded; assymetry of shaft normal for species-group (slight). Female genitalia: sternum VIII with ventral surface of either half bearing low anteroposteriorly-oriented ridge with excavated area medial to it; 2nd gonocoxa with blunt tooth at anterior margin of ventral notch, and with area between notch and apex excavated but without margins delineated and without tubercles formed around bases of setae. Larva: primary pronotal setae 6 and 7 absent; pronotal coloration dark violet-bronze with green reflections; fixed spine of inner hook of abdominal tergum V 1/e of length of entire hook; pygopod surrounded by 18 setae. Pupa: no diagnostic specific characters.

Synonymic notes. *C. purpurea* received additional names by authors apparently unaware of the original description. I have not had access to these publications and will not comment on them

further here. Status of the name *Cicindela superba* Dahl requires review of the letter, if still extant, cited by E. D. Harris and Leng (1914). Until such a review is made, the name should be considered a *nomen nudum*.

Relationships. See discussion of *purpurea*-subgroup.

Subspecies. A review of this species over its entire extensive range is needed to clarify the status and interrelationships of some of the named forms. I recognize five subspecies, one of which requires a new name (Leffler, in press). Geographic limits of three of the subspecies are unclear, and I shall, in the present report, delineate the ranges of the other two. Other taxonomic problems exist and I shall treat them in their appropriate contexts.

I arrange the subspecies in two subspecies-sections which are diagnosed as follows:

purpurea-section: Dorsal surface of elytron gently arched in transverse cross-section; tendency toward polychromatism; green color, when present, decidedly olivaceous; aedeagus with ventral face of apex shallowly concave; range east of Cascade and Sierra Nevada Mountains. Included subspecies: *audubonì*, *cimarrona* and *purpurea*.

lauta-section: Dorsal surface of elytron not arched in transverse cross-section; not polychromatic (except for frequent blue cast in *lauta*); green color Lime-Green (*fide* Palmer, 1962); aedeagus with ventral face of apex straight; range west of Cascade

and Sierra Nevada Mountains. Included subspecies: *lauta* and new name Leffler.

The following are brief diagnoses and range outlines of the subspecies of *C. purpurea*. Exact geographic limits of some subspecies are incompletely documented. My Figures 38 and 41 present the entire known range of the *lauta*-section subspecies.

C. p. purpurea Olivier, 1790. Maculation limited to middle band, apical dot and apical lunule; elytral color rich cupreous-violet with green lateral margin, melanic phase also (Frost, 1932); female abdominal sternum VIII with ratio from Table 28 <40%. Range: southern and western boundaries uncertain, but definitely from S. Ontario and Quebec (Graves, 1965; Larochelle, 1974) south to GA. (Huber, in litt., 1976) and west probably to near east side of Mississippi River but not as far south as TE. (Graves and Pearson, 1973). No synonyms.

C. p. audubonì Le Conte, 1845. Maculation as in *C. p. purpurea*; elytral color ranging from brownish-violet to olivaceous green with varying amounts of cupreous and all combinations between; melanic phase also; female abdominal sternum ratio from Table 28 >50%. Range: outlined in subspecies account beyond. Included synonyms discussed in detail beyond.

C. p. cimarrona Le Conte, 1868. Maculation with complete humeral and apical lunules and middle band completely connected by marginal line; color ranging from dull green to reddish-brown to

Table 28. Proportion and character of parts of left half of sternum VIII in subspecies and intergrade of female *Cicindela purpurea*: Ratio, lateral margin to lateral edge of median ventral ridge/greatest breadth of entire left half.

Subspecies or Intergrade	No.	Range and $\bar{X}$ of Ratio in %	Shape of Apex
C. p. audubonii	7	50.0-61.5 (56.67)	rounded
C. p. cimarrona	9	42.3-56.5 (49.19)	ranging from pointed to rounded
C. p. purpurea	1	36.90	pointed
C. p. lauta	3	55.6-56.5 (56.20)	rounded and broad
C. p. lauta x new name Leffler	2	55.3-57.0 (56.15)	pointed but broad
C. p. new name Leffler	3	50.0-60.4 (54.17)	pointed but broad

Fig. 37. Left half of sternite VIII in females of subspecies of *Cicindela purpurea*. X 20.

A. *C. p. purpurea*

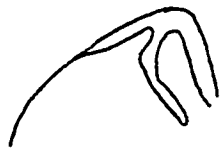
B. *C. p. audubonì*

C. *C. p. cimarrona*

D. *C. p.* new name Leffler

E. *C. p. lauta*

A



B

C

D

E

dull violet-brown, melanic phase also; female abdominal sternum VIII with ratio from Table 28 40-57%. Range: AZ., S. CO., NM. and perhaps S. UT.; exact boundaries not documented. Synonym: *C. p. ardelio* Casey, a narrowly maculate variation.

C. p. lauta Casey, 1897. Maculation as in *C. p. purpurea*; color: humeral umbo lacking pale spot in both sexes, elytra Lime-Green with varying amounts of blue wash, and legs uniformly metallic green. Range: presented in detail in subspecies account beyond. Synonym: *franciscana* Casey.

C. p. new name Leffler. Maculation as in *C. p. purpurea*; color: humeral umbo with pale spot in male, elytra Lime-Green with cupreous only along basal margin, and legs metallic cupreous. Range: presented in detail in subspecies account beyond.

C. p. audubonii Le Conte, 1845

Cicindela audubonii Le Conte, 1845. Boston J. Nat. Hist., 5:207.

Cicindela purpurea var. *audubonii* Le Conte, 1857 *nec* Le Conte, 1845. Trans. American Phil. Soc., Ser. 2, 11:37.

Cicindela purpurea var. *graminea* Schaupp, 1883-1884. Bull. Brooklyn Ent. Soc., 6:89.

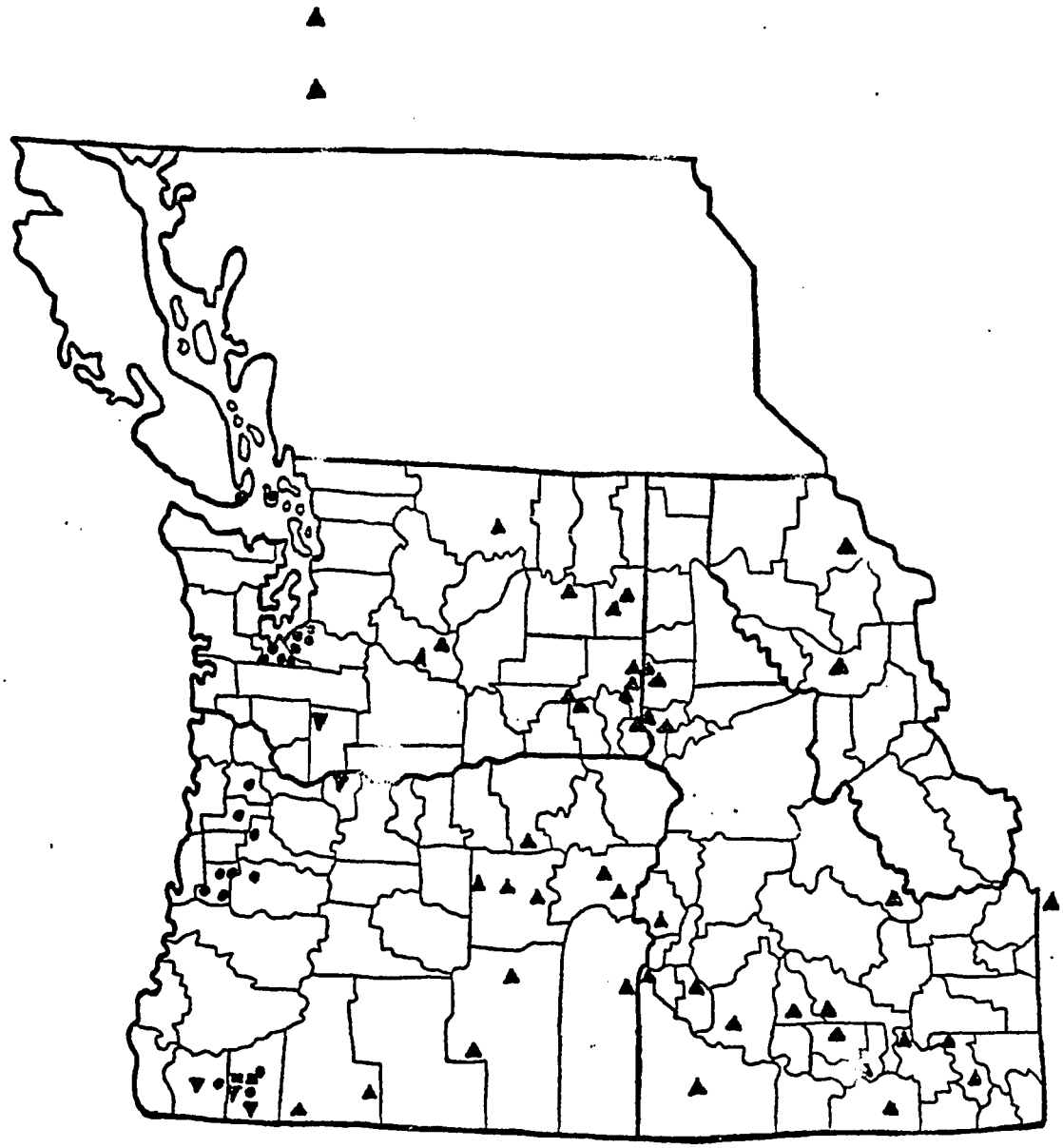
Cicindela purpurea inducta Casey, 1913. Mem. Col., 4(1):22.

Cicindela purpurea audubonii Le Conte. Casey, T. L. 1916, Mem. Col., 7(1):27.

Fig. 38. Pacific Northwest distribution of *Cicindela purpurea*. See Appendix I for tabulation of localities.

Symbols:

● - *C. p.* new name Leffler
▲ - *C. p. audubo·i*
▼ - *C. p. lauta*
■ - *C. p. lauta* x new name Leffler



Cicindela purpurea var. *nigerrima* Leng, 1918. J. New York Ent. Soc., 26:139.

Diagnosis. Characters of *purpurea*-section of *purpurea*-subgroup of *formosa*-group of subgenus *Cicindela*; maculation limited to middle band, apical dot, apical lunule, and, occasionally, humeral dot; elytral color ranging from brownish-violet to olivaceous-green, with varying amounts of cupreous, and all combinations in between, melanic phase also; female abdominal sternum VIII ratio of lateral margin to lateral edge of median ventral ridge/greatest breadth of left half >50%.

Synonymic notes. Le Conte's (1845) original description applied to the green morph of this subspecies. Confusion as to the correct date of this publication was ended by Leech (1941) Le Conte (1857) used the name *auduboni* for the black morph, thus creating further confusion which was confounded by Schaupp (1883-1884) who renamed the green morph *graminea* and Leng (1918) who used *nigerrima* for the black morph. Casey (1913) employed the name *inducta* for a black morph with a small humeral dot but not

otherwise distinctive. As far as I can determine, it was Casey (1916) who first used the same rank for *auduboni* as is used today, although he retained the black morph *nigerrima* as a subspecies as well. Wallis (1961) recognized that *nigerrima* is only a color phase of *auduboni*. It is well-known that black and green color phases occur together, but the genetical interactions have never been studied.

Typology. The type locality of *C. p. auduboni* is Fort Union, now a National Historical Site, located at the confluence of the Yellowstone and Missouri Rivers in Williams Co., North Dakota (Huber, in litt., 1976). Le Conte's type, if still extant, may be in the Museum of Comparative Zoology, Harvard University, where types of his more recently described taxa are housed; provenance of the type of *auduboni* should be ascertained for certain.

Auduboni Le Conte, 1857, and *graminea* Schaupp, 1883-1884, are replacement names.

Casey (1913) based *inducta* on a male from Colorado, no further data, a specimen I have examined.

Dahl (1941) designated a male from CO. Jefferson Co., Chimney Gulch, Golden as lectotype of *C. p. nigerrima* Leng, a specimen preserved in the American Museum. Lectotype examined.

Variation. The extensive synonymy under *C. p. auduboni* arose from its polychromatic nature. Color varies from completely black ("*nigerrima*") to every shade between brownish-violet to violet-washed olivaceous-green. The violet phase resembles *C. p. purpurea*,

but the color of the nominate subspecies is cupreous-violet rather than brownish-violet, a small distinction but readily apparent upon direct comparison of the two subspecies. It was the violet phase that led Hatch (1938) to record *C. p. purpurea* from the Pacific Northwest. Complete lack of violet wash is unknown for *auduboni*, such pure green morphs that I have seen so identified in collections from the Pacific Northwest actually being *C. pugetana* or *plutonica*.

Melanics are common east of the Rocky Mountains, and, if specimens from Utah (Tanner, 1929) are correctly identified, are also found in the eastern Great Basin. Melanic *purpurea* were not listed by La Rivers (1946) or Sumlin (1976). I have seen no melanics from the Pacific Northwest. I do not think that mere lack of melanism ought to be used as a subspecific criterion for the Pacific Northwest populations until the genetic or physiological nature of the character is understood. Browning (1900:582) reported "dark indigo" specimens from UT. Salt Lake Co., Salt Lake Valley near the Jordan River.

Maculation is uniform except for the occasional occurrence of a humeral dot. Casey's (1913) *inducta* was based on a melanic with a humeral dot.

Dates of occurrence. Published records all refer to the spring and fall dates for the subspecies. Leffler and Pearson (1976) gave the following dates for Washington: 7 April - 13 June and 9 September - 9 October.

Range. The eastern margin of the range of *auduboni* has not been delineated, although it is the subspecies found in Iowa (Eckhoff, 1939), Kansas (Willis, 1970) and Oklahoma (Drew and Bartholemew, 1962). Graves and Pearson (1973) suggested that *auduboni* and not *purpurea* is found in Mississippi and Tennessee. The species is unknown in Alabama (Nicolay and Weiss, 1932), or Texas (Gaumer and Murray, 1971). La Rivers (1946) and Sumlin (1976) gave Nevada records and Tanner (1929) listed Utah records. I have seen no specimens from California. Wallis (1961) presented the Canadian distribution. The range in the Pacific Northwest is given in the present paper.

Intergrades. Wallis (1961) and Willis (1968) stated that *C. p. purpurea* intergrades with *auduboni* in the northern Great Plains. Casey (1913:21) described *C. p. auguralis* from Colorado, no further data. I have studied specimens and consider the form to be an intergrade between *auduboni* and *cimarrona*. It has the humeral and apical lunules complete to broadly divided and with the marginal line not confluent with either lunule.

C. p. lauta Casey, 1897

Cicindela lauta Casey, 1897. Ann. New York Acad. Sci., 9:296.

Cicindela lauta franciscana Casey, 1913. Mem. Coleop., 4(1):23.

Cicindela purpurea lauta Casey. E. D. Harris and Leng, 1916, Cicindelinae of North America, New York:4.

Diagnosis. Characters of *lauta*-section of *purpurea*-subgroup of *formosa*-group of subgenus *Cicindela*; maculation limited to middle band, apical portion of apical lunule, and, occasionally apical and humeral dots; both sexes lacking pale humeral umbonal spot reddish dorsal coloration, when present, not sharply delineated into defined areas and dingy in tone; humeral umbone without pale spot; legs metallic green.

Synonymic notes. Casey's name *lauta* had been applied to populations west of the Cascade and Sierra Nevada Mountains by E. D. Harris and Leng (1916), W. Horn (1930), and Leng (1902). Nicolay and Weiss (1932) united *lauta* under *auduboni*, but Nicolay (1934), perhaps convinced by Smyth (1933), returned *lauta* to separate subspecific status and separated it from "*mirabilis* (= new name Leffler)." Unfortunately, Hatch (1953) retained *lauta* in synonymy under *auduboni*. My treatment in the

present report will hopefully clarify the relationships in the *lauta*-section.

I have examined the holotypes of *lauta* and *franciscana*. Casey (1913) distinguished *franciscana* on its "more obscure" color and transverse middle band lacking a posterior arm. Characters of *franciscana* are not distinctive if the holotype is placed among a series of *lauta*, which I have done.

Typology. The holotype of *C. p. lauta* is a male, NM no. 45734, from *CA. Siskiyou Co.* The holotype of *C. lauta franciscana* is a male, NM no. 45935, from *CA*, no further data. Both holotypes examined. I herewith fix the type locality of *lauta* as *CA. Siskiyou Co., Dunsmuir.*

Variation. *C. p. lauta* varies in extent and intensity of cupreous coloration, even in series from the same locality. Some individuals lack all trace of cupreous color and are uniformly green including the propleura. Others have cupreous propleura, pronotal discs, and areas on the head. The cupreous has a bronzy tone and is more nebulous compared with the rich cupreous, sharply delineated areas in *C. p.* new name Leffler. There is variation in the intensity of blue wash on the elytra, some individuals lacking all traces and others having as much as completely blue lateral margins. Casey (1913) was misled by the variation in angulation and completeness of the middle band. Most specimens have uniformly metallic green legs but some have brassy

highlights, never uniformly cupreous as in the other *lauta*-section subspecies.

Dates of occurrence. A survey of specimens in the AM, NM, UC, and UI collections gave the following dates: 10 April-21 June and 28 July-14 October.

Range. I shall treat this in detail beyond.

Intergrades. I shall treat this in detail beyond.

C. p. new name Leffler, in press

Cicindela mirabilis Casey, 1914 *nec* Dejean, 1831. Mem. Coleop. 5(5):358-359.

Cicindela lauta mirabilis Casey. Casey, T. L., 1916, Mem. Coleop., 7(1):27.

Cicindela purpurea lauta Casey, pars. Harris, E. D., and C. W. Leng, 1916, Cicindelinae of North America, New York:4.

Cicindela purpurea mirabilis, Casey. Smyth, E. G., 1933, Ent. News, 44(8):202.

Diagnosis. Characters of *lauta*-section of *purpurea*-subgroup of formosa-group of subgenus *Cicindela*; maculation limited to middle band, apical portion of apical lunule, and, occasionally apical and humeral dots; male usually with pale humeral umbonal spot,

absent in female; cupreous dorsal coloration delineated into defined markings on head, pronotal disc, propleura, and basal margins of elytra, brilliant in tone; legs metallic cupreous.

Synonymic notes. Casey (1914:358-359) described *C. mirabilis*. However, that name is preoccupied by *Cicindela mirabilis* Castenau, 1835 (= *Prothyma fulvipes* Dejean, 1831). I have (Leffler, in press) proposed a replacement name. The subspecies has vacillated in the literature between suppression (E. D. Harris and Leng, 1916; and W. Horn (1930) and varying taxonomic rankings. Smyth (1933) first used the name in the same context in which I use it.

Typology. The holotype, a female, NM no. 45936, was collected 28 February, 1909, by G. R. Pilate at CA. Placer Co., Dutch Flat.

Variation. There is minor variation in intensity and extent of the cupreous markings on the head (see fig. 39, A and B), and elytral color ranges from lime-green (*fide* Palmer, 1962) to blue-green. There is sexual dimorphism in development of a pale spot on the humeral umbo: present in males, absent in females. However, one male out of 10 examined lacks the umbonal spots. I shall discuss size variation beyond.

Dates of occurrence. Results of a pooling of all available dates for this subspecies over its entire range are: 28 February-20 May and 4 September-9 October and a single July

Fig. 39. Color pattern of head in subspecies of *Cicindela purpurea*.

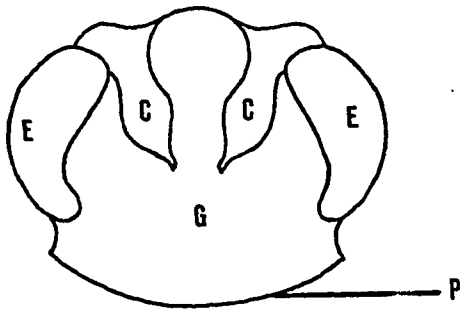
A. *C. p.* new name Leffler, OR. Jackson Co., Medford (OSU)

B. *C. p.* new name Leffler, CA. Placer Co., Dutch Flat (AM-Topotype)

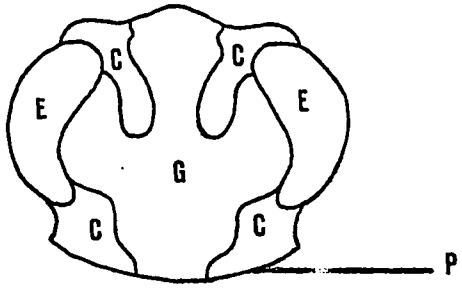
C. *C. p. lauta* Casey, OR. Hood River Co., Hood River (AM).

Legend for abbreviations:

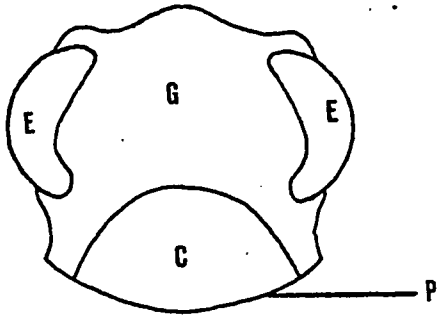
C - cupreous coloration
E - eye
G - green coloration
P - posterior margin



A



B



C

Fig. 40. Dice graphs of lengths of left elytron of samples from three localities of *Cicindela purpurea* new name Leffler.

A. CA. Placer Co., Dutch Flat (type locality).
Sample size: male, 7; female, 4.

B. OR. Jackson Co., several localities.
Sample size: male, 1; female, 5.

C. WA. Thurston Co., Rocky Prairie, 4.8 Km. N Tenino.
Sample size: male, 2; female, 1.

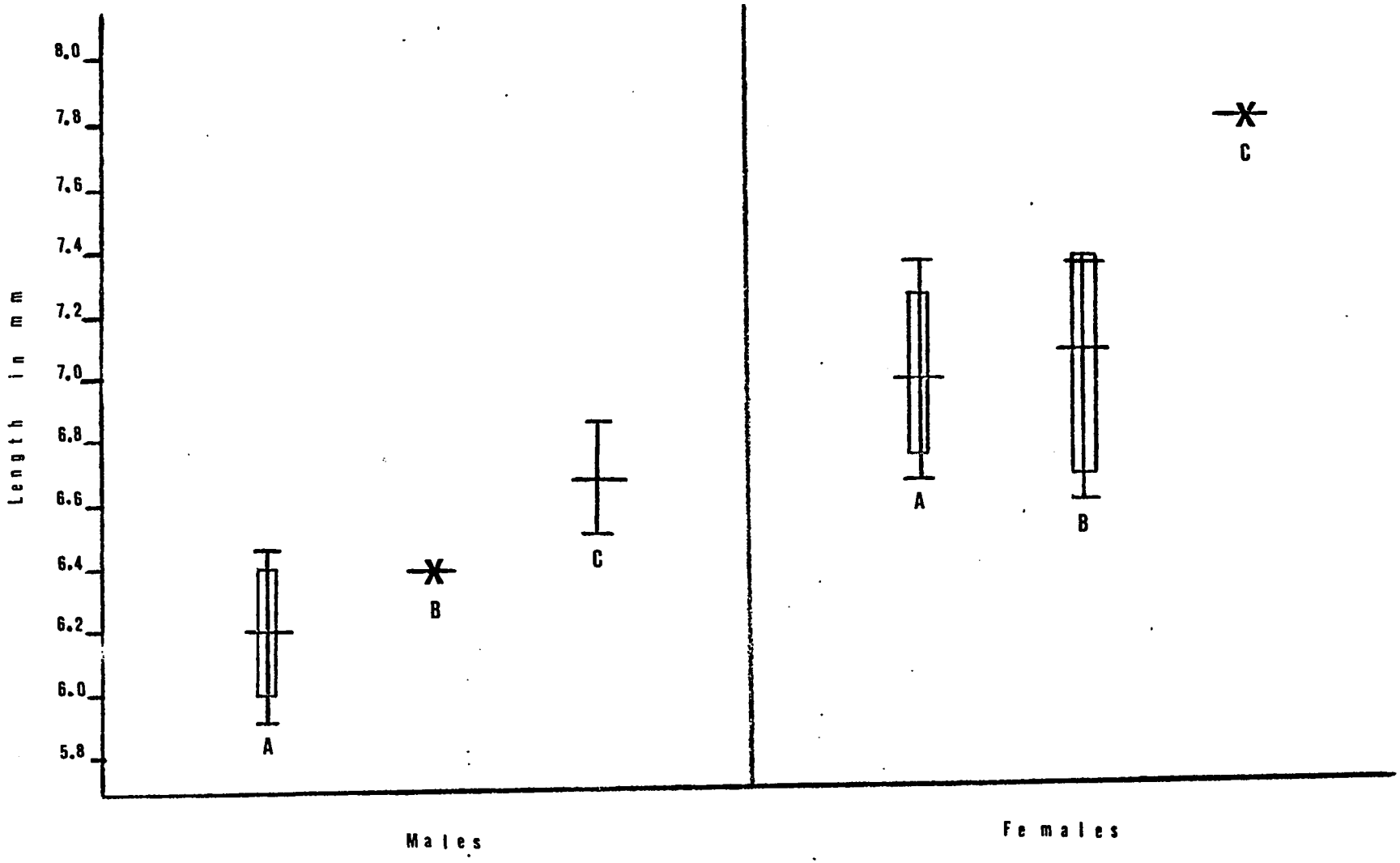
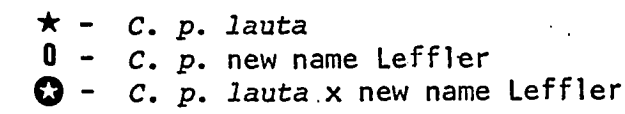
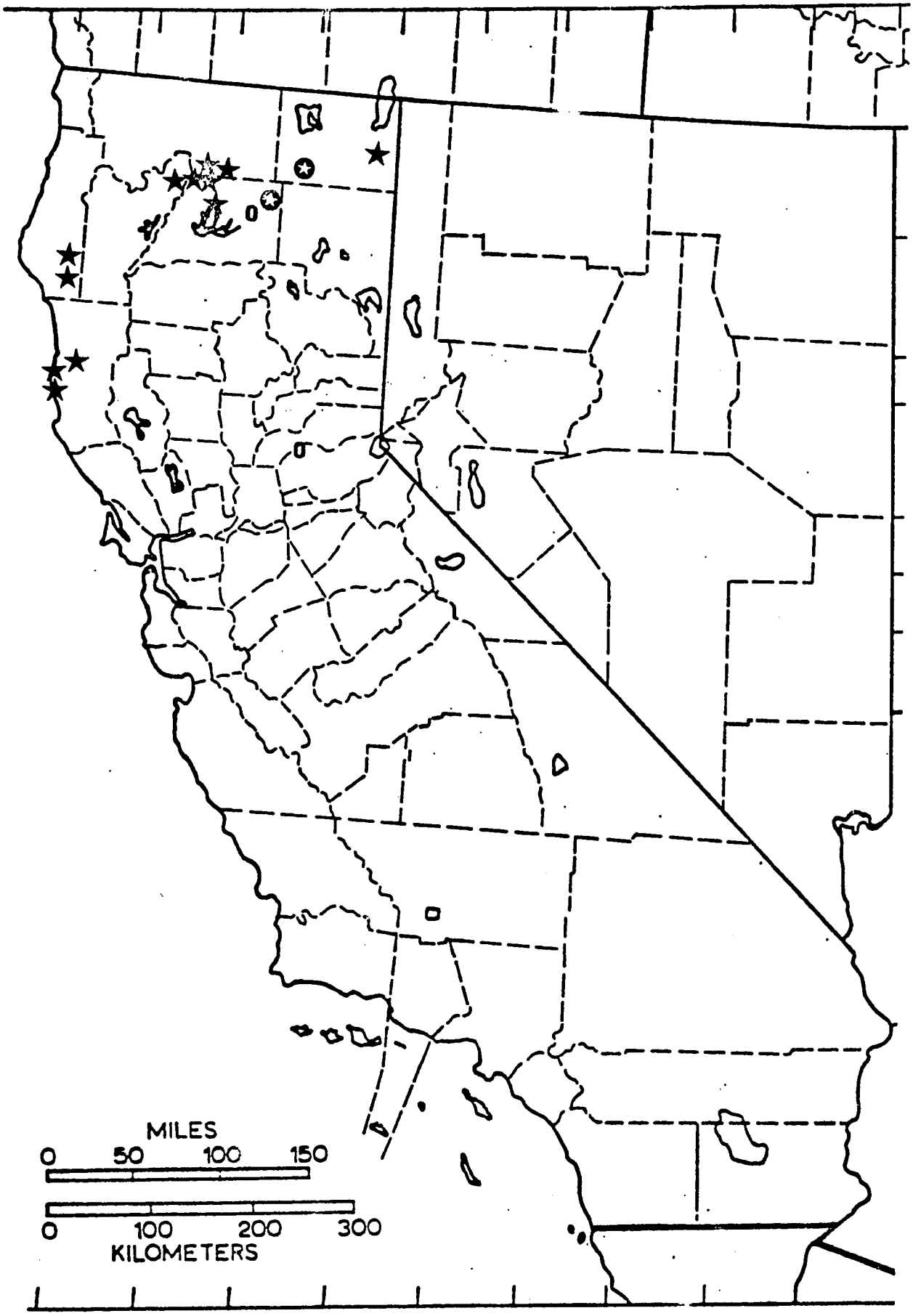

8.0
7.8
7.6
7.4
7.2
7.0
6.8
6.6
6.4
6.2
6.0
5.8
Length in mm
A
B
C
Males
A
B
C
Females

Fig. 41. California distribution of *Cicindela purpurea, lauta, C. p.* new name Leffler, and intergrade populations.




MILES
0 50 100 150
0 100 200 300
KILOMETERS

record (no day). California records are all for February (28th only) and March, certainly an aberration of collecting.

Range. I shall treat this in detail beyond.

Intergrades. I shall treat this in detail beyond.

Distribution and Intergradation of the *lauta*-section Subspecies

Typical individuals of *C. p. lauta* may be distinguished from typical individuals of *C. p.* new name Leffler by differences in the tone of the reddish markings, coloration of the legs, and presence or absence of the humeral umbo spot in the males. The two subspecies are also parapatric. However, in areas of the northern Sierra Nevada Mountains of California and the western foothills of the Cascades in southern Oregon, the subspecies intergrade resulting in animals ranging from pure *lauta* to pure new name Leffler at the same locality.

I have identified five localities in Oregon and California where the two subspecies intergrade. I have also surveyed collections at AM, NM, OSU, UC, and UI for distributional records of the two subspecies. Figure 38 and the appropriate section in Appendix I present the ranges and localities in the Pacific Northwest. Fig. 41 maps the California records which are as follows:

C. p. new name Leffler

CALIFORNIA. Placer Co.: Dutch Flat (AM, NM-type locality)

Shasta Co.: Burney (NM).

C. p. new name Leffler X *lauta* intergrades

Note: I am repeating Oregon records for completeness' sake.

CALIFORNIA. Modoc Co.: Hackamore (AM). Shasta Co.: McArthur (UC).

OREGON. Jackson Co.: Gold Hill (NM); Rogue Riffles (OSU).

C. p. lauta

CALIFORNIA. Humboldt Co.: Blocksburg (UC); Fort Seward (AM).
Mendocino Co.: Caspar (NM); Mendocino (AM); Ryan Creek, 8 km. N. Willits (UC). Modoc Co.: Cedar Pass (AM). Shasta Co.: Carbon (AM); Castella (NM); Echo Lake, 13 Km. WNW Castella (NM). Siskujou Co.: Dunsmuir (AM); Upper Soda Springs (NM). Trinity Co.: Carrville (UC).

A brief discussion of variation of the intergrade populations is in order.

1. CA. Modoc Co., Hackamore: The sample consists of two specimens. The female is typical of new name Leffler. The male is colored like *lauta* but has the tibiae brassy rather than green and the pale umbo spot absent.

2. CA. Shasta Co., McArthur: The one specimen, a male, has the cupreous head and pronotol color of new name Leffler, but the legs are completely green and the pale umbo spot is absent.

3. OR. Jackson Co., Rogue Riffles: The one specimen, a male is colored dorsally like *lauta* and lacks the pale umbo spots, but the legs, except for the brassy-washed green metafemora, are cupreous.

4. OR. Jackson Co., Gold Hill: A series of six males presents a complete transition from *lauta* to new name Leffler. The one specimen most like the latter has pale umbonal spots, but dull cupreous dorsal coloration, and green femora, however.

I shall discuss my hypothesis as to how the geographic distributional relationships may have developed in "Historical Geology" beyond.

Integrity of *C. p.* new name Leffler

When I began this study, I believed that two taxa were represented, one restricted to the Sierra Nevada Mountains and the other found in western Oregon and Washington. However, my examination of specimens revealed no characters other than a northward clinal increase in size to distinguish two taxa. I still lack sufficient material from the northern part of the range, but plotting of elytral lengths of three populations (see fig. 40) reveals some overlap. Student's t-tests showed no significant differences at the 95% level of significance. In coloration as well the populations are identical. Thus, I consider the entire population to represent a single subspecies.

Cicindela (Cicindela) plutonica Casey, 1897

(Figures 22 O, 43)

Cicindela plutonica Casey, 1897, Ann. New York Acad. Sci. 9:296-297

Cicindela tranquebarica plutonica Casey. W. Horn, 1908-1915, Gen. Insect., 82:1-486.

Cicindela plutonica leachi Cazier, 1936, Pan-Pacific Ent., 12(3):123-124. NEW SYNONYMY.

Cicindela purpusea ab. *plutonica* Casey. Hatch, M. H., 1953, Univ. Washington Publ. Biol., 16:38.

Diagnosis. Adult: characters of *purpurea*-subgroup of *formosa*-group of *Cicindela*; labrum pale in male, black in female; mesepisternal coupling sulcus Type B; elytral sculpture shallowly punctuate, not granulate, giving shiny lustre; maculation ranging from traces of middle band and apical lunule to immaculate: dorsal coloration forming transitional series from green to black. *Aedleagus*: beak elongate; lateral apical flanges extremely narrow, nearly obsolescent, not forming triangular point; assymetry of shaft normal for

species-group (slight). Female genitalia: lateral lobes of syntergum IX + X of equal breadth for entire length; sternum VIII with apices blunt, emargination broadly rounded, and ventral surface of either half bearing low anteroposteriorly-oriented ridge with excavated area medial to it; second gonocoxa with blunt tooth at anterior margin of ventral notch, without excavation between notch and apex, but with tubercles formed around bases of setae. *Larva*: unknown. *Pupa*: unknown.

Synonymic notes. Casey (1897) described *C. plutonica* as a full species belonging to the *purpurea*-group, but later (1909) placed it in the *tranquebarica*-group. W. Horn (1908-1915) considered it only a subspecies of *tranquebarica*. Cazier (1936) gave it specific rank although still related to *tranquebarica* and described *C. p. leachi* as a green subspecies. As the green morph, as well as blue ones and blue-black ones, occurs throughout the range of the species, I consider this so-called *"leachi"* to be merely a color-phase and place it in synonymy. The male genitalia of *C. plutonica* ally it clearly with *C. purpurea*, but differences

in the genitalia, male and female, and the elytral sculpture, and sympatry with *C. purpurea* in Oregon and Idaho, lead me to consider it a full species.

Relationships. See discussion of *purpurea*-subgroup.

Subspecies. With reduction of *leachi* to synonymy, there are no longer subspecies of *C. plutonica*.

Typology. The holotype of *C. plutonica*, a male, NM no. 45948, is from CA. Placer Co. Holotype examined. I do not know the provenance of the holotype of *C. p. leachi*. Since it is not in the American Museum collection, I presume it is at the University of California at Berkeley. The holotype, a female, is from CA. Modoc Co., Warner Mountains, 9000-10,000 ft.

Variation. *C. plutonica* is polychromatic. Color ranges from bright shining green through blue-green, blue, blue-black, to black. There is minor variation in maculation: of 12 specimens available for study, one has a trace of the transverse arm of the middle band, eight have narrow apical spots (one also being the same specimen with the middle band), and four are immaculate. Sexual dimorphism is seen in labral color and depth of elytral punctures: males have pale labra and shallow punctures, and females have black labra and deep punctures. A single male (of nine seen) has weak, indistinct elytral granules, but not at all as developed in *C. purpurea*.

Dates of occurrence. A summary of records from specimens and literature (Andrews, 1975; Beer and Maser, 1973; and Cazier, 1936,

1939) is as follows: 12 March-8 July and 12 September-14 October. The March, April, and some October dates are from ID. Canyon Co., Parma, elevation 685 m. Andrews (1975) and Cazier (1936, 1939) gave June and July dates for localities in California, elevation 2,600 m. This suggests correlation between temporal and elevational occurrence. Andrews' (1975:40) record for 27 January 1965 at CA. Lassen Co., Doyle, 5,000 ft. is probably of a diapausing individual. Andrews said nothing about diapause but did state that the specimen was found beneath a rock.

Range. The Pacific Northwest distribution is presented in this report. *C. plutonica* is known from California (Andrews, 1975; Casey, 1897; and Cazier, 1936, 1939) and Nevada (La Rivers, 1946, and Sumlin, 1976), but details of its southern distribution are poorly known.

Cicindela (Cicindela) pugetana Casey, 1914

Cicindela pugetana Casey, 1914, Mem. Coleop., 5(1):20-21.

Cicindela purpurea pugetana Casey. Horn, W., 1908-1915, Gen. Insect., 82:1-48b.

Cicindela denverensis pugetana Casey. Casey, T. L., 1916, Mem. Coleop., 7(1):27.

Cicindela splendida pugetana Casey. Nicolay, A. S., and H. B. Wiess, 1932, Ent. News, 40(3):353.

Fig. 42. Pacific Northwest distribution of *Cicindela pugetana*. See Appendix I for tabulation of localities.

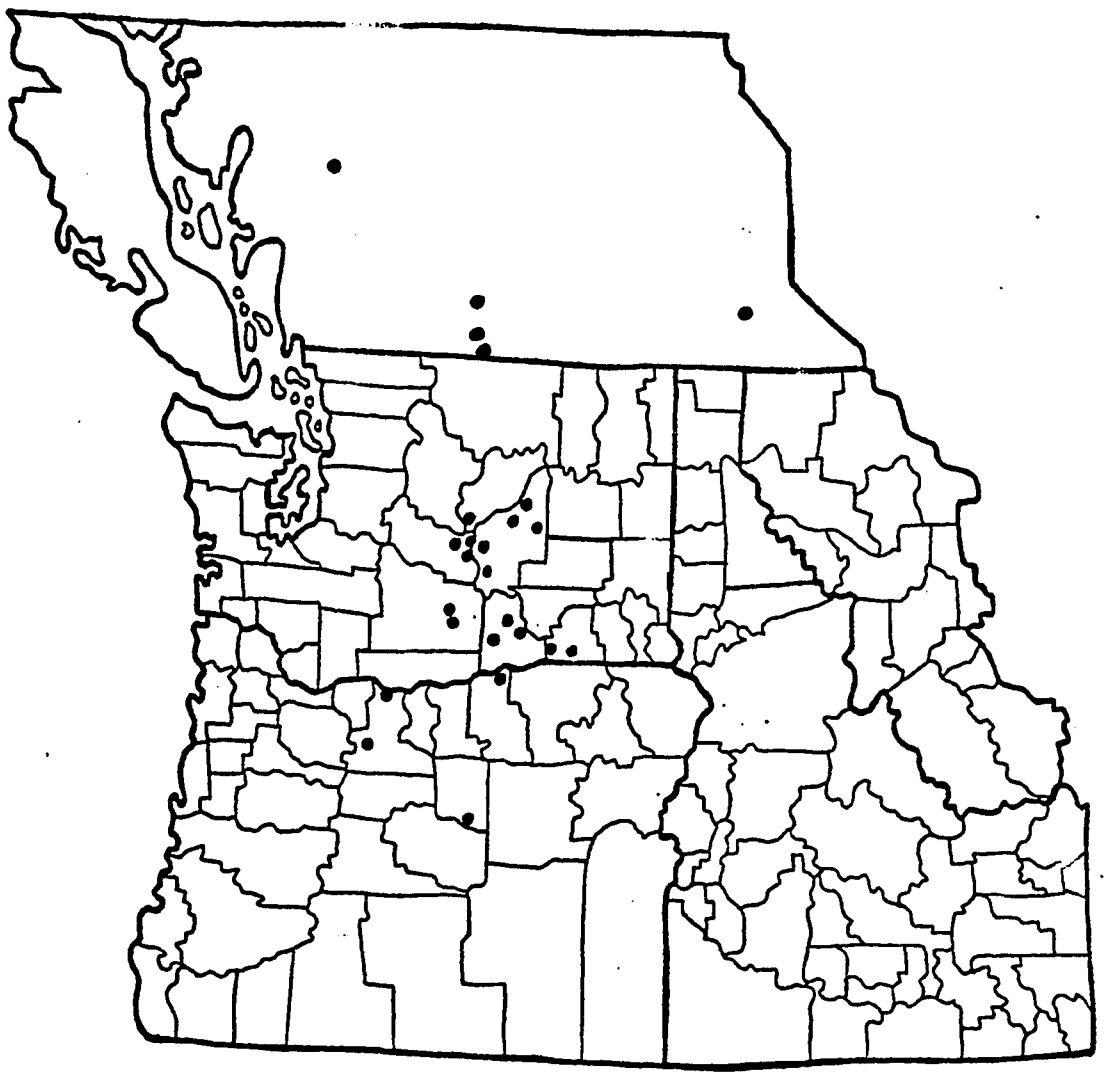
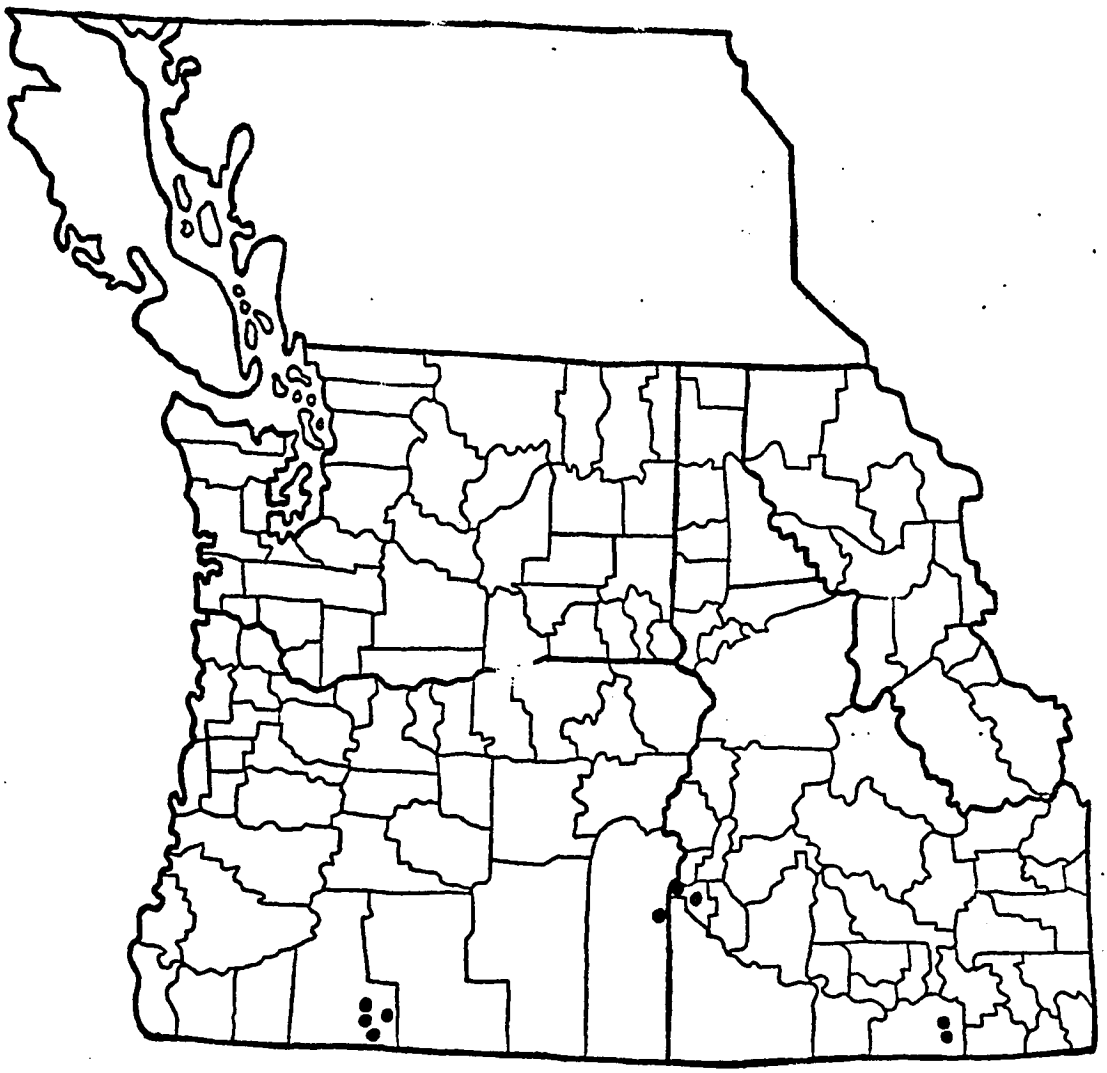


Fig. 43. Pacific Northwest distribution of *Cicindela plutonica*. See Appendix I for tabulation of localities.



Cicindela purpurea var. *pugetana* ab. *nigerrimoides* Hatch, 1938, Univ. Washington Publ. Biol., 1(5):232-233.

Cicindela limbali pugetana Casey. Rivalier, E., 1954, Rev. Française d'Ent., 21:253.

Diagnosis. Adult: characters of *purpurea*-subgroup of *formosa*-group of *Cicindela*; labrum pale in male, usually black in female; mesepisternal coupling sulcus Type B; elytral sculpture obsolescently punctate-strongly granulate, giving dull lustre; maculation ranging from complete middle band, apical dot, and apical lunule to immaculate; color forming transitional series from green to blue and black. *Aedeagus*: beak elongate; lateral apical flanges narrow but with tiny triangular earlike points; shaft decidedly assymetrical with left skew. *Female genitalia*: lateral lobes of syntergum IX + X of equal breadth for entire length; sternum VIII with apices pointed, emargination narrowly rounded, and ventral surface of either half bearing low anteroposteriorly-oriented ridge with

excavated area medial to it; second gonocoxa with blunt tooth at anterior margin of ventral notch, without excavation between notch and apex, but with tubercles formed around bases of setae. *Larva*: primary pronotal setae six and seven absent; pronotal coloration metallic red-violet with blue reflections; fixed spine of inner hook of abdominal tergum V one-half of length of entire hook; pygopod surrounded by 22-24 setae. *Pupa*: unknown.

Synonymic notes. Casey (1914) described *C. pugetana* as a full species of his *purpurea*-group. Other authors have retained this association but have placed *pugetana* as a subspecies of *denverensis* (Casey, 1916), *limbalis* (Rivalier, 1954), *purpurea* (E. D. Harris and Leng, 1916; Hatch, 1938, 1953; W. Horn, 1908-1915; and Willis, 1967), or *splendida* (Nicolay and Weiss, 1932).

Hatch (1938) described *nigerrimoides* as a black aberration. This black morph, as well as blue-green and blue ones, occurs throughout the range of the species, and I, like Wallis (1961), consider it a synonym of *C. pugetana*. Its characters ally *pugetana* with *purpurea* but differences in the genitalia, male and

female, and elytral sculpture, and sympatry with *purpurea* in Washington, lead me to consider it a full species.

Relationships. See discussion of *purpurea*-subgroup.

Subspecies. With reduction of *nigerrimoides* to synonymy, there are no longer subspecies of *C. pugetana*.

Typology. The holotype of *C. pugetana*, a male, NM no. 45942, is from BC, no furth r data. The holotype of *C. purpurea* var. *pugetana* ab. *nigerrimoides* Hatch, a male, is in the Hatch Collection, now at OSU, was collected 15 April, 1928, by Merton C. Lane WA. Yakima Co., Buena. Both holotypes examined.

Variation. *C. pugetana* is polychromatic. Color ranges from dull green through blue-green to blue; melanics are common, but, unlike *plutonica* there are no morphs intermediate between blue and black. Maculation varies from possession of a complete middle band, apical dot, and apical lunule to completely immaculate, with a range of intermediates. Of a series of 27 specimens, six (22.2%) have maculation complete for the species, but only one is completely immaculate. Sexual dimorphism is present in labral color: males have pale labra, and females have black labra. However, one female, of 13 available, has a pale labrum.

Dates of occurrence. Leffler and Pearson (1976) gave the following dates, modified by subsequent collecting:
5 March-12 June and 21 September-25 October.

Range. The entire range of the species is presented in Figure 42 and Appendix I.

The *silvatica*-group

Diagnosis. Adult: labrum long: ratio, length/basal breadth > 60% (except *C. gemmata* Gebler); frons excavated with vertex boss; mesepisternal coupling sulcus Type B. *Aedeagus:* shaft of middle lobe symmetrical; beak produced; dorsal surface of apex strongly concave in anteroposterior direction; flagellum short and thickened; sclerite six well-developed and strongly sclerotized.

Rivalier (1950, 1954) united a number of species as his group I, with *C. silvatica* as its "type." Mandl (1935, 1936, and 1937) revised *C. silvatica* and *C. soluta*, but the characters and species limits of the remaining six species are poorly understood. The species-group was based on the short, thick aedeagal flagellum in combination with a sclerotized sclerite six. In addition, the species have the frons strongly excavated between the eyes and, except for *C. gemmata* Gebler, a long labrum (ratio, length/basal breadth > 60%). Detailed review of the Palearctic species is needed. I have been able to study two Palearctic species (*silvatica* and *soluta*) in detail and three others superficially, and, thus, I feel that comparisons with the Nearctic species are unwise at present.

Relationships. The *silvatica*-group is apomorphic in labral proportions, frontal excavation, mesepisternal coupling sulcus anatomy, elytral sculpture, sclerotization of the aedeagal sclerite 6, and (based on *C. nebraskana*) pupal morphology. The eight included species differ widely in chaetotaxy, labral morphology, elytral sculpture, and (as far as known) male and female genitalia, indicating either incorrect grouping by Rivalier (1950, 1954) or the diverse remnants of a group whose connecting lineages are now extinct. If the *silvatica*-group is monophyletic, its relationships to other species-groups in the subgenus *Cicindela* are unclear. Of the other eight species-groups, the *maritima*-group is so generalized that it shows no more similarity to the *silvatica*-group than to any other group. The *campestris, chinensis, formosa, hybrida, pudibunda, pulchra,* and *transbaicalica*-groups all have one or another male genitalic modifications that eliminate them from consideration. The *silvatica*-group perhaps arose from an ancestor which had sclerite 6 sclerotized but in which the flagellum was not elongated. The two Nearctic species are no more similar to one another than to any of the Palearctic species and may represent separate invasions from the Old World.

Accounts of the Pacific Northwest species of the *silvatica*-group

Uncertainty as to the number and delineation of Nearctic species and subspecies caused by confusion in the literature and identification in museum collections has led me to perform

statistical analyses. I have had 487 specimens from museum and private collections and have been able to study types of most of the named taxa.

Table 29 is a list of localities with members and provenances of specimens.

Descriptions of Characters Used in Analysis of Species and Subspecies of the *silvatica*-group

I chose 18 characters and ratios in analyzing the species and subspecies of *Cicindela longilabris* and *C. nebraskana*. Characters will be referred to by number in the text (e.g., "Character 1").

1. Length of left elytron from apex of scutellum. This measurement was used as the best representation of body size. I consider it superior to total length because it is unbiased by telescoping of body segments and problems of differential drying. Length is measured from the level of the apex of the scutellum to the apical edge of the left elytron (the right elytron was measured in case of any damage).

2. Breadth of head at widest point including the eyes. This measurement is another indication of body size. It represents the widest point across the dorsum of the head including both eyes.

3. Ratio: breadth of head/length of elytron. Self-explanatory.

Table 29. Localities of *Cicindela longilabris* and *C. nebraskana* used in statistical analyses.

Locality	N		Provenance
	Male	Female	
C. l. perviridis			
WA. Clallam Co., Olympic Nat. Park	4	6	OSU, SL
WA. Okanogan Co., Black Canyon	3	3	NM
WA. Snohomish Co., Miner's Ridge, NE of Glacier Peak	1	10	OSU
WA. King and Chelan Co., vic. Stevens Pass	4	4	OSU, SL
OR. Clackamas Co., Government Camp	10	14	OSU, NM
OR. Jackson Co., Mount Ashland	10	10	ODA
CA. Placer Plumas, Sierra, and Tuolumne Cos.	5	5	NM

Table 29 (continued)

Locality	N		Provenance
	Male	Female	
C. l. laurentii X *perviridis*			
BC. Creston	20	20	NM, SL, UBC
BC. crest Rocky Mountains above 1000 m, several localities	2	7	NM, UALTA
ALTA, Banff	3	8	UALTA
MT. Missoula Co., several localities	17	18	UMT
MT. Silver Bow and Jefferson Cos., vicinity of Butte	3	5	OSU, SL
MT. Lewis and Clark Co., Helena	1	10	NM
OR. and WA. north of Wallowa Mtns., several localities	8	12	NM, OSU
OR. Baker and Grant Cos., several localities	7	8	NM, OSU, SL

Table 29 (continued)

Locality	N		Provenance
	Male	Female	
C. l. laurenti			
ALTA. 152 Km. N Coleman, Gorge Creek	9	11	UALTA
MT. Meagher Co., 15 Km. S Neihart, Sheep Creek	4	1	NM
SD and WY. Black Hills, several localities	0	4	NM
CO. Jefferson and Larimer Cos., several localities	3	2	NM
CO. Mineral Co., Creede	3	2	NM
SW.UT and NW.AZ. several localities	4	1	AM, NM

Table 29 (continued)

Locality	N		Provenance
	Male	Female	
C. n. chamberlaini			
BC. Copper Mountain	5	2	NM
WA. Chelan, King, and Kittitas Cos., several localities	2	18	NM, OSU, SL
WA. Skamania and Yakima Cos., several localities	3	4	OSU, SL
WA. Whitman Co., Pullman	5	5	NM, OSU
OR. Harney Co., Steens Mountains (Topotypes)	7	8	NM, OSU
CA. Alpine Co., Sonora Pass	1	7	NM
UT. Utah Co., vicinity of Provo	2	4	NM

Table 29 (continued)

Locality	N		Provenance
	Male	Female	
C. n. nebraskana X *chamberlaini*			
ALTA. 152 Km. N Coleman, Gorge Creek	0	3	UALTA
WY. Teton Co., Yellowstone Nat. Park	2	6	NM
ID. Bear Lake Co., Copenhagen Basin	12	13	OSU
ID. Caribou Co., Pocatello	2	2	NM, OSU
ID. Caribou Co., Soda Springs	7	8	OSU
C. n. nebraskana			
ALTA. Medicine Hat	3	8	NM
SASK. Gull Lake	6	11	AM
SASK. Coteau Lakes, and MT. Roosevelt Co., 25 Km. S Scobey	4	7	AM

4. Length of labrum including median tooth. The labrum is measured along the midline from the clypeal margin to the apex of the median tooth.

5. Basal breadth of labrum. The labrum is measured along the base (clypeal margin).

6. Ratio: length of labrum/breadth of labrum. Self-explanatory.

7. Ratio: length of labrum/length of elytron. Self-explanatory.

8. Apical outline of labrum. Specimens may be either (a): tridentate, or (b): unidentate (see figs. 44 A and B).

9. Color of labrum. There are three color patterns.

   a. uniformly pale except, perhaps, for darkened apical edge

   b. apical edge and midrib broadly darkened or mottled

   c. uniformly darkened, or nearly so (care must be taken to ascertain that the labrum is not merely greasy).

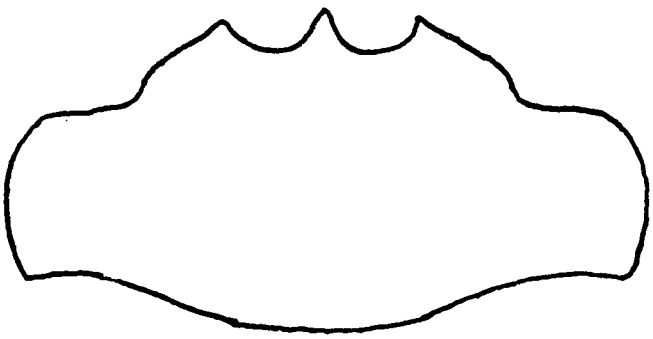
10. Length of left metatibia. The left metatibia (the right one is substituted in case of damage) is measured along the lateral surface.

11. Length of left metatarsus. Lengths of each of the five left tarsal articles (the right tarsus is substituted in case of missing articles) are taken and summed. Claws are excluded.

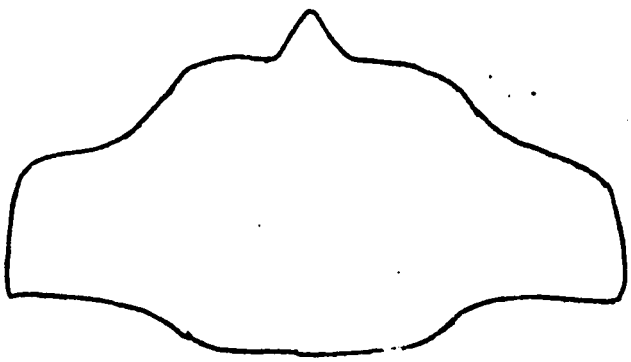
Fig. 44. Labra of *silvatica*-group to illustrate states of character 8. X 50.

A. Tridentate (variable 1)

B. Unidentate (variable 2)



A



B

12. Ratio: length metatibia/length metatarsus. Self-explanatory.

13. Form of elytral sculpture. The two species and the groups of subspecies of *C. longilabris* may be distinguished by the elytral sculpture.

a. *nebraskana*-type: *C. nebraskana* (fig. 48C) has large, defined punctures arranged in fairly regular and straight transverse rows with smooth ridges lacking granules.

b. *perviridis*-type: *C. longilabris* differs from *C. nebraskana* in that the punctures are shallow, irregular in outline, often confluent to varying degrees, and arranged randomly rather than in discrete rows. *C. l. perviridis* (fig. 49B) have the granules composed of distinct but appressed divisions.

c. *longilabris*-type: *C. l. longilabris* and *laurenti* have the granules undivided (fig. 49A).

14. Number of elytral punctures in a selected 2 mm^2 area. The tool illustrated in fig. 45 is placed over the basal half of the left elytron and the number of complete and partial punctures visible at 30X are counted.

15. Color of elytron. Fifteen different color shades are recognizable among various populations of *C. longilabris* and *C. nebraskana*. These were coded a-o, inclusive.

Fig. 45. Tool used in counting elytral punctures in species of silvatica-group of *Cicindela*. The pin is held by the head and placed on the specimen with the free edge of the plastic piece along the suture and the notch along the basal margin. Complete and partial punctures within the 2 mm. diameter hole are counted under 30 X magnification. Measurements of the pin and plastic are unimportant; only the diameters of the hole applies to observations made.

Legend:

h - 2 mm. diameter hole
n - notch
p - pin
pp - sturdy piece of transparent plastic

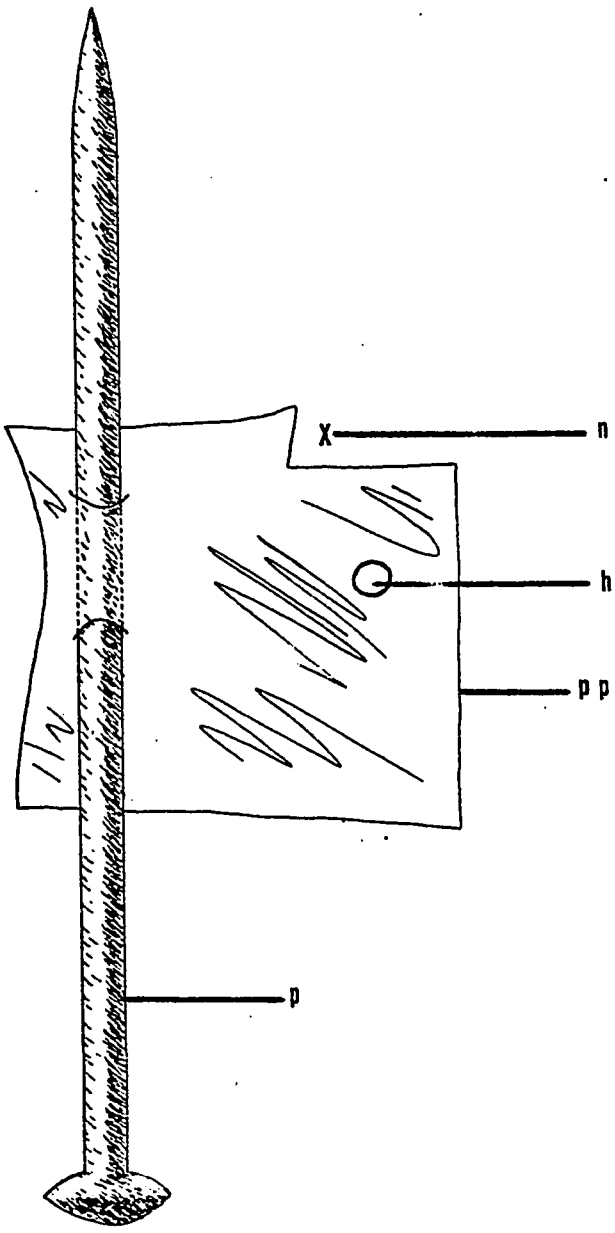

X
n
h
p p
p

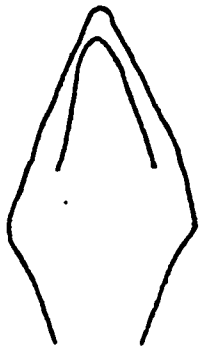
Fig. 46. Male genitalia in species of *silvatica*-group of *Cicindela*. X 20.

A. *Cicindela longilabris*: apical third, ventral view

B. *Cicindela longilabris*: apical half, left side

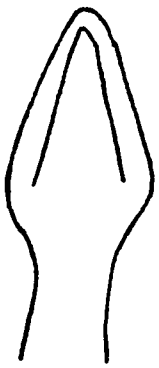
C. *Cicindela nebraskana*: apical third, ventral view

D. *Cicindela nebraskana*: apical half, left side



A

B



C

D

Fig. 47. Female genitalia in species of *silvatica*-group of subgenus. *Cicindela*. X 24.

A. *C. longilabris*: syntergum IX + X, dorsal view

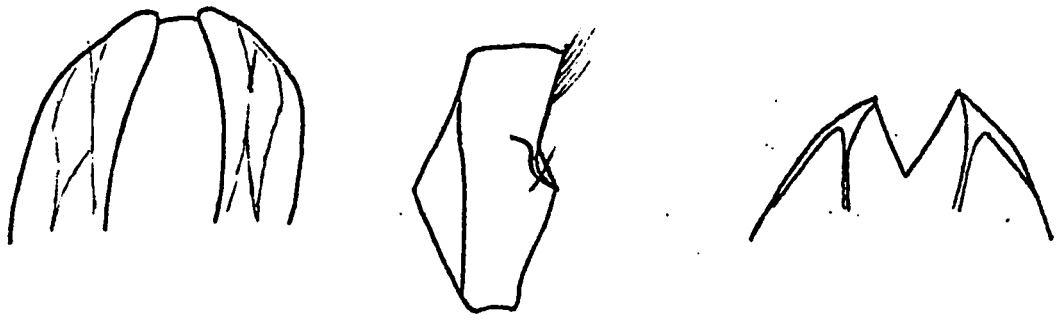
B. *C. longilabris*: left 2nd gonocoxa, ventral view

C. *C. longilabris*: sternite VIII, ventral view

D. *C. nebraskana*: syntergum IX + X, dorsal view

E. *C. nebraskana*: left 2nd gonocoxa, ventral view

F. *C. nebraskana*: sternite VIII, ventral view



A B C

D E F

Fig. 48. Scanning electronmicrographs of elytral sculpture of species of *silvatica*-group of *Cicindela* (orientation same as for fig. 36).

A. *Cicindela longilabris longilabris* (X 202)

B. *Cicindela longilabris perviridis* (X 192)

C. *Cicindela nebraskana chamberlaini* (X 191)

Fig. 49. Scanning electronmicrographs of elytral granules of two subspecies of *Cicindela longilabris* (orientation same as for Fig. 36).

A. *Cicindela longilabris longilabris* (X 970)

B. *Cicindela longilabris perviridis* (X 970)

a. olive-green

b. dark dull green, with or without brassy reflections

c. bright green

d. greenish-blue

e. blue

f. bluish-violet

g. greenish-brown

h. green, with cupreous tinge

i. cupreous, with green tinge

j. cupreous

k. bronzy-brown

l. brownish-black

m. brownish-black, tinged with green

n. uniformly black

o. black with green speckles

16. Maculation pattern. Seventeen different patterns of maculation are recognizable among various populations of *C. longilabris* and *C. nebraskana*. These were coded a-q, inclusive, and are illustrated in fig. 50, a-q.

17. Approximate measurement of angle of bend of middle band. This angle was not actually measured but could be easily assigned to one of three arbitrary classes, a-c, inclusive, by inspection.

a. greater than 45°

b. less than 45°

Fig. 50. Elytral maculation patterns in *silvatica*-group species of *Cicindela*, character 16 of statistical analysis: A-Q. X 6.

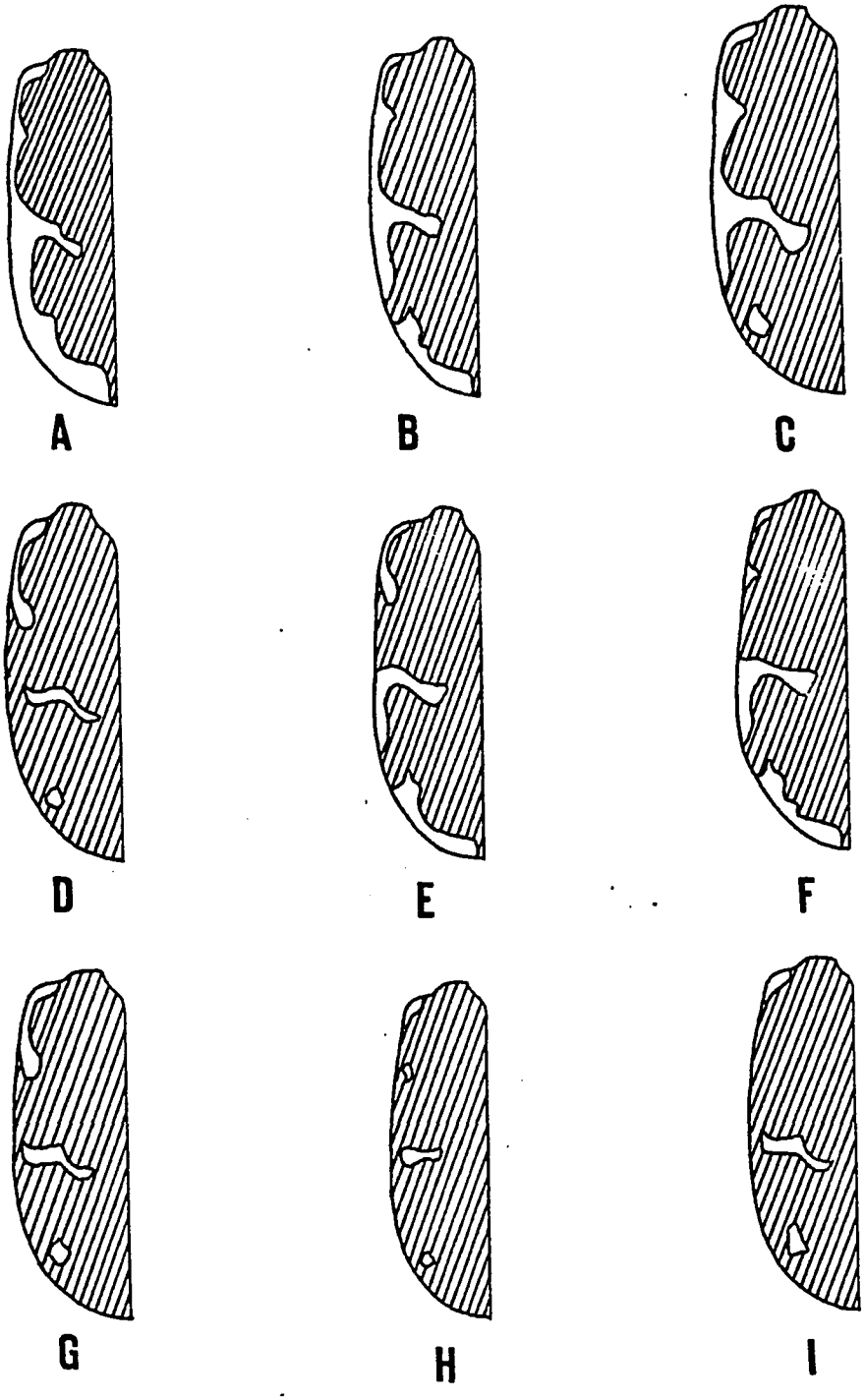
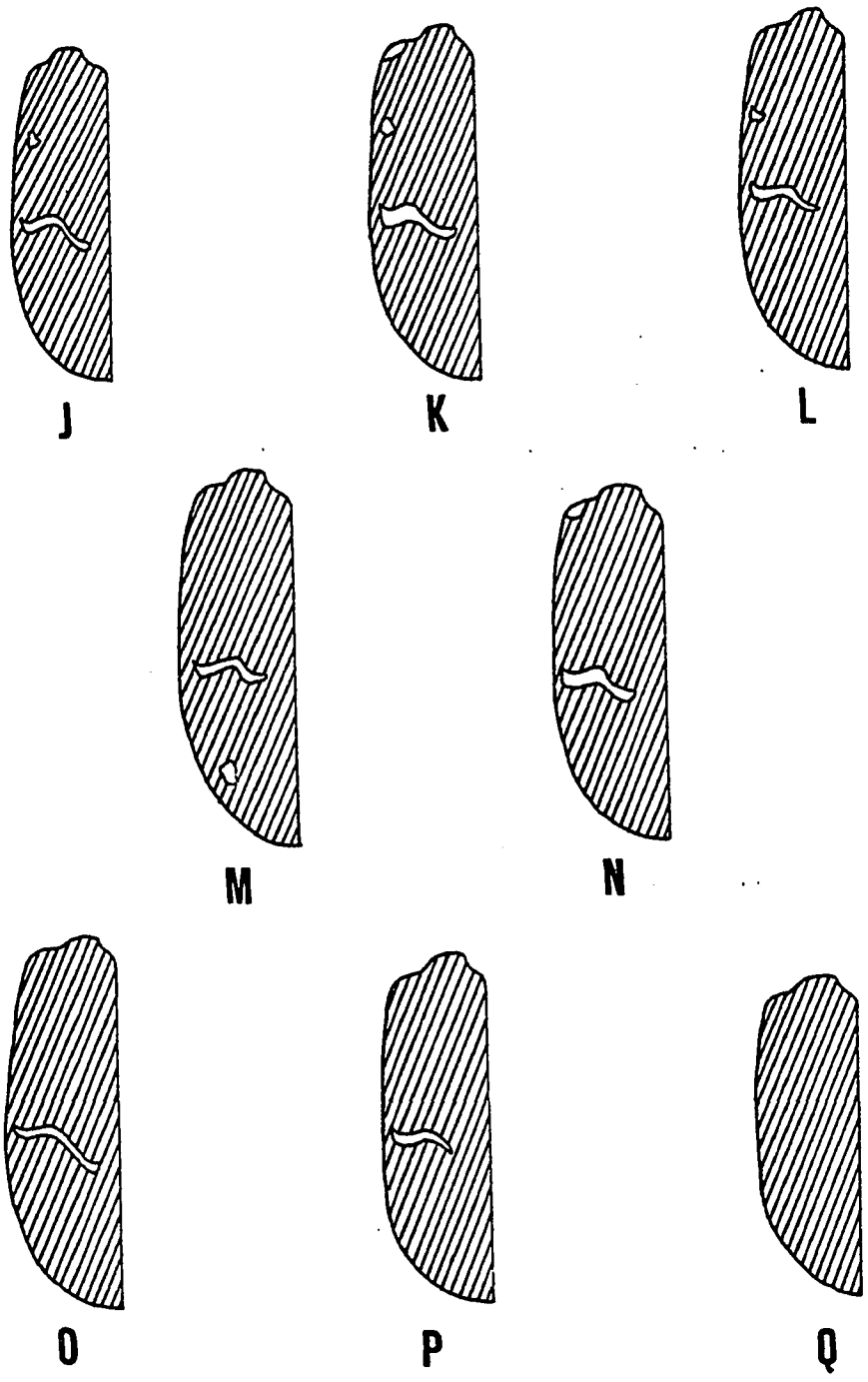

A
B
C
D
E
F
G
H
I

Figure 50 (continued)



c. too incomplete for measurement (corresponding to class p of character-state 16) or middle band absent (corresponding to class q of character-state 17)

18. Ventral abdominal coloration. Seven different color shades are recognizable among various populations of *C. longilabris* and *C. nebraskana* for sterna 1-4 (males) or 1-5 (females). The terminal sternite in both sexes is often non-metallic and brownish or black, and is thus not included. The seven color shades are coded a-g, inclusive.

a. metallic green

b. metallic bluish-green, with or without violet reflections

c. metallic blue

d. metallic bluish-violet

e. black, with green, blue, and/or violet reflections

f. uniformly black

g. brown, with green, blue, and/or violet reflections

Tables 30 to 68 present results of a discriminant analysis of 11 quantitative characters of *C. longilabris* and *C. nebraskana*. Table 69 is a summary of the discrimination rankings, that is, the order of usefulness of the characters as determined by computer analysis. The rankings will hereafter be called Rank X where X = 1-11, corresponding to the 11 characters. For example, Rank 1

Table 30. Pooled within groups covariance matrix for species of the *silvatica*-group of *Cicindela*.

A. Males

B. Females

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.20699										
C2	.04915	.02985									
C3	-.51746	.10823	4.25218								
C4	.02861	.00969	-.03453	.01137							
C5	.04700	.01579	-.06017	.00916	.02161						
C6	-.08410	-.02524	.21569	.26641	-.22412	20.03041					
C7	-.07731	.01645	.63913	.07896	.01579	3.39819	1.19699				
C10	.12300	.03570	-.22678	.02450	.03558	.06421	.04938	.12832			
C11	.12591	.03738	-.22499	.02416	.03609	.03733	.03490	.11767	.14316		
C12	.02873	.01144	.03313	.03078	.01655	.00714	.38219	.30086	-.21864	11.31411	
C14	-.00336	-.00871	-.07221	.01069	-.00385	.19154	.17086	.07169	.02753	1.02596	1.92733

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.20202										
C2	.04961	.02798									
C3	-.38950	.08789	3.00393								
C4	.02641	.00701	-.01929	.01140							
C5	.03890	.01557	-.00608	.00926	.02040						
C6	.01796	-.05330	-.66428	.24193	-.19100	16.05114					
C7	-.08535	.00955	.54811	.08228	-.03281	2.89491	1.13768				
C10	.11006	.03075	-.16933	.01765	.02821	-.04331	-.00567	.10910			
C11	.10663	.03220	-.12399	.01877	.02735	.02766	.01025	.09763	.12522		
C12	-.35585	-.35149	-2.27131	.10488	-.08663	7.18419	2.00705	.34536	-.61234	2911.73730	
C14	.05336	-.00096	-.25390	.02112	.00692	.77699	.13913	.02711	.05197	-6.00988	1.35152

Table 31. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) for males of *Cicindela longilabris* (1) and *C. nebraskana* (2). * shows a group centroid. The table shows complete separability of the two species.

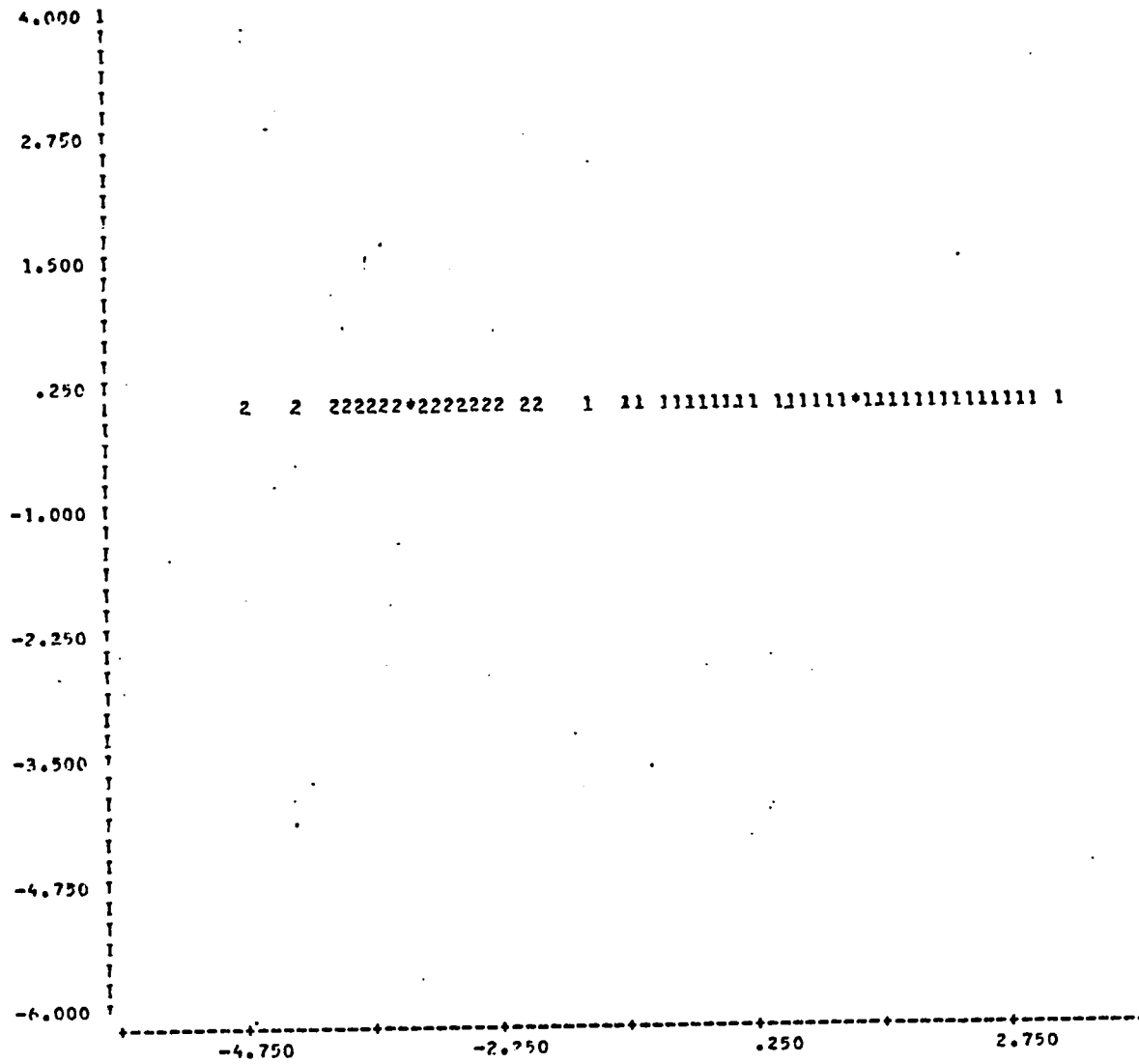

4.000
2.750
1.500
.250
-1.000
-2.250
-3.500
-4.750
-6.000
-4.750
-2.250
.250
2.750

Table 32. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) for females of *Cicindela longilabris* (1) and *C. nebraskana* (2). * shows a group centroid. The table shows complete separability of the two species.

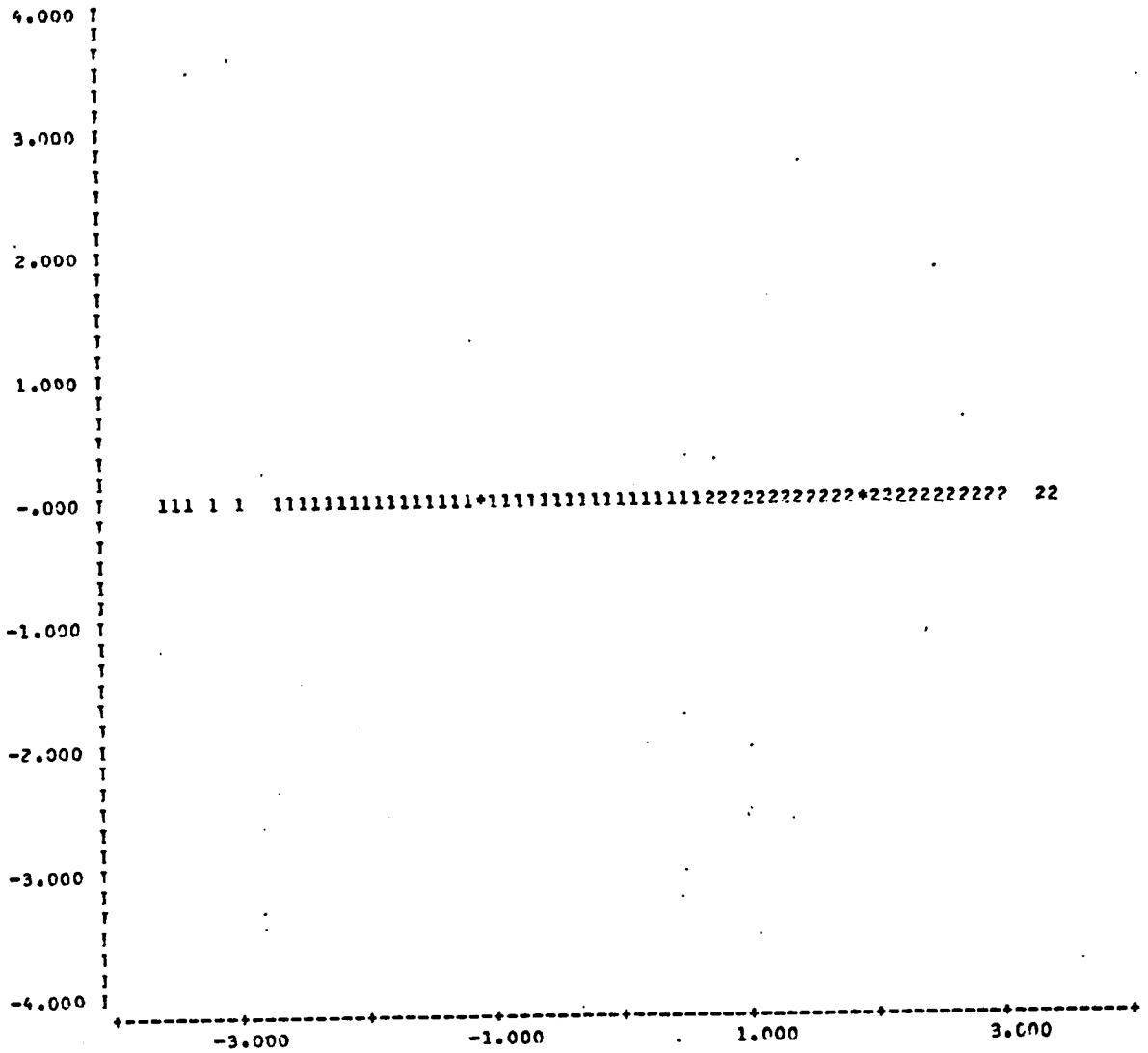

4.000
3.000
2.000
1.000
-.000
-1.000
-2.000
-3.000
-4.000
111 1 1 1111111111111111*1111111111111111122222222222*22222222222 22
-3.000
-1.000
1.000
3.000

Table 33. Pooled within groups covariance matrix for *Cicindela longilabris laurenti* and *C. l. perviridis*.

A. Males

B. Females

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.09717										
C2	.02179	.01412									
C3	-.23934	.06297	2.05861								
C4	.01116	.00522	.00740	.00722							
C5	.01657	.00722	.00474	.00382	.00919						
C6	.03612	.02718	.15020	.23196	-.09849	14.30998					
C7	-.05717	.02157	.58577	.04592	.01516	2.72103	.92648				
C10	.05396	.01856	-.04442	.01187	.01582	.10185	.04366	.07904			
C11	.05575	.02044	-.03325	.01037	.01677	-.00779	.02019	.04115	.08236		
C12	.04352	.00492	-.35521	.05724	.01467	2.48210	.55238	.49124	-.17354	12.14091	
C14	-.02231	.00663	.20421	.01183	.02223	-.14592	.19410	.08513	.01648	1.49989	1.65108

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.10176										
C2	.03218	.02128									
C3	-.11105	.09380	1.61933								
C4	.01704	.00621	-.00874	.00944							
C5	.01655	.01046	.04251	.00602	.01156						
C6	.27955	-.03041	-1.66824	.25196	-.07212	13.79151					
C7	.00464	.01135	.11316	.07700	.03907	2.37175	.98649				
C10	.03926	.01981	.03380	.00984	.01165	.10359	.04039	.05502			
C11	.04261	.02463	.03124	.01273	.01572	.10351	.06649	.05616	.12643		
C12	-.01180	.04295	.61617	-.02476	.01458	-1.63254	-.27812	.22761	-.03325	7.56556	
C14	-.02974	-.00484	.08050	-.01221	.00683	-.71918	-.07005	-.01225	.04210	-.64939	1.81347

Table 34. Statistical information from discriminant analysis of males of *Cicindela longilabris laurenti* (groups 5, 8, 9) and *C. l. perviridis* (groups 1-3) based on 11 characters. See text for explanation of characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	20.	10.	19.	0	15.	0	0	2.	1.

UNGROUPED.

NUMBER 57.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	8.77350	8.68300	8.64263	0	8.48400	0	0	3.48000	8.71000
C2	3.61500	3.43700	3.57368	0	3.71400	0	0	3.65000	3.78000
C3	41.22250	39.59600	41.34789	0	43.78600	0	0	43.07500	43.40000
C4	1.43500	1.44200	1.44789	0	1.43600	0	0	1.45500	1.47000
C5	2.21650	2.14800	2.18632	0	2.19000	0	0	2.23000	2.20000
C6	64.80600	67.11200	66.28421	0	65.45600	0	0	65.26000	70.43000
C7	16.35200	16.59100	16.75474	0	16.89000	0	0	17.18000	16.60000
C10	4.96950	4.86200	5.01474	0	4.78200	0	0	4.46000	5.40000
C11	5.21950	5.09800	5.22632	0	5.12000	0	0	4.66000	5.64000
C12	95.25650	95.35300	92.27842	0	93.47800	0	0	96.13500	95.74000
C14	10.85000	10.10000	9.52632	0	9.40000	0	0	10.50000	12.00000

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	.33908	.27170	.24859	0	.32622	0	0	.32527	1.00000
C2	.15783	.07243	.16194	0	.15209	0	0	0	1.00000
C3	1.28679	.89521	1.41543	0	1.12311	0	0	1.64756	1.00000
C4	.08685	.10530	.05580	0	.15614	0	0	.04958	1.00000
C5	.12132	.08284	.09789	0	.15749	0	0	.02709	1.00000
C6	3.35495	4.01665	4.08821	0	3.27891	0	0	.67682	1.00000
C7	.84386	.84072	.89448	0	1.22195	0	0	1.24451	1.00000
C10	.22853	.24997	.23448	0	.25577	0	0	.01414	1.00000
C11	.24228	.22720	.49886	0	.31169	0	0	0	1.00000
C12	2.99540	2.28622	2.70555	0	3.10763	0	0	.30406	1.00000
C14	1.22582	.56765	1.17229	0	1.14018	0	0	.70711	1.00000

Table 34 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3	4	5
C1	9.01498	12.74400	9.29167	-3.32172	4.87332
C2	-13.85603	-10.42775	-14.78531	-.05557	-11.44680
C3	11.14121	10.67970	13.98785	.58974	10.73795
C4	6.69781	1.45655	6.69585	-1.25701	1.09870
C5	-2.97061	4.09405	-.00132	5.16424	4.30144
C6	-2.88234	5.25699	.20429	6.29182	5.38914
C7	-2.74849	-7.24622	-7.20817	-6.25665	-6.87911
C10	5.25740	3.51316	-.09009	1.31703	-2.27375
C11	-4.01222	-3.26797	-.74913	-.40283	1.00774
C12	-3.93907	-2.74757	-.29131	-1.34109	1.12335
C14	.53262	.99407	-.01952	-.23736	-.08290

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3	4	5
C1	27.4057	38.7420	28.2468	-10.0981	14.8150
C2	-33.2007	-116.657	-89.7807	-.333663	-48.7341
C3	5.56621	9.80028	7.33671	.309404	5.63360
C4	60.1577	15.0305	60.0343	-12.0701	11.3445
C5	-26.9134	38.2502	-.852989	48.2281	40.1730
C6	-.746969	1.36237	.5204135-01	1.63055	1.39602
C7	-2.44755	-6.45291	-6.41893	-5.59831	-6.12590
C10	15.7219	11.1741	-.286346	4.19539	-7.23201
C11	-12.4427	-10.1346	-2.32009	-1.24926	6.19537
C12	-1.01084	-.705079	-.7218916-01	-.344379	.298427
C14	.338535	.631600	-.1240246-01	-.150808	-.5266306-01
CONSTANT	-60.5227	-351.319	-202.325	-6.20824	-233.037

CENTROIDS OF GROUPS IN REDUCED SPACE

	1	2	3	4	5
GROUP 1	.86969	.83070	.07898	.86936	-.09415
GROUP 2	.81214	-.63398	1.25632	-.47149	-.19712
GROUP 3	.39444	-1.16979	-.76205	-.06609	.32172
GROUP 5	-4.44723	-.79262	.49962	.53592	-.11428
GROUP 8	-.79034	2.11565	.01480	-.69952	.67621
GROUP 9	-.40922	.79627	-1.23257	-.68647	-1.25074

Table 35. Statistical information from discriminant analysis of females of *Cicindela longilabris laurenti* (groups 5, 8, 9) and *C. l. perviridis* (groups 1-3) based on 11 characters. See text for explanation of characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	20.	10.	19.	0	5.	0	0	2.	1.

UNGROUPD.

NUMBER 57.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	8.77350	8.68300	8.64263	0	8.49400	0	0	8.48000	8.71000
C2	8.61500	3.43700	3.57368	0	3.71400	0	0	3.45000	3.78000
C3	41.22250	39.59600	41.34789	0	43.78600	0	0	43.07500	43.40000
C4	1.43500	1.44200	1.44789	0	1.43600	0	0	1.45500	1.62000
C5	2.21650	2.14800	2.18632	0	2.19000	0	0	2.23000	2.30000
C6	64.60600	67.11200	66.28421	0	65.45600	0	0	65.26000	70.43000
C7	16.35200	16.59100	16.75474	0	16.83000	0	0	17.18000	18.60000
C10	4.96950	4.86200	5.01474	0	4.78200	0	0	4.48000	5.40000
C11	5.21950	5.09800	5.22632	0	5.12000	0	0	4.66000	5.64000
C12	95.25650	95.35300	92.27842	0	93.47800	0	0	96.13500	95.74000
C14	10.85000	10.10000	9.52632	0	9.40000	0	0	10.50000	12.00000

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	.38908	.27170	.24059	0	.32822	0	0	.32527	1.00000
C2	.15793	.07243	.16194	0	.15209	0	0	0	1.00000
C3	1.20679	.89521	1.41543	0	1.12311	0	0	1.64756	1.00000
C4	.09685	.10830	.08580	0	.15614	0	0	.04950	1.00000
C5	.12132	.09284	.08789	0	.15749	0	0	.09899	1.00000
C6	3.35495	4.01565	4.08821	0	3.27891	0	0	.67882	1.00000
C7	.94386	.84072	.89448	0	1.22195	0	0	1.24451	1.00000
C10	.22853	.24997	.23448	0	.25577	0	0	.01414	1.00000
C11	.24228	.22720	.49886	0	.31169	0	0	0	1.00000
C12	2.99540	2.28622	2.70555	0	3.10763	0	0	.30405	1.00000
C14	1.22582	.56765	1.17229	0	1.14018	0	0	.70711	1.00000

Table 35 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3	4	5
C1	-1.44086	7.90022	12.33462	1.68393	2.93650
C2	.99492	-8.31871	-14.99631	-3.84440	-9.94574
C3	-1.79535	8.52390	12.97177	3.98599	8.80100
C4	-7.59685	2.63522	-15.31743	-12.49183	13.65262
C5	6.06933	-2.74224	11.10952	11.70441	-3.20950
C6	7.69974	-2.87907	12.40432	13.15351	-3.28671
C7	-1.38054	.89752	.05151	-3.44573	-8.77671
C10	-1.10187	-1.11795	-1.06646	.16909	-.18808
C11	.55202	.10617	.54138	.05906	.72260
C12	1.09932	.43019	-.14763	-.23209	.03782
C14	.46290	.27951	-.89519	.16912	-.03842

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3	4	5
C1	-4.53069	24.8417	38.7853	5.29501	8.91917
C2	6.17461	-51.6968	-83.0687	-24.4793	-61.7243
C3	-1.08356	5.14448	7.82803	2.37551	5.36609
C4	-79.2324	27.4844	-159.755	-130.181	142.392
C5	65.4085	-25.7364	104.265	109.849	-30.1219
C6	2.09040	-.777899	3.35154	3.55397	-.888041
C7	-1.43431	1.03636	.535152E-01	-3.57092	-9.11850
C10	-4.25793	-4.32008	-4.12109	.648544	-.730259
C11	1.52295	.292899	1.49360	.160176	1.99356
C12	.362735	.146749	-.491607E-01	-.772900E-01	.125026E-01
C14	.374455	.226101	-.724147	.186810	-.310780E-01
CONSTANT	-105.094	-188.568	-521.529	-292.003	-14.8222

CENTROIDS OF GROUPS IN REDUCED SPACE

	1	2	3	4	5
GROUP 1	.96323	.19173	-.25527	.51974	.05043
GROUP 2	1.39377	-.60326	.26976	-.78503	.14231
GROUP 3	-1.19133	-.81070	.19325	.03209	-.14931
GROUP 5	-1.76476	2.03124	.41809	-.20274	.53247
GROUP 8	.87684	3.33124	.77716	-.48518	-1.03510
GROUP 9	-1.49585	.79253	-4.90878	-1.18725	-.19693

Table 36. Results of discriminant analysis in assignment of populations of *Cicindela longilabris laurenti* (groups 5, 8, 9 in vertical axis) and *C. l. perviridis* (groups 1-3 in vertical axis).

A. Males

B. Females

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 1	1	12	10. 83.3 PCT	0 0 PCT	1. 8.3 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	1. 8.3 PCT
GROUP 2	2	10	1. 10.0 PCT	7. 70.0 PCT	2. 20.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 3	3	14	0 0 PCT	0 0 PCT	13. 92.9 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	1. 7.1 PCT
GROUP 5	5	4	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	4. 100.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 8	8	6	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	5. 83.3 PCT	1. 16.7 PCT
GROUP 9	9	4	1. 25.0 PCT	0 0 PCT	1. 25.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	2. 50.0 PCT

82.0 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 1	1	20	19. 95.0 PCT	1. 5.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 2	2	10	1. 10.0 PCT	8. 80.0 PCT	1. 10.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 3	3	19	1. 5.3 PCT	2. 10.5 PCT	16. 84.2 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 5	5	5	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	5. 100.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 8	8	2	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	2. 100.0 PCT	0 0 PCT
GROUP 9	9	1	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	1. 100.0 PCT

89.5 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

Table 37. Plot of Discriminant #1 (horizontal axis) vs. Discriminant #2 (vertical axis) for males of *Cicindela longilabris laurenti* (5, 8, 9) and *C. l. perviridis* (1-3). * shows a group centroid.

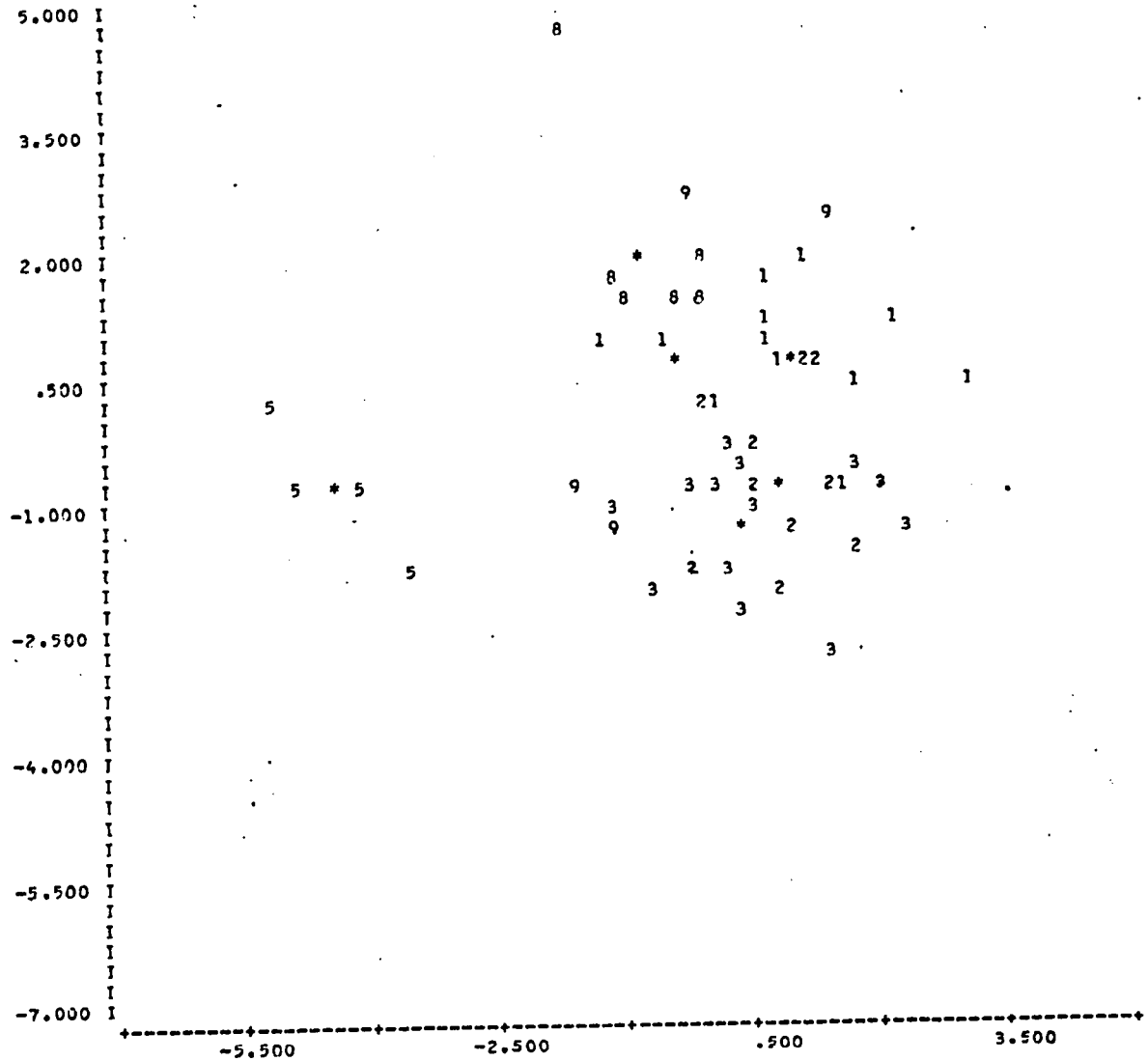

5.000
3.500
2.000
.500
-1.000
-2.500
-4.000
-5.500
-7.000
-5.500
-2.500
.500
3.500

Table 38. Plot of Discriminant #1 (horizontal axis) vs. Discriminant #2 (vertical axis) for females of *Cicindela longilabris laurenti* (5, 8, 9) and *C. l. perviridis* (1-3). * shows a group centroid.

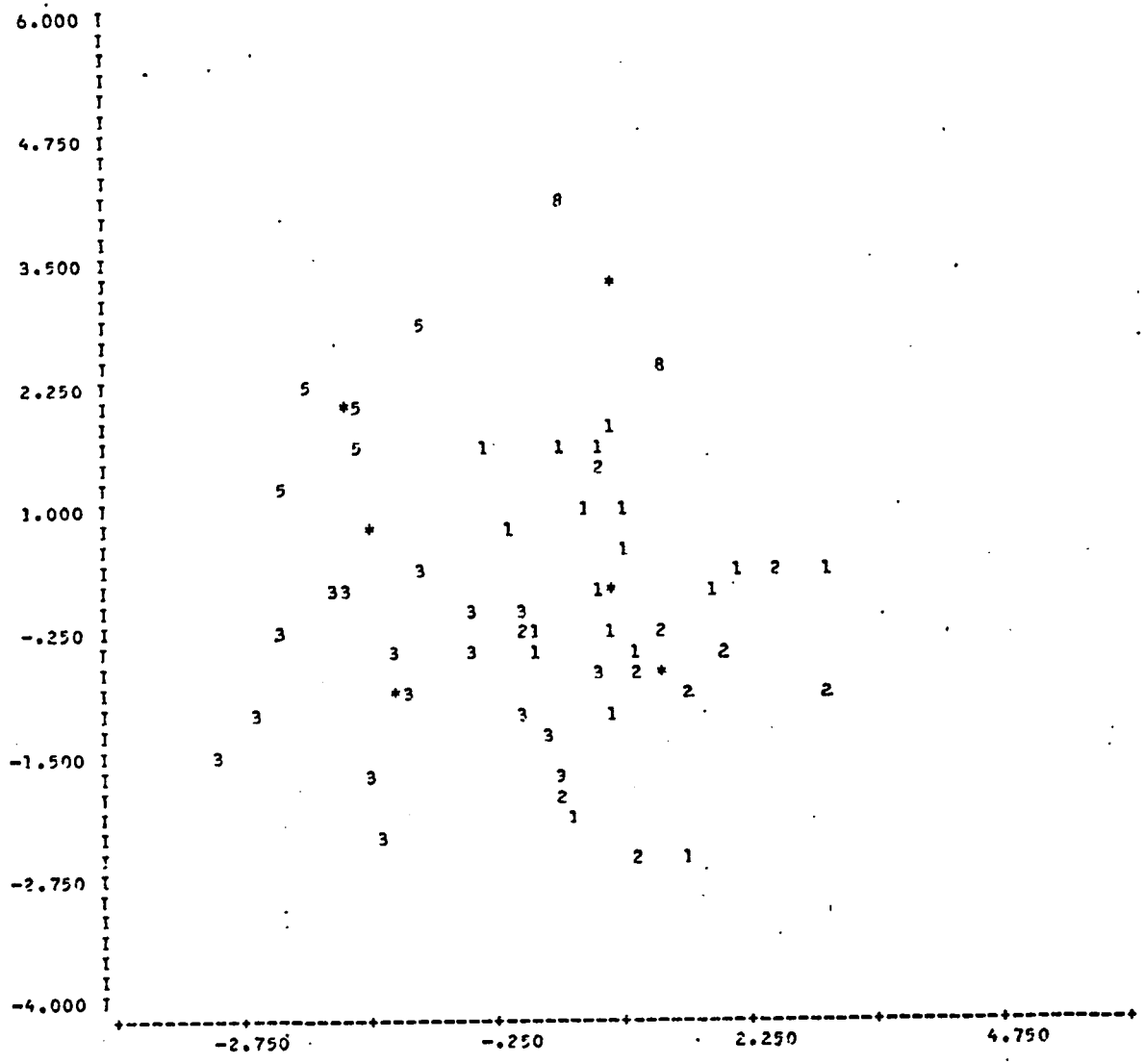

6.000
4.750
3.500
2.250
1.000
-.250
-1.500
-2.750
-4.000
-2.750
-.250
2.250
4.750

Table 39. Pooled within groups covariance matrix for *Cicindela longilabris perviridis* and *C. l. laurenti* x *perviridis* intergrades.

A. Males

B. Females

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.09384										
C2	.03038	.02720									
C3	-.12037	.11696	2.11034								
C4	.01386	.00779	.02452	.00949							
C5	.01911	.00953	.02195	.00558	.01492						
C6	.08034	.06413	.32049	.28805	-.18557	19.64257					
C7	-.04328	.02652	.57053	.05137	.02496	3.18997	1.17859				
C10	.04930	.02249	.02045	.01343	.01591	.15934	.05746	.09632			
C11	.05242	.02448	.02947	.01508	.01421	.28925	.06496	.07307	.09902		
C12	.09161	.01931	-.23707	.01346	.06442	-1.28307	.06404	.41314	-.20144	11.10253	
C14	-.01577	-.02648	-.24355	-.01446	-.01800	-.17938	-.07936	.08641	.02804	1.30150	1.85390

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.15450										
C2	.04286	.02510									
C3	-.25250	.08361	2.24504								
C4	.02168	.00827	-.03124	.00265							
C5	.02558	.01184	.00876	.00681	.01702						
C6	.18337	-.06796	-1.62562	.23546	-.19063	16.26308					
C7	-.04750	-.00952	.12753	.06935	.02756	2.35624	.38511				
C10	.03354	.02509	-.07663	.01474	.02213	.01166	.01150	.03829			
C11	.07953	.02874	-.04807	.01529	.02016	.09088	.02494	.07000	.10624		
C12	-.22470	-.01773	-5.02816	.21525	-.23000	14.19246	4.33743	.50796	-1.39537	5833.52172	
C14	.06342	-.01017	-.39584	.01918	.00474	.73032	.09726	-.02013	.03432	-11.45861	2.25447

Table 40. Statistical information from discriminant analysis of males of *Cicindela longilabris perviridis* (groups 1-3) and *C. l. laurenti* x *perviridis* ingtergrades (group 4) based on 11 characters. See text for explanation of characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	12.	10.	14.	56.	0	0	0	0	0

TOTAL

NUMBER 92.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	8.23667	8.07600	7.89143	8.03804	0	0	0	0	0
C2	3.41000	3.24400	3.25714	3.43464	0	0	0	0	0
C3	41.40833	40.17200	41.28429	42.74714	0	0	0	0	0
C4	1.36250	1.25800	1.32214	1.32625	0	0	0	0	0
C5	2.09083	1.99000	2.02000	2.09821	0	0	0	0	0
C6	65.19000	63.17800	65.51714	63.33250	0	0	0	0	0
C7	16.54000	15.57100	16.77786	16.49518	0	0	0	0	0
C10	4.97583	4.66200	4.84071	4.84089	0	0	0	0	0
C11	5.60667	5.13300	5.36357	5.48411	0	0	0	0	0
C12	89.54083	90.48400	90.31143	88.23446	0	0	0	0	0
C14	10.50000	9.70000	9.64286	9.60714	0	0	0	0	0

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	.22087	.22591	.26047	.32072	0	0	0	0	0
C2	.13080	.10700	.11364	.16385	0	0	0	0	0
C3	.99274	.89896	1.13888	1.65548	0	0	0	0	0
C4	.07967	.10528	.06963	.10482	0	0	0	0	0
C5	.09090	.12365	.09958	.13365	0	0	0	0	0
C6	3.04443	2.96095	3.53939	5.01802	0	0	0	0	0
C7	.70373	1.09930	.80890	1.19762	0	0	0	0	0
C10	.17789	.49039	.22612	.28624	0	0	0	0	0
C11	.25857	.40980	.22853	.32439	0	0	0	0	0
C12	3.19254	3.78758	3.78523	3.16093	0	0	0	0	0
C14	1.00000	1.33749	1.15073	1.47314	0	0	0	0	0

Table 40 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3
C1	-1.47314	13.50210	4.84929
C2	1.86608	-15.42442	-5.30714
C3	-.36656	12.62813	4.88954
C4	-7.97866	1.20551	-1.38409
C5	6.83127	-1.28690	.89195
C6	7.54440	-1.43197	1.01768
C7	-.38297	.22196	-.40793
C10	-1.16432	2.84149	-1.81718
C11	1.25599	-3.09439	.95978
C12	.35026	-2.22438	1.04000
C14	.19802	.51943	-.30975

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3
C1	-4.67353	42.8354	15.3844
C2	11.1984	-92.5618	-32.3882
C3	-.216334	7.45273	2.88565
C4	-80.5773	12.1441	-13.9431
C5	53.9224	-10.1581	7.04055
C6	1.69285	-.321727	.229290
C7	-.343077	.193052	-.26 825
C10	-3.89430	9.50395	-6.07792
C11	3.75543	-9.25230	2.86976
C12	.102821	-.652987	.30522[illegible]
C14	.136866	.378107	-.225475
CONSTANT	-110.983	-264.030	-151.449

CENTROIDS OF GROUPS IN REDUCED SPACE

	1	2	3
GROUP 1	-.39214	.98892	-.61838
GROUP 2	-1.79971	.30240	.68569
GROUP 3	-.88100	-.91882	-.42768
GROUP 4	.62387	-.03622	.11698

Table 41. Statistical information from discriminant analysis of females of *Cicindela longilabris perviridis* (groups 1-3) and *C. l. laurenti* x *perviridis* intergrades (group 4) based on 11 characters. See text for explanation of characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	20.	10.	19.	83.	0	0	0	0	0

UNGROUPD.

NUMBER 132.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	8.77350	8.68300	8.64263	8.69602	0	0	0	0	0
C2	3.61500	3.43700	3.57368	3.65241	0	0	0	0	0
C3	41.22250	39.58600	41.34789	42.00783	0	0	0	0	0
C4	1.43500	1.44200	1.44789	1.46064	0	0	0	0	0
C5	2.21550	2.14800	2.18527	2.21955	0	0	0	0	0
C6	64.80500	67.11200	66.28421	65.95241	0	0	0	0	0
C7	16.35200	16.59100	16.75474	16.80614	0	0	0	0	0
C10	4.98950	4.84200	5.01474	4.94012	0	0	0	0	0
C11	5.21950	5.09800	5.22632	5.33265	0	0	0	0	0
C12	95.25650	95.35300	92.27842	103.08627	0	0	0	0	0
C14	10.85000	10.10000	9.52637	9.56627	0	0	0	0	0

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	.38908	.27170	.24859	.43308	0	0	0	0	0
C2	.15783	.07243	.16194	.16453	0	0	0	0	0
C3	1.28679	.89521	1.41543	1.61027	0	0	0	0	0
C4	.08685	.10830	.08580	.10202	0	0	0	0	0
C5	.12132	.08284	.08789	.14390	0	0	0	0	0
C6	3.35405	4.01685	4.08821	4.16898	0	0	0	0	0
C7	.94386	.84072	.89449	.96021	0	0	0	0	0
C10	.22852	.24027	.23448	.32676	0	0	0	0	0
C11	.24728	.22720	.49866	.30322	0	0	0	0	0
C12	2.28548	2.28622	2.70555	95.40304	0	0	0	0	0
C14	1.22582	.56765	1.17229	1.68344	0	0	0	0	0

Table 41 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3
C1	-.90809	-.70244	-.40217
C2	-.92392	.48769	-.45961
C3	-.10211	.21413	-.05203
C4	3.56950	.58640	.10177
C5	-1.34940	.53464	2.06014
C6	-1.45602	.30276	1.8[illegible]540
C7	-1.84567	-1.23137	-1.79801
C10	.71315	.01145	-1.54554
C11	-.71224	-.26461	.61009
C12	-.14398	.13177	.19276
C14	.32295	.93841	-.05072

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3
C1	-2.31213	-1.78850	-1.02397
C2	-5.61585	2.01155	-2.74391
C3	-.628513E-01	.131802	-.320245E-01
C4	36.5701	6.00778	1.04263
C5	-10.3330	4.09402	15.7755
C6	-.361656	.752021E-01	.458375
C7	-1.95463	-1.30407	-1.90415
C10	2.40989	.386934E-01	-[illegible].22269
C11	-2.15671	-.801251	1.84738
C12	-.190376E-02	.174236E-02	.254878E-02
C14	.297448	.536560	-.325785E-01
CONSTANT	66.4795	-2.80634	1.58597

CENTROIDS OF GROUPS IN REDUCED SPACE

	1	2	3
GROUP 1	.62739	.72520	-.02845
GROUP 2	1.43119	-.53409	.42531
GROUP 3	.43702	-.32642	-.52525
GROUP 4	-.42365	-.03568	.06742

Table 42 . Results of discriminant analysis in assignment of populations of *Cicindela longilabris perviridis* (groups 1-3 in horizontal axis) and *C. l. laurenti* intergrades (group 4 in vertical axis).

A. Males

B. Females

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 1	1	12	5. 41.7 PCT	0 0 PCT	0 0 PCT	7. 58.3 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 2	2	10	0 0 PCT	6. 60.0 PCT	2. 20.0 PCT	2. 20.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 3	3	14	1. 7.1 PCT	0 0 PCT	8. 57.1 PCT	5. 35.7 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 4	4	56	1. 1.8 PCT	0 0 PCT	4. 7.1 PCT	51. 91.1 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT

76.1 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 1	1	20	5. 25.0 PCT	1. 5.0 PCT	0 0 PCT	14. 70.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 2	2	10	0 0 PCT	5. 50.0 PCT	1. 10.0 PCT	4. 40.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 3	3	19	2. 10.5 PCT	1. 5.3 PCT	3. 15.8 PCT	13. 68.4 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 4	4	83	5. 6.0 PCT	3. 3.6 PCT	1. 1.2 PCT	74. 89.2 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT

65.0 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

Table 43. Plot of Discriminant #1 (horizontal axis) vs. Discriminat #2 (vertical axis for males of *Cicindela longilabris perviridis* (1-3) and *C. l. laurenti* x *perviridis* intergrades (4). * shows a group centroid.

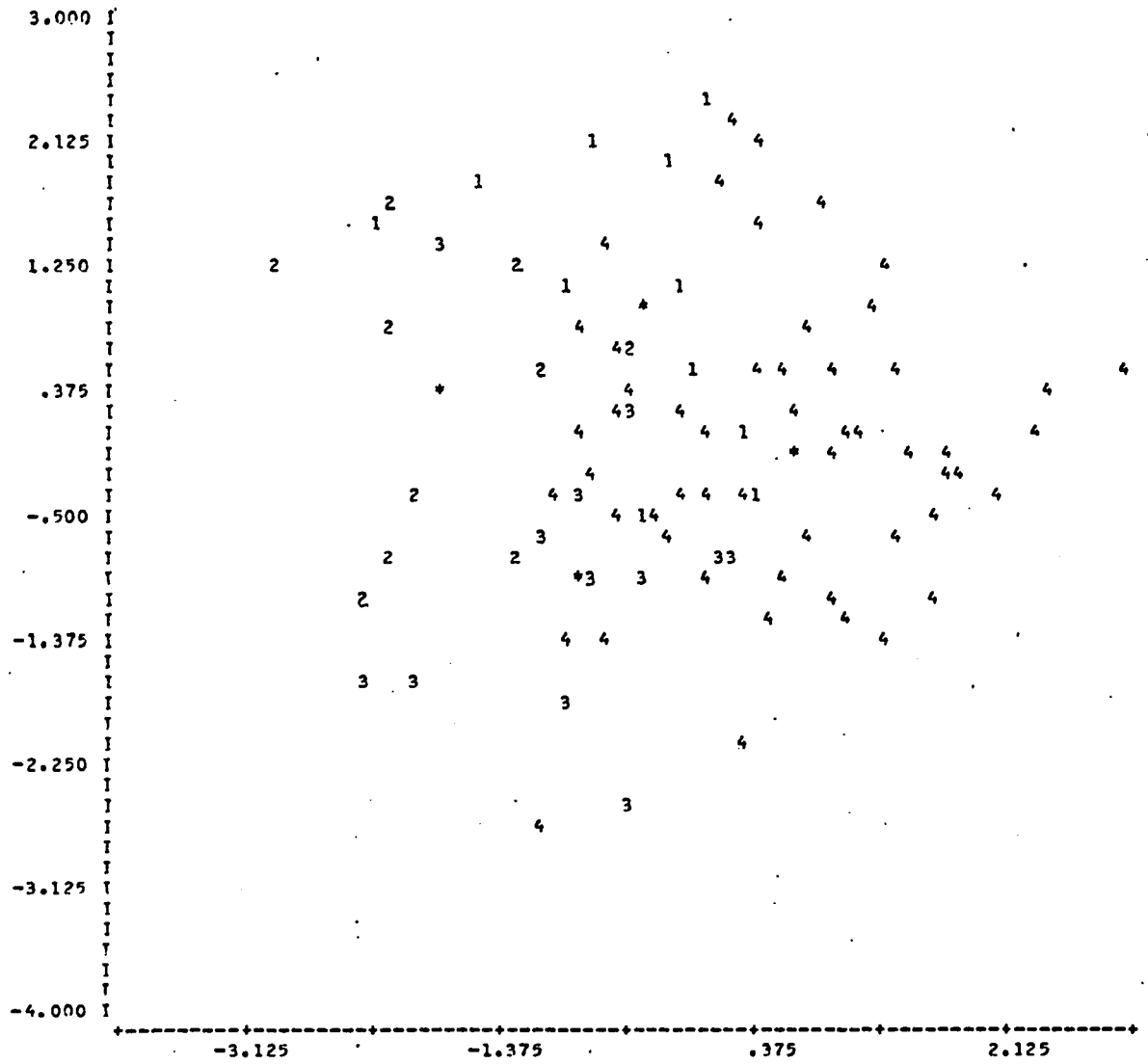

3.000
2.125
1.250
.375
-.500
-1.375
-2.250
-3.125
-4.000
-3.125
-1.375
.375
2.125

Table 44. Plot of Discriminant #1 (horizontal axis) vs. Discriminant #2 (vertical axis for females of *Cicindela longilabris perviridis* (1-3) and *C. l. laurenti* x *perviridis* intergrades (4). * shows a group centroid.

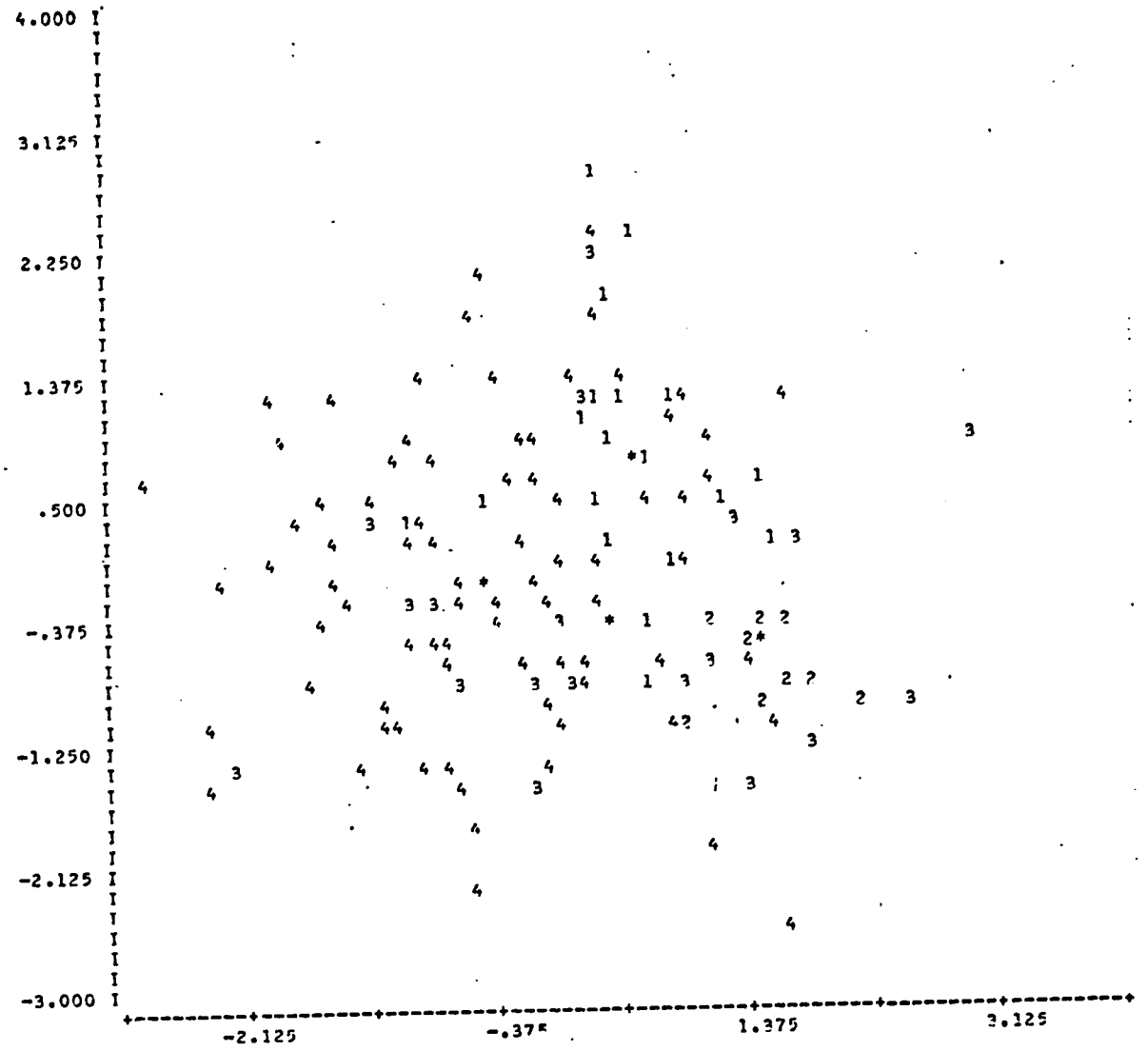

4.000
3.125
2.250
1.375
.500
-.375
-1.250
-2.125
-3.000
-2.125
-.375
1.375
3.125

Table 45. Pooled within groups covariance matrix for *Cicindela longilabris laurenti* and *C. l. laurenti* x *perviridis* intergrades.

A. Males

B. Females

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.09510										
C2	.02370	.01707									
C3	-.20600	.08969	2.23323								
C4	.01161	.00471	-.00201	.00706							
C5	.01626	.00654	-.00303	.00372	.00984						
C6	.06854	.02494	-.06871	.22713	-.11706	14.47794					
C7	-.04566	.01153	.39727	.06366	.01457	2.62214	.88146				
C10	.05441	.01582	-.04857	.01222	.01554	.12866	.04771	.07641			
C11	.05194	.02077	-.01109	.00959	.01490	.01164	.01814	.05538	.07501		
C12	.16752	.03699	-.76326	.07738	.04191	2.64094	.66442	.54000	-.16653	13.05623	
C14	-.01592	.00713	.17478	.01130	.03177	-.41124	.17484	.08091	.01962	1.29254	1.57595

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.09990										
C2	.03186	.02276									
C3	-.13237	.11087	1.84143								
C4	.01251	.00626	.01484	.00937							
C5	.01526	.01050	.04928	.00575	.01192						
C6	.11545	-.02971	-.81638	.25557	-.09411	14.51558					
C7	-.05062	.01115	.40733	.08658	.03867	2.79556	1.13857				
C10	.03819	.02077	.05985	.00949	.01270	.05460	.03723	.05459			
C11	.03395	.02648	.11404	.01174	.01470	.08686	.05814	.05427	.11617		
C12	.01512	.02511	.27007	-.01654	.04278	-2.04635	-.21611	.22414	-.07978	8.01745	
C14	-.04140	-.00342	.16018	-.00537	-.00555	-.06152	.02991	-.00592	.05191	-.77310	1.31181

Table 46. Statistical information from discriminant analysis of males of *Cicindela longilabris laurenti* (groups 5, 8, 9) and *C. l. laurenti* x *perviridis* (groups 1-3) based on 11 characters. See text for explanation of characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	12.	10.	14.	0	10.	0	0	6.	4.

TOTAL

NUMBER 56.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	8.23667	8.07600	7.99143	0	7.92700	0	0	7.98833	8.29250
C2	3.41000	3.24400	3.25714	0	3.48300	0	0	3.43167	3.49000
C3	41.40833	40.17300	41.28429	0	43.94900	0	0	43.61500	42.01250
C4	1.36250	1.25800	1.32214	0	1.27300	0	0	1.41833	1.42000
C5	2.09083	1.99000	2.02000	0	2.09500	0	0	2.09833	2.10000
C6	65.19000	63.17800	65.51714	0	60.97900	0	0	67.61500	64.30250
C7	16.54000	15.57100	16.77786	0	16.07600	0	0	17.74833	17.23750
C10	4.97583	4.66200	4.84071	0	4.79000	0	0	4.96833	5.30250
C11	5.60667	5.13300	5.36357	0	5.16200	0	0	5.30333	5.59000
C12	88.54083	90.48400	90.31143	0	92.76800	0	0	93.67333	94.59750
C14	10.50000	9.70000	9.64286	0	8.10000	0	0	11.83333	11.75000

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	.29087	.29591	.26047	0	.32782	0	0	.40841	.35283
C2	.13090	.10700	.11964	0	.18617	0	0	.08298	.08794
C3	.99274	.89896	1.13888	0	1.78884	0	0	2.76114	1.80432
C4	.07967	.10528	.06863	0	.07304	0	0	.11339	.05715
C5	.09090	.12365	.08858	0	.10773	0	0	.05845	.11516
C6	3.04443	2.96085	3.53839	0	4.22570	0	0	5.51154	4.74996
C7	.70373	1.09930	.80990	0	1.03508	0	0	1.05804	1.15570
C10	.17789	.48039	.22612	0	.21019	0	0	.19691	.22384
C11	.26857	.40980	.22953	0	.23412	0	0	.09026	.31123
C12	3.10254	3.78758	3.76523	0	4.50248	0	0	2.75446	1.28256
C14	1.00000	1.33749	1.15073	0	.87560	0	0	.98819	2.75379

Table 46 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3	4	5
C1	5.68798	4.94448	9.03406	-2.29882	-2.70579
C2	-6.58429	-5.97542	-12.04360	-1.75095	9.04349
C3	5.39601	6.70540	11.74044	2.10036	-7.97185
C4	1.86233	.90394	6.86164	4.23392	-2.57239
C5	-2.07731	.41037	-2.19725	2.39097	-3.00386
C6	-1.73341	.48385	-2.61561	2.95148	-4.34794
C7	.54542	-.96210	-3.94766	-7.14290	6.38559
C10	5.27315	.56853	.19792	1.60560	2.37065
C11	-4.19702	-.76355	-1.30639	-.86665	-1.94592
C12	-4.01532	-.28412	-.36890	-1.46388	-1.05508
C14	1.00504	.61250	.32901	-.21759	-.07003

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3	4	5
C1	17.3093	15.0467	27.4918	-6.99561	-8.23409
C2	-40.2099	-36.4916	-73.5497	-10.6929	40.1212
C3	2.73732	3.40155	5.95576	1.06548	-4.04401
C4	18.9760	9.21056	69.9160	43.1412	-26.2172
C5	-19.0677	3.76677	-20.1896	21.9469	-27.5725
C6	-.416417	.116235	-.628348	.695011	-1.04449
C7	.511914	-.871063	-3.57411	-6.46608	5.78134
C10	17.0381	1.83696	.639494	5.19785	7.65979
C11	-13.1702	-2.39601	-4.09939	-2.71954	-6.10628
C12	-1.00991	-.714607E-01	-.927837E-01	-.368184	-.265366
C14	.602900	.367424	.197364	-.130527	-.420084E-01
CONSTANT	-12.6062	-147.038	-149.371	31.8993	153.595

CENTROIDS OF GROUPS IN REDUCED SPACE

	1	2	3	4	5
GROUP 1	1.35487	.14602	-.04741	.80099	-.07393
GROUP 2	.59506	-1.02245	1.24533	-.31019	.11630
GROUP 3	.35074	-.80753	-.90684	-.28117	-.17796
GROUP 5	-3.32421	.08271	.03688	.24472	.06718
GROUP 8	.37332	2.22367	.38797	-.53829	-.59102
GROUP 9	.97069	1.40213	-.47128	-.36774	1.27247

Table 47. Statistical information from discriminant analysis of males of *Cicindela longilabris laurenti* (groups 5, 8, 9) and *C. l. laurenti* x *perviridis* intergrades (groupx 1-3) based on 11 characters. See text for explanation of characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	20.	10.	19.	0	15.	0	0	2.	1.

UNGROUPED.

NUMBER 67.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	8.77350	8.68300	8.64263	0	8.42867	0	0	8.48000	3.71000
C2	3.61500	3.43700	3.57369	0	3.69400	0	0	3.65000	3.78000
C3	41.22250	39.58600	41.34789	0	43.71667	0	0	43.07500	43.40000
C4	1.43500	1.44200	1.44789	0	1.43967	0	0	1.45500	1.62000
C5	2.21650	2.14800	2.19632	0	2.20667	0	0	2.23000	2.20000
C6	64.80600	67.11200	66.28421	0	64.85867	0	0	65.25000	70.43000
C7	16.35200	16.59100	16.75474	0	16.98733	0	0	17.18000	18.62000
C10	4.94950	4.86700	5.01474	0	4.70200	0	0	4.48000	5.40000
C11	5.21950	5.09800	5.22632	0	5.03267	0	0	4.66000	5.14000
C12	95.25650	95.15300	92.27842	0	93.49867	0	0	96.13500	95.74000
C14	10.25000	10.10000	9.52632	0	8.66667	0	0	10.50000	12.00000

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	.38908	.27170	.24859	0	.30877	0	0	.32527	1.00000
C2	.15783	.07243	.16194	0	.16813	0	0	0	1.00000
C3	1.28679	.89521	1.41543	0	1.57837	0	0	1.64756	1.00000
C4	.08665	.10830	.08580	0	.11573	0	0	.04950	1.00000
C5	.12142	.08284	.08789	0	.13004	0	0	.02999	1.00000
C6	3.35495	4.01665	4.08821	0	4.00970	0	0	.67862	1.00000
C7	.94386	.84072	.89448	0	1.46207	0	0	1.24451	1.00000
C10	.22853	.24997	.23448	0	.23683	0	0	.01414	1.00000
C11	.24228	.22720	.49886	0	.27086	0	0	0	1.00000
C12	2.98540	2.28622	2.70555	0	3.17164	0	0	.30406	1.00000
C14	1.22582	.56765	1.17229	0	1.29099	0	0	.70711	1.00000

Table 47 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3	4	5
C1	-6.28477	3.39885	8.31531	-10.67730	-4.80220
C2	7.74426	-4.50316	-10.54284	12.53828	7.96630
C3	-8.76274	4.55586	9.25618	-12.43472	-7.80964
C4	4.56297	-1.32368	-7.90066	14.28764	-3.49569
C5	-3.77200	2.36002	6.08986	-10.45769	.78832
C6	-4.51508	2.68230	7.00672	-11.96389	.57351
C7	.71993	-1.56920	-.44794	.43591	2.84208
C10	.84634	-1.63569	-.74384	-.16452	.24372
C11	-.16981	.50471	.59374	-.17364	-1.15635
C12	.13460	1.08756	.02117	.34353	-.46002
C14	.68446	.67541	-.64100	-.17253	.27201

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1	2	3	4	5
C1	-19.0365	10.2951	25.1870	-32.3415	-14.5458
C2	46.7171	-27.1652	-63.5995	75.6369	48.0566
C3	-4.67854	2.43257	4.94228	-6.63943	-4.16990
C4	47.5838	-13.9036	-82.3900	148.995	-36.4539
C5	-34.9945	21.7795	56.2004	-96.5090	7.27596
C6	-1.19333	.702864	1.83603	-3.13499	.150282
C7	.664972	-1.44941	-.413747	.402636	2.62513
C10	3.11198	-6.01441	-2.73509	-.604919	.896140
C11	-.480374	1.42774	1.67962	-.491203	-3.27115
C12	.442426E-01	.357477	.699952E-02	.112916	-.151206
C14	.489496	.483026	-.458418	-.123390	.194530
CONSTANT	244.443	-158.767	-304.452	476.383	134.171

CENTROIDS OF GROUPS IN REDUCED SPACE

	1	2	3	4	5
GROUP 1	.83353	.80275	-.23012	-.47089	-.05058
GROUP 2	1.41848	.55674	.86608	.60699	-.10314
GROUP 3	.35426	-1.46362	-.01648	-.03734	.14541
GROUP 5	-2.43875	.06641	.06773	.05919	-.14453
GROUP 8	-1.50553	2.76384	-.52543	.66951	.97746
GROUP 9	2.00592	-.33731	-3.71030	1.83072	-.50671

Table 48. Results of discriminant analysis in assignment of populations of *Cicindela longilabris laurenti* (groups 5, 8, 9 in vertical axis) and *C. l. laurenti* x *perviridis* (groups 1-3 in vertical axis).

A. Males

B. Females

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 1	1	12	11. 91.7 PCT	0 0 PCT	1. 8.3 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 2	2	10	1. 10.0 PCT	8. 80.0 PCT	1. 10.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 3	3	14	0 0 PCT	1. 7.1 PCT	12. 85.7 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	1. 7.1 PCT
GROUP 5	5	10	0 0 PCT	0 0 PCT	1. 10.0 PCT	0 0 PCT	9. 90.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 8	8	6	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	6. 100.0 PCT	0 0 PCT
GROUP 9	9	4	1. 25.0 PCT	0 0 PCT	1. 25.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	2. 50.0 PCT

85.7 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 1	1	20	18. 90.0 PCT	1. 5.0 PCT	1. 5.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 2	2	10	1. 10.0 PCT	8. 80.0 PCT	1. 10.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 3	3	19	2. 10.5 PCT	2. 10.5 PCT	15. 78.9 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 5	5	15	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	15. 100.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 8	8	2	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	2. 100.0 PCT	0 0 PCT
GROUP 9	9	1	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	1. 100.0 PCT

88.1 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

Table 49. Plot of Discriminant #1 (horizontal axis) vs. Discriminant #2 (vertical axis) for males of *Cicindela longilabris laurenti* (5, 8) and *C. l. laurenti* x *perviridis* intergrades (1-3, 5). * shows a group centroid.

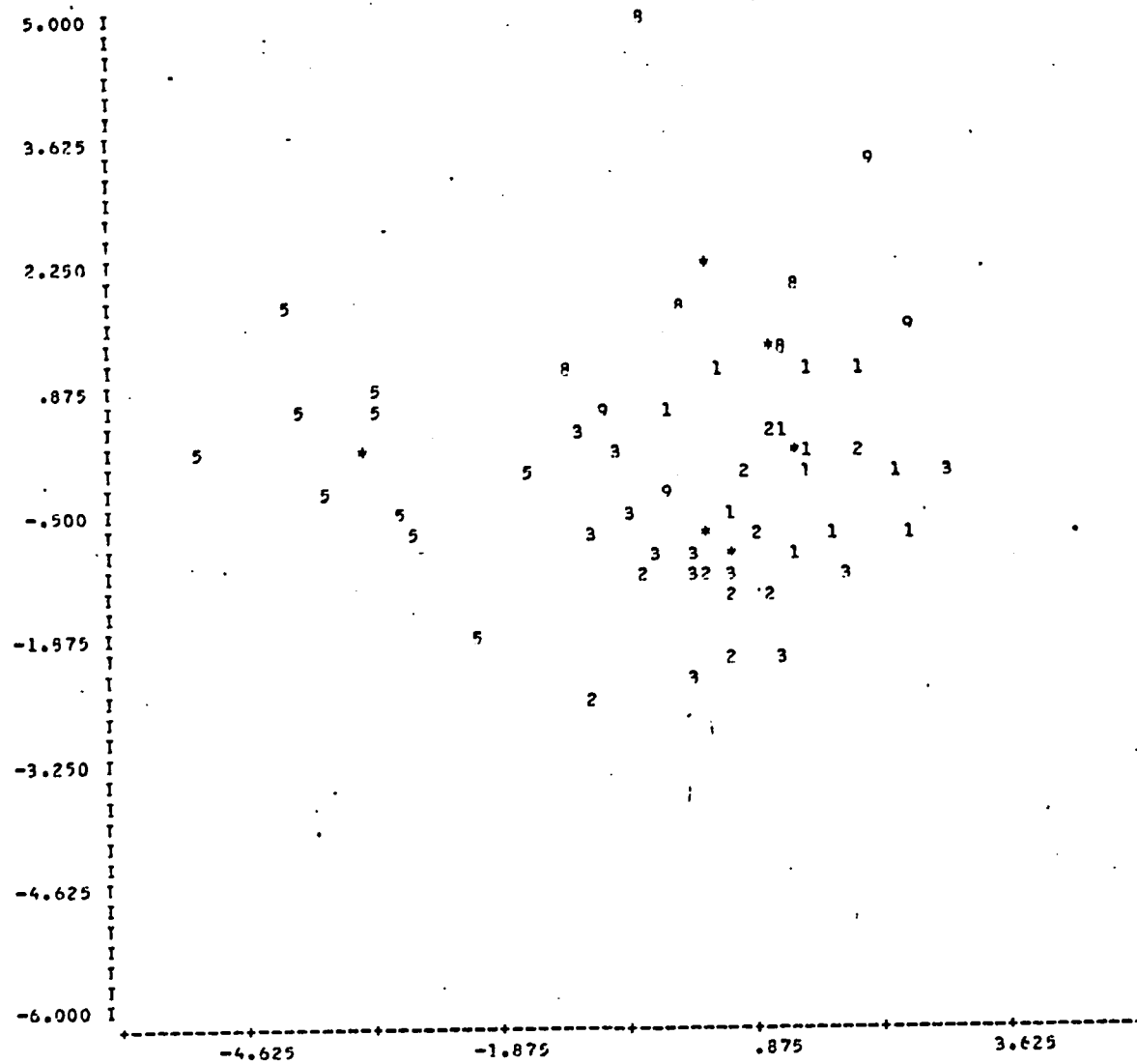

5.000
3.625
2.250
.875
-.500
-1.875
-3.250
-4.625
-6.000
-4.625
-1.875
.875
3.625

Table 50. Plot of Discriminant #1 (horizontal axis) vs. Discriminant #2 (vertical axis) for females of *Cicindela longilabris laurenti* (5, 8) and *C. l. laurenti* x *perviridis* intergrades (1-3, 5). * shows a group centroid.

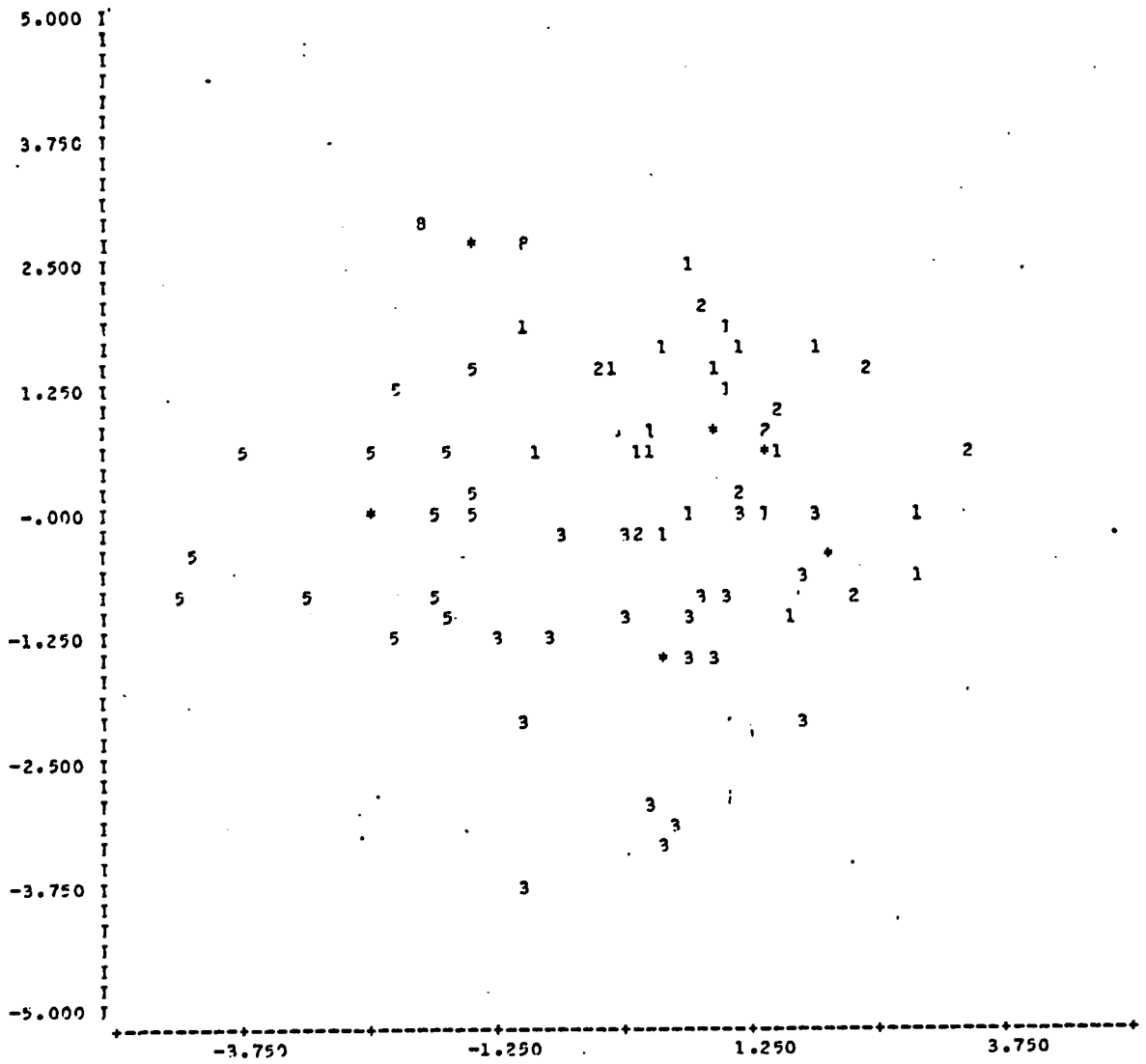

5.000
3.750
2.500
1.250
-.000
-1.250
-2.500
-3.750
-5.000
-3.750
-1.250
1.250
3.750

Table 51. Pooled within groups covariance matrix for *Cicindela nebraskana chamberlaini* and *C. n. nebraskana*.

A. Males

B. Females

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.22093										
C2	.04542	.01630									
C3	-.65346	-.04699	3.07606								
C4	.03004	.00610	-.09982	.00913							
C5	.05471	.01220	-.16364	.00761	.01939						
C6	-.35866	-.03892	.95398	.21124	-.27058	20.71316					
C7	-.07724	-.01752	.21705	.05308	-.02333	3.55534	.83824				
C10	.09202	.01393	-.26534	.01430	.02527	-.15750	-.01448	.05923			
C11	.05234	.01944	-.21452	.01230	.02285	-.17550	-.02011	.05467	.05714		
C12	.12795	-.01139	-.09984	.02789	.02391	.53071	.09047	.04600	-.09832	3.26056	
C14	-.11478	-.02632	.26238	-.01400	-.01030	-.54415	.04010	-.03053	-.04216	.24627	.58870

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.19581										
C2	.05774	.02924									
C3	-.20434	.07998	2.41374								
C4	.02544	.01104	.03284	.01317							
C5	.03295	.01444	.02250	.00956	.01823						
C6	.12062	.03304	.84101	.31297	-.12952	19.99373					
C7	-.03374	.02474	.61123	.10776	.05032	3.50285	1.47031				
C10	.08769	.02989	-.03772	.01652	.02002	.12519	.02506	.06475			
C11	.07457	.02699	-.00890	.01393	.01663	.11701	.01821	.05334	.05753		
C12	.23957	.05565	-.50412	.05011	.06725	.09198	.16572	.21765	-.10067	5.71485	
C14	.01975	.03209	.20343	.02093	.00481	.78971	.21458	.02502	.03282	-.13470	.99869

Table 52 . Statistical information from discriminant analysis of males of *Cicindela nebraskana chamberlaini* (group 1) and *C. n. chamberlaini* x *nebraskana* intergrades (group 2) based on 11 charactesr. See text for explanation of characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	23.	0	12.	0	0	0	0	0	0

TOTAL

NUMBER 35.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	3.25913	0	7.13417	0	0	0	0	0	0
C2	3.41793	0	3.21333	0	0	0	0	0	0
C3	41.45926	0	45.12583	0	0	0	0	0	0
C4	1.34739	0	1.16417	0	0	0	0	0	0
C5	2.11000	0	1.82000	0	0	0	0	0	0
C6	63.88957	0	64.28750	0	0	0	0	0	0
C7	16.31609	0	16.34250	0	0	0	0	0	0
C10	5.35565	0	4.45583	0	0	0	0	0	0
C11	5.30130	0	4.40583	0	0	0	0	0	0
C12	101.13326	0	101.17417	0	0	0	0	0	0
C14	7.56522	0	7.91667	0	0	0	0	0	0

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	.48192	0	.44531	0	0	0	0	0	0
C2	.12544	0	.13200	0	0	0	0	0	0
C3	1.67876	0	1.89474	0	0	0	0	0	0
C4	.10541	0	.07179	0	0	0	0	0	0
C5	.12649	0	.16006	0	0	0	0	0	0
C6	4.00044	0	5.48930	0	0	0	0	0	0
C7	.91913	0	.91033	0	0	0	0	0	0
C10	.25170	0	.22577	0	0	0	0	0	0
C11	.23227	0	.23957	0	0	0	0	0	0
C12	1.41654	0	2.40177	0	0	0	0	0	0
C14	.78775	0	.90034	0	0	0	0	0	0

Table 52 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	.58222
C2	1.78503
C3	-1.77501
C4	2.73335
C5	-5.94783
C6	-4.05520
C7	1.79887
C10	7.49409
C11	-10.72194
C12	-1.62329
C14	-.20594

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	.816910
C2	11.1743
C3	-.718253
C4	21.1873
C5	-30.4202
C6	-.903621
C7	1.99414
C10	15.1319
C11	-21.8208
C12	-.912458
C14	-.247491
CONSTANT	172.891

CENTROIDS OF GROUPS IN REDUCED SPACE

	1
GROUP 1	-1.57674
GROUP 3	3.02209

Table 53. Statistical information from discriminant analysis of females of *Cicindela nebraskana chamberlaini* (group 1) and *C. n. nebraskana* (group 3) based on 11 characters. See text for explanation characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	45.	0	25.	0	0	0	0	0	0
	UNGROUPED								
NUMBER	70.								

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	8.79244	0	8.01960	0	0	0	0	0	0
C2	3.59000	0	3.44560	0	0	0	0	0	0
C3	40.65778	0	42.98440	0	0	0	0	0	0
C4	1.43533	0	1.35560	0	0	0	0	0	0
C5	2.18156	0	2.00920	0	0	0	0	0	0
C6	65.96400	0	67.65560	0	0	0	0	0	0
C7	16.32956	0	16.92440	0	0	0	0	0	0
C10	5.21956	0	4.58960	0	0	0	0	0	0
C11	5.09289	0	4.43880	0	0	0	0	0	0
C12	102.54022	0	103.41800	0	0	0	0	0	0
C14	6.95556	0	7.20000	0	0	0	0	0	0

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	.49985	0	.30968	0	0	0	0	0	0
C2	.18992	0	.12931	0	0	0	0	0	0
C3	1.69716	0	1.24632	0	0	0	0	0	0
C4	.12031	0	.10377	0	0	0	0	0	0
C5	.13284	0	.13598	0	0	0	0	0	0
C6	3.51960	0	5.60116	0	0	0	0	0	0
C7	1.09171	0	1.40742	0	0	0	0	0	0
C10	.27966	0	.20011	0	0	0	0	0	0
C11	.26601	0	.18240	0	0	0	0	0	0
C12	2.58133	0	2.60950	0	0	0	0	0	0
C14	1.13726	0	.70711	0	0	0	0	0	0

Table 53 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	-1.04341
C2	-.16368
C3	-.45782
C5	.71482
C6	.41743
C7	-.61607
C10	3.37961
C11	-1.46943
C12	-.93400
C14	-.11219

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	-1.81142
C2	-.891906
C3	-.247121
C5	4.53093
C6	.945943E-01
C7	-.497832
C10	9.60063
C11	-3.71625
C12	-.357925
C14	-.112294
CONSTANT	33.8996

CENTROIDS OF GROUPS IN REDUCED SPACE

	1
GROUP 1	1.16195
GROUP 3	-2.09151

Table 54. Results of discriminant analysis in assignment of populations of *Cicindela nebraskana chamberlaini* (group 1 in vertical axis) and *C. n. nebraskana* (group 3 in vertical axis).

A. Males

B. Females

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 1	1	23	20. 87.0 PCT	3. 13.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 2	2	20	3. 15.0 PCT	17. 85.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT

84.0 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 1	1	45	40. 88.9 PCT	5. 11.1 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 2	2	31	13. 41.9 PCT	18. 58.1 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT

76.3 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

Table 55. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) for males of *Cicindela nebraskana chamberlaini* (1) and *C. n. nebraskana* (3). * shows a group centroid.

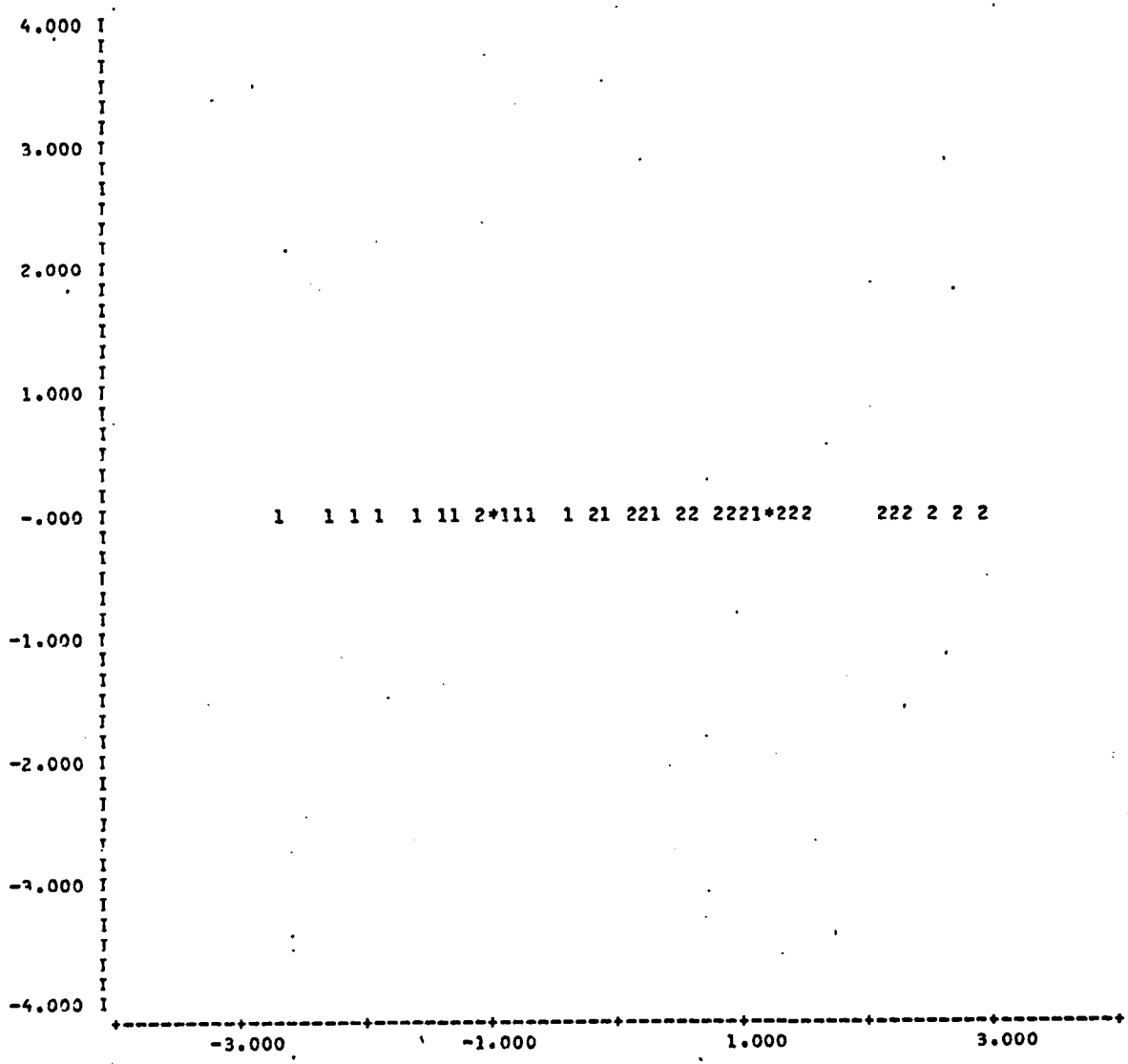

4.000
3.000
2.000
1.000
-.000
-1.000
-2.000
-3.000
-4.000
1 1 1 1 1 11 2*111 1 21 221 22 2221*222 222 2 2 2
-3.000
-1.000
1.000
3.000

Table 56. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) for females of *Cicindela n. chamberlaini* (1) and *C. n. chamberlaini* x *nebraskana* intergrades (2). * shows a group centroid.

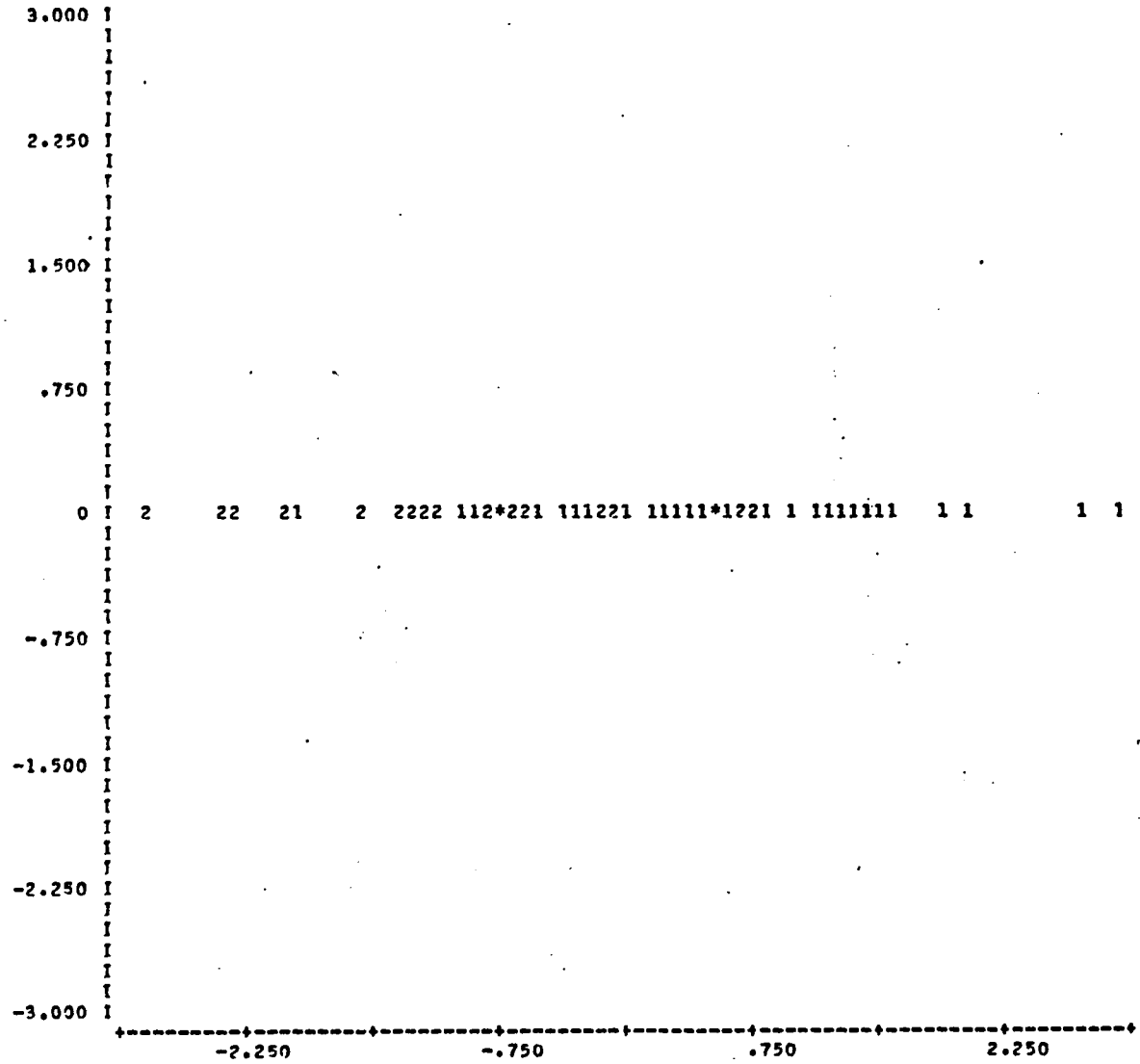

3.000
2.250
1.500
.750
0
-.750
-1.500
-2.250
-3.000
2 22 21 2 2222 112*221 111221 11111*1221 1 1111111 1 1 1 1
-2.250
-.750
.750
2.250

Table 57. Pooled within groups covariance matrix for *Cicindela nebraskana chamberlaini* and *C. n. chamberlaini* x *nebraskana* intergrades.

A. Males

B. Females

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.21416										
C2	.04468	.02059									
C3	-.61073	.01780	3.65127								
C4	.02758	.00597	-.07787	.00933							
C5	.05041	.01155	-.13107	.00787	.01779						
C6	-.17245	-.05754	.13961	.20660	-.15853	14.83419					
C7	-.07493	-.01183	.23396	.05043	-.00057	2.84667	.86902				
C10	.10673	.02307	-.30597	.01748	.02782	-.02104	.00298	.09117			
C11	.10870	.02307	-.32493	.01710	.02922	-.08680	-.00683	.09264	.09990		
C12	-.15714	-.01614	.84080	-.01162	-.06542	1.57446	.19186	-.10843	-.23007	2.80601	
C14	-.12070	-.01709	.43833	-.01193	-.01412	-.16157	.09217	-.06221	-.06432	.04814	.48423

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.24546										
C2	.06421	.08237									
C3	-.34316	.06002	2.83040								
C4	.03743	.01388	-.00859	.01273							
C5	.04693	.01015	-.00758	.01117	.01913						
C6	.28678	.08830	-.20028	.24159	-.05662	12.51315					
C7	-.03280	.03193	.56128	.07659	.04182	2.21593	.95400				
C10	.10146	.02908	-.12029	.01971	.02318	.19129	.03734	.08558			
C11	.09134	.02932	-.06687	.01834	.02005	.19791	.03973	.07594	.08133		
C12	.10177	-.01557	-1.02479	.01929	.03562	-.22081	-.06688	.16142	-.14131	6.12591	
C14	.01146	.00767	.06232	.01506	-.00596	.88229	.15152	.02967	.04675	-.35087	.88633

Table 58. Statistical information from discriminant analysis of males of *Cicindela nebraskana chamberlaini* (group 1) and *C. n. nebraskana* (group 3) based on 11 characters. See text for explanation of characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	23.	20.	0	0	0	0	0	0	0

TOTAL

NUMBER 43.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	8.25913	7.82500	0	0	0	0	0	0	0
C2	3.41783	3.37650	0	0	0	0	0	0	0
C3	41.45826	43.21850	0	0	0	0	0	0	0
C4	1.34739	1.29550	0	0	0	0	0	0	0
C5	2.11000	1.98150	0	0	0	0	0	0	0
C6	63.88957	63.30000	0	0	0	0	0	0	0
C7	16.21609	16.01700	0	0	0	0	0	0	0
C10	5.35565	4.36950	0	0	0	0	0	0	0
C11	5.30130	4.71050	0	0	0	0	0	0	0
C12	101.13826	101.29650	0	0	0	0	0	0	0
C14	7.56522	7.30000	0	0	0	0	0	0	0

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	.48192	.43958	0	0	0	0	0	0	0
C2	.12544	.16191	0	0	0	0	0	0	0
C3	1.67876	2.14844	0	0	0	0	0	0	0
C4	.10541	.08525	0	0	0	0	0	0	0
C5	.12699	.14042	0	0	0	0	0	0	0
C6	4.00044	3.67156	0	0	0	0	0	0	0
C7	.22813	.24926	0	0	0	0	0	0	0
C10	.25170	.35126	0	0	0	0	0	0	0
C11	.23927	.38637	0	0	0	0	0	0	0
C12	1.41654	1.93175	0	0	0	0	0	0	0
C14	.78775	.97124	0	0	0	0	0	0	0

Table 58 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	2.94040
C2	-.03243
C3	-.21380
C4	-5.31713
C5	2.34502
C6	1.90907
C7	2.07920
C10	3.96677
C11	-3.66070
C12	-1.03326
C14	-.51085

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	5.50948
C2	-5.21734
C3	-.116627
C4	-46.6232
C5	16.7138
C6	.542769
C7	2.14085
C10	13.1992
C11	-12.4239
C12	-.785173
C14	-.528389
CONSTANT	13.8319

CENTROIDS OF GROUPS IN REDUCED SPACE

	1
GROUP 1	.53963
GROUP 2	-.78334

Table 59. Statistical information from discriminant analysis of females of *Cicindela nebraskana chamberlaini* (group 1) and *C. n. nebraskana* (group 3) based on 11 characters. See text for explanation fo characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	45.	31.	0	0	0	0	0	0	0

UNGROUPED.

NUMBER 76.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	8.79244	8.48323	0	0	0	0	0	0	0
C2	3.52000	3.59032	0	0	0	0	0	0	0
C3	40.85778	42.38097	0	0	0	0	0	0	0
C4	1.43533	1.39258	0	0	0	0	0	0	0
C5	2.10156	2.12387	0	0	0	0	0	0	0
C6	65.26400	65.54419	0	0	0	0	0	0	0
C7	16.32956	16.41903	0	0	0	0	0	0	0
C10	5.21956	5.06452	0	0	0	0	0	0	0
C11	5.07289	4.92903	0	0	0	0	0	0	0
C12	102.51022	102.78323	0	0	0	0	0	0	0
C14	6.95556	7.45161	0	0	0	0	0	0	0

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	.43985	.48242	0	0	0	0	0	0	0
C2	.13772	.16416	0	0	0	0	0	0	0
C3	1.69714	1.66047	0	0	0	0	0	0	0
C4	.12031	.10083	0	0	0	0	0	0	0
C5	.13234	.14594	0	0	0	0	0	0	0
C6	3.51960	3.56479	0	0	0	0	0	0	0
C7	1.04171	.77792	0	0	0	0	0	0	0
C10	.27968	.31043	0	0	0	0	0	0	0
C11	.26601	.31119	0	0	0	0	0	0	0
C12	2.58133	2.31037	0	0	0	0	0	0	0
C14	1.12726	.56796	0	0	0	0	0	0	0

Table 59 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	-12.68066
C2	6.29661
C3	-6.50771
C4	1.47659
C5	2.58133
C6	2.08436
C7	-3.30973
C10	8.30277
C11	-9.85594
C12	-1.75536
C14	-.59878

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	-25.0102
C2	43.9389
C3	-3.11894
C4	13.9160
C5	17.5744
C6	.546072
C7	-3.54613
C10	23.2998
C11	-26.6846
C12	-1.05953
C14	-.840609
CONSTANT	261.981

CENTROIDS OF GROUPS IN REDUCED SPACE

	1
GROUP 1	-1.04673
GROUP 2	1.20374

Table 60. Results of discriminant analysis in assignment of populations of *Cicindela nebraskana chamberlaini* (group 1 in vertical axis) and *C. n. chamberlaini* x *nebraskana* intergrades (group 3 in vertical axis).

A. Males

B. Females

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 1	1	23	22. 95.7 PCT	0 0 PCT	1. 4.3 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 3	3	12	0 0 PCT	0 0 PCT	12. 100.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT

97.1 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 1	1	45	44. 97.8 PCT	0 0 PCT	1. 2.2 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 3	3	25	1. 4.0 PCT	0 0 PCT	24. 96.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT

97.1 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

Table 61. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) for males of *Cicindela n. chamberlaini* (1) and *C. n. chamberlaini* x *nebraskana* (2). * shows a group centroid.

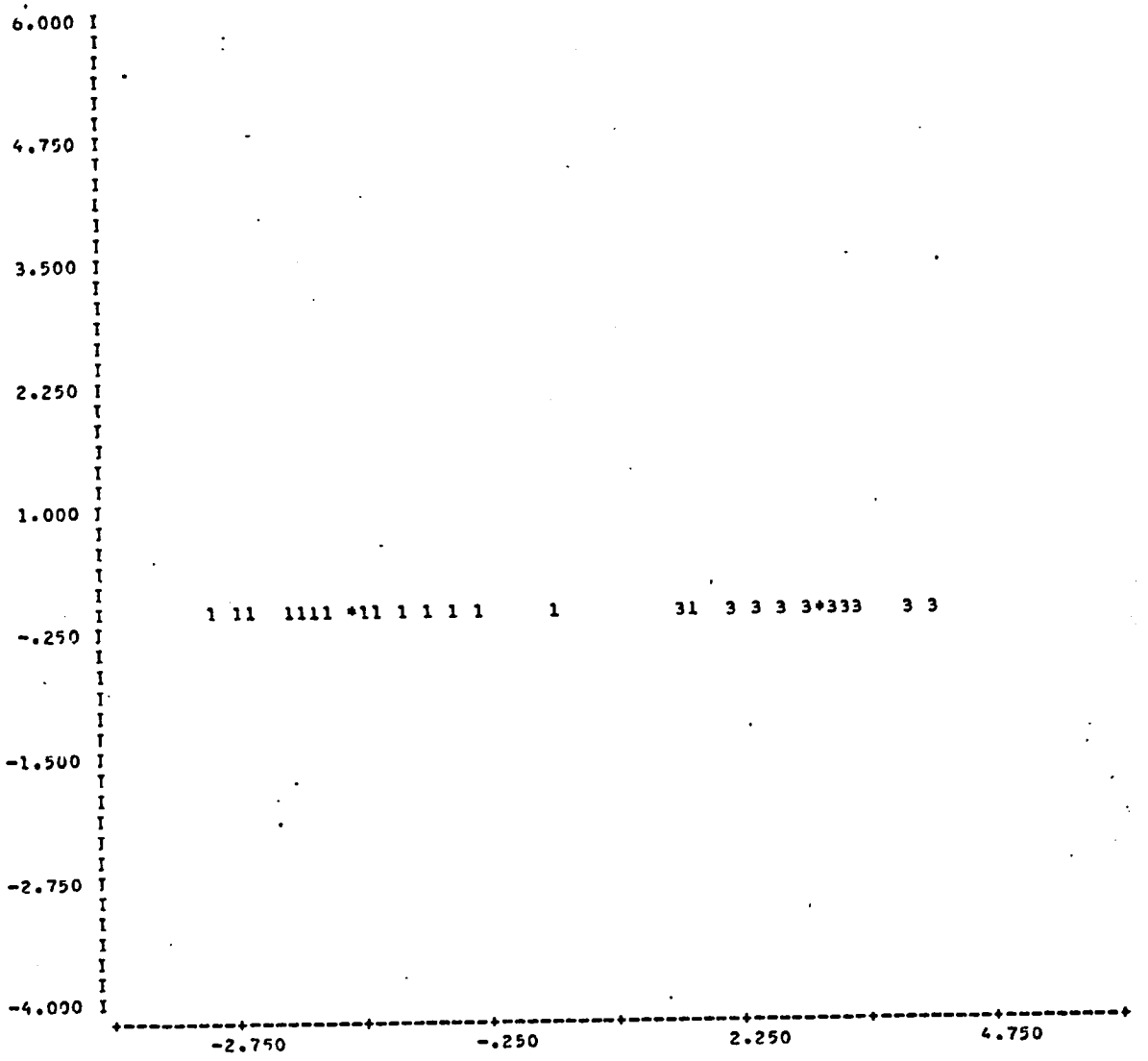

6.000
4.750
3.500
2.250
1.000
-.250
-1.500
-2.750
-4.000
-2.750
-.250
2.250
4.750

Table 62. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) of females of *Cicindela nebraskana chamberlaini* (1) and *C. n. nebraskana* (3). * shows a group centroid.

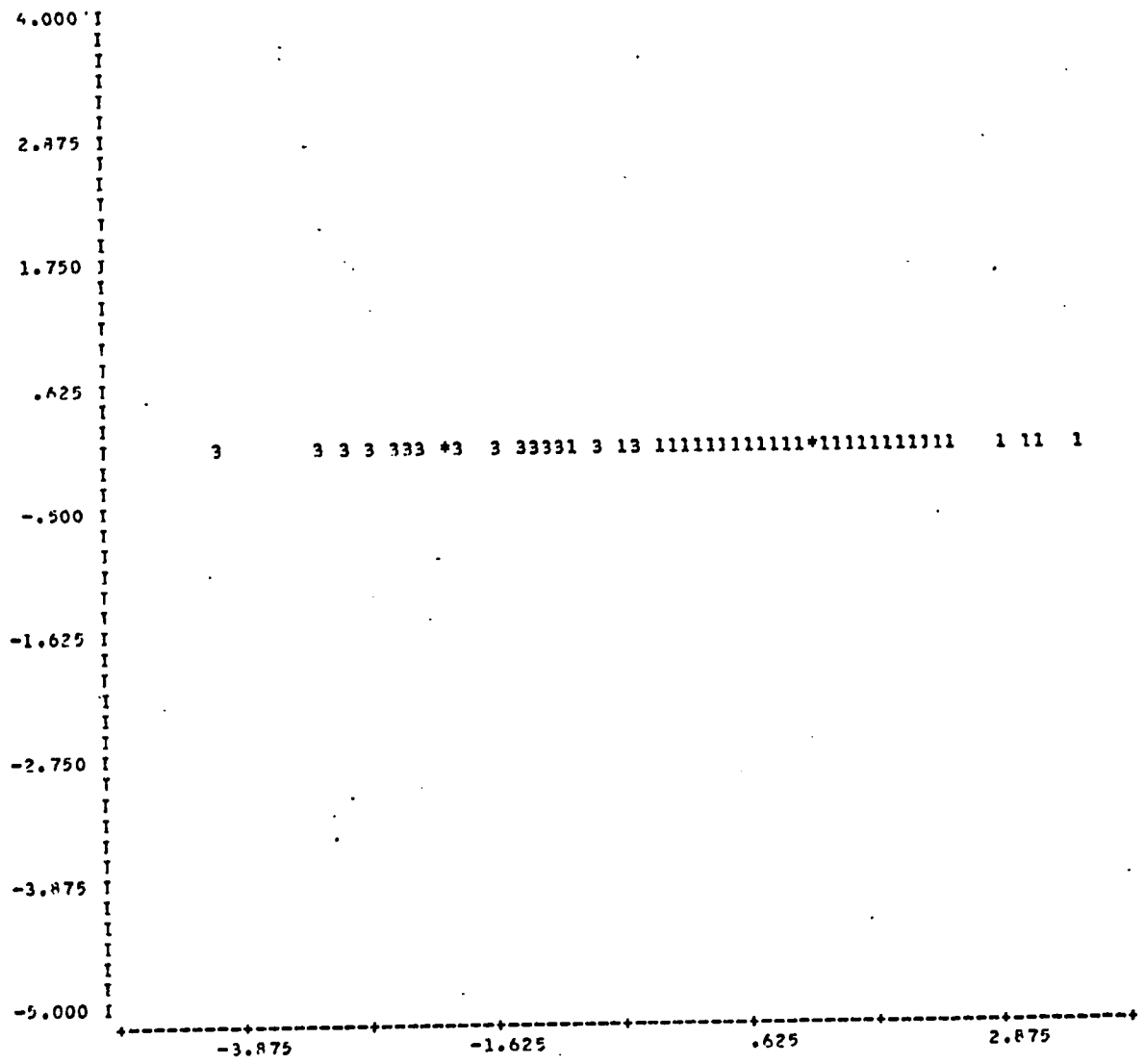

4.000
2.875
1.750
.625
-.500
-1.625
-2.750
-3.875
-5.000
-3.875
-1.625
.625
2.875

Table 63 . Pooled within groups covariance matrix for *Cicindela nebraskana nebraskana* and *C. n. chamberlaini* x *nebraskana* intergrades.

A. Males

B. Females

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.19509										
C2	.04135	.02299									
C3	-.59700	.04458	4.24250								
C4	.01945	.00406	-.06513	.00649							
C5	.05294	.01284	-.15195	.00680	.02188						
C6	-.75990	-.21571	1.79151	.10729	-.38797	19.58600					
C7	-.15292	-.03694	.41638	.04207	-.02384	3.10164	.87338				
C10	.10537	.02334	-.32417	.01112	.03380	-.40101	-.08438	.09683			
C11	.11211	.02465	-.34606	.01249	.03637	-.60685	-.08064	.10229	.11543		
C12	-.20270	-.03741	.76221	-.04008	-.06929	.03337	-.09790	-.16474	-.34913	4.47850	
C14	-.04819	-.01886	.03549	-.00529	-.00063	-.36442	.03202	-.04171	-.06591	.59717	.50387

	C1	C2	C3	C4	C5	C6	C7	C10	C11	C12	C14
C1	.17570										
C2	.04617	.02241									
C3	-.35334	.03158	2.22433								
C4	.02200	.00600	-.01662	.01043							
C5	.03903	.01446	-.02774	.00811	.02042						
C6	-.18538	-.07862	.04768	.24408	-.27304	21.00337					
C7	-.08543	.00511	.51655	.08415	.02197	3.35720	1.21657				
C10	.07330	.01676	-.17415	.01261	.01720	.05036	.00658	.07133			
C11	.06701	.01485	-.16492	.01101	.01330	.10053	-.00110	.06376	.06858		
C12	.09782	.03687	-.05346	.03043	.07760	-1.08801	.19364	.13125	-.14017	5.99198	
C14	.02050	-.00560	-.16270	.00585	-.00111	.31358	.04114	.02590	.02444	.03768	.40143

Table 64. Statistical information from discriminant analysis of males of *Cicindela nebraskana nebraskana* (group 3) and *C. n. chamberlaini* x *nebraskana* intergrades (group 2) based on 11 characters. See text for explanation of characters.

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	0	20.	12.	0	0	0	0	0	0

TOTAL

NUMBER 32.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	0	7.82500	7.13417	0	0	0	0	0	0
C2	0	3.27650	3.21333	0	0	0	0	0	0
C3	0	43.21850	45.12583	0	0	0	0	0	0
C4	0	1.25550	1.16417	0	0	0	0	0	0
C5	0	1.98150	1.82000	0	0	0	0	0	0
C6	0	63.30000	64.28750	0	0	0	0	0	0
C7	0	16.01700	16.34250	0	0	0	0	0	0
C10	0	4.96950	4.45583	0	0	0	0	0	0
C11	0	4.91050	4.40583	0	0	0	0	0	0
C12	0	101.28650	101.17417	0	0	0	0	0	0
C14	0	7.30000	7.91667	0	0	0	0	0	0

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	0	.43958	.44531	0	0	0	0	0	0
C2	0	.16191	.13200	0	0	0	0	0	0
C3	0	2.14844	1.69476	0	0	0	0	0	0
C4	0	.09525	.07179	0	0	0	0	0	0
C5	0	.14042	.14006	0	0	0	0	0	0
C6	0	3.67154	5.44930	0	0	0	0	0	0
C7	0	.94526	.91039	0	0	0	0	0	0
C10	0	.35126	.22577	0	0	0	0	0	0
C11	0	.38637	.23857	0	0	0	0	0	0
C12	0	1.93175	2.40177	0	0	0	0	0	0
C14	0	.57124	.90034	0	0	0	0	0	0

Table 64 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	-7.17051
C2	1.94523
C3	-1.98313
C4	-.35361
C5	5.06606
C6	3.35107
C7	-3.13173
C10	35.20593
C11	-38.17186
C12	-8.30494
C14	.45135

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	-12.9996
C2	11.4843
C3	-.709007
C4	-3.88098
C5	30.5572
C6	.764970
C7	-3.35504
C10	88.6980
C11	-91.6925
C12	-3.98784
C14	.592833
CONSTANT	451.412

CENTROIDS OF GROUPS IN REDUCED SPACE

	1
GROUP 2	-.88628
GROUP 3	1.47713

Table 65. Statistical information from discriminant analysis of females of *Cicindela nebraskana nebraskana* (group 3) and *C. n. chamberlaini* x *nebraskana* intergrades (group 2) based on 11 characters. See text for explanation of characters.

GROUP COUNTS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
NUMBER	0	31.	25.	0	0	0	0	0	0

UNGROUPED.

NUMBER 55.

MEANS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	0	8.48323	8.01960	0	0	0	0	0	0
C2	0	3.59032	3.44560	0	0	0	0	0	0
C3	0	42.38097	42.98440	0	0	0	0	0	0
C4	0	1.39258	1.35560	0	0	0	0	0	0
C5	0	2.12387	2.00220	0	0	0	0	0	0
C6	0	65.64419	67.65560	0	0	0	0	0	0
C7	0	16.41903	16.92440	0	0	0	0	0	0
C10	0	5.06452	4.58960	0	0	0	0	0	0
C11	0	4.92903	4.43880	0	0	0	0	0	0
C12	0	102.78323	103.41800	0	0	0	0	0	0
C14	0	7.45161	7.20000	0	0	0	0	0	0

STANDARD DEVIATIONS

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
C1	0	.48942	.30968	0	0	0	0	0	0
C2	0	.14416	.12936	0	0	0	0	0	0
C3	0	1.66047	1.24832	0	0	0	0	0	0
C4	0	.10083	.10377	0	0	0	0	0	0
C5	0	.14594	.13898	0	0	0	0	0	0
C6	0	3.56478	5.60116	0	0	0	0	0	0
C7	0	.77792	1.40742	0	0	0	0	0	0
C10	0	.31043	.20011	0	0	0	0	0	0
C11	0	.31118	.18240	0	0	0	0	0	0
C12	0	2.31037	2.60950	0	0	0	0	0	0
C14	0	.56796	.70711	0	0	0	0	0	0

Table 65 (continued)

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	3.92180
C2	-7.41080
C3	5.93304
C4	6.98226
C6	-.22779
C7	-6.33395
C10	11.29903
C11	-10.35981
C12	-3.46403
C14	.20597

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS

	1
C1	9.23886
C2	-44.8751
C3	8.96627
C4	67.9564
C6	-.429657E-01
C7	-5.64561
C10	31.7040
C11	-28.9782
C12	-1.41603
C14	.321642
CONSTANT	50.9532

CENTROIDS OF GROUPS IN REDUCED SPACE

	1
GROUP 2	.99259
GROUP 3	-1.23081

Table 66. Results of discriminant analysis in assignment of populations of *Cicindela nebraskana nebraskana* (group 1 in vertical axis) and *C. n. chamberlaini* x *nebraskana* intergrades (group 2 in vertical axis).

A. Males

B. Females

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 2	2	20	0 0 PCT	17. 85.0 PCT	3. 15.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 3	3	12	0 0 PCT	1. 8.3 PCT	11. 91.7 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT

87.5 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

ACTUAL GROUP NAME	CODE	N OF CASES	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5	GROUP 6	GROUP 7	GROUP 8	GROUP 9
GROUP 2	2	31	0 0 PCT	27. 87.1 PCT	4. 12.9 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT
GROUP 3	3	25	0 0 PCT	3. 12.0 PCT	22. 88.0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT	0 0 PCT

87.5 PERCENT OF KNOWN CASES CORRECTLY CLASSIFIED

Table 67. Plot of Discriminant Score 1 (horizontal axis) vs. Discriminat Score 2 (vertical axis for males of *Cicindela n. nebraskana* (3) and *C. n. chamberlaini* x *nebraskana* (2). * shows a group centroid.

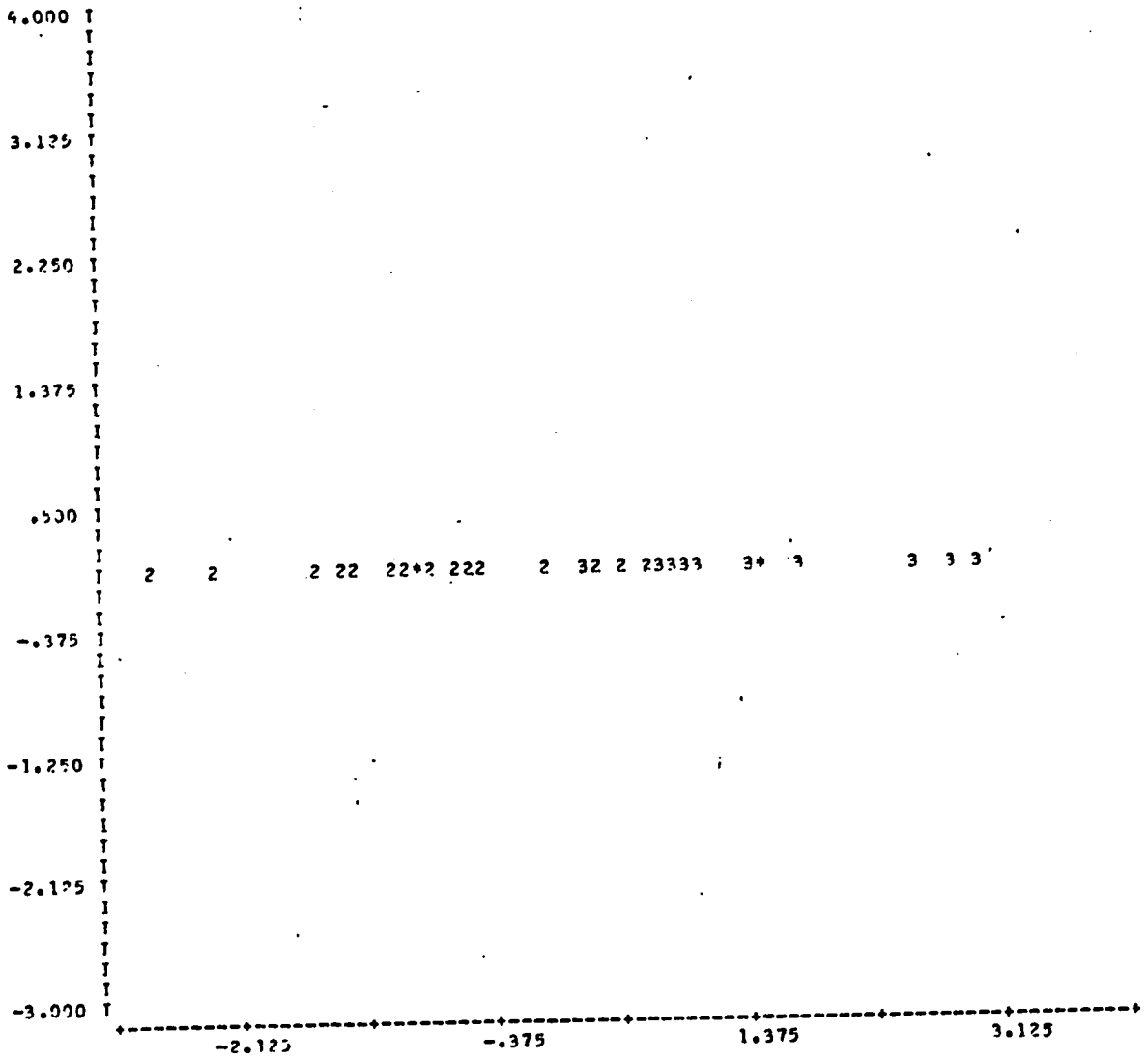

4.000
3.125
2.250
1.375
.500
-.375
-1.250
-2.125
-3.000
-2.125
-.375
1.375
3.125

Table 68 . Plot of Discriminant Score 1 (horizontal axis) vs. Discriminant Score 2 (vertical axis) for females of *Cicindela n. nebraskana* (3) and *C. n. chamberlaini* x *nebraskana* (2). * shows a group centroid.

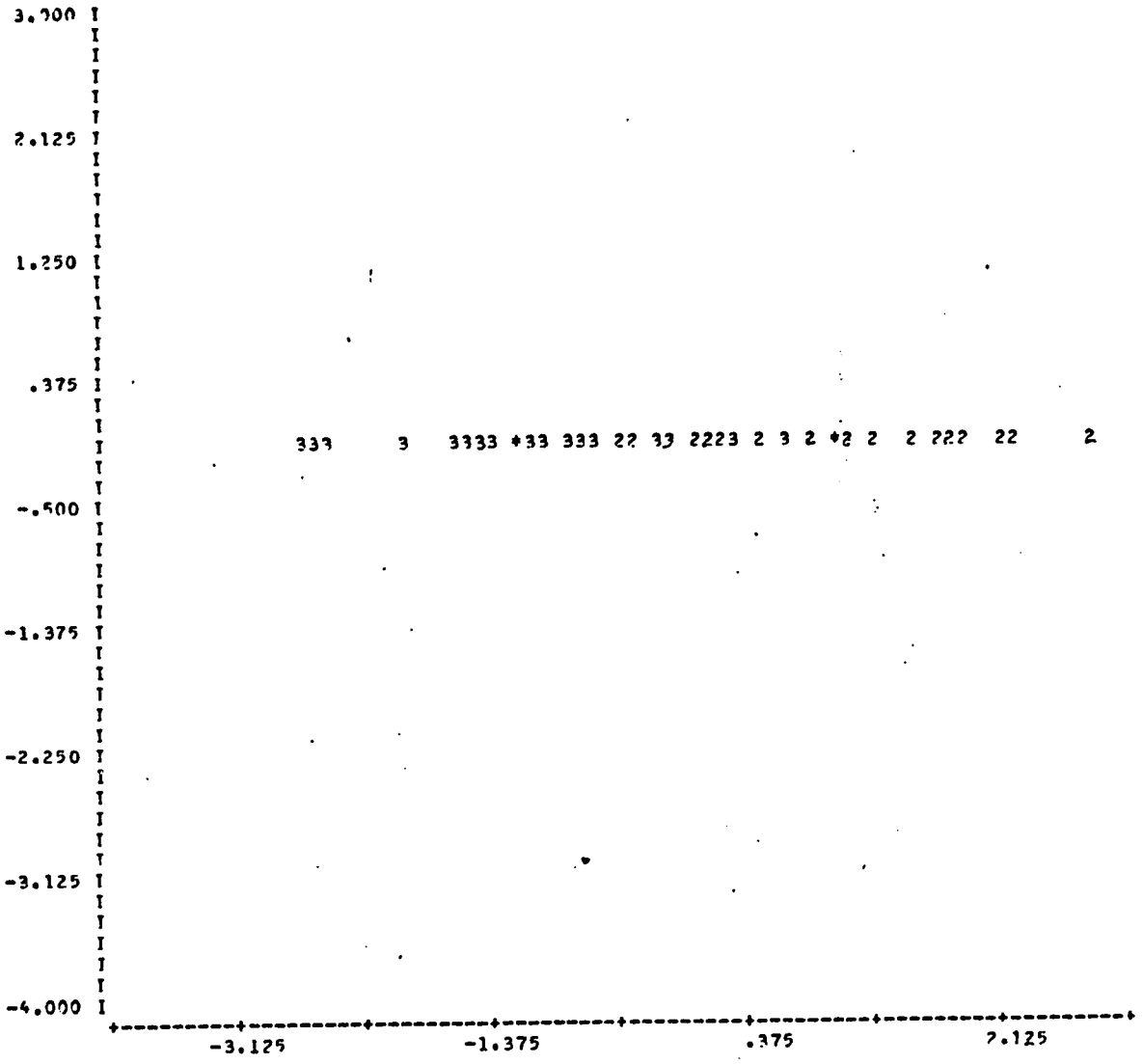

3.000
2.125
1.250
.375
-.500
-1.375
-2.250
-3.125
-4.000
-3.125
-1.375
.375
2.125

Table 69. Discrimination rankings of 11 character-states from discriminant analysis of species, subspecies, and intergrade populations of Nearctic members of the *silvatica*-group. See text for explanation of symbol at heads of ranking lists.

Male								Female							
Discrimination Rankings	Character-State Number							Discrimination Rankings	Character-State Number						
	LN	pl	pi	li	cn	ci	ni		LN	pl	pi	li	cn	ci	ni
1	12	2	3	14	11	10	10	1	14	3	3	3	11	3	11
2	14	14	11	3	2	14	14	2	11	10	11	14	3	14	6
3	5	11	1	12	12	3	12	3	10	12	14	10	1	11	3
4	11	7	10	6	10	12	4	4	5	14	10	12	6	12	7
5	10	4	14	10	3	11	11	5	1	1	2	1	10	7	10
6	6	12	12	1	1	7	5	6	12	4	7	11	14	2	12
7	2	10	6	11	14	6	1	7	6	2	12	4	12	1	14
8	4	3	2	2	6	1	2	8	7	11	4	2	5	5	4
9	3	1	5	5	4	2	6	9	3	5	5	5	7	6	2
10	1	6	4	7	5	4	7	10	2	6	6	6	2	4	1
11	7	5	7	4	7	5	3	11	4	7	1	7	4	10	5

means that the character is the most useful in distinguishing two given taxa. Three arbitrary ratings have been given to the ranks:

Ranks 1-4 - most useful

Ranks 5-7 - of limited usefulness

Ranks 8-11 - least useful

I have used symbols for the populations I am comparing, and these are employed in Table 69:

LN- *C. longilabris* and *C. nebraskana* species discrimination

pl- differentiation of *c. l. perviridis* and *C. l. laurenti*

pi- differentiation of *C. l. perviridis* and *perviridis* X *laurenti* intergrades

li- differentiation of *C. l. laurenti* and *perviridis* X *laurenti* intergrades

cn- differentiation of *C. n. chamberlaini* and *C. n. nebraskana*

ci- differentiation of *C. n. chamberlaini* and *chamberlaini* X *nebraskana* intergrades

ni- differentiation of *C. n. nebraskana* and *chamberlaini* X *nebraskana* intergrades

In the following accounts, I shall summarize results of the discriminant analysis for each of the 11 characters and their taxonomic implications.

Character 1

Elytral length is useful (Rank 3) only in distinguishing *C. n. nebraskana* and *C. n. chamberlaini*, the difference between the means being 8.76%.

Characters 2 and 3

Head breadth is one of the most important characters in distinguishing males of subspecies of both *C. longilabris* (Rank 1) and *C. nebraskana*. In both species, the character shows subspecific differences and slight sexual dimorphism in *C. nebraskana*, the males having proportionally slightly broader heads. The westernmost subspecies of both species have the narrowest heads, the easternmost subspecies the broadest heads, and the intergrade populations the intermediate condition. The character of head breadth is most readily understood in terms of character 3, the ratio head breadth/elytral length. Examination of my tables shows that elytral length of all of the subspecies and intergrades is similar except for the small *C. n. nebraskana*. Thus, it is head breadth differences that produce the sexual and subspecific variation. The results are summarized in Table 77.

Characters 4-6

Labral proportions are of limited value, the apparent usefulness stemming from the inclusion of the small *C. n. nebraskana*

in the analysis. Character 6, the ratio labral breadth/length, shows generally low rankings indicating that *C. n. nebraskana* is uniformly a smaller animal.

Character 7

Male p! and female ni both show Rank 4 for the ratio, labral length/elytral length. There is a 5.8% difference between the means for labral lengths of *perviridis* and *laurenti* compared with only 0.74% for elytral lengths, *perviridis* being the smaller subspecies in both measurements. Equivalent differences between female *nebraskana* and *chamberlaini* X *nebraskana* intergrades are 3.99% and 5.42%, the latter reflecting the small size of *C. n. nebraskana*. According to the formulae of Amadon (1949), the differences are not significant even at the 75% level.

Characters 10-12

Relative proportions of the metatibia and metatarsus are important in distinguishing the two species and may reflect differences in mechanical advantage of the hind limb. Actual lengths of the limb segments do not correlate with body size differences, since elytral length ranks low and limb segment lengths rank quite high. Thus, limb segments show useful differences in distinguishing the species. This is shown best by the ratio, metatibial length/metatarsal length. No specimen of *C. longilabris* has a ratio greater than 98.81%, and this species averages 91.58%. Conversely, no specimen of *C. nebraskana* has a

ratio less than 100.0%, and this species averages 102.02%. The difference between the means is 10.23% and the difference between the extremes is 1.19%.

The significance of the differences between the two species is probably related to mechanical advantage of the proportions of the limb segments. Hamilton (1973:101) stated: "If the mechanical advantage of the locomotory muscles is high then a slow powerful action is indicated . . . a low mechanical advantage . . . indicates a weak but rapid action and is characteristic of cursorial animals . . . [Therefore] the mechanical advantage . . . may be used to measure the degree of cursorial adaptation attained." Similarly, Miller (1911) showed that ". . . shortening of the power arm . . . would . . . diminish the [power] of the limb" in fossil eagles. Hence, the high ratio of *C. nebraskana* suggests a slower runner, and the lower ratio of *C. longilabris* indicates a fast runner. It would be useful to experiment with the two species to prove these predictions.

A second interpretation (the two interpretations may both be correct and not mutually exclusive) is that the ratios involve adaptations to soil types. Unfortunately, I have not been able to study enough specimens of species characteristically of sand or clay soils. The means of the ratios (N = 5) of two arenicolous species, *C. arenicola* and *C. bellissima*, are 117.32% and 125.58%, respectively. *C. tranquebarica* which typically inhabits compact soils, often clayey, has a mean ratio (N = 5) of 98.74%. Analysis

of soil samples from localities inhabited by *C. longilabris* and *nebraskana* (see "Soil Analysis") showed that *longilabris* (low ratio) is found on clayier soils than *nebraskana* (high ratio). More work is needed to corroborate the relationship between soil type and limb proportions.

Character 14

The density of elytral punctures gives excellent separation between the two species and between some of the subspecies and their intergrades. Density in *longilabris* ranges from 6-13 punctures/2 mm^2, with 66.3% of the total sample (183 of 276 total) between nine and 11. Density in *nebraskana* ranges from 4-9 punctures/2 mm^2, with 55.1% (192 of 167 total) between six and seven. Overlaps between the species are: *longilabris* with density less than 10 punctures-22.5%; *nebraskana* with density more than seven punctures-41.3%. I have found no references in the literature concerning this character.

Tables 70 to 76 present analysis of seven qualitative characters of *C. longilabris* and *C. nebraskana*. For this analysis, localities are grouped so that six entities are represented, indicated by the numbers 1-6 on the X-axis of the tables:

1. *C. l. perviridis*
2. *C. l. perviridis* X *laurenti*
3. *C. l. laurenti*
4. *C. n. chamberlaini*

5. *C. n. chamberlaini* X *nebraskana*

6. *C. n. nebraskana*

Categories in the y-axis correspond to the divisions of characters 8, 9, 13, and 15-18 which I have previously defined. Because of possible differences from sexual dimorphism, sexes are treated separately for characters 8 and 9. Sexes are pooled for characters 13 and 15-18.

Cramer's V was computed for each of the seven characters. Nie (1975:225) described Cramer's V as a measure of the strength of association of the data. A high value means that a high degree of association exists. For example, character 13 has a Cramer's V of 0.81, showing that data are clustered, defining two categories corresponding to the two species *longilabris* and *nebraskana*. Thus, character-state 13 is useful in distinguishing the two species. Conversely, Cramer's V for character 8 (males) is 0.28, showing little clustering and, thus, high variability of the character. Therefore, character-state 8 is of low taxonomic value. In the following accounts, I shall summarize results of this analysis of each of the eight characters and the taxonomic implications. The results are presented graphically in Tables 70 to 76.

Character 8

The low Cramer's V for both sexes, 0.28 for males and 0.26 for females, shows limited difference between the two species.

Table 70. Sample percentages of forms of distal outline of labrum (character-states for Character 8) in species and subspecies of the *silvatica*-group of *Cicindela*. Numbers 1-2 in the vertical axis refer to the two character-states (1-2); numbers 1-6 in the horizontal axis refer to the subspecies and intergrade populations of the two species: see text for identification of character-states and taxa.

C8	COUNT / COL PCT / TOT PCT	TYPE 1	2	3	4	5	6	ROW TOTAL
1		10	15	8	14	12	8	67
		27.0	26.3	34.8	56.0	52.2	61.5	37.6
		5.6	8.4	4.5	7.9	6.7	4.5	
2		27	42	15	11	11	5	111
		73.0	73.7	65.2	44.0	47.8	38.5	62.4
		15.2	23.6	8.4	6.2	6.2	2.8	
COLUMN TOTAL		37	57	23	25	23	13	178
		20.8	32.0	12.9	14.0	12.9	7.3	100.0

RAW CHI SQUARE = 13.79289 WITH 5 DEGREES OF FREEDOM. SIGNIFICANCE = .0170
CRAMER'S V = .27337

C8	COUNT / COL PCT / TOT PCT	TYPE 1	2	3	4	5	6	ROW TOTAL
1		1	23	3	14	8	9	58
		1.9	26.7	14.3	29.2	25.0	34.6	21.9
		.4	8.7	1.1	5.3	3.0	3.4	
2		51	63	18	34	24	17	207
		98.1	73.3	85.7	70.8	75.0	65.4	78.1
		19.2	23.8	6.8	12.8	9.1	6.4	
COLUMN TOTAL		52	86	21	48	32	26	265
		19.6	32.5	7.9	18.1	12.1	9.8	100.0

RAW CHI SQUARE = 18.15195 WITH 5 DEGREES OF FREEDOM. SIGNIFICANCE = .0028
CRAMER'S V = .26172

Table 71. Sample percentages of labra coloration (character-states for Character 9) in species and subspecies of the *silvatica*-group of *Cicindela*. Numbers 1-3 in the vertical axis refer to the three character-states (1-3); numbers 1-6 in the horizontal axis refer to the subspecies and intergrade populations of the two species: see text for identification of the character-states and taxa.

C9	TYPE 1	2	3	4	5	6	ROW TOTAL
1	36	54	22	25	19	12	168
	97.3	90.0	95.7	100.0	82.6	92.3	92.8
	19.9	29.8	12.2	13.8	10.5	6.6	
2	1	3	1	0	4	1	10
	2.7	5.0	4.3	0	17.4	7.7	5.5
	.6	1.7	.6	0	2.2	.6	
3	0	3	0	0	0	0	3
	0	5.0	0	0	0	0	1.7
	0	1.7	0	0	0	0	
COLUMN TOTAL	37	60	23	25	23	13	181
	20.4	33.1	12.7	13.8	12.7	7.2	100.0

RAW CHI SQUARE = 14.57355 WITH 10 DEGREES OF FREEDOM. SIGNIFICANCE = .1484
CRAMER'S V = .20065

C9	TYPE 1	2	3	4	5	6	ROW TOTAL
1	45	73	18	14	7	0	157
	66.5	83.9	65.7	29.2	21.9	0	59.0
	16.9	27.4	6.8	5.3	2.6	0	
2	7	10	2	15	10	3	47
	13.5	11.5	9.5	31.3	31.3	11.5	17.7
	2.6	3.8	.8	5.6	3.8	1.1	
3	0	4	1	19	15	23	62
	0	4.6	4.8	39.6	46.9	88.5	23.3
	0	1.5	.4	7.1	5.6	8.6	
COLUMN TOTAL	52	87	21	48	32	26	266
	19.5	32.7	7.9	18.0	12.0	9.8	100.0

RAW CHI SQUARE = 149.21904 WITH 10 DEGREES OF FREEDOM. SIGNIFICANCE = .0000
CRAMER'S V = .52961

Table 72. Sample percentages of forms of elytral sculpture (character-states for Character 13) in species and subspecies of the *silvatica*-group of *Cicindela*. Numbers 1-3 in the vertical axis refer to the three character-states (1-3); numbers 1-6 in the horizontal axis refer to the subspecies and intergrade populations of the two species: see text for identification and character-states and taxa.

C13

C13	TYPE 1	2	3	4	5	6	POW TOTAL
1	0	0	0	73	53	39	165
	0	0	0	100.0	96.4	100.0	36.9
	0	0	0	16.3	11.9	8.7	
2	89	82	7	0	2	0	180
	100.0	55.8	15.9	0	3.6	0	40.3
	19.9	18.3	1.6	0	.4	0	
3	0	65	37	0	0	0	102
	0	44.2	84.1	0	0	0	22.8
	0	14.5	8.3	0	0	0	
COLUMN TOTAL	89	147	44	73	55	39	447
	19.9	32.9	9.8	16.3	12.3	8.7	100.0

RAW CHI SQUARE = 594.63935 WITH 10 DEGREES OF FREEDOM. SIGNIFICANCE = 0
CRAMER'S V = .81556

Table 73. Sample percentages of elytral coloration (character-states for Character 15) in species and subspecies of the *silvatica*-group of *Cicindela*. Numbers 1-15 in the vertical axis refer to the 15 character-states (A-O); numbers 1-6 in the horizontal axis refer to the subspecies and intergrade populations of the two species: see text for identification of character-states and taxa.

C15

C15	TYPE 1	2	3	4	5	6	ROW TOTAL
1	0	0	1	0	0	0	1
	0	0	2.3	0	0	0	.2
	0	0	.2	0	0	0	
2	0	13	1	0	0	0	14
	0	8.6	2.3	0	0	0	3.1
	0	2.9	.2	0	0	0	
3	39	21	1	0	0	0	61
	43.8	14.3	2.3	0	0	0	13.6
	8.7	4.7	.2	0	0	0	
4	28	9	0	1	0	0	38
	31.5	6.1	0	1.4	0	0	8.5
	6.3	2.0	0	.2	0	0	
5	14	0	0	0	0	0	14
	15.7	0	0	0	0	0	3.1
	3.1	0	0	0	0	0	
6	1	0	0	0	0	0	1
	1.1	0	0	0	0	0	.2
	.2	0	0	0	0	0	
7	2	0	2	0	0	0	4
	2.2	0	4.5	0	0	0	.9
	.4	0	.4	0	0	0	
8	4	39	3	0	0	0	46
	4.5	26.5	6.8	0	0	0	10.3
	.9	8.7	.7	0	0	0	
9	0	40	7	0	0	0	47
	0	27.2	15.9	0	0	0	10.5
	0	8.9	1.6	0	0	0	
10	0	3	9	0	0	0	12
	0	2.0	20.5	0	0	0	2.7
	0	.7	2.0	0	0	0	
11	0	2	4	0	0	0	6
	0	1.4	9.1	0	0	0	1.3
	0	.4	.9	0	0	0	
12	0	4	5	1	0	2	12
	0	2.7	11.4	1.4	0	5.1	2.7
	0	.9	1.1	.2	0	.4	
13	1	4	5	0	0	0	10
	1.1	2.7	11.4	0	0	0	2.2
	.2	.9	1.1	0	0	0	
14	0	10	6	58	46	27	147
	0	6.8	13.6	79.5	83.6	69.2	32.9
	0	2.2	1.3	13.0	10.3	6.0	
15	0	2	0	13	9	10	34
	0	1.4	0	17.8	16.4	25.6	7.6
	0	.4	0	2.9	2.0	2.2	
COLUMN TOTAL	89	147	44	73	55	39	447
	19.9	32.9	9.8	16.3	12.3	8.7	100.0

RAW CHI SQUARE = 729.01254 WITH 70 DEGREES OF FREEDOM. SIGNIFICANCE = 0
CRAMER'S V = .57144

Table 74. Sample percentages of elytral maculation (character-states for Character 16) in species and subspecies of the *silvatica*-group of *Cicindela*. Numbers 1-17 in the vertical axis refer to the 17 character-states (A-Q); numbers 1-6 in the horizontal axis refer to the subspecies and intergrade populations of the two species: see text for identification of character-states and taxa.

C16

C16	TYPE							
COUNT / COL PCT / TOT PCT	1	2	3	4	5	6	ROW TOTAL
1	0	1	4	0	0	0	5
	0	.7	9.1	0	0	0	1.1
	0	.2	.9	0	0	0	
2	3	13	4	0	0	0	20
	3.4	8.8	9.1	0	0	0	4.5
	.7	2.9	.9	0	0	0	
3	12	1	1	0	0	0	14
	13.5	.7	2.3	0	0	0	3.1
	2.7	.2	.2	0	0	0	
4	14	2	0	0	0	0	16
	15.7	1.4	0	0	0	0	3.6
	3.1	.4	0	0	0	0	
5	0	0	1	0	0	0	1
	0	0	2.3	0	0	0	.2
	0	0	.2	0	0	0	
6	0	0	1	0	0	0	1
	0	0	2.3	0	0	0	.2
	0	0	.2	0	0	0	
7	11	26	5	0	0	0	42
	12.4	17.7	11.4	0	0	0	9.4
	2.5	5.8	1.1	0	0	0	
8	1	0	0	0	0	0	1
	1.1	0	0	0	0	0	.2
	.2	0	0	0	0	0	
9	4	1	0	0	0	0	5
	4.5	.7	0	0	0	0	1.1
	.9	.2	0	0	0	0	
10	3	21	3	2	1	0	30
	3.4	14.3	6.8	2.7	1.8	0	6.7
	.7	4.7	.7	.4	.2	0	
11	0	0	4	0	0	0	4
	0	0	9.1	0	0	0	.9
	0	0	.9	0	0	0	
12	0	2	1	2	0	0	5
	0	1.4	2.3	2.7	0	0	1.1
	0	.4	.2	.4	0	0	
13	16	23	2	2	1	0	44
	18.0	15.6	4.5	2.7	1.8	0	9.8
	3.6	5.1	.4	.4	.2	0	
14	3	3	2	0	0	0	8
	3.4	2.0	4.5	0	0	0	1.8
	.7	.7	.4	0	0	0	
15	20	39	6	49	30	2	146
	22.5	26.5	13.6	67.1	54.5	5.1	32.7
	4.5	8.7	1.3	11.0	6.7	.4	
16	2	7	2	16	19	2	48
	2.2	4.8	4.5	21.9	34.5	5.1	10.7
	.4	1.6	.4	3.6	4.3	.4	
17	0	8	8	2	4	35	57
	0	5.4	18.2	2.7	7.3	89.7	12.8
	0	1.8	1.8	.4	.9	7.8	
COLUMN TOTAL	89	147	44	73	55	39	447
	19.9	32.9	9.8	16.3	12.3	8.7	100.0

RAW CHI SQUARE = 592.52160 WITH 80 DEGREES OF FREEDOM. SIGNIFICANCE = 0
CRAMER'S V = .51489

Table 75. Sample percentages of angle of bend of middle band (character-states for Character 17) in species and subspecies of the *silvatica*-group of *Cicindela*. Numbers 1-3 in the vertical axis refer to the three character-states (1-3); numbers 1-6 in the horizontal axis refer to the subspecies and intergrade populations of the two species: see text for identification of character-states and taxa.

C17		TYPE 1	2	3	4	5	6	ROW TOTAL
	1	62	114	30	32	26	2	266
		69.7	77.6	68.2	43.8	47.3	5.1	59.5
		13.9	25.5	6.7	7.2	5.8	.4	
	2	20	18	4	23	5	0	70
		22.5	12.2	9.1	31.5	9.1	0	15.7
		4.5	4.0	.9	5.1	1.1	0	
	3	7	15	10	18	24	37	111
		7.9	10.2	22.7	24.7	43.6	94.9	24.8
		1.6	3.4	2.2	4.0	5.4	8.3	
COLUMN TOTAL		89	147	44	73	55	39	447
		19.9	32.9	9.8	16.3	12.3	8.7	100.0

RAW CHI SQUARE = 166.13113 WITH 10 DEGREES OF FREEDOM. SIGNIFICANCE = 0
CRAMER'S V = .43108

Table 76. Sample percentages of ventral abdominal coloration (character-states for Character 18) in species and subspecies of the *silvatica*-group of *Cicindela*. Numbers 1-7 in the vertical axis refer to the seven character-states (1-7); numbers 1-6 in the horizontal axis refer to the subspecies and intergrade populations of the two species: see text for identification of character-states and taxa.

C18 by TYPE

COUNT / COL PCT / TOT PCT	1	2	3	4	5	6	ROW TOTAL
1	14	10	0	0	0	0	24
	15.7	6.8	0	0	0	0	5.4
	3.1	2.2	0	0	0	0	
2	47	127	39	1	0	0	214
	52.8	86.4	88.6	1.4	0	0	47.9
	10.5	28.4	8.7	.2	0	0	
3	6	0	0	0	0	0	6
	6.7	0	0	0	0	0	1.3
	1.3	0	0	0	0	0	
4	21	3	0	1	1	0	26
	23.6	2.0	0	1.4	1.8	0	5.8
	4.7	.7	0	.2	.2	0	
5	0	4	4	69	54	28	159
	0	2.7	9.1	94.5	98.2	71.8	35.6
	0	.9	.9	15.4	12.1	6.3	
6	0	3	1	0	0	0	4
	0	2.0	2.3	0	0	0	.9
	0	.7	.2	0	0	0	
7	1	0	0	2	0	11	14
	1.1	0	0	2.7	0	28.2	3.1
	.2	0	0	.4	0	2.5	
COLUMN TOTAL	89	147	44	73	55	39	447
	19.9	32.9	9.8	16.3	12.3	8.7	100.0

RAW CHI SQUARE = 577.66979 WITH 30 DEGREES OF FREEDOM. SIGNIFICANCE = 0
CRAMER≠S V = .50839

Table 77. Summary of means and standard deviations of Ratio, head breadth/elytral length for sexes, subspecies, and intergrades of *Cicindela longilabris* and *C. nebraskana*.

Taxon	Male (in %)	Female (in %)
C. l. perviridis	40.95 ± 1.01	40.72 ± 1.20
C. l. perviridis X *laurenti*	42.75 ± 1.66	42.01 ± 1.61
C. l. laurenti	43.47 ± 2.05	43.42 ± 1.26
C. n. chamberlaini	41.46 ± 1.68	40.86 ± 1.70
C. n. chamberlaini X *nebraskana*	43.22 ± 2.15	42.38 ± 1.66
C. n. nebraskana	45.13 ± 1.90	42.98 ± 1.25

In *C. longilabris*, 33 of the 117 males (28.2%) have tridentate labra, but only 27 of the 159 females (17.0%). Only one female of 52 *C. l. perviridis* was tridentate.

In *C. nebraskana*, 34 of the 61 males (55.7%) are tridentate, as opposed to 31 of the 106 females (29.2%).

My data refute Casey's (1913:5) statement: ". . . formation of the labrum is different in the male and female. In [the Nearctic species of the *silvatica*-group, the margin] is usually tridentate in the male . . . and purely unidentate in the female. . . ." The unidentate state is actually most common in both sexes of both species except in the males of *C. nebraskana* where about half the sample shows one or the other state.

Character 9

The low Cramer's V for males (0.20) shows that labral color is of limited value in distinguishing males of the two species. A Cramer's V of 0.53 for females indicates greater value for the character in distinguishing females.

In *C. longilabris*, 112 of the 120 males (93.3%) have pale labra; and 136 of 160 females (85.0%). Percentages of black labra are 2.5% of the males and 3.1% of the females.

In *C. nebraskana*, 56 of the 61 males (91.8%) have completely pale labra and 21 of the 106 females (19.8%). Percentages of black labra are 0.0% of the males and 53.8% of the females. In *C. n. nebraskana* none of the females (N = 26) has a completely pale labrum, but 29.2% (14 out of 48) of

C. n. chamberlaini females have pale labra. This less-than-complete degree of sexual dimorphism of *chamberlaini* shows somewhat greater plesiomorphy in this character-state compared with *nebraskana*.

Character 13 (see figs. 48 and 49)

The two species are nearly completely separable on the basis of elytral sculpture. No *longilabris* examined had *nebraskana*-type sculpture, and two females from ALTA. Gorge Creek (UALTA) had sculpture resembling that of *C. l. perviridis*, although with the low density of punctures (Character-state 14) of *nebraskana*. A Cramer's V of 0.82 corroborates the separability.

Intergrades *C. l. perviridis* X *laurenti* are fairly equally divided between *perviridis*-and *longilabris*-type sculpture (55.8% and 44.2% respectively), to be expected of intergrade populations. All specimens of *perviridis* show *perviridis*-type sculpture. Of 44 specimens of *laurenti*, only seven (15.9%), all from Colorado, show *perviridis*-type rather than *longilabris*-type.

Casey, in several papers mentioned elytral sculpture as being important in distinguishing taxa in this species group, but he gave few details. Later authors, except for Willis (1968), largely ignored the character. My data show the character excellent in separating the two species and useful in separating some subspecies of *longilabris*.

Character 15

My analysis of elytral coloration shows how variable this character is in distinguishing subspecies of *longilabris*, although the character gives nearly perfect species separation. In *longilabris* only 18 specimens out of 280 (6.4%) are black or black with green speckles (codes 14 and 15), whereas only four specimens of *nebraskana* out of 167 (2.4%) are not black. A Cramer's V = .57 corroborates the species separation.

In *longilabris*, at the subspecific level, only *perviridis* shows strong separability: 81 of the 89 specimens (91.0%) are codes 3-5 (bright green, greenish-blue, or blue). The series of *laurenti* are fairly evenly distributed among the various codes. The intergrade specimens show peaks at codes 2-4 (dark dull green, bright green, and greenish-blue)--29.3%; and codes 8-9 (green with cupreous tinge and cupreous with green tinge)--53.7%. Therefore, although green or blue coloration is characteristic of *perviridis*, I do not believe coloration should have been used by Casey, Leng, and Schaupp in distinguishing the taxa that I unite as *C. l. laurenti* (*estesiana*, *oslari*, and *uteana*). This is also one of the reasons why I believe that a proposed subspecies of *longilabris* from southwestern Utah and northern Arizona, mentioned by Lawton (1972b), should not be recognized.

Character 16

My analysis of elytral maculation shows that this character, like coloration, has received too much emphasis in

previous studies of this species-group. *C. longilabris* tends to be more maculate than *nebraskana*, but 100 of the 280 specimens (35.7%) have maculation of codes 13-17 (see figs. 50 M-Q). Conversely, only eight out of 112 *nebraskana* (7.1%) have codes 1-14. A moderately high Cramer's V of .51 reflects the partial species separability yet variability of *longilabris*.

Maculation is of no value in subspecies discrimination. Neither the series of *perviridis* nor *laurenti* show tendencies toward any particular range of codes. Three peaks appear in the series of *perviridis:* codes 2-4 = 32.6%, codes 7-10 = 21.3%, and codes 13-16 = 46.1%. No completely maculate or completely immaculate specimens of *perviridis* (codes 1 and 17 respectively) occur in the series of 89. Four peaks occur in the series of 44 *laurenti*: codes 1-3 = 20.5%, codes 5-7 = 15.9%, code 15 = 13.6%, and code 17 = 18.2%. This represents a complete range from fully maculate to completely immaculate. All four of the fully maculate specimens are of the proposed but still unpublished subspecies from Utah and Arizona mentioned by Lawton (1972b), but other specimens from the same locality in Utah (UT. Iron Co., Cedar Breaks National Monument) are less maculate. Thus, neither the black elytral coloration and complete maculation are unique or even uniform in this population. Its other characteristics (elytral sculpture and broad head) are as in *laurenti*. The five samples of *laurenti* show a north-to-south clinal increase in maculation, although there is overlap. The northern samples vary greatly but

tend to have maculation of codes 7-17. Only two of the specimens from Arizona, Colorado, and Utah (Total N = 15) rate more than code 7. The series of *perviridis* are too variable at all localities to show any recognizable clines.

Character 17

This character partly correlates with maculation: code 17 of character-state 16 (immaculate) results in code 3 of character-state 17 (middle band too incomplete for measurement). Few *longilabris* (32 specimens out of 280 = 11.4%) show code 3, but this code is more widely seen in *nebraskana* (79 specimens out of 167 = 47.3%). A Cramer's V of 0.43 reflects this difference. An angle greater than 45° is seen in more specimens of both species than an angle less than 45° (83.1% of *longilabris* and 68.2% of *nebraskana*, excluding immaculate specimens). No notable differences occur between subspecies or intergrades as Table 75 shows.

Character 18

Ventral abdominal coloration was used by Willis (1968) in separating *C. longilabris* and *montana* (= *C. nebraskana sensu mihi*). My data generally corroborate the value of the character. Only 4.6% of the *longilabris* (13 of 280 specimens) are largely black (Codes 5-7) and 1.8% of the *nebraskana* (three of 167 specimens) are not black (codes 1-4). My data also show virtually no differences

between subspecies or intergrades in either species. Thus, the character is useful at the specific but not at the subspecific level.

Cicindela (Cicindela) longilabris Say, 1825

(Figures 44-52)

Cicindela longilabris Say, 1825. Appendix in Keating, W. J. Narrative of expedition to source of St. Peter's River. London, 2:16.

Cicindela (Cicindela) longilabris Say. Rivalier, E., 1954. Rév. Française d'Ent., 21:252.

Diagnosis. Adult: characters of *silvatica*-group of *Cicindela*; labrum pale in 93.3% of males and 85.0% of females, and completely black in only 2.5% of males and 3.1% of females; midline of labrum with low, broad, longitudinal keel; frons sparsely setose; genae glabrous; scape plurisetose in addition to subapical sensory setae; elytral sculpture (see figs. 48 - 49) consisting of small punctures (6-13 punctures/2 mm^2 area with

66.3% of sample with 9-11 and only 22.5% with less than 10 punctures/2 mm^2 area) not obviously arranged in rows and with scattered granules of form varying subspecifically; elytral microserrae weakly developed; ventral abdominal color metallic green, blue, or violet, or combinations of these colors, black in only 4.6% of sample; abdominal sternites sparsely setose in addition to long sensory setae; ratio, metatibial length/metatarsal length not greater than 98.81% and averaging 91.58%. *Aedeagus*: beak produced but distinctly more slender than preceeding portion of apex (fig. 46); keels on ventral face of apex converging apically and extending not as far proximally as earlike angles of lateral apical keels. *Female genitalia*: distal edge of lateral portion of syntergum IX + X slanting diagonally with medial side farther distal and lateral angle gently rounded; median lobe of syntergum IX + X narrower distally than basally; sternite VIII

with apical emargination narrowly rounded but near acute, and ridge on ventral face of either lateral lobe oriented longitudinally near midline of lobe; second gonapophysis with two setae near base on ventral face. *Larva*: pronotum rufous with strong cupreous, violet, brassy, and blue-green reflections; setae of head and pronotum white. *Pupa*: unknown.

Synonymic notes. Systematic problems have resulted from the inability of most workers to distinguish *C. longilabris* and *C. nebraskana*. I have, through discriminant analysis and analysis of addi ional qualitative characters as well as study of larvae and male and female genitalia, presented evidence as to why I believe that two species should be recognized.

Relationships. The form of the labrum, frons, mesepisternal coupling sulcus (at least of *C. longilabris, nebraskana,* and *silvatica*), and aedeagus indicate relationship of the species comprising the *silvatica*-group of Rivalier (1950, 1954). However, the many differences in sculpture, chaetotaxy, and details of male and female genitalia indicate that the several species are distinct. Certainly, sculpture, chaetotaxy, hind limb proportions, and larval characters differ so greatly between

C. longilabris and *nebraskana* that these species should not be considered conspecific. The differences suggest long evolutionary separation and neither species appears to be particularly closely related to any of the Palearctic species.

Subspecies. Based on my statistical analysis and study of specimens and most of the types of the 11 named divisions of *C. longilabris* (Lawton, 1972b, mentioned an additional as-yet-unnamed subspecies of N. L. Rumpp), I recognize three subspecies. The following are diagnoses, synonymic notes, and ranges of the subspecies as I interpret them.

C. l. longilabris Say, 1825. Appendix in Keating, W. J., Narrative of expedition to source of St. Peter's River. London, 2:16.

Synonyms:

C. albilabris Kirby, 1837, in Richardson, J., Fauna boreali-americana, Norwich, London, 4:12.

C. l. novaterrae Leng, 1918, J. New York Ent. Soc., 26:140.

Diagnosis. Ratio, head breadth/elytral length for males: 38.26-45.49% (N = 8, $\bar{X}$ = 42.79%), for females: 37.05-42.26%

(N = 11, $\bar{X}$ = 40.32%); lateral edge of medial basal elytral boss steeply declivous (see fig. 51B); elytral granules of *longilabris*-type (see fig. 49A).

Synonymic notes. Wallis (1961:48) discussed the identity of *C. albilabris* Kirby. Leng (1918) based *C. l. novaterrae* on green specimens from eastern Newfoundland, but Lindroth (1955) found complete transitions from the dull black color usual in *C. l. longilabris* and the bright green of some eastern Newfoundland specimens.

Intergrades. A series of three males and eight females from the vicinity of ALTA, Edmonton (UALTA, NM) have the broad head (ratio, head breadth/elytral length in males: 42.68-45.65%, $\bar{X}$ = 43.86%; in females: 41.10-45.68%, $\bar{X}$ = 42.88%) and tendency to brown dorsal coloration of *C. l. laurenti* and the basal medial elytral form of *C. l. longilabris*. The locality, near both the east slope of the Canadian Rockies (*laurenti*) and the Canadian boreal forest (*longilabris*), is where intergrades are to be expected.

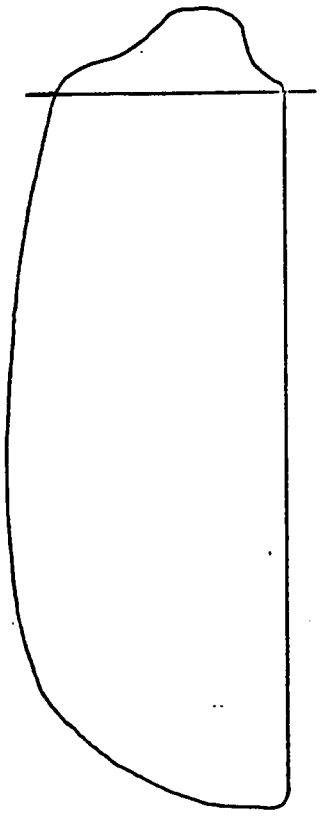
Range. Wallis (1961) had a concept of *C. longilabris* and *nebraskana* different from mine; hence, his map 10 serves only for the Canadian range from Ontario eastward. I have seen *C. l. longilabris* also from NWT. Yellowknife (UBC); Yukon Terr. Whitehorse and Dawson (UALTA, NM, UBC); and AK. Fairbanks (SL).

Fig. 51. Elytral structure in subspecies of *Cicindela longilabris*. X 12.

A. Outline of left elytron showing level which cross-section represents.

B. Cross-section of *C. l. longilabris*

C. Cross-section of *C. l. perviridis*



A

B

C

The approximate United States range can be pieced together from the literature: the species has been definitely reported from IL (Leng, 1902), ME (Leng, 1902), MG (Graves, 1963), MI (NM, SL), NY (W. Horn, 1930), and WI (NM). The species was not found in IN by Montgomery and Montgomery (1931) or IO by Eckhoff (1939). W. Horn (1930) reported the species from NE but his record may refer to *C. nebraskana* from NW.NE; *longilabris* could possibly occur in NE.NE. I have seen no published records south of NY but the species might be expected to extend south in the Appalachian Mountains.

Typology:

longilabris. Wallis (1961:48) narrowed down the type locality as "between Victoria Beach, Manitoba, and Lake Superior, or perhaps even farther east to Lake Ontario." The holotype has been apparently destroyed and a neotype and an exact type locality should be designated.

albilabris. Kirby's material probably came from the area north of the Great Lakes. Presumably the holotype is in the British Museum.

novaterrae. Dahl (1941:188) designated a female from Newfoundland, Bay St. George (AM) as lectotype.

C. l. laurenti Schaupp, 1883-1884

C. l. var. *laurenti* Schaupp, 1883-1884. Bull. Brooklyn Ent. Soc., 6:87.

Synonyms:

C. l. var. *oslari* Leng, 1902. Trans. American Ent. Soc., 28:121.

C. l. var. *vestalia* Leng, 1902. Trans. American Ent. Soc., 28:121-122.

C. montana uteana Casey, 1924, Mem. Coleap., 11:12.

C. oslari denissima Casey, 1924. Mem. Coleop., 11:12-13.

C. oslari estesiana Casey, 1924. Mem. Coleop., 11:13.

Diagnosis. Ratio, head breadth/elytral length for males: 40.21-48.60% (N = 23, $\bar{X}$ = 43.47%), for females: 40.87-45.67% (N = 21, $\bar{X}$ = 43.42%); lateral edge of medial basal elytral boss gently sloped (see fig. 51B); elytral granules of *longilabris*-type (see fig. 49A).

Synonymic notes. I have examined holotypes and lectotypes of all six taxa. This examination and my statistical analyses have resulted in the above synonymy. Collections I have studied have usually used *laurenti* for highly maculate specimens, *oslari* for less maculate ones, and *vestalia* for immaculate ones. My studies show

that maculation and coloration are too variable to permit recognition of subspecies based on these characters. Casey (1924:12) compared his *uteana* only with the black "*montana*," and is indistinguishable from bronzy, nearly immaculate specimens of *C. l. laurenti*. Holotypes of *denissima* and *estesiana* are respectively *laurenti* with character-state 15K coloration and 16F maculation; and 15h coloration and 16e maculation.

Lawton (1972b) mentioned an as-yet-unnamed subspecies of N. L. Rumpp from UT. Iron Co., Cedar Breaks National Monument. Typical specimens have blackish color with complete maculation. However, specimens with these characters occur elsewhere (even in *C. l. perviridis* and *C. l. laurenti* X *perviridis*) and I have seen specimens from the same localities where Rumpp's morph occurs that are green or cupreous and even nearly immaculate. The SW. UT and NE.AZ populations have the broad heads and elytral granules of *C. l. laurenti*. There is a weakly defined north-to-south clinal increase in maculation and trend to darker coloration and the southern population merely represents the extreme expression of those clines. I recommend against recognizing the southwestern population as a distinct subspecies.

Intergrades. I have discussed *C. l. longilabris* X *laurenti* intergrades in my *C. l. longilabris* account. I have included *C. l. laurenti* X *perviridis* intergrades in my statistical analyses and have listed localities elsewhere. The intergrade zone extends from the vicinity of ALTA. Banff and includes populations from

SE.BC, E.WA, ID, W.MT, and NE.OR. Intergrades are intermediate between the parent subspecies in range and head breadth, and are extremely variable in coloration, maculation, and in the form of the elytral granules.

Range. ALTA. 152 Km. N Coleman, Gorge Creek, is my northernmost record of this subspecies. I have also identified specimens from C.MT, E.WY, SE.SD, CO, E. and SW.UT, NC.NM, and NE.AZ. The lack of adequate material prevents me from a more complete delineation of the subspecies' range.

Typology:

laurenti. The type locality is Colorado. I do not know the provenance of the holotype if one exists.

oslari. Dahl (1941) designated a lectotype female (AM) from CO. Dolores Co., SW slope Mt. Wilson, 12,000 ft.

vestalia. Dahl (1941) designated a lectotype female (AM) from MT. Fergus Co., Maiden.

uteana. The holotype, a male, is from UT. Utah Co., Provo. The holotype is presumably in the Casey Collection but I did not find it.

denissima. The holotype, a female (NM 45895), is from an unrecorded locality but "probably Colorado (Casey, 1924:13)."

estesiana. The holotype, a female (NM45806) is from Colorado.

C. l. perviridis Schaupp, 1883-1884. See subspecies account.

C. l. perviridis Schaupp, 1883-1884

Cicindela longilabris var. *perviridis* Schaupp, 1883-1884. Bull. Brooklyn Ent. Soc., 6:87.

Cicindela ostenta Casey, 1913, Mem. Coleop., 4:17.

Cicindela perviridis placerensis Casey, 1913, Mem. Coleop., 4:18.

Cicindela oslari terracensis Casey, 1924, Mem. Coleop., 11:13.

Cicindela ostenta columbiana Casey, 1924, Mem. Coleop., 11:13.

Diagnosis. Ratio, head breadth/elytral length for males: 38.71-42.99% (N = 38, $\bar{X}$ = 40.95%), for females: 38.31-44.32% (N = 51, $\bar{X}$ = 40.72%); lateral edge of medial basal elytral boss gently sloped (see fig. 51C); elytral granules of perviridis-type (see fig. 49B); 91.0% of sample dorsally green, greenish-blue, or blue.

Synonymic notes. Schaupp (1883-1884) based his *perviridis* on green specimens from CA, OR, UT, and Newfoundland. Types may not exist and the type locality should be restricted to CA and OR as the Utah and Canadian specimens are respectively *laurenti* and *longilabris* on zoogeographic grounds.

Casey's (1913, 1924 respectively) *ostenta* and *columbiana* have incomplete type locality data, the former being from California and

the latter from British Columbia. Both show characteristics of *C. l. perviridis*. British Columbia has both *perviridis* and *laurenti* X *perviridis* intergrades, but the holotype of *columbiana* has the rough sculpture typical of unworn specimens of northwestern Washington *perviridis*. Casey's tarsal characteristics are too variable to be of value.

C. perviridis placerensis was proposed by Casey (1913:18) for bluish specimens from CA. Placer Co. Casey (1924:13) placed it in synonymy under *C. perviridis*.

C. oslari terracensis was proposed by Casey (1924:13) for a black specimen from BC. Terrace. I have studied the holotype and a topotype (UALTA), finding them to indistinguishable from *C. l. perviridis* in elytral structure and sculpture. The black coloration is unusual for *perviridis* but I have seen black *perviridis* from BC. Boston Bar (SL) and WA. Whatcom Co., Mt. Baker (DL).

Typology.

perviridis: A holotype may never have been designated. The type locality is restricted to CA and OR.

ostenta: The holotype, a male (NM 45898), is from CA.

placerensis: The holotype, a male, is from CA. Placer Co. I did not record the number.

terracensis: The holotype, a male (NM 45899), is from BC. Terrace.

columbiana: The hototype, a male (NM 45899), is from BC.

Variation. I have covered this topic in the discussion of statistical analyses. An additional point of importance is the difference in roughness of elytral sculpture between specimens from WA and BC and those from OR and CA. In unworn northern specimens, the edges of the punctures are sharper giving a decidedly rougher texture and a duller lustre. Unworn OR and CA specimens have smoother sculpture and slightly shinier lustre. Casey's (1924) holotype of *columbiana* has the rough sculpture of the northern population. The roughness disappears with wear. This characteristic alone is insufficient for recognition of a subspecies insofar as other characteristics are within the range of variation of southern populations.

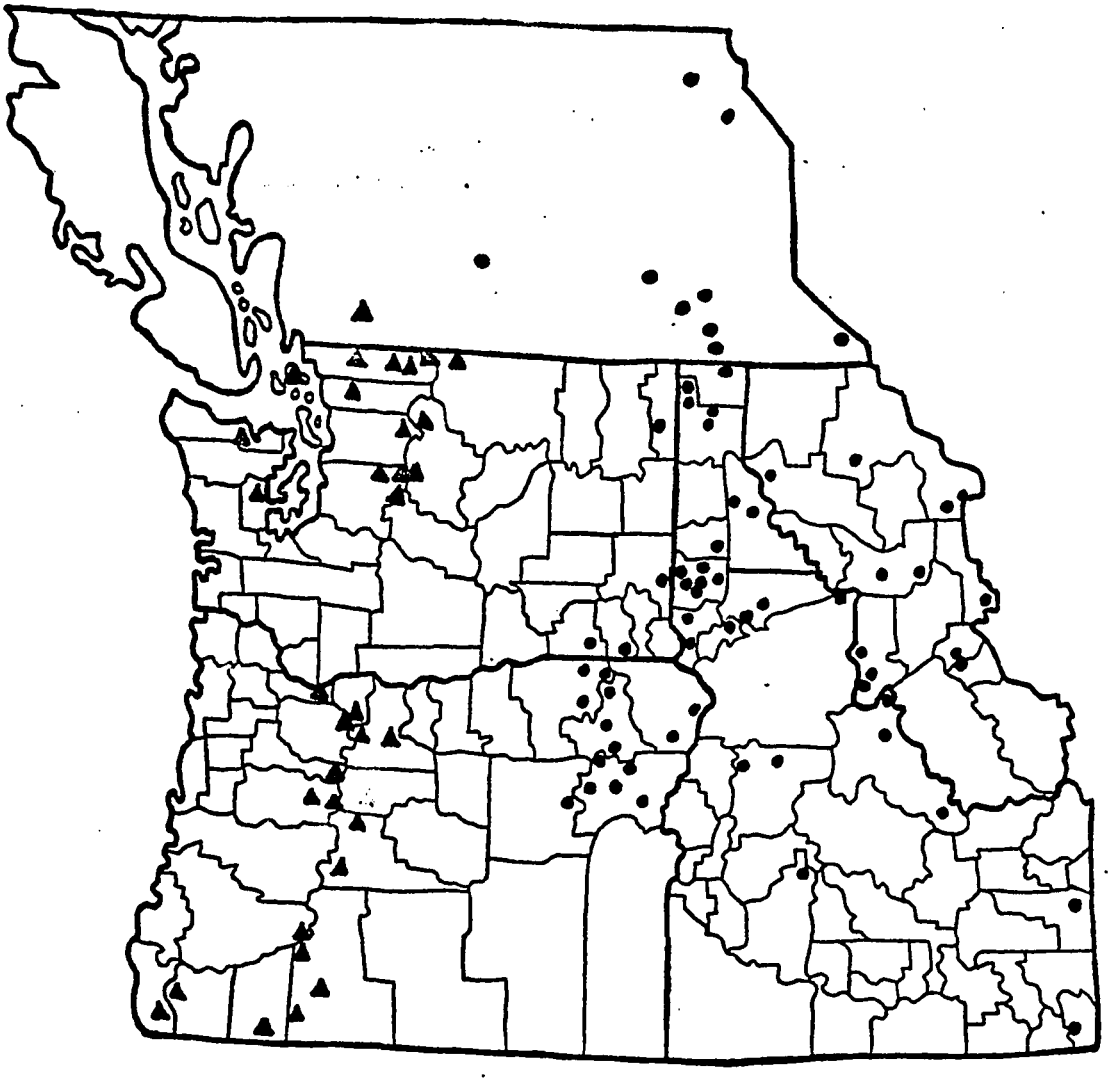
Dates of occurrence. I have records from museums and my personal collection from 14 March-2 October with most records from May to August. The high elevations at which this subspecies occurs result in compression of the activity period into the summer months. The unworn nature of late summer specimens is characteristic of a Type A life history pattern.

Range. BC. Terrace is the northernmost record for the subspecies. *C. l. perviridis* ranges from W.BC south to the Olympic Peninsula and northern Cascades in Washington and again in the Oregon Cascades south to the central California Sierra Nevada Mountains. Neither Sumlin (1976) nor La Rivers (1946) reported the subspecies from the Nevada portion of the Sierras but it is to be expected there. R. L. Huber (in litt., 1976) informed

Fig. 52. Pacific Northwest distribution of *Cicindela longilabris*. See Appendix I for tabulation of localities.

Symbols:

▲ - *C. l. perviridis*
● - *C. l. laurenti* x *perviridis*



me that he received a specimen from CA, San Diego Co., Santa Rosa Mountains. Lack of material from the northern and southern Sierras either represents incomplete collecting or a post-Hypsithermal restriction in distribution.

Intergrades. I have discussed *C. l. laurenti* X *perviridis* intergrades in my statistical analysis section and the account of *C. l. laurenti*.

Cicindela (Cicindela) nebraskana Casey, 1909

(Figures 44-50, 53)

Cicindela montana LeConte, 1861 *nec* Charpentier, 1825, Proc. Philadelphia Acad. Sci., 1861:338.

Cicindela longilabris montana LeConte. LeConte, J. L., 1875, Trans. American Ent. Soc., 5:157.

Cicindela montana nebraskana Casey, 1909, Canadian Ent., 41:238.

Cicindela nebraskana Casey. Casey, T. L., 1914, Mem. Coleop., 5:17-18.

Diagnosis. Adult: characters of *silvatica*-group of *Cicindela*; labrum pale in 91.8%, mottled in 8.2%, and black in 0.0% of males, and, respectively, 18.9%, 27.3%, and 53.8% of females; midline of labrum with low, broad, longitudinal keel; frons glabrous except

for supraorbital sensory setae; genae glabrous; scape with two setae in addition to subapical sensory setae; elytral sculpture (see fig. 48C) consisting of large punctures (4-9 punctures/2 mm^2 area with 55.1% of sample with 6-7 and 41.3% with more than 7 punctures/2 mm^2 area) obviously arranged in transverse rows and without granules; elytra not microserrate; ventral abdominal color normally non-metallic black (non-black in 1.8% of sample) usually with green, blue, and violet reflections on sternites 3-4; abdominal sternites glabrous except for long sensory setae; ratio, metalibial length/metatarsal length not less than 100.0% and averaging 102.02%.

Aedeagus: beak well-developed and only gradually more slender than preceeding portion of apex (fig. 46); keels on ventral face of apex converging apically and extending proximally to level of earlike angles of lateral apical keels. *Female genitalia*: distal edge

of lateral portion of syntergum IX + X slanting diagonally with medial side farther distal and lateral angle lobed and broadly rounded; median lobe of syntergum IX + X broader distally than basally; sternite VIII with apical emargination sharply V-shaped, and ridge on ventral face of either lateral lobe curved and located near medial edge of lobe; second gonapophysis with two setae near base on ventral face. *Larva*: pronotum uniformly maroon with brassy-green and blue reflections; setae of head and pronotum light brown. *Pupa*: median frontal boss pronounced, extending posteriorly to occiput, and delineated laterally from tempora by broad, shallow frontal sulci.

Synonymic notes. *C. montana* Leconte is preoccupied by *C. montana* Charpentier, 1825. The next available name is *C. nebraskana* Casey, 1909, originally described as a subspecies of *montana* but raised to species rank by Casey (1914:17-18).

Relationships. See account for *C. longilabris*.

Subspecies. Based on my statistical analysis and study of specimens and all of the types except that of LeConte's (1861) *C. "montana,"* I recognize two subspecies. The following are diagnosis, synonymic notes, and ranges of the subspecies as I interpret them.

C. n. nebraskana Casey, 1909, Canadian Ent., 41:238.

Synonyms:

C. montana canadensis Casey, 1913, Mem. Coleop., 4:17-18.

C. spissitarsis Casey, 1913, Mem. Coleop., 4:18.

C. calgaryana Casey, 1914, Mem. Coleop., 5:18.

Diagnosis. Labral color completely pale in 92.3%, mottled in 7.7%, and completely black in 0.0% of males (N = 13), and pale in 0.0%, mottled in 11.5%, and completely black in 88.5% of females (N = 26); ratio, head breadth/elytral length for males: 41.95-47.96% (N = 13, $\bar{X}$ = 45.13%), for females: 40.68-45.50% (N = 26, $\bar{X}$ = 42.98%); elytral length for males: 6.36-7.58 mm (N = 13, $\bar{X}$ = 7.13 mm), for females, 7.45-8.54 mm (N = 26, $\bar{X}$ = 8.02 mm).

Synonymic notes. The three synonyms have resulted from Casey's lack of understanding of variation. Casey (1913:17-18) based *canadensis* on small specimens from ALTA. Calgary. He (1913:18) used *spissitarsis* for a female from MAN. Aweme with green bottoms in the elytral punctures, my character-state 15 o and which occurs in 32 of my entire sample of 167 *C. nebraskana* (19.2%). *C. calgaryana* (Casey, 1914:18) was based on a female with the apex of abdominal sternite VII feebly notched, structure resulting from differential drying of the specimen.

Intergrades. See account of *C. n. chamberlaini*.

Typology:

nebraskana. The holotype, a female (NM 45902) is from NE.

canadensis. The holotype, a female (NM 45903) is from ALTA, Calgary.

spissitarsis. The holotype, a female (NM 45904) is from MAN, Aweme.

calgaryana. The holotype, a female (NM 45901) is from ALTA, Lethbridge.

C. n. chamberlaini Knaus, 1925

Cicindela montana LeConte, 1861 *nec* Charpentier, 1825. Proc. Philadelphia Acad. Nat. Sci., 13:388-389.

Cicindela longilabris chamberlaini Knaus, 1925, Pan-Pacific Ent., 1(4):182.

Cicindela nebraskana chamberlaini Knaus, 1925. NEW STATUS.

Diagnosis. Labral color completely pale in 100.0%, mottled in 0.0%, and completely black in 0.0% of males (N = 25), and pale in 27.1%, mottled in 33.3%, and completely black in 39.6% of females (N = 48); ratio, head breadth/elytral length for males: 38.90-46.01% (N = 25, $\bar{X}$ = 41.46%), for females: 38.52-44.62% (N = 48, $\bar{X}$ = 40.86%); elytral length for males: 6.89-8.91 mm (N = 25, $\bar{X}$ = 8.26 mm), for females: 7.70-9.65 mm (N = 48, $\bar{X}$ = 8.79 mm).

Synonymic notes. LeConte (1861:388-389) described *Cicindela montana*, but Huber (1969:21) showed this name is preoccupied by *Cicindela montana* Charpentier, 1825, itself a synonym of *C. hybrida riparia* Dejean. The next available name for the species is *C. nebraskana* Casey, proposed for what I consider to be the eastern population of the species. The western subspecies is left without a name even though the apparent type locality of *C. montana* LeConte is within the range of this western population. Knaus (1925) proposed *C. longilabris chamberlaini* and this name is available for the western subspecies.

Typology. LeConte (1861) described *C. "montana"* from "Valleys of the Rocky Mountains." R. L. Huber (in litt., 1976) presented the following account: "LeConte described *montana* from the 'valleys of the Rocky Mountains,' but his 'types' in MCZ-Harvard are labelled Bitter Root Mountains. . . . Lieutenant Mullan's wagon expedition up the Hell-Gate River may have been the source of LeConte's types in 1854." If this interpretation is correct, the type locality is near MT. Mineral Co., Saltese. This situation is covered by Article 60a of the International Rules of Zoological Nomenclature, 1964 revised edition (after Mayr, 1969) which states that the oldest available synonym ". . . must be adopted, with its own authorship and date."

The type locality of *C. longilabris chamberlaini* is OR. Harney Co., Steens Mountains. The holotype is a male and was stated by Knaus (1925) to be in his personal collection.

Variation. I have covered this topic in the discussion of statistical analyses.

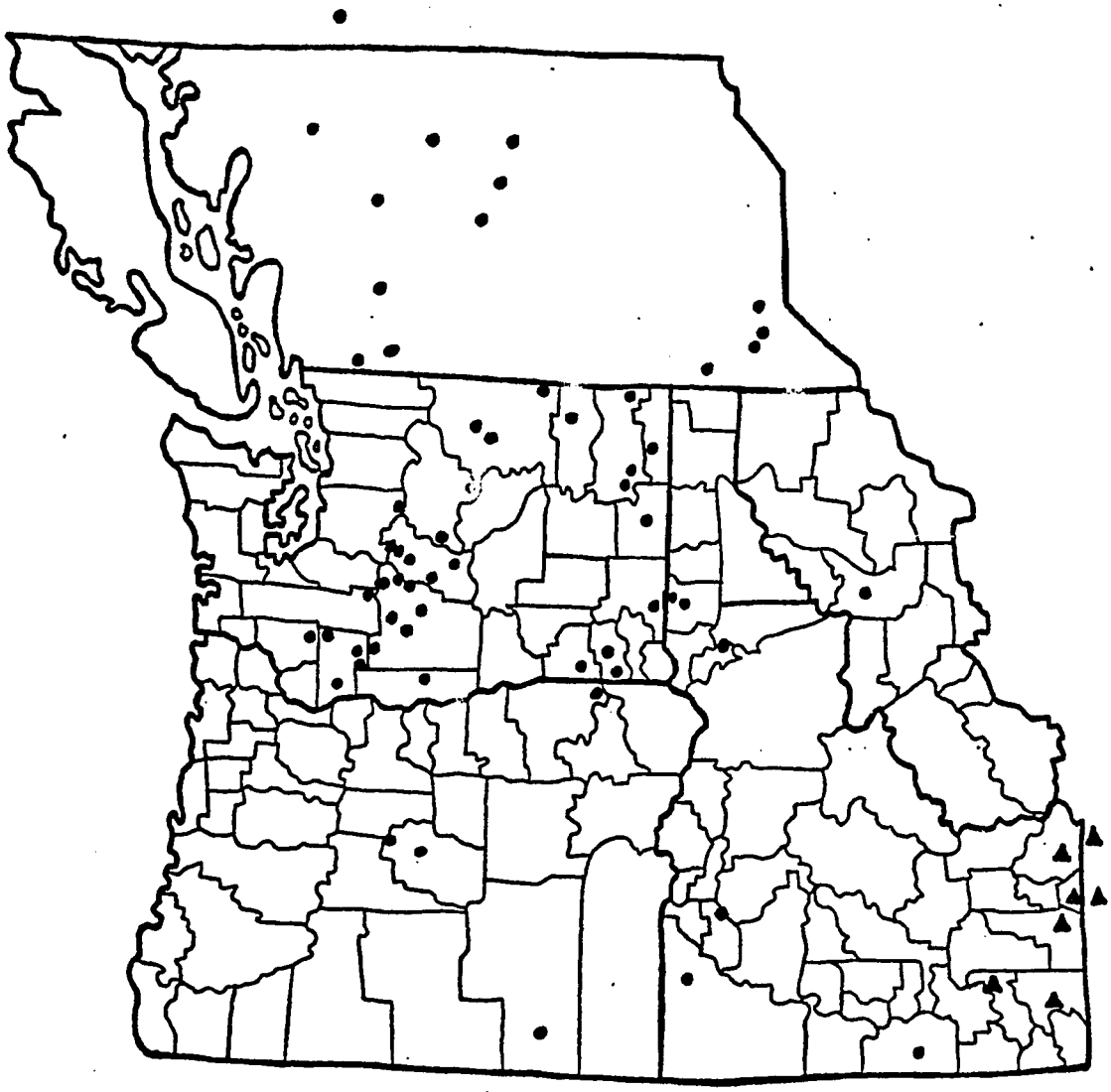
Dates of occurrence. I have records from museum and my personal collection from 5 March-6 October with dates distributed evenly throughout this period. Specimens I have collected in September are teneral indicating a life history pattern A. I collected LL3 23 June 1974 which pupated in captivity within a few weeks, further substantiating the Type A pattern.

Range. The Pacific Northwest distribution is presented in Fig. 53 and Appendix I. Southernmost records I have found from

Fig. 53. Pacific Northwest distribution of *Cicindela nebraskana*. See Appendix I for tabulation of localities.

Symbols:

- *C. n. chamberlaini*
- *C. n. chamberlaini* x *nebraskana*



museum collections are: CA. Alpine Co., Sonora Pass (NM); NV. White Pine Co., Lehman Caves National Monument (NM); and UT. Utah Co., Provo (NM).

Intergrades. Specimens from ALTA. 152 Km. N Coleman, Gorge Creek (UALTA), SE. ID (various collections), and NW.WY (various collections) are intermediate between *C. n. nebraskana* and *chamberlaini* in elytral length and head breadth.

The *pulchra*-group

Diagnosis. Adult: antennal scape setose in addition to apical sensory setae; frons densely setose; genae glabrous; labrum tridentate; elytral sculpture consisting of deep, rounded punctures arranged in transverse rows, and completely separated by distances greater than breadth of individual punctures. *Aedeagus*. ventral surface of apex with two parallel submedian low ridges confluent apically; dorsal notch between beak and orifice long and shallow; beak elongate; flagellum sinuate and nearly as long as inner sac; schlerite 6 approximately elongate-triangular and strongly chitinized.

Female genitalia: middle lobe of syntergum IX + X extended apically beyond apices of lateral lobes; sternum VIII with apices pointed, with seven setae on lateral margins, and with emargination deep and V-shaped; notch of second gonocoxa shallow, with parallel-sided excavation extending distally, margined with linearly arranged stout medial and fine lateral setal rows; ventral surface of second gonapophysis with long setae near base. *Larva:* no diagnostic group characters; seven pairs of primary pronotal setae; antennal chaetotaxy 1:5-6, 2:9-10, 3:2, 4:3-4. *Pupa:* unknown.

Rivalier's (1954) Group VIII of the subgenus *Cicindela*, with *C. pulchra* Say as its "type," was reviewed in part by Rumpp (1977) and Willis (1967) and contains four species: *C. fulgida* Say, *parowana* Wickham, *pimeriana* LeConte, and *pulchra* Say. Rivalier (1954) defined the *pulchra*-group on the basis of the elongate flagellum (at least elongate for the subgenus), the strongly chitinized sclerite 6 on the right flank of the inner sac, and the brilliantly metallic coloration. The four species are similar in chaetotaxy, elytral sculpture, male and female genitalia, and, as

far as they are known, larvae. Rumpp (1977: fig. 3) presented a phylogeny which my research generally corroborates. However, I strongly disagree with Rumpp's inclusion of a chronological aspect without fossil evidence. Rumpp considered *fulgida, parowana*, and *pimeriana* most closely related, and *pulchra* a separate offshoot. I have not been able to study female specimens of *pulchra*; Freitag (1974) described the mesepisternal coupling sulcus, but the female genitalia remain undescribed. Also, I question the correctness of Hamilton's (1925) identification of the *pulchra* larva; the *pimeriana* larva is unknown.

Characters and interrelationships of *pulchra*-group species

Table 78 compares some of the more important character-states of the four species of the *pulchra*-group. *C. pulchra* is not notably more primitive than the other species. It has supernumerary setae on the antennal scape, and the elongate flagellum and large field C of the aedeagal sac are apomorphic. A broadened mesepisternal coupling sulcus represents an evolutionary direction different from those seen in the other species. *C. pimeriana* and *fulgida* are more like another than to *parowana* in both male and female genitalic features. *C. fulgida* and *parowana* agree in the form of the mesepisternal coupling sulcus, macular pattern, the finely rugose sculpture between the elytral punctae, and Type II hypopleuron of the larva.

Table 78. Comparisons of species of *pulchra*-group.

Character-State	Species			
	C. pulchra	*C. pimeriana*	*C. fulgida*	*C. parowana*
External features				
Ratio labral length/breadth	(N = 1) 42.1	(N = 2) < 47% $\bar{X}$ = 46.85	(N = 7) < 50% $\bar{X}$ = 43.5	(N = 7) > 55% $\bar{X}$ = 59.7
Setae on antennal scape (besides apical sensory setae)	numerous	3-5	3-5	4-6
Mesepisternal coupling sulcus (terminology of Freitag, 1974)	Type B	Type D	Type N to SC	Type N to SC
Elytral sculpture between punctae	smooth	smooth	slightly rugose	slightly rugose
Maculation	reduced to dots	absent except occasionally with humeral dot only	average to confluent	average to confluent
Aedeagus				
Beak	laterally compressed, elongate	not compressed, not elongate	not compressed, elongated	not compressed, not elongate
Sculpture on beak	fine reticulation over entire surface	aculeate on apex only	aculeate on ventral face only	aculeate on ventral face only
Ventral apical ridges	extended half length of middle lobe	extended only length of apex	extended only length of apex	extended only length of apex
Lateral apical flanges	barely developed	narrow, with basal angle	narrow, with basal angle	absent
Flagellum	sinuate, length of inner sac	arcuate, half length of inner sac	slightly sinuate, half length of inner sac	sinuate, nearly length of inner sac
Field C of inner sac	large bulge	small, elongate-oval area	small, ovoid bulge	large bulge

Table 78 (continued)

Character-State	Species			
	C. pulchra	*C. pimeriana*	*C. fulgida*	*C. parowana*
Female genitalia				
Shape of lateral lobe of syntergum IX + X	?	apically evenly rounded	rounded but diagonally truncate	strongly diagonally truncate
Ventral ridges on apices of sternum VIII	?	extended 3/4 of distance from apex to depth of emargination	extended full distance from apex to depth of emargination	absent
Form of excavation distal to ventral notch of second gonocoxa	?	broad, parallel-sided, stout setae on medial edge, fine on lateral edge	broad, ovoid, stout setae on medial edge, fine on lateral edge	narrow, parallel sided, fine setae on medial and lateral edges

C. fulgida is the most generalized of the four species and appears most like a structural ancestor for the group. The elongated ridges on the apices of the female sternum VIII is perhaps apomorphic. Willis (1967) illustrated differences between the aedeagal beaks of *C. f. fulgida* and *westbournei*. The shorter, blunter less constricted beak of the latter is probably more plesiomorphic: it is most like the form in *C. parowana* and *pimeriana*.

I hypothesize that *C. pimeriana* evolved from a *fulgida*-like ancestor by losing most of its maculation and developing a Type D mesipisternal coupling sulcus while retaining the ancestral genitalic form. *C. parowana* diverged much further. It developed proportionally long legs and a much longer labrum. The aedeagus retained a short beak but lost the lateral apical flanges and, like *C. pulchra*, evolved a large, bulging field C. The female genitalia lost the apical ridges on sternum VIII and the lateral lobes of syntergum IX + X became diagonally truncated rather than evenly apically rounded. The excavation distal to the ventral notch of the second gonocoxa in *C. parowana* differs from both the ovoid form of *fulgida* and the broad but parallel-sided form of *pimeriana*. Thus my interpretation of the phylogeny of the *pulchra*-group differs from that of Rumpp (1977) only in that I believe *fulgida* rather than *pulchra* to be closest to the common ancestor of the species group.

Fig. 54. Male genitalia in species of *pulchra*-group of subgenus *Cicindela*. X 24, except C, D, G, H, K, and L which are X 100.

A. *C. pimeriana*: apical half, ventral view

B. *C. pimeriana*: apical half, left view

C. *C. pimeriana*: sclerite 6

D. *C. pimeriana*: flagellum

E. *C. pulchra*: apical half, ventral view

F. *C. pulchra*: apical half, left view

G. *C. pulchra*: sclerite 6

H. *C. pulchra*: flagellum

I. *C. parowana*: apical half, ventral view

J. *C. parowana*: apical half, left view

K. *C. parowana*: sclerite 6

L. *C. parowana*: flagellum

M. *C. fulgida*: apex, ventral view

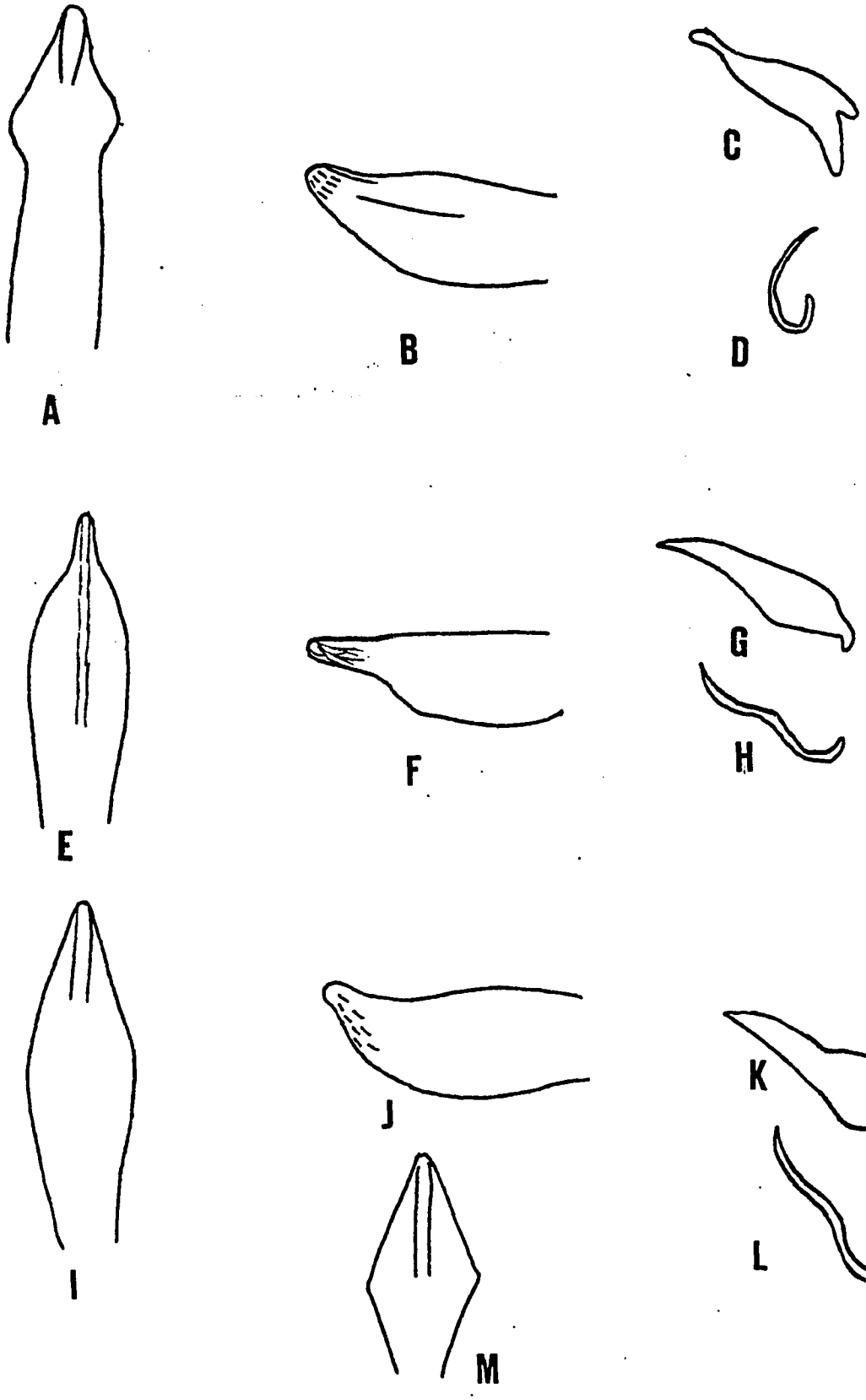

A
B
C
D
E
F
G
H
I
J
K
L
M

Fig. 55. Female genitalia in species of *pulchra*-group of subgenus *Cicindela*. X 24.

A. *C. pimeriana*: syntergum IX + X, dorsal view

B. *C. pimeriana*: left 2nd gonocoxa, ventral view

C. *C. pimeriana*: sternite VIII, ventral view

D. *C. fulgida*: syntergum IX + X, dorsal view

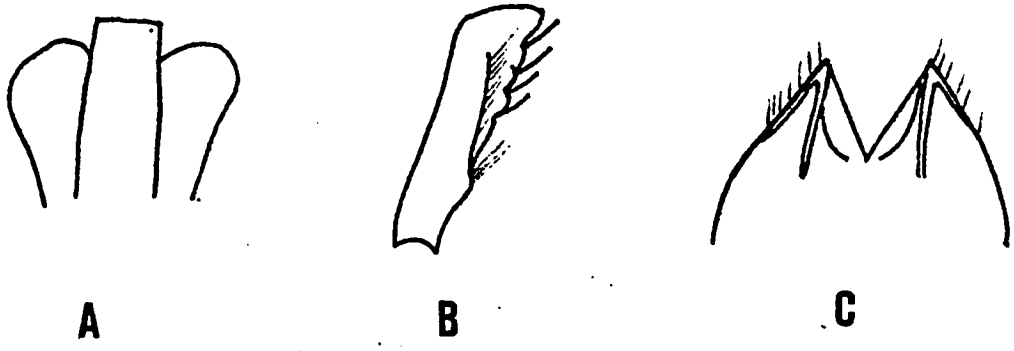
E. *C. fulgida*: left 2nd gonocoxa, ventral view

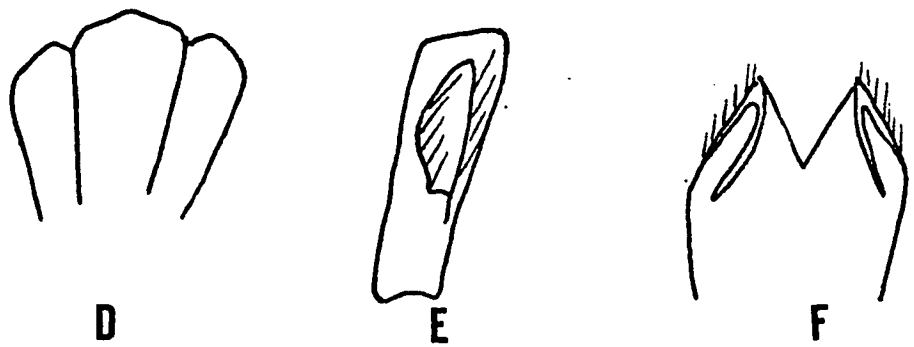
F. *C. fulgida*: sternite VIII, ventral view

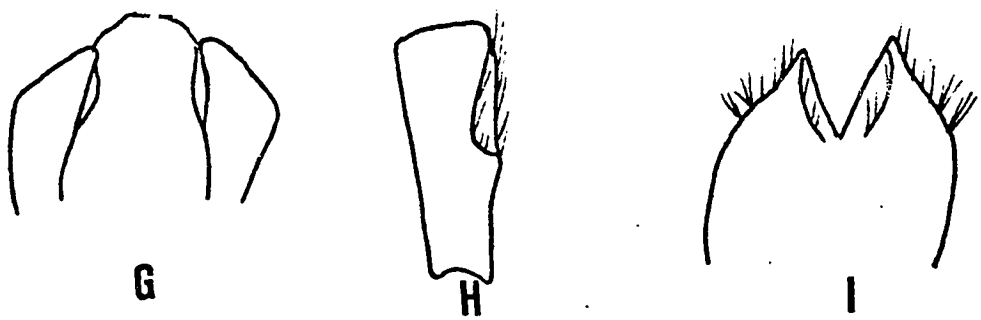
G. *C. parowana*: syntergum IX + X, dorsal view

H. *C. parowana*: left 2nd gonocoxa, ventral view

I. *C. parowana*: sternum VIII, ventral view


A
B
C


D
E
F


G
H
I

Hamilton's supposed *C. pulchra larva*

Hamilton (1925:51-53) described larvae tentatively identified as *C. pulchra* and *C. obsoleta*. None of the specimens in question was reared, and even Hamilton was not completely certain of the determinations. He even stated that the species identified as *pulchra* might be *obsoleta* and vice-versa. My purpose in the present section is to cast further doubt on both identifications, although I have not seen Hamilton's specimens and I do not have larvae of *C. pulchra* available. Through the kindness of Dr. David L. Pearson, Pennsylvania State University, I have obtained specimens of *C. obsoleta*. They differ from Hamilton's descriptions of *pulchra* and *obsoleta* in pronotal coloration and details of chaetotaxy. Unfortunately, Hamilton did not mention the character I find diagnostic of the subgenus *Cicindelidia*, namely that the distal seta on the median hook of tergum V is directed dorsally rather than anterodorsally as in the other setae: my specimens of *obsoleta* show this *Cicindelidia* character. The differences between my *obsoleta* and Hamilton's description are so great as to prove that Hamilton's specimens are misidentified. His descriptions of *pulchra* and *obsoleta* are virtually identical. He differentiates the two "species" on minor size differences and the anterior extent of the anterolateral pronotal angles. It is possible that both are the same species. If Hamilton's fig. is correct then his *pulchra* is probably *C. purpurea* because as far as known only *purpurea*, *pugetana*, and *formosa* lack pronotal

primary seta 7. Hamilton's specimen is from Colorado, thus eliminating *C. pugetana* from consideration. *C. formosa* differs in pronotal coloration. Hamilton's specimens should be reexamined with identification as *C. purpurea* in mind: its characters are close to those given by Hamilton for his supposed *pulchra* and *obsoleta*. Willis (1967) described the larva of *C. fulgida* and that of *parowana* is described in the present paper. They are similar to one another and greatly different from Hamilton's *pulchra*, thus casting further doubt on the veracity of that identification.

Cicindela (Cicindela) parowana Wickham, 1905

Cicindela parowana Wickham, 1905, Canadian Ent., 37:165.

Cicindela fulgida parowana Wickham. W. Horn, 1930, Trans. American Ent. Soc., 56:82.

Cicindela (Cicindela) fulgida parowana Wickham. Rivalier, E., 1954, Rév. Française d'Ent., 21:253.

Diagnosis. Adult: antennal scape with 4-6 setae in addition to apical sensory setae; labrum tridentate, moderately long (ratio, length/basal breadth > 55%); mesepisternal coupling sulcus varying from Type D to SC; ratio, mesotibia/elytral length > 43%; ratio,

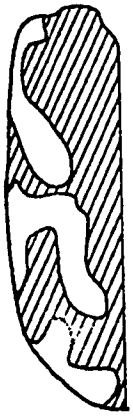
Fig. 56. Elytral patterns of populations of *Cicindela parowana*. X 6.

A. *C. p. wallisi*: WA. Grant Co., Lower Crab-Creek WRA

B. *C. p. parowana*: UT. Iron Co., Little Salt Lake (Topotype)

C. *C. p. parowana*: ID. Owyhee Co., J.C. Strike Reservoir

D. *C. p. platti*: CA. Mono Co., Benton's Crossing (Paratype; type locality)



A

B

C

D

metatibia/elytral length > 56%; elytral sculpture slightly rugose between punctae, producing "greasy" appearance; maculation of average breadth to confluent: posterior arm of humeral lunule directed diagnonally posteriorly and transversely broadened, and apex of posterior arm of middle band directed diagonally, without angulate bend. *Aedeagus*: beak moderately long, not laterally compressed, aculeate on ventral face only; ventral apical ridges short, parallel, confluent apically; ventral face of apex moderately concave; lateral apical flanges absent; inner sac with flagellum nearly length of entire sac; field C of inner sac large and bulged. *Female genitalia*: lateral lobe of syntergum IX + $\bar{X}$ diagonally truncate; ventral surface of apices of sternum VIII unridged; excavation distal to ventral notch of second gonocoxa narrow, parallel-sided. *Larva*: no diagnostic specific characters; Type II hypopleuron; spine of inner hook of

tergum V half of length of entire hook; pygopod surrounded by 20 setae.

Pupa: unknown.

Synonymic notes. W. Horn (1930) considered *C. parowana* to be a subspecies of *C. fulgida*. Cazier (1937) gave ample evidence for its specific distinctness, although Rivalier (1954) still referred to it as a subspecies of *C. fulgida*.

Relationships. I have already treated these in the *pulchra*-group account.

Subspecies. All three subspecies are known from the Pacific Northwest and are treated in the separate subspecies accounts.

C. p. parowana Wickham, 1905

Cicindela parowana Wickham, 1905, Canadian Ent., 37:165.
Cicindela parowana remittens Casey, 1924, Mem. Coleop., 11:14-15.

Diagnosis. Size (see Table 79) similar to that of *wallisi*, smaller than *platti*; maculation without tendency to confluence; portion of posterior branch of marginal line extended nearly to apical lunule.

Table 79. Elytral length in subspecies of *C. parowana*. Values are limits of observed range followed in parentheses by the arithmetic mean and standard deviation. The number of specimens in each category is given at the head of each column.

Subspecies	Sex	
	Male	Female
	N = 6	N = 9
parowana	5.61-6.11 (5.85 ± .20)	5.94-6.27 (6.12 ± .13)
		N = 2
platti		6.49-6.71 (6.60 ± .10)
	N = 7	N = 7
wallisi	5.45-6.00 (5.72 ± .20)	5.94-6.60 (6.10 ± .22)

Synonymic notes. *C. p. remittens* was proposed by Casey (1924:14-15) for the cupreous color morph of *C. p. parowana*. Not all topotypes of *remittens* are cupreous, and cupreous individuals occur elsewhere. Cazier (1937b:160) and Tanner (1929:85) both considered *remittens* as merely a variable color phase of *parowana* and I follow them.

Typology. The holotype, a male, NM 56136, is from UT. Iron Co., Little Salt Lake, NW of Parowan. The holotype of *C. p. remittens*, a female, is from UT. Juab Co., Callao. I have examined the type of *C. p. parowana* in the regular type collection of the National Museum. I did not find the holotype of *remittens* in the Casey Collection in December, 1976.

Variation. *C. p. parowana* is uniform in maculation but varies in color. Of a series of 15 specimens from four localities, eight are dorsally cupreous, the rest dark blue-green. Two are violet ventrally, the remainder green to blue-green.

Dates of occurrence. Data from a series of 15 specimens and records from Cazier (1937b) and Tanner (1929) are:
5 June-11 August.

Remarks. *C. p. parowana* is geographically associated with the extent of Pluvial Lake Bonneville and Tertiary Lake Idaho.

C. p. platti Cazier, 1937

Cicindela parowana platti Cazier, 1937, Bull. S. California Acad. Sci., 35:161-162.

Diagnosis. Size (see Table 79) largest of species; maculation very broad to completely confluent; marginal line in specimens without confluent markings posteriorly extended nearly to apical lunule.

Synonymic notes. None.

Typology. The holotype, a male, AM 1202, was collected 14 August 1935 by M. A. Cazier and T. R. Platt CA. Mono Co., Benton's Crossing. This locality, no longer known as such, is located along the Owens River near its source at the southeast corner of Crowley Lake.

Variation. Variation has been briefly outlined by Cazier (1937b) and Sumlin (1976). Color varies from blue-green, green-brown, cupreous, and even black with cupreous reflections. Maculation ranges from very broad but separated lunules to completely confluent.

Dates of occurrence. Data from two specimens and records from Cazier (1937b) and Sumlin (1976) are: 17 July-15 September.

Remarks. *C. p. platti* is geographically associated with the extent of Pluvial Lake Lahontan and drainages to the north and east.

Intergrade specimen. A single male in the American Museum collection from OR. Lake Co., Coleman Lake has the extremely broad markings (not confluent) of *platti*, but the elytral length is 5.83 mm. Although I have not had available males of unquestioned *platti* for measurement, elytral lengths of two females average 7% larger than females of *parowana* and, indeed, the smaller *platti* is 3.4% larger than the largest of a series of nine female *parowana*. Differences between the means of the sexes of *parowana* and *wallisi* from Table are 4.4 and 6.2% respectively. If *platti* has similar sexual dimorphism, even a 6% difference would yield a mean for the males of 6.2 mm, 6% larger than the Coleman Lake specimen. I contend that the specimen is an intergrade between *platti* and *parowana*, showing the size of *parowana* and maculation of *platti*. Another alternative explanation is that the specimen is a runt, but I have seen no noticeable runts among 77 specimens. Coleman Lake is part of the drainage system of Pluvial Lake Lahontan but in the northeastern portion. Thus, the locality is at the northeastern margin of the range of *platti*, where one might expect intergradation with *parowana*. Only further specimens will solve the problem. I tentatively call the specimen *C. p. parowana* X *platti*.

C. p. wallisi Calder, 1922

Cicindela azurea Calder, 1922, *nec* Knausse, 1910, Canadian Ent., 44:62.

Cicindela wallisi Calder, 1922, Canadian Ent., 44:191.

Cicindela fulgida parowana Wickham, *pars*. Horn, W., 1930, Trans. American Ent. Soc., 56:82.

Cicindela fulgida fulgida Say, *pars*. Cazier, M., 1937, Bull. S. California Acad. Sci., 35:159.

Cicindela parowana wallisi Calder. Wallis, J. B., 1961, *Cicindelidae* of Canada, Univ. Toronto Press, 53-54.

Diagnosis. Size (see Table 79) similar to that of *parowana*, smaller than *platti*; maculation without tendency to confluence; portion of posterior branch of marginal branch extended less than 50% of distance between middle band and apical lunule.

Synonymic notes. *C. p. wallisi* was originally described as a full species by Calder (1922) whose character distinguishing it from *C. parowana* actually is a feature of *parowana* and not *fulgida* as Calder intimated. Several authors refused *wallisi* recognition until Wallis (1960) quoted a letter from Cazier

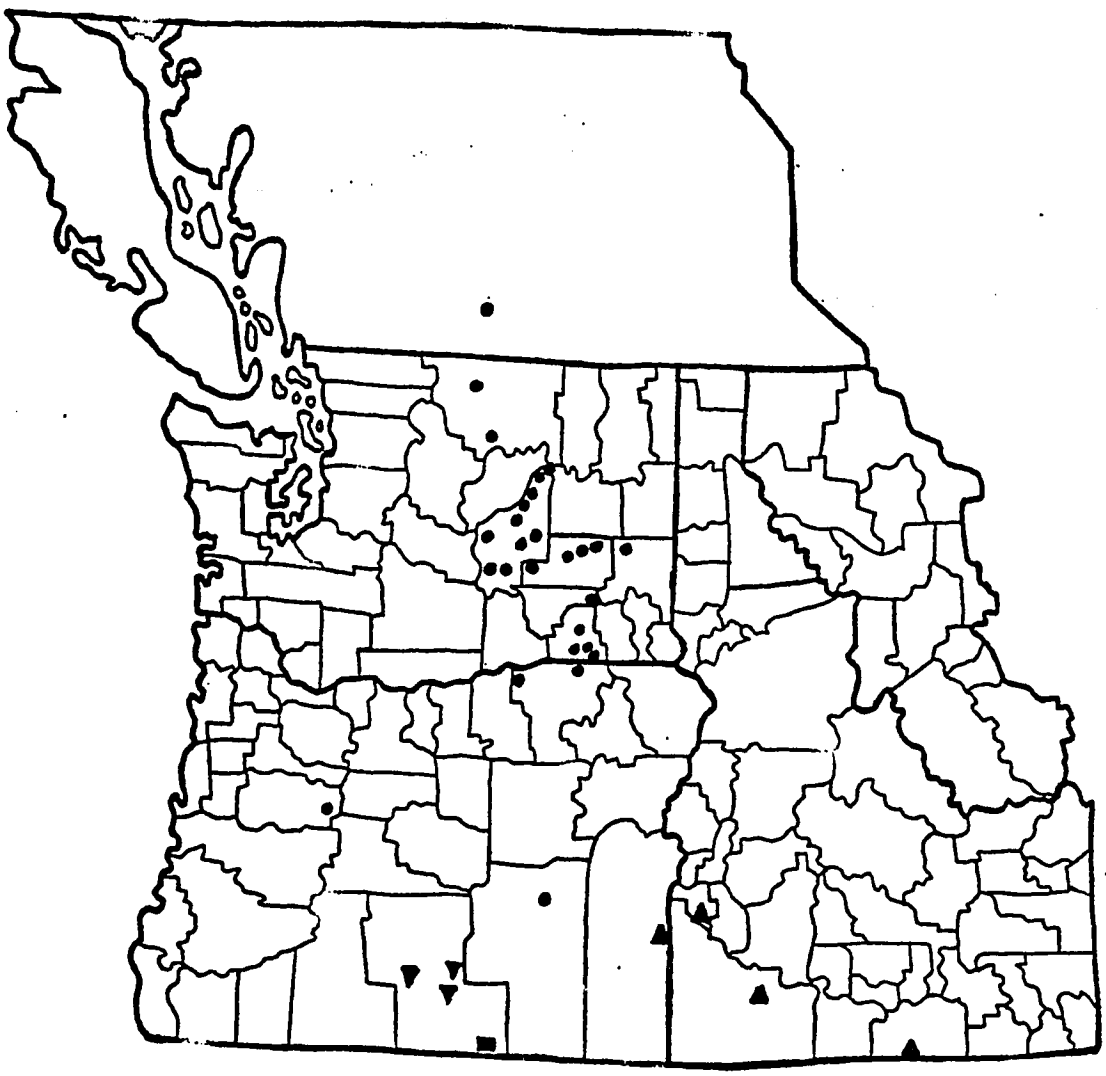
Fig. 57. Pacific Northwest distribution of *Cicindela parowana*. See Appendix I for tabulation of localities.

▲ - *C. p. parowana*

▼ - *C. p. platti*

■ - *C. p. parowana* x *platti*

● - *C. p. wallisi*



stating that the form is distinct. *C. p. wallisi* is similar to *C. p. parowana*, but the differentiating character of the marginal line is constant and the two subspecies are widely allopatric.

Typology. The type locality is BC. Penticton. Holotype not examined.

Variation. *C. p. wallisi* is uniform in maculation. Color is usually cupreous-tinged green dorsally, but two specimens out of 61 examined lack all traces of the cupreous tinge. One specimen is uniformly reddish-brown, but is senescent.

Dates of occurrence. Leffler and Pearson (1976) gave the dates as 23 March-21 June and 25 August-10 September. This Pattern A set of dates differs from the summer dates of *C. p. parowana* and *platti*. The apparent Pattern B of these other subspecies may be an adaptation to different conditions of the Great Basin, paralleling dates of *C. tenuicincta*, another form related to lineages showing Pattern A life histories.

Subgenus *Cicindelidia* Rivalier, 1954

(Subgenotype. *Cicindela (Cicindelidia) carthagena* Dejean, 1831)

Cicindelidia Rivalier, 1954. Rév. Française d'Ent., 21:255-258.

Diagnosis. Adult: *Cicindela* with eyes of moderate development; female mesepisternal coupling sulcus not developed as cavity (except SC in southern

populations of *C. abdominalis)*. *Aedeagus*: Inner sac of auricular type; flagellum elongate, circumvolutory but not concentric. *Female genitalia*: apices of sternite VIII with 3-4 short, stout setae. *Larva*: Median hooks of abdominal tergite V with distalmost seta directed dorsally, others directed anteriorly (based on *C. amargosae, haemorrhagica, nigrocoerulea, obsoleta,* and *willistoni)*. Life History Pattern: B except for A in *willistoni*-group.

Synonymic notes. Rivalier (1954) united a large number of species as his genus *Cicindelidia*, stating that they are a New World group with an aedeagal inner sac structure ". . . perfectly identical with that of [the Old World] *Lophyridia* when it is only moderately evolved and *Lophyra* when its development is complete." Willis (1967) appeared to have accepted the group with some reservation. Freitag (1974) used Rivalier's group intact, adding some species Rivalier omitted, and substituting the numeral IV for the formal subgeneric name. Rumpp (1967, 1977) refused *Cicindelidia* even subgeneric rank, reducing it to synonymy, under the subgenus *Cicindela*. I shall discuss

Rivalier's and Rumpp's contentions in more detail beyond under "Subgeneric validity."

Subgeneric validity. After reviewing Cazier (1954) and Rivalier (1954) I include 57 species in this strictly New World subgenus. Twenty-two are found completely or in part north of Mexico, and three (*amargosae, haemorrhagica,* and *willistoni)* range into the Pacific Northwest. I cannot accept Rumpp's (1977) contention that *Cicindelidia* should be synonymized under *Cicindela (S.S.)*, based on only one character. Rumpp based his conclusion on the 25° angle between the axes of the everted inner sac and the approximate centerline of the aedeagus. A 25° angle is characteristic of nine of the 12 Nearctic Rivalier subgenera, suggesting true relationship. However, other characters of the inner sac, larval features, and differences in life history patterns argue for greater taxonomic subdivision among these nine than Rumpp's arrangement allows were his reasoning extended to all of them.

I have studied larvae of five species of *Cicindelidia (amargosae, haemorrhagica, nigrocoerulea, obsoleta,* and *willistoni)*. All agree with one another and differ from species I have had available of other subgenera in the arrangement of the setae on the median hooks of abdominal tergite V stated in my diagnosis. Hamilton (1925) unfortunately did not use this character in his descriptions of *abdominalis, ocellata,* and *punctulata.*

The subgenus was characterized by Rivalier on the auricular-type aedeagal sac (Rivalier, 1950:219-220). Papp (1952: fig. 3:1-4, 8; 5:1, 9; 11 [this notation, not used by Papp, refers to fig. 3, subfigs. 1-4, etc.]) and Rivalier (1950:219-220) illustrated 10 of the 57 species, and I have examined two additional. The flagellar convolutions form the evolutionary sequence seen in Rivalier's figures arranged fig. 3b-d-c. *C. amargosae, senilis,* and *willistoni* are generalized in having only a proximal loop with the remainder sinuate. I call this Type I and it is illustrated in Rivalier's fig. 3b. *C. abdominalis, cyaniventris, obscura,* and *sedecimpunctata* represent Type II (Rivalier, fig. 3d) in which there is a proximal loop but in which a distal loop is only imperfectly developed. Type III is found in *C. haemorrhagica, ocellata, punctulata,* and *sommeri* (Rivalier, fig. 3c) in which both proximal and distal loops are equally developed. Finally, *C. euthales* (Papp. fig. 3:1) represents Type IV which has the loops of Type III additionally complex.

Distribution of pro- and mesotrochanteric setae, unfortunately, does not correlate perfectly with flagellar types. The setae are present in all three species having a Type I flagellum. Of Types II and III, some species have the setae and some do not. Those Nearctic species which lack the setae have red abdominal sternites. The Mexican *C. sommeri* has a red abdomen but also has the setae present. Pilosity among the various species is generally

Fig. 58. Idealized flagellar types in *Cicindelia*. (adapted from Rivalier, 1954: fig. 3, b-d).

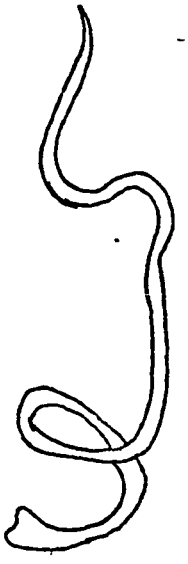
A. Type I (*willistoni*-group)

B. Type II (*carthagena*-group)

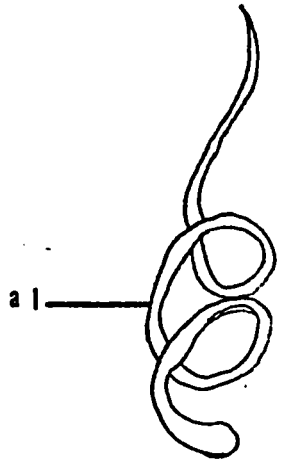
C. Type III (*euthales*-group)

Legend:

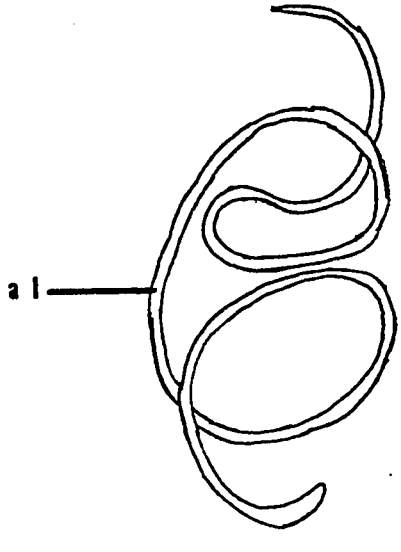
al - auriculate-loop form



A



B



C

similar. Except for western subspecies of *C. willistoni*, *C. amargosae, senilis,* and *willistoni* have the frons setose; in other species the frons is largely glabrous. These combinations of characters show evolutionary sequences from a basal stock with frons setose, pro- and mesotrochanteric setae present, abdominal sternites metallic blue or green, and Type I flagellum to groups with frons glabrous, pro- and mesotrochanteric setae absent, abdominal sternites red, and Types II, III, or IV flagella. Such evolutionary sequences are to be expected in so large a species group.

Another character in which Nearctic species, at least, agree is that they have Life History Pattern B so far as the scanty available data indicate.

The problem is whether we should follow Rivalier (1954) in recognizing the aedeagal form of *Cicindelidia*, characters involving both the flagellum and the auricular-type inner sac membrane, as worthy of taxonomic recognition; or if we should follow Rumpp (1977) who used the angle between the axes in synonymizing *Cicindelidia* with *Cicindela* (S.S.). I believe Rivalier's classification to be better and recommend, with reservations, continued use of his broadly-conceived subgenus, with the realization that some species may be added and others removed.

Relationships. Before Rivalier (1954) presented his classification, the species he included in his subgenus *Cicindelidia*

had been arranged by various authors among several species groups often on superficial similarities. Willis (1967) considered *Cicindelidia* to be derived from *Cicindela (S.S.)*. Rumpp (1977) did not afford *Cicindelidia* even subgeneric distinction from *Cicindela (S.S.)*.

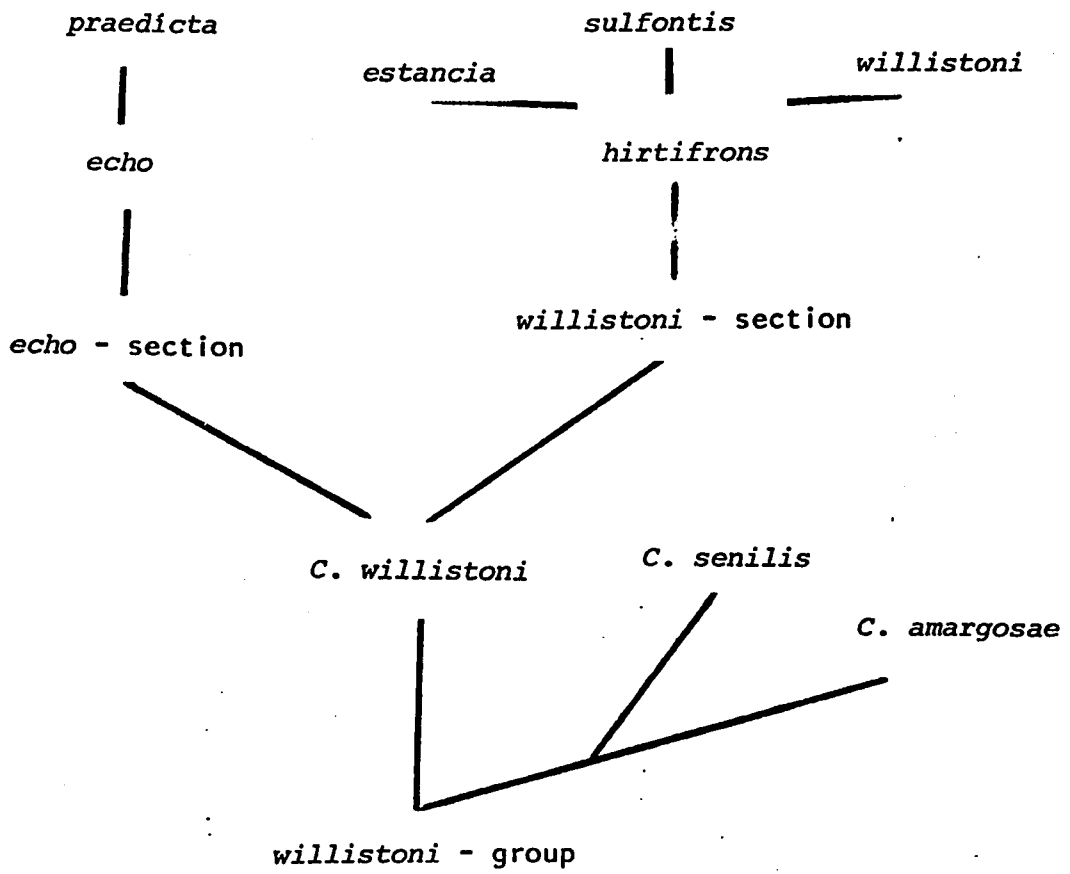
Rivalier (1954) stated that the aedeagal structure of *Cicindelidia* is identical to those of the Old World *Lophyra* and *Lophyridia*, thus implying, although not actually stating, that these three groups are related. Rivalier's implication involves difficult zoogeographic considerations. Some of the involved species are widespread and presumably geologically old, suggesting long independent evolution. Such possible relationships are beyond the scope of the present study. I would prefer to seek species-groups related to *Cicindelidia* among New World forms since it is a strictly New World group as formulated. Rumpp's character relates it to nine of the 12 Nearctic subgenera. The interrelationships of these have not been worked out but *Cicindela* (S.S.) is probably the common ancestor.

There is a striking similarity among the inner sac sclerites, between the subgenera *Cicindelidia* and *Tribonia*, particularly schlerites 2 and 5. In both, sclerite 2 is enlarged and heavily sclerotized and sclerite 2 evenly crescentic, at least when not secondarily modified (e.g., *C. willistoni*). *Tribonia* has a cloaked-type inner sac membrane which superficially differs from the auriculate-type of *Cicindelidia*, but both types agree in that

the membrane is supported by a proximal loop and the distally-directed main shaft of the flagellum which extends along the right surface. The cloaked-type appears to represent the auriculate-type in elongate form. Of the remaining subgenera: *Cicindela* (S.S.) and *Pachydela* have simple flagella lacking the proximal loop, the remaining sclerites relatively unmodified except for twisting or thickening in some species; and *Brasiella, Eunota, Habroselimorpha, Microthylax,* and *Opilidia* all show fusion of some of the sclerites. The form of the female second gonocoxa in *Cicindela* (S.S.), *Tribonia*, and the *willistoni*-group of *Cicindelidia* (Freitag, 1972, and Tanner, 1927) is quite similar. Chaetotaxy, elytral sculpture, and the mesepisternal coupling sulcus form are also similar.

Wallis (1961:60) considered the inner sac structure of *C. willistoni* intermediate between those of *C. tranquelbarica* and the *punctulata*-group of *Cicindelidia*. On the basis of the limited but strong evidence presented above, I concur. My suggestions as to the relationships of the subgenera are presented in fig. 59. The very generalized *willistoni*-group of *Cicindelidia* and *C. (Tribonia) tenuicincta* are both nearest the basal stock of their respective subgenera. Further research is needed to determine which, if any, of the living species-groups of *Cicindela (S.S.)* is closest to this common ancestry. Such an ancestor may be a now-extinct group. Of the four species-groups, the *pulchra*- and *silvatica*-groups shows modifications of the sclerites difficult

Fig. 59. Suggested phylogeny of *willistoni*-group of subgenus *Cicindelidia*.


praedicta
sulfontis
estancia
willistoni
echo
hirtifrons
willistoni - section
echo - section
C. willistoni
C. senilis
C. amargosae
willistoni - group

to reconcile with an ancestral form, but the *maritima*- and *formosa*-groups, being completely generalized, are most likely nearest the primitive stock.

Species Groups. Rivalier (1954) listed 45 species in *Cicindelidia*. By correlating his list with revisions by Cazier (1954) and Willis (1968) this number is altered. Name changes, descriptions of new species by Cazier (1954) and Sumlin (1977), synonymies, and elevation of former subspecies to full specific rank account for the alteration. The species I include in this subgenus are as follows. I separate *C. amargosae* from *senilis* for reasons given beyond in the present study, and consider the southeastern United States *C. scabrosa* distinct from *C. abdominalis* on the basis of its much larger size and very different elytral sculpture. Species found north of the Mexican border are marked with an asterisk (*).

**abdominalis*	*craveri*	*ioessa*	**ocellata*
aeneicollis	*cyaniventris*	*klugi*	*papillosa*
**amargosae*	*dysentrica*	*longicornis*	*phosphora*
aterrima	*euthales*	*luteolineata*	**politula*
aurora	*favergeri*	**marginipennis*	**punctulata*
beneshi	**fera*	*mathani*	*radians*
bradti	*flohri*	*nebuligera*	**roseiventris*
carthagena	*guerrerensis*	*nigrilabris*	**rufiventris*
**cazieri*	**haemorrhagica*	**nigrocoerulea*	*rufoaenea*
chrysippe	**hornii*	*nudata*	*rugatilis*
clarina	*hydrophoba*	**obsoleta*	**scabrosa*

**schauppi*	**senilis*	*sommeri*	**trifasciata*
**sedecimpunctata*	*sinaloae*	**tenuisignata*	*vasseleti*
semicircularis	*smaragdina*	*thalestris*	*viridiflavescens*
			**willistoni*

Cazier's study of the Mexican fauna and Rivalier's classification were published the same year so, presumably, neither had the advantage of the other's work. Additionally, the Central and South American species are poorly known. Unless I were able to study these species personally from the standpoint of their interrelationships I would not properly be able to include these Neotropical forms in a classification of my own formulation. Many of the 36 species found entirely south of the United States are related to Nearctic species, but relationships of the rest are too uncertain. Thus, in my arrangements into species-groups below, I am including only those 21 species found north of Mexico. I have personally examined most of them and useful literature exists on some of the others.

C. willistoni-group. Antennal scape with eight or more setae in addition to barge apical sensory setae; frons abundantly setose (except for westward clinal trend to glabrousness in *C. willistoni*); pro- and mesothoracic setae present; abdominal sternites metallic blue or green; Type I flagella; female second gonocoxa with notch at midpoint along mesial edge, notch having proximal tooth present; life history pattern A.

Included species: *amargosae, senilis,* and *willistoni.*

C. punctulata-group. Antennal scape with 0-2 setae in addition to large apical sensory setae; frons glabrous except for supraocular setae; pro- and mesothoracic setae present; abdominal sternites metallic blue or green; Types II or III flagellum; female second gonocoxa elongate and narrow and lacking notch along mesial edge; life history pattern B.

Included species: *hornii, marginipennis, nigrocoerulea, obsoleta, punctulata, tenuisignata,* and *trifasciata.*

C. carthagena-group *(C. carthagena* ranges from Mexico southward but it is the subgenotype and a sibling species of the Nearctic *C. haemorrhagica* (Cazier, 1954), so it is proper to base this species-group on it). Antennal scape glabrous except for large apical sensory setae; frons glabrous except for supraocular setae; pro- and mesothoracic setae absent; abdominal sternites non-metallic; Types II and III flagellum: female second gonocoxa elongate and narrow and having very shallow notch along mesial edge, with proximal teeth; life history pattern B.

Included species: *abdominalis, cazieri, fera, haemorrhagica, ocellata, politula, roseiventris, rufiventris, scabrosa,* and *schauppi.*

Cicindela (Cicindelidia) amargosae Dahl, 1939

(Figures 22U, 60)

Cicindela willistoni amargosae Dahl, 1939, Bull. Brooklyn Ent. Soc., 30:221-222.

Diagnosis. Adult: characters of *willistoni*-group of *Cicindelidia*; frons moderately setose; mesepisternal coupling sulcus Type D; elytra strongly depressed; elytra very weakly microserrulate; elytral maculation usually with apical dot only. *Aedeagus*: lateral apical flanges very weakly developed; notch between beak and orifice deep; ventral surface of apex unkeeled; inner sac with Type I flagellum and sclerite 2 evenly crescentic in shape. *Female genitalia*: apical notch of sternite VIII V-shaped. *Larva*: setae on head elongate; pronotal margin along posterior and lateral edges continuously carinate to and including anterolateral angles; abdominal hypopleuron consisting of several small setiferous tubercles only.

Synonymic notes. Dahl (1939) described this species as a subspecies of *C. willistoni*. Rumpp (1956) raised it to full specific status stating (p. 133) ". . . that two distinct subspecies of the same species cannot exist sympatrically, that no

interbreeding with [the sympatric subspecies of *C. willistoni*] has ever been observed, and that no hybrids have ever been found. . . ." Willis (1968) considered it a subspecies of *C. senilis*, the species to which I consider it most closely related yet specifically distinct for reasons I shall bring out beyond.

Relationships. Chaetotaxy and aedeagal characters show *C. amargosae* to be most closely related to *C. senilis* and *willistoni*. These three species comprise what I call the *willistoni*-group of the subgenus *Cicindelidia*. It is more closely related to *C. senilis* with which it agrees in the very weak elytral microserrulation (well-developed in *C. willistoni*), having a deep notch between the aedeagal beak and orifice (shallow in *willistoni*), and in having the inner sac sclerite 2 evenly crescentic (complex in *willistoni*). There are at least three important characters distinguishing larvae of *C. amargosae* and *willistoni*, and I have presented these in the specific diagnosis; unfortunately, the *C. senilis* larva is still unknown.

Specific distinctness. Willis (1968) included *C. amargosae* as a subspecies of *C. senilis*. I maintain that the two are very closely related but distinct species on the basis of the following characters:

1. *C. amargosae* has distinctly depressed elytra as seen in lateral view. In *C. senilis*, there is no such depression.

2. Elytral maculation of *C. amargosae* consists usually of the apical dot only, although occasional individuals have traces of the

middle band. *C. senilis* is completely maculate, although some specimens of the northern *C. s. senilis* have the humeral lunule divided.

3. The apical notch of the female sternite VIII is V-shaped in *C. amargosae*, and broadly U-shaped in *C. senilis*.

4. *C. amargosae* is associated with the Amargosa River drainage and the western and northern portions of Pluvial Lake Lahontan. *C. senilis* is found around San Francisco Bay, the southwestern San Joaquin Valley and adjacent western drainages, and coastal Los Angeles and Orange County tidelands, all in western California. The ranges have been separated for at least a million years if not longer by the Sierra Nevada Mountains.

Subspecies. Rumpp (1956) provided ample characterizations of the two subspecies of *C. amargosae*. They differ in color and size. *C. a. amargosae* is dark green, *C. a. nyensis* black. Rumpp (1956) published a table of measurements of the total lengths of large samples of topotypes of each subspecies. I used Rumpp's figures and applied formula 3 of Amadon (1949) to calculate the 97% rule for separating subspecies. Using total lengths of pooled sexes and females, the subspecies are separable at the 97% level of confidence. Males do not give such separation, however.

C. (C.) a. nyensis Rumpp, 1956

Cicindela amargosae nyensis Rumpp, 1956, Bull. S. California Acad. Sci., 55(3):140-142.

Diagnosis (in part after Rumpp, 1956). Characters of *C. amargosae* with dorsal coloration sericeous black with very faint green and blue reflections; total length of pooled sexes and of females less than that of *C. a. amargosae* with separation at 97% level; elytra distinctly softer than *C. a. amargosae*.

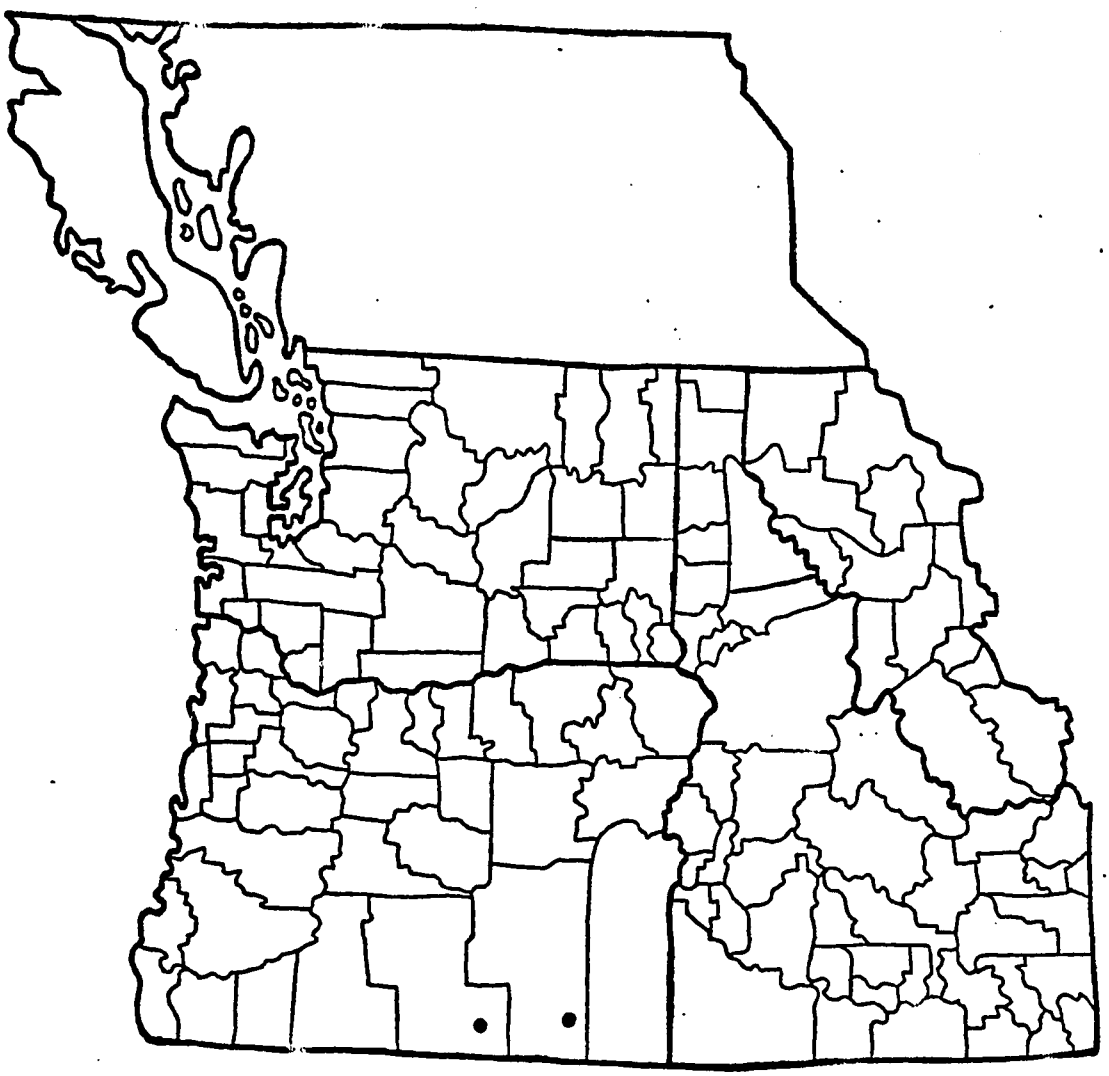
Synonymic notes. Beer and Maser (1973) called this subspecies *C. senilis nyensis*, apparently following Willis (1968).

Typology. The type locality is NV. Nye Co., 1.6 mi S Springdale. The holotype, a female, is preserved in the American Museum of Natural History, New York.

Variation. Occasional individuals have traces of the middle band present. Dahl (1940) pointed out the occurrence of bronzy and dark green variants in northwestern Nevada and northeastern California.

Dates of occurrence. Available dates from Oregon specimens in the Hatch Collection, OSU, and Beer and Maser (1973) extend from 14 June-29 August. Dahl (1940) and Rumpp (1956) reported a number of April dates for California and Nevada. Rumpp (1956:133, 142)

Fig. 60. Pacific Northwest distribution of *Cicindela amargosae nyensis*. See Appendix I for tabulation of localities.



wrote that *C. amargosae* is one of the earliest species to emerge (April) and disappears by June at Death Valley National Monument. The intense summer heat of the California locality and the cool early spring in southeastern Oregon probably account for these differences.

The note by Blaisdell (1912) on hibernation of *C. senilis* indicates that this species also has a life history pattern A. Presence of this pattern coupled with a long summer survival period is what might be considered intermediate between patterns A and B. Since the *willistoni*-group is a primitive transitional group anatomically between *Cicindela (S.S.)* which are pattern A and the other species-groups of *Cicindelidia* which are pattern B, such intermediacy is to be expected.

Larval collections from California in the UI Collection 16 April 1965 include an L2 and several young L3 indicating that the species overwinters as an L2.

Cicindela (Cicindelidia) willistoni LeConte, 1879

(Figures 22T, 61)

Cicindela willistoni LeConte, 1879, Bull. U.S. Geol. and Geog. Sur. Terr., 5(3, art. 25):507.

Cicindela (Cicindelidia) willistoni LeConte. Rivalier, E., 1954, Rév. Française d'Ent., 21:255.

Diagnosis. Adult: characters of *willistoni*-group of *Cicindelidia*; frons with setal distribution depending on subspecies; mesepisternal coupling sulcus type N; elytra of normal degree of arching; elytra weakly microserrulate; elytral maculation depending on subspecies. *Aedeagus*: lateral apical flanges well-developed, with proximal angulate point; notch between beak and orifice short and shallow; ventral surface of apex keeled; inner sac with Type I flagellum, and sclerite 2 sickle-shaped with "handle" distal. *Female genitalia*: apex of sternite VIII broadly V-shaped. *Larva*: setae on head short to medium, pronotal margin along posterior and lateral edges carinate only to midpoint along lateral edge; abdominal hypopleuron with one enlarged sclerite and three small setiferous tubercles.

Synonymic notes. This species has been placed in its own species-group throughout its taxonomic history, notably Cazier (1937b) and Leng (1902).

Relationships. Relationships of *C. willistoni* to other species of the *willistoni*-group have been discussed in the account of *C. amargosae*. The two lineages in this group, *amargosae* and *senilis* on one hand and *willistoni* on the other, are not closely related, and neither is completely more generalized than the other. The extensive fragmented range of *willistoni* and the restricted range of the *amargosae-senilis* lineage are both indicative of ancient species. A formerly continguous range has been modified by geological events, particularly orogeny and drainage basin alterations. A time scale for such events is well-established and has been discussed by Axelrod (1957), Rumpp (1956, 1961), and Willis (1967). Each lineage probably had a contiguous range until the mid-Pliocene. Discussion before that time would be baseless conjecture.

The modified sclerite 2 and the keel and modified flanges on the aedeagal apex are apomorphic character-states of *C. willistoni*. Also, an enlarged larval abdominal hypopleural sclerite is certainly apomorphic. On these bases, it is the less generalized of the two lineages.

Subspecies. Willis (1967) revised *C. willistoni*. Except for *C. w. psendosenilis* which I have already discussed, I accept his arrangement. Rotger (1972) and Rumpp (1977) each described an additional subspecies since Willis' review. Willis (1975:18) cast doubt on the validity of Rotger's *C. w. funaroi*, suggesting that it

may be but ". . . a slightly different population of the variable *C. w. hirtifrons*."

C. willistoni consists of two groups of subspecies. One centers around *hirtifrons* which is generalized in its very setose frons and average maculation. It has the most centralized and largest range and also is the most variable in coloration. There is a southwestward cline through New Mexico in the number of frontal setae which culminates in *sulfontis*, a form which differs also in that a small majority of the population (54%) are green, whereas in *echo* only an occasional specimen is anything but brown or greenish-brown. Two isolated subspecies, *estancia* and *willistoni*, differ from *hirtifrons* in their greatly expanded maculation. The *hirtifrons*-group is most like *C. senilis* and probably is the more generalized of the two.

The second subspecies group contains *echo* and *praedicta*. These have few or no frontal setae. *C. w. echo* has the coloration and maculation of *hirtifrons*, and like *hirtifrons* has the largest range and greatest color variation. It intergrades with *praedicta* at localities in Inyo and Kern Counties, California.
C. w. praedicta closely resembles *C. a. amargosae* with which it is not, however, sympatric, although their respective ranges are only a single drainage system apart. They agree in color and maculation, but may be distinguished on the basis of more fundamental specific characters. The resemblance is the result of convergence perhaps caused by similar climatic and edaphic factors.

The following are brief diagnoses and range outlines of subspecies-groups and subspecies of *C. willistoni*. Willis (1967: fig. 160; 1975: fig. 4) mapped the range of the species. My fig. gives additional localities in the Pacific Northwest.

willistoni-section: frons mainly setose, labrum long

estancia

hirtifrons

sulfontis

willistoni

C. w. willistoni Leconte, 1879. Elytral color reddish-brown; maculation very broad to partly confluent; frons strongly setose; labrum relatively long, width/length ratio usually less than 2.0. Range: restricted to vicinity of WY. Albany Co., Medicine Bow (see Willis, 1967: fig. 160).

C. w. hirtifrons Willis, 1967. Elytral color ranging from cupreous to violet-cupreous, bronze, green-bronze, or green; maculation generally of average breadth; frons with more than 15 setae; labrum relatively long, width/length ratio usually less than 2.0. Range: KS, NM, OK, TX (see Willis, 1975). Includes *C. w. funaroi* as synonym.

C. w. estancia Rumpp, 1961. Elytral color except for maculation reddish-brown; maculation confluent and nearly covering elytral surface; frons strongly setose; labrum relatively long, width/length ratio usually less than 2.0. Range: restricted to type locality, NM. Torrance Co., 7 mi. E. Willard.

C. w. sulfontis Rumpp, 1977. Elytral color green (54%), greenish-brown (4%), or brown (42%); maculation uniform and moderately broad; frons with "a few hairs on vertex (Rumpp, 1977:171); "labral dimensions not presented in original description. Range: restricted to vicinity of type locality, A2. Cochise Co., 5.6 Km. WSW Willcox.

echo-section: frons largely glabrous, labrum short

echo

praedicta

C. w. echo Casey, 1897. Elytral color usually bronzy-brown, with occasional reddish-brown or greenish brown individuals; maculation of average breadth, but when broad, never confluent; frons with four or fewer setae; labrum relatively short, width/length ratio usually greater than 2.0. Range: CA, ID, NV, OR, UT, WY (see Willis, 1967, and Appendix I of the present paper). Includes *C. w. amedeensis* and probably *C. w. spauldingi* as synonyms (I consider *C. w. pseudosenilis* to be an intergrade between *echo* and *praedicta*).

C. w. praedicta Rumpp, 1956. Elytral color blue or bluish-green; maculation absent or reduced to apical dot only; frons glabrous; labrum relatively short, width/length ratio usually greater than 2.0. Range: restricted to type locality, CA. Inyo Co., 3.5 mi. S Shoshone.

C. (C.) w. echo Casey, 1897

Cicindela echo Casey, 1897, Ann. New York Acad. Sci., 9:298.

Cicindela willistoni echo Casey. W. Horn, 1908-1915, Gen. Insect., 82:378.

Cicindela amedeensis Casey, 1909, Canadian Ent., 41:272.

Cicindela spauldingi Casey, 1924, Mem. Coleop., 11:14.

Diagnosis. *C. willistoni* with elytral coloration normally dull bronzy brown with greasy appearance; maculation complete and of average breadth (except for "*spauldingi*" morph with expanded but not confluent markings; frons with number of setae averaging 5.6-6.2 in males, 5.8-6.8 in females; labral width/length ratio averaging less than 2.0 in 93.6% of specimens.

Synonymic notes. W. Horn (1908-1915:378) was the first author to place *echo* in *C. willistoni*, an allocation denied by Casey (1909:272). Cazier (1937b:157-159) retained "*spauldingi*" as a distinct subspecies but synonymized "*amedeensis*" with *echo*. Willis (1967) revised the entire species and the synonymy used in the present study follows his work.

C. w. amedeensis was based on larger than average, dark brown specimens found with typical *echo* and not worthy of taxonomic recognition; in this I concur with Cazier (1937b) and Willis (1967). *C. spauldingi* was based on a bright green specimen with very wide markings. The status of this form is uncertain. Bright green is a color only approached in some *echo* X *praedicta* intergrades. I have seen Oregon specimens with markings nearly as wide as those of the type of *spauldingi*. Until this isolated population is studied more closely, I prefer to synonymize it with *echo*. The form called *C. w. pseudosenilis* W. Horn from CA. Inyo Co., Owens Lake was retained as a subspecies by Willis (1967). It appears to be intermediate in measurements between *echo* and *praedicta* (Willis, 1967), has the maculation of the former, and is either blue-green or brown or even anteriorly blue-green and posteriorly brown. Its mosaic of characters leads me to consider it *C. w. echo* X *praedicta*.

Typology. The type localities of *C. w. echo* and its synonyms are as follows:

echo. UT. Salt Lake Co., Great Salt Lake. Provenance of type not reported.

amedeensis. CA. Lassen Co., Amedee. Type, female, in NM.

spauldingi. UT. Toole Co., Callao. Type, male, in NM.

Variation. This has been treated by Willis (1967). Willis (op. cit.: tables 45-46) indicated that his Oregon samples, his smaller series of the two analyzed, are larger in four measurements

in the males, and smaller in three but larger in the fourth in the females. However, Willis' figures show that these populations are not statistically separable.

Dates of occurrence. Willis (1967: figs. 88-89) has determined that adult *C. willistoni* in Kansas are at peak abundance from March to April. He had no fall records but expected a fall activity peak. Rumpp (1956:133, 142) stated that *C. willistoni* is the first species to appear at localities in California and Nevada he studied. I have records of this species from June through August (see also Willis, 1975) from California, New Mexico, and Oregon. I collected teneral adults 7 September 1976 at ID. Owyhee Co., 7.8 Km. N Bruneau. These data indicate a Life History Pattern A species but one which either has a prolonged spring emergence period or which survives through the summer. Further collections, marking, and noting of earliest dates of collections of teneral specimens are needed to answer the question. I have discussed this problem already in the *C. a. nyensis* account.

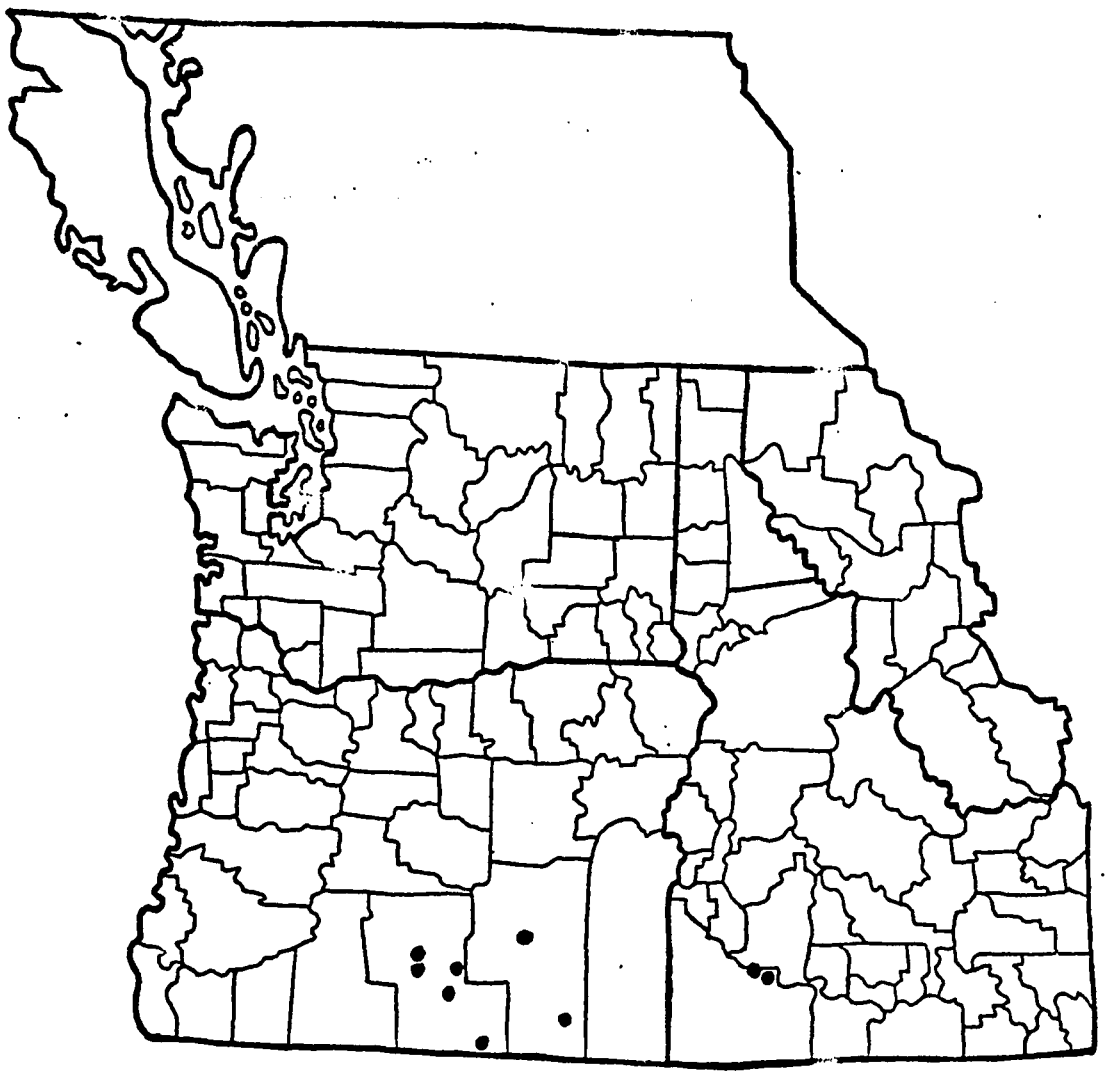
Cicindela (Cicindelidia) haemorrhagica LeConte, 1851

(Figures 22V, 62, 63)

Cicindela haemorrhagica LeConte, 1851, Ann. Lyc. Nat. Hist. New York, 5:171.

Cicindela carthagena haemorrhagica LeConte. Cazier, 1948, Amer. Mus. Nov. 1382:11.

Fig. 61. Pacific Northwest distribution of *Cicindela willistoni echo*. See Appendix I for tabulation of localities.



Diagnosis. Adult: characters of *carthogena*-group of *Cicindelidia*; elytra widest at middle or basal third, only moderately expanded at basal third in females; maculation subject to individual variation but never expanded along margin; abdominal sternites non-metallic red; mesepisternal coupling sulcus Type D. *Aedeagus*: lateral apical flanges well-developed, with proximal angulate point; ventral surface of apex unkeeled; inner sac with Type III flagellum. *Female genitalia*: apex of sternite VIII V-shaped. *Larva*: setae of head of moderate length; margin along posterior and lateral edges carinate, carina ending in point halfway to anterolateral angle along lateral margin; abdominal hypopleuron consisting of several small setiferous tubercles only.

Synonymic notes. This species was never united with any other species until Cazier (1948) considered it a subspecies of *C. carthagena*. Cazier (1954) afforded both distinct specific status.

Relationships. Relationships between species of *Cicindelidia* have never been worked out in detail. Cazier (1954) pointed out relationships between small groups of species, but indicated no broader alliances. His statements and figures suggest that *C. beneshi, carthagena, haemorrhagica*, and *roseiventris* are related. They agree with one another and differ from all other Nearctic and Mexican species in that the elytra are widest at or anterior to the midpoint. They may be distinguished by means of the following key (modified from Cazier (1954: 236-237 and figs. 87-88, 90-94, 184-185, and 187-191):

1. Labrum with basal margin strongly convex; abdominal sternites dark brown; marginal line continuous with middle band and elongated along lateral margin ——— *C. beneshi*

   Labrum with basal margin only weakly arcuate; abdominal sternites testaceous; marginal line consisting only of postmedia lateral spot except in *C. r. roseiventris* and *C. h. arizonae* ——— 2

2. Elytral apices strongly and regularly microserrulate ——— *C. roseiventris*

   Elytral apices feebly and irregularly microserrulate ——— 3

3. Female with elytral margins broadly expanded at basal third ——————————————— *C. carthagena*

Female with elytral margins only feebly expanded at basal third ——————————————— *C. haemorrhagica*

Subspecies. *C. haemorrhagica* needs taxonomic review over its entire extensive range. Cazier (1948, 1954) studied the southern populations and I agree with him in part, at least. I have studied limited material of all the named forms and present the following accounts as a basis for a more detailed revision. I recognize 5 subspecies. The extremely variable *C. h. haemorrhagica* has the most extensive and centralized range. The remaining four subspecies have smaller ranges peripheral to that of the nominate race and show little variability in maculation. Cazier (1954) stated that there are differences between the male genitalia of eastern, southern Californian, and Baja California samples, but did not say what these differences are. My examination of aedeagi indeed reveals minor differences. *C. h. haemorrhagica* and *nigroides* are identical in the ratio of lateral breadth/length from apex to angle of flanges being less than 50% and in the nearly straight outline of the ventral surface proximal to the apex. *C. h. arizonae* and *miniscula* have a ratio 60% or greater and an outline distinctly concave, strongly so in *miniscula*. *C. h. woodgatei* has the outline concave like *arizonae* but the ratio is 52.4% in the one available specimen; thus, *woodgatei* is intermediate between *haemorrhagica* and *arizonae*. My findings corroborate Cazier's statement as to the

Fig. 62. *Cicindela haemorrhagica*, left side of apex of aedeagus.

A. *C. h. arizonae*, UT. Washington Co., St. George (AM).

B. *C. h. haemorrhagica*, CA. Inyo Co., SW shore Owens Lake (SL).

C. *C. h. miniscula*, Baja California del Sur, Santa Rosa (AM).

D. *C. h. nigroides*, WA. Grant Co., 9.4 mi S Moses Lake (SL).

E. *C. h. woodgatei*, AZ. Cochise Co., 6 mi. S Willcox (AM).

A

B

C

D

E

distinctness of *miniscula* although I have been able to examine only a single specimen.

In maculation, *haemorrhagica* varies from completely maculate to completely immaculate. Such variation occurs within a single population. This variability has led authors to create three synonyms based on degrees of maculation. The totally immaculate morph ("*pacifica*") may even dominate some populations. The other subspecies are remarkably invariate in maculation. Variation in coloration of *nigroides* will be treated in more detail beyond.

The following are brief diagnoses and range outlines of the subspecies of *C. haemorrhagica*. Cazier (1948) and Leffler and Pearson (1976) partially mapped the range of the species. My fig. 62 gives the Pacific Northwest range.

C. h. arizonae Wickham, 1899. Size average for species; elytral coloration cupreous-brown with green punctures, sutures brown; thoracic sternites metallic blue-green; maculation relatively invariate, complete for species; aedeagus with outline of ventral surface proximal to apex broadly concave, and ratio of lateral breadth/length from apex to angle of flanges > 60%. Range: NW AZ and SW UT (see Cazier, 1948).

C. h. haemorrhagica LeConte, 1851. Size average for species; elytral coloration black with strong green reflections and punctures, sutures metallic green; thoracic sternites metallic blue-green; maculation ranging from completely maculate (for species) to completely immaculate; aedeagus with outline of ventral

surface proximal to apex nearly straight, and ratio of lateral breadth/length from apex to angle of flanges < 50%. Range: Baja, California, CA, NV, and UT (except SW). Specimens from along the Colorado River between CA and AZ (see Leffler, 1975) are intergrades between *haemorrhagica* and *woodgatei*, and those from N.NV and NWUT are intergrades between *haemorrhagica* and *nigroides*. Includes *bisignata* Dokhturov, *nevadiana* Casey, and *pacifica* Schaupp as synonyms.

C. h. miniscula Cazier, 1948. Size small for species; elytral coloration black with slight green reflections and green punctures, sutures brown; thoracic sternites metallic blue-green; maculation relatively invariate, complete for species; aedeagus with outline of ventral surface proximal to apex strongly arcuate, and ratio of lateral breadth/length from apex to angle of flanges > 60%. Range: Baja California del Sur (see Cazier, 1948, 1954).

C. h. nigroides Hatch, 1938. Size average for species; elytral coloration black without green reflections, color of punctures varying clinally from black in north to green in south, sutures metallic cupreous; thoracic sternites varying clinally from non-metallic black in north to metallic blue-green in south; maculation relatively invariate, complete for species; aedeagus with outline of ventral surface proximal to apex nearly straight, and ratio of lateral breadth/length from apex to angle of flanges < 50%. Range: ID, OR, WA, NWWY.

C. h. woodgatei Casey, 1913. Size average for species; elytral coloration black with only slight green reflections, punctures black, sutures brown; thoracic sternites metallic blue-green; maculation relatively invariate, complete for species; aedeagus with outline of ventral surface proximal to apex broadly concave, and ratio of lateral breadth/length from apex to angle of flanges 50-55%. Range: SE.AZ, N.NM.

C. h. nigroides Hatch, 1938

Cicindela carthagena haemorrhagica, var. *nigroides* Hatch, 1938, Univ. Washington Publ. Biol., 1(5):236.

Diagnosis. *C. haemorrhagica* with elytra black, lacking green reflections, and with sutures metallic cupreous; maculation relatively invariate, complete for species; aedeagus with outline of left surface proximal to apex nearly straight, and ratio of lateral breadth/length from apex to angle of flanges < 50%.

Synonymic notes. Hatch (1938:236) named this subspecies as a variety of *C. carthagena haemorrhagica*. Under Articles 10b and 17

of the Rules of International Nomenclature, an infrasubspecific or varietal name published before 1961 becomes available for use.

Typology. The type locality is WA. Walla Walla Co., Walla Walla. The holotype is, at the time of writing, in the Hatch Collection, OSU.

Variation. This subspecies shows two characters that vary clinally from north to south as the range of *C. h. haemorrhagica* is approached. Washington and Oregon specimens have the thoracic sternites and propleura non-metallic black. Those from southern Idaho agree with all other populations of *C. haemorrhagica* in that the sternites are metallic blue-green and the propleura are metallic cupreous becoming blue-green ventrally. Northern populations have the elytral punctures black, whereas the Idaho material has them green.

Occasional specimens from southern Idaho have a greenish luster to the elytra, thus resembling the nominate race. Also, some have the elytral sutures metallic green rather than metallic cupreous, but such individuals occur in populations in which the characters of *nigroides* predominate. Leffler and Pearson (1976:54-55) reported two specimens from Washington, taken in company with typical *nigroides*, with characters of *haemorrhagica*. I consider the southern Idaho populations to be *nigroides* but tending toward *haemorrhagica*. Specimens from NV. Humboldt Co., Winnemucca Lake, and UT. Box Elder Co., Promontory Point (both UI collection) are truly intermediate in having a greenish tinge to

the elytra and sutures that are metallic green with cupreous reflections.

C. h. nigroides is invariate in macular pattern except in the size of the postmedian marginal spot. There is great variation in body length, but this probably reflects the effects of larval nutrition.

Dates of occurrence. I have records from 13 May to 30 September, with most of the dates from late June to mid August. I have 3rd-instar larvae in early May and have collected 2nd-instar larvae in mid-September. These data indicate that the larvae probably overwinter as L2 or young L3. The adult dates are typical for Life History Pattern B.

Subgenus *Tribonia* Rivalier, 1954

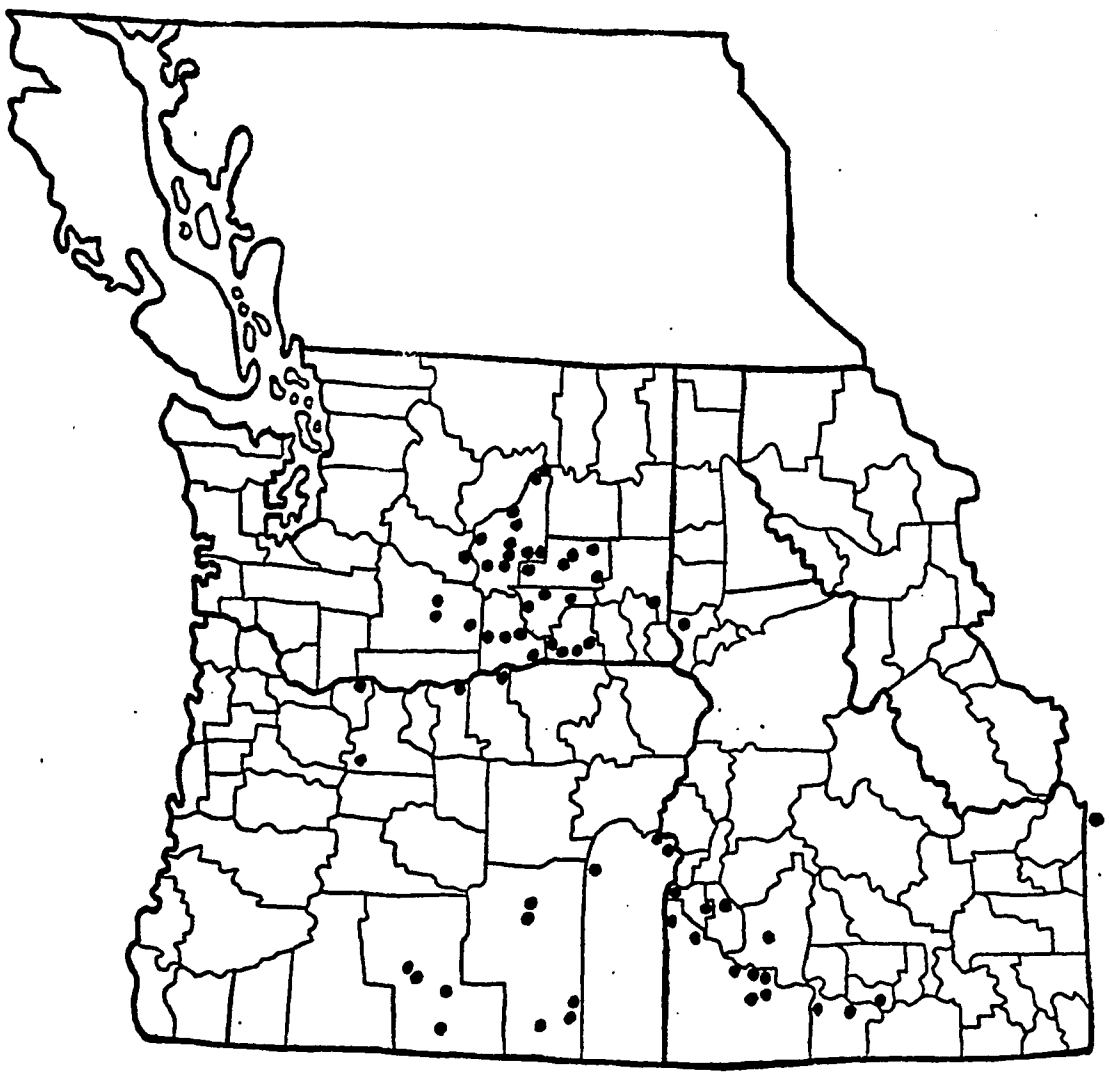
(Subgenotype. *Cicindela (Tribonia) tranquebarica* Herbst, 1806)

Cicindela (Tribonia) Rivalier, 1954. Rev. Francaise d'Ent., 21:254.

Cicindela Linnaeus, 1758 (*pars*). Willis, H. L., 1967, Univ. Kansas Sci. Bull., 47(5):230.

Diagnosis. Adult: *Cicindela* with eyes moderately developed; labrum tridentate (except *C. tenuicincta*) and medium (ratio length/basal breadth 52-63%); antennal scape plurisetose; frons setose; female mesepisternal coupling sulcus not

Fig. 63. Pacific Northwest distribution of *Cicindela haemorrhagica nigroides*. See Appendix I for tabulation of localities.



developed as cavity; pro- and meso-trochanters both with apical sensory setae. *Aedeagus*: Inner sac of cloak-type; flagellum elongate and with proximal loop only. *Female genitalia*: apex of sternite VIII V-shaped, with medial edges thin, and apices with several fine setae along laternal margins. *Larva*: no diagnostic subgeneric larval characters; 5-8 setae on antennal scape; Type I hypopleuron (based on *C. latesignata* [after Hamilton, 1925], *lengi*, and *tranquebarica*). *Pupa*: medial edge of eye concave; triangular depressions between medial edges of eyes; narrow, posteriorly-directed interocular extension of median frontal boss; lateral pronotal margin thickened; single isolated seta present on posterolateral face of lateral spine of tergite V. Life History Pattern: A.

Synonymic notes. Rivalier (1954:254) erected *Tribonia* as a subgenus of *Cicindela* to contain five species. He mentioned *propinqua* and *plutonica* as subspecies of *C. tranquebarica*. The former is a preoccupied name for *C. arida* which I consider a

species distinct from yet related to *C. tranquebarica*. The latter is a species related to *C. purpurea* and has already been discussed. Willis (1967) included *Tribonia* in *Cicindela* without further comment as to its validity.

Subgeneric validity. The subgenus was characterized by Rivalier on the cloak-type aedeagal inner sac (Rivalier, 1950:220). Seven of Rivalier's 55 "genera" *(Calochroa, Chaetodera, Hipparidium, Neolaphyra, Rhopaloteres, Tribonia,* and *Tribonophora)*, involving 76 species, have a cloak-type inner sac. I shall discuss the possible interrelationships of these beyond but, to summarize here, I do not consider *Tribonia* related to any of the Old World "genera."

The cloak-type inner sac is unique among Nearctic *Cicindela*, although it is most like an elongated modification of the auricular-type of *Cicindelidia*. Chaetotaxy and larval characters show relationship of *Tribonia* and generalized members of *Cicindela (S.S.)* and *Cicindelidia*. The inner sac and the numerous pupal features argue for systematic separation. The six genera show easily traceable lineages and thus form a definable taxonomic unit for which I am retaining Rivalier's subgenus *Tribonia*. Further discussion is contained under "Subgeneric Validity" in my section on *Cicindelidia*.

Relationships. Before Rivalier (1954) erected the subgenus *Tribonia*, its various species were usually associated with one another, although, frequently, *C. lengi* was considered related to

C. formosa, and, occasionally, extraneous species such as *C. plutonica* were included in *C. tranquebarica* (W. Horn, 1930:81).

Six of Rivalier's 55 "genera" have a cloak-type aedeagal inner sac. I have reviewed accounts of the species involved in W. Horn (1908-1915) and have been able to study the external morphology of *C. (Tribonophora) laetescripta*. The six "genera" involve 76 species worldwide: 6 Nearctic, 4 Palaearctic, 45 Ethiopian (one shared with Oriental), and 22 Oriental. After comparing chaetotaxic and labral characters I have concluded that only *C. (Tribonophora) laetescripta* (the "genus" was placed in *Chaetodera* by Rivalier, 1961) resembles *Tribonia* in any detail. However, it differs strikingly in having dense, decumbent lateral clypeal setae and a Type C mesepisternal coupling sulcus in the female. Thus, I believe that the Nearctic *Tribonia* is unrelated to any of the Old World groups and its cloak-type inner sac has evolved independently.

Tribonia shares with 9 of the 12 Nearctic subgenera a 25° angle between the axes of the everted inner sac and the shaft of the aedeagus. The subgenus is divisible into two species groups which I shall characterize under "Species Groups." The more generalized of the two groups, the *lengi*-group, has the cloak-type inner sac membrane, but the flagellar form and the evenly crescentic shape of sclerite II are much as in the primitive members of the *willistoni*-group of *Cicindelidia*. Wallis (1961:60) considered the inner sac structure of *C. willistoni* intermediate between those of *C. tranquebarica* and the *punctulata*-group of *Cicindelidia* and

I concur. *C. (T.) tenuicincta* and the *willistoni*-group are nearest the basal stock of their respective subgenera. I do not know what group of *Cicindela (S.S.)* is closest to this common ancestry. The *pulchra*- and *silvatica*-groups have modifications of inner sac sclerites. The *maritima*- and *formosa*-groups are completely generalized and are most likely nearest the primitive stock. My suggestions as to the relationships of the subgenera are presented in fig. 65.

Species Groups. Rivalier (1954) indicated that two groups of species differed in the development of the intermediate portion of the flagellum. In one group, this is unmodied, and, in the other, this portion is distinctly arcuate. It is on this basis that I recognize two species-groups in *Tribonia*. Argument for placement of *C. tenuicincta* in its own monotypic species-group could be made, but its characters, as will be elucidated in its own species account beyond, ally it with the *lengi*-group. It has the generalized flagellar type and I am placing it in that group.

C. lengi-group. Intermediate portion of flagellum only weakly arcuate if at all.

C. tenuicincta

C. lengi

C. ancocisconensis

C. tranquebarica-group. Intermediate portion of flagellum strongly arcuate.

Fig. 64. Male genitalia in species of subgenus *Tribonia*. X 24.

A. *C. tenuicincta*: apex, ventral view

B. *C. tenuicincta*: apex, left view

C. *C. ancocisconensis*: apex, ventral view

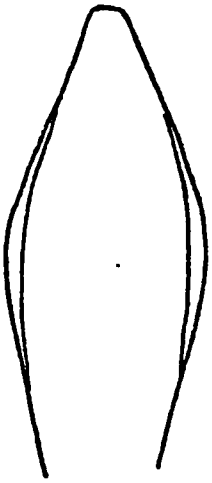
D. *C. lengi*: apex, ventral view

E. *C. lengi*: apex, left view

F. *C. tranquebarica*: apex, ventral view

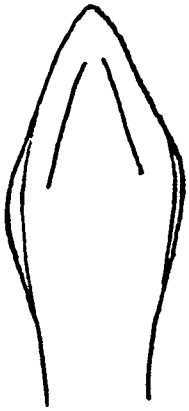
G. *C. tranquebarica*: apex, left view

H. *C. latesignata*: apex, ventral view



A

B



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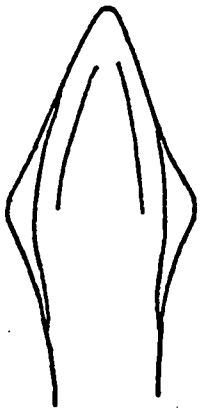

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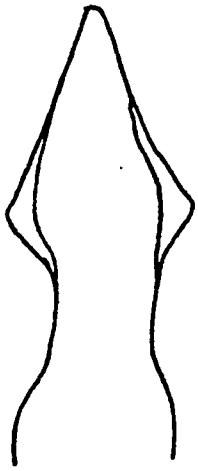
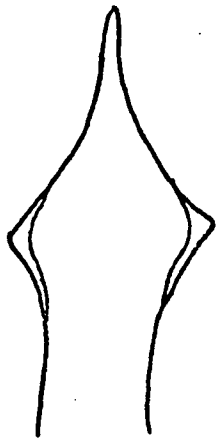


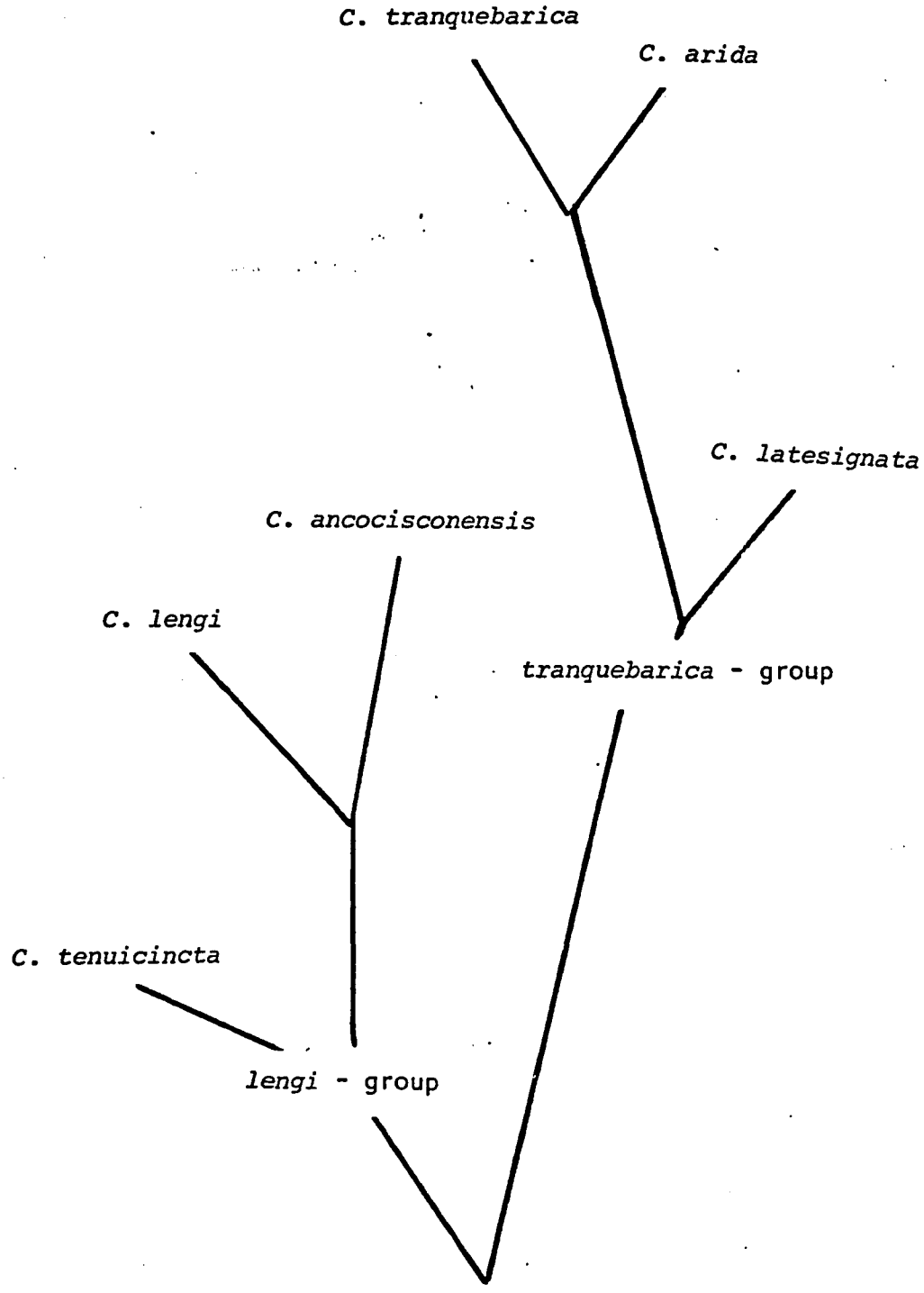
F

G



H

Fig. 65. Phylogeny of species of subgenus *Tribonia*, based on morphological characteristics.


C. tranquebarica
C. arida
C. latesignata
C. ancocisconensis
C. lengi
tranquebarica - group
C. tenuicincta
lengi - group

C. tranquebarica

C. arida

C. latesignata

Cicindela (Tribonia) tenuicincta Schaupp, 1884

(Figures 22P, 64, 66)

Cicindela latesignata var. *tenuicincta* Schaupp, 1884, Bull. Brooklyn Ent. Soc., 6:122.

Cicindela tenuicincta Schaupp. Leng, C. L., 1902. Trans. American Ent. Soc., 28:138.

Cicindela (Tribonia) tenuicincta Schaupp. Rivalier, E., 1954. Rév. Française d'Ent., 21:254.

Diagnosis. Adult: Size medium; color dull blackish-brown dorsally (light green or reddish-brown when teneral) with weak cupreous and bluish highlights, metallic green ventrally; marginal line complete except for gap anterior to apical lunule; space between posterior end of humeral lunule and bend of middle band as broad or broader than anteroposterior breadth of former; labrum short (ratio, length/basal breadth < 46%) and unidentate, but lobes on either side of median tooth well-developed; genae

glabrous; gula glabrous; prosternum glabrous; length metatarsus/length metatibia ratio < 78%. *Aedeagus*: Apex lanceolate with tip only gradually narrowed and not hooked, and left surface of apex only very slightly concave and lacking submarginal ridges; dorsal and ventral flanges well-developed but arcuate; neck of apex proximal to dorsal and ventral surfaces evenly arcuate; inner sac with intermediate portion of flagellum not strongly arcuate. *Female genitalia*: No specimens available. *Immature stages:* No specimens available.

Synonymic notes. *Cicindela tenuicincta* was originally described by Schaupp (1884:122) as a variety of *C. latesignata*. Leng (1902) considered it to be a distinct species and has been followed by subsequent authors. There are no named subspecies.

Relationships. *C. tenuicincta* has always been associated with at least some of the species to which I consider it to be related. Schaupp (1884) called it a variety of *C. latesignata* and related to *C. formosa* and *tranquebarica*. Leng (1902) included it in his *formosa*-group which contained *formosa, lengi,* and *latesignata* also. Rivalier (1954) placed it in his subgenus *Tribonia* as one of the

species in which the intermediate portion of the aedeagal flagellum is only weakly arcuate, the other two species being *C. ancocisconensis* and *lengi*. It differs from these species in lacking the submarginal ridges on the left surface of the apex of the aedeagus, and in lacking the concavity of the same left surface. These characters agree with conditions in *C. arida, latesignata,* and *tranquebarica*, indicating that the ridging and concavity of *ancocisconensis* and *lengi* are apomorphic.

The unidentate, short labrum, short metatarsi, relatively unmodified aedeagus, restricted range, and limited variation in maculation all show a primitive species, perhaps nearest the ancestral stock of the subgenus.

Typology. The holotype, a female (NM 1204), was collected by J. B. Smith supposedly in Colorado and received by Schaupp from H. Edwards. The species has never again been collected in Colorado and it is doubtful that the originally-stated type locality is correct. The Utah-Colorado state line is separated from the Great Basin, the true range of the species, by 275 air Km. of unsuitable habitat. Under Recommendation 72E, sec. 4, to Article 72 of the Rules of Zoological Nomenclature, a first reviewer can redesignate a type locality. I hereby designate the new type locality of *C. tenuicincta* as UTAH. Salt Lake Co., Saltair, SE shore Great Salt Lake, 18.5 Km. W Salt Lake International Airport, 1.285 m. The species is common around the southern and eastern shores of Great Salt Lake, and Leng (1902:138)

specifically mentions Saltair as a locality. The resort, Saltair, no longer exists, but it was located west of the airport along US Hwy. 40.

Variation. Teneral specimens are light green or reddish-brown and darken to brownish or greenish-black. Maculation varies slightly in breadth. Shelford (1918) illustrated some of the variations. The lobes on either side of the median labral tooth vary in development, but the labrum is never truly tridentate.

Dates of occurrence. 28 May-15 June; 1-16 August. Mating pairs have been taken in mid-June by F. M. Beer (pers. comm.). Teneral specimens were collected by Beer 16 August. I have seen specimens from California and Utah collected between 17 May and 19 September. Dates for July are included (15, 21, and 24).

Cicindela (Tribonia) lengi W. Horn, 1908

(Figures 22Q, 67)

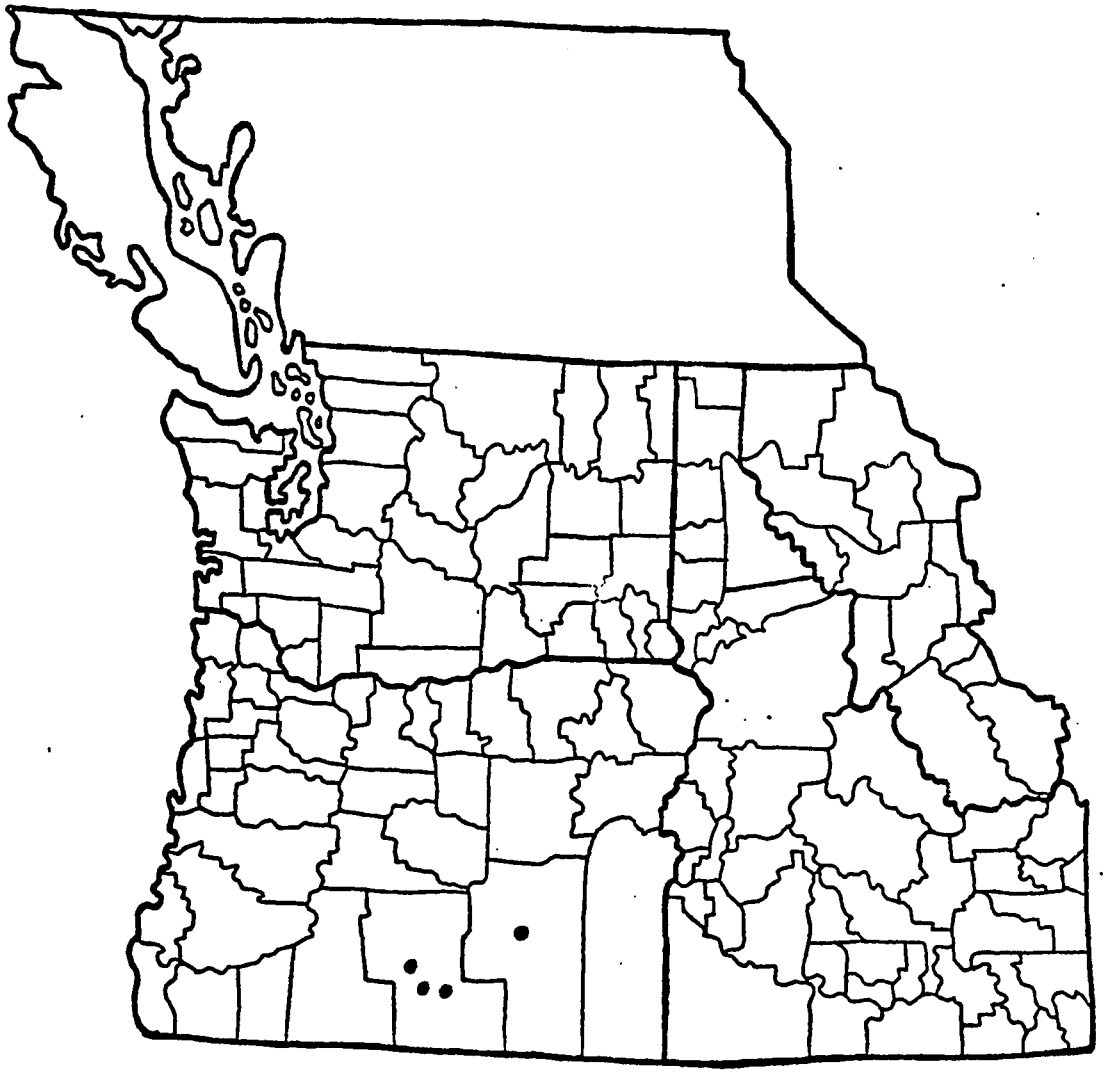
Cicindela venusta Leconte, 1848, An. Lyc. Nat. Hist. New York, 4:179, *nec* Laferté-Sénèctre, 1841, Rév. Zool.:1841:37.

Cicindela lengi W. Horn, 1908, Deutsch. Ent. Zeitsch., 1908:738.

Cicindela (Tribonia) lengi W. Horn. Rivalier, E., 1954, Rév. Française d'Ent., 21:254.

Diagnosis. Adult: characters of *lengi*-group of *tribonia*; size medium; color brassy-green to reddish-brown

Fig. 66. Pacific Northwest distribution of *Cicindela tenuicincta*. See Appendix I for tabulation of localities.



dorsally, metallic green to cupreous-green ventrally; color of propleuron variable according to subspecies; maculation variable according to subspecies, but, when lunules not coalesced, posterior end of humeral lunule touching or nearly touching bend of middle band, and marginal line usually complete; labrum medium (ratio, length/basal breadth < 63%) and tridentate; genae setose; gula glabrous; prosternum glabrous; ratio length metatarsus/length metatibia > 91%. *Aedeagus*: apex lanceolate with beak only gradually narrowed and not hooked, and ventral surface of apex broadly concave and bearing low submarginal ridges converging apically; lateral apical flanges well-developed and angulate; neck of apex proximal to lateral apical flanges short, only slightly constricted, and with lateral surfaces evenly arcuate; *lengi*-group type flagellum. *Female genitalia*: apex of sternite VIII V-shaped. *Larva*: unique diagnostic characters not present; pronotal coloration

black with violet reflections; pygopod surrounded by 18 setae. *Pupa:* unknown.

Synonymic notes. *Cicindela lengi* was originally described by Leconte (1848) as *C. venusta*, a name previously used for *C. dorsalis venusta* by LaFerté Sénectère (1841). It was renamed by W. Horn (1908).

Relationships. *C. lengi* has always been associated with species to which I consider it to be related (see Leng, 1902). Rivalier (1954) placed it in his subgenus *Tribonia* as one of the three species in which the intermediate portion of the flagellum is only weakly arcuate, the feature that characterizes what I am calling the *lengi*-group in the present study. The aedeagus agrees closely with that of *C. ancocisconensis*, differing only in the more angulate dorsal and ventral apical flanges. This angulate condition is apomorphic, but, probably, the maculation of *C. lengi* is more plesiomorphic than that of *ancocisconensis*. Thus, these two species are slightly divergent branches from a common ancestor rather than one being ancestral to the other.

Subspecies. Three well-marked subspecies are recognized, although no revisionary studies have been made, particularly in the Great Plains where ranges of two of them meet. Rotger (1974) compared the subspecies, and Huber (in Ferris, 1969) and Willis and Stamatov (1971) discussed intergrade populations in Wyoming.

The three subspecies differ in different combinations of macular breadth and propleural coloration. There is intergradation

between *C. l. lengi* and *versuta* in southern Wyoming where most of the populations are *versuta* but contain individuals with the blue-green propleura of *lengi*. Southern Wyoming is an area of intergradation of eastern and western subspecies of *C. cinctipennis* and *C. nebraskana*, and apparently *C. lengi* is affected similarly.

It is difficult to choose between *lengi* and *versuta* as being more generalized, if either is. Cupreous propleural coloration is characteristic of most species considered generalized. *C. l. versuta* has the propleura cupreous but tends to have rather broad maculation. It also has the most extensive range. *C. l. lengi*, conversely, has blue-green propleura and rather narrow maculation, and inhabits a narrow area parapatric to the eastern margin of that of *versuta*. *C. l. jordai*, with blue-green propleura and largely confluent maculation, is restricted to only a few localities in central New Mexico and is clearly apomorphic. Whether it was derived from a *lengi*-like or *versuta*-like ancestor is unknown, although the range of *versuta* is most geographically approximate. A *lengi* ancestor probably had cupreous propleura and maculation intermediate between that of *lengi* and *versuta*. *C. l. versuta* has a range approximating the long-grass prairie of the Great Plains, an area drier than the short-grass prairie inhabited by *C. l. lengi*.

The following are brief diagnoses and range outlines of the subspecies of *C. lengi*. Wallis (1961) and Willis (1970) mapped the

distributions for Canada and Kansas, respectively, and my fig. presents localities in the Pacific Northwest.

C. l. jordai Rotger, 1974. Elytral maculation greatly expanded to confluent; propleura blue-green. Range: C. NM.

C. l. lengi W. Horn, 1908. Elytral maculation narrow and not confluent; propleura blue-green. Range: NE. CO, KS, NE, and OK (intergrading with *versuta* in S. WY).

C. l. versuta Casey, 1913. Elytral maculation broad but not confluent; propleura cupreous to golden. Range: Alberta, British Columbia, CO, ID, Manitoba, MT, NM, ND, Saskatchewan, SD, and WY.

Cicindela lengi versuta Casey, 1913

Cicindela venusta versuta Casey, 1913, Mem. Coleop., 4:24.
Cicindela venusta gracilenta Casey, 1913, Mem. Coleop., 4:25.
Cicindela lengi (pars) W. Horn, 1908. W. Horn, 1915, in 1908-1915 Gen. Insect., 82c:372.

Diagnosis. *C. lengi* with elytral maculation broad and often touching but not confluent; propleura cupreous to golden.

Synonymic notes. *C. l. versuta* was described by Casey (1913:24) as *C. venusta versuta*, Casey being apparently still unaware that W. Horn (1908) had replaced the preoccupied specific

name. W. Horn (1915 in 1908-1915:372) denied *versuta* even subspecific status but gave no reasons.

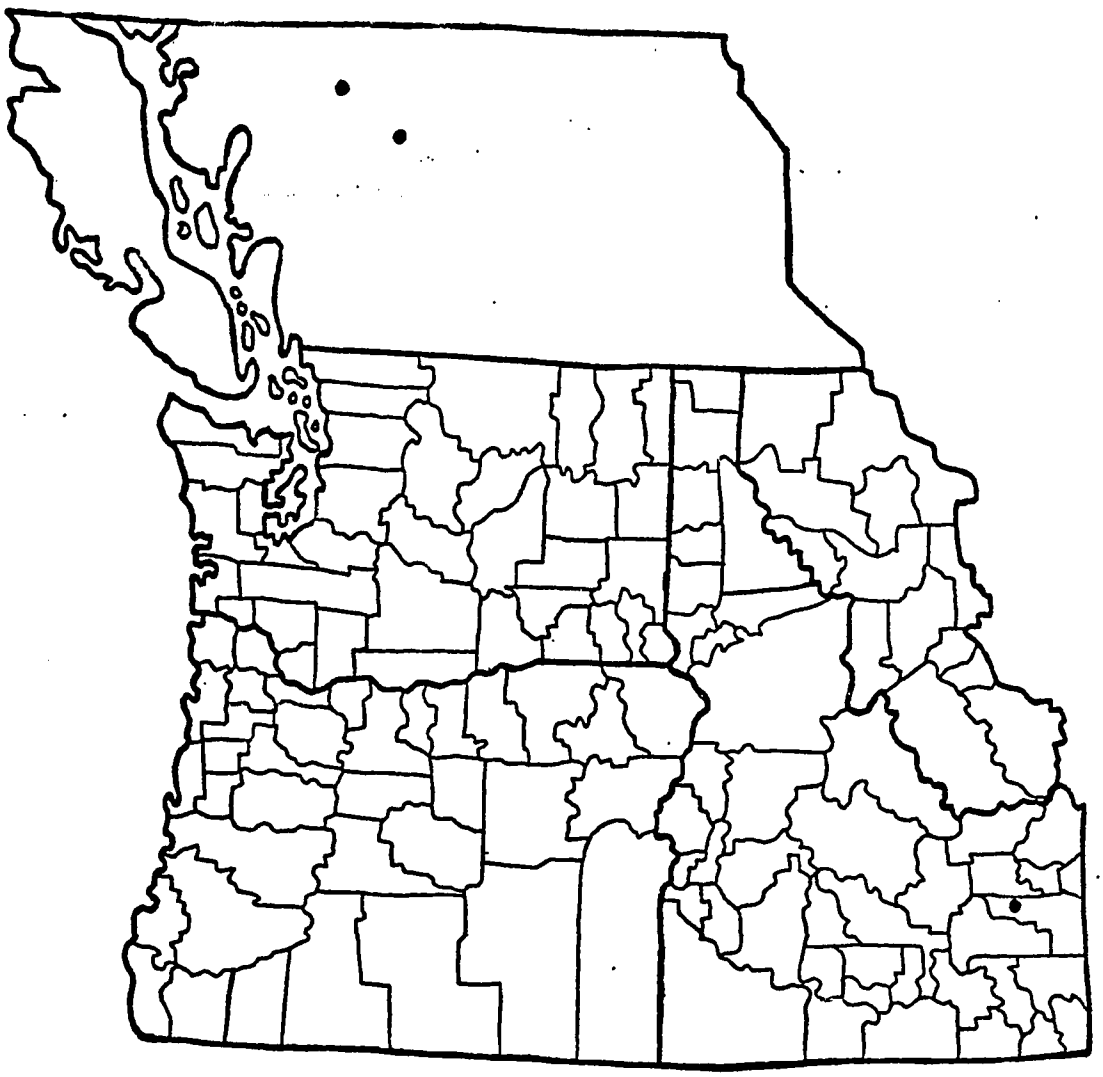
Casey (1913:25) described *C. venusta gracilenta* on the basis of a small male from Montana (no further locality). The holotype is indistinguishable from *C. l. versuta*.

Typology. The type locality of *C. l. versuta* is Manitoba, *aweme*. The holotype, a female, is NM 45973. The holotype of *C. l. gracilenta* is NM 45972.

Variation. Elytral coloration varies from brassy-green in fresh specimens to reddish-brown in senescent ones. Maculation is always broad and sometimes confluent where lunules touch. Ferris (1969) and Willis and Stamatov (1971) described variations in propleural coloration, their material from southern Wyoming apparently representing introgression of *C. l. lengi* into *versuta* populations or actual intergradation.

Dates of occurrence. The few Pacific Northwest records are from March and April. Ferris (1969) attempted to collect the earliest emergents near Laramie, Wyoming, finding this species 3 May 1969. Willis and Stamatov (1971) collected *C. l. lengi* in Nebraska 6 June 1970. I have taken Colorado specimens 22 June 1976. Rotger (1974:11) deduced September edosion and May to early June breeding in New Mexico, indicating a Life History Pattern A. An L3 I collected 22 June 1976 corroborates such a pattern.

Fig. 67.. Pacific Northwest distribution of *Cicindela lengi versuta*. See Appendix I for tabulation of localities.



Cicindela (Tribonia) tranquebarica Herbst, 1806

(Figures 22R and S, 68)

Cicindela tranquebarica Herbst, 1806. Berlin, Pauli, 10:178.

Cicindela vulgaris Say, 1818, Trans. American Phil. Soc., n.s., 1:409.

Cicindela (Tribonia) tranquebarica Herbst. Rivalier, E., 1954. Rév. Française d'Ent., 21:254.

Diagnosis. Adult: characters of *tranquebarica*-group of *Tribonia*; size large; color variable according to subspecies and individual variation; color of propleuron variable according to subspecies and individual variation; maculation variable according to subspecies, but with marginal line, when maximally developed, interrupted anterior and posterior to marginal middle band extensions; space between posterior end of humeral lunule and middle band variable according to subspecies, but usually greater than anteroposterior breadth of posterior end of lunule; labrum medium (ratio, length/basal breadth < 53%), tridentate; genae sparsely setose along ventral margin; gula glabrous; prosternum

glabrous; ratio length metatarsus/length metatibia > 93% (N = 10, $\bar{X}$ = 98.7%). *Aedeagus*: apex lanceolate with beak only gradually narrowed and not hooked, and ventral surface not concave and lacking submarginal ridges; lateral apical flanges well-developed and angulate; neck of apex proximal to lateral apical flanges long and constricted, and with lateral surfaces broadly arcuate; *tranquebarica*-group type flagellum. *Female genitalia*: apex of sternite V-shaped. *Larva*: unique diagnostic characters not present; pronotal coloration violet to violet-bronze with green reflections; pygopod surrounded by 22 setae.

Synonymic notes. Say (1818) created a synonym *C. vulgaris* for *C. tranquebarica* Herbst. Other proposed names now refer to subspecies or their synonyms.

Relationships. *C. tranquebarica* has always been associated with some of the species to which I consider it to be related, only Leng (1902) having placed it in a group by itself. W. Horn (1930) associated *C. plutonica* with it, but the genitalia certainly do not bear this out. *C. arida* was first associated with *C. tranquebarica* as a subspecies by W. Horn (1930:81). I consider these two as closely

related but separate species, differing in that *C. arida* has glabrous genae, proportionally shorter and straighter-sided elytra, and longer, narrower, and more acute apices of the female sternite VIII.

Rivalier (1954) placed *C. tranquebarica* and four other species in his subgenus *Tribonia*, making it the subgenotype. *C. latesignata, arida,* and *tranquebarica* comprise the *tranquebarica*-group of *Tribonia*, characterized by the strongly arcuate intermediate portion of the flagellum. The extremely narrowed beak of the aedeagus of *latesignata* and its setose gula and prosternum set it apart from the other two species. Thus, the closest relative of *C. tranquebarica* in the *tranquebarica*-group is *C. arida*. Of the three species of the *lengi*-group, aedeagi of *lengi* and *ancocisconensis* have characters different from those of the *tranquebarica*-group (see fig. and my account of *C. lengi*), and *tenuicincta* is too generalized. Thus, there are no living species near the immediate ancestry of *tranquebarica*.

Subspecies. This species needs revision over its entire range. I have examined specimens, including many of the holotypes, of all of the named subspecies. Tentatively, I recognize 15 subspecies with the full realization and expectation that some of these will eventually be synonymized and, perhaps, others proven valid. I divide the species into two subspecies-sections based on whether or not the humeral lunule is divided. Importance of such a character might seem questionable in view of the great individual variation in coloration and macular breadth, but this particular

character is largely invariate geographically: the lunule is widely broken in the three westernmost subspecies *sierra, vibex,* and *viridissima*, and complete in all others. Thus, I recognize a *tranquebarica*-section and a *vibex*-section. I have examined larvae of *admiscens* and *moapana (tranquebarica*-section) and *vibex (vibex*-section) and found no differences in coloration or chaetotaxy. Adults, likewise, show no differences in aedeagal form or distribution of pilosity. Thus, I am confident that both subspecies-sections are properly retained as a single species. Casey (1913) recognized several species within the *tranquebarica*-complex but considered all of them closely related. His characters were primarily those of coloration and maculation.

tranquebarica-section: humeral lunule complete; primarily subspecies of the Great Basin, Intermontane area, eastward, excluding Pacific Northwest except southern Idaho and southeastern Oregon.

admiscens

cibecuei

inyo

"kirbyi"

minor

moapana

parallelonota

tranquebarica

tranquebarica-section subspecies of uncertain validity:

diffracta

lassenica

turbulenta

uintana

vibex-section: humeral lunule widely broken; Pacific Northwest, Sierra Nevada Mountains and westward subspecies.

sierra

vibex

viridissima

The following are diagnoses, synonymic notes, and range outlines of the subspecies of *C. tranquebarica* as I interpret them.

tranquebarica-section

C. t. admiscens Casey, 1913. Elytral maculation wide, apex of humeral lunule sometimes touching bend of middle band, middle band lengthened anteriorly and posteriorly along marginal line; elytral color brick-red to reddish-brown. Range: NE.AZ, CO, N.NM, E. UT, and S. WY. Type locality: NM. Sandoval Co., Jemez Springs. Holotype examined.

C. t. cibecuei Duncan, 1958. Elytral maculation wide, some lunules touching in some specimens (see Duncan, 1958:43); elytral color dark navy blue. Range: reported only from type locality, AZ. Gila Co., Cibecue Creek, near Cibecue. Holotype examined.

C. t. lassenica Casey and *C. t. uintana* resemble *cibecuei* in their dark blue or black coloration and wide maculation. The type locality of *lassenica* was given simply as "California" by Casey (1914), and that of *uintana* (Casey, 1924) is UT. Washington Co., Zion Canyon. The three forms may be synonymous. I shall comment further on this possibility.

C. t. inyo Fall, 1917. Elytral maculation of moderate breadth, no tendency toward confluence, middle band lengthened anteriorly and posteriorly along marginal line; elytral coloration varying seasonally from bright green in teneral form to dull black in senescent individuals. Range: CA. Inyo Co., Owens Valley. Type locality: CA. Inyo Co., Olancha. Holotype not seen.

Fall (1917:106) named as varieties *inyo* and *owena*, the first for the green early seasonal form (April and May) and the latter for the black form (late May and June). *C. t. inyo* has line priority and *owena* is reduced to synonymy.

C. t. "kirbyi." See subspecies account beyond.

C. t. minor Leng, 1910. Maculation very narrow; elytral coloration dark chocolate brown. Range: SE US, exact limits uncertain (small western Canada specimens were called *minor* by Wallis, 1961:57, but geographically are either *tranquebarica* or *"kirbyi"*). Type locality: Leng (1910:80) reported on a collection from GA. Rabun Co., Clayton but did not designate a type locality (nor did Dahl, 1941:171-172). No type or lectotypes were designated.

The small size and uniformly chocolate color of *tranquebarica* from the southeastern United States suggest that the name *minor* is probably useful for these populations. E. D. Harris (1911) referred to them as *vulgaris-minor*. Leng (1910) stated that Harris had called the form *minor*. However, Leng characterized the form properly and Harris' published name is improperly formulated and predated by Leng's. Thus *vulgaris-minor* E. D. Harris becomes a synonym of *minor* Leng. Casey (1913) named *crinifrons* from North Carolina. It agrees closely with *minor* in size and color, although punctures are green. Five of Casey's series of nine have the humeral lunule divided (not so in the holotype). I consider *crinifrons* to be a synonym of *C. t. minor*. Casey (1916) mentioned the synonymy of *minor* and *crinifrons* but remarked that the former had no designated type or type locality.

C. t. moapana Casey, 1914. Maculation of moderate breadth, no tendency toward confluence, middle band without marginal extensions; elytral coloration deep reddish-violet tending to blackish-violet after death. Range: NV and W UT (largely corresponding to area of Pluvial Lake Bonneville). Type locality: NV. White Pine Co., McGill, 6500 ft. Holotype examined.

Characteristic of typical *moapana* in life is its deep reddish-violet color. I reared a specimen from UT. Salt Lake Co., Saltair, and subjected the newly-ecloded adult to high humidity by saturating its substrate soil while it developed its coloration; temperature averaged about 24° C. The developed color was

greenish-black, precisely the color of many Great Basin specimens reported in the literature as "*borealis* (see Cazier, 1939; LaRivers, 1946; and Lawton and Willis, 1974)." Variation results from a complex interaction of evolutionary (subspecific), seasonal, and microclimatic factors. The problem can only properly be solved through study of collections from single populations at various seasons, marking experiments, and rearing under controlled experiments. I believe that the Great Basin population is *C. t. moapana* with intergradation to varying degrees as well as partial coexistence with *C. t. "kirbyi."* There is the possibility that *cibecuei, lassenica, parallelonota,* and *uintana* are also involved in the problem.

C. t. parallelonota Casey, 1914. Maculation of moderate breadth, no tendency toward confluence, middle band without marginal extensions; elytral coloration bright green to greenish-blue. Range: S. NV and SW. UT. Type locality: NV. Clark Co., Las Vegas. Holotype examined.

Lawton (1972b) and Sumlin (1976) both stated that this form occurs with the reddish *moapana* without signs of intergradation, although Lawton mentioned "hybridization" in southwestern Utah. Further collecting is needed to delineate the range. It is possible that *parallelonota* represents only a green color phase. If so, the name has page priority over *moapana*.

C. t. tranquebarica Herbst, 1806. Maculation narrow, no tendency toward confluence, middle band with short or no marginal

extensions; elytral coloration variable but usually bronzy-brown. Range: SE Canada, NE quadrant of United States; western and southern limits of range not documented (see Graves, 1965, for Ontario; Larochelle, 1974, for Quebec; and Willis, 1970, for Kansas). Type locality: uncertain. Holotype: perhaps not extant.

Variation in the widely distributed eastern subspecies has resulted in creation of several synonyms. The variation has been discussed by Wickham (1906), and Shelford (1918) considered causal factors (1918). Wickham (op. cit.:43) stated: "In some districts a form may occur which, within a limited [geographic] area, seems to be definable by features of constancy and apparent importance--and we are tempted into describing it as a new race of subspecies. But in another locality, we find these characters utterly unstable and consequently have to abandon them as bases of subspecific separation, unless we make the citation of a locality label the most important part of our diagnosis."

Eight names are involved in the synonymy of *C. t. tranquebarica*. *C. vulgaris* was used by Say (1818) for the same form named *C. tranquebarica* by Herbst (1806:178). There is question as to whether Herbst's name is properly applied to this species, but such useage dates at least from Wickham (1906) and perhaps legal action by the International Committee on Zoological Nomenclature will result in it being validated as a *nomen conservandum*.

The holotype of *obliquata* Dejean came from the east end of the Great Lakes, probably Lake Erie, well within the range of

C. t. tranquebarica (R. H. Huber, in litt., 1976). The names *obliquata* Kirby *nec* Dejean and *kirbyi* LeConte refer to Dejean's *obliquata* and become synonyms of *C. t. tranquebarica* (see also my account of *C. t. "kirbyi"*).

Leng (1902) named *C. t.* var. *horiconensis* for the cupreous and green-bronze individuals occurring sporadically with the typical dark brown morphs of *C. t. tranquebarica*. It has been relegated to synonymy by Eckhoff (1939) and Wallis (1961) among others. Varas Arangua (1927) proposed *viridula* for bright green individuals. The name is preoccupied by *Prothyma viridula* Quensal, 1806 (see Huber, 1969). As this synonym requires a new name, I propose *deciperata* (Latin--"deceived," in reference to Varas Arangua being deceived into naming a mere color variety). *C. t. deciperata* Leffler now falls into synonymy under *C. t. tranquebarica*. So too does *wichitana* proposed by Casey (1914) for small individuals that are well-within the size-range of *C. t. tranquebarica*.

The following four subspecies are of uncertain validity:

C. t. diffracta Casey, 1909. This name was based on a male from NM. San Miguel Co., Las Vegas. Casey (1909:273) suggested that it is allied to *C. cinctipennis lunalonga*. I examined the holotype (NM 45950) and found that it is a small *C. tranquebarica* with narrow, eroded maculation. *C. t. admiscens* is known from Sandoval County (Casey, 1913), New Mexico, its type locality. Portions of the range of *C. t. tranquebarica* near northeastern New Mexico are: southwestern Kansas (Willis, 1970), western

Oklahoma (Drew and Van Cleave, 1962), and northern Texas (Gaumer and Murray, 1971). As *diffracta* is known from only a single specimen, its status is uncertain and awaits further collecting.

C. t. lassenica Casey, 1914. The holotype is a male collected from "California," without further locality data. The specimen is black with dull longitudinal reflections of green and violet on the elytra and the venter is dull brownish-black and not metallic. It is most like *cibecuei* and *uintana*. Because the type locality is so uncertain, it is perhaps best considered a *nomen oblitum*.

C. t. turbulenta Casey, 1913. This was based on a large female with reddish-brown elytra from MI. Warren Co., Vicksburg. It is more-than-likely an aberrant *C. t. tranquebarica* but material from the Mississippi coastal plain should be reassessed to put this morph into proper perspective.

C. t. uintana Casey, 1924. The holotype is a female from UT. Washington Co., Zion Canyon. It is bluish-black dorsally with green reflections and punctures and metallic green and blue-violet ventrally. The extremely wide maculation resembles some weakly maculated specimens of *C. latesignata*. *C. t. admiscens* and *moapana* are geographically the most proximate but the specimen looks like a widely maculate *cibecuei*. The status of *uintana* must remain uncertain until specimens from southwestern Utah and northern Arizona have been better studied.

vibex-section

C. t. sierra Leng, 1902. Elytral maculation greatly reduced, humeral lunule almost lacking; elytral coloration varying from brilliant to dark green. Range: Sierra Nevada Mtns., California, from Sierra south to Calaveras Counties. Type locality: CA. Sierra Co. Lectotype examined.

This is a distinctive alpine subspecies with bright green coloration and greatly reduced markings. It closely resembles *C. arida* but differs in having the genae setose and the lateral elytral margins arcuate, both characters of the species *tranquebarica*. The humeral lunule when maximally developed consists of a small humeral dot and a very narrow oblique dash.

C. t. vibex G. Horn, 1866. See subspecies account beyond.

C. t. viridissima Fall, 1910. Elytral maculation narrow, no tendency for confluence or marginal expansion; elytral coloration bright green. Range: sc. CA, exact limits unknown but Fall (1910) reported it from western Riverside and San Bernardino Counties and Tulane County and I have seen specimens (DL) from CA. San Luis Obispo Co., Soda Lake. Type locality: "Southern California." Holotype not examined.

Fall (1910:89) stated that darker specimens approaching *vibex* were collected in Tulare County but did not say whether they were taken with *viridissima*. *C. t. viridissima* closely resembles *C. t. vibex* but is of a much brighter green than even the

"roguensis" morph of *vibex*. The small series I have seen are uniform in coloration.

Cicindela tranquebarica "kirbyi" auct.

Cicindela kirbyi LeConte, 1866, Proc. Acad. Nat. Sci. Philadelphia, 1866:362.

Cicindela obliquata Kirby 1837 *nec* Dejean. Fauna Boreali-Americana, 4:10.

Cicindela tranquebarica "kirbyi" auctorum.

Diagnosis. *C. tranquebarica* of *tranquebarica*-section with maculation moderately broad, little tendency toward confluence; middle band often expanded marginally; typical elytral coloration rich brassy brown with green punctures.

Synonymic notes. LeConte (1866:362) created the name *kirbyi* as a replacement name for *obliquata* Kirby, 1837. However, Kirby's name (Kirby, 1837:10) refers to a different insect than the *obliquata* of Dejean (1825:73). Dejean's form is described as aeneous-black dorsally and Huber (*in litt.*, 1976) informed me that the type came from the east end of the Great Lakes. The locality and color are both characteristic of *C. t. tranquebarica*. Thus, *C. t. obliquata* Dejean becomes a junior synonym of *C. t. tranquebarica*.

Kirby distinguished his *obliquata* from *C. vulgaris* Say (= *C. t. tranquebarica*) on the basis of greenish-copper *vs.* nearly black dorsal coloration. Thus, the two are not the same and *obliquata* Kirby needs a different name. LeConte's name *kirbyi* was intended to serve as a replacement name for *obliquata* Kirby but, as it was proposed to replace a name that is a junior synonym, it too becomes a junior synonym of *C. t. tranquebarica*. A new name is still needed for the distinctive subspecies of the northern Great Plains and northern Rocky Mountains. None of Casey's names is applicable. I do not have material from the region in question and since a review of *C. tranquebarica* over its entire range is still needed in order to delineate the ranges of and define the various subspecies, I shall not propose a new name. Thus, I shall continue to use the name *C. t. "kirbyi" auct.*

Typology. Neither Kirby (1837) nor LeConte (1866) mentioned a type locality. LeConte (1866:362) stated that the type is in the British Museum collections.

Variation. There is confusion as to the identity of the populations in the Great Basin. Cazier (1939), La Rivers (1946), and Lawton and Willis (1974) referred to greenish-black material with complete humeral lunules as *borealis*. However Harris (1911) clearly described his *borealis* as a dark brown insect with the lunule broken. Furthermore, the type locality of *borealis* is the Kootenay of southeastern British Columbia. I consider the Great Basin populations to consist of various mixes of *"kirbyi,"*

moapana, and perhaps other subspecies as well, and certainly not *borealis* which is the brown morph of *vibex*. Sumlin (1976) described some of the peculiar Great Basin variants.

The typical "*kirbyi*" from the northern Great Plains is usually a rich brassy brown, although other color morphs occur. The series of 22 in the Casey Collection, National Museum, range in color from greenish to rich brown to dark brown, with the marginal extensions of the middle band varying from absent to elongate.

In southern Idaho, "*kirbyi*" intergrades with *vibex*. Specimens from Fremont County are typical "*kirbyi*," rich brassy brown with moderately wide markings. I have studied a series of 13 specimens in the University of Idaho collection and was given 5 additional by Mr. Richard L. Wescott, Oregon Department of Agriculture entomologist, from ID. Lincoln Co., Dietrich, a total of 18 specimens examined. Of these, 7 (37.8%) are typical "*kirbyi*," 3(16.4%) have the lunules narrowly broken but are richly colored, and 8 (45.8%) have the lunules widely broken and rich coloration.

Sign of this intergradation with *vibex* continues westward along the Snake River and can be seen in material from Ada and Owyhee Counties. The population from ID. Owyhee Co., Bruneau Dunes St. Park are intergrades, but a large proportion are dark greenish-blue (UI). Specimens from nearby but drier Hot Springs Falls are rich brown.

Range. Details of the range of *C. t.* "*kirbyi*" remain to be worked out. I have seen specimens from Alberta, eastern Montana,

Nebraska, North Dakota, and South Dakota (AM, DP, NM). Localities in the Pacific Northwest are presented in Appendix I. Cazier (1939) stated that *"kirbyi"* extends through the Mohave Desert to the San Joaquin Valley and to the Pacific coast in Santa Barbara County, California. Specimens in UBC from Mackenzie and BC. Terrace are deep brown and are probably *C. t. tranquebarica* on the basis of their narrow markings. Wallis (1961) reported *"kirbyi"* and *borealis (= C. t. vibex)* from Mackenzie. Ft. Smith, but stated that they are ecologically separated: *"borealis"* was found on sandy areas and *"kirbyi"* where ". . . the soil was heavy and alkaline." If *"kirbyi"* is properly applied to the form over such an extensive distribution, it crosses or touches the ranges of 7 other subspecies *(admiscens, inyo, moapana, parallelonota, tranquebarica, vibex,* and *viridissima)*.

Dates of occurrence. I have few Pacific Northwest records for this form, but dates range from 21 March to 24 June. Collecting trips in July and early September yielded other Pattern A species but not *C. t. "kirbyi."* Freitag and Tropea (1971) obtained it 8 July 1970.

Cicindela tranquebarica vibex G. Horn, 1866

Cicindela vibex G. Horn, 1866, Proc. Acad. Nat. Sci. Philadelphia, 1866:395.

Cicindela vulgaris var. *vibex* G. Horn. Schaupp, 1883-1884. Bull. Brooklyn Ent. Soc., 6:94.

Cicindela vulgaris var. *roguensis* E. D. Harris, 1901. Canadian Ent., 33:226.

Cicindela tranquebarica vibex G. Horn. Wickham, 1906. Ent. News, 17:45.

Cicindela obliquata var. *borealis* E. D. Harris, 1911. List of NA. Cicindelidae in the Harris Collection. Truan Press, Yonkers, New York:19.

Diagnosis. *C. tranquebarica* of *vibex*-section with maculation narrow but lunules always present and unbroken (except diagnostic humeral break), no tendency toward confluence; middle band not expanded marginally; elytral coloration extremely variable but never light green.

Synonymic notes. *C. t. vibex* was originally proposed by G. Horn (1866) as a species but thereafter has had universal ranking as a subspecies or variety of *C. tranquebarica*. The extreme variation in color has led to naming of two of the variants as subspecies, *borealis* and *roguensis*. I shall treat these in more detail under "Variation."

Typology. The type localities of *vibex* and its two synonyms are as follows:

borealis: "Kootenay region of British Columbia" (E. D. Harris, 1911:19)

roguensis: OR. Jackson Co., Gold Hill (Huber, in litt., 1976)

vibex: OR. Klamath Co., Ft. Klamath (G. Horn, 1866:395)

Variation and taxonomic notes. I have studied a large series of *C. tranquebarica vibex* from the Pacific Northwest and conclude that this name should be used for a subspecies showing little variation in maculation but a great deal in color. I have found nine elytral color variants in the Pacific Northwest: bright, dark green (to be called green); greenish-blue; blue; greenish-black; black; bronzy to cupreous-green (to be called greenish-brown); violet-brown; reddish-brown; and brown.

G. Horn (1866) based *C. vibex* on a "bright green" form from Fort Klamath, Oregon. E. D. Harris (1901) named *C. vulgaris* var. *roguensis* as the "dull coppery green" variant from western Oregon. Harris (1911) used *borealis* for specimens from the Kootenay of British Columbia (the southeastern portion) in which color ". . . varies from cupreous-brown to dark green, the latter prevailing." All three forms have the broken humeral lunule characteristic of the *vibex*-section. Wickham (1906:45-46) considered that the distinction between *roguensis* and *vibex* is ". . . merely the evanscent one of depth or brilliance in color." Wallis (1961:59) similarly considered the distinction to be only

". . . an unstable color character--dark green versus bright green [respectively]."

E. D. Harris (1911:19) clearly used *borealis* for a form with a broken humeral lunule and color varying from cupreous brown to dark green and based it on specimens from southeastern British Columbia. Cazier (1939), LaRivers (1946), and Lawton and Willis (1974) have all referred specimens from California and Nevada to *borealis*, the last mentioning the dark green color. Sumlin (1976) applied *"borealis"* to a brown or black form with very narrow lunules. None of these authors referred to any break in the humeral lunule. I contend that *borealis* should not be used for Great Basin forms with complete humeral lunules, and what these authors have is either *"kirbyi"* or *moapana*, both of these, and/or intergrades.

The three names, *borealis, roguensis,* and *vibex*, are all based on coloration: *borealis,* cupreous brown to dark green; *roguensis,* dull greenish-brown; and *vibex*, bright green. Table 80 shows that these color morphs are not restricted in the Pacific Northwest to region or season. In general, populations west of the Cascade Mountains have a larger proportion of the bright green morph and those from east of the range have a higher percentage of the brown morph. Also, the proportion of green or greenish-brown individuals from east of the range is greater in the late summer and fall (N = 87, % = 36.5) than in the spring and early summer (N = 11, % = 12.1). The table shows, however, that, at many localities, several color morphs occur regardless of season.

Table 80. Survey of color variation in *Cicindela tranquebarica vibex* from selected localities in the Pacific Northwest.

Localities	Σ	Color Morph								
		Green "vibex"	Green-Blue	Blue	Green-Black	Black	Green-Brown "roguensis"	Violet-Brown	Red-Brown	Brown "borealis"
Spring and Early Summer										
West of Cascade Range										
1. WA. Island Co., sev. locs. 20 April-10 July	24	8 (33.3%)			6 (25.0%)	1 (4.2%)	6 (25.0%)			3 (12.5%)
2. WA. San Juan Co., San Juan Is. 16 May-10 July	15	15 (100.0%)								
3. OR. Douglas and Josephine Cos., sev. locs. (north and west) of type locality of "*roguensis*" respectively 10 May-9 June	16	8 (50.0%)			4 (25.0%)					4 (25.0%)
Σ	55	31 (56.4%)			10 (18.2%)	1 (1.8%)	6 (10.9%)			7 (12.7%)

Table 80 (continued)

Localities	Σ	Color Morph: Green "vibex"	Green-Blue	Blue	Green-Black	Black	Green-Brown "roguensis"	Violet-Brown	Red-Brown	Brown "borealis"
East of Cascade Range										
1. BC. Kootenay (type locality of "*borealis*") 23 April-14 June	15						1 (6.7%)			14 (93.3%)
2. WA. Chelan Co., Holden Village 6 July	3	1 (33.3%)	1				1 (33.3%)			1 (33.3%)
3. WA. Spokane Co., Cheney 9 April-22 May	22						1 (4.5%)		1 (4.5%)	20 (91.0%)
4. WA. Walla Walla Co., SW part of county (sev. locs.) 2 April-19 June	15	4 (26.7%)	4 (26.7%)	1 (6,7%)				1 (6.7%)		5 (33.3%)
5. OR. Morrow and Umatilla Cos., sev. locs. 25 April-27 May	6	2 (33.3%)				2 (33.3%)	1 (16.7%)			1 (16.7%)
6. ID. Kootenai and Latah Cos., sev. locs. 5 April-1 July	30	1 (3.3%)					1 (3.3%)	1 (3.3%)		27 (90.1%)
Σ	91	8 (8.8%)	4 (4.4%)	1 (1.1%)		5 (5.5%)	3 (3.3%)	2 (2.2%)	1 (1.1%)	76 (83.5%)

Table 80 (continued)

Localities	Σ	Color Morph: Green "ylbex"	Green-Blue	Blue	Green-Black	Black	Green-Brown "roguensis"	Violet-Brown	Red-Brown	Brown "borealis"
					Late Summer and Autumn					
					East of Cascade Range					
1. BC. Kootenay (type locality of "*borealis*" August	23	9 (39.1%)					9 (39.1%)			5 (21.8%)
2. WA. Columbia and Garfield Cos., Blue Mtns. 2 September	16	3 (18.8%)					10 (62.4%)			3 (18.8%)
3. WA. Pend Oreille Co., 7 mi. W Locke 26 September	23	6 (26.1%)					2 (8.7%)		4 (17.4%)	11 (47.8%)
4. OR. Morrow and Umatilla Cos., sev. locs. 6 September	8									8 (100.0%)
5. ID. Benewah Co., Palouse Divide 2 October	10									10 (100.0%)
Σ	80	18 (22.5%)					21 (26.3%)		4 (5.0%)	41 (51.2%)
Grand Total	239	57 (23.9%	4 (1.7%)	1 (0.4%)	10 (4.0%)	6 (2.5%)	30 (12.6%)	2 (0.8%)	5 (2.1%)	124 (51.9%)

Material from the two counties (Douglas and Josephine) north and west of the type locality of *"roguensis"* included none of this green-brown morph. Nineteen (50%) of a sample from BC. Kootenay *("borealis")* were not brown.

The reason for such variation is not certain. Shelford (1918) carried out laboratory experiments with *C. tranquebarica* showing that temperature and humidity influenced color and macular breadth. My own experiments are limited (one was mentioned regarding *C. t. moapana*). A single larva each from BC. W shore Columbia Lake, Kooteney and OR. Grant Co., Dixie Pass, both localities where the brown morph is abundant, were reared and the freshly-emerged imagines allowed to develop coloration at high humidity (the substrate soil was saturated) and ambient temperature averaging 24° C. Both developed bright green coloration. Further work along such lines is still needed but I believe that microclimatic factors produce the several color morphs. Perhaps imagines developing nearer plant roots are subjected to greater humidity than those in exposed situations, for example. At any rate, the several color morphs do not fulfill criteria for subspecies: uniform morphological characteristics within a defined geographic area.

Another point of variation occurs at low frequency. I use the broken humeral lunule as the character defining the *vibex*-section. Out of over 300 specimens examined from the Pacific Northwest, three have at least one humeral lunule complete or nearly so, one

specimen each from: WA. Island Co., Whidbey Island, Greenbank (OSU), WA. Spokane Co., Nine Mile Falls (SL); and OR. Marion Co., Salem (ODA). Such variation is common at localities in southern Idaho, but here populations are intergrades between *vibex* and *"kirbyi,"* the intergradation also shown by intermediate coloration.

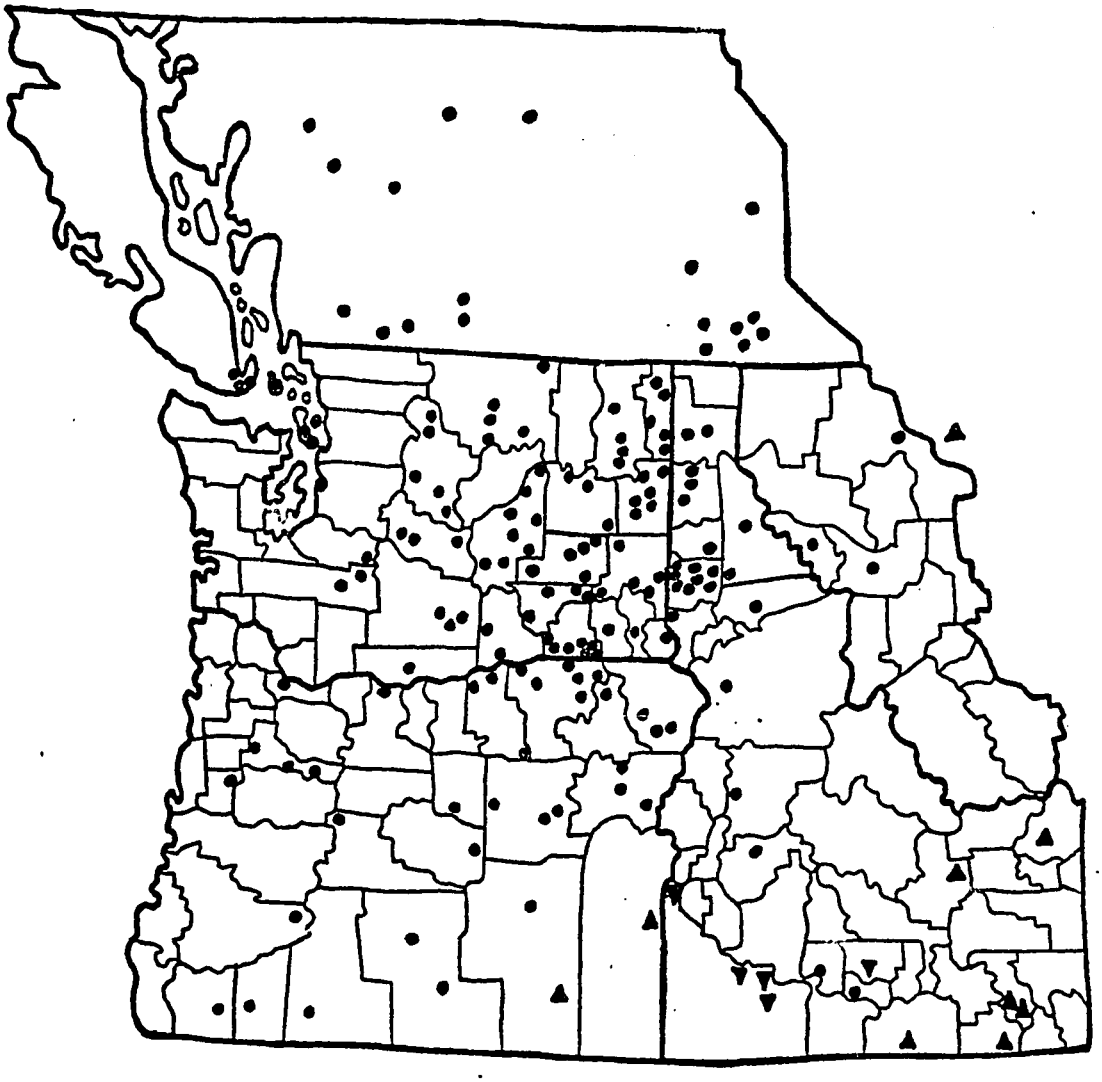
Range. The northern and southern range limits of *C. t. vibex* remain to be delineated, but from published statements and specimens I have seen, the subspecies appears to extend from the Northwest Territories (Wallis, 1961) south to Tulare County, California (Fall, 1910). Its range in eastern California and Nevada is uncertain because of identifications that I question. I have seen a specimen from MT. Glacier Co., Blackfoot (UMT) that is clearly *C. t. "kirbyi,"* and this form is reported from Alberta (Wallis, 1961), so I consider the continental divide in the northern Rocky Mountains to be the eastern boundary. The Pacific Northwest range is presented in fig. 68 and Appendix I.

Dates of occurrence. My records for the Pacific Northwest are 4 April-19 June and 19 August-10 October. A completely dried female, clearly senescent from her blunted mandibles and second gonocoxae, was found dead WA. Chelan Co., 5.6 Km. E Stevens Pass 18 July 1976. I have collected LL3 at several localities in May and June and LL2, which shortly moulted, in mid-June. All of these records are typical of a Pattern A species.

Fig. 68. Pacific Northwest distribution of *Cicindela tranquebarica*. See Appendix I for tabulation of localities.

Symbols:

● - *C. t. vibex*
▲ - *C. t. "kirbyi"*
▼ - *C. t. "kirbyi" x vibex*



Subgenus *Cylindera* Westwood, 1831

(Figures 69-72)

(Subgenotype. *Cicindela (Cylindera) germanica* Linnaeus, 1758)

Cylindera Westwood, 1831.

Diagnosis. *Aedeagus*: flagellum circumvolutory but not concentric, with from one to two full loops, and situated against left flank of inner sac, but not contained in membrane; sclerite 3 right-angled (équerre *fide* Rivalier), projecting into circle formed by flagellar loops.

Synonymic notes. Rivalier (1950, 1954, 1958, 1961, 1963) conserved the genus *Cylindera* of Westwood (1831) for 103 species (I have adjusted his list of Nearctic species and included *C. nahuelbutae* Peña; Rivalier (1961) stated that his Oriental list is tentative) arranged in 11 subgenera. The subgenera differ widely in pilosity, size, and labral chaetotaxy, but have generally similar male genitalia. If the same perspective used for other "genera" of Rivalier is applied to *Cylindera*, this taxon should be reduced to subgeneric rank within the genus *Cicindela* and divided into 11 species-groups. Validity of the various species-groups is beyond the scope of the present study. Only the *germanica*-group (subgenus *Cylindera ss. fide* Rivalier) has Nearctic species.

Subgeneric validity and Relationships. Rumpp (1977) included in *Cylindera* the species contained by Rivalier (1954) and Willis (1971b) in *Ellipsoptera* Dokhtourow. *Ellipsoptera* and *Cylindera* agree in having circumvolutory flagellar loops and the right-angled form of sclerite 3 (équerre of Rivalier) projecting into the orbit formed by the flagellar loops. The same arrangement is seen also in the Nearctic *Dromochorus* Guérin-Méneville and the Palearctic *Cephalota* Dokhtourow and *Homodela* Rivalier. These "genera" follow one another in the sequence given by Rivalier (1963) although *Spiralia*, which lacks the équerre-form of sclerite 3, is also part of this sequence. It is possible that the five "genera" are related but, as about 135 species are involved, revisionary studies ought to be undertaken to determine species limits and interrelationships before Rivalier's "genera" are dismissed.

I have discussed a character used by Rumpp (1967, 1977) in connection with my treatments of the subgenera *Cicindela*, *Cicindelidia*, and *Tribonia*. In these groups, the inner sac during copulation is extruded at about a 25° angle to the axis of the aedeagal shaft. In *Cylindera* and *Ellipsoptera* (I must state, however, that I have only examined two species of *Cylindera* and one of *Ellipsoptera*) the inner sac is extruded in the same axis as the shaft, thus forming no angle. If only the inner sac and its sclerites are used in the classification of subgenera of *Cicindela*, I would follow Rumpp in synonymizing *Ellipsoptera* with *Cylindera*, and include *Cephalota*, *Dromochorus*, and *Homodela* also. If we look

at other characters of *Dromochorus* and *Ellipsoptera*, we find that these groups differ as much from one another as they are from any of the Nearctic species of *Cylindera*. The three differ in adult body form, chaetotaxy, mesepisternal coupling sulcus morphology, and, so far as larvae are known, larval anatomy. I recommend that the three groups with Nearctic representatives be considered closely related but retained in separate subgenera. I am not, unfortunately, in any position at present to comment further on the Palearctic groups.

Species-groups. Rivalier (opp. cit.) divided his "genus" *Cylindera* into 11 "subgenera." These 11 groups agree closely in aedeagal form but differ in chaetotaxy, body form, and labral morphology. These differences are frequently of the sort that help delineate others "genera" of *Cicindela*, further emphasizing the inconsistencies existing in taxonomic limits. It is possible that studies of all biological aspects of the species involved will result in a better ranking and arrangement than now exists. Until then, I recommend that the 11 "subgenera" be retained as species-groups. It is the *germanica*-group (Rivalier's subgenus *Cylindera*) that has Nearctic representatives. Eight species of the *germanica*-group are found north of Mexico (*celeripes, cinctipennis, cursitans, debilis, lemniscata, terricola, unipunctata,* and *viridisticta*). Little is known of the interrelationships of these species. As only *C. cinctipennis* is found in the Pacific Northwest, I shall treat relationships only as it applies to this species.

The *germanica*-group

Diagnosis. Adult: labrum with 4-8 submarginal setae; antennal seta with one subapical sensory seta; frons glabrous; proepisternum glabrous; protrochanteric seta always present, mesotrochanteric seta present in some species.

As modified from the lists of Rivalier (*opp. cit.*), I count 34 species in this group on a world-wide basis, eight of which are Nearctic (north of Mexico) and eight Palearctic. The Nearctic species differ widely in body form, mesepisternal coupling sulcus morphology, and elytral sculpture. Larvae are known only of *C. cinctipennis, germanica,* and *unipunctata* and these differ greatly. I am not convinced that the eight Nearctic species are all particularly closely related but am in no position to speculate further.

Cicindela (Cylindera) cinctipennis LeConte, 1848

Cicindela cinctipennis LeConte, 1848, Ann. Lyc. Nat. Hist. New York, 4:182-183.

Cicindela pusilla cinctipennis LeConte. Horn, W., 1908-1915, Gen. Insect., 82:1-486.

Cylindera cinctipennis. (LeConte). Rivalier, E., 1954, Rév. Francaise d'Ent., 21:265.

Diagnosis. Adult: labrum with eight submarginal setae, unidentate but with margin excavated on either side of tooth; mesepisternal coupling sulcus Type N; elytra gradually broadening to within level of apical 1/6th; elytral sculpture consisting of shallow, irregular-sized, variably-confluent punctures, most numerous anteriorly and suturally, and deepest laterally, non-granulate; hindwings functional; mesotrochanteric seta present. *Aedeagus*: lateral apical flanges located ventro-laterally and extending 40% of length of shaft of middle lobe; ventral face of apex weakly convex between lateral apical flanges. *Female genitalia*: apices of tergum VIII with three stout setae and pairs of fine setae laterally along the margin. *Larva*: inner spine of abdominal tergum V with hook rudimentary. *Pupa*: setae on lateral spine of abdominal tergum V arranged in patch on anterior face of apical portion.

Synonymic notes. LeConte (1848) described this as a distinct species. Casey (1913, 1914), Leng (1902), and Schaupp (1883-1884) all retained this specific status. W. Horn (1908-1915) united it with *C. "pusilla (= C. terricola sensu mihi),"* and has been followed by subsequent authors.

Status of *C. "pusilla" auct.* Huber (1969:21) showed that *C. pusilla* Say, 1817, is preoccupied by *Cicindela pusilla* Schreber, 1759, itself a synonym for the carabid *Notiophilus aquaticus* Linnaeus. Four names have been proposed although none as a replacement for *pusilla:*

name	author	characterization
pusilla	Say (1817)	color black; maculation consisting of humeral and apical lunules and middle band, no marginal band
terricola	Say (1824)	color black; maculation reduced to traces of humeral lunule and complete apical lunule, or immaculate
cyanella	LeConte (1857)	color blue or green; maculation as in *pusilla*
sayella	Casey (1914)	color dull cupreous-brown; maculation as in *pusilla* but only horizontal arm of middle band present

C. terricola Say is the first available replacement name for the species. Although I have had only limited material for study and cannot delineate their ranges, I recognize two subspecies (characterization of the species is presented beyond):

C. t. terricola Say. Color black; maculation reduced to traces of humeral lunule and complete apical lunule, or immaculate; eastern portion of range: NE north to SE. Saskatchewan and S. Manitoba (Leng, 1902; Wallis, 1961).

C. t. cyanella LeConte. Color variable: black, brown, blue, or green; maculation consisting of humeral lunule, middle band, and apical lunule; western part of range: MT (Yellowstone River is type locality), NW.NE, and "Dakota" (Leng, 1902, and personal examination of specimens. Synonym: *sayella* Casey.

Differences between *C. cinctipennis* and *terricola*. Treatments subsequent to W. Horn's (1908-1915) arrangement have united these two species as *C. pusilla*. However, they differ in elytral sculpture, labral morphology, and aedeagal form. Table 81 and figs. 69-71 present these differences. These differences are, I believe, sufficient to show that two species are represented, species probably not particularly closely related.

Relationships. Harris and Leng (1916) arranged what are now the Nearctic members of *Cylindera* into three species groups, following W. Horn (1908-1915). This has been the only attempt at

Table 81. Differences between *C. cinctipennis* and *C. terricola*.

Character	C. cinctipennis	C. terricola
Labrum (see fig. 70)	unidentate with margin excavated on either side of tooth	tridentate with lateral teeth not acute
Elytral sculpture (see fig. 71)	large, shallow punctures of irregular size, variable amounts of confluence; nongranulate	small, deep, regularly-sized, evenly-spaced punctures each with anterior granule
Aedeagus (see fig. 69)	lateral apical flanges located ventrolaterally and extending anteroposteriorly > 40% of length of middle lobe; ventral surface of apex between lateral apical flanges weakly evenly convex.	lateral apical flanges located ventrally and extending anteroposteriorly < 30% of length of middle lobe; ventral surface of apex between lateral apical flanges shallowly concave

Fig. 69. Genitalia of *Cicindela* (*Cylindera*) spp. X 13.

A. *C. cinctipennis*: aedeagus, ventral view

B. *C. cinctipennis*: aedeagus, lateral view

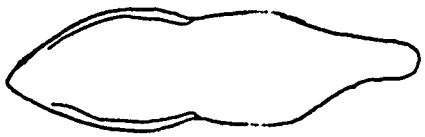
C. *C. terricola*: aedeagus, ventral view

D. *C. terricola*: aedeagus, lateral view

E. *C. cinctipennis*: female syntergum IX + X, dorsal view

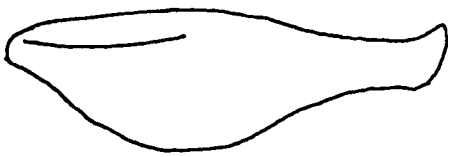
F. *C. cinctipennis*: 2nd gonocoxa and 2nd gonapophysis

G. *C. cinctipennis*: sternite VIII, ventral view



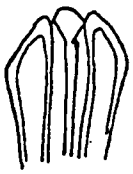
A

B



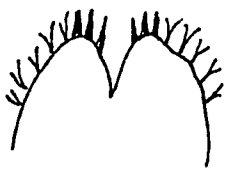
C

D



E

F

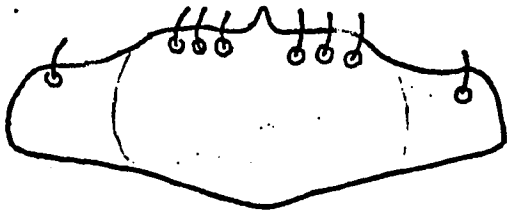


G

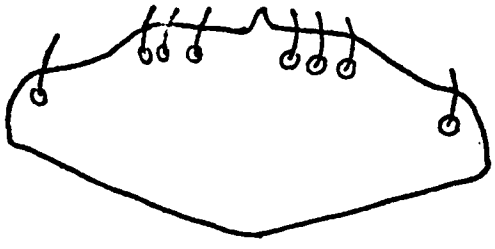
Fig. 70. Labra in species of *Cicindela* (*Cylindera*) (X 24).

A. *Cicindela terricola*

B. *Cicindela cinctipennis*



A



B

Fig. 71. Scanning electronmicrographs of elytral sculpture of species of *Cicindela* (*cylindera*) (orientation same as for fig. 36).

A. *Cicindela terricola* (X 202)

B. *Cicindela cinctipennis* (X 202)

determining relationships. Two of the groups contain species not now included in *Cylindera*, placing doubt on the entire arrangement. The treatment does underline how diverse the Nearctic species are. It is possible that they do not form a natural grouping. *C. viridisticta* has the same body form and elytral sculpture as *cinctipennis* but differs greatly in chaetotaxy and aedeagal form. No other species known to me resembles *cinctipennis*. Its relationships might best be sought among Palearctic species.

Subspecies. I recognize five subspecies of *C. cinctipennis*, one of which has not yet been formally described (I have examined a series of the new subspecies in the AM).

C. c. cinctipennis LeConte. Maculation consisting of complete submarginally located marginal band, humeral and apical lunules, and middle band; color variable: black, brown, or green. Range: western Great Plains from S. Alberta and Saskatchewan (Wallis, 1961) south to N.NM and NE.AZ (AM and NM specimens); eastern limits poorly known. I have seen specimens from NW.CO, NW.NE, and S.WY, but Willis (1970), Drew and Bartholemew (1962), and Gaumer and Murray (1971) stated the species to be absent from KS, OK, and TX, respectively. Type locality: "near Rocky Mountains (LeConte, 1848)."

C. c. continua Knaus. Maculation consisting of humeral and apical lunules, middle band expanded marginally and reaching apical lunule, marginal band absent; color variable: brown or blue.

Range: SE.CA, CW.NV. Type locality: CA. San Bernardino Co., San Bernardino Mountains, Baldwin Lake near Pine Knot (Knaus, 1922).

C. c. imperfecta LeConte. Treated beyond.

C. c. lunalonga Schaupp. Maculation variable, usually with slender humeral and apical lunules and middle band, marginal line absent; color variable: black, brown, or green. Range: CA (specimens seen or recorded in literature from Mono, Sierra, Tulare, and Tuolumne Cos.--an AM specimen from CA. Lassen Co., Facht is identified as *lunalonga* but is actually *imperfecta*), NV (Reno), AZ (Prescott), and Baja, California (Sierra San Pedro Martir--Cazier, 1954). Includes as synonyms: *tularensis* Casey, *tuolumnae* Leng, and *wagneri* Cazier.

C. c. n. ssp. Rumpp. Immaculate; color black. Range: restricted to CA. Inyo Co., Owens Valley.

C. c. imperfecta LeConte, 1851

(Fig. 22W, 72)

Cicindela imperfecta LeConte, 1851, Ann. Lyc. Nat. Hist. New York, 5:171.

Cicindela cinctipennis var. *imperfecta* LeConte. Schaupp, F. S., 1883-1884, Bull. Brooklyn Ent. Soc., 6:96-97.

Cicindela pusilla imperfecta LeConte. Horn, W., 1908-1915, Gen. Insect., 82:1-486.

Diagnosis. Elytral coloration variable, usually dull brown, but also black, green, and blue-green; maculation consisting of complete humeral and apical lunules, middle band, and connective between humeral lunule and middle band, marginal band absent.

Synonymic notes. LeConte (1851) described *C. imperfecta* as a full species. Schaupp (1883-1884) considered it a variety of *C. cinctipennis*, in effect giving it subspecific rank. Leng (1902) retained *imperfecta* as a distinct species but suggested that more material than was available to him might lead him to treat it as a geographic race of *C. cinctipennis*. W. Horn (1908-1915) and subsequent authors have used *imperfecta* as a subspecies of an expanded *C. pusilla*.

Typology. LeConte (1851:171) gave the type locality as "California borealis." I take this to be the state of California as opposed to Baja California, Mexico. LeConte's list of localities and corresponding dates of collection are unclear in determining the actual source of the type specimen. Presumably, the holotype, if still extant, is in the LeConte Collection, Museum of Comparative Zoology, Harvard University.

Variation. This subspecies varys widely in elytral color, dull brown being the most common coloration, but with green, blue-green, and black individuals also known. A larva

I collected WA. Grant Co., 6.4 Km E Beverly was subjected to 100% humidity at temperature averaging 24° C when the adult ecloded. Final coloration developed by the imago was green, suggesting that the green morph results from high soil moisture following eclosion. This is a result I have found in *C. longilabris* and *tranquebarica* and agrees with some conclusions reached by Shelford (1918).

Macular extent of this subspecies is quite constant. However, intensity varies, some specimens appearing immaculate unless subjected to microscopic examination under reflected light.

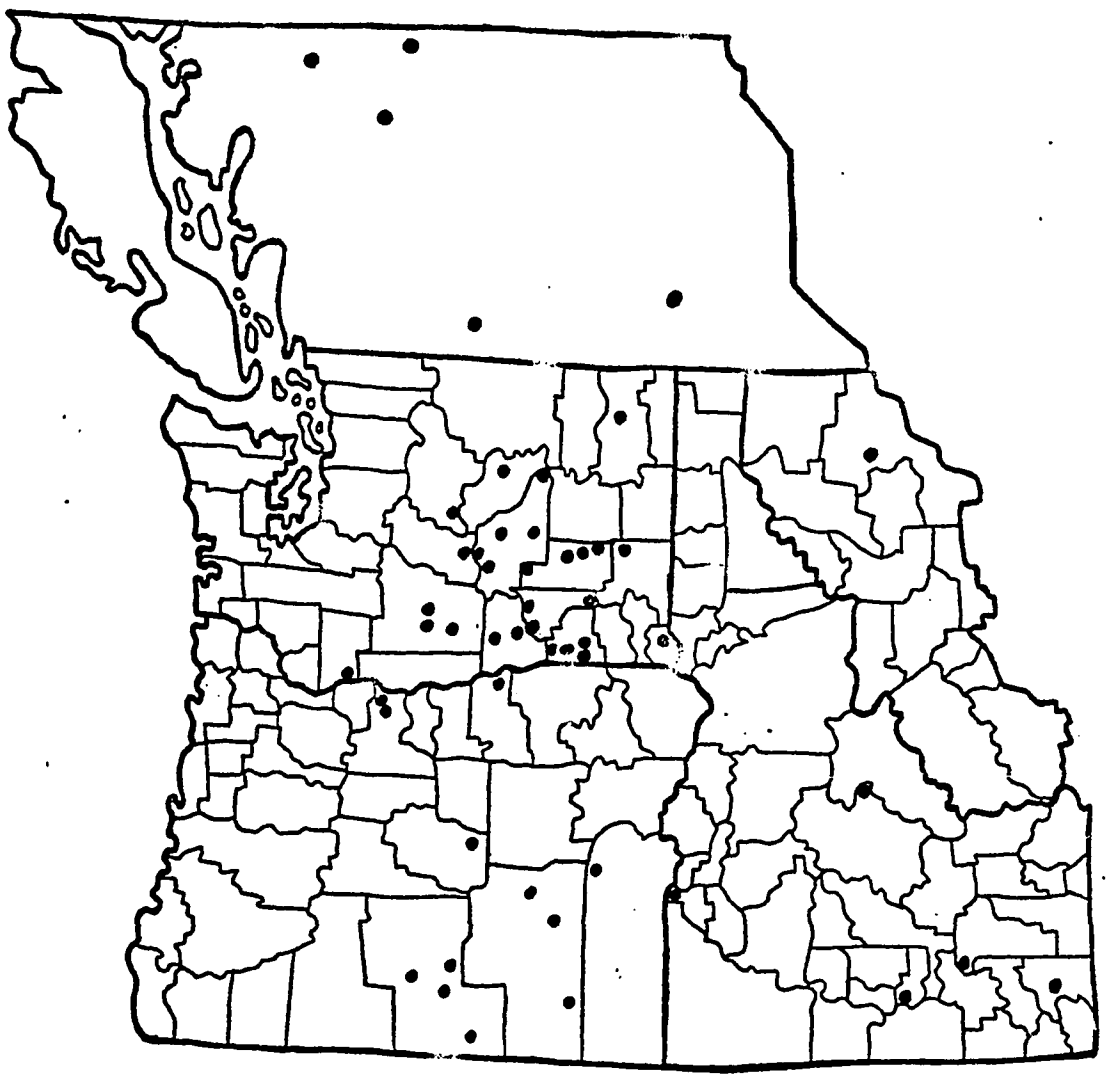
Dates of occurrence. Leffler and Pearson (1976) gave the following dates for adults: 16 May-18 August. Most of the records are for June. I have collected full-sized L3 in May and a young L2 in early July. These larval dates, winter diapause as L3 and late spring oviposition, would correlate with a Life History Pattern B.

Intergrades. I have examined specimens in the AM from S. WY, finding *C. c. cinctipennis* ranging west as far as Carbon Co., Baggs, and Sweetwater Co., Green River. I have studied *imperfecta* from localities in Bear Lake Co., Idaho. Specimens in which the marginal band is present but interrupted between the middle band and apical lunule have been seen from WY. Sweetwater Co., 26 mi S Green River and Uinta Co., Fort Bridger. This region of S.WY appears to form a zone of intergradation and perhaps dispersal for other species, mountains to the north and south probably restricting such species movements. Species so affected include

C. decemnotata, nebraskana, and *purpurea,* in addition to *C. cinctipennis.*

Range. The Pacific Northwest distribution is presented in fig. 72 and Appendix I. La Rivers (1946) and Tanner (1929) respectively gave NV and UT localities but these need review against the possibility that other subspecies might be included. I have seen a specimen (AM) from CA. Lassen Co., Facht. The remainder of the CA range is unreported.

Fig. 72. Pacific Northwest distribution of *Cicindela cinctipennis imperfecta*. See Appendix I for tabulation of localities.



SOIL ANALYSIS

Rationale

I contend that edaphic factors are among the most important limits in defining tiger beetle habitats. The female adult chooses oviposition sites. Also, the entire larval stage is passed in a burrow. Many species are restricted to soils of particular types, clayey, sandy, or alkali-encrusted, among others. In conference with Dr. Fiorenzo Ugolini, I have chosen three soil parameters to aid in defining the soil types inhabited by Pacific Northwest cicindelid species.

pH. Tiger beetle habitats range from acid podzolic soils of forested lands to the extremely alkaline soils on the shores of alkaline bodies of water. pH measured directly in the field is subject to fluctuations resulting from temperature and moisture changes. Therefore, in the interest of uniformity, I have tested air-dried samples in the laboratory. Although minor changes in pH may occur during the process of air-drying from loss of volatile gases, chemical changes, and decomposition of organic matter, uniformity in technique under laboratory conditions hopefully minimizes them.

Electroconductivity. A mesaure of the amount of soluble ions in a given soil is found by determining electroconductivity. Surface horizons of a pozol subject to high precipitation will have fewer ions than an alkaline, xeric soil. Although an electroconductivity test does not identify the various ions or measure their proportions, such refinements are of little significance because local lithic features vary widely over the range of a given tiger beetle species.

Particle size and distribution. Sandy soils have large pores which are few in number compared with clayey soils. They do not form aggregates unless cemented. Such a soil is dry unless in close contact with water. Thus, a sandy soil may be a limiting factor to a hydrophilous species. A species must be specially adapted to the dry conditions to which a sandy soil far from water subjects it. Also, a larva must be able to produce artificial aggregation of the particles of the burrow walls to keep the burrow from collapsing. Such species secrete material, perhaps saliva, as they dig their burrows. This secretion maintains the integrity of the burrow wall so well that parts of the burrow may remain intact as it is dug up.

Poorly aggregated silt soils are non-porous and compact. These factors make such soils unsuitable to tiger beetles unless wet. Because of the tendency for silt soild to puddle, a larva is subjected to flooding of its burrow.

Clay soils tend to form aggregates and have greater porosity per unit volume compared with sandy soils. Aggregated clay soils are friable and easily worked and retain their structure unless disturbed. A large number of tiger beetle species are associated with clay soils.

Elaboration on the types of soils represented in my samples is irrelevant to this study but here is a brief statement on the basis of soil textural classes for the reader's benefit. Brady (1974: 45-49) summarized the now standard United States Department of Agriculture Classification System:

Sand. Soils in which sand comprises 70% or more by weight.

Clay. Soils in which clay comprises at least 35% by weight.

Loam. Soils in which neither sand nor clay predominate.

Particle size and distribution are measured by several methods. Most are based on Stokes' Law which states that velocity of a particle falling through a liquid column is directly proportional to the size of the particle, the largest particles falling fastest. I used the Hydrometer Method, a process which sorts soil particles into classes based on size.

Results

I have collected at least one soil sample for 19 of the 24 Pacific Northwest species. Samples for *Omus californicus*, *Cicindela amargosae*, *lengi*, *plutonica*, and *tenuicincta* were not collected. In all, 37 samples were analyzed. Results are presented in Table 82.

Species Accounts

Omus dejeani. Three of the four samples are clayey soils. The remaining sample (WA. Thurston Co., Rocky Prairie) is loamy sand, a glacial outwash area with a thin layer of poorly sorted ice-smoothed pebbles, soil, and humus overlying compacted gravel. The soil becomes soupy when wet and very hard when dry. The large amount of humus probably produces properties otherwise caused by clay.

O. audouini. See numbers for *O. dejeani*. The two species are frequently found in the same general vicinity but not together. *O. audouini* prefers exposed situations, whereas *O. dejeani* lives in closed-canopy situations.

Cicindela oregona. This species inhabits a full range of soil classes, emphasizing its eurytopy. It is also tolerant of a wide range of pH and ion concentrations.

C. depressula. Two samples for *C. d. depressula* ranged from loam to clay. Samples for *C. d. eureka* were not studied but this subspecies inhabits riparian sand bars, a habitat distinct from the dry, bare areas at high elevations inhabited by *C. d. depressula*.

C. repanda. This species distinctly prefers soils tending toward sand. It is also highly tolerant of high pH and ion concentrations, although I have never found it on salt-pan. Larval burrows are always located on sand near water's edge or among scattered grasses where the moisture or roots help maintain the integrity of the burrows.

C. hirticollis. The analyses showed a range from sand to clay. Habitat of this species is ordinarily sand bars or aeolian dunes. Riparian sand bars are largely sand, whereas aeolian dunes would be expected to contain a high percentage of finer particles... I have found larvae in wet sand but, also, in protected depressions in dunes dry at the surface but with a high water table.

C. arenicola. Samples represent two of the three localities comprising this species' entire range. It inhabits aeolian dunes whose high clay content may maintain the integrity of the larval burrows. These are also wet dunes, dry at the surface but with a high water table.

C. columbica. Only one sample was available because most of the habitat of this species has been destroyed. The one sample is from a riparian sand bar. Larvae were not found but presumably the wetness from the adjacent Snake River helps maintain the burrows.

C. bellissima. Two samples, both from ocean dunes, were studied. One is nearly pure sand, the other quite clayey. Larvae are found near low, sparse vegetation, and their burrows extend into the wet soil beneath the dry surface layer.

C. decemnotata. Only one sample was available for this rare species. It consists of silt loam. The soil is apparently well-drained as evidenced by flourishing *Artemisia tridentata*. This soil becomes extremely compacted beneath a deep surface layer of dust from June to August, limiting the species activities to times of precipitation.

C. purpurea. Two samples each for *C. p. audubonì* and *C. p.* new name Leffler were studied. The former is found on loamy to clayey soil and the latter on loamy sand. The latter inhabits glacial outwash prairies in Washington, discussed under *O. dejeani*. The extremely low pH of the sample from WA. Whitman Co., Pullman may reflect the large quantities of chemical fertilizers used for crops in the Palouse,

C. pugetana. Both available samples are loam, both with a rather large percentage of particles greater than 2 mm. diameter (23.44% and 15.44% respectively). Both localities are heavily grown to *Artemisia tridentata* and have a large portion of the area covered by basalt outcroppings, indicating well-drained local pockets of shallow, poorly-sorted loamy soil.

C. longilabris. All five available samples are clayey soils, generally well into the clay range. The samples average low in percentage of sand ($\bar{X}$ of % of sand for five samples is 28.6% compared with 50.7% for *C. nebraskana)*.

C. nebraskana. All five available samples are sandy clay, remarkably similar in components considering the extensive geographic distribution represented. They are near the low end of the clay range compared with the samples for *C. longilabris*. See remarks for *C. longilabris* also.

C. parowana. The one available sample for this rare species has a high electroconductivity but does not really reflect the halophilic tendencies of the species.

C. tranquebarica. Like *C. oregona*, this species inhabits all soil types and with a wide range of pH and ionic concentrations. I have found larvae in soild ranging from sand to clay. Those from sand are found near vegetation or on wet soil. I have never found larvae on open dunes; even adults are rare in such situation.

C. willistoni. Rumpp (1967) recorded this species from ID. Owyhee Co., Bruneau Dunes St. Park. This is atypical habitat and perhaps the species visits the area only temporarily from adjacent, more suitable habitat. Willis (1967) discussed this species' habits at length, regarding it as a true halophile. I agree based on my personal experiences at localities in California, Idaho, New Mexico, and Utah. The other sample (ID. Owyhee Co., 7.8 km N. Bruneau) was taken from a flat area heavily encrusted with salts and grown to *Distichlis* and *Sarcobates*. The salt is reflected in the extremely

high pH and electroconductivity readings. Wet lake shores are typical habitat. This locality is near although not adjacent to the Snake River, but the entire area has a high water table.

C. haemorrhagica. At WA. Walla Walla Co., 4.0 km E. Wallula Jct., larvae were collected from the non-alkaline well-drained low bluff on the south edge of the Walla Walla River, in a mixed aggregation with *C. decemnotata* larvae. Other samples for this species are sandy to loamy, frequently with an alkaline crust, and reflect this species' usual halophily.

C. cinctipennis. This is a halophile and inhabits sandy to loamy soil, often alkali-encrusted, and with grasses for shelter for the adults and soil stability afforded by the roots for larval burrows.

Correlation Between Proportions of 2nd gonapophysis and Soil Particle Size Distribution

The chelicerate 2nd gonapophyses (terminology following Freitag, 1966) of the ovipositor are used in digging the egg burrow (Willis, 1967, and personal observation of *Cicindela purpurea* and *Omus dejeani* in captivity). The 2nd gonapophysis resembles a mitten, with a fixed, short, dorsal and medial "thumb" and a movable (dorsoventral direction), long, ventral and lateral "finger" portion. Freitag (1966, 1972) and Tanner (1927) may be consulted for homologies and terminologies of the various parts (Freitag's terminology supersedes that of Tanner). The presence of the two styli is unique among Adephaga and probably among beetles in general, based on Tanner's description of 66 families, other groups lacking the short, fixed stylus ("thumb"). The 2nd gonapophyses act to physically pick up and move soil particles.

Differences in proportions of the movable stylus among several species led me to hypothesize about a possible correlation between the proportions of the stylus (ratio, basal breadth/length) and the size of the particles in the soil. I had observed that in species living in sandy soil the stylus was long and narrow, and in those found on clayey soils the stylus is short and broad. I was able to correlate stylus proportions and soil particle size for 15 species. Proportions are presented in Table 82 and soil particle size distributions are presented in Table 82. Labelled examples of the extremes of styli are shown in Fig 73.

In order to test the hypothesis that stylus proportions are correlated with soil particle size distribution, I performed a discriminant analysis using four means for each of the 15 species: ratio, stylus basal breadth/length; percentage of sand in soil sample; percentage of silt in soil sample; and percentage of clay in soil sample.

The results of the discriminant analysis are as follows:

Type of Soil	Correlation %
Sand	91
Silt	78
Clay	98

Thus, there is excellent correlation between stylus proportions and the percentages of sand, silt, and clay in the soil. The lower correlation for silt is to be expected because silt particles are intermediate in size (>.05 mm.) and clay (<.02 mm.). The conclusion to be reached is that species with long, narrow styli are found in soils with a high proportion of sand, and those with short, narrow styli inhabit highly

clayey soils. A cautionary note: specimens for examination must be chosen with regard to the time of year (those closest to the time of eclosion although not necessarily teneral or at least early during the time of oviposition) because digging activitiy wears down the styli altering the proportions and giving misleading results.

The results presented here are preliminary. Samples are small because accurate measurement requires a completely extruded ovipositor, a condition infrequently found in museum specimens. Also, I pooled all subspecies in order to build as large of sample sizes for each species as possible. Probably, if subspecies of *Cicindela depressula*, *purpurea*, and *tranquebarica* could be considered separately, for example, differences could be found and further refinements in developing this line of evidence made.

Table 82. Ratios, basal breadth/length of styli of 2nd gonapophysis in 15 species of Pacific Northwest Cicindelidae (subspecies pooled).

SPECIES	N	Ratio (Range and $\bar{X}$) in %
Omus dejeani	2	64.52 - 67.57 (66.05)
O. audouini	1	(54.84)
Cicindela oregona	3	24.56 - 32.76 (28.28)
C. depressula	5	40.74 - 52.17 (46.38)
C. repanda	5	36.11 - 58.11 (44.25)
C. bellissima	2	37.50 - 40.74 (39.13)
C. arenicola	1	(48.00)
C. decemnotata	1	(62.50)
C. pugetana	2	52.00 - 66.67 (59.34)
C. purpurea	7	47.22 - 65.22 (55.12)
C. longilabris	6	48.44 - 71.15 (56.75)
C. nebraskana	6	44.83 - 66.67 (56.95)
C. parowana	2	38.10 - 46.43 (42.27)
C. tranquebarica	4	42.86 - 64.71 (55.02)
C. haemorrhagica	5	50.00 - 55.00 (52.97)

Table 82. Results of soil analyses for Pacific Northwest tiger beetle collecting sites.

Abbreviations:
L. = Loamy
S. = Sandy
S.C. = Sandy Clay

SPECIES	LOCALITY	pH	EC	% sample > 5 mm.	% sample 2-5 mm.	% sample < 2 mm.	% <2 mm. Sand	% <2 mm. Silt	% <2 mm. Clay	Soil Class
O. dejeani	1. WA King Co., Seattle, Univ. WA Campus	4.74	30.0	1.59	21.68	76.73	33.40	16.60	50.00	Clay
	2. WA Thurston Co., Rocky Prairie	7.34	20.0	11.84	5.19	82.97	92.55	8.35	9.10	L. Sand
	3. OR Marion Co., 3.5 km W Mill City	5.02	21.5	1.30	3.22	95.48	47.50	5.40	47.10	S. Clay
	4. OR Douglas Co., 5.7 km S Curtin	4.96	25.5	1.18	19.03	79.79	51.10	4.90	44.00	S. Clay
O. audouini	1. WA King Co., Seattle, Univ. WA Campus	4.74	30.0	1.59	21.68	76.73	33.40	16.60	50.00	Clay
	2. WA Thurston Co., Rocky Prairie	7.34	20.0	11.84	5.19	82.97	82.55	8.35	9.10	L. Sand
C. oregona	1. BC 31.7 km W Creston	6.15	35.5	7.21	7.41	85.38	56.40	9.50	34.10	S.C. Loam
	2. BC 11.7 km N Creston	5.43	46.0	14.31	24.74	60.95	50.00	4.80	45.20	S. Clay
	3. WA King Co., 10.7 km W Steven's Pass	5.25	39.0	0.83	1.21	97.96	64.85	29.99	5.16	S. Loam
	4. WA Chelan Co., 24.4 km W Cole's Corner	4.63	18.5	0.70	2.87	96.43	16.30	30.30	53.40	Clay
	5. WA Grant Co., 1.8 km E Beverly	7.97	900.1	0.00	0.00	100.00	11.00	69.00	20.00	Silt Loam
	6. WA Grant Co., 6.7 km E Beverly	7.30	80.1	0.00	0.00	100.00	96.25	2.45	1.30	Sand
	7. WA Walla Walla Co., 0.8 km W Touchet	8.54	152.9	0.98	8.86	90.16	32.50	52.70	14.80	Loam
	8. WA Adams Co., 16.7 km W Washtucna	7.13	88.1	0.00	0.05	99.95	92.53	4.75	2.72	Sand
	9. OR Klamath Co., 18.9 km E Daisy	5.71	45.4	2.34	12.40	85.26	45.70	31.00	23.30	Loam
	10. ID Owyhee Co., 27.9 km S Nampa	7.25	275.1	0.00	0.00	100.00	77.70	15.55	6.75	L. Sand
	11. ID Owyhee Co., Bruneau Dunes St. Pk.	7.05	39.1	0.00	0.00	100.00	78.00	15.25	6.75	L. Sand
C. depressula	1. WA King Co., 10.7 km W Steven's Pass	5.25	39.0	0.83	1.21	97.96	64.85	29.99	5.16	S. Loam
	2. WA Chelan Co., 24.4 km W Cole's Corner	4.63	18.5	0.70	2.87	96.43	16.30	30.00	53.40	Clay

Table 82 (continued)

SPECIES	LOCALITY	pH	EC	% sample > 5 mm.	% sample 2-5 mm.	% sample < 2 mm.	%<2 mm. Sand	%<2 mm. Silt	%<2 mm. Clay	Soil Class
C. rapanda	1. WA Grant Co., 6.7 km E Beverly	7.30	80.1	0.00	0.00	100.00	96.25	2.45	1.30	Sand
	2. WA Walla Walla Co., 0.8 km W Touchet	8.54	152.9	0.98	8.86	90.16	32.50	52.70	14.80	Loam
	3. ID Idaho Co., vicinity Slate Creek	7.55	36.5	0.00	0.07	99.93	78.20	16.70	5.10	L. Sand
	4. ID Owyhee Co., Bruneau Dunes St. Pk.	7.05	39.1	0.00	0.00	100.00,	78.00	15.25	6.75	
C. hirticollis	1. WA Grant Co., 6.7 km E Beverly	7.30	80.1	0.00	0.00	100.00	96.25	2.45	1.30	Sand
	2. ID Idaho Co., vicinity Slate Cr.	7.55	36.5	0.00	0.07	99.93	78.20	16.70	5.10	L. Sand
	3. ID Fremont Co., St. Anthony Dunes	7.33	30.1	0.00	0.00	100.00	48.60	9.20	42.20	S. Clay
C. arenicola	1. ID Owyhee Co., Bruneau Dunes St. Pk.	7.05	39.1	0.00	0.00	100.00	78.00	15.25	6.75	L. Sand
	2. ID Fremont Co., St. Anthony Dunes	7.33	30.1	0.00	0.00	100.00	48.60	9.20	42.20	S. Clay
C. columbica	1. ID Idaho Co., vicinity Slate Creek	7.55	36.5	0.00	0.07	99.93	78.20	16.70	5.10	L. Sand
C. bellissima	1. WA Clallam Co., Makah Bay	6.69	12.0	0.00	0.00	100.00	30.06	39.88	30.06	C. Loam
	2. OR Curry Co., 18.4 km S Gold Beach	6.55	14.0	0.00	0.00	100.00	95.04	2.33	2.63	Sand
C. decemnotata	1. WA Walla Walla Co., 4.0 km E Wallula Jct.	6.72	37.0	0.00	0.18	99.82	10.50	73.70	15.80	Silt Loam
C. purpurea	1. WA Pierce Co., Roy Prairie	7.35	34.9	1.80	5.62	92.58	82.58	8.39	9.03	L. Sand
	2. WA Thurston Co., Rocky Prairie	7.34	20.0	11.84	5.19	82.97	82.55	8.35	9.10	L. Sand
	3. WA Columbia Co., 15 km SE Starbuck	7.42	38.2	0.87	0.75	98.38	36.50	54.30	9.20	Silt Loam
	4. WA Whitman Co., Pullman	4.35	56.5	0.77	4.59	94.64	33.40	11.00	55.60	Clay
C. pugetana	1. WA Kittitas Co., 23.4 km E Ellensburg	6.17	47.8	12.06	11.38	76.56	50.20	34.50	15.30	Loam
	2. WA Grant Co., 8.3 km SW George	6.22	20.0	8.02	7.42	84.56	48.50	39.80	11.70	Loam

Table 82 (continued)

SPECIES	LOCALITY	pH	EC	% sample > 5 mm.	% sample 2-5 mm.	% sample < 2 mm.	%<2 mm. Sand	%<2 mm. Silt	%<2 mm. Clay	Soil Class
C. longilabris	1. BC 11.7 km N Creston	5.43	46.0	14.31	24.74	60.95	50.00	4.80	45.20	S. Clay
	2. WA King-Chelan Co., Steven's Pass	4.68	30.5	7.02	16.67	76.31	12.60	28.80	58.60	Clay
	3. WA Chelan Co., 24.4 km W Cole's Corner	4.63	18.5	0.70	2.87	96.43	16.30	30.30	53.40	Clay
	4. OR Grant Co., Dixie Pass	5.60	31.0	3.07	4.77	92.15	42.00	16.10	41.90	S. Clay
	5. MT Jefferson Co., Homestake Pass	4.94	26.5	10.47	29.29	60.24	22.20	24.80	53.00	Clay
C. nebraskana	1. BC 11.7 km N Creston	5.43	46.0	14.31	24.74	60.95	50.00	4.80	45.20	S. Clay
	2. WA Chelan Co., 31.2 km S Leavenworth	5.74	19.8	2.04	4.67	93.29	55.60	8.40	36.00	S. Clay
	3. WA Kittitas Co., 2.5 km S Send Lake Katches	5.72	17.5	9.70	11.39	78.91	43.40	12.10	44.50	S. Clay
	4. WA Kittitas Co., 12.5 km SE Cle Elum	5.40	40.9	4.47	11.31	84.22	60.20	17.80	39.80	S. Clay
	5. ID Fremont Co., 18 km N Ashton	5.62	33.0	13.80	18.48	67.72	44.40	16.00	39.60	S. Clay
C. parowana	1. WA Grant Co., 6.7 km E Beverly	7.30	80.1	0.00	0.00	100.00	96.25	2.45	1.30	Sand
C. tranquebarica	1. BC 6.7 km N Canal Flats	8.06	309.0	0.00	0.00	100.00	76.10	12.00	11.90	L. Sand
	2. WA Chelan Co., 24.4 km W Cole's Corner	4.63	18.5	0.70	2.87	96.43	16.30	30.30	53.40	Clay
	3. WA Kittitas Co., 11.7 km E Easton	5.30	26.2	5.33	4.48	90.19	68.60	18.80	12.60	L. Sand
	4. WA Grant Co., 6.7 km E Beverly	7.30	80.1	0.00	0.00	100.00	96.25	2.45	1.30	Sand
	5. WA Adams Co., 16.7 km W Washtucna	7.13	88.1	0.00	0.05	99.95	92.53	4.75	2.72	Sand
	6. OR Marion Co., 3.3 km E Gates	6.00	71.6	28.81	30.52	40.67	51.20	25.80	23.00	S.C. Loam
	7. OR Grant Co., Dixie Pass	5.60	31.0	3.07	4.77	92.15	42.00	16.10	41.90	S. Clay
	8. ID Owyhee Co., Bruneau Dunes St. Pk.	7.05	39.1	0.00	0.00	100.00	78.00	15.25	6.75	L. Sand
	9. ID Fremont Co., St. Anthony Dunes	7.33	30.1	0.00	0.00	100.00	48.60	9.20	42.20	S. Clay
C. willistoni	1. ID Owyhee Co., 7.8 km N Bruneau	10.07	9090.0	0.00	0.00	100.00	3.00	69.80	27.20	Silt Loam
	2. ID Owyhee Co., Bruneau Dunes St. Pk.	7.05	39.1	0.00	0.00	100.00	78.00	15.25	6.75	L. Sand

Table 82 (continued)

SPECIES	LOCALITY	pH	EC	% sample > 5 mm.	% sample 2-5 mm.	% sample < 2 mm.	%<2 mm. Sand	%<2 mm. Silt	%<2 mm. Clay	Soil Class
C. haemorhagica	1. WA Grant Co., 1.8 km E Beverly-	7.97	900.1	0.00	0.00	100.00	11.00	69.00	20.00	Silt Loam
	2. WA Grant Co., 6.7 km E Beverly	7.30	80.1	0.00	0.00	100.00	96.25	2.45	1.30	Sand
	3. WA Adams Co., 16.7 km W Washtucna	7.13	88.1	0.00	0.05	99.95	92.53	4.75	2.72	Sand
	4. WA Walla Walla Co., 4.0 km E Wallula Jct.	6.72	37.0	0.00	0.18	99.82	10.50	73.70	15.80	Silt Loam
	5. WA Walla Walla Co., 0.8 km W Touchet	8.54	152.9	0.98	8.86	90.16	32.50	52.70	14.80	Loam
	6. ID Owyhee Co., Bruneau Dunes St. Pk.	7.05	39.1	0.00	0.00	100.00	78.00	15.25	6.75	L. Sand
	7. ID Owyhee Co., 7.8 km N Bruneau	10.07	9090.0	0.00	0.00	100.00	3.00	69.80	27.20	Silt Loam
C. cinctipennis	1. WA Douglas Co., 9.9 km NW Leahy Jct.	7.72	2190.0	0.00	0.00	100.00	72.95	4.90	21.15	S.C. Loam
	2. WA Grant Co., 6.7 km E Beverly	7.30	80.1	0.00	0.00	100.00	96.25	2.45	1.30	Sand
	3. WA Walla Walla Co., 0.8 km W Touchet	8.54	152.9	0.98	8.86	90.16	32.50	52.70	14.80	Loam

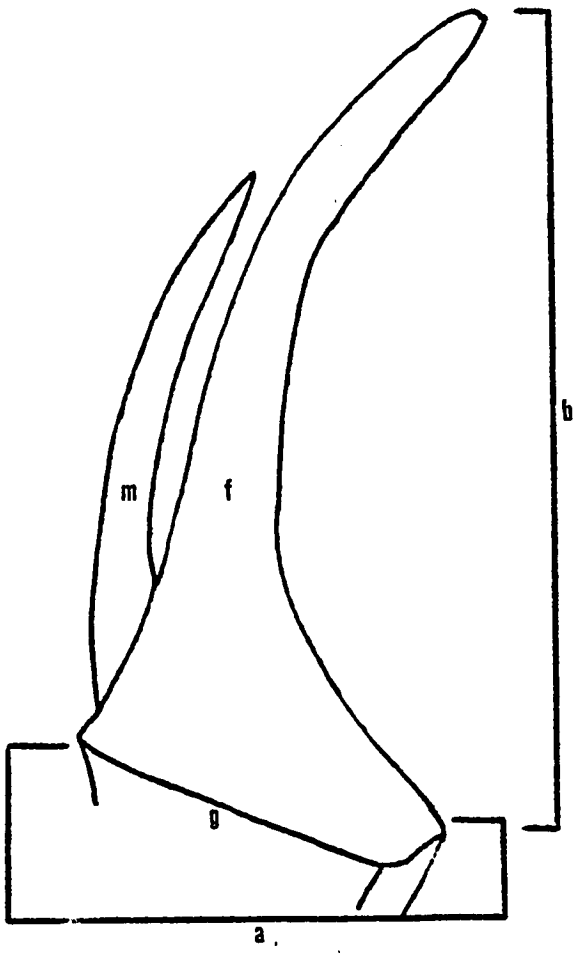
Fig. 73. 2nd gonapophyses of two species of *Cicindela*, ventral view (X 33).

A. *C. oregona*: an example of the long, narrow type correlating with sandy soils

B. *C. nebraskana*: an example of the short, broad type correlating with clayey soils

Legend:

a - basal breadth
b - length
f - fixed stylus
g - apex of 2nd gonocoxa
m - movable stylus
s - seta



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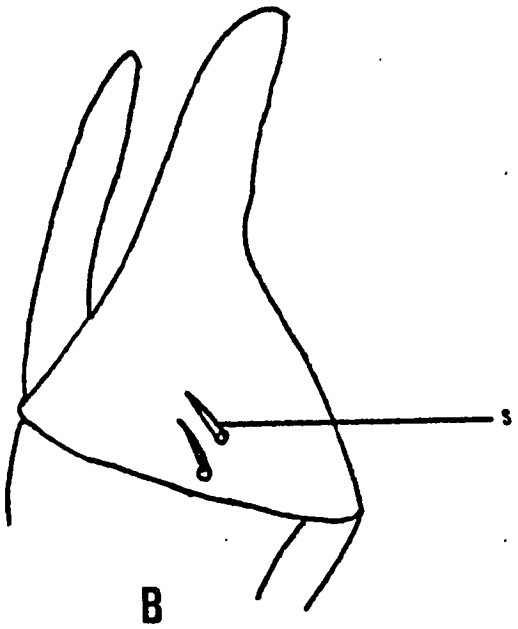


B

BEARING OF HISTORICAL GEOLOGY OF THE PACIFIC NORTHWEST ON CICINDELID DISTRIBUTION

Willis (1967) summarized the negligible Nearctic cicindelid fossil record (Matthews, 1978, has since added an Arctic occurrence). With no meaningful fossil record, dispersal routes must be reconstructed with caution. Hwever, by examining contemporary distributions, geographic variation, and interspecific relationships, and correlating these data with the geological history of an area, some hypotheses as to the direction of dispersal can be developed. I contend that a geological chronology aids in predicting the sequence of events as to when a species might have evolved and entered a particular region, not when it actually did. Therefore, I am reviewing the historical geology of the Pacific Northwest in order to show the various events and environmetns that may have either fostered or hindered cicindelid dispersal and colonization.

A summary of the historical geology of the Pacific Northwest is presented in Appendix III, first an overview, then regional treatments in order to put some of the local occurrences into better perspective along with effects of the more widespread events. I have divided the Pacific Northwest into 14 areas based strictly on convenience and not intended to have anything to do with physiographic provinces, although some coincide. The geological histories of these areas is treated in Appendix III. The present treatment is of the influence on the cicindelid faunas.

1. Southwestern British Columbia including Vancouver Island. Presence of glaciers over all of southwestern British Columbia until 11,000 yBP precluded the existence of any tiger beetles in the region.

Therefore, both *Omus dejeani* and *O. audouini* have entered since that time. Dispersal north of the Fraser River delta has been blocked to northward movement until only 100 years ago, and most of the Coastal mountains are too rugged for any species except *Cicindela depressula* and *longilabris*. Time of entry of *C. oregona* may have occurred at any time during the past 11,000 years since it probably followed the shorelines of Puget Sound and the Pacific Ocean. *C. purpurea* probably entered during the Hypsithermal when there was a northward dispersal of plant species during that time. *C. bellissima* has not become established on Vancouver Island because of a lack of proper habitat. *C. tranquebarica* is to be expected in southwestern British Columbia as it is found in the San Juan Islands. Its presence has possibly escaped detection because of inadequate collecting.

2. Olympic Highlands. *Omus* probably existed throughout the lowland areas throughout the Pleistocene except for parts covered by ice. *C. oregona* also reinvaded newly exposed habitat when available. *C. bellissima* may have existed along the Oregon and southern Washington coast where the ocean moderated the extreme cold of the Pleistocene. After the ice had receded from Cape Flattery, a population became established and developed into *C. b.* n. ssp. Leffler. *C. depressula eureka* may have been present in lowland areas and hybridized with *C. depressula* which was forced to lower elevations by alpine glaciation producing intergrade populations at intermediate elevations in the Hoh and Bogachiel drainages, whereas *C. d. depressula* in pure form could invade the highlands. The heavy rainfall and its effects on drainage and forest growth of the lowlands has destroyed available habitats of

C. d. eureka. *C. longilabris perviridis*, like *C. d. depressula*, was probably forced by alpine glaciation to adjacent lower elevations perhaps on the south slopes of the Olympic Mountains and has since returned to the higher areas as well as remaining in small numbers at intermediate elevations such as at Lake Cushman, Mason Co. Finally, *C. hirticollis* ssp. B is rare in Washington. It is found on sand bars at river mouths along the ocean shore, a habitat scarce on the west side of the Olympic Peninsula.

3. Coastal strip of Washington (excluding Olympic Peninsula) and Oregon. The region has only five cicindelid species. Ancestors of *Omus dejeani* and *O. audouini* may have existed in the area since its Miocene emergence having entered from adjacent land areas. When *Cicindela oregona* became established and from what direction is unknown. *C. bellissima* may have differentiated from an ancestral form after uplift of the Cascades and has existed on the ocean dunes throughout the Pleistocene. The entry point onto the coastal strip may have been by way of the Columbia River. The history of *C. hirticollis* ssp. B may have been similar to that of *C. bellissima*. Its greater abundance in Oregon either reflects a southern origin or more extensive habitat afforded by the larger number of rivers than in Washington.

4. Klamath Mountains and adjacent coast. The Klamath Mountains, which correspond to the Klamath Mountain Physiographic Province *fide* Franklin and Dyrness (1973), is an area of great floral endemism (Whittaker, 1961). The limited cicindelid fauna reflects some of this endemism but the region serves more as a blend zone between two depauperate faunas. Three species of *Omus* are found here: *O. dejeani* and *O. audubonii*

reach their southern limits, and *O. californicus* its northern limit in the coastal mountains. *Cicindela purpurea* extended its range northward to Vancouver Island during the Hypsithermal. Following that time *C. p. lauta* dispersed westward through the Siskiyou Mountains to the ocean from the southernmost Cascades. *C. bellissima* has nearly reached the California border along the coast but has not entered California, although suitable habitat exists. Its presence is perhaps quite recent in origin. *C. tranquebarica vibex* has crossed the Cascades at several points and has become established in the Rogue River Valley. *C. oregona* has probably existed in the area through the Pleistocene but the date and direction of dispersal is obscure. *C. longilabris perviridis* is found in the Cascades as well as the Klamaths. It probably existed *in situ* moving to adjacent lower elevations only in response to advancing Pleistocene alpine glaciers.

5. Puget lowlands. *Omus dejeani* and *O. audouini* and their ancestors had probably inhabited the region throughout the Teritary, adapting to a gradually cooler climate and changes in forest composition from *Metasequoia*-hardwood to *Tsuga-Pseudotsuga-Alnus* associations. During the glaciation, they were shifted southward and have since reinvaded. *Cicindela o. oregona* similarly has entered the area since the glaciation. *C. depressula eureka* may have existed along rivers through the pre-Pleistocene redwood forests and the northern populations have perhaps been able to maintain parts of their range even though the California populations have retained the ancestral habitat preference. *C. purpurea* new name Leffler entered during the Hypsithermal from the south. Its distribution coincides with the areas with climate that is ". . . humid, microthermal (and), with inadequate summer precipitation" as outlined by

Hansen (1947: 50), prairies south of Puget Sound and the San Juan Islands. *C. tranquebarica vibex* crossed the Cascades probably quite recently and has established populations on Whidbey Island and in the San Juan Islands. There are old records for Seattle, but perhaps urbanization has caused extirpation of this species, even though *C. oregona* thrives in vacant lots, parks, and golf courses! *C. longilabris* is found in the San Juan Islands. The large Mt. Constitution population suggests long, successful occupation rather than mere survival of wind-wafted drifters from the mainland.

6. Willamette and lower Columbia Valleys. The cicindelid fauna is the same as that of the Puget Sound lowlands except for three additional species, and the same remarks given for that area apply here, except that displacement by glacial ice did not occur. *Cicindela repanda* and *C. hirticollis* ssp. A have followed the Columbia River from east of the Cascades and have established populations in the Willamette Valley and at and down stream along the Columbia from Portland and Vancouver. *C. bellissima* also appears to have penetrated the Columbia Valley but the present status of its Portland population requires further study.

7. Cascade Range. The Cascades cicindelid fauna is small but consists both of wideranging and characteristically montane forms. The former include: *Omus dejeani* has apparently crossed 923 m. high Snoqualmie Pass for it has been collected in the vicinity of Easton; *Cicindela oregona* is found at several passes; *C. nebraskana chamberlaini* extends to the crest of the central Washington Cascades, has crossed to to the west side at WA. King Co., Red Mountain, and apparently replaces *C. longilabris* throughout the southern Washington Cascades. The montane forms are: *C. d. depressula* found throughout the Cascades, the Washington

and Oregon populations representing a blend of stocks from the north and south; *C. longilabris perviridis* has a disjunct distribution, being absent in the Washington Cascades south of Stevens Pass, an absence I am at a loss to explain, but present again in the northern Oregon Cascades; *C. purpurea lauta* has a distribution at intermediate elevations on the west slope of the Oregon Cascades, and has penetrated northward at least to Skamania Co., WA. *C. p. lauta* and *C. l. perviridis* both extend to California and probably survived *in situ* throughout the Pleistocene or at adjacent lower elevations.

8. Rocky Mountains and adjacent ranges. All of the tiger beetle species are wideranging and have entered the region since the last glaciation. *Cicindela repanda* is restricted to riparian habitats and has followed large rivers probably from the east, perhaps at a time when the upper Salmon River was part of the Missouri River drainage system in the late Pliocene (Anderson, 1947; Hobbs and Miller, 1948). Intergrade populations between *C. o. oregona* and the Rocky Mountain *C. o. guttifera* occur eastward from eastern Idaho, representing a meeting of postglacial expansion of the ranges of both stocks. *C. longilabris* populations of this region are also intergrades, between the narrow-headed stock of the Cascades and Sierras and the broad-headed form of the Rockies. Glaciation separated the two stocks and they have since formed a broad blend zone. In northwestern Alberta, the Rocky Mountain form *C. l. laurenti* contacts the eastern North American *C. l. longilabris* forming intergrade populations, also of stock presumably separated by glaciation. This is the area described by Freitag (1965) where *C. oregona* and *C. duodecimguttata* hybridize, the result of a meeting of glacially-separated stocks. The

dry conifer forest of this region is characteristic habitat of *C. tranquebarica vibex*. Its Pleistocene populations were probably merely shifted southward by advancing glaciation and it has since reinvaded its former range. *C. d. depressula* may have extended into the Canadian Rockies from an Alaskan Pleistocene refugium. There is an as-yet-unverified northern Idaho record for the species, a locality not unexpected in view of the ample suitable habitat between the Idaho locality (ID. Clearwater Co., Elk City) and the Kootenay.

Three other species must be considered for this region although they are not characteristic of it. *C. haemmorhagica* has been collected in Yellowstone National Park. The population undoubtedly originated from the Snake River Plains. Presumably the strong winds so typical of that area have wafted individuals eastward into the high mountains where a viable population thrives on the alkaline soil around hot springs. The eastern edge of southern Idaho is a zone of intergradation between the western *C. nebraskana chamberlaini* and the Great Plains *C. n. nebraskana*. Stock of the latter probably crossed southern Wyoming. Finally, populations of *C. cinctipennis imperfecta* have become established in southeastern Idaho derived from Great Basin stock and inhabiting areas which, if they were not geographically located in the Middle Rockies, would be considered as part of the Great Basin.

9. Wallowa-Blue Mountains. The cincindelid fauna of the area is sparse and easily derived from surrounding areas. The region is part of the zone of intergradation between the Cascades and Rocky Mountains populations of *C. longilabris*. *C. nebraskana chamberlaini* is found in drier, more open forest situations. The wide-ranging *C. oregona* and *C. tranquebarica* are found throughout the region. *C. columbica* is not

properly a member of the fauna of this region because it inhabits riparian sand dunes. However, routing of the Snake River between Idaho and Oregon has enabled the range of this species to make a connection between the middle Snake and Columbia River systems. It may have been a corridor also for dispersal of *C. oregona*, *repanda*, and *hirticollis*. *C. pugetana* has undoubtedly entered the Ochoco Mountains from the Umatilla Basin.

10. Palouse Grasslands. With the clearing of the forestlands, *C. longilabris* and *C. nebraskana* disappeared from the region, although there are numerous specimens collected about 1900. The only other species in the region, *C. purpurea*, inhabits bunchgrass habitat and is even found in agricultural areas.

11. Columbia Basin and Okanogan. Zoogeographically, the Columbia Basin is related to parts of Oregon now included in the Basin and Range Physiographic Province (Hubbs and Miller, 1948) offering a logical source for the tiger beetle species shared between the two regions. Of the ten forms in the Columbia Basin, three are endemic, four are wideranging, one is restricted to the Snake-Columbia drainage, and two are derived from the south. If there was indeed a glacial refugium along the Yakima River drainage it would have been ideally located for the differentiation and survivial of *Cicindela pugetana* and *C. parowana wallisi*. The former developed *in situ* from a *C. purpurea* ancestor. The latter is closely related to the Great Basin form of its species and may have been isolated by uplift of the High Lava Plains of central Oregon, uplift that broke the drainage connectives between the Harney Basin and the Columbia River and perhaps also influenced the Snake

River. It is, however, possible that *C. p. wallisi* entered the Columbia Basin during the Hypsithermal.

C. decemnotata n. ssp. Clifford may have entered the Pacific Northwest during the grassland incursions of the Hypsithermal and now exists only as scattered relict populations, or like *C. p. wallisi* and *C. pugetana*, may have existed *in situ* in a glacial refugium.

Cicindela columbica is restricted to parts of the Columbia, Snake and Salmon River drainages. Wheter it developed along the Columbia River and entered the Snake and Salmon River Canyons after the latter became part of the Columbia drainage pattern in the early Pleistocene or if the reverse is true is unknown. I favor the former hypothesis because if the latter were true, one might expect *C. columbica* populations still existing in southern Idaho. Its origin is from the breakup of a wideranging Rocky Mountain stock, and this breakup must have occurred in the Pliocene when there was a major uplift of the Rockies.

There are four wideranging species *C. oregona repanda hirticollis,* and *tranquebarica*, which are largely riparian. *C. repanda* may represent a rather recent immigrant as it is found only along the Columbia and Snake Rivers and their immediate tributaries and very sparingly in Oregon and California. It may have entered during the Hypsithermal, following the Clark Fork and Snake Rivers, the headwaters of both of which are close to those of the Missouri system. *C. haemorrhagica* and *C. cinctipennis* both have extensive ranges to the south and undoubtedly entered the Northwest during the Hypsithermal. has since evolved a weakly defined northern race, *C. h. nigroides*, which is stable in its characteristics compared with the southerly nominate

race. Intergradation occurs only where incursions of Pluvial Lake Bonneville had extended into southern Idaho, most of the ranges being separated by the Owyhee Uplands and some of the Great Basin ranges.

A single specimen of *Omus audouini* was collected by Dr. L. R. Rogers WA. Benton Co., 16 km. NW Richland, representing a relict population. The Saddle Mountains from whence the specimen came are an eastern continuation of the Simcoe Anticline, the western part of which has a continuation of eastern Cascades flora. The population has probably survived since the early Postglacial when the whole Columbia Basin was more forested.

12. High Lava Plains. Habitat for tiger beetles is sparse in this region, the importance of the area being its nature as a barrier. *C. longilabris* intergrades are known from the Ochoco National Forest.

13. Snake River Plains. Faunally, the Snake River Plains has three components besides some wideranging species. Four forms and, at least originally two others, are derived from the east. The eastern part of the Snake River Plains has two Great Plains forms, *C. lengi versuta* and *C. tranquebarica "kirbyi"*, and two intergrade populations each with an eastern subspecies as one parent stock, *C. oregona oregona* x *guttifera* and *C. nebraskana nebraskana* x *chamberlaini*. The hydrographic boundray between the eastern and western parts of the Snake River Plains coincides with the edge of the zone of intergradation between *C. o. oregona* and *C. o. oregona* x *guttifera* and *C. t. vibex* and *"kirbyi"*. *C. purpurea* and *decemnotata* are widespread but their primary distributions are east of the Rocky Mountains.

A second component consists of six species of predominantly Great

Basin origin. *C. haemorrhagica nigroides* has differentiated from the southern nominate race. *C. cinctipennis* is widespread throughout the Great Basin. *C. plutonica* is a Great Basin form but its peculiar habitat adaptations point to an origin perhaps in some of the western Great Basin mountain ranges. The other three species, *C. parowana*, *willistoni*, and *tenuicincta*, are all associated with the former extents of Pluvial Lakes Bonneville and Lahontan.

C. oregona, *repanda*, *hirticollis*, and *tranquebarica vibex* are all widespread forms. *C. oregona* and *t. vibex* have probably lived in the area for a long time being originally derived from the south or west. *C. repanda* and *hirticollis* are both rather recent immigrants from the east.

C. arenicola is endemic to the Snake River Plains. Its two subspecies are found each in the two parts of the region and the integrade population is found at the hydrographic boundary between the two parts.

14. Great Basin. Only two species are influenced by the drainage basins, the other ten being common to both and having most of their ranges to the south or elsewhere. These include: *C. oregona*, *nebraskana*, *purpurea*, *plutonica*, *decemnotata*, *tenuicincta*, *willistoni*, *haemorrhagica*, and *cinctipennis*. *C. purpurea* and *plutonica* are sympatric in the Fremont National Forest, Klamath Co., Oregon, an area floristically closer to the Cascades although included in the Basin and Range Province *sensu* Franklin and Dyrness (1973).

C. parowana platti is associated with Pluvial Lake Lahontan and, where the outlying parts of that system extend into Oregon, so does the subspecies. A southeastern Oregon population consists of intergrades between *C. p. platti* and the Bonneville form *C. p. parowana*. The two drainages had connections during the early postglacial and the beetles may have interdispersed then or during the Hypsithermal. *C. amargosae* is restricted to the Lahontan system and extends into Oregon following the outlying drainages of that system.

Methods of Cicindelid Dispersal

I postulate 5 dispersal methods for portions of tiger beetle populations.

1. Wind dispersal. In open habitats subject to strong winds, flying beetles are know to be carried long distances; there is no reason to believe this would not be true for tiger beetles. Some species, such as *Cicindela oregona*, have long, sailing flights. Most of the Pacific Northwest species fly fairly close to the ground, decreasing the likelihood of their being caught by wind gusts. Schneider and Kramer (1974), however, showed experimentally that *Cicindela* orients in flight into the wind. Of course, high wind velocity would overcome any efforts by a beetle. Usually during high winds, tiger beetles are loath to fly and often take shelter. Despite such wind avoidance behavior, wind probably has been an important factor in cicindelid dispersal.

2. Walking (or running). It is well-known that larvae leave their burrows upon the advent of unfavorable environmental conditions. On 15 July 1974, I captured one L2 and one L3 *C. oregona* at WA. Benton Co.,

Plymouth, as they crawled upon the open, dry sand dunes. Such behavior enables larvae to seek optimal habitat, and, over a period of time of gradual displacement of habitats, might result in a geographical shift of the population. Adults are also subject to such habitat shifts and, during their daily activities, could walk (or run!) to adjacent areas. Nothing has been reported of homing in cicindelids: if such behavior does not occur and if the new habitat is favorable, the beetles might stay in the new situation (see also no. 5 further on in this section).

3. Swimming. Virtually nothing has been documented of swimming ability of Cicindelidae. I once placed an *Omus dejeani* larva in a container of water finding that it sank immediately and writhed about, showing no swimming ability whatsoever. Bubbles developed over the entire body indicating a hydrophogic integument. The larva was unaffected by more than one hour's submergence. This observation suggests that larvae can survive under water at least short period of time. Although they cannot swim, they might be able to move by wriggling or, perhaps, crawling on the bottom of small ponds or creeks and maybe even survive being washed from their burrows by flooding. This could be a means of short-distance, accidental dispersal.

I have thrown adult *Cicindela repanda* onto the surface of a slow-moving river. They swam buoyantly and quickly back to shore using oar-like motions of the legs. Cazier (1942: 29) stated that *Omus* adults were collected in a reservoir fed by a flume which traversed favorable habitat: the beetles had apparently fallen into the flume during their nightly activities and were carried into the reservoir. Cazier quoted F. W. Nunenmacher who saw *Omus* adults walk into the ocean and crawl under

stones. Cazier suggested that the adults might actually be attracted by water, indicating that streams might be dispersal avenues.

4. Following river courses or shorelines. This has probably been of major importance in the dispersal of riparian and littoral species. Some have undoubtedly followed major river courses in the past and are, presumably, still doing so. The ranges of several Great Basin species correspond with the former shorelines of pluvial lakes. Dune habitat along the Pacific Ocean shore is not completely continuous. *Cicindela bellissima* probably dispersed along the shore, establishing aggregations wherever favorabld conditions occurred.

5. Cycles of formation and destruction of habitat by gradual or catastrophic events. As a biotic community develops through time, it is colonized by a succession of tiger beetle species (Shelford, 1912). Gradual climatic changes can also alter the habitat. Elevation of the Cascades through the middle and late Tertiary changed the floral assemblages east of this range from a mesic conifer-hardwood association to the modern xeric sclerophyll flora. Before the middle Pliocene, the habitat was totally unsuitable for the tiger beetle fauna now living there except for riparian species or those so eurytopic that they could exist in almost any situation. Cycles of gradual formation and destruction of habitat have occurred in the past and are ongoing in the present with corresponding changes in the tiger beetle fauna.

On the other hand, catastrophic events such as vulcanism and large-scale flooding can quickly destroy a habitat, returning it to the lowest level of a seral progression. An entire biota is destroyed and can only recolonize an area when conditions allow. Tectonic events

occurred frequently during the Cenozoic throughout much of the Northwest. The Cascades and the area west of them have been subjected to nearly continuous volcanic activity since the Eocene, and much of the region east of the Cascades was inundated during the middle Miocene by basalt flows. In addition, postglacial eruptions of Glacier Peak and Mt. Mazama led to great accumulations of volcanic ash. Such activity must have had locally devastating effects on the biota, although Kittleman (1973) suggested that conditions at any given time were probably little different than those in parts of Hawaii or Alaska today, for example.

Glacial ice covered much of British Columbia, northern Washington and Idaho, and western Montana, and, in addition, alpine glaciation affected local montane areas of other parts of the Pacific Northwest. The area covered by ice was obviously incapable of supporting permanent life, although adjacent uncovered land probably was inhabited. Evidence exists (Dillon, 1956; Hansen, 1947) that life zones were compressed southward by the advancing ice rather than being destroyed. Thus, the ice had a catastrophic effect on the area it covered, but there has been a gradual recolonization after the ice receded.

Finally, flooding may have occurred on the local level, but nothing could have compared with the effects of the pluvial lakes or the Spokane Flood. The former covered vast tracts of land, and the latter scoured a broad swath of territory in eastern Washington, probably extirpating nearly all life in its path.

Each of these 5 phenomena have occurred alone or in concert to effect cicindelid colonization and dispersal. One or another of the phenomena have affected the distributions of each of the 24 Pacific

Northwest species, but specific hypotheses would be sheer speculation. One can surmise the direction of colonization based on present distributions and, perhaps with some species, even the geological time.

Theoretical Sequence of Cicindelid Colonization of the Pacific Northwest

Details of the distributions of the Cicindelidae of the Pacific Northwest are given elsewhere in the present report, but a brief outline of the range of each species is in order before I present a theoretical sequence of colonization by the several species. Ranges of very few species of Nearctic Cicindelidae have been mapped. A number of regional papers have mapped the various ranges for their respective areas but distributional details are sketchy or lacking for large portions of the ranges of most species. Hence, I must resort to summary of the wholly unsatisfactory range outlines presented by Leng (1902) and Horn (1930) rather than being able to present concise maps. In the following outlines I have made use of numerous references as well as specimens and correspondence. It is often impossible to pinpoint the original source of some of the information, so references are given only when a source of data is definite. The remaining range statements are mainly based on Leng (1902), and Horn (1908-1915, 1930).

Omus dejeani (Cazier, 1942; Leffler and Pearson, 1976). This species is endemic to the Pacific Northwest. It ranges from southwestern British Columbia (including Vancouver Island) south to the Oregon-California border west of the Cascades. Its entire range is presented in map

Omus californicus (Cazier, 1942). This species has a wide distribution in California. *O. c. californicus*, widely distributed in California, barely penetrates southwestern Curry Co., Oregon.

Omus audouini (Cazier, 1942; Leffler and Pearson, 1976). This species ranges from southwestern British Columbia (including Vancouver Island) south to northwestern California and extends into central Washington. Its entre range is presented in maps and

Cicindela oregona (Freitag, 1965). *C. oregona* ranges from Alaska to the Mexican border west of the Rocky Mountains. Its entire range has been mapped by Freitag (1965). There are four subspecies, one of which, *C. o. oregona*, is the most widespread and which is found throughout most of the Pacific Northwest. *C. o. oregona* shows much variation over its range mainly in elytral coloration, suggesting that it has not yet stabilized. It is most closely related to *C. o. maricopa* of the southwestern states. As Freitag showed, the intergrade populations are variable in propleural coloration indicating that the parent subspecies differentiated rather recently. Probably, the direction of *C. o. oregona* into the Pacific Northwest has been from the south, perhaps since the last glaciation. *C. o. oregona* contacts *C. o. guttifera* in the western parts of the Rocky Mountains and intergrades are found in eastern Idaho and western Montana.

Cicindela depressula (Freitag, 1965). This species ranges from southeastern Alaska south to the central Sierra Nevada Mountains of California. Its entire range was mapped by Freitag (1965). There are two subspecies. *C. d. eureka* is a lowland form with disjunct populations in the Puget Sound region, the Willamette Valley, and

northwestern California. Its uniform size, color and maculation suggest an old stable form whose range is probably restricted by the limited number of rivers with extensive sand bars west of the Cascade and Siskiyou Ranges. The rivers that are present are subject to heavy flooding. Perhaps the species had a more extensive range prior to the final uplift of the mountains when rivers were less high-grade and could build up dune deposits and which were less subject to winter and spring floods.

Freitag (1965) considered that *C. d. depressula* represents a merger of two pre-Pleistocene stocks. The Alaskan and Californian populations are less variable than those from Washington and Oregon where the two stocks have merged. Presence of *C. d. depressula* in the Canadian Rockies and its absence in those of the United States indicates that, in this area, it is part of a southward dispersal since the retreat of the Cordilleran glacier after the Pleistocene, a dispersal that has not been completed and which is presumably still under way.

C. d. depressula and *eureka* are in contact at four localities in western Washington and Oregon, all at about 700 m. elevation. The parent stocks are found at higher or lower elevations near all but one of these localities. Only on the Olympic Peninsula is *C. d. eureka* absent, although *C. d. depressula* is present at higher elevations. An intermediate elevation intergrade population may be the result of a meeting of the parent stocks followed by local extinction of *C. d. eureka* perhaps by destruction of suitable lowland habitat following melting of all but the alpine glaciers.

Cicindela repanda. This species is found throughout southern Canada and most of the United States except for much of Oregon, California, Nevada, and Arizona. Most of this range is occupied by *C. r. repanda* which varies little over such a wide region. In view of its scarcity or absence in the far west, it has perhaps dispersed from the east. It has been present west of the Cascades only along theColumbia River and in the Willamette Valley probably only in postglacial times.

Cicindela hirticollis. This species is presently being revised by R. C. Graves (in litt.). Until his study is published, we will not know precisely the geographic and anatomical limits of the several species and subspecies within what is now known as *C. hirticollis*. The various forms collectively range from southern Canada to southern Mexico and from the Atlantic to the Pacific coasts. There are two subspecies in the Pacific Northwest, herein called subspecies A and B.

Subspecies A is generally distributed east of the Cascades on riparian sand dunes. It has followed the Columbia River west of the Cascades but is unknown north or south of this river indicating a recent dispersal.

Subspecies B is restricted to the mouths of rivers entering the Pacific Ocean. It may either represent part of an old stock isolated along the coast by the rise of the Cascades or may be related to *C. h. gravida* of southwestern California. The absence of *C. hirticollis* from the nearly 1200 km. between the ranges of *gravida* and subspecies B makes the latter possibility unlikely. Presence of a different

stock in the Great Valley of California probably also resulted from isolation by uplift of western Mountains, lending further credence to the theory of this type of origin for ssp. B.

Cicindela arenicola (Rumpp, 1967). This species is found on aeolian dunes along the southern Idaho portion of the Snake River and some of its tributaries. Its closest relatives have similarly restricted ranges except for *C. limbata* which extends in a narrow band from Manitoba to Utah. Rumpp (1961, 1967) postulated that the range of a widespread arenicolous ancestor was dissected by various uplifts during the Plio-Pleistocene orogeny of the Rocky Mountains and that *C. arenicola* was isolated at this time. Because of the scattered occurrence of suitable sand dunes, its range is necessarily discontinuous. *C. a. arenicola* is restricted to the St. Anthony Sand Dunes, Fremont Co. and *C. a.* n. ssp. Clifford to dunes immediately northwest of Bruneau Sand Dunes, Owyhee Co. An intergrade population is found on dunes east of Rupert, Minidoka Co. Flooding, including the catastrophic Bonneville flood in early postglacial time, and powerful winds have probably created and destroyed dunes frequently since the Pleistocene. Populations geographically intermediate between those currently existing periodically flourished and died out as the habitats changed. The species may be considered endemic and its entire range is shown on map

Cicindela columbica (Beer, 1971; Leffler and Pearson, 1976; and Rumpp, 1967). This species was restricted to riparian dunes along the Salmon, Snake, and lower Columbia Rivers in Idaho, Oregon, and Washington. It is extinct over most of its range because of habitat

destruction by dams. It is a derivative of the *C. limbata*-group of species. It probably retains an ancestral habitat preference and became restricted to the shores of large, ancient rivers before they formed the deep canyons through which they now flow. The species may be considered endemic and its entire range is shown on map

Cicindela bellissima (Leffler and Pearson, 1976; and Maser, 1973). This species is found on ocean dunes from the northwest tip of Clallam Co., Washington, south to Curry Co., Oregon. There is no proper habitat for it presently on Vancouver Island and it has not been found in apparent suitable situations in northwestern California (Maser, 1973). It probably developed as a coastal isolate from a *columbica*-like ancestor following the Plio-Pleistocene uplift of the Coast Ranges. Perhaps the route of dispersal followed the ancestral Columbia River and from its mouth extended north and south along the coast. Its absence from California may indicate that it reached southern Oregon fairly recently. The nominate subspecies, *C. b. bellissima*, occupies most of the range. It has also been taken at Portland, probably having been carried up the Columbia Valley by wind. *C. b.* n. ssp. Leffler is restricted to Clallam Co., Washington, separated from the populations to the south by about 120 km. of unsuitable habitat. This locality was covered by glacial ice until about 11,000 yBP, so this subspecies has differentiated since that time. The species may be considered endemic and its entire range is shown on map

Cicindela longilabris. This is a polytypic species ranging from the Pacific to the Atlanatic coasts in Canada and the northern United States and extends southward to Arizona and New Mexico through the

Rocky Mountains and to central eastern California through the Cascade and Sierra Nevada Ranges. Much of its present range coincides with areas glaciated during the Pleistocene. Whether it was restricted to refugia during the Pleistocene or has immigrated after having been driven south is unknown, but the latter is most likely. The eastern subspecies shows little variation, whereas some of the western forms are extremely variable. The western forms have probably contacted the eastern ones in British Columbia and Idaho since the glaciation so that characters have not yet stabilized.

C. l. perviridis has a disjunct range, being found in the northern Cascades, San Juan Islands, Olympic Mountains, and from the Oregon Cascades and Klamath Mountains south to the central Sierras (R. L. Huber, in litt., has a specimen from the Santa Rosa Mountains of southwestern California). I cannot explain absence of the form from the Washington Cascades south of Stevens Pass. In this region, it has been replaced by *C. nebraskana*, normally not a montane form. *C. l. perviridis* varies little and has probably existed *in situ* for a long time, its range only being affected by glaciation.

Throughout southeastern British Columbia, eastern Washington and Oregon, Idaho and western Montana, the *C. longilabris* populations are intermediate in proportion and sculpture between the western *perviridis* and *laurenti* of the Rocky Mountains, and extremely variable in color and maculation. This indicates recent contact of the stocks without stabilization. I postulate that the parent stocks were separated by one or another of the Pleistocene glaciations, probably even earlier,

in view of their many differences, and have since recontacted, forming a broad blend zone.

Cicindela nebraskana. This species is parapatric with *C. longilabris*, inhabiting lower elevations or adjacent drier life zones. It is found at moderate elevations in the northwestern quadrant of the continent excluding the coast and extreme northwestern Canada and Alaska. Its range approximates that of *Pinus ponderosa*. It is found with *C. longilabris* at a few localities in eastern Washington and Oregon and northern Idaho and replaces it at high elevations in the southern Washington Cascades. It shows little variation over its wide range and has porbably inhabited it for a long time. The two subspecies are found east and west of the Rocky Mountains with intergrades in southeastern Idaho and western Alberta. Except for the intergrades, only *C. n. chamberlaini* is found in the Pacific Northwest and extends south into Utah, Nevada, and eastern California.

Cicindela purpurea. The species is found throughout the southern half of Canada and all of the contiguous United States except the southern tier of states. I recognize 6 subspecies, generally associated with grasslands.

C. p. audubonì has a wide range west of the Mississippi Valley. Populations west of the Rocky Mountains show none of the melanism common to those east of these mountains. Since, on morphological grounds, *C. purpurea* is ancestral to both *C. pugetana* and *plutonica*, both polychromic species, and, on geographical grounds an *audubonì*-like form is the most likely ancestor, as opposed to the very different *lauta*-group or *cimarrona*, probably the ancestor was also polychromic and,

following isolation from Great Plains stock by the rising Rocky Mountains, the western *audubonì* populations have lost their melanistic tendencies. *C. p. audubonì* is widely distributed throughout southern Idaho and eastern Oregon, but, in Washington, it is known only along the eastern and northern edges of the state and in Kittatas County. Its absence from the rest of the east slope of the Washington Cascades either represents a recent and still-incomplete incursion into the state or insufficient collecting. It contacts the related *C. plutonica* and *pugetana* without hybridization, showing a lengthy phylogenetic separation.

C. p. lauta and *C. p.* new name Leffler are the two subspecies found in or west of the Cascades and Sierra Nevadas. They intergrade in southeastern Shasta County, California, and Jackson County, Oregon. They became separated from the range of the parent stock by the Plio-Pleistocene rise of the Cascades and Sierras. *C. p. lauta* ranges from southern Washington through the Cascades and Siskiyous to northern California. *C. p.* new name Leffler has a disjunct range from southern Vancouver Island, San Juan Island, the Puget Sound prairies, the Willamette and Rogue River Valleys, and the west edge of the central Sierras. I hypothesize that, following the Pleistocene, *C. p. lauta* was restricted to montane situations and *C. p.* new name Leffler was found in adjacent lower elevations in northern California. During the Hypsithermal, *C. p.* new name Leffler was part of the biota that extended northward, and, with the onset of the cooler Late Postglacial, its range became fragmented leaving relict populations. Also, following the Hypsithermal, the Siskiyou Mountains acquired a cooler climate, allowing *C. p. lauta*

to extend westward to the ocean, transecting the range of new name Leffler. A mixture of parent forms and intergrades is present in the Klamath Mountains.

Cicindela plutonica. This species ranges from the Fremont National Forest, southeastern Oregon south to the Central Sierra Nevada Mountains California, and, also, in southwestern Idaho and the Owyhee Uplands of Oregon. The details and limits of its range are poorly known. It probably developed as a southwestern segregate from *C. purpurea* whose range it touches in Oregon and Idaho but from which it is reproductively and ecologically separated.

Cicindela pugetana. This is another segregate of a *C. purpurea* stock which ranges from the Okanagan, British Columbia, south through the Columbia Basin, Washington, and from the Umatilla Basin to the north edge of the High Lava Plains, Oregon. As most of its range was once glaciated or flooded following the glaciation, it may have developed and survived in unforested refugia, perhaps in the rain shadow along the east side of the Cascades if such refugia did, indeed, exist there. Larval, elytral sculpture, and habitat differences suggest long separation from *C. purpurea*, a suggestion also indicated for *C. plutonica*. It was probably wind-wafted to high elevations in the Ochoco Mountains in Wheeler County, Oregon. *C. pugetana* may be considered endemic and its entire range is presented in map

Cicindela decemnotata. This species ranges from southwestern Yukon Territory south to northwestern Nebraska (Willi, 1970: 8), Colorado and Utah. Two subspecies are found in the Pacific Northwest, the nominate form from southern Idaho, and n. ssp. Clifford from southern British Columbia and Washington.

C. d. decemnotata inhabits most of the range of the species and exhibits an erythritic tendency. It intergrades with a third, as-yet-unnamed, subspecies from Utah in northeastern Utah, close to the Idaho border. *C. d.* n. ssp. Clifford shows more of the erythritic tendency of the nominate subspecies. It has not yet been found in Oregon, probably an artifact of collecting. The subspecies probably developed in its present range perhaps following a northward spread of xeric vegetation during the Hypsithermal.

Cicindela parowana. This species is closely related to *C. fulgida*. Willis (1967: 269) postulated that the two evolved from a common ancestor widespread in the western United States and Canada. Its range was divided by the rise of the Rocky Mountains in the late Tertiary. *C. parowana* is divided into three subspecies. *C. p. parowana* inhabits the area around Pluvial Lake Bonneville and *C. p. platti* is found in the vicinity of Pluvial Lake Lahontan and some of thepluvial lakes west and north of it. These two intergrade in southeastern Oregon in an area geographically between the two pluvial lake basins. *C. p. wallisi* is restricted to alkaline soils north of the High Lava Plains, Oregon As the High Lava Plains between Newberry Crater and the Strawberry Mountains have been uplifted recently, I believe their uplift isolated *C. p. wallisi* from the southern populations. Perhaps it, like *C. decemnotata* n. ssp. Clifford and *C. pugetana*, survived glaciation and flooding in refugia, and, since that time, it has extended its range into southcentral British Columbia. The subspecies may be considered endemic and its entire range, along wiht the Pacific Northwest portion of those of its southern relatives, are shown on map

Cicindela tenuicincta. The type locality was given by Schaupp (1884: 122) as Colorado, certainly in error as the species is associated with the basins of Pluvial Lakes Bonneville, Lahontan, Owens, Mathew, Warner, and Chewaucan (Hubbs and Miller, 1948) in Utah, Nevada, California, Oregon and Idaho. Elsewhere in this paper, I have emended its type locality. It probably had a more continuous range but the drying up of the pluvial lakes since the Pleistocene has disrupted its distribution.

Cicindela lengi. This species has an extensive range from southcentral Canada through the Great Plains to central New Mexico. Most of this area is occupied by *C. l. versuta* which extends westward to northwestern Colorado. Its presence in southeastern Idaho is perhaps rather recent as it is known only from near Idaho Falls. Its occurrence in southcentral British Columbia is difficult to explain as the species is unknown elsewhere in the Pacific Northwest. The British Columbia population may be a relict from a Pleistocene refugium.

Cicindela tranquebarica. The species ranges over most of Canada and the continguous United Staes. It is uniform in color and maculation over the eastern part of its range, but the western part has been much dissected by geological events resulting in complex intersections and isolations of the ranges of some of the subspecies. Two and perhaps even three or four subspecies are present in the Pacific Northwest. *C. t. vibex* is a variable form inhabiting almost the entire area except for southeastern Oregon and parts of southern Idaho. It has crossed to the west side of the Cascades at several points in Washington and Oregon and is locally abundant on Whidbey Island and the San Juan Islands although unknown from Vancouver Island.

C. t. "kirbyi" is widespread from northern Canada (Wallis, 1961) south through the east slope of the Rocky Mountains and western Great Plains to Wyoming and the Great Basin. It intergrades with *C. t. vibex* in southern Idaho. Its variability in color and maculation in the Great Basin may have resulted from interbreeding of several stocks as well as incorrect reference of some of the populations to *"kirbyi"*. The truth of the latter possibility depends on a needed revision of the species in the Great Basin. *C. t. admiscens* is found from southern Wyoming south to Arizona and hypothetically may occur in southeastern Idaho. *C. t. moapana* is found over much of western Utah and eastern Nevada. A specimen in the collection of the University of Idaho from "Rea," Idaho is this subspecies, but I cannote locate this locality. Since Pluvial Lake Bonneville, where *moapana* is found, was once hydrographically continuous with the Snake River it is possible that this form may enter Idaho by this route.

Cicindela amargosae (Beer and Maser, 1973; Dahl, 1940; La Rivers, 1946; Rumpp, 1956). The range of this species coincides with the west edge of Pluvial Lake Lahontan and immediately adjacent lake basins in California and Oregon. Most of this area is occupied by *C. a. nyensis* which extends from southcentral Oregon south to Nye Co., Nevada.

Cicindela willistoni (Willis, 1967). This species is composed of 6 subspecies ranging from southwestern Kansas to Arizona and northward throughout the Great Basin to southern Oregon and Idaho, with an isoalted subspecies in southeastern Wyoming. Most of the range was mapped by Willis (1967). There is an east-to-west cline in decreasing pilosity. *C. w. echo*, the Great Basin subspecies, is intermediate in this regard.

This suggests that the original dispersal route was from east to west, a hypothesis in line with the fact that the area from the Great Plains southward through Mexico has the greatest diversity of species of the subgenus *Cicindela* and, thus, is probably the place of origin. *C. w. echo* barely enters southern Oregon and Idaho and has probably entered the Pacific Northwest since the time of the pluvial lakes with whose extent it is associated.

Cicindela haemorrhagica. This is the westernmost member of a wide-ranging species-complex. It ranges from southcentral British Columbia and northwestern Wyoming south from central Washington and southern Idaho through Arizona and New Mexico to Sonora and west to southwestern California. Most of this area is occupied by *C. h. haemorrhagica* with four peripheral subspecies that lack the extreme variability of the nominate form. *C. h. nigroides* is present in the Pacific Northwest and intergrades with *C. h. haemorrhagica* in northern Nevada. *C. h. nigroides* may be considered endemic to the Pacific Northwest and its entire range is presented on map

Cicindela cinctipennis. This species consists of 5 parapatric subspecies ranging over much of southwestern Canada and the western half of the United States excluding the coast. Most of the range belongs to *C. c. cinctipennis*, east of the Rocky Mountains, and *C. c. imperfecta*, from southcentral British Columbia south through the Great Basin. Intergrades are found in southwestern Wyoming (American Museum Collection). *C. c. imperfecta* varies greatly throughout its range in color, size and maculation, and has apparently not yet become stabilized genetically. It probably developed when the Rocky

Mountain uplift divided the range of the ancestral form before the Pleistocene, and has probably dispersed northward into the Pacific Northwest from the Great Basin.

Future Trends and Human Effects

It is perhaps folly to speculate on future cincindelid distribution. Wolfe (1969: 108) stated: "The (biotic) changes that have occurred in the . . . Pacific Northwest during the Neogene indicate strongly that the present associations are also probably transitory." Barring the occurrence of major changes from unforeseen but probable future geological events and ignoring detrimental human influences on the environment, I can make a few predictions as to changes in cicindelid distribution in the northwest over succeeding years:

1. As alpine glaciers continue to recede from lowlands west of Mt. Garibaldi, B.C., *Omus* ssp. will extend their ranges northward along the coast.

2. *Cicindela tranquebarica* will become more widespread west of the Cascades.

3. Both *C. repanda* and *hirticollis* ssp. A will reach the mouth of the Columbia River and then northward and southward along the coast. *C. h.* sspp. A and B will intergrade, resulting in loss of the latter as a distinct subspecies.

4. The prairies south of Puget Sound are rapidly being replaced by forest, and habitat suitable for *C. purpurea* new name Leffler in Washington will be restricted.

5. *C. p. lauta* will extend father north into the Washington Cascades from its present known limit of northern Skamania County

(it may already occur in adjacent montane areas which have as yet been poorly collected).

6. *C. d. depressula* will range throughout much of the United States portion of the Northern Rockies. A still-unsubstantiated Clearwater Co., ID., record suggests that such dispersal has already begun.

7. The area of intergradation of the subspecies of *C. nebraskana* in southern Idaho will increase.

8. *C. limbalis* will follow roadcuts across lower divides across the Northern Rockies into western Montana.

9. *C. punctulata* will range into southern Idaho from Colorado and Utah.

Human influence on habitat is certain to affect adversely some species. *C. columbica* is already extinct over most of its former range because of flooding by dams. Conversion of natural vegetation in the Columbia Basin and Snake River Lava Plains to croplands will affect species such as *C. decemnotata*, *plutonica*, and *pugetana*. Off-road vehicles on beaches, inland dunes, and rangeland damage those habitats.

Human activities have benefited some species. Logging roads up the east slope of the Washington Cascades offer good habitat for *C. nebraskana*. Alkali bee husbandry results in excellent habitat for *C. cinctipennis*, *haemorrhagica*, and *parowana*, and has permitted these to flourish in eastern Walla Walla County, WA., a mesic grassland area otherwise unsuitable for these xeric, halophilic species. Preservation of parts of the Cascade and Olympic Mountains as parks and

primitive areas has permitted large populations of *C. longilabris* and *depressula* to thrive. Protection of Oregon coastal dunes from off-road vehicles protects habitat of *C. bellissima* and *hirticollis*.

Finally, human activities appear to have had little effect on a few species. A viable population of *C. purpurea* inhabits a dirt-bike track and an adjacent lawn on the Washington State University campus. *Omus dejeani* and *audouini* both occur on campuses of Oregon State University and the Universities of Washington and British Columbia and also in brushy gardens in those campuses' respective cities, Corvallis, Seattle, and Vancouver. *C. oregona* can be found in suburban vacant lots, city parks, and even around sand and water traps on golf courses! Since all four of these species are also to bound in "natural" habitats, such synanthropic occurrences merely indicate very tolerant species.

PHYSIOGRAPHIC PROVINCES OF THE PACIFIC NORTHWEST AND FAUNAL COMPARISONS

In another section, I outlined the historical geology of the Pacific Northwest and hypothesized about its effect on the time of differentiation and dispersal of the various cicindelid species. The present section concerns the zoogeography of these species from physiographic provinces into which the Pacific Northwest is divided.

There has been no consensus in the literature as to the terminology for biogeographical divisions of an area. VanDyke (1919, 1926) employed the biotic province concept first outlined by Vestal (1914). Dice (1943) used the same concept, but the number, names, and geographic boundaries of his provinces do not correspond to those of VanDyke. Kaiser *et al.* (1972) criticized use of biotic provinces on the basis that precise boundaries are difficult to define for some of the provinces. Elements of their criticisms are valid but they ignored some of Vestal's guidelines, thus diminishing the brunt of their argument for abandoning the entire concept.

Merriam (1892, 1894, 1898) used temperature as the basis for his life zone concept, one now considered largely inadequate because it fails to take into account time and climatic and edaphic factors. Belicek (1971: 354) pointed out that the " . . . basic difference between biotic province and life zone is that the first is based on composition of the [biotic] assemblage in a given area, whereas the life zone is basically ecological . . ." VanDyke's biotic provinces are, in my view, far more satisfactory than Dice's, but, with only two recognizable in the Pacific Northwest, the Vancouveran

and Sonoran, his divisions are too broad to be of much use in determining details of faunal resemblances. Some of Merriam's life zones are definable in the Pacific Northwest, but alterns cause a complex mosaic pattern, and many cicindelid species have ranges corresponding to edaphic factors rather than vegetational zones. Also, many species are so wide-ranging and eurytopic that the life zone concept becomes meaningless.

I attempted to adapt the technique of Nimmo (1971) of comparing total range outlines of the 24 species of the Pacific Northwest cicindelids in order to discover similar patterns. Unfortunately, I found eighteen different patterns based on available data, incompletely documented for many species, and thus I abandoned this method as inapplicable.

Franklin and Dyrness (1973: 5) employed the principle of physiographic provinces which ". . . are broad stratifications of relatively homogeneous areas (that) reduce complexity to manageable proportions." I have found it necessary to make use of some concept in making my faunal study manageable and have accepted the work of Franklin and Dyrness because of its scope, detail and ready applicability. It removes the necessity of creating and defining my own regions. Franklin and Dyrness treated Washington and Oregon only. I have expanded their ideas to include the rest of the Pacific Northwest for which no comparable comprehensive treatments exist. My divisions of southern British Columbia area based on Cowan and Guiguet (1965) and McKee (1972); for western Montana, McKee (1972); and for Idaho, Gittens *et al.* (1976), Maser and Storm (1970), and McKee (1972). The nineteen provinces have been defined ecologically,

geographically, geologically, and, in part, botanically and zoologically by these several authors. I have made minor changes in the outlines presented by Franklin and Dyrness (1973): western Cowlitz and Clark Counties, Washington, are included in the Willamette Valley Province rather than in the Puget Trough Province because of the proximity and geological history; included inthe Columbia Basin Province are extension northward along the Okanogan River into southcentral British Columbia to Kamloops, and along the Snake River to the Joseph Plains, Idaho Country, Idaho (following Daubenmire, 1970); and the Palouse Grasslands Province is recognized as distinct from the Columbia Basin Province (following Daubenmire, 1970). The provinces are shown in Figure 74 and listed in the legend for that map, along with the numbers used on the map and abbreviations used in Tables 83 and 84.

Following consultation with Mr. Daniel Geiszler, University of Washington College of Forest Resources, I employed the formula of Jaccard (1908) to calculate faunal resemblances. Jaccard's formula, following Long (1963), is as follows:

$$\% \text{ faunal resemblance} = C\,(100)/(N_1 + N_2 - C)$$

where

C = no. species in common between two faunas being compared

N_1 = no. species in first fauna

N_2 = no. species in second fauna

Jaccard's formula measures the percentage of species in common to two areas, and it is useful because the relative sizes of the two faunas are not considered.

The subspecies (intergrades are counted as a separate subspecies for the purposes of this analysis)--species if no subspecies are recognized--is the unit used in the analysis. Table 83 presents a faunal list with physiographic provinces included in the range of each form. The percentages of faunal resemblances for the nineteen provinces are presented in Table 84 in matrix form for ready comparison.

Discussion

A detailed analysis of Table is unnecessary because the results are obvious through inspection. However, some generalizations are in order.

1. Higher elevation provinces such as those encompassing the Cascades, Rockies, Klamaths, Okanogan Highlands, Blue Mountains, and High Lava Plains show the greatest faunal resemblance. The depauperate Olympic Mountains are an exception.

2. The lowland areas west of the Cascades resemble one another closely and differ strongly from adjacent mountains.

3. Similarity of the Columbia Basin and Plaouse Grasslands faunas results from the sharing of three wide-ranging species (*C. oregona*, *C. repanda*, and *C. tranquebarica*) and is thus misleading.

4. The Palouse Grasslands and the High Lava Plains correlate 100%, and also very strongly with the Blue Mountains, perhaps reflecting the shared mixed conifer and grassland habitat. The similarity with the Northern Rockies may be the result of the forcing southward of fauna of the Rockies during glaciation. The Middle Rockies do not share the same correlation of these areas with the Northern Rockies

suggesting that the species did not follow the mountain ridge southward upon the onset of glaciation but, instead, spread to adjacent lowlands.

5. The Snake River Lava Plains and the Basin and Range Provinces correlate strongly. Differences result from endemism and an eastern influence on the former, and separation of the latter into drainage basins of Pluvial Lakes Bonneville and Lahontan. The Lahontan drainage contains a few forms (*C. amargosae* and *C. parowana platti*) not found in either the Bonneville system or the Snake River Lava Plains. Limiated similarity to these provinces of the Owyhee Uplands is because of that region's depauperate fauna (four species, of which two, *C. oregona* and *C. nebraskana*, are wide-ranging).

Table 83. Cicindelid faunal list of the physiographic provinces of the Pacific Northwest
Abbreviations follow the legend for Fig.

TAXON	QIH	CR	PT	WV	NC	SWC	WC	HC	KM	OKH	CB	PG	HLP	BR	BM	OU	SLP	NR	MR
O. dejeani		X	X	X		X			X										
O. c. californicus									X										
O. audouini		X	X	X		X			X	X									
C. o. oregona		X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X
C. o. oregona x guttifera																	X	X	
C. d. depressula	X				X	X		X										X	
C. d. eureka			X	X															
C. d. depressula x eureka		X	X				X												
C. r. repanda				X							X	X	X		X		X	X	
C. hirticollis					X					X	X				X		X		
C. h. ssp. B		X																	
C. a. arenicola																	X		
C. a. n. ssp. Clifford																	X		
C. a. arenicola x n. ssp.																	X		
C. b. bellissima		X		X															
C. b. n. ssp. Leffler		X																	
C. columbica				X							X				X				
C. l. perviridis	X		X		X			X	X										
C. l. perviridis x laurenti												X	X		X			X	X
C. nebraskana chamberlaini						X				X	X	X	X	X	X	X	X	X	
C. n. chamberlaini x nebraskana																	X		X
C. purpurea auduboni					X				X	X		X	X	X	X		X	X	
C. p. new name Leffler			X	X					X										
C. p. lauta					X	X	X	X											

Table 83 (continued)

TAXON	OIH	CR	PT	WV	NC	SWC	WC	HC	KM	OKH	CB	PG	HLP	BR	BM	OU	SLP	NR	MR
C. pugetana											X				X				
C. plutonica														X		X	X		
C. d. decemnotata														X			X		X
C. d. n. ssp. Clifford											X								
C. parowana platti														X					
C. p. platti x parowana														X					
C. p. parowana																	X		
C. p. wallisi											X								
C. tenuicincta														X			X		
C. lengi versuta											X						X		
C. tranquebarica "kirbyi"																X	X		
C. t. vibex			X	X	X	X	X	X	X	X	X	X	X		X		X	X	
C. t. "kirbyi" x vibex																		X	
C. amargosae nyensis														X					
C. willistoni echo														X			X		
C. haemorrhagica nigroides											X			X			X		X
C. cinctipennis imperfecta											X			X			X		X
TOTAL NUMBER OF TAXA	2	7	8	10	4	7	4	5	10	5	13	6	6	12	9	4	20	9	6

Table 84. Faunal resemblance matrix for physiographic provinces of the Pacific Northwest. Values are in percent.

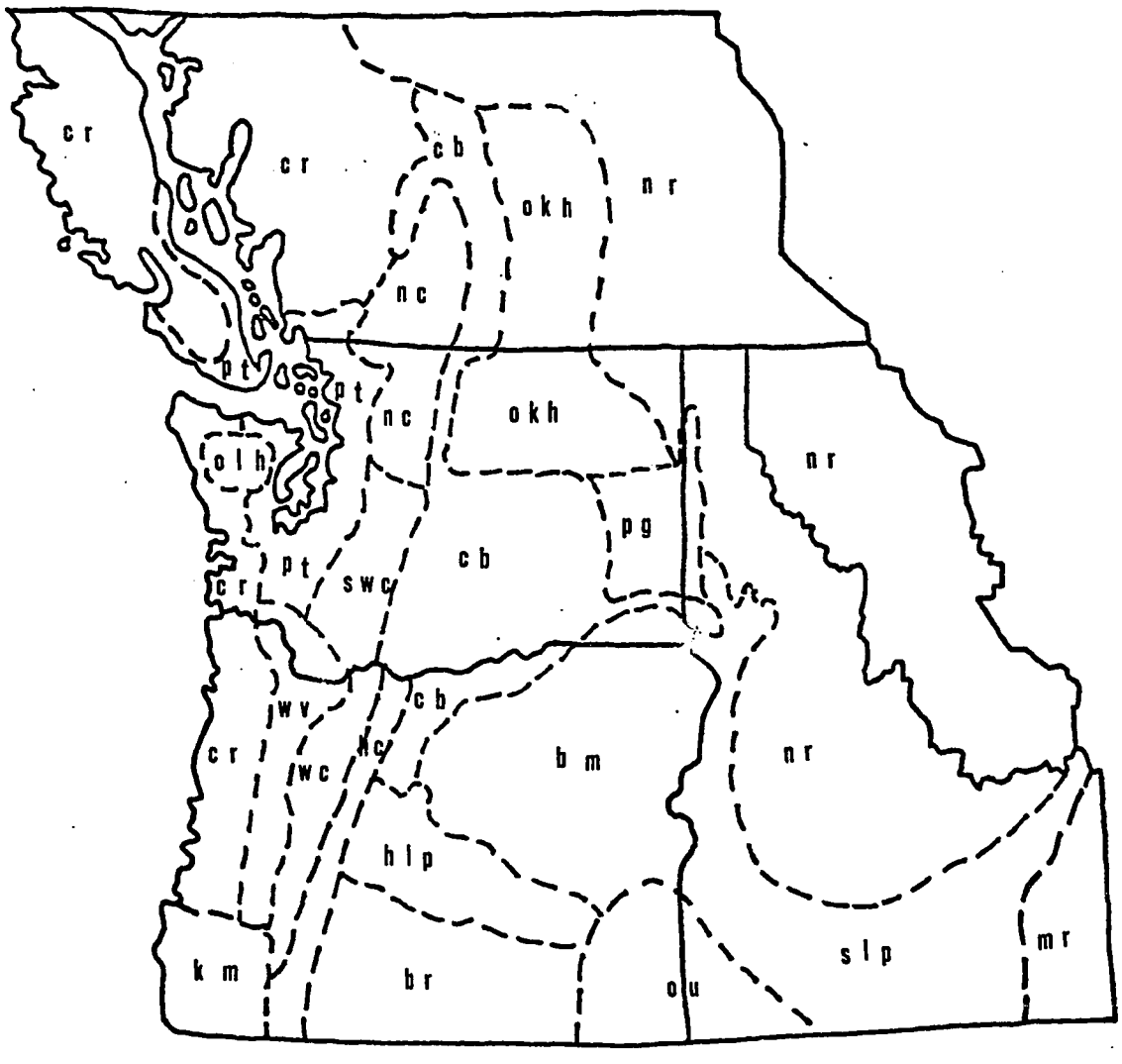
	OIH	CR	PT	WV	NC	SWC	WC	HC	KM	OKH	CB	PG	HLP	BR	BM	OU	SLP	NR	MR
OIH	----																		
CR	00.0	----																	
PT	11.1	36.4	----																
WV	00.0	30.8	50.0	----															
NC	20.0	00.0	7.7	8.3	----														
SWC	12.5	27.3	30.7	30.8	20.0	----													
WC	00.0	22.2	16.7	18.2	14.3	37.5	----												
HC	16.7	9.1	15.4	16.7	28.6	50.0	50.0	----											
KM	00.0	21.4	33.3	35.7	16.7	41.7	27.3	36.4	----										
OKH	00.0	9.1	25.0	27.3	28.6	20.0	28.6	25.0	25.0	----									
CB	00.0	11.1	35.3	37.5	6.3	25.0	13.3	12.5	15.0	28.6	----								
PG	00.0	8.3	23.1	25.0	25.0	30.0	25.0	22.2	23.1	57.1	26.7	----							
HLP	00.0	8.3	23.1	25.0	25.0	30.0	25.0	22.2	23.1	57.1	26.7	100.0	----						
BR	00.0	5.6	4.8	5.0	6.7	11.8	6.7	6.3	10.0	21.4	25.0	20.0	20.0	----					
BM	0.00	6.7	12.5	35.7	18.2	23.1	18.2	16.7	18.8	55.6	46.7	66.7	66.7	15.8	----				
OU	0.00	10.0	7.7	8.3	00.0	22.2	14.3	12.5	7.7	28.6	13.3	25.0	25.0	23.1	18.2	----			
SLP	00.0	3.8	15.4	16.0	9.1	12.5	9.1	8.7	11.1	25.0	37.5	23.8	23.8	45.5	26.1	20.0	----		
NR	10.0	6.7	18.8	20.0	30.0	33.3	18.2	27.3	18.8	40.0	22.2	66.7	66.7	40.0	50.0	18.2	26.1	----	
MR	00.0	8.3	6.7	7.1	00.0	8.3	11.1	10.0	6.7	10.0	26.7	20.0	20.0	28.6	15.4	11.1	23.8	15.4	----

Fig. 74. Map showing locations of the 19 physiographic provinces in the Pacific Northwest.

Legend:

(Letters are in parentheses are abbreviations for each province)

1. Olympic Highlands
2. Coast Range (CR)
3. Puget Trough (PT)
4. Willmaette Valley (WV)
5. Northern Cascades (NC)
6. Southern Washington Cascades (SWC)
7. Western Cascades (WC)
8. High Cascades (HC)
9. Klamath Mountains (KM)
10. Okanogan Highlands(OKH)
11. Columbia Basin (CB)
12. Palouse Grasslands (PG)
13. High Lava Plains (HLP)
14. Basin and Range (BR)
15. Blue Mountains (BM)
16. Owyhee Uplands (OU)
17. Snake River Lava Plains (SLP)
18. Northern Rocky Mountains (NR)
19. Middle Rocky Mountains (MR)


cr
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HABITAT CHARACTERISTICS AND COMPETITION

This section is not intended to be an exhaustive review of niche characteristics, but, rather, is a summary of habitat preferences and information on how the several species may coexist while minimizing competition. Some species discussed here range outside of the Pacific Northwest and habits may differ elsewhere, but the following accounts refer to characteristics in the Pacific Northwest only.

Omus dejeani. Maser (1977: 35) stated that, at least along the Oregon coast, this species is ". . . primarily associated with successional stage plant communities [with the requirement of] . . . an abundance of dead-and-down woody material for cover." The species extends to higher elevations in the Cascades than does *O. audouini*. Its preference for denser canopy situations perhaps allows it to exploit such higher elevations where the canopy moderates, at least to some extent, extremes of temperature more than the exposed situations preferred by *O. audouini*. My observations (6 localities for *O. dejeani* and two for *O. audouini*, both shared with *dejeani*) show that *dejeani* larvae are found often, but not exclusively, on steep, often vertical, embankments. Burrows extend through the O and A horizons and penetrate the B_2 hir horizon but stop short of deeper levels presumably because such soils have higher water content or lack sufficient friability. Adults are usually found in the general vicinity of the larvae, often in rotting logs or beneath leaf litter. I collected an adult female WA. Thurston Co., Rocky Prairie, crossing a dirt road at 1000 PDT, 4 May 1974, air temperature 21° C, sky clear, some 100 m. from the nearest larval burrows and trees. This observation along with

Maser's (1977a, 1977b) and Cazier's (1942) data show that the adults are not restricted to forested areas, but disperse and perhaps forage in open regions.

The habitat is shared mainly only by *O. audouini*. *Cicindela oregona*, *purpurea*, and *tranquebarica* may contact *O. dejeani* adults, but the *Cicindela* species are smaller and do not enter forested situations. Adults of both species of *Omus* may be caught in the same pitfall traps, showing that the cruising ranges (*sensu* Mayr, 1963) can overlap at a given locality, even though optimal habitat preferences differ. Mr. Ronald Herschi, California Department of Fish and Game (pers. comm., 1974) studied the two species on the University of Washington campus. He found that *O. audouini* adults will fall prey to the much larger *O. dejeani*. This suggests that *audouini* adults may be excluded from the range of *dejeani* through predation.

Omus audouini. See also account of *O. dejeani*. Maser (1977b) stated that *O. audouini* is ". . . primarily an inhabitant of forest/meadow ecotones with orientation toward meadows in many areas." Whereas *O. dejeani* prefers closed canopy situations, *audouini* adults and larvae are usually found in open canopy areas or even in open situations adjacent to forests. Such habitat has greater exposure to sunlight and, hence, soils are subject to greater extremes of temperature and wetting or drying. *O. audouini* has been collected at fewer stations than *O. dejeani*, but is more widely distributed and tends to be more abundant at any given locality. *O. audouini* does not extend to so high of elevation in mountains as *dejeani*. Larvae may be found on steep embankments as in *dejeani*, but in situations where they are exposed to at least some

direct sunlight. On the University of Washington campus I have found *audouini* burrows along the margins of paved paths and bicycle trails distant from any tree cover. Differences in structure of the larval burrow suggest that the *audouini* burrow is a more effective trap than that of *dejeani*, perhaps a compensation for life in a drier soil where food is not as abundant.

Maser (1977b: 48) found a preference by *audouini* for the centipede *Scolopendra sexspinosa* Newport, also abundant in forest/meadow ecotones. Unfortunately, no information was presented for *O. dejeani*.

Preference for drier habitats might bring *O. audouini* into conflict with *Cicindela* spp., but *audouini* is usually found beneath rocks, slash, and litter so intergeneric competition would be minimized. *O. audouini* and *californicus* are parapatric in northwestern California. The range of *californicus* appears to coincide with that of *Sequoia sempervirens* in this region, whereas *audouini* is found in drier inland situations or on coastal headland praries.

Omus californicus. See also account of *O. audouini*. Most of the range of this species is in California and thus extralimital to the present study. *O. californicus* is the only species of *Omus* found at the single Northwest station inhabited by *californicus*.

Cicindela oregona. This is the most eurytopic of any of the 21 species of *Cicindela* found in the Pacific Northwest. I have collected it in almost every situation except forestlands, dry grasslands, and open sagebrush tracts. I have records for sea level along the ocean beaches to about 3000 m. in the Rocky Mountains. I have found larvae on sandbars, clayey soils, and even highly alkaline soils subject to periodic

C. arenicola. This species inhabits saddles in aeolian dunes. Other species may be found around the margins of such habitats only and do not appear to come into direct competition with *arenicola*.

C. decemnotata. This species appears to be restricted to well-drained silty soils grown largely to *Artemisia*. In the Pacific Northwest, it has been found in valleys formerly occupied by rivers larger than their modern counterparts such as the Raft and Big Lost Rivers of Idaho. *C. d.* new ssp. Clifford ranges through the east edge of the Columbia Basin of Washington, also silty soils in sagebrush tracts but with still viable rivers and pothole lakes.

C. decemnotata is a Pattern A species which minimizes competition from Pattern B species inhabiting the same regions. *C. purpurea* is partly sympatric but usually prefers grassland microhabitat. *C. pugetana* is parapatric in nearly identical habitat in Washington although both species have extended up the Okanogan River into southcentral British Columbia. *C. decemnotata* is a somewhat larger species than *pugetana* and thus could capture larger prey species.

C. purpurea. Except for *C. p. lauta*, this is a grassland species, usually in situations with bare areas between clumps of grass. The species is able to cope with human activities and utilizes footpaths and dirt-bike tracks. A typical escape behavior is to veer at a right angle from a trail into clumps of grass where its green color renders a beetle invisible.

Only *C. decemnotata*, *nebraskana*, *plutonica*, *pugetana*, and *tranquebarica* are of a similar enough size to bring them into potential conflict with *purpurea auduboni*. *C. decemnotata*, *pugetana*, and

temporary flooding. It is tolerant of human activities and may be found in urban situations in vacant lots, city parks along paths, and even sandtraps of golf courses. In the Pacific Northwest, it appears to be replaced in higher Cascades by *C. depressula*, although both species have been collected at WA. Lewis-Yakima Co. line, Mt. Rainier National Park, Chinook Pass, 1590 m.

In eastern Idaho and northwestern Montana, the western *C. o. oregona* and the Rocky Mountain *C.o. guttifera* intergrade at elevations above 760 m. Because the species is restricted to riparian habitats in this region, probably the change in elevation and concomitant climatic factors have influenced interactions of the two subspecies where their ranges meet.

Because of its wide distribution and eurytopy, *C. oregona* may potentially compete with virtually every other species of *Cicindela* in the Pacific Northwest. Having a life history pattern A eliminates competition with pattern B species. *C. oregona* is of small to medium size (elytral length, 5.5-7.0 mm.) and would be expected to utilize smaller prey than larger species such as *C. longilabris*, *nebraskana*, *purpurea*, and *tranquebarica*. *C. oregona* may frequently found in company with such species as *bellissima*, *columbica*, *hirticollis*, and *repanda*. Usually *bellissima* and *hirticollis* prefer loose sand of dunes, and *columbica* and *repanda* are found on wet sand near rivers. *C. oregona* adults are also found in the same situations, but they and their larvae are most abundant on drier soils with some clay or at least humus from vegetation. Eurytopy of the species is seen when other species are not present at a given locality.

Cicindela depressula. The two subspecies are allopatric except at points of intergradation. *C. d. depressula* in the Pacific Northwest is found along roadsides and bare areas at elevations above 1200 m., and usually not directly associated with water. *C. d. eureka* is riparian and at elevations near sea level. Intergrade populations are found in riparian situations at elevations between 240-600 m.

C. d. depressula may associate with *C. longilabris*, *nebraskana*, and *oregona*. The first two species are much large (elytral length > 7 mm.) and, presumably, utilize larger prey items. *C. oregona* is the same size as *depressula* but is not typically found at such high elevations. Only *C. oregona* and *repanda* are sympatric with *C. d. eureka*. *C. repanda* may be only a recent immigrant west of the Cascades and is common only along the Columbia River where *eureka* has not yet been found. *C. oregona* can be found with *eureka* in mixed aggregations both as larvae and adults. Both are about the same size and both are Pattern A. Competition may be minimized by some aspect of resource utilization about which data are lacking.

Cicindela repanda. This species is restricted to riparian situations. Its presence west of the Cascades is restricted to only a few localities along the Columbia and Willamette Rivers, suggesting a rather recent immigration. Adults and larvae are found in areas of wet sand immediately adjacent to the edge of rivers.

C. columbica, *hirticollis*, and *oregona* all may be associated with *repanda*, larvae of these are usually found in drier situations.

Cicindela hirticollis. There are two Pacific Northwest subspecies. Ssp. A is found on drier portions of riparian dunes, although I have found both adults and larvae associated with wet sand. Ssp. B is restricted to sandy areas at the mouths of rivers where they meet the ocean.

See accounts of *C. oregona* and *repanda* for discussions of potential competition of ssp. A with those species. Ssp. A is also found at the same localities as *C. arenicola*, but *arenicola* inhabits saddles much farther onto the dunes than does *hirticollis*. Ssp. B might compete with *C. oregona* and *C. bellissima*. I have found *oregona* in soil with more humus and vegetation in oceanside situations, and *bellissima* is found in foredune saddles or in less vegetated portions of the deflation plains, whereas ssp. B is found near mouths of rivers.

Cicindela columbica. This species was restricted to riparian dunes along parts of the Columbia, Salmon, and Snake Rivers, but most of its habitat has been destroyed through dam construction. Larvae are still unknown, and interactions of *columbica* adults with other species have not been studied. Its few remaining localities are of limited extent and lack dune development. Other riparian species inhabit the same localities, and, unless food is abundant enough to support four species of similar ecologies, the future of *C. columbica* is questionable.

C. bellissima. Maser (1973) and Leffler (in press) have discussed ecology of this species at length. It is restricted to ocean foredune saddles and the less vegetated portions of the deflation plains. See accounts of *C. hirticollis* and *oregona* for comments on potential competition.

tranquebarica normally inhabit areas with sparse grass growth if any. At WA. Kittitas Co., Colockum Pass, both *purpurea* and *pugetana* are found, but *purpurea* is found in the bunchgrass (*Agropyron-Festuca*) areas and *pugetana* in limited-grass sagebrush (Artemisia) tracts. Beer and Maser (1973) reported *C. purpurea* and *plutonica* from OR. Lake Co., vicinity of Bly. *C. purpurea* inhabits grassland situations and *plutonica* is found in broken-rock scablands. *C. nebraskana* is usually found in less grassy situations at higher elevations.

C. p. new name Leffler is found in grassy prairies in western Washington and Oregon and is usually the only cicindelid found in such situations (see also *Omus* spp.). *C. p. lauta* is found on paths in forested areas usually near creeks or small lakes. *C. oregona* is the only potential competitor of the same size but is not normally found in forested tracts.

C. pugetana. See also accounts of *C. decemnotata* and *purpurea*. This species is found on bare areas of sagebrush tracts where it is usually the only cicindelid species present.

C. plutonica. See also account of *C. purpurea*. This species is restricted to broken-rock scabland habitat not typically inhabited by other species.

C. longilabris. This high elevation (over 1000 m.) species is rarely found with other species. *C. oregona* and *depressula* may share its habitat but are smaller in size. *C. nebraskana* and *tranquebarica* are known from some of the same localities: at the lower elevational range of *longilabris*, intermediate for *nebraskana*, and high for *tranquebarica*.

C. nebraskana and *tranquebarica* usually are found where there is less canopy cover than is *longilabris*. My analyses of soils from 5 localities each of *longilabris* and *nebraskana* showed that those of *longilabris* had a higher percentage of clay.

C. nebraskana. See also accounts of *C. longilabris*, *purpurea*, and *tranquebarica*. This species is usually found at elevations from 700-1500 m., and is normally not associated with other cicindelid species. It prefers dry forest situations such as ponderosa-parkland with little if any grass. It replaces *C. longilabris* in the southern Washington Cascades perhaps because of edaphic factors not yet known. My analyses of soils from 5 localities each of *longilabris* and *nebraskana* showed that those of *nebraskana* were clay soils but with higher proportions of sand than those inhabited by *longilabris*.

Cicindela parowana. This is a Pattren A halophile. Preferred habitat is soils encrusted with alkali. Dazier (1937b) stated that it is ". . . collected along irrigation ditches leading out of reservoirs, and around the reservoirs." The type series of *C. p. platti* was collected on dry, powdery soil on a hillside with scattered bunchgrass about 30 m. from water. The species is locally abundant on plots prepared for husbandry of alkali bees (family Halictidae: *Nomia melanderi* Cockerell), but is otherwise quite rare.

Its size and life history pattern could bring *C. parowana* into competition with *oregona* and *willistoni*. Study is needed to delinate habitat distinctions of these species.

Cicindela amargosae. Rumpp (1956) reported habitat of this species as ". . . along mud flats at the edge of small rivulets, in patches of

short grasses." Pacific Northwest localities have alkaline soils found throughout much of the range of *C. a. nyensis*. Rumpp's (1956) dates are of a Pattern A species.

Rumpp's discussion indicates that this species prefers moist grassy areas, whereas other Pattern A halophiles of similar size, *oregona*, *parowana*, and *willistoni*, inhabit more open and often drier situations.

Cicindela willistoni. See also accounts of *C. amargosae* and *parowana*. This is a halophilic Pattern A species found typically on salt flats with heavy incrustations of alkali. Both Rumpp (1956: 133) and Willis (1967: 214, fig. 89) found *willistoni* to be the earliest emergent at localities they studied.

Cicindela haemorrhagica. This is a Pattern B species whose adults reach peak numbers by late June when Pattern A adults have declined or disappeared. I have found it typically but not exclusively on alkaline soils and, although it is usually found on moist ground, I have seen it on dry hardpan far from water.

The only other Pattern B halophile occurring with *haemorrhagica* is *cinctipennis*, a much smaller species which prefers grassier situations and reaches peak abundance in early rather than late June. Behavior of the two species also differs: *haemorrhagica* is gregarious and flies readily when threatened, an aggregation dispersing suddenly in all directions and showing the red abdomens, serving to frighten and confuse potential predators; *cinctipennis* is solitary, rarely flies, and usually runs and hides in clumps of vegetation.

Cicindela tenuicincta. I have found adults on alkali-encrusted soils of the shores of saline bodies of water. I have not collected its

larvae. Records indicat a Pattern A species but one whose summer adult survival overlaps activity times of Pattern B species.

Size, habitat, and activity period would bring this species into competition with *oregona*, *parowana*, and *willistoni*, but interactions require study.

Cicindela lengi. This is a Pattern A species of moderate size typically found at the margins of sand hills where there is sparse grass growth for soil stability.

As this species has only been found at three localities in the Pacific Northwest, little can be said regarding competition. is its mostly likely chief competitor.

Cicindela tranquebarica. This Pattern A. species is nearly as eurytopic as *C. oregona*. Its large size would reduce competition with most Pacific Northwest species. I have usually found it to be solitary and unassociated with other species at the same locality. *C. nebraskana* and *longilabris* are of similar size and may be found at the same locality as *tranquebarica*. *C. longilabris* is more typical of higher elevations, and *nebraskana* is most often found where there is some conifer canopy; *tranquebarica* is usually found in completely open situations. Clayey soils of blocky structure at open sites at low to moderate elevations (0-1000 m.) are mostly likely to support *tranquebarica* populations. Larvae may be found on level sites or moderately steep embankments in soils ranging from clay to sand, alkaline or non-alkaline.

C. cinctipennis. See also account of *C. haemmorhagica*. This is a Pattern B halophile whose small size and preference for sites with growth of grasses reduces potential competition by other species.

SUMMARY

1. Systematics and some other biological aspects of the 24 species of Cicindelidae of the Pacific Northwest (the section one-third of British Columbia, Montana west of the continental divide) are treated.

2. Larval descriptions of 19 species representing two genera are presented (13 for the first time). Larval characteristics are analyzed and assessed as to their systematic value. A key is given in Appendix IV.

3. Pupal descriptions of 11 species representing two genera are presented. Pupal characteristics are analyzed and assessed as to their systematic value. A key is given in Appendix IV.

4. Synonymies and diagnoses of each of 24 species are given as well as of the family, subfamilies, tribes, subtribes, genera, subgenera, species-groups, and subspecies. Information on validity of morphological characters, adaptations, interrelationships, and distributions are presented. The type locality for *Cicindela tenuicincta* is changed from Colorado to UT. Salt Lake Co., Saltair, and that of *C. purpurea lauta* is restricted to CA. Siskiyou Co., Dunsmuir. One new taxon is proposed: *Cicindela tranquebarica deciperata* Leffler, to replace the preoccuped *C. t. viridula*; *C. t. deciperata* is then synonymized under *C. t. tranquebarica* Herbst. A key is given in Appendix IV.

5. These edaphic factors are analyzed based on soil samples from 37 localities representing 19 species: pH, electroconductivity, and soil particle size distribution. The ratio of breadth and length

of the immovable stylus of the 2nd gonapophyses of specimens of 15 species are calculated and compared with proportions of sand, silt and clay in the appropriate soils: discriminant analysis gives correlations of 91% for sand, 78% for silt and 98% for sand. A long, narrow stylus correlates with sandy soil and a short, broad stylus correlates with clayey soil.

6. A theoretical overview of the influence of historical geology on the present distributions of Pacific Northwest is presented. Details of major geological events are given in Appendix III.

7. The Pacific Northwest is divided into 19 physiographic provinces. Faunal resemblances of these provinces are calculated by means of Jaccard's formula which measures similarities regardless of differences in sizes of the faunas being compared.

8. A summary of habitat preferences of each of the 24 species and information on how certain species may coexist while minimizing competition.

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APPENDIX I

PACIFIC NORTHWEST TIGER BEETLE LOCALITIES

The following is a compilation of localities in (and, in some instances, near) the geographic region treated in this report where tiger beetles have been collected. All records I include are based on specimens I have either personally examined or are from publications or lists whose correctness I do not question. Abbreviations in parentheses are for institutions, private collections, or publications listed in the Materials section. The reader will note some distances and elevations in metric units and others in British units. I have copied data directly from the original sources, most of which have used British units. Because such data may represent units that have been rounded off or some based on air distance and some on distance by road, conversion of all British units to metric might compound minor inaccuracies.

O. audouini

BRITISH COLUMBIA.

Vancouver Island: Saanich (BCP); Tod Inlet, S of Brentwood (AM); Victoria (AM, BCP).

Mainland: Merritt, Midday Valley (BCP).

WASHINGTON.

Benton Co.: 10 mi. NW Richland (L-P).

Clallam Co.: Seiku (SL).

Cowlitz Co.: Ariel (L-P).

Grays Harbor Co.: Ocean Shores (L-P).

Island Co.: Whidbey Island, Coupeville (L-P).

King Co.: Bothell (L-P); 6 mi. NW Carnation (SL); Cedar Mountain (L-P); Maury Island (L-P); Mercer Island (L-P); Renton (L-P); Richmond (L-P); Seattle, University of Washington campus (SL).

Kitsap Co.: Keyport (L-P).

Klickitat Co.: Husum (L-P).

Lewis Co.: Gilbert Forest, Chehalis (L-P).

Mason Co.: Shelton (L-P).

Pierce Co.: La Grande (AM); Ohop Lake (L-P); Puyallup (L-P); Tacoma (L-P).

San Juan Co.: Cypress Island (L-P).

Skamania Co.: Cook (L-P); Stevenson (SL).

Thurston Co.: 2.3 mi. SW Bucoda (L-P); Olympia (L-P); Rochester (L-P); Rocky Prairie, 3 mi. N Tenino (SL).

Whatcom Co.: Bellingham (L-P).

OREGON.

Benton Co.: Alpine (OSU); Alsea (ODA); 2 mi. N Coffin Butte (SL); Corvallis (ODA, OSU); 5 mi. W Corvallis (SL); McDonald Forest, 5 mi. N Corvallis (OSU); Monroe (OSU); 6 mi. SW Philomath (OSU); 1 mi. N Summit (SL); 3.5 mi. NE Summit (OSU).

Clackamas Co.: Colton, 8 mi. ENE Molalla (AM; Gladstone (ODA); Sandy (UCD).

Coos Co.: 15 mi. S Reedsport (OSU)

Curry Co.: Cape Sebastian St. Park (OSU); Gold Beach (OSU); Humbug St. Park (OSU); Pistol River (OSU); Winchuck River (SL).

Douglas Co.: Tenmile (OSU).

Jackson Co.: Ashland (OSU); 1 mi. E Brownsboro (OSU); Medford (OSU, UC).

Josephine Co.: Grants Pass (AM); Selma-Waldo (NM).

Klamath Co.: Upper Klamath Lake (NM).

Lane Co.: Eugene (UW); 10 mi. W Junction City (SL); 5 mi. SW Noti (JS); Siltcoos Outlet (UW); Spencer's Butte, 5 mi. E Eugene (OSU); Vida (OSU); Wendling (JS).

Lincoln Co.: 0.5 mi. W Digger Mountain Store (SL); 2 mi. W Harlan (OSU); Nashville (AM); Newport (UC).

Linn Co.: Cascadia (OSU); 6 mi. E Sweet Home (OSU).

Marion Co.: Salem (ODA); Turner (UCD).

Multnomah Co.: Portland (AM, UI).

Polk Co.: Dilley (AM); Forest Grove (OSU); North Plains (ODA).

Yamhill Co.: Gaston (AM); McMinnville (OSU).

O. californicus californicus

OREGON.

Curry Co.: Red Mountain Prairie, 53 Km. (by road) NE Brookings, 998 m. (ODA).

O. dejeani

BRITISH COLUMBIA.

Vancouver Island and islands in strait of Georgia: Colwood (BCP); Copper Canyon, ENE Crofton (BCP); Courtenay (UBC); Cowitchan Bay (BCP, UBC); Duncan (BCP, UBC); Esquimault (BCP); Goldstream (BCP); Gordon Head, E Royal Oak on coast (BCP); Ladysmith (UBC); Livingston (BCP); Mt. Arrowsmith, SE Port Alberni (BCP); Mt. Benson (UBC); Mt. Douglas (BCP); Pender Harbour (UBC); Rithets Creek, N edge Sooke Lake (BCP);

Royal Oak (UBC); Saanich (UBC); Salt Spring Island (UBC); Shawnigan Lake (OSU); Sooke (BCP); Sydney (BCP); Tod Inlet, S Brentwood (UBC); Tofino (UBC); Victoria (BCP); Wellington (UBC).

Mainland: Agassiz (BCP); Copper Canyon (BCP); Hollyburn, W North Vancouver (BCP); Hope (UBC); Koksiloh Mtns. (BCP); New Westminster (BCP); North Lonsdale, NNE North Vancouver (BCP); North Vancouver (BCP, UBC); Vancouver (BCP).

WASHINGTON.

Clallam Co.: Sol Duc Hot Springs (L-P).

Clark Co.: Washougal (L-P).

Cowlitz Co.: Ariel (L-P); Kelso (L-P); Longview (L-P).

Grays Harbor Co.: Aberdeen (L-P); Copalis Beach (L-P); 5 mi. S Humptulips (SL); Montesano (WSU); Quinault (L-P); Westport (OSU).

Island Co.: Camano Island (L-P); Greenbank (L-P); Oak Harbor (L-P).

Jefferson Co.: Brinnon (L-P); 16 mi. SE Forks (L-P); Hoh River (L-P); Port Townsend (L-P).

King Co.: Bothell (L-P); Cedar Mountain (L-P); Enumclaw (L-P); Green River (L-P); Issaquah (L-P); Kent (L-P); Lester (L-P); North Bend (L-P); Rattlesnake Lake, S North Bend (SL); Renton (L-P); Richmond (L-P); Seattle (L-P); Snoqualmie Falls (L-P);

Kitsap Co.: Gig Harbor (L-P); Point Blakley (L-P); Winslow (L-P).

Kittitas Co.: Eastern (L-P).

Lewis Co.: Chehalis (L-P); 0.75 mi. E Mossyrock (VC); 5 mi. E Mossyrock (L-P).

Mason Co.: Shelton (L-P).

Pacific Co.: Naselle River (L-P); 6 mi. N Nemah (SL); Seaview (L-P); South Bend (L-P).

Pierce Co.: Fort Lewis (L-P); 3 mi. SW Graham (VC); Lake Kapowsin (L-P); Longmire (L-P); Parkland (L-P); Tacoma (L-P).

San Juan Co.: Cypress Island (L-P); San Juan Island (L-P, WSU).

Skagit Co.: Fidalgo Island (L-P); Sedro Woolley (L-P).

Snohomish Co.: Darrington (L-P); Marysville (L-P); Monroe (L-P); 3 mi. NW Silvana (WSU); Snohomish (L-P).

Thurston Co.: Olympia (L-P); Rocky Prairie, 3 mi. N Tenino (SL); 1.5 mi. E Vail (VC).

Whatcom Co.: Bellingham (L-P); Lummi Island (L-P); 1 mi. NW Lynden (L-P).

OREGON.

Benton Co.: Alsea Mountain (OSU); Corvallis (OSU); Mary's Peak (OSU, ODA).

Clackamas Co.: Bull Run (NM): Colton 8 mi. ENE Molalla (AM); Estacada (ODA); 8.0 Km. SW Government Camp, US Hwy. 26, 750 m.; Milwaukie (OSU); Oregon City (ODA).

Clatsop Co.: Astoria (WSU); Cannon Beach (OSU); Saddle Mountain (ODA).

Coos Co.: Charleston (OSU), AM); Coos Bay (OSU); Fairview (OSU); North Bend (ODA).

Douglas Co.: 3.5 mi. S Curtin (SL).

Jackson Co.: Medford (OSU); Woodruff Meadows (UC).

Lane Co.: 7 mi. S Florence (OSU); Glenada (OSU).

Lincoln Co.: Boiler Bay (AM); 2 mi. W Harlan (OSU); Newport (AM, ODA, OSU); 15 mi. S Newport (ODA); Taft, 1 mi. S Lincoln City (AM); Toledo (ODA); Yachats (ODA).

Linn Co.: Cascadia (OSU); 8 mi. E Sweet Home (OSU).

Marion Co.: 2 mi. E Gates (SL); Salem (JS, ODA).

Multnomah Co.: Portland (OSU).

Polk Co.: Black Rock (OSU).

Tillamook Co.: Oceanside (OSU); Pacific City (OSU).

Washington Co.: Beaverton (JS); Dilley (AM); Gales Creek (OSU).

Yamhill Co.: Bald Peak St. Park (OSU); McMinnville (OSU).

C. amargosae nyensis

OREGON.

Harney Co.: Alvord Hot Springs, 5 mi. N Andrews (Beer and Masen, 1973).

Lake Co.: Crump Lake, 6 mi. N. Adel (Beer and Maser, 1973).

C. arenicola

C. a. arenicola

IDAHO.

Fremont Co.: 2 mi. N, 5 mi. W Parker (SL); St. Anthony Sand Dunes, 8 mi. NNE St. Anthony (Rumpp, 1967); Sand Creek, 15 mi. NNE St. Anthony (Freitag and Tropea, 1971).

C. a. n. ssp. Clifford

IDAHO.

Owyhee Co.: NW of NW corner Bruneau Dunes St. Park (VC).

C. a. arenicola x n. ssp. Clifford

IDAHO.

Minidoka Co.: Snake River, Jackson Dune area (VC).

C. bellissima

C. b. bellissima

WASHINGTON.

Grays Harbor Co.: Copalis Beach (L-P); Grayland (L-P); Moclips (L-P); Twin Harbors St. Park (L-P); Westport (L-P).

Pacific Co.: Bay Center (L-P); Klipsan Beach (WSU); Leadbetter Point (L-P); Long Beach (L-P); Nahcotta (L-P); 1.5 mi. N North Cove (Willis and Stamatov, 1971); Ocean Park (SL); Oysterville (L-P); Seaview (L-P); Snag Island (L-P).

OREGON.

Clatsop Co.: Ft. Stevens (Maser, 1973); Seaside (OSU).

Coos Co.: N of Bandon (Maser, 1973); 1 mi. W Charleston (Univ. Missouri Coll.); Hauser (OSU); 3.5 mi. N North Bend (OSU); Upper Cherry Creek, 15 mi. SW Powers (OSU).

Curry Co.: mouth Pistol River (SL).

Douglas Co.: Gardiner (OSU); Tahkenitsch Lake (Maser, 1973); Winchester Bay (OSU).

Lane Co.: Florence (OSU); Westlake (VC).

Lincoln Co.: Devil's Lake St. Park (OSU); Lost Lake (OSU); Newport (AM); Ona St. Park, 6 mi. S Newport (OSU); Seal Rock (OSU); Taft, Lincoln City (Maser, 1973); Alsea Bay, Waldport (OSU).

Multnomah Co.: Sauvie Island, Portland (OSU).

Tillamook Co.: Manzanita (OSU); Nskowin (OSU); Rockaway (OSU); Sandlake (J. B. Karren coll.); Woods (OSU).

C. b. n. ssp. Leffler

WASHINGTON.

Clallam Co.: Mukkaw Bay (L-P); Neah Bay (L-P)

C. cinctipennis imperfecta

BRITISH COLUMBIA.

Mainland. Fairview (UBC); Goldstream to Downie Creek, Selkirk Mountains (UI); Kamloops (UBC); Lillooet (BCP); Midday Valley, Merritt (BCP, UBC); Oliver (UBC).

WASHINGTON.

Adams Co.: Hampton Lake, Columbia Wildlife Refuge (L-P); Lind (L-P); Paha (L-P); Riz ille (L-P).

Asotin Co.: Schumaker Grade, 1.8 mi. S Asotin (WSU).

Benton Co.: Irrigation Experimental Station (L-P); Prosser (L-P); 2 mi. W West Richland (L-P); Roza Experimental Station (L-P).

Chelan Co.: Wenatchee (L-P).

Douglas Co.: 5.9 mi. NW Leahy Junction (SL).

Franklin Co.: Pasco (AM); Perry (L-P); near Ringold (L-P).

Grant Co.: Beverly to 4.2 mi. E Beverly (L-P, SL); Black Lake, 9 mi. NE Moses Lake (L-P); Ephrata (L-P); Grand Coulee (L-P); 2 mi. S Vantage (L-P).

Kittatas Co.: Vantage (L-P).

Walla Walla Co.: College Place (L-P); Gardena (L-P); Lowden (L-P); Reese (L-P); vicinity of Touchet (L-P); Walla Walla (L-P, OSU, UI); Wallula (L-P).

Whitman Co.: Ewan (L-P).

Yakima Co.: Granger (L-P); North Yakima (L-P); Outlook (L-P); Tampico (L-P); Toppenish (L-P); Yakima (L-P).

OREGON.

Crook Co.: Paulina Creek, N of Paulina (OSU).

Harney Co.: Alvord Hot Springs, 5 mi. N Andrews (OSU); 6 mi. S, 2 mi. E. Burns (VC); Malheur Lake (OSU).

Lake Co.: N end Abert Lake (FMB); 6 mi. N Adel (Beer and Maser, 1973); NW shore Alkali Lake (OSU); Summer Lake (OSU).

Malheur Co.: Castle Rock, 6 mi. NW Beulah (OSU).

Morrow Co.: Boardman (OSU).

Wasco Co.: Maupin (OSU); Tygh Valley (OSU).

IDAHO.

Bingham Co.: 0.5 mi. E Aberdeen (RB).

Canyon Co.: Parma (UI).

Caribou Co.: Soda Springs (UI).

Custer Co.: 12 mi. N Challis (OSU).

Minidoka Co.: Paul (UI).

MONTANA.

Flathead Co.: Big Fork, Mt. Aneas (OSU).

C. columbica

WASHINGTON.

Asotin Co.: Clarkston (L-P).

Franklin Co.: Perry (L-P).

Skamania Co.: Cook (L-P).

Whitman Co.: 15 mi. NW Clarkston (L-P); Moses (UI); Wawawai (UI); 4.6 mi. E. Wawawai (SL); 14 mi. SE Wawawai (L-P).

OREGON.

Gilliam Co.: Arlington (Beer, 1971); 3.5 mi. E Blalock (RW).

Hood River Co.: Hood River (OSU).

Sherman Co.: Biggs (Beer, 1971); Rufus (Beer, 1971).

Umatilla Co.: Umatilla (Beer, 1971).

Wasco Co.: 3 mi. E The Dalles (Beer, 1971).

IDAHO.

Idaho Co.: vicinity Slate Creek (Willis and Stamatov, 1971).

C. decemnotata

C. d. n. ssp. Clifford

BRITISH COLUMBIA.

Mainland: "South and southwest" (Wallis, 1961: 40); Quesnel (OSU).

WASHINGTON.

Adams Co.: Lind (L-P); Ritzeville (L-P).

Franklin Co.: Perry (L-P).

Grant Co.: Black Lake, 9 mi. NNE Moses Lake (L-P).

Okanogan Co.: 2 mi. SE Tonasket (SL).

Walla Walla Co.: 2.4 mi. E Wallula Junction (L-P).

Whitman Co.: Ewan (L-P).

C. d. decemnotata

IDAHO.

Bannock Co.: Pocatello, 4483 ft. (OSU).

Bear Lake Co.: Bloomington Lake, 6500 ft. (OSU).

Bingham Co.: Blackfoot, 4500 ft. (UI).

Butte Co.: 2 mi. NW Arco (UI); 20 mi. NE Howe (UI).

Cassia Co.: 3 mi. E Idahome (ODA); Malta (UI); 5 mi. NE Malta

(UI); 7 mi. SE Malta (AM, UI).

Clark Co.: Crystall Falls Cave (ODA, UI).

Jefferson Co.: 4.5 mi. NW Terreton (UI).

Lincoln Co.: Richfield (UI); 6 mi. NE Richfield (UI); 10 mi. NE Richfield (UI); Shoshone (UI).

C. d. decemontata x n. ssp. Rumpp

UTAH.

Rich Co.: Bear Lake, Summit Logan Canyon, 7800 ft. (AM).

C. depressula

C. d. depressula

BRITISH COLUMBIA.

Mainland: Diamond Head Trail, Mt. Garibaldi Provincial Park (F65); Jade Lake Trail, Mt. Revelstoke Nat. Park (F65).

WASHINGTON.

Chelan Co.: 3 mi. E Stevens Pass (SL); E side Cascade Pass Trail (SL).

Clallam Co.: Olympic National Park, Bogachiel (L-P).

Cowlitz Co.: Silverlake (L-P).

King County: 5.8 mi. W Stevens Pass (SL).

Kittitas Co.: Cle Elum (L-P).

Lewis Co.: Longmire (L-P); Skate Creek Rd., Nisqually River (VC).

Mason Co.: Lake Cushman (L-P).

Pierce Co.: Mt. Rainier National Park, several localities (L-P).

Skagit Co.: W side Cascade Pass Trail (SL): Granite Mountain, 1433 m. (SL).

Skamania Co : Goat Mountain Trail (L-P); Mount Adams, 1 mi. W Tahklakn Lake (JS); Mount St. Helens, Windy Pass (DF); North Fork Toutle River, 2000 ft. (DF); Steamboat Mountain (CM).

Snohomish Co.: Arlington (L-P); Meadow Mountain (L-P); Mount Pilchuck (L-P); Stillaguamish River (L-P); Verlot (L-P).

Whatcom Co.: Glacier (DF); Heather Meadows, near Mount Baker Ski Lodge, 4300 ft. (WSU); 1 mi. N north end Nooksack Glacier, 3000 ft. (SL); Silver Lake, 4 mi. N Maple Falls (L-P); Sourdough Mountain (L-P); Twin Lakes, 4 mi. NE Shuksan (L-P).

Yakima Co.: American River (L-P); 0.5 mi. E Chinook Pass (SL); 5 mi. E Chinook Pass (L-P); Mount Adams, Bench Lake (L-P); Naches (L-P); Soda Springs (L-P).

OREGON.

Clackamas Co.: Mount Hood (F65).

Deschutes Co.: Elk Lake (OSU); Sparks Lake (OSU); Three Creeks (OSU); Three Sisters Mountains (OSU); Todd Lake Meadows (F65).

Douglas Co.: Diamond Lake (F65); Three Lakes (UI).

Jackson Co.: Mount Ashland (F65); Rogue Riffles (OSU).

Jefferson Co.: Mount Jefferson (F65).

Klamath Co.: Crater Lake Nat. Park (OSU); Summit Lake (F65).

Lane Co.: Linton Meadows, near Three Sisters Mountains (F65); Scott Lake (F65); Wickiup Plains (F65).

Linn Co.: Big Lake (OSU); Cash Creek, Santiam Road (OSU); Hoodoo Bowl (F65); Marion Mountain (DS); Santiam Pass, summit (OSU).

C. d. eureka

BRITISH COLUMBIA.

Vancouver Island: Tod Inlet, S of Brentwood (BCP).

WASHINGTON.

King Co.: Canation, Tolt River Campground (SL); Seattle (L-P).

Skagit Co.: mouth Finney Creek (L-P).

Snohomish Co.: Darrington (L-P); 6 mi. N Darrington, 2000 ft. (L-P); 6 mi. W Darrington (L-P); Monroe, Snohomish River (L-P).

Whatcom Co.: Deming, 200 ft.

OREGON.

Benton Co.: Corvallis (OSU).

Lincoln Co.: Seal Rock Beach (HLW).

Linn Co.: Albany (F65); Peoria (OSU).

Marion Co.: Salem (Cazier, 1939).

Tillamook Co.: Tillamook (OSU).

Washington Co.: Forest Grove (Field Museum, Chicago).

Yamhill Co.: McMinnville (OSU).

C. d. depressula x *eureka*

WASHINGTON.

Clallam Co.: Forks (L-P).

Jefferson Co.: Hoh River, 550 ft. (L-P); Quinault River, 400 ft. (L-P).

Pierce Co.: Ashford (SL); Crocker, Carbon River (DE).

Whatcom Co.: 4.2 mi. NE Deming (Willis and Stamatov, 1971).

C. haemorrhagica nigroides

WASHINGTON.

Adams Co.: Columbia Nat. Wildlife Refuge (L-P); Lake McElroy, Paha (L-P); Lind (L-P); Ritzville (L-P); 10 mi. W Washtucna (WSU).

Benton Co.: Benton City (UI); 5 mi. E McNary Dam (L-P); Prosser (L-P); Roga Exp. Station (L-P); 2 mi. W West Richland (L-P).

Franklin Co.: Connell (L-P); Kahlotus (L-P); Ringold (WSU).

Grant Co.: 2.2-5.5 mi. E Beverly (L-P); Columbia Nat. Wildlife Ref. (L-P); 5 mi. W Corfu (L-P); Crescent Bar (L-P); 9.1 mi. S, 0.3 mi. W Electric City (L-P); Grand Coulee (L-P); Lake Lenore (L-P); Moses Lake (L-P); 9.9 mi. S Moses Lake (L-P); O'Sullivan Dam (L-P); Soap Lake (L-P); Stratford (L-P).

Kittitas Co.: Vantage (L-P).

Walla Walla Co.: Burbank (UMt); Reese (L-P); 4 mi. W Reese (L-P); 0.5 mi. W Touchet (L-P); Walla Walla (L-P); Wallula (L-P); 2.4 mi. E Wallula Jct. (SL).

Whitman Co.: 15 mi. NW Clarkston (L-P).

Yakima Co.: North Yakima (L-P); Sunnyside (L-P); Toppenish (L-P); Yakima (L-P).

OREGON.

Gilliam Co.: 7 mi. E Arlington (OSU).

Harney Co.: Alvord Hot Springs, 9 mi. N Andrews (Beer and Maser, 1973); 6 mi. S Alvord Ranch (OSU); Harney Lake (OSU); Hot Lake, 5 mi. SE Fields (OSU); 20 mi. W Malheur Lake (ODA).

Hood River Co.: Hood River (OSU).

Lake Co.: Albert Lake (OSU); Lakeview (ODA); Rest Lake, near Summer Lake (OSU); Summer Lake (OSU).

Malheur Co.: Castle Rock (OSU); Ontario (OSU); Snake River, 24 mi. N Ontario (OSU).

Morrow Co.: Boardman (OSU).

Wasco Co.: 2 mi. S Simnasho (OSU).

IDAHO.

Ada Co.: Boise River, Boise (G. Shook coll.).

Canyon Co.: Nampa (UI); Parma (UI); 4.6 mi. SW Roswell (UI).

Elmore Co.: 9 mi. N Mountain Home (UI).

Jerome Co.: Hazelton (UI).

Nez Perce Co.: Arrow Jct., 2 mi. NE Spaulding (R. L. Wescott coll.).

Owyhee Co.: 7.8 Km. N Bruneau (SL); 19 Km. S Bruneau (SL); Bruneau Dunes St. Park (SL); Crane Falls Reservoir (UI); Grandview (UI); Homedale (UI); Hot Creek Falls, Bruneau Canyon (OSU); 5 mi. NW Murphy (UI).

Twin Falls Co.: 6 mi. W Castleford (UI); Twin Falls (UI).

WYOMING.

Teton Co.: Yellowstone Nat. Park (OSU).

Localities where *haemmorhagica*-morphs have been collected with *nigroides* populations

WASHINGTON.

Benton Co.: 2 mi. W West Richland, 1 of 3 (WSU).

Grant Co.: 1 mi. SE Beverly, 1 of many observed (SL).

IDAHO.

Elmore Co.: 9 mi. N Mountain Home, 1 of 24 (UI).

Owyhee Co.: Grandview, 1 of 4 (UI).

C. haemorrhagica haemorrhagica x nigroides

NEVADA.

Humboldt Co.: Winnemucca Lake (UI).

UTAH.

Box Elder Co.: Promontory Point (UI).

C. hirticollis

C. h. ssp. A

BRITISH COLUMBIA.

Mainland: Kamloops (UBC); Wasa Lake, near Kimberly (Wallis, 1961); Oliver (UBC).

WASHINGTON.

Asotin Co.: Clarkston (L-P).

Cowlitz Co.: Kalama (SL).

Franklin Co.: Pasco (L-P); Perry (L-P).

Grant Co.: 1.8 mi. E Beverly (VC); 4.2 mi E Beverly (SL); 11.2 mi. S Vantage (SL).

Kittitas Co.: Vantage (L-P).

Skamania Co.: Cook (L-P).

Spokane Co.: Spokane (L-P).

Walla Walla Co.: Walla Walla (UI).

Whitman Co.: 1.7 mi. W Lewiston (L-P); North Lyon's Ferry (L-P); Pullman (L-P); Wawawai (L-P); 14 mi. SE Wawawai (L-P); Wilma (L-P).

Yakima Co.: Toppenish (L-P).

OREGON.

Baker Co.: Homestead (U. Mass. coll.); Robinette, Brownlee Reservoir (ODA).

Benton Co.: Corvallis (AM).

Multnomah Co.: Rooster Rock St. Park (U. Mich. coll.).

Umatilla Co.: Umatilla (AM).

IDAHO.

Fremont.: 8 mi. NNE St. Anthony (Willis and Stamatov, 1971).

Idaho Co.: 1 mi. SW Slate Creek (Willis and Stamatov, 1971); Whitebird (UI).

Nez Perce Co.: Lapwai (U. Mass. coll.); Lewiston (Ohio St. U. coll.).

C. h. ssp B

WASHINGTON

Grays Harbor Co.: Moclips (L-P).

Pacific Co.: Ocean Park (L-P).

OREGON.

Coos Co.: Hansen (UCD)

Lane Co.: vicinity Florence (AM); Siltcoos Outlet (OSU); Westlake (VC).

Lincoln City: vicinity Waldport (OSU); Yaquina Bay, Newport (U. Nebraska coll.).

Tillamook Co.: Neskowin (J. Knudsen coll.); Pacific City (Ohio St. U. coll.); Sand Lake (OSU); Twin Rocks (OSU); Woods (OSU).

C. lengi versuta

BRITISH COLUMBIA.

Mainland: Chilcotin (CN); Lillooet (BCP).

IDAHO.

Bonneville Co.: 3 mi. SE Idaho Falls (UI).

C. longilabris

BRITISH COLUMBIA.

Mainland: Hope Mountains (BCP).

WASHINGTON.

Chelan Co.: Holden Lake, 5700 ft (L-P); Stevens Pass, 1240 m. (L-P, SL).

Clallam Co.: Olympic Nat. Park, Blue Mountain (L-P); Olympic Nat. Park, Deer Park (L-P); Olympic Nat. Park, Hurricane Ridge (L-P).

King Co.: North Fork Skykomish River, 5000 ft. (L-P); west side Stevens Pass (OSU).

King-Kittitas Co. Line: Deception Pass (L-P).

Mason Co.: North Fork Skokomish River, 1525 m. (OSU).

Okanogan Co.: Black Canyon (NM); Cascade Crest Trail, Windy Pass (L-P).

San Juan Co.: Orcas Island, Mount Moran (L-P).

Skagit Co.: Sauk (L-P).

Snohomish Co.: Glacier Peak, 6400 ft (L-P); Miner's Ridge, east of Glacier Peak, 6400 ft. (L-P).

Whatcom Co.: Copper Mountain, 6000 ft. (L-P); Devil's Pass, east of Ross Lake (L-P); Sourdough Mountain (L-P).

OREGON.

Clackamas Co.: Government Camp, 4000 ft. (NM); Mount Hood (NM).

Curry Co.: Red Mountain Prairie, 53 Km. (by road NE Brookings, 998 m. (ODA).

Deschutes Co.: 10 mi. SW Bend (ODA); Cache Mountain (R. Turnbow coll.); Indian Ford Creek (R. Turnbow coll.).

Douglas Co.: Diamond Lake (OSU).

Hood River Co.: 3 mi. NE Cloud Gap Inn (ODA); 20 mi. S Hood River (ODA).

Jackson Co.: Mount Ashland, 7000 ft. (ODA); Union Creek (NM).

Jefferson Co.: Culver (CM).

Josephine Co.: 25 mi. E Gold Beach (ODA).

Klamath Co.: Crater Lake Nat. Park (OSU); Lake of the Woods (UCD); Cherry Creek, Upper Klamath Lake (OSU).

Linn Co.: Iron Mountain (OSU); Lost Prairie (OSU); Monument Peak (OSU); summit Santiam Pass (NM); Tombstone Prairie (NM).

Marion Co.: Ollalie Lake (AM).

Multnomah Co.: Larch Mountain (ODA).

Wasco Co.: Bear Springs (OSU); Flag Point (ODA); Maupin (OSU).

C. l. laurenti x perviridis

Note: I have listed only those localities from which I have personally examined specimens.

BRITISH COLUMBIA.

Mainland: Ainsworth Hot Springs (NM); Creston (BCP); 11.3 Km. N Creston (SL); Fernie (AM); Hosmer (AM); Kaslo (NM); Lamb Creek (AM); Little Vermillion River (UALTA); New Denver (AM); Okanogan (BCP); Sanca (NM) Wyndel (NM); Yoho Valley (AM).

WASHINGTON.

Columbia Co.: Blue Mountains, Godman Springs, 6000 ft. (L-P); Blue Mountains, Lewis Peak, 4000 ft. (L-P).

Pend Oreille Co.: 7 mi. W Locke (L-P).

Walla Walla Co.: Walla Walla (WSU).

Whitman Co.: Pullman (L-P).

OREGON.

Baker Co.: Anthony Lake (NM); Baker (OSU); Pine Creek, near Baker (NM); Durkee (OSU); Cable Cove, near Sumpter (NM); Big Creek, 26 mi. SE Union, 4200 ft. (WSU).

Grant Co.: summit, Dixie Pass, 1609 m. (SL).

Umatilla Co.: Athena (AM); Deadman's Pass (VC); Tollgate (UCD).

Union Co.: Elgin (ODA); Phillips Canyon, 6.8 Km. NE Elgin, 915 m. m. (SL); 8 mi. E La Grande (HLW); North Powder (Univ. Kansas coll.).

Wallowa Co.: Hot Point, 6982 ft. (OSU); French Forest Camp, Lastine River (OSU); Wallowa Lake (OSU).

IDAHO.

Bear Lake Co.: Bloomington Lake, 8200 ft. (OSU).

Benewah Co.: Emerald Creek (RB); 21.5 mi. NE Potlatch (SL).

Bonner Co.: Priest Lake (UI); Priest River (UI); Sandpoint (UI); 8 mi. N Sandpoint (UI).

Bonneville Co.: Swan Valley (UCD).

Boundary Co.: Brush Lake (UI).

Clearwater Co.: Green (UI); Pierce (UI).

Elmore Co.: Atlanta (NM).

Idaho Co.: Lolo Pass (RB).

Kootenai Co.: Athol (UI); Chilco (UI); Coeur d'Alene (UI).

Latah Co.: Bovill (UI); Cedar Mountain (JS); Harvard (UI); Laird Park, 5 mi. NE Harvard (UI); Sand Creek, 7 mi. SE Harvard (UI); Moscow (UI); Moscow Mountain (UI); 6 mi. N Moscow (UI); Tomer's Butte, 3 mi. SE Moscow (UI); Potlatch (UI); Troy (UI); Viola (UI).

Lemhi Co.: Gibbonsville (U. CO coll.); 6 mi. W Gilmore (ODA); 11 mi. SW Tendoy (UI).

Lewis Co.: 10 mi. N Nez Perce (UI).

Nez Perce Co.: Lake Waha (UI); Spaulding Park (WSU).

Shoshone Co.: Pine Creek, S of Pinehurst, 2700 ft (Carnegie Mus. coll.); Wallace (UI).

Valley Co. Egger's Creek, 4800 ft. (RB); McCall (UI); Yellowpine (UI).

MONTANA.

Flathead Co.: 8 mi. S. Kila (UMT).

Jefferson Co.: Homestake Pass, 1949 m. (SL).

Lewis and Clark Co.: Helena (NM).

Missoula Co.: Blue Mountain (UMT); Greenough (UMT); Kitchen Creek (UMT); Missoula (UMT); Pattee Canyon (UMT).

Ravalli Co.: Darby (NM); 10 mi. SW Darby (UI); 6 mi. NW Hamilton (NM).

Sanders Co.: White Pine (NM).

Silver Bow Co.: Butte (NM).

C. nebraskana

C. n. chamberlaini

BRITISH COLUMBIA.

Mainland: Aspen Grove (AM); Chilcotin (AM, UBC); Copper Mountain (NM); Cranbrook (AM); Creston (AM, UBC); Kamloops (UBC); Lac La Hache (BCP); Lilloet (BCP); Goodfellow Creek, Manning Prov. Park (BCP); Marysville (UBC); Nicola (AM); Okanagan (BCP); Salmon Arm (AM, BCP, NM); Skookumchuck (UBC); Vernon (NM).

WASHINGTON.

Chelan Co.: Lake Chelan (L-P); 18.7 mi. S Leavenworth (SL).

Columbia Co.: Blue Mountains Lewis Peak (L-P); Dayton (L-P).

Cowlitz Co.: Goat Mountain (VC).

Ferry Co.: 15 mi. S Republic (L-P).

King Co.: Red Mountain (L-P).

Kittitas Co.: Cle Elum (OSU); 5 mi. W Cle Elum (L-P); Colockum Pass (L-P); Easton (NM); Ellensburg (L-P); Lake Cle Elum (NM); 1.7 mi. S Lake Katchees (SL); Rocky Run, 2.9 Km. S Snoqualmie Pass (SL); Stampede Pass (SL); Robinson Canyon, 5 Km. SW Thorp (D. E. Wood coll.).

Klickitat Co.: Satus Pass (L-P).

Lewis Co.: North Fork Cowlitz River, Mt. Rainier Nat. Park, 2900 ft. (L-P).

Okanogan Co.: 5.5 mi. E Chesaw (L-P); Gibson Creek, 1 Km. N Conconully (VC); 14 mi. SE Omak (L-P).

Pend Oreille Co.: 7 mi. W Locke (L-P).

Skamania Co.: Little Huckleberry Mountain (OSU); Goat Mountain Trail, 5 mi. N Spirit Lake (L-P); Steamboat Mountain, 5425 ft. (L-P); 10 mi. N Trout Lake (L-P).

Spokane Co.: Spokane (OSU).

Stevens Co.: Blacktail Mtn., 3400 ft. (OSU); Deer Lake, 12 mi. SE Chewelah (WSU); 1.5 mi. E Loonlake (L-P); Northport (L-P); Springdale (L-P).

Walla Walla Co.: Walla Walla (NM).

Whitman Co.: Pullman (L-P).

Yakima Co.: 10 mi. S Bald Mountain (L-P); Bethel Ridge (L-P); Chinook Pass (L-P); Sawmill Flat, 5 Km. N Cliffdel (AM); Mount Adams (L-P); Rimrock Lake (OSU); Tampicco (L-P).

OREGON.

Crook Co.: Grizzly Mountain, 13 Km. NW Prineville (OSU); 23 mi. E Prineville (OSU).

Harney Co.: Steens Mountains (NM, OSU).

Umatilla Co.: Tollgate (OSU).

IDAHO.

Ada Co.: Mile High, 8 mi. NE Boise (G. Shook coll.).

Cassia Co.: 9 mi. W Elba (UI).

Latah Co.: Cedar Mountain (UI); Moscow (WSU); 6 mi. N Moscow (WSU); Moscow Mountain (SL).

Lewis Co.: 10 mi. N Nez Perce (UI).

Owyhee Co.: Silver City (UI).

MONTANA.

Missoula Co.: Missoula (RB).

C. n. nebraskana x *chamberlaini*

IDAHO.

Bannock Co.: Pocatello (NM).

Bonneville Co.: Swan Valley (UI); 11 mi. NE Swan Valley (UI).

Caribou Co.: Soda Springs (AM, NM).

Fremont Co.: 11 Km. NE Ashton (NM).

Teton Co.: Driggs (UI).

WYOMING.

Park Co.: Lake Creek Camp, 13 mi. SE Cooke City (MT), 7200 ft. (AM).

Teton Co.: Teton Nat. Park (AM); Yellowstone Nat. Park (AM, NM).

C. n. nebraskana

(westernmost records only; not included on map)

ALBERTA.

Calgary (NM); Gorge Creek, 160 Km. N Coleman (NM); Empress (NM); Fort McLeod (NM); Lethbridge (NM); Medicine Hat (NM); Paine Lake (NM).

MONTANA.

Gallatin Co.: Bozeman (NM); Gallatin (NM); Lake Hebgen (NM).

Roosevelt Co.: 20 mi. S Scobey (NM).

Wheatland Co.: 15 mi. S Harlowtown (UI).

WYOMING.

Carbon Co.: Bottle Creek Camp, 7 mi. SW Encampment, 8800 ft. (AM).

Hot Springs Co.: Owl Creek Mountains (NM).

Sweetwater Co.: Green River (AM).

C. oregona

C. o. oregona

(all records are from Freitag, 1965, unless otherwise stated)

BRITISH COLUMBIA.

Vancouver Island: Comox; Courtney; Cowitchan Lake; Duncan; Elk Lake; Gabriola; Goldstream; Nanaimo; Pender Harbour; Tod Inlet, S of Brentwood; Victoria.

Mainland: Abbotsford; Agassiz; Ainsworth Hot Springs; Cherryville; Chilliwack; Columbia Lake; Cranbrook; Creston; Selkirk Mountains, 19 mi. W Creston (SL); Fairmont Hot Springs; Field, Yoho National Park; Garibaldi Prov. Park; Harrison Hot Springs; Hatzic; Hope; Howser; Huntingdon; Kamloops; Kaslo; Keremeos; Lillooet; Lynn Valley, 3 Km. E North Vancouver; Lytton; Mabel Lake; Merritt; Mission City; North Bend; Okanagan Lake; Oliver; Osoyoos; Peachland; Penticton; Powell River; Radium Hot Springs; Riondel; Rock Creek; Salmon Arm; Sanca; Shuswap Falls; Stillwater; Summerland; Vancouver; Vaseaux Lake; Vernon; Windemere; Wyndel.

WASHINGTON.

Adams Co.: Othello; 12 mi. W Washtucna (WSU).

Asotin Co.: Asotin; Clarkston.

Benton Co.: 5 mi. N McNary Dam (Freitag and Tropea, 1971); Paterson.

Chelan Co.: Leavenworth; Stehekin; 3.5 mi. E Stevens Pass (SL); Wenatchee.

Clallam Co.: Clallam Bay (SL); Mukkah Bay (SL); Neah Bay (SL); Port Angeles.

Columbia Co.: Huntsville.

Douglas Co.: Moses Coulee.

Franklin Co.: 12 mi. W Eltopia (SL); Kahlotus; Pasco.

Grant Co.: Beverly; 4.2 mi. E Beverly (SL); Dry Falls (OSU); Goose Lake; Grand Coulee (OSU); Half Moon Lake (OSU); Lake Lenore (OSU); Moses Lake; O'Sullivan Dam; Park Lake (OSU); Potholds (OSU); Stratford; 2.3 mi. S Vantage (SL); 11.1 mi. S Vantage (SL).

Grays Harbor Co.: Grayland (DP); Hoquiam Airport (E. W. Stiles coll.); Moclips.

Island Co.: Whidbey Island, Coupeville; Whidbey Island, Deception Pass (DP); Whidbey Island, West Beach (OSU).

Jefferson Co.: Fort Flagler St. Park (SL); Port Townsend.

King Co.: Auburn; Bothell; Tolt River Campground, Carnation (SL); Enumclaw (OSU); Maple Valley; Renton; Lake Sammamish; Seattle; Selleck; Snoqualmie; 7 mi. W Stevens Pass (SL).

Kitsap Co.: Bremerton; Chico; Gorst; Keyport; Kingston; Manchester; Seabeck (OSU).

Kittitas Co.: Cle Elum (OSU); Ellensburg; 7 mi. E Ellensburg (E. W. Stiles coll.); Ginkgo St. Park, Vantage.

Klickitat Co.: 11 mi. E Glenwood (SL); Goldendale; 32.3 mi. N Goldendale.

Lewis Co.: Chehalis.

Lincoln Co.: Sprague.

Mason Co.: Lake Cushman.

Okanogan Co.: Brewster; 7 mi. WNW Pateros, 2900 ft. (J. P. Pelham coll.).

Pacific Co.: Bay Center; Chinook (OSU); Ilwaco; Leadbetter Point (DP); Long Beach; Nahcotta; 1.5 mi. N North Cover (Willis & Stamatov, 1971); Ocean Park.

Pend Oreille Co.: Newport.

Pierce Co.: Buckley; Chinook Pass; Mt. Rainier Nat. Park (OSU); near Roy (P. Joos coll.); Spanaway (P. Joos coll.); Sumner; Tacoma.

San Juan Co.: San Juan Island, False Bay; San Juan Island, Friday Harbor.

Skagit Co.: Anacortes.

Skamania Co.: Little Huckleberry Mountain (OSU).

Snohomish Co.: Darrington; 6 mi. W Darrington (R. Werner coll.); Everett; Index; Lynnwood (SL); Monroe (DF); Silverton, Stillaguamish (OSU); Sultan; Verlot.

Spokane Co.: Medical Lake; Nine Mile Falls (SL); Spokane.

Stevens Co.: Springdale (OSU); Wellpinit.

Thurston Co.: Olympia; Tenino.

Walla Walla Co.: Dixie; Lowden; 0.5 mi. W Touchet (SL); Wallula (Freitag and Tropea, 1971); 3 mi. E Wallula Junction (SL).

Whatcom Co.: Baker Lake (CM); Bellingham; Deming, 200 ft. (DP); 4.2 mi. NE Deming (Willis and Stamatov, 1971); Mt. Baker (? = lodge); North Fork Sauk Creek (OSU); Silver Lake (OSU).

Whitman Co.: Almota; Granite Point (SL); 1.8 mi. W Lewiston (SL); North Lyon's Ferry (SL); Pullman; Steptoe Canyon (WSU); Wawawai; 4.6 mi. E Wawawai (SL); 14 mi. SE Wawawai (SL).

Yakima Co.: North Yakima (OSU); Toppenish; White Swan; Yakima.

OREGON.

Baker Co.: Pine Creek, near Baker (OSU); Durkee (OSU); Farewell Bend St. Park (OSU); Richland.

Benton Co.: Corvallis.

Clackamas Co.: Estacada.

Clatsop Co.: Cannon Beach.

Columbia Co.: Rainier.

Coos Co.: Cape Arago St. Park; Charleston; Coos Bay.

Curry Co.: mouth Hunter's Creek (SL); Humbug Mountain St. Park; mouth Pistol River (SL); Port Orford.

Grant Co.: John Day River gorge (OSU).

Harney Co.: Alvord Hot Springs (OSU); Donner und Blitzen Valley (OSU); Frenchglen; Malheur Lake; Steens Mountains (OSU).

Hood River Co.: Hood River; Mount Hood; Parkdale.

Jackson Co.: Medford; Ruch.

Josephine Co.: Grants Pass; Murphy.

Klamath Co.: 8-9 mi. E Bly (Beer and Maser, 1973); Crater Lake Nat. Park; Klamath Lake; Lake of the Woods; 21.9 mi. E Pinehurst.

Lake Co.: Abert Lake (SL); Crump Lake (OSU); Paisley; 4 mi. E Summer Lake (FMB).

Lane Co.: Eugene; 3 mi. N Florence; Strawberry Hill (SL); 5 mi. S Yachats.

Lincoln Co.: Depoe Bay; Devil's Lake St. Park (OSU); Lost Creek St. Park (SL); Newport; Waldport.

Linn Co.: Cascadia.

Malheur Co.: Succor Creek Campground.

Marion Co.: Detroit.

Multnomah Co.: Portland.

Polk Co.: Buell (OSU).

Tillamook Co.: Pacific City; Tillamook; Woods.

Umatilla Co.: Echo; Hermiston; Meacham Lake (OSU); Umatilla.

Union Co.: Starkey Exp. Forest (Maser, 1976).

Wallowa Co.: Lake Creek, Lostine River (OSU).

Wasco Co.: The Dalles; Tygh Valley.

Yamhill Co.: Dayton; McMinnville.

IDAHO.

Ada Co.: Boise.

Blaine Co.: Carey.

Bonner Co.: Hope; Priest Lake; Sandpoint.

Canyon Co.: Lake Lowell (OSU); Nampa.

Elmore Co.: Atlanta.

Gooding Co.: Hagerman.

Idaho Co.: 9.2 mi. N Riggins (Willis and Stamatov, 1971); 1 mi. N Slate Creek (SL).

Jerome Co.: Jerome.

Kootenai Co.: Cataldo; Coeur d'Alene; Medimont.

Latah Co.: Moscow; Troy.

Nez Perce Co.: S bank Clearwater River, Lewiston (SL); Clearwater River, 0.3 mi. W Lenore (SL).

Owyee Co.: Snake River, 5 mi. NE, 1 mi. E. Bruneau (Willis and Stamatov, 1971); 19 Km. S Bruneau (SL); Bruneau Canyon (OSU); Bruneau Dunes St. Park (SL): Homedale.

Power Co.: American Falls.

Shoshone Co.: Wallace.

Valley Co.: Cascade.

C. o. oregona x *guttifera*

BRITISH COLUMBIA.

Mainland. Athalmer, north of Windemere; Canal Flats; Fernie; Kootenay Nat. Park; Moyie; Wasa; Yoho Nat. Park.

IDAHO.

Bannock Co.: Pocatello.

Bear Lake Co.: Bloomington Lake, 8200 ft.

Custer Co.: Salmon River, 12 mi. N Challis (OSU).

Fremont Co.: 14 mi. NE St. Anthony (Freitag and Tropea, 1971); Parker.

Lemhi Co.: Salmon River, 21 mi. N Salmon; Salmon River, 17 mi. S Salem (SL).

MONTANA.

Flathead Co.: Hungry Horse; Kalispell.

Lake Co.: Moiese Nat. Bison Range (OSU).

Lewis and Clark Co.: Craig; Helena.

Lincoln Co.: Troy.

Missoula Co.: Frenchtown; Missoula (UMT).

Ravalli Co.: Darby; Florence; Hamilton; Lost Horse Canyon.

Sanders Co.: Whitepine.

Silver Bow Co.: Butte.

WYOMING.

Teton Co.: Yellowstone Nat. Park, Beaver Lake (OSU).

C. parowana

C. p. parowana

OREGON.

Malheur Co.: Crooked Creek (VC, SL).

IDAHO.

Canyon Co.: Nampa Canyon (UI).

Cassia Co.: 3 mi. E Idahome (UI).

Owyhee Co.: Jack Creek, 7 mi. S Bruneau (VC, SL).

C. p. platti

OREGON.

Lake Co.: Abert Lake (FMB): Alkali Lake (FMB); 4 mi. E Summer Lake (FMB).

C. p. parowana x *platti*

OREGON.

Lake Co.: Coleman Lake (AM).

C. p. wallisi

BRITISH COLUMBIA.

Mainland: Penticton (AM).

WASHINGTON.

Adams Co.: Lind (L-P); Paha (L-P); Potholes (D.E. Wood coll.); Ritzville (L-P).

Franklin Co. Perry (L-P).

Grant Co.: 4.2 mi. E Beverly (SL); Black Lake, 9 mi. NE Moses Lake (L-P): Blue Lake (L-P); 3-5 mi. W Corfu (L-P); Coulee City (L-P); Dry Falls (L-P); Electric City (L-P); Grand Coulee (L-P); 4 mi. N Moses Lake (L-P); Quincy (WSU); Stratford (L-P).

Okanogan Co.: Goose Lake, 22 mi. W Nespelem (WSU); 2 mi. SE Tonasket (SL).

Walla Walla Co.: 5 mi. W College Place (L-P); Lowden (L-P); Prescott (L-P); Touchet (L-P); Walla Walla (L-P).

Whitman Co.: Ewan (L-P).

OREGON.

Linn Co.: Lost Prairie, 9 mi. E Upper Soda (JS).

Harney Co.: Burns (ODA).

Umatilla Co.: Ordnance (ODA); 2.3 mi. W. Umapine (ODA).

C. plutonica

OREGON.

Klamath Co.: 10 mi. N Beatty (Beer and Maser, 1973); 8-9 mi. E Bly (Beer and Maser, 1973); 8 mi. N, 12 mi. E Bonanza (Beer and Maser, 1973); 7 mi. SE Lorella (FMB).

Malheur Co.: 10 mi. S Adrian (ODA).

IDAHO.

Canyon Co.: Caldwell (OSU); Parma (OSU).

Cassia Co.: 5 mi. NE Malta (UI); 7 mi. SE Malta (UI); 8 mi. SE Malta (UI).

C. pugetana

BRITISH COLUMBIA.

Mainland: Lytton (UBC); Marysville (UALTA); Oliver (UBC); Osoyoos (UBC); Penticton (UBC).

WASHINGTON.

Benton Co.: Prosser (UI, WSU); Richland (L-P); 10 mi. NW Richland, Rattlesnake Mountain, Hanford Reservation (L-P); 2 mi. W West Richland (WSU).

Douglas Co.: Rock Island (L-P).

Grant Co.: Adrian, 5 mi. SW Stratford (NM); 4 mi. E Beverly (L-P); Black Lake (VC); Dead Man's Lake (OSU); Dry Falls (L-P); 5 mi. SW George (L-P); Half Moon Lake (L-P).

Kittitas Co.: Colockum Pass (L-P); 14 mi. E Ellensburg (SL); Vantage (L-P); Saddle Mountains, 12 mi. N Vantage (L-P).

Walla Walla Co.: Lowden (NM); Touchet (L-P); Wallula (UI).

Yakima Co.: Buena (L-P); Toppenish (L-P).

OREGON.

Morrow Co.: Boardman (ODA).

Wasco Co.: Bear Springs, Wapinitia (OSU); The Dalles (OSU).

Wheeler Co.: Pisgah Lookout, Ochoco Nat. Forest, 7 mi. SSW Mitchell, 6812 ft. (ODA).

C. purpurea

C. p. auduboni

BRITISH COLUMBIA.

Mainland: Quesnel (UBC); Williams Lake (UBC).

WASHINGTON.

Asotin Co.: Clarkston (L-P).

Columbia Co.: 15 Km. SE Starbuck, 305 m. (SL).

Franklin Co.: Perry (L-P).

Kittitas Co.: Colockum Pass, 4600 ft. (L-P); Ellensburg, Rob Canyon (L-P).

Lincoln Co.: Hawk Canyon, 8.5 mi. NW Davenport (L-P).

Okanogan Co.: Tunk Mountain, 20 Km. SE Tonasket (VC).

Spokane Co.: Cheney(L-P); Spokane (L-P).

Whitman Co.: Kamiak Butte St. Park (L-P); Palouse (L-P); Pullman, Washington St. Univ. campus (L-P); Wawawai (L-P); Wilma (L-P).

OREGON.

Baker Co.: Durkee (OSU); Pine Creek, near Baker (OSU).

Grant Co.: 12.3 mi. S Kimberly (SL); 3.4 mi. S Long Creek (VC); 12 mi. NE Prairie City (ODA).

Harney Co.: Burns (OSU); Hart Mountains Nat'l. Antelope Ref. (OSU); 5 mi. E Page Springs Campbround, 5500 ft. (WSU).

Klamath Co.: 8-9 mi. E Bly (Beer and Maser, 1973); Klamath River (OSU).

Malheur Co.: 20 mi. S Adrian (ODA); Succor Creek Canyon (VC).

Umatilla Co.: 20 mi. N Dale (VC).

IDAHO.

Ada Co.: Boise (UI); 7 mi. E Boise (RB).

Adams Co.: 5 mi. N Council (UI).

Bannock Co.: Arimo (UI); Pocatello (OSU).

Blaine Co.: 2 mi. E Magic Reservoir (UI); Picabo (UI); 20 mi. N Shoshone (UI).

Camas Co.: Fairfield (NM).

Canyon Co.: Parma (NM).

Cassia Co.: 7 mi. SE Basin (ODA).

Elmore Co.: Dixie (ODA).

Latah Co.: Kendrick (UI); Moscow (UI); Moscow Mountain (UI); Potlatch (UI).

Lemhi Co.: 7 mi. W Gilmore (UI).

Lincoln Co.: Richfield (UI); 7 mi. NE Richfield (UI).

Minidoka Co.: Paul (UI).

Nez Perce Co.: Lewiston (UI).

Owyhee Co.: 10 mi. N Grasmere (RB).

Power Co.: Crystal Ice Cave (ODA).

MONTANA.

Flathead Co.: Kalispell (NM).

Missoula Co.: Blue Mountain (UMT); Missoula (UMT).

WYOMING.

Teton Co.: Yellowstone Nat. Park (NM).

C. p. new name Leffler

BRITISH COLUMBIA.

Vancouver Island: Victoria (BCP).

WASHINGTON.

Pierce Co.: 5 mi. W Graham (L-P); McKenna (L-P); 10 mi. S Parkland (L-P); 2.5 mi. E Puyallup (L-P); 5 mi. S, 2 mi. W Puyallup (L-P); Roy Prairie (L-P); 5 mi. S Roy (L-P); Spanaway (L-P).

San Juan Co.: San Juan Island, Friday Harbor (L-P).

Thurston Co.: 1.5 mi. W Lake Lawrence (L-P); Olympia (L-P); Rochester (L-P); Rocky Prairie, 3 mi. N Tenino (L-P); Vail (L-P).

OREGON.

Benton Co.: Alsea (ODA); Corvallis (ODA, OSU); McDonald Forest, 5 mi. N Corvallis (ODA); Monroe (ODA); Philomath (OSU).

Jackson Co.: 11 mi. SSE Butte Falls (ODA); Medford (OSU).

Josephine Co.: Grant's Pass (OSU).

Linn Co.: Lacomb (OSU).

Marion Co.: West Woodburn (OSU); Woodburn (ODA).

Washington Co.: Forest Grove (OSU).

Yamhill Co.: McMinnville (OSU).

C. p. lauta

WASHINGTON.

Skamania Co.: Dead Man's Lake (VC-sight record).

OREGON.

Hood River Co.: Hood River (NM).

Jackson Co.: Talent (OSU); Wimer (UI).

Josephine Co.: Finley Bend, Rogue River, 8 mi. W Grant's Pass (FMB).

C. p. lauta x new name Leffler

OREGON.

Jackson Co.: Gold Hill (NM); Rogue Riffles (OSU).

C. r. repanda

BRITISH COLUMBIA.

Mainland. Canal Flats (UBC); Creston (UBC); Vancouver (BCP); Yale (BCP).

WASHINGTON.

Asotin Co.: 2 mi. S Asotin (L-P); Couse Creek Canyon, 14 mi. S Asotin (L-P); Clarkston (L-P); Grand Ronde River (L-P).

Benton Co.: Prosser (WSU).

Clark Co.: Washougal (L-P); Reed Island, Washougal (L-P).

Cowlitz Co.: Kalama (SL).

Franklin Co.: Pasco (L-P); Perry (L-P).

Garfield Co.: Central Ferry (L-P).

Grant Co.: 4 mi. E Beverly (SL); Crescent Bar (L-P); Grand Coulee (L-P); 11.2 mi. S. Vantage (SL); White Bluffs Ferry, 7 mi. SW Taunton (WSU).

Kittitas Co.: Vantage (L-P).

Okanogan Co.: Omak (L-P).

Pend Oreille Co.: Newport (L-P).

Walla Walla Co.: 4 mi. W Reese (L-P); 0.5 mi. W Touchet, E bank Toucher River (L-P); 3 mi. E Wallula Junction (L-P).

Whitman Co.: Almota (L-P); 15 mi. NW Clarkston (L-P); 1.7 mi. W Lewiston, N shore Snake River, 830 ft. (L-P); North Lyon's Ferry (L-P); Palouse Falls St. Park (L-P); Penewawa (L-P); Pullman (L-P); Uniontown (L-P); Wawawai (L-P); 4.6 mi. E Wawawai (L-P).

OREGON.

Baker Co.: Robinette, Brownlee Reservoir (ODA).

Benton Co.: Corvallis (OSU).

Gilliam Co.: Arlington (AM).

Grant Co.: John Day Gorge (OSU).

Jackson Co.: 5 mi. NE Medford (OSU).

Lincoln Co.: Delake, Lincoln City (AM).

Linn Co.: Albany (OSU); Peoria (OSU).

Marion Co.: Santian River, 15 mi. S Salem (ODA).

Morrow Co.: Boardman (NM); Irrigon (R. Turnbow coll.).

Multnomah Co: Portland (AM).

Polk Co.: Brodie (OSU).

Tillamook Co.: Woods (OSU).

Umatilla Co.: Hat Rock, 7 mi. ENE Umatilla (OSU).

Yamhill Co.: Dayton (OSU); McMinnville (OSU); Newberg (OSU).

IDAHO.

Bear Lake Co.: N end Bear Lake (AM).

Bonner Co.: 2 mi. S Hope (NM); Priest River (NM).

Canyon Co.: Old Fort Boise, Snake River (G. Shook coll.); Parma (AM).

Clearwater Co.: 8 mi. W Orofino (UI).

Idaho Co.: 9.2 mi. N Riggins (H. L. Willis coll.); 17 mi. N Riggins (UI); vicnity Slate Creek (SL).

Nez Perce Co.: Arrow Junction, 2 mi. W Spaulding (UI); Lapwai (OSU); 0.3 mi. W Lenore (SL); 5 mi. E Lewiston (UI).

Owyhee Co.: 5 mi. NE, 1 mi. E Bruneau (HLW).

Payette Co.: Payette (AM).

MONTANA

Lincoln Co.: Troy, Kootenai River, 1800 ft. (OSU).

Mineral Co.: Alberton, 3000 ft. (OSU).

Missoula Co.: NW of Huson, Clark Fork River (SL).

Sanders Co.: 16 mi. NE St. Regis (OSU); Thompson Falls, 2400 ft. (OSU).

C. tenuicincta

OREGON.

Harney Co.: Harney Lake (OSU).

Lake Co.: Abert Lake (FMB, OSU); 8 mi. W Paisley (OSU); 3 mi. E Summer Lake (OSU).

C. tranquebarica

C. t. "kirbyi"

OREGON.

Harney Co.: Alvord Hot Springs, 5 mi. N Andrews (OSU).

Malheur Co.: Crooked Creek (VC).

IDAHO.

Butte Co.: 12 mi. N Howe (UI).

Caribou Co.: Bancroft (OSU); Soda Springs (U. Nebraska coll.).

Cassia Co.: Almo (UI).

Fremont Co.: St. Anthony Sand Dunes (UI).

Oneida Co.: 0.5 mi. N Samaria (JS).

MONTANA.

Glacier Co.: Blackfoot (UMT).

C. t. "kirbyi" x vibex

IDAHO.

Canyon Co.: Parma (OSU).

Lincoln Co.: Dietrich (SL).

Owyhee Co.: Bruneau Dunes St. Park (SL); 12 mi. W Bruneau (UI); Hot Creek Falls (RB); Hot Springs Falls (SL).

C. t. vibex

BRITISH COLUMBIA.

Vancouver Island: Colwood (BCP); Goldstream (BCP); Victoria (BCP).

Mainland: Boston Bar (SL); Cameron Lake, NW Ft. Steele (UALTA); W shore Columbia Lake (SL); Copper Mountain (UBC); Creston (UBC); Kamloops (UBC); Kaslo (BCP); Lillooet (BCP); Lytton (UBC); Manning Prov. Park (BCP); Marysville (UBC); Merritt, Midday Valley (BCP, UBC);

Moyie Lake, Moye (UALTA); Nicola (UBC); Okanagan Falls (BCP); Penticton (UBC); Salmon Arm (UBC); Sanca (UBC); Wasa Lake, Wasa (UALTA); Wyndel (UBC).

WASHINGTON.

Adams Co.: Lind (H38); Lake McElroy, PAHA (DP); Othello (OSU); Ritzville (UMT); 6 mi. W Washtucna (WSU); 10 mi. W Washtucna (WSU); 12 mi. W Washtucna (WSU).

Asotin Co.: 13 mi. S Asotin (WSU).

Benton Co.: Paterson (L-P); Prosser (WSU).

Chelan Co.: Holden Village (L-P); 18 mi. NNW Leavenworth (ODA); Stehekin (JS); 3.5 mi. E Stevens Pass (SL); Tumwater Rec. Area, 8 mi. W Leavenworth (DP); Wenatchee (UCD).

Columbia Co.: Dayton (H38).

Franklin Co.: Connell (R. W. Dawson coll.); Sand Hills Park, 10 mi. N Kahlotus (WSU); Pasco (L-P); Perry (L-P).

Garfield Co.: Misery Spring, 28 mi. S Pomeroy (WSU).

Grant Co.: 4.2 mi. E Beverly (SL); Black Lake, 9 mi. NE Moses Lake (VC); Corfu (LOP); The Potholes (L-P); Soap Lake (L-P).

Island Co.: Camano Island (L-P); Coupeville, Whidbey Island (L-P); Ebeyer's Landing, Whidbey Island (L-P); Greenbank, Whidbey Island (L-P); Sunnyside, Coupeville, Whidbey Island (L-P); West Beach, Whidbey Island (L-P).

King Co.: Seattle (L-P).

Kittitas Co.: Cle Elum (L-P); Colockum Pass (SL); Easton (L-P); East Nelson Siding, 7 mi. E Easton (L-P).

Klickitat Co.: Goldendale (DP).

Lewis Co.: Cowlitz River, Packwood (VC); 7 mi. SW Packwood (VC); Randle (VC); 7.5 mi. E Randle (VC).

Lincoln Co.: Hawk Canyon, 8.5 mi. NW Davenport (L-P); Lincoln (H38); Sprague (H38).

Okanogan Co.: Brewster (L-P); 5.5. mi. E Chesaw (L-P); 10 mi. W Colville Indian Agency (D. R. Paulson coll.); Omak (L-P); 14 mi. S Omak (DP).

Pend Oreille Co.: Bead Lake (L-P); 7 mi. W Locke (L-P); Metalline Falls (DP); Newport (L-P); Sullivan Lake (L-P).

Pierce Co.: Mt. Rainier Nat. Park (R. C. Graves coll.).

San Juan Co.: American Camp, San Juan Island (L-P); Friday Harbor, San Juan Island (L-P); Kanaka Bay, San Juan Island (L-P).

Spokane Co.: Cheney (L-P); Mount Spokane St. Park, 5200 ft. (L-P); Nine-Mile Falls (L-P); Spokane (L-P); 5 mi. S Spokane (VC); Turnbull Wildlife Refuge (L-P).

Stevens Co.: Chewelah (WSU); Deer Lake, 12 mi. S Chewelah (WSU); Colville (DP); 1.5 mi. E Loon Lake (VC); Springdale (L-P).

Walla Walla Co.: Burbank (H38); 5 mi. W College Place (CM); Dixie (DP); Kooskooskie (L-P); Lowden (DP); Prescott (L-P); Touchet (L-P); Walla Walla (L-P); 3 mi. S Wallula (WSU); 3 mi. E Wallula Junction (L-P).

Whitman Co.: Almota (H38); Ewan (H38); North Lyon's Ferry (L-P); Palouse Falls St. Park (DP); Penewawa (DP); Pullman (L-P); S end Rock Lake (L-P); 5.6 mi. SE Sprague (SL); 6.6 mi. SE Sprague (SL); Wawawai (L-P); 4.6 mi. E Wawawai (L-P); 9 mi. E Wawawai (SL).

Yakima Co.: Granger (L-P); Satus (H38); Toppenish (H38).

OREGON.

Baker Co.: Baker (OSU); Durkee (OSU); Big Creek 26 mi. SE Union, 4200 ft. (WSU).

Benton Co.: Corvallis (OSU).

Crook Co.: Suplee (OSU).

Deschutes Co.: Indian Fork Creek, 6 mi. W Sisters (OSU).

Douglas Co.: Cow Canyon (OSU).

Grant Co.: Dixie Pass, 5200 ft. (SL); 12.3 mi. S Kimberly (SL); Prairie City (ODA).

Harney Co.: 6 mis. S, 2 mi. E Burns (VC).

Jackson Co.: Gold Hill (E. D. Harris, 1901).

Josephine Co.: Wonder (OSU).

Klamath Co.: Fort Klamath (G. Horn, 1866).

Lake Co.: Abert Lake (JS); Fossil Lake (OSU).

Marion Co.: 1 mi. N Detroit (SL); 2.1 mi. E Mill City (SL); Salem (ODA).

Morrow Co.: Boardman (OSU); Cecil (OSU); 20 mi. N Dale (VC).

Mulnomah Co.: Portland (DP).

Umatilla Co.: Cold Springs, Blue Mountains (OSU); Echo (ODA); 5-7.8 mi. W Langdon Lake (ODA); Meacham Lake (OSU); Milton-Freewater (OSU); Tollgate (WSU, UCD); 5 mi. W Tollgate (ODA): Umatilla (OSU, UI).

Union Co.: 5 mi. S. Elgin (VC).

Wallowa Co.: Hurricane Canyon, 1.6 mi. S, 2.3 mi. W Joseph (SL); Lostine River (OSU); Wallowa Lake (OSU).

Wasco Co.: Moody (DP); The Dalles (OSU).

Wheeler Co.: Summit Prairie (JS).

IDAHO.

Benewah Co.: Palouse Divide, 21.5 mi. NE Potlatch (SL).

Boise Co.: Lowman (G. Shook coll.).

Bonner Co.: Priest Lake (UI); Sandpoint (UI).

Clearwater Co.: Pierce (UI).

Gooding Co.: Hagerman (UI).

Idaho Co.: Whitebird (UI); Wild Goose Camp (UMT).

Kootenai Co.: Athol (UI); Chilco (UI); Coeur d'Alene (UI); 12 mi. N Coeur d'Alene (U. Kansas coll.).

Latah Co.: Bovill (UI); 5 mi. W Clarkia (SL); Laird Park, 5 mi. NE Harvard (WSU); Sand Creek, 7 mi. SE Harvard (WSU); 3 mi. S Helmer (WSU); Moscow (WSU); Moscow Mountain (SL); Potlatch (UI); Troy (UI); Viola (UI); Yale (UI).

Nez Perce Co.: Lewiston (UI).

Shoshone Co.: Clarkia (UI); Wallace (UI).

Valley Co.: Donnelly (UI).

MONTANA.

Flathead Co.: Glacier Nat. Park, Camas Creek (OSU); McWiniger's (UMT).

Missoula Co.: base Blue Mountain (UMT); Missoula (UMT).

Sanders Co.: 12 mi. NE St. Regis (OSU).

C. willistoni echo

OREGON.

Harney Co.: Alvord Hot Springs, 5 mi. N Andrews (Beer and Maser, 1973); Harney Lake (OSU).

Lake Co.: Abert Lake (FMB); Alkali Lake (FMB); Coleman Lake (NM); Rest Lake, near Summer Lake (OSU); 4 mi. E Summer Lake (FMB).

IDAHO.

Owyhee Co.: Bruneau Dunes St. Park (Willis and Stamatov, 1971); 7.8 Km. N Bruneau, St. Hwy. 51, 778 m. (SL).

APPENDIX II

TYPOLOGY

Four Pacific Northwest subspecies are either in press or the proposing papers have not yet been prepared. Thus, they are not included in this list. They are:

Cicindela arenicola n. ssp. Clifford

Cicindela bellissima n. ssp. Leffler

Cicindela decemnotata n. ssp. Clifford

Cicindela purpurea new name Leffler

Pacific Northwest Type Localities of Cicindelidae

BRITISH COLUMBIA.

1. British Columbia. *Cicindela ostenta columbiana* [*Cicindela longilabris laurenti* x *perviridis*].
2. Kootenay. *Cicindela obliquata* var. *borealis* [*Cicindela tranquebarica vibex*].
3. Penticton. *Cicindela pugetana*; *Cicindela wallisi* [*Cicindela parowana wallisi*].

WASHINGTON.

Franklin Co.:

4. Perry. *Cicindela bellissima columbica* [*Cicindela columbica*].

King Co.:

5. Seattle. *Omus audouini distans* [*Omus audouini*]; *Omus dejeani robustus* [*Omus dejeani*].

Pierce Co.:

6. Tacoma. *Omus audouini tacomae* [*Omus audouini*].

Walla Walla Co.:

7. Walla Walla. *Cicindela carthagena* var. *nigroides* [*Cicindela haemorrhagica nigroides*].

Yakima Co.:

8. Buena. *Cicindela purpurea* ab. *nigerrimoides* [*Cicindela pugetana*].

OREGON.

"Oregon Territory and northern California as far as San Francisco (LeConte, 1957: 41)":

9. *Cicindela oregona* [*Cicindela oregona oregona*].

Oregon (state only):

10. *Omus audouini*; *Omus audouini delicatulus* [*Omus audouini*]; *Omus audouini parvulus* [*Omus audouini*]; *Omus borealis* [*Omus audouini*]; *Omus dejeani*.

"Mittel-Oregon (W. Horn, 1903)":

11. *Omus vandykei* [*Omus audouini*].

Clackamas Co.:

12. Bull Run. *Omus dejeani foveatus* [*Omus dejeani*].

Harney Co.:

13. Steens Mountains. *Cicindela longilabris chamberlaini* [*Cicindela nebraskana chamberlaini*].

Jackson Co.:

14. Gold Hill. *Cicindela vulgaris* var. *roguernsis* [*Cicindela tranquebarica vibex*].

Josephine Co.:

15. Selma and Waldo. *Omus aequicornis* [*Omus audouini*]; *Omus oregonensis* [*Omus audouini*].

Klamath Co.:

16. Fort Klamath. *Cicindela vibex* [*Cicindela tranquebarica vibex*].

17. Upper Klamath Lake. *Omus thoracicus* [*Omus audouini*].

Lincoln Co.:

18. Yaquina Bay. *Cicindela bellissima* [*Cicindela bellissima bellissima*].

IDAHO.

Fremont Co.:

19. St. Anthony Dunes. *Cicindela arenicola* [*Cincdela arenicola arenicola*].

APPENDIX III

SUMMARY OF THE HISTORICAL GEOLOGY OF THE PACIFIC NORTHWEST

Overview of Historical Geology of the Entire Pacific Northwest

Carpenter (1953) outlined the fossil record of insects, noting that Coleoptera first appeared by the late Permian. Thus, it is with the Permian that I begin this account.

Permian (Schuchert, 1935).

Throughout the Permian, most of the Pacific Northwest was non-marine. In early Permian, only southwestern Oregon had a marine environment. By middle Permian a broad marine embayment extended from southwestern Oregon to southern Idaho, western Montana, and parts of southeastern British Columbia, and northeastern Washington. By late Permian, the entire region was again non-marine.

Mesozoic (Lawson, 1936; Smith and Packard, 1919).

In the late Jurassic, a marine embayment extended from Nevada across eastern Oregon to the Oregon-Idaho border. It is probable that the Sierra-Nevada and central Idaho batholiths are continuous and of Jurassic age. They consist of laminated argillite characteristic of deposition on a sea floor remote from high-grade streams.

In the Cretaceous, the Klamath and Blue Mountains had emerged, and, between them, the Chico Sea extended from California to the southwestern flanks of the Blue Mountains. Much of the Cretaceous history consisted of essentially continuous igneous activity with the development of large intrusive masses.

Tertiary.

Because of the complexity of the geological history of parts of the Pacific Northwest, I will present an overview of the Tertiary history of the entire area first, follows by more detailed treatment of certain regions under separate headings.

General Tertiary History

At the start of the Tertiary (Snavely and Wagner, 1963), western Washington and Oregon were submerged from Skagit County, Washington, to

the Klamath Mountains, Oregon. The coastline was just east of the Cascade Mountains crest. Correlation of the Pacific Northwest fossil floras with estimated average elevation of the Cascade Range and its effect on annual precipitation is given in Table modified from Smiley (1963).

Eocene: In the early Eocene, a broad, low-lying swampy coastal plain with large, meandering streams covered the western part of the regoin except for highlands in northern Washington and southwestern Oregon. East of this plain was a region of low, forested terrain extending to the present-day Rocky Mountains area but interrupted by highlands in the Blue Moutntains and central Idaho. Fossil floras (Chaney, 1925) from Oregon (Ashland, Cherry Creek) indicated climatic conditions like the modern coastal California redwood forest: frequent and heavy sea fogs, temperatures rarely below -9° C or above +38° C, annual precipitation 0.5-1.5 m., mainly as winter rains. The fossil floras consisted of a forest of conifers dominated by *Metasequoia* and broad-leafed evergreen angiosperms, characteristic of a subtropical climate.

Table. 85 . Correlation of Pacific Northwest fossil floras with estimated average elevation of the Cascade Range and its effect on annual precipitation (adapted from Smiley, 1963, who gave annual precipitation for members of the Ellensburg formation only.)

FLORA		AGE	CASCADES ELEVATION (in meters)	ANNUAL PRECIPITATION (in meters)
Alturas	(NE. CA)	Middle Pliocene	———	———
Deschutes	(C. OR)		———	———
Post Ellensburg	(C. WA)		762-914	0.6-0.8
Alvord Creek	(SE. OR)	Early Pliocene	———	
Upper Ellensburg	(C. WA)		610	0.8-0.9
Upper Dalles	(NC. OR)		———	
Middl Ellensburg	(C. WA)	Mio-Pliocene	457	1.0-1.2
Lower Dalles	(NC. OR)	Late Miocene	———	———
Lower Idaho (Weiser)	(SWC. ID)		———	———
Thorn Creek	(SWC. ID)		———	———
Lower Ellensburg	(C. WA)		91-305	1.0-1.2
Payette	(SWC. ID)		———	———
Upper Cedarville	(NE. CA)		———	———
Trout Creek	(SE. OR)		———	———
Succor Creek	(SE. OR)		———	———
Stinking Water	(SE. OR)		———	———
Vantage	(C. WA)	Middle Miocene	91	———
Blue Mountains	(NE. OR)		———	———
Mascall	(C. OR)		———	———
Latah	(E.WA, NW.ID)		———	———
Eagle Creek	(NE. OR)	Early Miocene	———	———

By late Eocene, the platform of the Cascade Range had developed through volcanic activity and the Olympic Mountains had begun to lift.

Oligocene: A gradual general uplift over the entire region eliminated much of the swampy coastal plain, although the general aspect of the flora remained the same as in the Eocene. The flora consisted of a mixture of the Arcto-Tertiary, Neotropical-Tertiary, and Paleotropical-Tertiary Geofloral elements of the Eocene with widespread *Metasequoia* forests. The palms of the Eocene were absent, showing a cooling trend toward a subtropical climate. Also, presence of a flora characteristic of well-drained slopes indicates progressively impaired drainage. Coastal volcanism ended the coal-forming environment as well as cutting off drainage in the northern part (Chaney, 1925; Snavely and Wagner, 1963).

Miocene: The early Miocene situation was little different than that of the Oligocene. The general trend of drying continued because of continued uplift of the Cascade Range. The effect on the flora was the beginning of an influx of the Madro-Tertiary Geoflora and the gradual elimination of Neotropical- and Paleotropica-Tertiary Geofloral elements.

A major geological event occurred in the middle Miocene when great volumes of basalt flowed from numerous fissures throughout eastern Washington, eastern Oregon, and southern Idaho, some of the flows extending west of the Cascades. Kittleman (1973) stated that the abundant fossils showed that life flourished despite the volcanic actvity.

General uplift occurred so that the maximum inland marine extent was only in the Grays Harbor Basin of western Washington and just south of the mouth of the present-day Columbia River. By the late Miocene, the Puget-Willamette lowlands contained large, shallow lakes. The Cascade, Coast, and Olympic Ranges were developing and reduced the area of marine deposition.

Pliocene: The region west of the Cascades was marked by periodic uplift and erosion along the coast and a period of laterization in the Willamette Valley (Baldwin, 1976). The early Pliocene Troutdale flora just east of Portland, Oregon (Chaney, 1944), retains several Miocene species including East American and East Asian elements nearly extinct east of the Cascades. A climate similar to that of modern coastal Oregon is indicated. Upwarping and folding at the close of the Pliocene raised the basement of the Cascades to its present elevation.

Climate east of the Cascades was only slightly more mesic than it is today. The elevation of the Cascades produced a continental climate of saesonal extremes and reduced total annual precipitation. Available fossil floras show elimination of elements requiring summer rainfall. Leopold (1969: 407) stated that the late Miocene Trapper Creek flora of southwestern Idaho contains 35% of genera now foreign to the area and only 9% by the Pliocene-Pleistocene boundary. The Deschutes flora (late middle Pliocene) showed that conifer forest was no longer present near sites of deposition in some areas east of the Cascades, reflecting developing of a rain shadow created by

elevation of the range (Wolfe, 1969). The modern landscape of canyons, plateaus, and mesas had largely developed by the end of the Pliocene (Baldwin, 1976).

Pleistocene: By the start of the Pleistocene[(0.5-2 myBP (Kulp, 1961)], the Rocky Mountains (Walker, 1966), the Owyhee Uplands (Kittleman, 1973), the Okanogan and Olympic Highlands (Snavely and Wagner, 1963), and the platform of the Cascade Range (Baldwin, 1976) had neared their present elevations. Only the development of the major volcanic cones in the Cascades, further rising of the Rocky Mountains, and the Coast Range Orogeny have occurred since (Walter, 1966).

Besides orogenic and tectonic events, the Pleistocene has been marked by successive advances and retreates of alpine and continental glaciation in the Cascade Range, Okanogan Highlands, northern Puget Sound Trough, and in the Rocky Mountains and their western front ranges.

Dawson (1890) named the continenal ice sheet that extended westward from the Rocky Mountains ". . . the Cordilleran Glacier in order to distinguish it from the second and larger ice-cap by which the northeastern part of the continent was . . . covered." At its maximum, it extended from off the Pacific Ocean shore east to the Rocky Mountains, north from latitude 63° B south to latitude 48° N, with several lobes extending north and south along mountain ranges and large low-lying districts, with the main gathering ground between 55°-59° N latitudes. The ice sheet was not uniform throughout the entire region and was even locally absent in the Cranbrook and Moyle areas and parts

of the Cariboo, British Columbia where valleys are V-shaped and glacial scarring occurs only on high peaks (Rice, 1936).

The ice sheet consisted of a coalescence of valley glaciers from the Rocky Mountains and Cascades and the mass flowed northwest at the north end and southeast at the south end (Flint, 1935). In portions of British Columbia and northern Washington, the ice sheet surface was at an elevation up to 2356 m. as evidenced by absence of moraines, grooving, and scratches above that height (Rice, 1936).

In addition to the ice sheet covering the northern portion of the Pacific Northwest, there was extensive but localized alpine glaciation in portions of the Olympic, Oregon and southern Washington Cascade, Wallowa, and Wasatch Ranges, and in the Klamath, Steens, and middle Rocky Mountains.

Glacial-Interglacial terminology of North American has been based on the eastern or Laurentide ice sheet. Much uncertainty remains as to details of correlation between these "classic" advances and retreats and those of the Rocky Mountains and west of the Cascades. There is a standard terminology for the Rockies and a sequence for the lobes that covered the Puget Trough. Correlation is difficult because of differences in local conditions. Although details of contemporaneity vary, there were basically four glacial periods separated by three interglacial periods. The several advances and retreats were not uniform in extent and duration and one or more were multiple or even partial.

It was the final glacial advance (Wisconsin in the Great Plains, Pinedale in the Rocky Mountains, and Vashon west of the Cascades) that

was most extensive. There is a nearly complete record of Quaternary climates for the southern Great Plains (Taylor, 1965), but lack of older records make correlation with the Pacific Northwest impossible before postglacial times (Leopold, 1967).

Dillon (1956) and Hanson (1947) summarized evidence that biotic zones were not eliminated by the advancing ice but, rather, were compressed from north to south. Dillon (1956: fig. 11) suggested that of the life zones of Merriam (1899): the Alpine-Arctic covered Washington, northern Idaho, and western Montana; Hudsonian covered the Cascades and the eastern third of Oregon; and Canadian extended over the remainder. The Transitional and Upper Sonoran zones, so extensive in modern time, were no closer than 500 km to the south. However, it is possible that the Cascade Range exerted a mollifying protective effect on the area immediately adjacent to the east resulting in a northern extension of biotic zones. Many species were driven south of their present ranges, but there was extensive commingling of biota (Leopold, 1967).

Postglacial period: Heusser (1977: 300-301) estimated that late Wisconsin July climatic conditions in the Cascades and Olympics approximated the modern situation in the St. Elias Range along the Alaska-Yukon border. Mean July temperature and annual precipitation for the St. Elias Range are +2° C and 2.1 m. at 1765 m. elevation and -2° C and 1.3 m. at 2620 m. elevation, +12° C and 4.4 m. at nearby sea level. Colder and drier climates must have occurred east of the Cascades where climate-moderating effects of the ocean were blocked. Regions west of the Cascades were certainly milder.

There is evidence for an abrupt temperature rise on a global level, the time of which marks the end of the Pleistocene. Antevs (1931) defined the beginning of the Postglacial period as the time when temperatures, particularly summer temperatures, in the southern parts of the newly deglaciated area had risen to those of the present time. Broecker *et al.* (1960) summarized evidence from several geographic systems that the temperature change occurred in a period of less than one thousand years duration, resulting in a climate similar to that of modern times. Their data indicate that climate change was not uniform, minor fluctuations having occurred. Lamb (1960) showed that the climate change occurred at about 10,000 yBP, based on biological evidence from central Europe, the Nethlands, and in tropical Atlantic surface waters. Similarly, Duncan *et al.* (1970) established the Pleistocene-Holocene boundary at 12,500 yBP based on deep-water faunal stratigraphy off the coasts of Washington and Oregon.

Hansen (1947: 35) calculated the rate of ice-front retreat from the Puget Trough at about 42 km/yr., thus requiring five thousand years for total ice-sheet withdrawal from Washington, too long a period insofar as wastage also was occurring from the north and west as well as the south. Some recession dates based on Heusser (1960: 180) are:

Locality	yBP
Sedro Woolley, WA	12,900 ± 330
Lower Fraser River Valley, BC	11,300
Queen Charlotte Islands, BC	10,850 ± 800
Juneau, AK	10,300 ± 400-600
Kenai Peninsula, AK	9,600 ± 650

The weight of the continental ice-sheet--McKee (1972: 296) claculated that it exerted a base pressure of 56.25 kg/cm.^{2} at Seattle --depressed the northern half of the continent as much as 122 m. below its present elevation, depression from which the region has as yet only partially recovered. Peacock (1935) stated that coastal British Columbia was depressed 488 m., but has since only rebounded 183 m. and the fjords are drowned intermontane valleys. Bretz (1919) stated that, immediately following recession of the ice-sheet, sea level in Puget Sound was 88 m. above the present level following a maximum depression of 24 m. Submergence lagged behind deglaciation, with highest-water levels not reached until the ice front had retreated 117-167 km.

Heusser (1960), following well-established terminology, divided the Postglacial period into three sections, each delineated by absolute dates:

Section	Beginning Date (yBP)	Climatic Trends
Late Postglacial	Juneau, AK (3,500)	
	WA (2,950)	As at present
	CA (2,500)	
Hypsithermal	Several localities	Maximum warmth
	(8,000)	and dryness
Early Postglacial	Juneau, AK (10,300)	
	S.W. BC (11,300)	Cool and moist
	N.W. WA (12,900)	

The Postglacial period had three events of major effect, and several of regional importance (these latter occurrences will be discussed in detail beyond under their respective regions):

1. Climatic changes. There is widespread synchroneity of dates for the three divisions of the Postglacial period and its concomitant temperature changes. The early Postglacial climate was abruptly warmer and wetter than that of the immediately preceding glacial period, but was colder than that of today. Heusser (1977) estimated that the mean July temperature at sea level on the Pacific coast of Washington was 12°-15° C, compared with 15°-16° C today. West of the Cascades, the pioneer forest of *Pinus contorta* and *P. monticola* was superseded by *Pseudotsuga menziesii* and *Tsuga heterophylla* within three to four thousand years (Hansen, 1947). East of the Cascades, the pioneer forest was replaced by *P. ponderosa* because of a gradual drying trend. Similarly, the Great Basin was extensively forested in the early Postglacial period with *P. contorta*. In northeastern Washington, northern Idaho, western Montana, and

southern British Columbia, the pioneer forest has persisted to the present.

The increase in temperature and decrease in precipitation during the Hypsithermal was expressed in a northward extension of xeric grasses and shrubs east of the Cascades and restriction of conifers to higher elevations. West of the Cascades, *Quercus garryana* and *Pinus ponderosa* invaded respectively from south and east, and *Picea sitchensis* was eliminated from the Puget Trough and Willamette Valley. Heusser (1977) reconstructed the coastal mean July temperature at 17° C, about at 12% increase.

There has been a lowering of temperature and an increase in precipitation since the Hypsithermal. The result has been relegation to relicit status of *Q. garryana* and *P. ponderosa* west of the Cascades and some restriction of xeric associations east of these mountains. The initial increased precipitation resulted in partial redevelopment of Great Basin pluvial lakes, but the precipitation increase was only temporary, and the lakes have been steadily declining in area and increasing in salinity. Jones (1925) calculated that Pluvial Lake Lahontan required only 1956 years to change from fresh water to the salinity of its present remnants.

The significance of the climatic changes to the Pacific Northwest Cicindelidae is that their effects on floral assemblages and edaphic factors have governed the extent of the ranges of some of the tiger beetle species. Ranges alternately expanded, contracted, or fragmented depending on the valences of the species involved.

Species intolerant of forested areas could not have entered the Columbia or northern Great Basin until Hypsithermal time unless islands of xeric conditions occurred. Similarly, forest species that may have inhabited what is now xeric scrub and grassland had their ranges restricted as these areas become deforested. Perhaps only riparian species were unaffected as long as waterways persisted.

2. Pluvial lakes. I have followed Hubbs and Miller (1948: 22) in referring to the periodically recurring late Pleistocene and postglacial lakes with the epithet "pluvial (e.g., Pluvial Lake Lahontan)". The extent of these lakes was shown by Feth (1961). These lakes developed in basins of internal drainage that were only interconnected at all at times of extremely high water-levels or before regional uplift destroyed such connections. For instance, Miller (1958) suggested a Pliocene or early Pleistocene connection between the now-separate Lahontan and Bonneville basins.

Morrison (1961b) listed three general deductions about the Bonneville and Lahontan systems which, from data from Hubbs and Miller (1948), also apply to adjacent Great Basin systems, and which are adapted as follows:

a. Fluctuations of the pluvial lake levels were similar and synchronous.

b. Fluctuations paralleled development of alpine glaciers: when lakes levels were high, glaciers were extensive.

c. Lakes dried up considerably or completely between deep-water intervals, correlating with reduction in size of the glaciers.

The significance of the pluvial lakes to Cicindelidae is that the lakes were alternately large or small in are through late Pleistocene and Postglacial time. Habitat suitable for the several lake shore Great Basin species was alternately extensive and contiguous or limited and widely discontinuous. At the present time, the lakes are declining in area. The surface elevation of remnants of Pluvial Lak Lahontan in western Nevada is 1180 m., compared with 1332 m. at the early Postglacial maximum (Morrison, 1961a: figure 329.1). During the entire postglacial period alone, there have been eight fluctuations, high-water marks of which averaged 26 m. above the present level. During the middle Wisconsin, Pluvial Lake Bonneville emptied into the Snake River (Trimble and Carr, 1961) as a catastrophic flood, but, since then, the highest water mark has been 64 m. lower than the lowest divide from the Snake River drainage (Red Rock Pass, Bannock Co., ID) an elevation of 1485 m. The lake had a surface elevation of 1280 m., 8000 yBP (Crittenden, 1963). It has fluctuated eight times since, with Great Salt Lake presently having a surface of 1334 m. (Morrison, 1961a: figure 329.1) at its south end, although the elevation has risen slightly because of isostacy following relief from the weight of the new evaporated water.

Beetle population may have not been isolated long enough to become reproductively incompatible (speciation) yet long enough to develop differences in color and maculation. Perhaps this is why the Great Basin fauna consists of only a small number of species and subspecies, some very variable.

3. Spokane Flood. There were at least 40 floods that affected the Columbia Basin during and since the Wisconsin glaciation. This flooding has been known by several names (Bretz or Missoula Flood, for instance), but "Spokane Flood" is generally the accepted name (McKee, 1972). The exact chronology is still under study, but Hansen (1947: 13) suggested that the floods corresponded with the end of the Wisconsin glaciation. A lobe of ice extended southward along the Purcell River in northern Idaho, damming up the Clark Fork River. The result was the periodic formation of Pluvial Lake Missoula, whose surface elevation was up to 1280 m.--Missoula, Montana, south of its center, has an elevation of 975 m. (Pardee, 1910)--and which covered as much as 4100 km.^{2}, about 30% of western Montana. When the ice dam broke up, the lake emptied as a catastrophic torrent southwestward across eastern Washington to enter the Columbia River at Wallula. The floods were up to 330 km. wide north to south and about 84 km.^{3} in volume, the giant ripple marks they left indicating a velocity of 12 km./hr. (Thornbury, 1965). The water stripped away much of the loessal and glacial outwash veneer from a six-county area, deeply eroding the underlying basalt and leaving the floodway known as the Channeled Scablands.

Isostatic depression of the land and wasting of the ice-sheet had raised sea level 88 m. above the present level. Thus, the enormous volume of water required some time to empty into the ocean. Narrowness of the Columbia Gorge further slowed down the flow. The backed up water in the Columbia Basin formed Pluvial Lake Lewis. Water also backed up the Snake River Canyon. The extent is not given by McKee (1972) or

Bretz (1919), but water undoubtedly filled one-third of the depth of the 760 m. deep canyon at Lewiston, Idaho (elevation 252.), and perhaps extended nearly to Hell's Canyon and well up Clearwater and Lochsa Canyons. Impaired drainage at the mouth of the Columbia River backed up water into the Willamette Valley and adjacent lowlands of southwestern Washington, Willamette Gulf thus formed extending south to Eugene, about 170 km. south of the Columbia River. Surface elevations are determined by positions of glacial erratics, boulders remaining after icebergs containing them had melted. On petrographic evidence, the erratics originated in southeastern British Columbia, large ones being over 4 $m.^3$ in volume (Allison, 1935; Bretz, 1919).

Some surface elevations indicating the level and extent of Pluvial Lake Lewis and Willamette Gulf are as follows (from Allison, 1935; and Bretz, 1919):

Locality	Present elevation	Elevation of erratic
Grand Coulee, WA	549 m.	391 m.
The Dalles, OR	30 m.	366 m.
Corvallis, OR	68 m.	76 m.
Eugene, OR	129 m.	122 m.

McKee (1972) estimated a duration of but a few weeks for passage of the flood waters. This was sufficient itme for deposition of a thick layer of siit and gravel on the floor of the water-covered area, fill as thick as 90 m. at Portland. Scrutiny of Hansen's (1947) pollen profiles from eastern Washington reveals no effects on vegetation, indicating a catastrophy too short in duration to register in the profiles, alhtough, admittedly, pollen profiles are probably not refined enough to show events of less than even a few hundred years' duration. Following

drainage of Pluvial Lake Lewis, the exposed deep silt formed the source of much of the upper portion of the loess mantle of the Palouse (McKee, 1972).

Significance of the Spokane Flood to Cicindelidae is that the fauna was extirpated from the affected area. Samll populations may have survived on islands, but habitat such as salt pan, riparian sand bars, and lake shores were surely completely destroyed. Such habitat would have to be redeveloped, requiring some length of time, before becoming suitable for cicindelid reoccupation. Willamette Valley forests were drowned and they and their fauna had to recolonize the flooded area from adjacent higher lands. River courses and prairies also required time for reestablishment.

Regional Historical Geology

The following accounts are treatment of 14 areas into which I have divided the Pacific Northwest for the sake of convenience. They present more detail about regional occurrences. These discussions are to be used in conjunction with the respective discussions of the associated cicindelid faunas presented in the body of the present report.

1. Southwestern British Columbia including Vancouver Island. This region has had an eventful Tertiary history (Johnston, 1923), but all the postglacial sequence is irrelevant to Cicindelidae because the entire area except for mountain peaks over 2100 m. elevation was covered by the Cordilleran ice-sheet. Immediately following the beginning of recession of the ice-sheet, forest, rather than tundra, covered the newly exposed land. A radiocarbon date for a bog in the Fraser Valley of c. 11,300 yBP gives the approximate time of glacial recession (Armstrong, 1956). The

only major vegetational change has been the seral one from a *Pinus contorta* pioneer assemblage to the present dominance of *Pseudotsuga* and *Tsuga*, although the heat of the Hypsithermal presumably increased fires which favored increased growth of alder (Heusser, 1960).

Isostatic emergence has occurred since the recession of the ice. Mathews (1951) mentioned marine clays and pelecypods at the head of Howe Sound occurring at 30.4 m. above present sea level. In addition to these isostatic changes, glaciers have been active until the nineteenth century A.D. between Mt. Garibaldi and the Georgia Strait effectively cutting off any dispersal route between the Fraser River and the coastal Massif.

2. Olympia Peninsula. The Olympic Peninsula consists of a central highland rising to over 2100 m. elevation, an eastern shoreline in the rain shadow of the highland, a gradual western slope of rain forest with several large rivers, and a shoreline of dune areas and headlands. The peninsula developed during a Miocene orogeny. The highlands were largley separated from southern land masses by marine embayments through the Pliocene. Connections eastward and northward were obliterated by Pleistocene glaciation (McKee, 1972).

The Juan de Fuca lobe of the Cordilleran ice-sheet extended along the northern ridge of the Peninsula and over the northwest corner to a point 10 km. south of the mouth of the Hoh River. The mountains were covered with expanded alpine glaciers. Pollen profiles from two localities on the west side document the history of the past 47,000 years (Heusser, 1977). They indicate a fluctuation between forest and non-forest flora corresponding to the third glacial period (34,000-47,000 yBP), a 6,000 year-long interglacial period dominated by *Tsuga* forest, a non-tree

sequence during the fourth glacial until 10,000 yBP, and, finally, the postglacial period which has changed from an *Alnus-Picea-Pseudotsuga* forest to one dominated by *Tsuga* and an increase of *Abies*.

3. Coastal strip of Washington (excluding Olympic Peninsula) and Oregon. This area corresponds to the Coast Range Pysiographic Province *fide* Franklin and Dyrness (1973), and consists of the Coast Range and a shoreline of interspersed sand dunes and headlands. By the middle Miocene, most of the Coast Range had been uplifted and had reached its present elevation by the Pleistocene (Snavely and Wagner, 1963). The shoreline has been an area of alternate uplift and subsidence with Pliocene terraces up to 487 m. above sea level, and, during the last 15,000 years, there has been a partial drowning of sections of the coast (McKee, 1972). The extensive dunes have developed where inshore hills are neither too close nor too high. They are best developed along the central Oregon and southern Washington coast. Other parts of the coast consist of rugged headlands unsuitable for extensive dune formation (McKee, 1972).

4. Klamath Mountains and adjacent coast. Southwestern Oregon contains some of the oldest rocks in the entire Pacific Northwest. The Klamath Range has been emergent since the late Triassic and except for some local late Cenozoic deposits in the highlands and terrace deposits along the coast, the entire region consists of rocks of Cretaceous age and older (McKee, 1972). Diller (1902) considered the highlands to have been peneplained, perhaps during the early Tertiary, as evidenced by the uniformity of mountain summit elevations. He also recorded sixteen periods of coastal uplift, subsidence and erosion, the latest being a recent subsidence resulting in drowning of some estuaries and river

river mouth valleys.

5. Puget lowlands. This area corresponds to the Puget Trough Physiographic Province *fide* Franklin and Dyrness (1973). All of it was covered by the Vashon lobe of the Cordilleran ice-sheet up to a depth of 1220 m., which withdrew at the rate of 167 m./yr. about 10,500 yBP (McKee, 1972). Plant succession was the same as that along the coast with allowances for lesser total annual precipitation because of effects of distance from the ocean and the Olympic Mountains (Neusser, 1977).

6. Willamette and lower Columbia Valleys. Until the middle Miocene this area was covered by ocean bordered by marshland. This was a time of warmth and high precipitation as shown by extensive bog deposits of limonite and bauxite. In the middle Miocene, basalt flows from east of the still-low Cascades extended down the Columbia River to the ocean. Redwoods survived through the Pliocene. The entire area became a lake as glaciers in Washington and the Oregon Cascades melted and the water backed up because of rising ocean level. This flooded area was called Willamette Sound by Condon (1902). The limited palynological data show presence of conifer forest at least during the late Pleistocene followed by Hypsithermal influxes of *Pinus ponderosa* and *Quercus garryana*, still present as relict stands.

7. Cascade Range. The Cascades began their gradual rise during the Oligocene and Miocene and achieved their present elevation by the Pleistocene except for the Recent volcanic cones (Smiley, 1963). The portion north from Stevens Pass largely consists of old metamorphic rock, whereas the rest of the range is volcanic in origin. The Pleistocene

saw extensive alpine glaciation, still occurring today although on a reduced scale. The several volcanoes in the Cascades date between Pleistocene and Recent. Mt. St. Helens lacks the extreme glacial scarring of the other cones and thus developed in the last twelve thousand years (McKee, 1972: 209). The volcanoes are considered dormant, although Mt. Baker is presently emitting steam and Mt. Rainier had a major mudflow within the last five thousand years. Glacier Peak erupted 6750 ± 200 yBP, sending volcanic ash eastward to central Montana and Alberta. Glacier Peak's eruption did not destroy its summit as did that of Mt. Mazama which formed a caldera 6453 ± 250 yBP (Heusser, 1960) and emitted another far-reaching ash blanket. Hansen (1947) showed that, at least, in Oregon, the ash fallout slowed down forest succession by deposition of a pumice mantle and its resultant sterile soil.

8. Rocky Mountains and adjacent ranges. I am considering under this heading a large area including the Kootenay of British Columbia, the Okanogan Highlands and northeastern corner of Washington, the northern half of Idaho, western Montana, and eastern Idaho. This area is considered together because of the similarity of the cicindelid fauna rather than geological similarity. The northern portion of the area was covered by the Cordilleran ice-sheet up to 2130 m. elevation, and much of the rest of the region had extensive alpine glaciation. Postglacial pollen profiles (Hansen, 1947) show a sequence of *Pinus contorta* followed during the Hypsithermal by an influx of grasses, and leading to the present *Pinus monticola* subclimax in the northern part of the region.

9. Wallowa-Blue Mountains. This area of southeastern Washington, northeastern Oregon, and an adjacent part of Idaho, is one of the geologically oldest in the Pacific Northwest, with deposits dating before the Devonian (Baldwin, 1976). The postglacial history based on a pollen profile from Anthony Lakes (Hansen, 1947) indicates altitudinal changes in tree assemblages which indicate great influence by fire. The Snake River Canyon has been an important corridor for some tiger beetle species. Wheeler and Cook (1954) have shown that its present course between the borders of Idaho and Oregon may only date from early Pleistocene. They stated that the original course may never be learned but hypothesize how through stream capture and deformation a northward flow from Teritary Lake Idaho was established.

10. Palouse Grasslands. This region is considered part of the Columbia Basin Physiographic Province by Frankin and Dyrness (1973) but its cicindelid fauna is so distinct that I wish to consider it separately here. The area was, until 75 years ago, ponderosa parkland-bunchgrass association, but, through logging and clearing of the forest for agricultural purposes, forest is now restricted to a few preserves and some river canyons. The Columbia Basalt bedrock is covered with a veneer of loess derived from glacial outwash into the Columbia Basin from the receding Cordilleran ice-sheet. None of the area was glaciated and only the western margin was touched by the Missoula flood.

11. Columbia Basin and Okanagan. This region receives the main effect of the rain shadow produced by the Cascade Range. Until the middle Pliocene, it was an area of mixed conifer and hardwood forest, but now it is an extremely arid region with a mosaic of riparian, halic, and thin,

drained soil habitats. Only the Okanagan was glaciated, but the remainder of the area was affected by glacial outwash and flooding. Fryxell (1962) showed that more than one major flood ravaged the region during the Pleistocene but the breaking of the Pluvial Lake Missoula ice-dam had the most recent effect, producing the channeled scablands and backing up water to form Pluvial Lake Lewis which had a depth up to 391 m. as evidenced by glacial erratics at Grand Coulee (Bretz, 1919). Feth (1961) showed a map of the extent of Pluvial Lake Lewis, and McKee (1972) stated that it may have existed only as long as the great volume of backed up water required for drainage into the ocean. Hansen's (1947) data showed that the postglacial period saw an influx of *Pinus monticola* followed by the xeric Hypsithermal assemblages and replaced by a mixture of late postglacial *Pinus ponderosa* and xeric floras. Halic situations may then be no older than the Hypsithermal and their associated cicindelid faunas probably entered from the south at that time.

12. High Lava Plains. This is a ridge of largely recent lava extending from the headwaters of the Deschutes River eastward to the Blue Mountains. Newberry Caldera, at the west end, developed during the Pleistocene and has continued activity up to the last few centuries, the youngest cinder cones being only four to five hundred years old (Williams, 1935). Hubbs and Miller (1948) presented evidence based on fish faunas that some lake basins just south of the ridge belong to the Columbia drainage rather than to the Lahontan Basin (e.g., Harney Basin).

13. Snake River Plains. Southern Idaho is traversed by a broad, inhospital expanse of Columbian Basalt. The Snake River which flows through the region has a peculiar drainage pattern. The source of water for the portion east of American Falls is the headwaters in the Rocky Mountains. The tributary's waters sink into the basalt plains and finally empty into the river in the form of springs in the vicinity of Hagerman. Most of the western portion was submerged under a large lake until the late Pliocene (Tertiary Lake Idaho) whose westward drainage is in doubt but may have been by way of the Owyhee, Humboldt, Pit, and Sacramento Rivers to the Pacific Ocean (Hubbs and Miller, 1948; Wheeler and Cook, 1954).

There was a catastrophic flood caused by overflow of Pluvial Lake Bonneville during its earlier stage and dated 30,000-40,000 yBP (Trimble and Carr, 1961). The overflow into the Snake River was by way of the Bonneville River, the boulders and gravels indicating a velocity of 20-60 km./hr. In addition, five fingers of Pluvial Lake Bonneville extended into Idaho at highest water, 200 m. above the present lake level (Antevs, 1925). Recent history of the region is noted for the heavy winds from southwest to northeast which have formed scattered areas of aeolian dunes.

14. Great Basin. This region includes part of southern Idaho south of the Snake River Plains and also southeastern Oregon. It is the continuation northward of the Great Basin of Nevada and Utah and is divisible into the eastern drainage basin of Pluvial Lake Bonneville and the western one of Pluvial Lake Lahontan.

Table 86. Type Localities of Valid Taxa of the Pacific Northwest

TAXON	TYPE LOCALITY	AUTHOR
Omus dejeani	Oregon	Reiche (1838)
Omus californicus californicus	CA. Marion Co., Pt. Reyes	Eschscholtz (1829)
Omus audouini	Oregon	Reiche (1838)
Cicindela repanda repanda	America septentrionale	Dejean (1825)
Cicindela oregona oregona	Ore. Territory & no. Calif. to San Francisco	LeConte (1857)
Cicindela depressula depressula	CA. Placer Co.	Casey (1897)
Cicindela depressula eureka	CA. Humboldt Co.	Fall (1901)
Cicindela hirticollis sspp.	- - - - - Currently under review by R. C. Graves - - - - -	
Cicindela bellissima bellissima	OR. Lincoln Co., Yaquina Bay, Newport	Leng (1902)
Cicindela bellissima n. ssp. Leffler	- - - - - Not yet published - - - - -	
Cicindela columbica	WA. Franklin Co., Perry	Hatch (1938)
Cicindela arenicola arenicola	ID. Fremont Co., St. Anthony Dunes	Rumpp (1967)
Cicindela arenicola n. ssp. Clifford	- - - - - Not yet published - - - - -	
Cicindela decemnotata decemnotata	On Missouri Riv. above confluence w/Platte Riv. (probably East Montana)	Say (1817)
Cicindela decemnotata n.ssp. Clifford	- - - - - Not yet published - - - - -	

Table 86 (continued)

TAXON	TYPE LOCALITY	AUTHOR
Cicindela purpurea auduboni	ND. Williams Co., Ft. Union	LeConte (1845)
Cicindela purpurea lauta	CA. Siskiyou Co.	Casey (1897)
Cicindela purpurea new name Leffler	CA. Placer Co., Dutch Flat	Leffler (in press)
Cicindela plutonica	CA. Placer Co.	Casey (1897)
Cicindela pugetana	BC.	Casey (1914)
Cicindela longilabris perviridis	CA. and OR.	Schaupp (1883-4)
Cicindela nebraskana chamberlaini	OR. Harney Co., Steens Mountain	Knaus (1925)
Cicindela parowana parowana	UT. Iron Co., Little Salt Lake, NW of Parowan	Wickham (1905)
Cicindela parowana platti	CA. Mono Co., Benton's Crossing SE of Crowley L.	Cazier (1939)
Cicindela parowana wallisi	BC. Penticton	Calder (1922)
Cicindela amargosae nyensis	NV. Nye Co., 1.6 mi. S Springdale	Rumpp (1956)
Cicindela willistoni echo	UT. Salt Lake Co., Great Salt Lake	Casey (1897)
Cicindela haemorrhagica nigroides	WA. Walla Walla Co., Walla Walla	Hatch (1938)
Cicindela tenuicincta	Redesignated in present paper: UT. Salt Lake Co., Saltair	Schaupp (1883-4)
Cicindela lengi versuta	Manitoba. Aweme	Casey (1913)
Cicindela tranquebarica vibex	OR. Klamath Co., Fort Klamath	G. Horn (1866)
Cicindela cinctipennis imperfecta	"California boreas," probably Colorado Desert in the state of California	LeConte (1851)

APPENDIX IV

KEYS TO PACIFIC NORTHWEST CICINDELID FAUNA

Larval Key

1A. Caudal frontal ridge transverse and confluent with posterior edge of frons (genus *Omus*).....2

B. Caudal frontal ridge U-shaped and anterior to and not confluent with posterior edge of frons (genus *Cicindela*).....4

(1A) 2A. Spine of inner hook of abdominal tergum V about twice as long as setae on shoulder of hook; pronotal color light rufous with irregular brown spots.....*Omus dejeani*

B. Spine of inner hook of abdominal tergum V about same length as setae on shoulder of hook; pronotal color other than above.....3

(2B) 3A. Pronotal color black with pale margin; caudal frontal margin with 3 setae.....*Omus audouini*

B. Pronotal color uniformly light brown; caudal frontal margin with 5 setae.....*Omus californicus*

(1B) 4A. Supernumerary pronotal setae numerous, >50, generally distributed, primary setae difficult to recognize.....5

B. Supernumerary pronotal setae if present few in number, <20, located in longitudinal row near midline, primary setae longer and stouter than secondary or supernumerary setae.....6

(4A) 5A. Supernumerary head and pronotal setae terete and pointed; pygopod surrounded by 20-24 setae.....*Cicindela bellissima*

B. Supernumerary head and ponotal setae flattened anteroposteriorly and square-ended; pygopod surrounded by 16 setae.....*Cicindela hirticollis*

(4B) 6A. Primary pronotal discal setae 6 and 7 absent.....7

B. Primary pronotal discal setae 6 and 7 present.....8

(6A) 7A. Head and pronotal color dark violet-bronze with green reflections; spine of inner hook of abdominal tergum V one-third of length of entire hook; pygopod surrounded by 18 setae.....*Cicindela pugetana*

B. Head and pronotal color metallic red-violet with blue reflections; spine of inner hook of abdominal tergum V one-half of length of entire hook; pygopod surrounded by 22-24 setae.....*Cicindela pugetana*

(6B) 8A. 1st antennal segment with 9 or more setae (true for couplet 5 also) (*maritima*-group).....9

B. 1st antennal segment with less than 9 setae.....11

(8A) 9A. Pronotum without longitudinal rows of secondary setae on either side of midline.....*Cicindela repanda*

B. Pronotum with longitudinal rows of secondary setae on either side of midline and incorporating primary setae 1 and 5.....10

(9B) 10A. Pronotum with blue reflections; pygopod surrounded by 18 setae.....*Cicindela oregona*

B. Pronotum with brassy-green reflections; pygopod surrounded by 20 setae.....*Cicindela depressula*

(8B) 11A. Distalmost seta of median hook of abdominal tergum V directed dorsally, other(s) directed anteriorly (subgenus *Cicindelidia*).....12

B. All setae of median hook of abdominal tergum V directed anteriorly.....14

(11A) 12A. Dorsal setae of head long; pygopod surrounded by 18 setae; Type I hypopleuron.....*Cicindela amargosae*

B. Dorsal setae of head short or moderate; pygopod surrounded by 16 setae; Type I or II hypopleuron.....13

(12A) 13A. Spine of inner hook of abdominal tergum V > one-third of length of entire hook; Type II hypopleuron.....*Cicindela willistoni*

B. Spine of inner hook of abdominal tergum V < one-quarter of length of entire hook; Type I hypopleuron.....*Cicindela haemorrhagica*

(11B) 14A. Type II hypopleuron.....*Cicindela parowana*

B. Type I hypopleuron.....15

(14B) 15A. Setae of head and pronotum yellow or brown.....16

B. Setae of head and pronotum glassy or white.....17

(15A) 16A. Setae of head and pronotum yellow; spine of inner hook of abdominal tergum V one-half of length of entire hook.....*Cicindela decemnotata*

B. Setae of head and pronotum brown; spine of inner hook of abdominal tergum V one-third of length of entire hook.....*Cicindela nebraskana*

(15B) 17A. Ventral elevations of abdominal sternum IX with 3 main setae.....18

B. Ventral elevations of abdominal sternum IX with 4 main setae.....19

(17A) 18A. Spine of inner hook of abdominal tergum V rudimentary.....*Cicindela cinctipennis*

B. Spine of inner hook of abdominal tergum V one-third of length of entire hook.....*Cicindela longilabris*

(17B) 19A. Pronotal color black with violet reflections; pygopod surrounded by 18 setae.....*Cicindela lengi*

B. Pronotal color violet with green reflections; pygopod surrounded by 22 setae.....*Cicindela tranquebarica*

Pupal Key

Note: Available material does not permit differentiation of species of the *maritima*- and *formosa*-groups.

1A. Pronotum trapezoidal in outline, long base anterior; setae on apex of spines of abdominal tergum V arranged in I-pattern; metathoracic wings rudimentary, not visible without deflecting mesothoracic wing (genus *Omus*).....2

B. Pronotum rectangular in outline, broader than long; setae on apex of spines of abdominal tergum V arranged randomly in patch; metathoracic wings well-developed and fully visible (genus *Cicindela*).....3

2A. Four short spines, arranged transversely on dorsum of abdominal tergum V, in addition to large dorsolateral spines; labrum with squared median apical lobe; basal depressions of pronotum rounded and not extending to basal margin.....*O. dejeani*

B. Abdominal tergum V with dorsolateral spines only; labrum with equilaterally triangular apical lobe; basal depressions of pronotum extending to basal margin.....*O. audouini*

(1B) 3A. Setae of dorsolateral spines of abdominal tergum V arranged in patch on anterior face of distal quarter of spine, not apically; medial edge of eye straight.....*C. (Cylindera) cinctipennis*

B. Setae of dorsolateral spines of abdominal tergum V arranged as patch on apex of spine; medial edge of eye concave or convex.....4

(3B) 4A. Dorsolateral spines of abdominal tergum V with isolated seta on posterolateral face; medial edge of eye concave; narrow, posteriorly-directed interocular extension of median frontal boss present....*C. (Tribonia) tranquebarica*

B. Dorsolateral spines of abdominal tergum V lacking isolated seta on posterolateral face; medial edge of eye convex; interocular extension of median frontal boss absent (except in *C. nebraskana*).....5

(4B) 5A. Lateral pronotal margins arcuate; vertex broad and shallowly concave in transverse cross-section.....*C. (Cicindelidia) haemorrhagica*

B. Lateral pronotal margins straight; vertex deeply concave and U-shaped in transverse cross-section (subgenus *Cicindela*).....6

(5B) 6A. Median frontal boss extending between eyes to occiput.....*C. (C.) nebraskana*

B. Median frontal boss restricted to area anterior to eyes.....remaining species of *Cicindela*

Adult Key

1A. Pronotum trapezoid in outline, long base anterior, with anterolateral angles extending anteriorly to level anterior of anterior margin of prosternum; metathoracic wings rudimentary; elytra fused along suture. (genus *Omus*).....2

B. Pronotum rectangular in outline, broader than long, with anterolateral angles extending no farther anteriorly than anterior margin of prosternum; metathoracic wings well-developed and functional; elytra not fused along suture (genus *Cicindela*).....4

(1A) 2A. Elytral punctures large, foveate, irregularly arranged, and each with seta; size large: greatest pronotal breadth of males > 5.8 mm., of females > 6.6 mm.....*Omus dejeani*

B. Elytral punctures variable in shape and arrangement but not foveate or setiferous; size not large: greatest pronotal breadth of males < 5.2 mm., of females < 5.9 mm.....3

(2B) 3A. Lateral pronotal margins steeply declivous, and with corners of anterolateral pronotal angles not completely visible in dorsal view; elytral punctures irregularly arranged and wider than smooth area between punctures.....*Omus audouini*

B. Pronotum in transverse cross-section evenly arcuate to flattened, and with corners of anterolateral pronotal angles completely visible in dorsal view; elytral punctures variable but, when developed, regularly arranged and equalling or narrower than smooth area between punctures.....*Omus californicus*

(1B) 4A. Pro- and mesotrochanters lacking subapical setae; venter of abdomen non-metallic reddish.....*Cicindela haemorrhagica*

B. Pro- and mesotrochanters both with subapical setae present; venter of abdomen not reddish.....5

(4B) 5A. Frons densely setose.....6

B. Frons glabrous, with clusters of setae anteromedial to eyes (may be only 2-4 setae per cluster), or with scattered setae.....17

(5A) 6A. Labrum unidentate.....7

B. Labrum tridentate.....11

(6A) 7A. Genae setose.....8

B. Genae glabrous.....9

(7A) 8A. Antennal scape with apical sensory setae only.....*Cicindela repanda*

B. Antennal scape with setae in addition to apical sensory setae.....*Cicindela arenicola*

(7B) 9A. Elytral maculation reduced to apical spot only.....*Cicindela amargosae*

B. Elytral maculation complete.....10

(9B) 10A. Antennal scape with 1-2 setae in addition to apical sensory setae.....*Cicindela hirticollis*

B. Antennal scape plurisetose in addition to apical sensory setae.....*Cicindela tenuicincta*

(6B) 11A. Ratio, basal breadth/length of labrum > 52%.....*Cicindela parowana*

B. Ratio, basal breadth/length of labrum < 52%.....12

(11B) 12A. Elytral sculpture granulate or punctate, not both.....13

B. Elytral sculpture granulate-punctate.....14

(12A) 13A. Elytral sculpture granulate with punctures obsolete or absent; elytral lustre dull....*Cicindela pugetana*

B. Elytral sculpture punctate; elytral lustre shiny.....*Cicindela plutonica*

(12B) 14A. Marginal line complete; humeral lunule long and oblique and often nearly touching middle band; OR all maculation confluent.....*Cicindela lengi*

B. Marginal line absent or reduced to no more than anterior and posterior extension of middle band.....15

(14B) 15A. Humeral lunule long and oblique.....*Cicindela tranquebarica*

B. Humeral lunule C-shaped, reduced to humeral dot, or absent.....16

(15B) 16A. Middle band long, angulate, distant from margin; Type N mesepisternal coupling sulcus.....*Cicindela decemnotata*

B. Middle band short, obtusely angulate, distant from margin; Type B mesepisternal coupling sulcus.....*Cicindela purpurea*

(5B) 17A. Ratio, basal breadth/length of labrum > 55%; frons concave.....18

B. Ratio, basal breadth/length of labrum < 55%, frons gently, evenly convex between eyes.....19

(17A) 18A. Elytral punctures irregularly arranged, not in distinct transverse rows; ratio, length metatibia/length metatarsus < 99%, usually < 95%.....*Cicindela longilabris*

B. Elytral punctures arranged in disting but sometimes wavy transverse rows; ratio, length metatibia/length metatarsus ≥ 100%.....*Cicindela nebraskana*

(17B) 19A. Elytral not microserrulate.....*Cicindela cinctipennis*

B. Elytral microserrulate.....20

(19B) 20A. Humeral lunule C-shaped.....21

B. Humeral lunule long and oblique or reduced to humeral dot.....22

(20A) 21A. Antennal scape glabrous except for apical sensory setae.....*Cicindela columbica*

B. Antennal scape shaft plurisetose.....*Cicindela willistoni*

(20B) 22A. Humeral lunule long and oblique; frons with scattered setae.....*Cicindela hellissima*

B. Humeral lunule reduced to humeral dot; frons with clusters or 2-4 setae anteromedial to eye.....23

(22B) 23A. Frons with cluster of 10-11 setae anteromedial to eye; anterior margin of transverse arm of middle band concave....*Cicindela oregona*

B. Frons with 2-4 setae anteromedial to eye; anterior margin of transverse arm of middle band straight.....*Cicindela depressula*

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