Systematics and ecology of the *sexguttata* species group, genus *Cicindela* (Coleoptera: Cicindelidae).

by

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ABSTRACT

The systematics of *Cicindela sexguttata* Fabricius and *Cicindela patruela* Dejean was studied. Various aspects of their holomorphology were considered, including: multivariate analysis of external characters, morphology of the genitalia, distribution, habitat, and life history. Colour of the exoskeleton is not a stable character in this group and is not used in taxonomic decisions. The species *C. denikei* Brown is a sibling species of *C. sexguttata*, not a subspecies as previously described. The egg and third instar larva of *C. denikei* are described for the first time. The larval burrow of *C. denikei* opens directly beneath rocks and stones, a habit unique in *Cicindela*. The species *C. sexguttata* occurs throughout Eastern North America and consists of several identifiable subpopulations which are characterized by ecophenotypic characters only, and are not recognized taxonomically. The species *C. patruela* consists of two subspecies, *C. p. patruela* and *C. p. consentanea* Dejean. The distributions, habitats, and life histories of *C. sexguttata*, *C. denikei*, *C. p. patruela*, and *C. p. consentanea* are described. The distribution of *C. sexguttata* is correlated with warm moist loamy soils. Populations of *C. denikei* are found on sandy silty till deposited by Lake Agassiz. Some of the variability in the populations of *C. sexguttata* is accounted for by differences in dominant soil type. Climate and geographic features

also account for some variability. The different number of mature eggs in the abdomens of adult females of *C. sexguttata* and *C. denikei* indicate that the fecundity of the two species differs. Adults of *C. denikei* are ambush predators that change ambush site frequently. Encounters with prey modify the behaviour of the beetles such that they remain in the vicintity of the encounter. The beetles have a defended territory that moves with them as they forage.

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

W. Kauuiaus

December 7, 1982

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INTRODUCTION

Many of the North American species of _Cicindela_ have large ranges, and within these species there is a great deal of variation in size, colour, maculation, and pilosity (Horn, 1908; Wallis, 1961). This variability has led to a proliferation of names and a general state of confusion about the gamma, and, to some extent, beta taxonomy of the genus. Recent work has cleared up the problems in some species groups (Freitag, 1965; Willis, 1967; Gaumer, 1977; Leffler, 1979), but problems remain in others (Wallis, 1961).

The species _C. sexguttata_ is highly variable (Leng, 1902; Shelford, 1917), with nine synonyms and one subspecies currently recognized (Boyd et al., 1982). The species _C. patruela_ has frequently been ranked as a subspecies of _C. sexguttata_ (Schaupp, 1884; Horn, 1930) and only recently has it been generally recognized as a species (Rivalier, 1954; Wallis, 1961). Recent authors have suggested that _C. sexguttata denikei_ Brown is in fact a sibling species of _C. sexguttata_ (Wallis, 1961; Willis, 1968; Leffler, 1979). Other authors have recognized or suggested the resurrection of names that had been synonymized (Eckhoff, 1939; Rivalier, 1954; Ward, 1971). Shelford (1917) speculated that much of the variation in body colour and maculation was due to differences in soils which affected larval developement. In view of these problems a taxonomic review of the _sexguttata_ species complex is in order.

The objectives of this study were as follows: determine whether

C. sexguttata denikei and C. sexguttata are sibling species, if so, conduct investigations on the life history and ecology of denikei and describe the immature stages; determine whether the various populations of C. sexguttata that had been named are subspecies or ecophenotypes; determine whether the variation in C. sexguttata is correlated to soils as postulated by Shelford (1917); determine whether C. p. consentanea is an ecophenotype, subspecies, or sibling species of C. patruela; determine the relationship of C. patruela to C. sexguttata and their relationship to other species in the genus Cicindela.

In determining the taxonomic rank of the populations, much evidence of the holomorphology of the forms are used; including multivariate analysis of morphological characters, morphology of the genitalia, distribution, habitat, and life history. In assigning the rank of species, subspecies, or ecophenotype to a population it is important to define what is meant by these terms, particularly as there is some debate as to their meaning and validity. The definitions used in this study are given below; for a thorough treatment see also Amadon (1949), Wilson and Brown (1953), Edwards (1954), Gosline (1954), Hubbel (1954), Parkes (1955), Smith and White (1956), Owen (1963) and Gaumer (1977).

Ecophenotype - "...the same genotype produces a different result under different circumstances. Such differences are nongenetic..." (Ross, 1974, p. 28).

Subspecies - " A subspecies is an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species" (Mayr, 1963, p. 210).

Species - "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1963, p. 12).

Materials and Methods

Material Obtained on Loan

Approximately 9085 specimens were examined in the course of this study, of which 4400 were used in numerical analysis. Much of this material was obtained on loan from the institutions and individuals listed below. In certain cases, I dealt with more than one individual at an institution; in recognition of their assistance, both names are given.

AMNH	American Museum of Natural History. Central Park West at 79th St. New York, New York. 10024
	L. Herman
BGSU	Bowling Green State University, Bowling Green, Ohio. 43403
	R. C. Graves
CASC	California Academy of Sciences, Golden Gate Park, San Francisco, California. 94118
	D. H. Kavanaugh and G. C. Hunter
CNCI	Canadian National Collection, K. W. Neatby Bldg. Ottawa, Ontario. K1A 0C6
	J. E. H. Martin and A. Smetana
CU	Carleton University, Ottawa, Ontario. K1S 5B6
	H. F. Howden
ICCM	Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania. 15213
	G. Ekis and R. Davidson
CUSC	Clemson University, Clemson, South Carolina. 29631
	J. C. Morse
CUIC	Cornell University, Comstock Hall, Ithaca, New York. 14853
	L. L. Pechuman

FMNH	Field Museum of Natural History, Roosevelt Rd. at Lakeshore Dr. Chicago, Illinois. 60605
	L. Watrous
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. 02138
	A. F. Newton
INHS	Illinois Natural History Survey, 172 Natural Resources Bldg. Urbana, Illinois. 61801
	D. W. Webb
KSUC	Kansas State University, Manhattan, Kansas. 66506.
	H. D. Blocker
MPM	Milwaukee Public Museum, 800 West Wells St. Milwaukee, Wisconsin. 53233
	G. Noonan
MSU	Montana State University, Boseman, Montana. 59717.
	S. Rose
NCSM	North Carolina State University, Box 5215, Raleigh, North Carolina. 27607
	C. S. Parron
OSEC	Oklahoma State University, Stillwater, Oklahoma. 74074
	W. A. Drew
PSUC	Pennsylvania State University, University Park, Pennsylvania 16802.
	D. L. Pearson
PURC	Purdue University, West Lafayette, Indiana. 47907
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W. F. Barr

UK University of Kansas. Lawrence, Kansas. 66045

G. Byers

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UMMZ University of Michigan. Ann Arbor, Michigan. 48109

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UWY University of Wyoming, Laramie, Wyoming. 82071

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A. & A. Morgan	University of Waterloo, Waterloo, Ontario. N2L 3G1
M. Palmer	Vassar College, Box 492, Poughkeepsie, New York. 12601
J. Walas	77 Farrand St., Thunder Bay, Ontario.

Type material examined

C. sexguttata denikei Brown; Holotype, Allotype, and six Paratypes, CNCI. Paratype, UA.

C. sexguttata harrisi Leng; Three Cotypes, AMNH.

C. illinoensis Mares; Holotype, INHS.

Collecting Sites

The principal collecting site for *C. denikei* was 54 km east of Kenora, Ontario, on gas pipeline road #50-2+15.71 which intersects Highway 17. The road is a seldom used sand and gravel track cleared on both sides. The behavioural studies on adults of *C. denikei* were conducted at this site. The surrounding area is boreal forest, predominantly Jack Pine (*Pinus banksiana*) and Birch (*Betula* spp.), with some Willow (*Salix* spp.) and Poplar (*Populus* spp.) in the moister low lying areas. Ground vegetation in the cleared area is a mixture of grasses and various opportunists such as Daisey (*Chrysanthemum leucanthemum*), Milfoil (*Achillea millefolium*) and Raspberry (*Rubus idaeus*). The soil is a silty sand with much exposed rock.

Adults of C. denikei were also collected at a number of similar sites along Highway 17 between Vermillion Bay and the junction of Highways 17 and 71. One specimen was collected at each of three sites along Highway 71 between Caliper Lake and the junction of Highways 17 and 71. Other specimens were taken at Ingolf Ontario, the type locality, and the Assinaka Nature Trail in Manitoba, four km west of Ingolf. The habitat around Ingolf is similar to the pipeline road described above.

The only collection of C. patruela was made in Todd Co. Minnesota, seven km north of Lincoln. The forest was an admixture of boreal and Appalachian elements with Jack Pine(P. banksiana) predominating.

Both adults and larvae of C. sexguttata were collected at many sites throughout Eastern North America, from Poughkeepsie, New York, to Torreya State Park, Florida, and as far west as Manhattan, Kansas. The general features of these collecting sites can be found in the section on habitat.

Collecting Techniques.

Most of the adults were captured with a standard insect net. Techniques of capturing adult tiger beetles are described in Larochelle (1978a). A few adults of C. denikei were caught using a Malaise trap. Some adults of C. denikei were kept alive for study in the laboratory, and all other captured beetles were immediately killed in either sodium cyanide or ethyl acetate. The beetles were then transferred to 70% alcohol, or Barbers fluid if they were to be dissected. Specimens preserved in alcohol were later dry mounted on #1 and #2 insect pins.

Larvae were removed from their burrows using the three methods described by Palmer (1979). Some larvae were kept alive for rearing; all others were killed and preserved in 70% alcohol.

Dispersal of *Cicindela denikei*.

Studies on dispersal of adult *C. denikei* were conducted at pipeline road 50-2+15.71, 54 km east of Kenora, Ontario. This site was chosen because it had the largest known colony of *C. denikei*. The pipeline road was marked at 3.0 m intervals for 420 m. Adult beetles were captured and marked on the elytra with Testors model paint in a manner similar to that of Willis (1974) and Palmer (1976). Marks were placed on the humeral lunule, the middle band, or the apical lunule of either elytra. With the use of four colours, it was possible to distinguish up to 90 individuals by putting one or two spots of paint on the beetle. Some marked individuals were kept in the laboratory and suffered no ill effects from the marking.

At the time of marking, the following information was recorded: sex of the individual; date and time of capture; and site of capture. The beetles were then released. If the beetles were recaptured, the site and time of the recapture was noted. If less than four hours had elapsed between recapture and previous capture, the beetle was not counted as a recapture. During a seven day period, 45 individuals were marked. There were 32 recaptures of 21 beetles.

Beetles were captured twice a day to minimize disturbance, once in the morning and once in the afternoon for one week. The road at both ends and the trees at the sides of the colony were checked for beetles daily.

Behaviour of <u>Cicindela denikei</u>.

The beetles were observed with binoculars from a two meter high embankment four meters from the pipeline road study site. Accurate observations of the beetles on the road could be made for ten meters in either direction. Observations were dictated into a portable tape recorder. The tapes were transcribed and timed in the laboratory. Behaviours noted were as follows:

Pause: The beetle does not move or change orientation for a full second or more.

Run/Stop: Adult tiger beetles usually move about in short dashes, here termed a "run/stop". In <u>C</u>. <u>denikei</u>, the runs cover 10 to 15 cm, averaging about 13 cm. The stops are brief and not noted as pauses.

Orient: The beetle changes the direction that it is facing or moving. The beetle frequently orients itself such that it faces parallel or perpendicular to the long axis of the road. The direction that a beetle faces is classed as being (i) "away", facing away from the observer towards the far side of the road, (ii) "towards", towards the observers side of the road (iii) "right", facing down the road to the observers right, or (iv) "left", the opposite of "right". All facings of the beetle are classed into one of the above four categories. All changes in orientation are noted except those occurring during a "move" (see below).

Run: The run differs from the run/stop in that the beetle does not pause during the course of the run. The beetle moves approximately 0.2 m/sec although the speed varies considerably.

Move: The move consists of crawling slowly over the ground, covering 1 - 6 cm/sec. This often occurs after a beetle strikes at prey, misses, and then tries to find it. The move also occurs when a beetle moves through dense vegetation and cannot run. The "move" includes many short pauses and changes in facing, all of which cannot be accurately recorded. Only the initial and final facing are noted for orientation.

Other recorded behaviours are: encountering conspecific, grappling with conspecific, mating, attempts to capture prey, prey handling, prey consumption, and flying. Whenever possible, the position of the beetle relative to certain reference points was noted, ie., vegetation on the sides of and in the middle of the road, numbered markers, and certain conspicuous rocks and plants. Twenty-six adult beetles were observed.

Rearing larvae.

Many species of Cicindela larvae have been successfully reared in the laboratory. Techniques have included the use of earth-filled vessels (Harris, 1828), two glass plates (Shelford, 1908) wooden chimneys (Shelford, 1917), terraria (Willis, 1967) and glass tubes (Palmer, 1979). The earth is kept moist and the larvae are fed small prey items (Palmer, 1979) or lean meat (Shelford, 1908). For unknown reasons, the adults reared from larvae often do not live long (Shelford, 1917).

The techniques used for rearing adults and larvae of *C. denikei* were the same as those described by Palmer (1979). Larvae were kept in glass tubes filled with soil from the collecting site. The tubes were placed vertically in a plastic bucket. Water in the bottom of the bucket kept the soil in the tubes moist; occasionally, it was necessary to water some tubes directly. The larvae were fed daily with live *Tribolium* sp. adults and larvae.

Adult beetles were kept in terraria. Some had soil in the bottom, others were lined with paper. Water was placed in small Stentor dishes or jar lids. The beetles were fed adults and larvae of *Tribolium* sp. daily. Folded pieces of cardboard, stiff paper, or jar lids were provided as shelters. Both the adults and larvae of *C. denikei* were kept at room temperature. The photoperiod was approximately 12 h light : 12 h dark with florescent day lights.

Dissections

The genitalia of approximately 180 specimens were examined of which approximately six specimens of each sex of *C. denikei*, *C. patruela patruela* and *C. patruela consentanea* were examined in detail. The genitalia of at least two specimens of each sex of *C. sexguttata* from Kansas, Nebraska, Louisiana, Mississippi, Texas, Florida, Ontario, Minnesota, New York, and Stamford New York were examined in detail. Other specimens were dissected to examine specific genitalic characters and were not studied in detail.

Dissection and preparation of the genitalia were as follows: Dry pinned specimens were relaxed in hot water for 10 to 15 minutes. The genitalia were then pulled from the abdomen with watchmaker forceps and cut off. Soft tissues were removed by placing the genitalia in hot 10% KOH. Male genitalia were kept in the KOH solution for two to five minutes, female genitalia for five to ten minutes. The softened genitalia were then rinsed with water. For detailed examination of the sclerites of the internal sac of the male, it was necessary to evert the internal sac. The internal sac was everted with the use of a #0 insect pin with a hooked point. To examine the internal genitalia of the female, it was necessary to remove Sternum 8 and Syntergum 9 + 10. With the use of watchmaker forceps, the membranes holding Sternum 8 were torn and the Sternum removed, and the process repeated for Syntergum 9 + 10. If detailed study was not required, Sternum 8 and Syntergum 9 + 10 were not removed. Instead, the genitalia were exposed by gripping the 2nd Gonapohpysis with forceps and gently pulling them out. The arc length of the 2nd gonapohpysis from the apex to the base was measured using a scalar micrometer accurate to $\pm$ 0.02 mm.

The abdomens of 62 female specimens were dissected for count of mature eggs. Specimens were relaxed in hot water for 10 to 15 minutes. The abdomen was then separated from the thorax and a cut was then made along the joint of the terga and sterna for the entire length of the abdomen. The terga were folded back or completely removed and the lower abdomen was examined for the presence of mature eggs.

Females of C. sexguttata and C. denikei were collected, preserved in Barbers fluid, and dissected. Eggs that had undergone, or were undergoing vitelligenesis were much larger than the oocytes and the yolk gave them a creamy orange/yellow colour. Eggs that were greater than 50% of laying size were classed as mature for the purposes of this study. Only mature females were used. Teneral females were distinguished by the extent of sclerotization and wear of the genitalia and by how early in the season they had been collected. These criteria were tested by comparing the number of mature eggs found in teneral and mature females of C. denikei (below). Females classed as teneral had no mature eggs, while those classed as mature had an average of 4.8 mature eggs.

	Number of mature eggs						
Teneral females	0	0	0	0	0	0	0
Mature females	4	6	6	7	2	2	7

Number of mature eggs found in the abdomens of teneral (n = 7) and mature (n = 7) females of C. denikei.

Preparation of Illustrations

Drawings of tiger beetle structures were made using a Wild Heerbrugg M5 stereo microscope with a *camera lucida* attachment.

Character States used for multivariate analysis.

Statistical analysis of character states was done to establish relationships between geographic populations and to aid in making taxonomic decisions. Thirteen adult characters of each species were used for the analysis. As C. patruela is recognized as a separate species from C. sexguttata and C. denikei, the two data sets were analyzed separately. Three criteria were followed in choosing characters for analysis. First, the character had to vary geographically. Second, the character had to be suitable for measurement or have at least two identifiable states. Third, the character had to be easy to observe to allow for the processing of several thousand individuals.

All specimens used for analysis were sexed. Character states were scored using a Wild Heerbrugg M5 stereo microscope. Characters that were bilaterally symmetrical were scored for one side of the beetle only, as noted in the discussion of the characters.

Although colour has been used as an important distinguishing character in these species, it was not used here for several reasons, but mainly because it is an ecophenotypic character. The colour and maculation of C. sexguttata varies widely (Shelford, 1917). Dawson and Horn (1928) noted that variation in markings are induced by different temperatures, moisture regimes, light conditions, soil types, and so on. Colour also varies with the age of a specimen (Shelford, 1908, 1917).

Equipment to measure colour accurately is required, as described in McKillop and Preston (1981) and Nelson (1982). Accurate measurements of colours are only worthwhile if it is known, or can be assumed, that the colours of the preserved specimens are the same as, or correspond to the colours of the specimens when they were alive.

The metallic colours in the exoskeleton of C. sexguttata specimens are produced by the multiple thin layers of the cuticle surface (Kennaught, 1963). The layers form a diffraction pattern and consist of dense and less dense electron layers. Different colour phases are produced by different thicknesses of the bilayer or different numbers of bilayers. Pressure and immersion do not have a pronounced effect on these colours, however, swelling agents will change blue-green to green (Mossakowski, 1979).

When the beetle is alive, the elytra are naturally swollen by vascularization and body fluids. With death and drying, the colour changes from blue-green/green to blue/blue-green. By altering the killing agent (sodium cyanide and ethyl acetate), method of preservation (fluid or dry), type of fluid preservative (Barbers fluid or 70% alcohol), and drying conditions (open air, weak ethyl acetate, or previously fluid preserved) a wide range of colours was produced that did not reflect the range or type of colouration found in the field population.

I suspect that the various conditions result in different rates of drying which causes different degrees of structural change in the colouration of the beetles. For this reason, colour was not considered a valid character for analysis.

Characters used for *C. sexguttata* and *C. denikei*

Maculation. Adults of *C. sexguttata* range from fully maculate to immaculate. Figure 1 shows an adult with almost complete maculation; more extensive maculation is rare. Each of the humeral spots (Fig. 1, A and B), middle band spots (C and D), and apical spots (E and F) were scored as present or absent. The spots varied considerably in size as well, but this was not considered. Scoring of maculation was done for the left elytron only.

Elytron length. The length of the left elytron was used to indicate body length. Measurement was made from the tip of the apex to the shoulder crease with a fine ruler accurate to 1/4 mm (Fig. 2).

Figure 1: Elytra of *C. sexguttata* showing code system for scoring of maculation. A and B, humeral lunule spots, C and D, middle band spots, E and F, apical lunule spots.

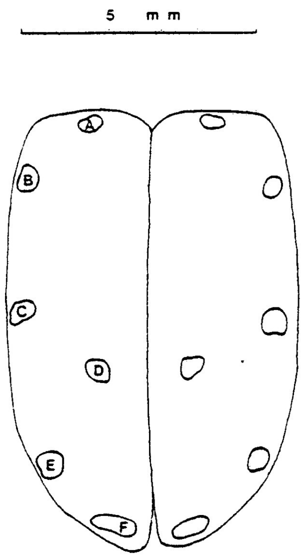
Figure 2: Adult *C. sexguttata* with length and width measurements indicated.

Figure 3: Right side of head of *C. patruela*, anterior view, indicating sensory, scape, and supraorbital setae.

Figure 4: Labral shapes of *C. sexguttata*, a. Type 1, b. Type 2, c. Type 3.

Figure 5: Elytra of *C. patruela* showing measurement of distances between lunule spots, dhl. distance between the spots of the humeral lunule, dal. distance between the spots of the apical lunule.

Figure 6: Dorsal view of the cardo and stipes on the right side of the head of *C. patruela*. Indicated are setal fields A, B, C, and D.



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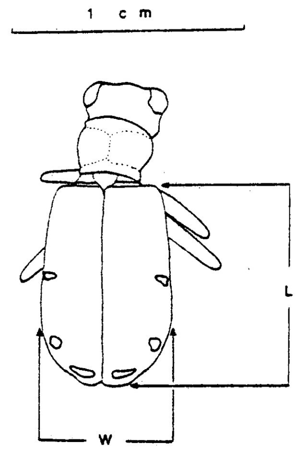

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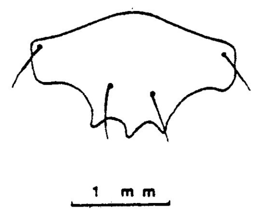

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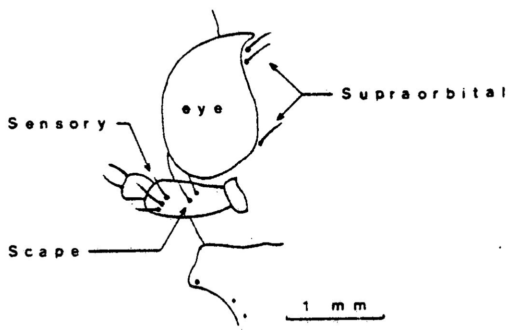

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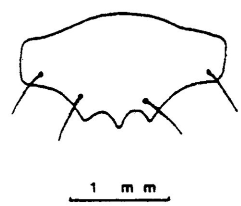

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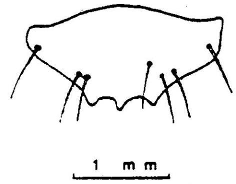

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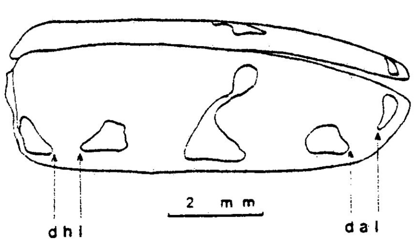

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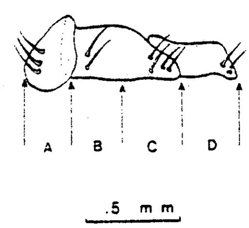


6

Body width. The width of the elytra at the widest point was measured in the same manner as described above.

Sensory setae of the antenna. The number of sensory setae on the apical end of the right antennal scape were counted. Setal pits rather than setae were counted as the setae are often missing (Fig. 3).

Setae of the scape. The number of non-sensory setae scape setae were counted. As with sensory setae, setal pits were counted as setae (Fig. 3).

Labral setae. The number of setae or setal pits on the labrum were counted (Fig. 4).

Handedness of the labrum. When there was an odd number of labral setae, the labrum was scored as left or right handed, depending on which side the extra seta occurred, generating variable H1 (Fig. 4c). Variable H2 indicated whether the pattern of labral setae was symmetrical (Fig. 4b) or asymmetrical (Fig. 4c).

Shape of the labrum. The shape of the labrum was classed as being Type 1, 2, or 3 (Fig. 4a, b, and c respectively). A Type 1 labrum has sharp outer angles and a deep convex curvature (Fig. 4a). Type 2 has the sharp outer angles of Type 1 but lacks the smooth convex curvature (Fig. 4b). Type 3 has obtuse outer angles and very little curvature, being almost or completely straight. This is a graded character and is scored subjectively. Usually, the determination is clear; however, if there is doubt, the character is given as Type 2.

Characters used for *C. patruela*

The following characters used for *C. patruela* were scored in the same manner as for *C. sexguttata* and *C. denikei*; length of the elytra, body width, sensory setae of the antenna, and setae of the scape. Characters used for *C. patruela* alone are given below.

Supraorbital setae. Most adult *C. patruela* have two pairs of supraorbital setae, but some have one or two extra setae (Fig. 3). The extra setae were scored as present or absent for the right side of the head.

Colour of the antenna. The first four antennal segments tend to be dark and heavily sclerotized. Antennal segments 5 - 11 range from very pale and lightly sclerotized to dark and heavily sclerotized. Antennal colouration was scored as dark or pale for segments 5 - 11 of the right antenna.

Maculation. In *C. patruela*, the apical and humeral lunules range from complete to two small dots. The distance between the two dots of each lunule is measured and scored separately (Fig. 5). Measurements are made to the nearest 1/4 mm. Complete maculation is scored as zero.

Setae on the cardo and stipes. Setae on the cardo and stipes occur in four distinct groups (Fig. 6, group A, B, C, and D). The number of setae in each group were counted. The cardo and stipes of the right side of the head were used.

Discriminant Analysis. Analysis of character states was done on the Lakehead University VAX 11/780 computer. The program used was the discriminant analysis from SPSS for FAX/VMS, Version M, Release 8.1, May 1, 1981. The discriminant analysis is described by Nie et. al. (1975).

Discriminant analysis is not the most appropriate form of analysis for this type of study, but was the best multivariate analysis available. The discriminant analysis is not used as a discriminant analysis *per se*, *i.e.*, to generate discriminant functions for use in a numerical key. The analysis is used to give measures of relative relationships among populations based on 13 character states. The minimum tolerance level for rejection of characters from the analysis was 0.001.

Significance levels. For most statistical analysis, the accepted levels of significance are 0.05 and 0.01. I feel that neither of these levels are appropriate to the discriminant analysis of character states done here because the analysis is complicated by several factors.

If available, at least 100 specimens from each state were used. Even though the sexes were analyzed separately, most tests used about 100 individuals or more. With large sample sizes, the analysis was very powerful and meaningless differences were detected.

The characters used were not all suitable for the discriminant analysis. Ideally, the analysis deals with continuous variables. A number of characters used were multi-state and were coded as continuous, which added unwarranted power to the analysis.

Ideally, a sample is representative of a population at a given time. If the time differences between samples is small, then any variation is meaningful. In this study, the specimens collected in the Eastern United States were 30 to 50 years older than those collected in the West. Variation may have occurred in response to changing climates or man's impact on the environment.

The specimens used in this study may represent biased sampling by collectors and curators. With common species, there is a tendency to keep a limited number of "typical" specimens, but to gather as many unusual forms as are available. This is particularly evident with the violet forms of C. sexguttata from Kansas and Nebraska. Although they are comparatively rare (Wickham, 1902; Smythe, 1905; Willis, 1967), they account for roughly 50% of the museum specimens from this region.

Because of these difficulties, guidelines were used to interpret results of the analysis. Tests were run in pairs, with data for males and females tested separately. If the levels of significance differed, the analysis showing the least significant difference was used for interpretation. The interpretation examines relative relationships of populations without regard to absolute differences. Within these criteria, a significance level of 0.001 indicates that the populations are different. No taxonomic decisions are based solely on the evidence of the discriminant analysis.

RESULTS AND DISCUSSION

Discriminant Analysis.

Few specimens were available from certain states and provinces and in these cases, the data were lumped with the data of adjacent areas in order to have sample sizes sufficiently large for analysis. For C. sexguttata, the data from Nova Scotia (16) and New Brunswick (2) were included with those of Maine, and the data from Delaware (2) were included with those of Maryland.

For the analysis of C. patruela, it was necessary to lump larger regions as only a few specimens from each state were available. The central region consists of data from Indiana, Ohio, Kentucky, and West

Virginia. The Northeastern region is the lumped data from New York, Massachusetts, and Rhode Island. The Southeastern region consists of data from Maryland, District of Columbia, Virginia, North and South Carolina, Georgia, and Tennessee.

Table 1. Canonical discriminant functions evaluated at group centroids for discriminant analysis of *C. sexguttata*.

TEST	SEX	GROUP	FUNC. 1	SIGNF.	FUNC.2	SIGNF.	FUNC.3	SIGNF.
1	F*	-	-	-	-	-	-	-
	M	VA	-0.17648		0.35099			
		MD	0.52016		-0.15365			
		DC	-0.68703	0.0841	-0.42679	0.4884		
2	F	ON	1.19129					
		MN	-2.19931	0.0000				
	M	ON	1.37460					
		MN	-2.36611	0.0000				
3	F	ON	-0.55169					
		NY	0.50755	0.0022				
	M	ON	0.41697					
		NY	-0.61477	0.0001				
4	F	ON	-0.37977					
		MI	0.25944	0.2861				
	M	ON	0.39448					
		MI	-0.38122	0.0043				
5	F	NY	0.64995		0.06512		0.00590	
		VT	-0.28413		-0.42393		-0.20613	
		NH	-0.59147		0.81884		-0.66999	
		ME	-0.44440	0.0008	0.12916	0.2088	0.35033	0.4042
	M	NY	0.52623		-0.03555		0.04889	
		VT	-0.46099		0.33506		0.07769	
		NH	-0.73448		-0.90385		0.32487	
		ME	-0.26392	0.0064	-0.21601	0.2613	-0.75234	0.4559

Table 1. Cont'd.

TEST	SEX	GROUP	FUNC.1	SIGNF.	FUNC.2	SIGNF.	FUNC.3	SIGNF.
6	F	NY	0.46778		0.31294		0.03653	
		VT	-0.67093		-0.07193		0.37231	
		NH	-0.87503		0.27750		-0.61215	
		MA	0.30356	0.0000	-0.65513	0.0201	-0.14735	0.1823
	M	NY	0.48200		-0.15638		0.10746	
		VT	-0.63993		0.26935		0.23032	
		NH	-0.75927		-0.55081		-0.38185	
		MA	0.36559	0.0001	0.58569	0.0787	-0.49720	0.1851
7	F	CT	0.51288		-0.02007			
		RI	-0.25138		-0.38747			
		MA	-0.21650	0.3767	0.39585	0.3568		
	M	CT	0.34968		-0.44946			
		RI	-0.81585		0.00901			
		MA	0.37926	0.0320	0.25260	0.7162		
8	F	NY	0.49055		0.03988			
		PA	-0.35530		-0.43604			
		NJ	-0.54162	0.0282	0.31578	0.5486		
	M	NY	0.60302		0.39120			
		PA	-0.93337		0.18092			
		NJ	0.19005	0.0000	-0.73211	0.0004		
9	F	MI	0.07840		0.28905			
		IN	-0.63717		-0.21590			
		OH	0.47220	0.0135	-0.39231	0.1597		
	M	MI	-0.22191		-0.14313			
		IN	0.65225		-0.03187			
		OH	-0.14440	0.1628	0.35941	0.7913		

Table 1. Cont'd.

TEST	SEX	GROUP	FUNC. 1	SIGNF.	FUNC.2	SIGNF.	FUNC.3	SIGNF.
10	F	MN	-1.36756		-0.29985		-0.37736	
		WI	-0.64113		-0.48871		0.28853	
		MI	0.94306		0.00285		-0.22429	
		IA	-0.84278		0.69168		0.06502	
		IL	0.44730	0.0000	-0.05062	0.0001	0.51530	0.0067
	M	MN	-1.19518		-0.19061		-0.63183	
		WI	-0.39874		-0.65065		0.45410	
		MI	0.95894		0.20547		-0.09361	
		IA	-1.57609		0.79919		0.43239	
		IL	0.86955	0.0000	-0.07038	0.0000	0.06995	0.0002
11	F	NB	-0.43214		-0.94064		0.21121	
		KS	-0.76709		0.34419		-0.17519	
		MO	2.21304		-0.33347		-0.38247	
		OK	0.96628	0.0000	0.75648	0.0000	0.48539	0.2173
	M	NB	-0.76311		-0.65528		-0.17983	
		KS	-0.62383		0.28946		0.22937	
		MO	2.53956		-0.25089		0.23610	
		OK	0.66229	0.0000	0.54879	0.0004	-0.67707	0.0645
12	F	IL	2.47205		-0.31727			
		KS	-1.96025		-0.04119			
		MO	1.64791	0.0000	0.65768	0.1663		
	M	IL	3.14512		0.27125			
		KS	-2.26261		0.04844			
		MO	1.81534	0.0000	-0.66184	0.4260		
13	F	NB KS OK AR TX LA MS MO	-1.36858					
		All other populations	0.40726	0.0000				
	M	NB KS OK AR TX LA MS MO	-1.28355					
		All other populations	0.37352	0.0000				

Table 1. Cont'd.

TEST	SEX	GROUP	FUNC.1	SIGNF.	FUNC.2	SIGNF.	FUNC.3	SIGNF.
14	F	KS MO AR LA	-0.47146					
		IA IL KT TN MS	0.71618	0.0000				
	M	KS MO AR LA	0.44760					
		IA IL KT TN MS	-0.68439	0.0000				
15	F	OK	-1.12419		0.28643		0.53715	
		TX	0.82880		-0.56872		0.21505	
		AK	0.93636		0.45823		-0.14476	
		LA	-0.99085	0.0000	-0.18487	0.0039	-0.41157	0.0462
	M	OK	-1.09579		0.76398		-0.19040	
		TX	0.96546		0.14557		0.30494	
		AK	0.80823		-0.20135		-0.36620	
		LA	-1.21038	0.0000	-0.35471	0.0152	0.11638	0.1902
16	F	MS	-1.07005		-0.35428			
		AL	-0.48262		1.24533			
		GA	0.87692	0.0002	-0.10598	0.1532		
	M	MS	-1.01747		0.37719			
		AL	-0.23950		-1.09742			
		GA	0.74474	0.0000	0.19062	0.0024		
17	F	TN	0.61601					
		GA	-0.34749	0.6529				
	M	TN	-0.73084					
		GA	0.29952	0.2673				
18	F	GA	0.66802					
		FL	-2.36844	0.0001				
	M	GA	0.76569					
		FL	-1.86828	0.0000				

Table 2. Canonical discriminant functions evaluated at group centroids for discriminant analysis of *C. patruela*.

TEST	SEX	GROUP	FUNC.1	SIGNF.	FUNC.2	SIGNF.	FUNC.3	SIGNF.
19	F	Central	0.98443		0.13851		0.01582	
		Northeastern	-0.53743		-0.45694		-0.64521	
		Southeastern	1.24300		0.18871		0.12336	
		Minnesota	-1.88949		0.75877		0.01189	
		Wisconsin	-1.00419		-0.06617		0.58678	
		Michigan	0.05596		0.71088		-0.33683	
		Pennsylvania	0.70246		-0.07465		0.12252	
		New Jersey	0.05512	0.0000	-0.42698	0.0000	0.16675	0.0000
	M	Central	0.74162		0.14388		0.09559	
		Northeastern	-0.40812		0.40278		-0.44657	
		Southeastern	1.13538		-0.00402		0.22366	
		Minnesota	-1.22813		0.09866		0.30066	
		Wisconsin	-0.97549		-0.15244		0.31372	
		Michigan	-0.28518		-0.58062		-0.17844	
		Pennsylvania	0.74268		-0.22809		-0.16356	
		New Jersey	0.06470	0.0000	0.54316	0.0366	0.22137	0.4201
20	F	*C. p. patruela*	0.10522					
		C. p. consentanea	-0.50990	0.0763				
	M	*C. p. patruela*	-0.08360					
		C. p. consentanea	0.65685	0.1802				
21	F	Pennsylvania	-0.46691					
		New Jersey	0.40944	0.0625				
	M	Pennsylvania	0.59268					
		New Jersey	-0.72815	0.0120				
22	F	Minnesota	1.10203		0.86754			
		Wisconsin	0.40058		-0.53057			
		Michigan	-0.92553	0.0000	0.20191	0.0025		
	M	Minnesota	0.82110		0.50026			
		Wisconsin	0.26290		-0.33869			
		Michigan	-0.54307	0.0774	0.12727	0.5773		

Table 2. Cont'd.

TEST	SEX	GROUP	FUNC.1	SIGNF.	FUNC.2	SIGNF.	FUNC.3	SIGNF.
23	F	Central	0.88705					
		Pennsylvania	-0.40462	0.0238				
	M	Central	-0.58436					
		Pennsylvania	0.29897	0.6644				
24	F	Central	1.10933					
		Michigan	-0.57685	0.0006				
	M	Central	1.04198					
		Michigan	-0.46783	0.0122				
25	F	Northeastern	-0.82244					
		Pennsylvania	0.88015	0.0000				
	M	Northeastern	-0.65852					
		Pennsylvania	0.81167	0.0001				

Table 3. Variables used in discriminant analysis of C. sexguttata. The 'X' indicates variables that failed the minimum tolerance test. The '+' indicates variables significant to the discrimination at the 0.005 level.

TEST	SEX	EL	EW	A	B	C	D	E	F	T	AS	ANS	LB	LBS	H1	H2
1	F*															
	M									X					X	
2	F	+	+		X					X			+		X	
	M	+	+			+	+	+	+	X	+		+	+	X	
3	F						+			X					X	
	M			+		X	+			X					X	
4	F								X	X					X	
	M	+	+		+					X					X	
5	F			X		X	+			X			+		X	
	M	+				X				X					X	
6	F			X		X	+			X			+		X	
	M	+	+			X				X					X	
7	F			X	X	X				X					X	
	M									X					X	
8	F		+	X		X				X					X	
	M		+							X			+	+	X	
9	F									X					X	
	M					X				X					X	
10	F	+	+			+	+	+	+	+	+					
	M	+	+	+		+	+	+	+		+	+				
11	F	+	+	X		+	+	+	+	X					X	
	M	+	+			+	+	+	+	X					X	
12	F	+	+	+		+	+	+	+	X		+	+		X	
	M	+	+			+	+	+	+	X					X	
13	F	+	+			+	+	+	+		+	+		+		
	M	+	+	+		+	+	+	+		+	+	+	+		
14	F	+	+			+		+	+	+						
	M	+	+			+		+	+		+	+				
15	F	+	+	X		+	+	+	+	+						
	M					+	+	+	+	+						
16	F			X				+		X					X	
	M				X	+		+	+	X	+		+		X	
17	F			X		X				X						
	M															
18	F			X				+	+	X					X	
	M	+	+		X	+		+	+	X					X	

Abbr.: EL - Elytron length; EW - Body width; A, B, C, D, E, F - Maculation of the elytron; T - Total maculation; AS - Sensory setae of the antenna; ANS - Setae of the scape; LB - Shape of the labrum; LBS - Labral setae; H1 - Handedness of labral setae; H2 - Symmetry of labral setae.

* Eigen values failed to converge, test could not be done.

Table 4. Variables used in discriminant analysis of C. patruela. The '+' indicates variables significant to the discrimination at the 0.005 level.

TEST	SEX	EL	EW	HL	AL	AC	SO	A	B	C	D	AS	ANS
19	F			+	+					+	+	+	
	M			+	+					+			
20	F												
	M												
21	F			+									
	M			+									
22	F			+	+						+	+	
	M			+									
23	F												
	M												
24	F			+	+					+		+	
	M									+			
25	F			+	+					+	+	+	
	M			+	+					+			

Abbr.: EL - Elytron length; EW - Body width; HL - Humeral lunule distance; AL - Apical lunule distance; AC - Colour of the antenna; SO - Supraorbital setae; A, B, C, D - Setae on the cardo and stipes; AS - Sensory setae of the antenna; ANS - Setae of the scape.

Table 5. Statistics for discriminant analysis of *C. sexguttata*.

TEST	SEX	n	FUNC.	% S^2	Canonical Corr.	Wilk's λ	χ^2	D.F.
1	F*	-	-	-	-	-	-	-
	M	144	1	68.97	0.4215756	0.7493860	38.80	28
			2	31.03	0.2977281	0.9113580	12.48	13
2	F	111	1	100	0.8528647	0.2726218	133.22	13
	M	166	1	100	0.8757933	0.2329861	.228.71	14
3	F	144	1	100	0.4702740	0.7788423	33.47	14
	M	193	1	100	0.4535792	0.7942660	42.49	13
4	F	170	1	100	0.3011019	0.9093377	15.34	13
	M	234	1	100	0.3629120	0.8682948	31.77	14
5	F	152	1	62.93	0.4931622	0.6318569	68.86	36
			2	22.98	0.3240483	0.8349159	27.06	22
			3	14.09	0.2590859	0.9328745	10.42	10
	M	166	1	58.30	0.4556594	0.6626884	64.39	39
			2	25.72	0.3219103	0.8363323	27.97	24
			3	15.97	0.2588100	0.9330174	10.85	11
6	F	179	1	57.44	0.4908038	0.6083213	84.49	36
			2	27.26	0.3617673	0.8013595	37.64	22
			3	15.31	0.2792296	0.9220308	13.80	10
	M	208	1	59.45	0.4578349	0.6648105	81.03	39
			2	23.02	0.3051474	0.8411200	34.34	24
			3	17.53	0.2692907	0.9274825	14.94	11
7	F	115	1	53.22	0.3313027	0.8031956	23.45	22
			2	46.78	0.3126897	0.9022251	11.00	10
	M	135	1	79.24	0.4849984	0.7077465	43.38	28
			2	20.76	0.2730767	0.9254291	9.726	13
8	F	156	1	75.30	0.4337647	0.7544860	41.41	26
			2	24.70	0.2658125	0.9293437	10.77	12
	M	197	1	65.48	0.5506806	0.5667076	106.20	30
			2	34.52	0.4320214	0.8133575	38.63	14

Table 5. Statistics for discriminant analysis of *C. sexguttata* (cont'd).

TEST	SEX	n	FUNC.	% S^2	Canonical Corr.	Wilk's λ	χ^2	D.F.
9	F	197	1	63.04	0.3702047	0.7894414	44.44	26
			2	36.96	0.2918583	0.9148188	16.73	12
	M	223	1	75.94	0.3416171	0.8478148	35.24	28
			2	24.06	0.2004270	0.9598290	8.753	13
10	F	269	1	74.37	0.6740742	0.4152689	228.06	48
			2	11.66	0.3398362	0.7610900	70.84	33
			3	8.84	0.3000730	0.8604638	38.99	20
			4	5.14	0.2332163	0.9456101	14.51	9
	M	337	1	75.38	0.7147606	0.3560077	338.24	48
			2	12.98	0.3904742	0.7278576	104.03	33
				10.03	0.3492718	0.8587987	49.85	20
				1.61	0.1479179	0.9781203	7.245	9
11	F	185	1	70.81	0.7316171	0.3081841	206.57	39
			2	23.98	0.5297218	0.6631373	72.09	24
			3	5.22	0.2796448	0.9217988	14.29	11
	M	210	1	81.86	0.7632745	0.3136422	231.90	42
			2	11.93	0.4111016	0.7513971	57.16	26
			3	6.21	0.3094944	0.9042132	20.13	12
12	F	181	1	97.57	0.9025366	0.1671720	306.77	28
			2	2.43	0.3137704	0.9015481	17.77	13
	M	155	1	98.52	0.9296329	0.1239335	303.81	28
			2	1.48	0.2954066	0.9127349	13.28	13
13	F	1500	1	100	0.5984968	0.6418016	661.67	12
	M	1881	1	100	0.5694741	0.6756993	743.23	12
14	F	330	1	100	0.5035548	0.7464325	94.16	12
	M	392	1	100	0.4851970	0.7645838	103.07	12
15	F	159	1	76.64	0.6990469	0.3897859	141.79	33
			2	13.67	0.3815772	0.7622929	40.84	20
			3	9.69	0.3283322	0.8921980	17.16	9
	M	199	1	83.25	0.7191408	0.3938211	177.05	36
			2	10.97	0.3516628	0.8156406	38.71	22
			3	5.78	0.2631682	0.9307425	13.63	10

Table 5. (Cont'd)

TEST	SEX	n	FUNC.	% S^2	Canonical Corr.	Wilk's λ	χ^2	D.F.
16	F	77	1	75.24	0.6794800	0.4198154	59.02	26
			2	24.76	0.4691683	0.7798811	16.90	12
	M	124	1	67.33	0.6200711	0.4723623	86.25	26
			2	32.67	0.4822551	0.7674300	30.44	12
17	F	61	1	100	0.4256881	0.8187897	10.49	13
	M	86	1	100	0.4278812	0.8169176	15.67	13
18	F	50	1	100	0.7889046	0.3776296	40.41	13
	M	86	1	100	0.7708764	0.4057495	69.90	13

* Eigen values failed to converge, test could not be done.

Table 6. Statistics for discriminant analysis of *C. patruela*.

TEST	SEX	n	FUNC.	% S^2	Canonical Corr.	Wilk's λ	χ^2	D.F.
19	F	380	1	60.56	0.6489811	0.3704172	366.46	84
			2	14.45	0.3846266	0.6399484	164.71	66
			3	11.94	0.3541450	0.7510582	105.63	50
	M	310	1	65.62	0.6076171	0.4699872	225.76	84
			2	14.61	0.3395540	0.7450636	87.991	66
			3	8.73	0.2687132	0.8421623	51.363	50
20	F	380	1	100	0.2262163	0.9488262	19.54	12
	M	310	1	100	0.2288541	0.9476258	16.24	12
21	F	122	1	100	0.4034003	0.8372682	20.24	12
	M	78	1	100	0.5540378	0.6930421	25.66	12
22	F	127	1	69.70	0.6223139	0.4806337	86.81	24
			2	30.30	0.4643066	0.7844194	28.77	11
	M	112	1	73.95	0.4627257	0.7170704	34.422	24
			2	26.05	0.2959107	0.9124369	9.4844	11
23	F	83	1	100	0.5185428	0.7311134	23.48	12
	M	65	1	100	0.3907988	0.8472763	9.44	12
24	F	76	1	100	0.6297451	0.6034211	34.35	12
	M	71	1	100	0.5779648	0.6659567	25.61	12
25	F	118	1	100	0.6512137	0.5759207	60.69	12
	M	96	1	100	0.5942357	0.6468839	38.33	12

C. sexguttata. Tests 1 and 2 were done as a base for the interpretation of the other tests. Test 1 compares the populations from Virginia, Maryland and District of Columbia. Most of the samples from Virginia and Maryland are from the environs of the District of Columbia. The three samples are from the same geographic population and are not expected to differ. In running the discriminant analysis on data for the females, the eigen values failed to converge and the test could not be run. The discriminant functions generated for data on the males were not significant (M - 0.0841, Table 1).

Test 2 compares data for C. sexguttata from Minnesota and C. denikei. At the time that this test was run, it had already been determined that C. denikei was a separate species and the two data sets were expected to be very different. The discriminations were highly significant (F - 0.0000, M - 0.0000, Table 1).

Tests 3 and 4 compare populations from habitats beside the St. Lawrence River, lower Great Lakes, and associated rivers to determine if they are barriers to dispersal. Test 3 compares populations from Ontario and New York. The discrimination is not significant for females (0.0022, Table 1) and significant for males (0.0001, Table 1). Test 4 compares the Ontario and Michigan samples. The discriminations for males and females are not significant (F - 0.0043, M - 0.2861, Table 1). The St. Lawrence River, lower Great Lakes, and associated rivers are not barriers to dispersal of C. sexguttata.

Test 5 compares the sample from New York with samples from Vermont, New Hampshire, and Maine. The populations from New York occur on a different dominant soil type (Alfisols and Inceptisols) than the New

England populations (Haplorthods); the test was run to see if the different soil types produced recognizably different populations. The primary discriminant functions separate New York from the New England states, but the functions are not signficant (F - 0.0008, M - 0.0064, Table 1).

Test 6 is similar to Test 5, except the Maine sample is replaced by a sample from Massachusetts. Maine experiences a climate different from New York; whereas Massachusetts is adjacent to New York and also has Haplorthod soils, which reduces the expected variation due to factors other than soils. In the analysis, the primary discriminant function is significant (F-0.0000, M - 0.0001, Table 1), but the grouping is not as predicted. The samples from New York and Massachusetts are separated from the New Hampshire and Vermont samples (Table 1). The populations of the northern New England states are different from adjacent populations, possibly due to climate. The differences cannot be attributed to soils.

Test 7 compares the populations from Connecticut, Massachusetts, and Rhode Island. The test was done to see if the apparent discontinuity between the populations of Rhode Island and Connecticut represent a true disjunction; if so, the analysis will indicate an affinity of the Massachusetts and Rhode Island populations. The primary disciminant functions for the sexes are different, and neither is significant (F - 0.3767, M - 0.0320, Table 1). There is no statistical evidence of a disjunction between the populations of Connecticut and Rhode Island.

Test 8 compares the populations from New Jersey, New York, and Pennsylvania. The test was done to determine if the Delaware River acts as a barrier to dispersal of C. sexguttata. The primary discriminant functions for both sexes indicate an affinity between the New York and New Jersey populations; however, only the analysis of males is significant (F - 0.0282, M - 0.0000, Table 1). The Delaware River does not act as a barrier between New Jersey and Pennsylvania.

Test 9 compares the populations of C. sexguttata from Michigan, Indiana, and Ohio. The test was done to establish relationships for reference with Test 10. The populations are geographically adjacent and on the same dominant soil type, and they are not expected to differ. The primary discriminant function is not significant for either sex (F - 0.0135, M - 0.1628, Table 1). The populations are not different.

Test 10 compares five populations from the northwestern part of C. sexguttata's range, Minnesota, Wisconsin, Michigan, Iowa and Illinois. The test was done to determine if Lake Michigan acted as a barrier between the populations of the northwest (Minnesota and Wisconsin) and Michigan. The primary discriminant function is significant for both sexes (F - 0.0000, M - 0.0000, Table 1). As expected, the populations of Minnesota, Wisconsin and Iowa form a group distinct from those of Michigan and Illinois. Lake Michigan forms a barrier between the northwest and Michigan. The second discriminant function is also significant for both sexes (F - 0.0001, M - 0.0000, Table 1). The second function indicates an affinity between Minnesota, Wisconsin, and Illinois. Probably two factors account for this function. The genetic link between the northwestern and central populations of C. sexguttata is through Illinois. Table 3 shows that size was an important variable in generating this function. The beetle populations of Iowa and Michigan are of a similar size, probably due to discordant variation of this character.

Test 11 compares populations from Nebraska, Kansas, Missouri and Oklahoma. The test was done to determine if the Kansas and Nebraska populations are a distinct population as stated by Knaus (1929). The primary discriminant function is significant for both sexes (F - 0.0000, M - 0.0000, Table 1). The populations of *C. sexguttata* from Kansas and Nebraska are different from neighbouring populations. The second discriminant function is also significant in both sexes (F - 0.0000, M - 0.0004, Table 1). This function pairs Kansas and Oklahoma as separate from Nebraska and Missouri. These affinities are probably soil related. The populations from Kansas and Oklahoma are found predominantly on Udolls, and the Nebraska and Missouri populations are found on the Haplaquolls of the Missouri River alluvium.

Test 12 compares the populations of *C. sexguttata* from Illinois, Kansas, and Missouri. The test was done to determine if the Kansas population is distinctly different, or if it is the distal end of a cline. The primary discriminant function is significant for both sexes (F - 0.0000, M - 0.0000, Table 1) and accounts for roughly 98% of the variance (Table 5). The beetles of Kansas are a distinct population, and not the end of a gradual cline.

Test 13 compares the populations of *C. sexguttata* from Nebraska, Kansas, Missouri, Oklahoma, Arkansas, Texas, Louisiana, and Mississippi with all other populations. The test was done to determine whether the populations of the south and west formed a marginal population distinct from the northeastern populations, as stated by Casey (1909). The discriminant functions are significant for both sexes (F - 0.0000, M -

0.0000, Table 1), which indicates that the marginal populations to the south and west are distinct from the main population in the northeast.

Test 14 compares the populations on either side of the lower Mississippi and Missouri Rivers. The test was done to see if the river systems act as a dispersal barrier between the southwestern marginal and northeastern central populations. The discriminant functions are significant for both sexes (F - 0.0000, M - 0.0000, Table 1). The lower Mississippi and Missouri Rivers act as a barrier.

Test 15 compares the populations from Oklahoma, Texas, Arkansas, and Louisiana. The test was done to determine whether the Texas population differed from the other marginal populations (Oklahoma and Louisiana) as indicated by Shelford (1917). The primary discriminant functions are significant for both sexes (F - 0.0000, M - 0.0000), separating Texas and Arkansas from Louisiana and Oklahoma. The Texas population is morphologically similar to the more central population, probably due to dry climate and Udult soils.

Test 16 compares the populations from Alabama, Mississippi and Georgia. The test was done to determine if populations from Alabama and Georgia were part of the marginal or central population of C. sexguttata. The discriminant functions are significant for both sexes (F - 0.0002, M - 0.0000, Table 1). The Georgia population is distinguished from those of Alabama and Mississippi. The Alabama population is part of the marginal population.

Test 17 compares the Georgia and Tennessee populations to determine if Georgia is part of the central C. sexguttata population. The discriminant functions are not significant for either sex (F - 0.6529, M - 0.2673, Table 1). The Georgia population is part of the central population.

Test 18 compares the Georgia and Florida populations. The discriminant functions are significant for both sexes (F - 0.0001, M - 0.0000, Table 1). The Florida population of C. sexguttata is distinct from the central population.

Variation in Significant Characters

From Table 3 it is evident that the characters most significant to the discriminant analysis of C. sexguttata were maculation and size. How these characters vary within the range of C. sexguttata will be considered, with total maculation as a measure of maculation, and elytron length as a measure of size. For the discussion,only the males will be considered. Female elytra differ from males in that they are generally about 0.6 mm longer and are somewhat more maculate, although there is some discordant variation in the sexual dimorphism.

Average length of the elytra in the main population ranges from 7.5 to 7.8 mm. Extent of maculation ranges from 3.5 to 5 spots per elytron. The beetles on the northeastern margin tend to be slightly smaller, but with the same maculation found in the central population. In the northwest, maculation ranges from two to three spots, and length from 7.3 to 7.5 mm. The beetles of the central mid-west have greatly reduced maculation, averaging less than one spot per elytron, and longer elytra (7.6 to 7.9 mm). The size and maculation of the Texas, Arkansas, and Missouri beetles is as in the central population. The beetles of Louisiana have longer elytra than adjacent populations, average 7.9 mm, whereas the beetles of Mississippi and Alabama have shorter elytra than adjacent populations, average 7.65 mm. The beetles of Louisiana and Mississippi average two spots per elytra, whereas the beetles of Alabama average 2.4 spots per elytra. The elytra of the beetles from Florida are long, average 8.2 mm, and have an average of two spots per elytron.

Overview. The species *C. sexguttata* consists of a central population surrounded by small marginal populations that differ from it. Geographically, the central population is bounded by Ontario, New York, and Massachusetts, and extends down the east coast of the United States into Georgia. In the west, the central population boundary is Michigan, Illinois, Missouri and Tennessee. The populations of Texas and Arkansas may represent an extension of the central population or a marginal population similar to the central population.

The marginal populations to the north are not very distinct. One in the northeast consists of the northern New England States and New Brunswick and Nova Scotia in Canada. In the northwest Minnesota, Wisconsin and Iowa form another indistinct marginal population. There is a distinct central mid-western population consisting of Nebraska, Kansas and northern Oklahoma. The populations of southern Oklahoma are associated with the Arkansas, Texas population, which may be an extension of the central population. There is a distinct Gulf population consisting of Louisiana Mississippi and Alabama, and a separate population in northern Florida.

Although I refer to a number of these populations as distinct, most bear clear affinities with neighbouring populations, or are themselves subdivided by geographic features (*eg.*, Mississippi River). The exception to this is the central mid-western population of Nebraska, Kansas, and northern Oklahoma, which does appear to be a distinct population.

C. patruela. Test 19 compares the eight data sets of *C. patruela*, which are: Central, Northeastern, Southeastern, Minnesota, Wisconsin, Michigan, Pennsylvania, and New Jersey. The primary discriminant function is significant for both sexes (F - 0.0000, M - 0.0000, Table 2). The primary function for the female data sets the Northeastern, Minnesota, and Wisconsin populations apart from the rest. The male data set is similar except the Michigan population is included with the Northeastern, Minnesota, and Wisconsin populations.

The second and third discriminant functions are significant for the females (0.0000, 0.0000 respectively, Table 2), but not for the males (0.0366 and 0.4201, Table 2). The population groupings by the two sets of discriminant functions are not comparable. These functions account for 23 to 26% of the variation (Table 6) and represent discordant variation.

Test 20 compares *C. p. patruela* with *C. p. consentanea*. The discriminant functions are not significant for both sexes (F - 0.0763, M - 0.1802, Table 2). The populations are not different.

Test 21 compares *C. p. patruela* from Pennsylvania with the *C. p. consentanea* of New Jersey. The amount of variation in the entire *C. p. patruela* population may have been so large as to mask differences between the subspecies. By comparing adjacent populations only local variation is considered. The discriminant functions are not significant for both sexes (F - 0.0625, M - 0.0120, Table 2). The populations are not different.

Test 22 compares populations from Minnesota, Wisconsin, and Michigan. The primary discriminant function is significant from females (0.0000, Table 2), and indicates that the Michigan population is different from populations of Minnesota and Wisconsin. The discriminant function for the males is the same as that for the females, but not significant (0.0774, Table 2). The Michigan population is not different from Minnesota and Wisconsin populations.

Test 23 compares the Pennsylvania and Central population. The discriminant functions for both sexes are not significant (F - 0.0238, M - 0.6644, Table 2). Test 24 compares the Michigan population with the central population. The discriminant function for the females is significant (0.0006, Table 2), but the function for the males is not (0.0122, Table 2). The populations are not different.

Test 25 compares the Pennsylvania population with the Northeastern population. The discriminant functions for both sexes are significant (F - 0.0000, M - 0.0001, Table 2). The populations are different.

Overview. Table 4 shows that the significant discriminating variables in the tests on populations of _C. patruela_ were maculation, pilosity of the stipes, and the number of sensory setae on the antennal scape. Based on the characters used in the analysis, the subspecies _C. p. consentanea_ is identical to _C. p. patruela_. Within the range of _C. patruela_, there are two identifiable northern populations and a main central population. The northeastern population geographically consists of New York, Massachusetts, and Rhode Island. The northwestern population includes Minnesota and Wisconsin, with an intergrade zone through Michigan. The two northern populations are similar (Test 19) despite a large geographic separation, suggesting that the differences are probably a response to climate, ie., an ecophenotypic cline.

The egg.

The eggs of nine species of Cicindela have been described (Moore, 1906; Shelford, 1908; Willis, 1967; Cutler, 1973). The size and shape of the egg does not seem to vary much from species to species; generally, they are ovoid, about 2.0 mm long and 1.0 mm wide. Some are conspicuously larger at the anterior end (Shelford, 1908) while others are only slightly so (Willis, 1967). The colour of the egg is translucent creamy yellow (Shelford, 1908) or light straw yellow (Willis, 1967). The egg is fastened to the substrate by a stalk or has a sticky posterior end (Willis, 1967). The egg hatches in 10 to 14 days (Shelford, 1908).

The egg of C. denikei is approximately 2.2 mm long and 1.2 mm wide. It is ovoid and not conspicuously larger at the anterior end (Figure 7). The colour ranges from a creamy off-white with a yellow tinge to a creamy orange/yellow. The eggs are fastened to the substrate with a short adhesive stalk.

The larva

The larvae of 40 species of Nearctic Cicindela have been described (Hamilton, 1925; Spangler, 1955; Leffler, 1979; Willis, 1967, 1980).

Figure 7: Eggs of <u>C. denikei</u>, a. newly laid, b. late blastula, c. early embryo (about one day old).

Figure 8: Dorsal aspect of <u>C. denikei</u> third instar larva, a. head, b. pronotum.

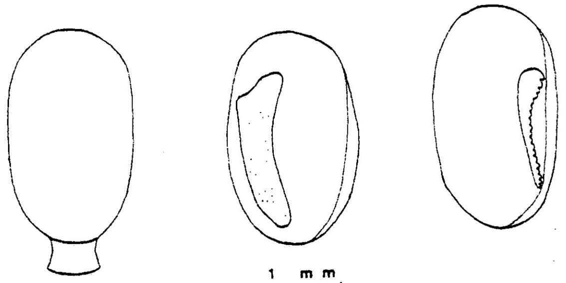
Figure 9: <u>C. denikei</u> third instar larva, left antenna, ventral aspect.

Figure 10: <u>C. denikei</u> third instar larva, third abdominal segment, lateral aspect of left half; ventrolateral suture dotted.

Figure 11: <u>C. denikei</u> third instar larva, dorsum of fifth abdominal segment, dorsal aspect.

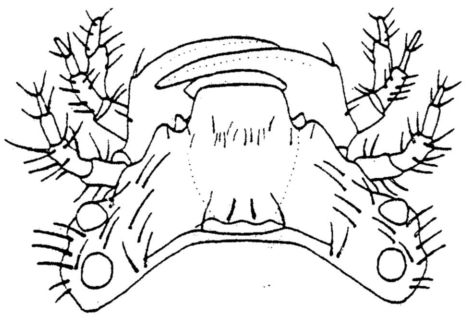
Figure 12: <u>C. denikei</u> third instar larva, ninth abdominal sternum, ventral aspect.

Figure 13: <u>C. denikei</u> third instar larva, pygopod, dorsal aspect.



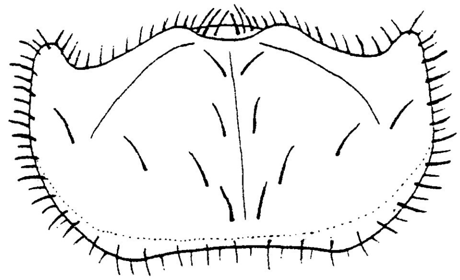
1 mm

7a b c



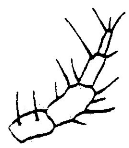
8a

1 mm



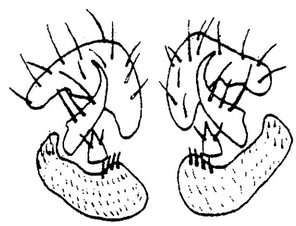
8b

1 mm



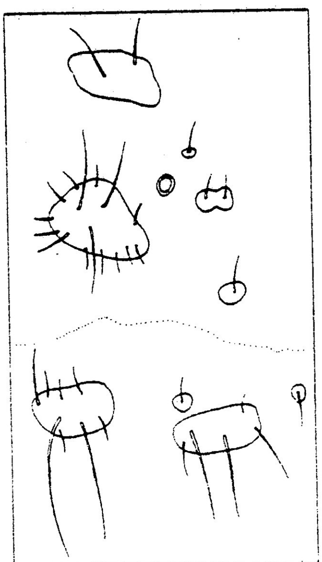
1 mm

9



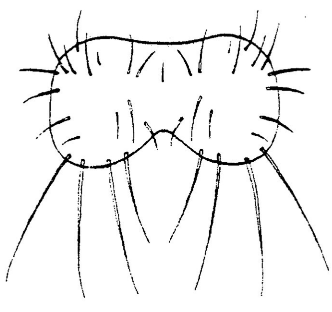
11

1 mm



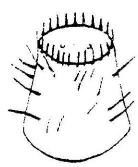
10

.5 mm



12

.5 mm



13

1 mm

Three morphologically similar larval instars occur, each larger than the previous one. In general, the larvae of *Cicindela* spp.are elongate and cylindrical. The body colour is white or some form of off-white. The head and prothorax are usually brown, black, or some other dark colour, often having metallic reflections. The head and prothorax are fused. The fifth abdominal tergite has a hump with two pairs of spines, both directed caudally. One pair of the spines are long and curved, the other pair are shorter and straight. The apex of the pygopod has a ring of stout setae. The spines of the fifth tergite and the setae of the pygopod are used to anchor the larva in its burrow (Shelford, 1908; Hamilton, 1925; Willis, 1967). The larva of *C. sexguttata* was partially described by Shelford (1908). Hamilton (1925) gave a complete description of the larva of *C. sexguttata* and included it in his key. Willis (1980) has described the larva of *C. patruela*.

The first larval instar is active for about two weeks before moulting. Moulting in all instars required about a week, but may take up to four weeks. The second larval instar is active for three to six weeks. The third larval instar stage may last from two months to two years (Criddle, 1907, 1910; Shelford, 1908; Willis, 1967; Palmer, 1978). The larva must attain a certain body weight before moulting (Palmer and Garrick, 1979). For the first instar larva, one meal is sufficient; later instar larva require more energy for the moult (Willis, 1967).

Description of the third instar larva of *C. denikei*.

Colour. Head and labrum black dorsally, with slight coppery and green reflections, ventrally light chestnut brown; pronotum dark brown or piceous black, lighter around the margin; mandibles rufo-piceous basally, otherwise black; maxillae and labium testaceous brown. Cephalic and pronotal marginal setae white; ventral pronotal primary setae brown; other setae yellow brown.

Head. (Figs. 8a, 9). Setae on dorsum prominant, long to short; diameter of stemma II subequal to that of stemma I and smaller than distance between I and II, front-clypeo-labral area longer than wide; ridge on caudal part of frons with two setae; antennae with distal segment 0.7 times as long as penultimate; proximal segment shorter than second segment; proximal segment with six setae, second with 9 - 10, third with two, and distal with three; maxillae with three setae on mesal margin of proximal segment of galea and five on distal segment; palpifer with seven setae, penultimate segment of palpus with two setae; distal segment of labial palpus with one ventral seta; penultimate with two long spurs and one inner short spur with two setae on either side of spurs; proximal with one long ventral seta; lingula with four setae.

Thorax (Fig. 8b). Pronotum with cephalolateral angles extending as far caphalad as mesal protion; lateral angles slightly carinate; primary setae long and stout, dorsal secondary setae few.

Abdomen (Figs. 10 - 13). Sclerotized areas distinct; secondary setae numerous, most long and slender, some short; eusternum of ninth segment bearing two groups of three long and one shorter seta caudally; median hooks of fifth segment strongly recurved, usually with three setae, inner hooks with two setae on a sloping shoulder and long spine about one-third to one-half the length of the hook; pygopod bearing 20 - 24 major setae, inner surface not sclerotized.

Measurements. Total length of larva, about 25 mm; width at third abdominal segment, 3.25 mm; length of pronotum, 2.4 mm; width of pronotum, 4 mm.

The larvae of *C. denikei* key out to couplet 18 in Hamilton's (1925) key. This is due to a problem in couplet 5 where the choice is "pronotum chestnut brown" or "pronotum not chestnut brown". In order to key out a larva of *C. sexguttata*, one must choose "pronotum chestnut brown", when in fact in the description of the *C. sexguttata* larva, the pronotal colour is given as dark chestnut brown, and I have seen specimens that were piceous to black. I offer the following modification to the couplet;

5. Primary pronotal setae brown ---------------------------- 5a
   Primary pronotal setae white ---------------------------- 5b

5a. Inner surface of pygopod lightly sclerotized ------------- *C. sexguttata*
   Inner surface of pygopod not sclerotized ---------------- *C. denikei*

5b. Pronotum chestnut brown --------------------------------- 6
   Pronotum not chestnut brown ----------------------------- 8

The pupa. The third instar larva of *Cicindela* closes its burrow and constructs a special pupal cell for pupation. The pupal cell may be an enlargement of the burrow or a special chamber adjoining it. The time between closure of the burrow and ecdysis is four to six weeks

(Willis, 1967). The pupa, and changes that occur during pupation, are described in detail by Shelford (1908, 1917) and Willis (1967). The newly emerged adult undergoes certain changes in sclerotization and colour. Most of these changes are complete within 70 hours of ecdysis, although colour may continue to change throughout the adult life of the beetle (Shelford, 1917).

Specimens of C. denikei pupae were not preserved for study. Two living specimens and three exuviae were examined. The pupa of C. denikei is not notably different from pupae of other species. Pupation in C. denikei takes about a month to complete.

Genitalia

The shape and size of the genitalia of both sexes of tiger beetles are useful in the identification of species as well as phylogenetic relationships. The male genitalia have been studied by Horn (1930), Papp (1952), Rivalier (1954, 1957, 1961, 1963), Rump (1957), Wallis (1961), Freitag (1965), and Leffler (1979). Papp (1952) described the male genitalia of C. sexguttata. Wallis (1961) indicates that he examined the male genitalia of C. sexguttata and C. denikei, but he did not describe them, noting only that he could find no difference between the two. Wallis also mentions that the male genitalia of C. sexguttata and C. patruela are similar. Nomenclature used here in describing the genitalia follows Freitag (1965) for the males and Freitag (1972) for the females.

Aedeagus and Parameres. C. sexguttata (Fig. 14a). The aedeagus is of average length and is somewhat stout. The parameres are long, roughly three-quarters the length of the aedeagus. The lateral flanges are well defined and extend to the apex, forming an apical tip.

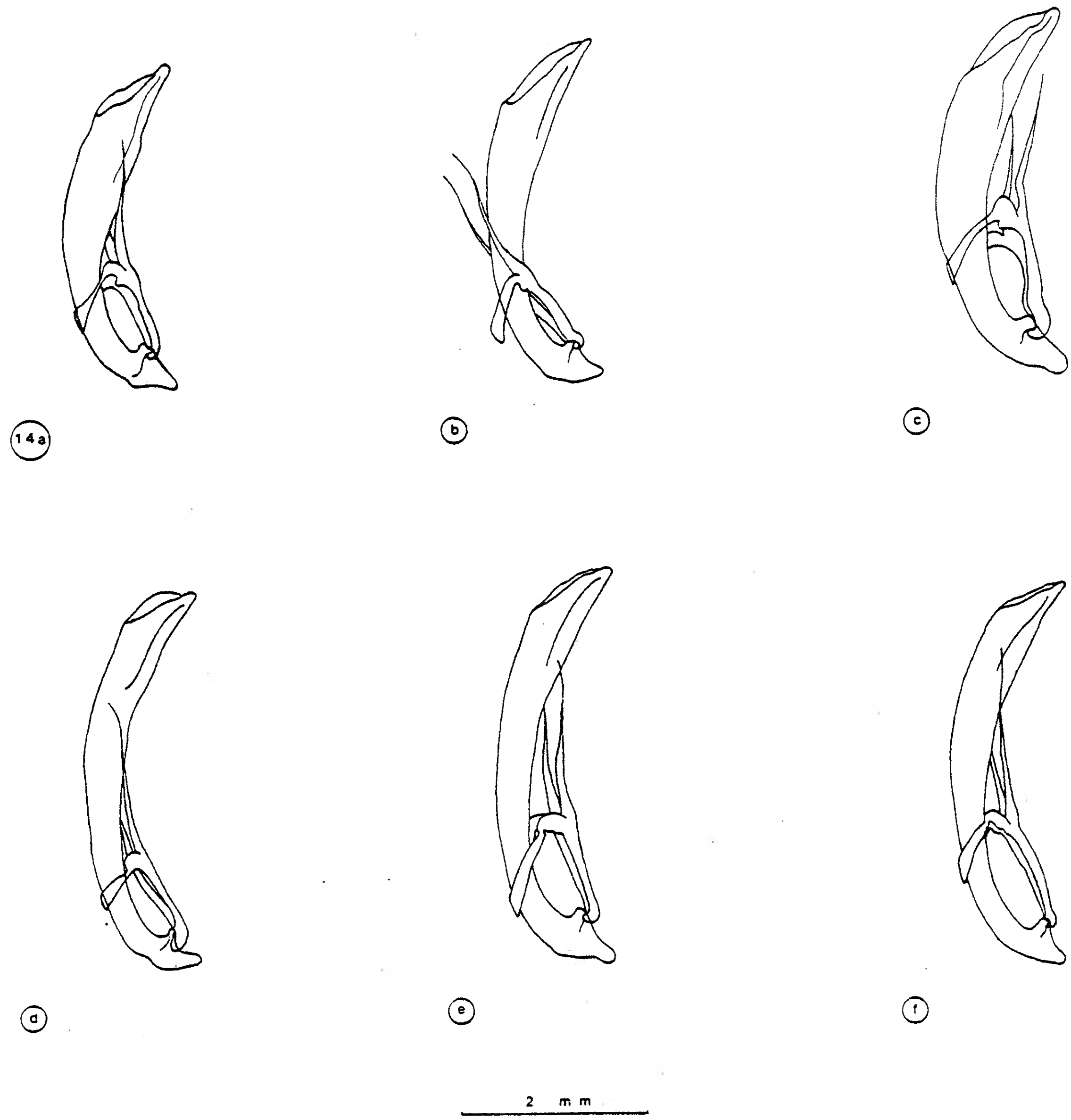
harrisii (Fig. 14b). The aedeagus of *harrisii* is morphologically identical to that of *C. sexguttata*. The example in Figure 14b was chosen to illustrate variation in the morphology of the aedeagus of *C. sexguttata*. The aedeagus is somewhat longer, thinner and not as curved as that in 14a. The lateral flanges are not as distinct, and the apical tip is longer and thinner.

C. denikei (Fig. 14c). The aedeagus is about 10% longer, more robust and less curved than in *C. sexguttata*. The lateral flanges are wider, more heavily sclerotized, and the apical tip is broader and blunter. The aedeagus of *C. denikei* is not within the normal variation of *C. sexguttata*; however, large specimens of *C. sexguttata* from Kansas, Nebraska, or Florida are very similar to *C. denikei* in the form of the aedeagus.

C. p. patruela (Figs. 14d, e). The aedeagus is longer, thinner, and not as curved as it is in *C. sexguttata*. The parameres are long, roughly three-quarters the length of the aedeagus, and the lateral flanges are thinner. The apical tip is not distinct and the head of the aedeagus is blunt. The first illustrated specimen (Fig. 14d) is from Wisconsin and the second (Fig. 14e) is from Pennsylvania. The variation in the form of the aedeagus is such that each could have come from either population.

C. p. consentanea (Fig. 14f). The aedeagus of *C. p. consentanea* is indistinguishable from that of *C. p. patruela*.

Figure 14: Aedeagus and parameres of a. *C. sexguttata*, b. *harrisii*, c. *C. denikei*, d. *C. p. patruela* (Wisconsin), e. *C. p. patruela* (Pennsylvania), f. *C. p. consentanea*.


14a
b
c
d
e
f
2 mm

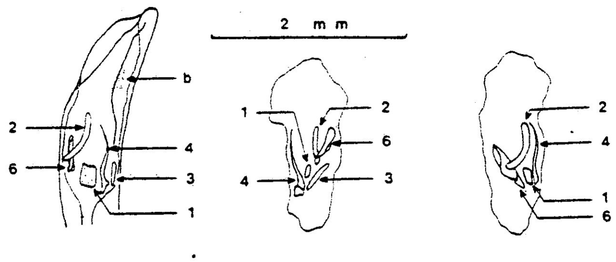
Internal Sac.

Figure 15a indicates the relative positions of the sclerites of the internal sac within the aedeagus. Figures 15b and c are respectively, the dorsal and ventral views of the internal sac. Note that sclerite 5 (see Freitag, 1965) is absent from these species. Scleral field b is larger and more sclerotized in *C. denikei* than in *C. sexguttata* and only very lightly sclerotized in *C. patruela*.

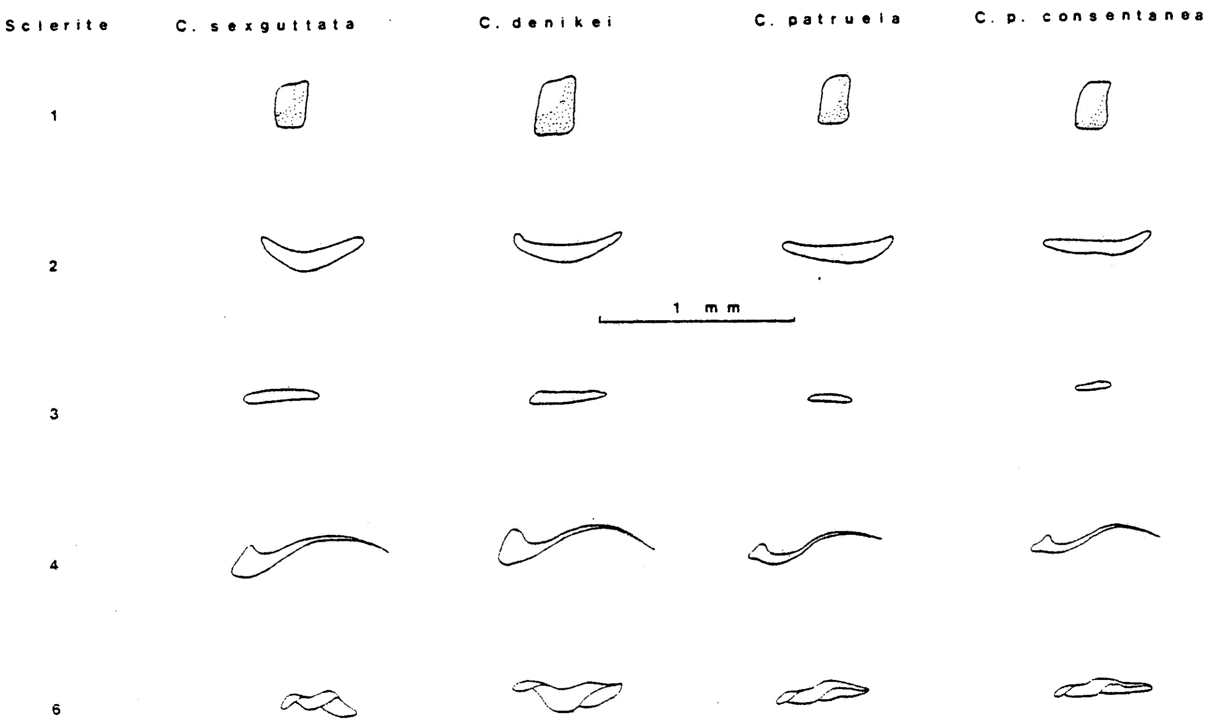
Figure 15d compares the sclerites of the internal sac of *C. sexguttata*, *D. denikei*, *C. p. patruela*, and *C. p. consentanea*. The sclerites of *C. sexguttata* and *C. denikei* normally differ, but specimens of each species will have similar sclerites. The internal sac sclerites of *C. p. consentanea* are morphologically identical to those of *C. p. patruela*.

Sclerite 1 (Fig. 15d) is more heavily sclerotized and has sharper corners in *C. sexguttata* and *C. denikei*. The sclerite is larger in *C. denikei*. Sclerite 2 is not as curved or as broad in *C. patruela* as it is in *C. denikei* and *C. sexguttata*. In *C. denikei*, the sclerite is not as curved as it is in *C. sexguttata*. Sclerite 3 of *C. patruela* is much smaller than it is in the other species. In *C. denikei*, the sclerite is slightly tapered at one end. Sclerite 4 is slightly shorter and conspicuously thinner in *C. patruela*. In *C. denikei*, the sclerite is stout. Sclerite 6 is shorter and more compressed in *C. patruela* than it is in *C. sexguttata* and *C. denikei*. The shape and size of sclerite 6 is highly variable in *C. sexguttata* and *C. denikei*. Although sclerite 6 as illustrated for *C. sexguttata* and *C. denikei* in Figure 15d shows differences, the differences are not consistent between the species.

Figure 15: Comparison of the sclerites of the internal sac of *C. sexguttata*, *C. denikei*, *C. p. patruela*, and *C. p. consentanea*, a. relative positions of the sclerites of the internal sac in *C. denikei*, lateral view, b. dorsal view, c. ventral view, d. comparison of the sclerites. Note that these species lack sclerite 5 (see Freitag, 1965).


2 mm
b
2
6
4
3
1
1
2
6
4
3
2
4
1
6

15a b c


Sclerite
C. sexguttata
C. denikei
C. patruela
C. p. consentanea
1
2
1 mm
3
4
6

d

In general, sclerite 6 tends to be larger and more robust in *C. denikei* than in *C. sexguttata*.

External female genitalia. As with the male genitalia; differences between *C. sexguttata* and *C. patruela* are consistent and distinct; differences between *C. sexguttata* and *C. denikei* are inconsistent and not distinct. Structure differences illustrated for *C. p. patruela* and *C. p. consentanea* indicate normal variation for a single population.

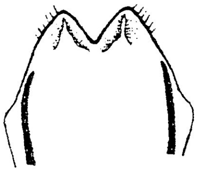
Figure 16 shows the 8th sternum of the female genitalia. The 8th sternum of *C. denikei* (Fig. 16c) tends to be broader and larger than it is in *C. sexguttata* (Fig. 16a). In *C. denikei* fewer setae occur along the margin and the ventral ridge is narrower. The 8th sternum illustrated for *harrisi* (Fig. 16b) shows normal variation for *C. sexguttata*; it is broader, the notch deeper, and the ventral ridge is not as distinct as in Figure 16a. The 8th sternum of *C. patruela* (Figs. 16d, e) has a deeper notch, the ventral ridge is narrower and more distinct, and the outer margin is more setose than in *C. sexguttata*.

The shape of syntergum 9 + 10 is similar in *C. sexguttata* (Figs. 18a, b) and *C. denikei* (Fig. 18c). The syntergum is slightly more sclerotized in *C. denikei*. Syntergum 9 + 10 is larger in *C. patruela* (Figs. 18d, e), the setae are longer, and the anterior end is rounded. The length of the four setae on the inner edge of the lateral lobes vary from very long (Fig. 18d) to the same length as the other setae (Fig. 18e).

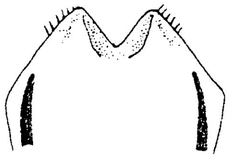
Figure 19 shows the oviduct sclerite (Fig. 19a) and the ventral (Fig. 19b) and lateral (Fig. 19c) views of the 2nd gonapophysis of

Figure 16: 8th sternum of adult female of a. *C. sexguttata*, b. *harrisii*, c. *C. denikei*, d. *C. p. patruela*, e. *C. p. consentanea*.

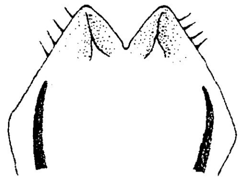
Figure 17: 8th sternum of adult female of a. *C. limbalis*, b. *C. purpurea*, c. *C. decemnotata*, d. *C. splendida*, e. *C. lengi*, f. *C. formosa*, g. *C. scutellaris*.



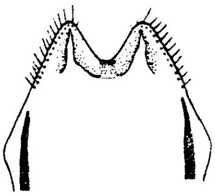
16a



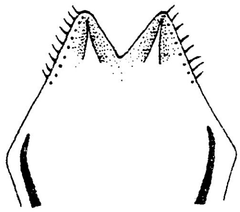
16b



16c

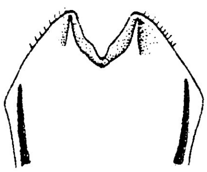


16d

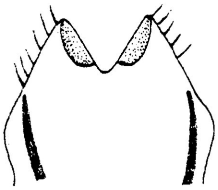


16e

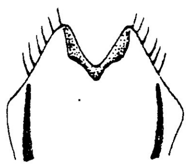
2 mm



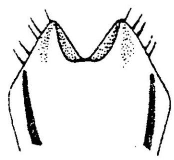
17a



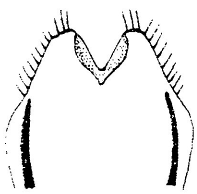
17b



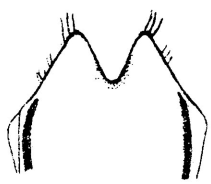
17c



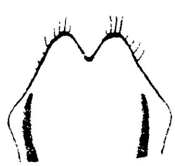
17d



17e



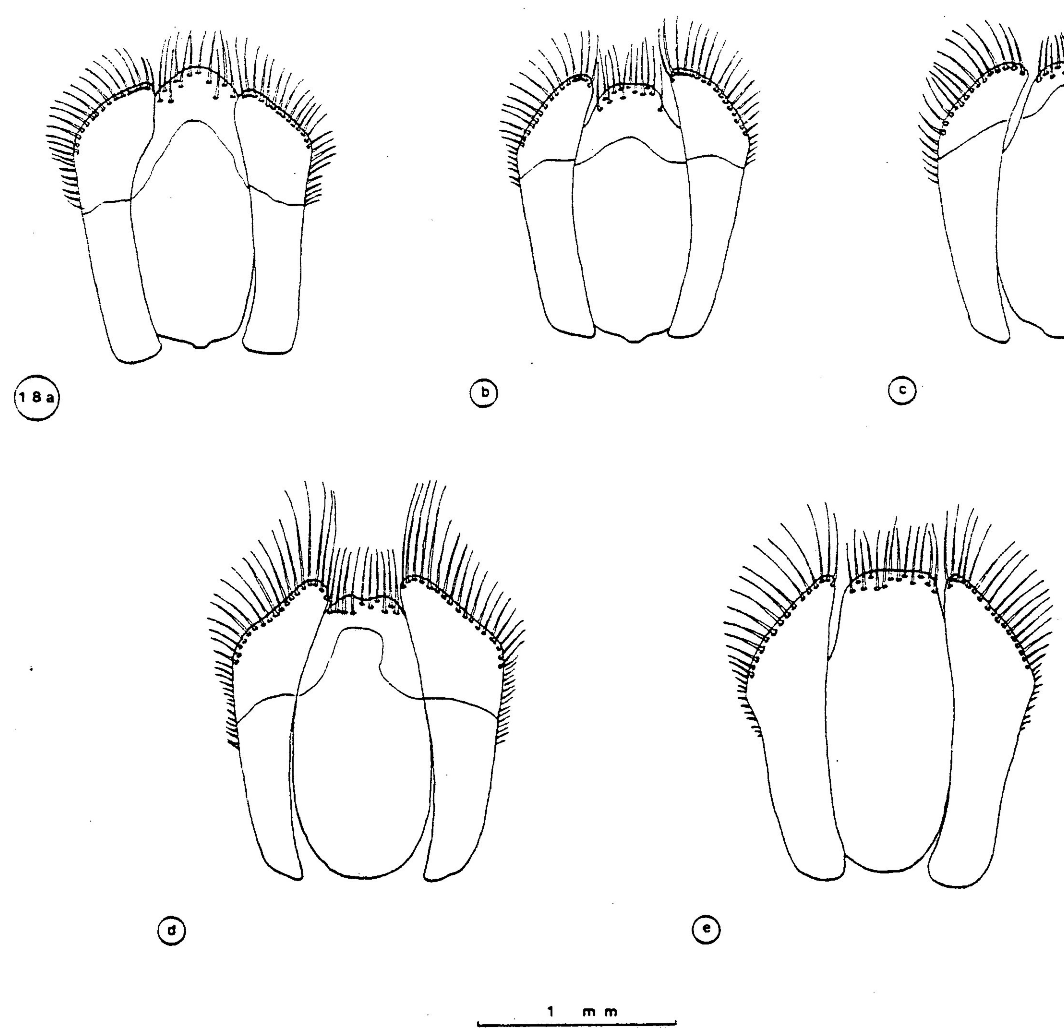
17f

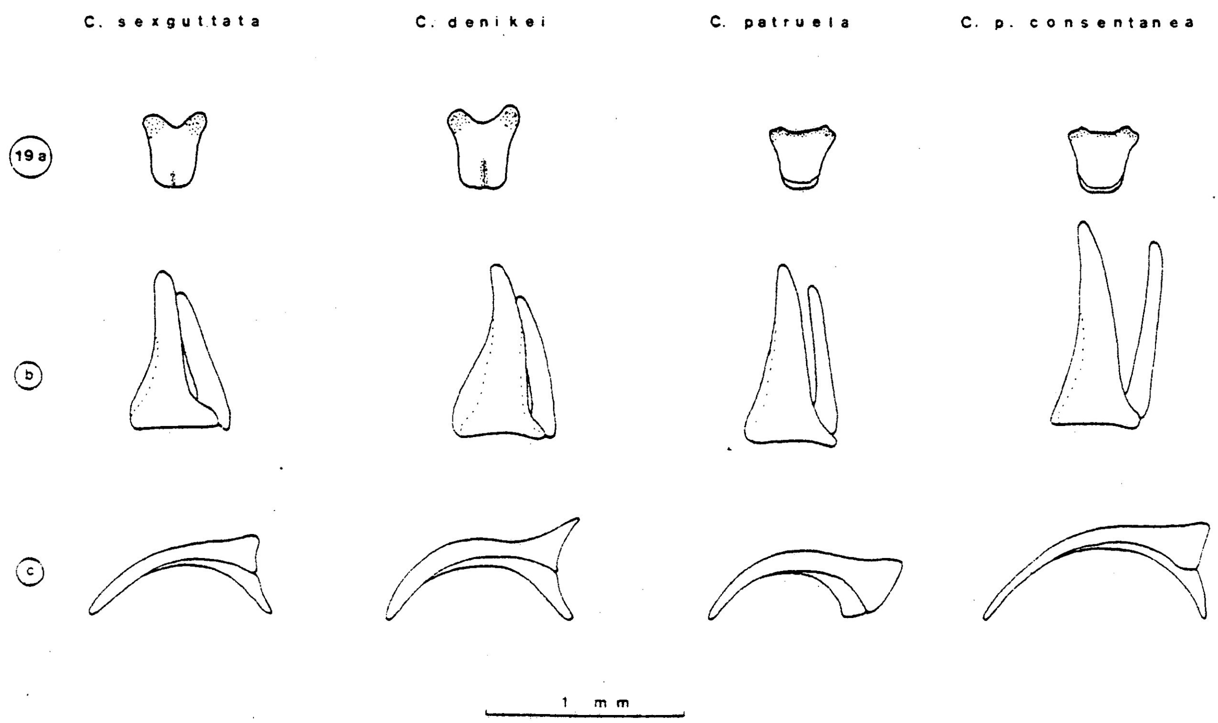


17g

Figure 18: Syntergum 9 + 10 of adult female of a. *C. sexguttata* b. *harrisii*, c. *C. denikei*, d. *C. p. patruela*, e. *C. p. consentanea*.

Figure 19: Comparison of structures of female genitalia of *C. sexguttata*, *C. denikei*, *C. p. patruela*, and *C. p. consentanea*, a. oviduct sclerite, b. 2nd gonapohpysis, ventral view, c. 2nd gonapohpysis, lateral view.


18a
b
c
d
e
1 mm


C. sexguttata
C. denikei
C. patruela
C. p. consentanea
19a
b
c
1 mm

C. sexguttata, C. denikei, and C. patruela. The lobes of the oviduct sclerite are truncate in C. patruela, and rounded in C. denikei and C. sexguttata. The 2nd gonapophysis of C. denikei is larger and more robust than that in C. sexguttata. The 2nd gonapophysis of C. patruela is longer and more curved than it is in the other two species.

Figure 20 compares the 2nd gonapophysis from a series of harrisii, including a cotype (Fig. 20f, left), with the gonapophysis of specimens from other localities. The 2nd gonapophysis of harrisii is much shorter, slightly narrower, and has a blunter tip than that in C. sexguttata. The geographic variation in the shape and length of the gonapophysis is slight (Fig. 21); generally, it is a conservative character. Leffler (1979) noted that the gonapophysis wears down as the beetle gets older, and that teneral adults should be used to determine the length. In the examined specimens of harrisii the gonapophysis showed signs of wear (pits, jagged margins), and the specimens were collected in the latter part of the season. Figure 22 shows the gonapophysis of three specimens of C. sexguttata collected from two localities in southern Ontario. The specimens were collected in May, June, and August (22a, b, and c respectively). The extreme wear in c is not typical for C. sexguttata, but illustrates that a gonapophysis similar to that of harrisii can be produced by wear.

Because wear could produce an extremely short gonapophysis the question became whether harrisii specimens were very old individuals of C. sexguttata with age related changes, that is colour and length of the gonapophysis. If true, it would be possible to calculate the rate of normal wear for the gonapophysis of C. sexguttata and extrapolate

Figure 20: Ventral and lateral views of the 2nd gonapohpysis of a., and b. _harrisii_, Stamford NY, c., and d. _C. sexguttata_, Ottawa ONT, e. left, _harrisii_ NY, right _C. sexguttata_ NY, f. left, cotype _harrisii_ NY, right _C. sexguttata_ NY.

Figure 21: Ventral and lateral views of the 2nd gonapohpysis of _C. sexguttata_ from a. Louisiana, b. Texas, c. Kansas.

Figure 22: Lateral view of 2nd gonapohpysis of specimens of _C. sexguttata_ collected in Ontario in a. May, b. June, c. August.

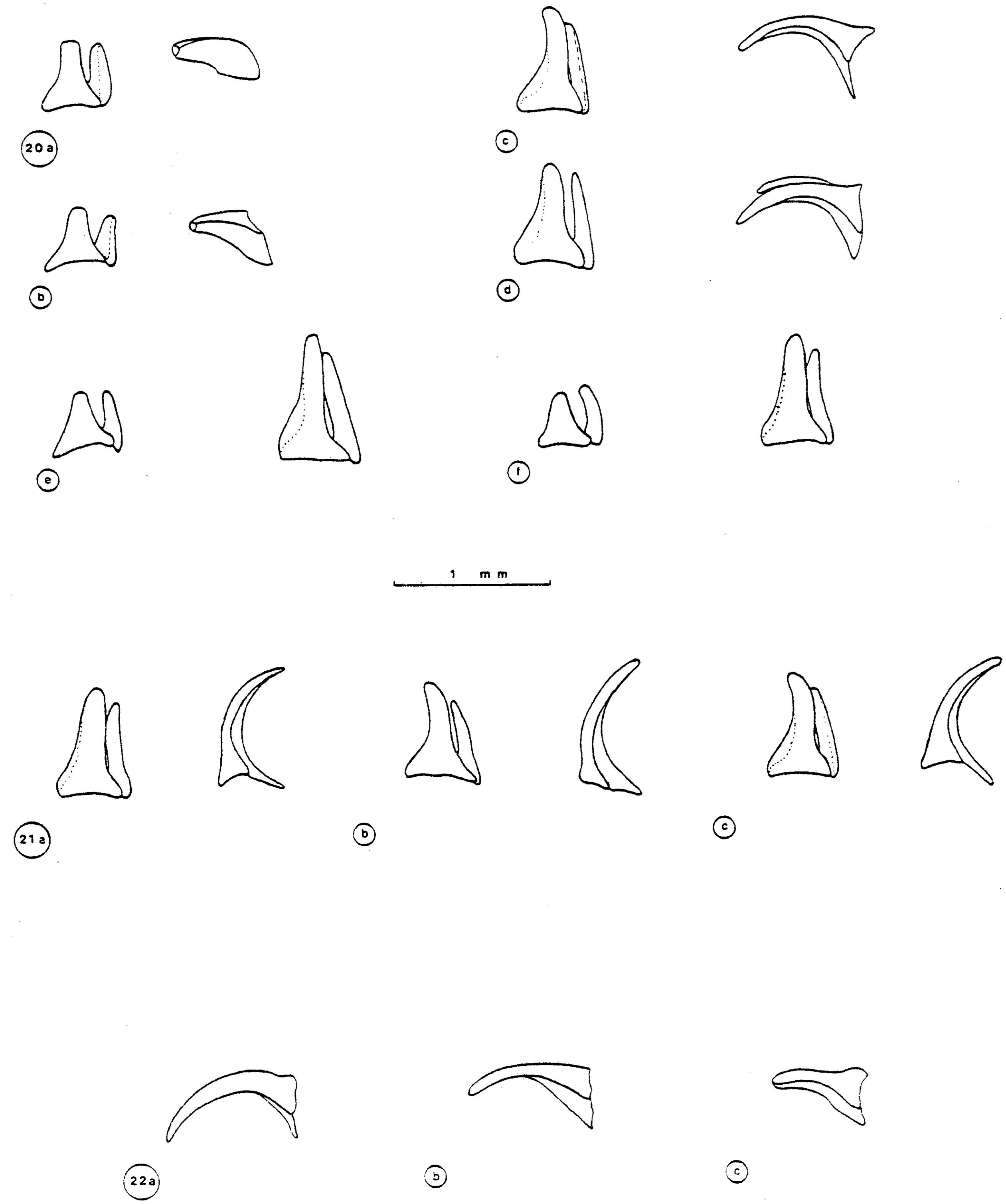
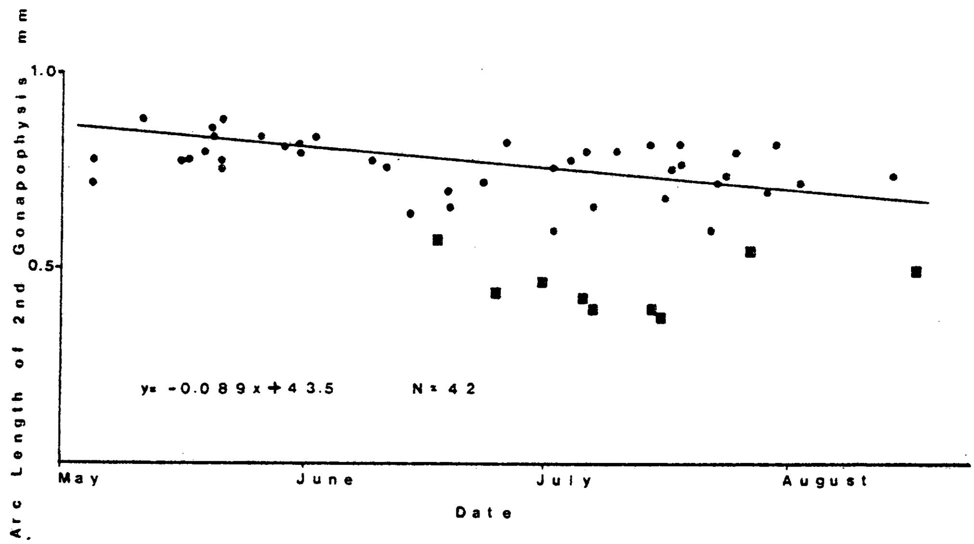
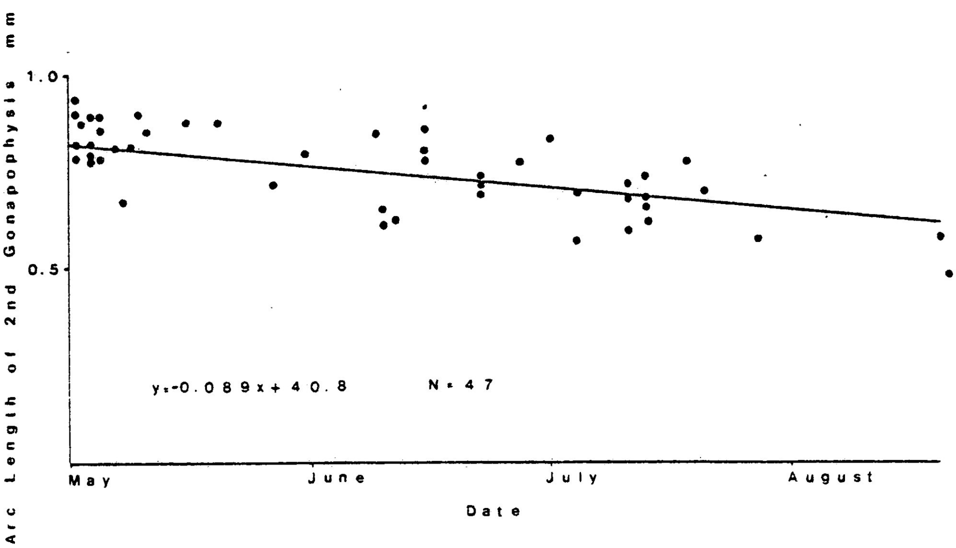

20a
b
c
d
e
f
1 mm
21a
b
c
22a
b
c

Figure 23: Arc length of 2nd gonapophysis plotted as a function of collection date. Circles are specimens of *C. sexguttata* collected in Vermont, squares are specimens of *harrisii* collected at Stamford NY. The regression line is calculated with data from Vermont only.

Figure 24: Arc length of 2nd gonapophysis plotted as a function of collection date for specimens of *C. sexguttata* collected in Arkansas.


Arc Length of 2nd Gonapophysis mm
1.0
0.5
y= -0.089x+43.5
N= 42
May
June
July
August
Date

(23)


Arc Length of 2nd Gonapophysis mm
1.0
0.5
y=-0.089x+40.8
N= 47
May
June
July
August
Date

(24)

that to tne end of the season, when harrisii is usually found. The arc length of the second gonapophysis was measured in 42 specimens of female C. sexguttata from Vermont, and in nine specimens of harrisii from New York. The results are plotted in Figure 23. The extremely short gonapophysis of harrisii could not be produced by "normal" wear, as defined by the Vermont population. To determine if the rate of wear for the Vermont population was typical for C. sexguttata, the study was repeated with 47 females from Arkansas (Fig. 24). The rate of wear of the gonapophysis of females in Vermont and Arkansas is identical. The arc lengths of the gonapophysis of the females from Vermont were compared to those of harrisii with a one-way ANOVA. The difference between the groups is highly significant (P less than 0.01, F = 136.3).

Systematics

The species Cicindela sexguttata Fabricius

Cicindela sexguttata Fabricius 1775:226. Type locality - Virginia.

Cicindele six mouchetee Olivier 1790:725. Type locality - none.

Cicindela varians Ljungh 1799:147. Type locality - extra-Europam.

Cicindela violacea Fabricius 1801:232. Type locality - Carolinas.

Cicindela thalissima Dejean in litt. Type locality - unknown.

Cicindela guttata Emmons 1854:35. Type locality - none.

Cicindela sexguttata var harrisii Leng 1902:128. Type locality - Appalachian mountains, North Carolina to Canada.

Cicindela quadriguttata Davis 1903:271. Type locality - Rhode Island and Massachusetts. Cicindela levettei tridens Casey 1909:271. Type locality - Vowells Mill Louisiana to Onaga Kansas.

Cicindela illinoensis Mares 1921:310. Type locality - Riverside Illinois.

Cicindela sexguttata kansanus Knaus 1929:24. Type locality - Kansas and Nebraska.

Recognition.

The species C. sexguttata has been described many times since the original description by Fabricius (1775). The best description is Leng (1902), but see also Fabricius (1775), Say (1818), Gould (1834), Schaupp, (1884), and the descriptions associated with synonyms (Ljungh, 1799; Fabricius, 1801; Emmons, 1854; Leng, 1902; Davis, 1903; Casey, 1909; Mares, 1921; Knaus, 1929).

The clearest and most consistent characters for differentiating specimens of C. sexguttata from specimens of C. patruela are elytral punctuation and morphology of the genitalia. The elytra of C. sexguttata are shallowly to deeply punctate, and those of C. patruela are granulate. Differences in the morphology of the genitalia are discussed in the section on genitalia. See the discussion of recognition of C. denikei for differentiating that species from C. sexguttata.

Notes on Synonomy and Taxonomic History

In 1775 Johan Fabricius described the species Cicindela sexguttata in Systema Entomologiae. The type locality was given as Virginia. Olivier (1790) translated a description of C. sexguttata and created the synonym C. six mouchetee. Ljungh (1799) described a species C. varians from "extra-Europam", a synonym of C. sexguttata.

In 1801 Fabricius described _C. violacea_ from the Carolinas. Dejean ranked _violacea_ as a variety of _C. sexguttata_ (Say, 1817); then Say (1818) ranked _violacea_ as a species. Schaupp (1884) ranked _violacea_ as a variety of _C. sexguttata_, but in doing so he referred to the bright violet forms of Kansas and did not mention the Carolinas. Leng (1902, 1920) recognized _violacea_ as a valid subspecies, whereas Horn (1915, 1926) called _violacea_ a sport or variety. Both authors refer to the western populations and do not mention the Carolinas. Knaus (1921) argued that the Kansas, Nebraska population was distinct from other populations, particularly the Carolinas, and that while the morphology of the two were similar the name _violacea_ did not apply to the western population. He proposed the name _kansanus_ for the western population, unfortunately, as a replacement for _violacea_, thereby creating an immediate synonym. Horn (1930) synonomized _kansanus_ with _violacea_. Leng and Mutchler (1933) recognized _kansanus_ as a valid subspecies, replacing _violacea_. Rivalier (1954) recognized _violacea_ as a subspecies. Both _kansasnus_ and _violacea_ are given as synonyms of _C. sexguttata_ by Boyd _et al._, (1982).

Dejean described _C. sexguttata_ as _C. thalissima_ in litt. (Leng, 1920; Horn, 1915), and later published the name without a description (Dejean, 1821).

In 1854 Emmons published a description of the species _C. guttata._ Emmons did not indicate that he was describing a new species, references Thomas Say after the description (no date given, probably Say, 1818), and associates the description with _C. patruela_. At the time, it was common to give the name of _C. sexguttata_ as _C. 6-guttata_, and it seems that Emmons was merely describing _C. sexguttata_, and a typographical error resulted in the creation of a synonym. The name is also a homonym of C. guttata Wiedman, published in 1823 (Huber, 1969).

The variety harrisii was described by Leng in 1902 as olivaceous green and found at elevations exceeding 1000 ft in the Appalachian mountains. Horn recognized harrisii as a mountain or seasonal form (1915), and later as just a mountain form (1930). Darlington (1931, in Dunn, 1978) regarded harisii as a synonym as it was not strictly alticoline, whereas Dunn (1978) argued that the distribution of harrisii is correlated to both elevation and altitude, being found at lower elevations in the north. Dunn (1978 unpub) recognized harrisii as a valid subspecies of C. sexguttata. Both Wallis (1961) and Boyd et al. (1982) regarded harrisii as a synonym of C. sexguttata.

In 1903, A. C. Davis published the name quadriguttata as a new variety of C. sexguttata. The variety differed in having four spots instead of six, and was found in Rhode Island and Massachusetts. The name was not recognized (Horn, 1908; Leng, 1920), and was found to be a homonym for C. quadriguttata Wiedmann (1821, in Huber 1969).

In 1909, Casey published two names, C. levettei, and C. l. tridens. The species C. levettei was described as different from C. sexguttata in colour, maculation, punctuation, and by having longer legs. The subspecies tridens differed in that it was largely immaculate, more elongate, and had coarser strigulation on the head. The distributions were given as Iowa and Louisiana to Kansas for C. levettei and C. l. tridens, respectively. Leng (1920) recognized C. levettei as a subspecies of C. sexguttata, and C. l. tridens as a synonym of C. s. levettei. At first Horn (1915, 1926) synonomized both names with C. sexguttata, but later recognized *tridens* as a form (1930). Eckhoff (1939) suggested that the name *tridens* be retained as a variety to differentiate the immaculate form of *C. sexguttata* found in Iowa, the locality Casey (1909) gave for *C. levettei*. Willis (1970) described *tridens* as a synonym for *C. sexguttata*. Ward (1971) examined specimens of *C. sexguttata* from Vowells Mills Louisiana and concluded "the appellation *tridens* should not be relegated to synonomy"; however, he added "Elevating *tridens* to the status of a valid subspecies...is also ill-advised". Boyd *et al.*, (1982) treated both *levettei* and *tridens* as synonyms.

Mares (1921) described a new species *C. illinoensis* from Riverside Illinois which differed from *C. sexguttata* in being completely black and having a more compressed prothorax. Horn (1926, 1930) recognized *illinoensis* as a variety of *C. sexguttata*, whereas Leng and Mutchler (1927) gave *illinoensis* species status, and Boyd et. al. (1982) regard it as a synonym.

Geographic Variation.

The discriminant analysis indicates a population in the southern states of Louisiana, Mississippi, and part of Alabama, which would correspond to Casey's name *tridens*. It is not recognized here because the population is not that distinct (see Leng, 1902), and the characters which would distinguish it are size, colour, and maculation, all of which are ecophenotypic in tiger beetles (Shelford, 1917; Dawson and Horn, 1928). Examination of external morphology and genitalia revealed no other characters which distinguished this population.

Another population indicated by the discriminant analysis is in the central mid-west, corresponding to Knaus's *kansanus*.

Of all of the populations of *C. sexguttata* analyzed, this was the most distinct; however, the characters that distinguished it were all ecophenotypic. There is reason to believe that the sample analyzed was not representative of this population. The large, bright violet specimens constituted 40 to 50% of the specimens examined, yet several authors have indicated that the violet specimens were rare (Knaus, 1900; Wickham, 1902; Smythe, 1905) and are now very rare or extinct (Willis, 1970; Brzoska, pers. com.).

Specimens of *harrisii* differ from *C. sexguttata* in colour (Leng, 1902), in the form of the gonapophysis, and they occur at high elevations, late in the season (Dunn, 1976), in habitats that are atypical for *C. sexguttata* (Wickham, 1902). These differences are explained if one postulates that *harrisii* are populations of *C. sexguttata* that occur in marginal habitats with different soils and cooler temperatures (*eg.*, at higher elevations). The differences between *harrisii* and *C. sexguttata* are all in ecophenotypic characters; and it is most parsimonius to view *harrisii* and *C. sexguttata* as one population rather than two sympatric subspecies. The name *harrisii* has no taxonomic rank within the species *C. sexguttata*.

Distribution.

Infomation on the distributions of *C. sexguttata*, *C. denikei*, and *C. patruela* is fragmentary and variable, and in catalogues, consists of a short, uninformative note. A number of authors have studied the distributions of species of *Cicindela* within restricted geographic regions. The largest geographic area examined was Canada by Wallis (1961). Others are Minnesota (Horn, 1928), Michigan (Graves, 1973), Ontario (Graves, 1965), Kansas (Willis, 1970), Quebec (Larochelle, 1972a), Arkansas, Mississippi, and Louisiana (Graves and Pearson, 1973), New Hampshire (Dunn, 1978) and New Jersey (Boyd, 1978). Otherwise, information on distributions is confined to publication of local records (eg., Gould, 1834; Davis, 1910; Davis, 1912; Kirk, 1969).

Figure 25 shows the known distribution of C. sexguttata. Since the map is constructed from collecting records, it represents the minimal distribution of the species. Further collecting would fill in the distribution; however, it is unlikely that the range extends much beyond that indicated in the Figure. The map represents historical information, and in some cases indicates populations that are probably extinct. County records of C. sexguttata collected in the United States are listed in Table 7.

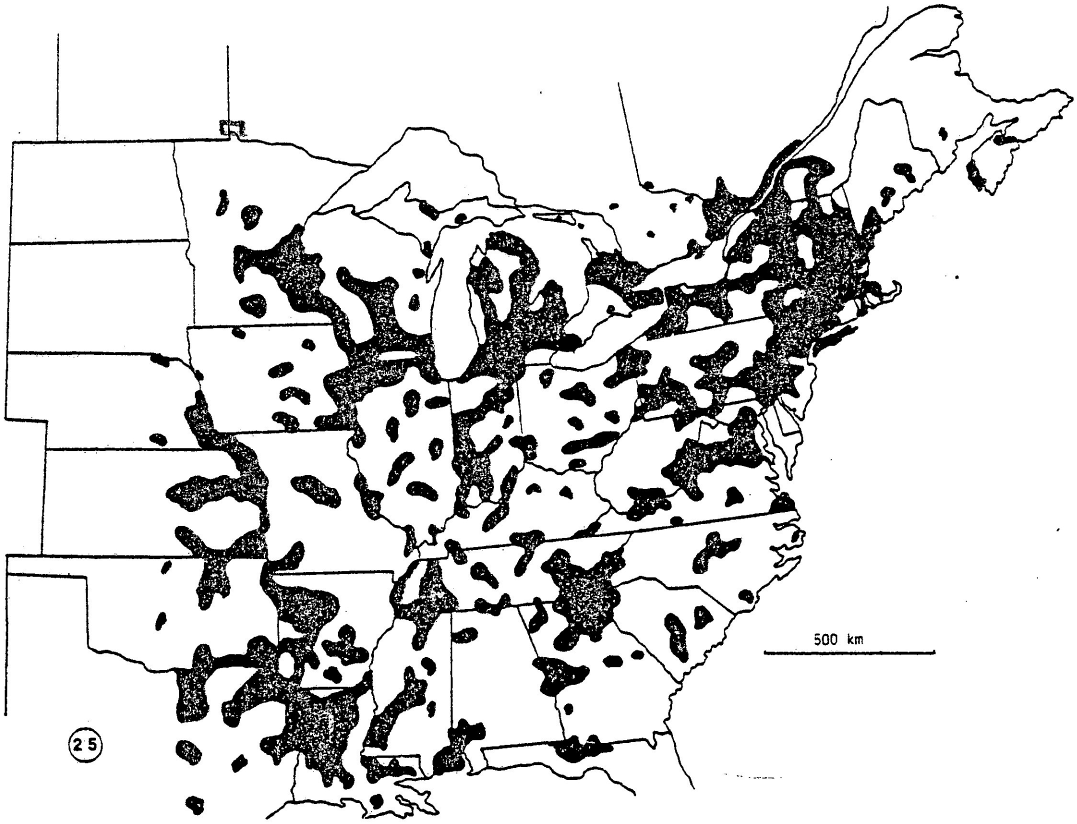
Doubtful distribution records

In his publication on the Cicindela of the Maritime Provinces, Larochelle (1980) reports C. sexguttata from Newfoundland. He cites as his sources Leconte (1860), Leng (1918), and Horn (1930). Horn (1930) does not give a source or a specific locality. Leng (1918) refers to Leconte (1860) as his source. The ultimate record for all three reports of a Newfoundland distribution is probably Leconte (1860), in which a specific locality is not given. No other records of a Newfoundland distribution are known, and the habitat of C. sexguttata is not found on Newfoundland. Leconte's (1960) record is probably a misidentification of the blue C. longilabris novaterrae Leng.

Leng (1920) reports C. sexguttata from New Mexico, while Acciavatti's

Figure 25: Distribution of *C. sexguttata*.

Figure 26: Distribution of *C. patruela*.


500 km
25

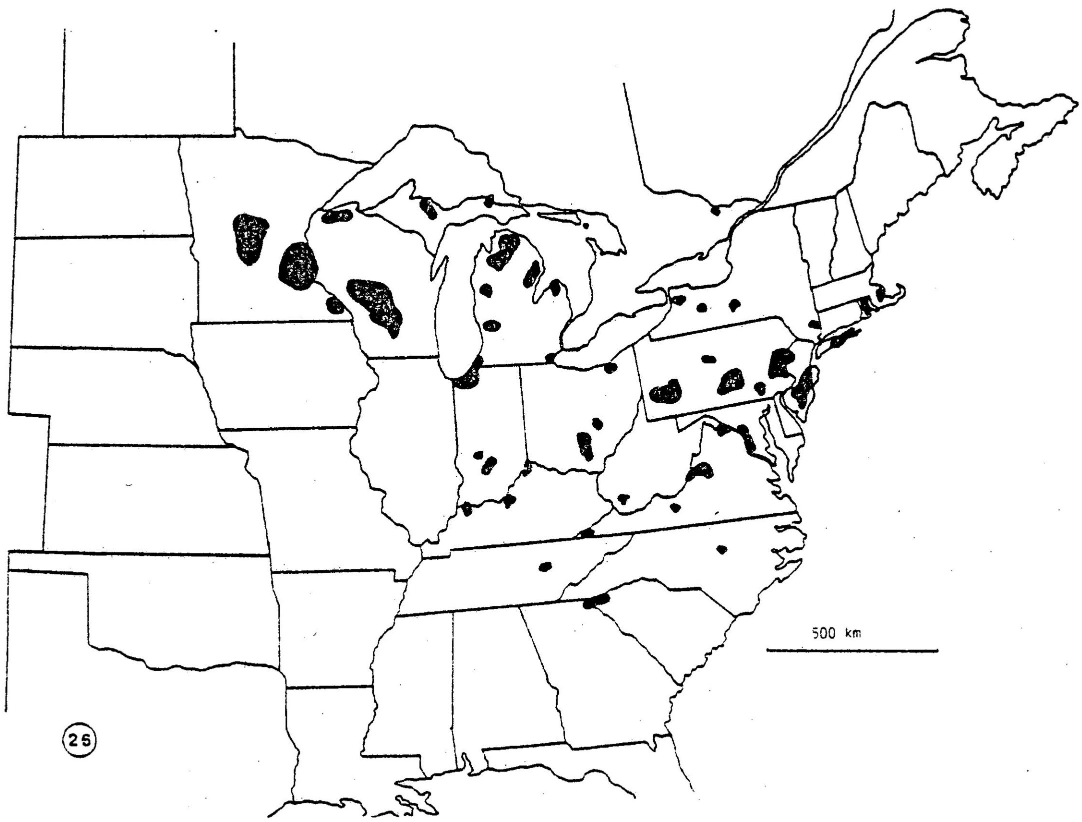

500 km
26

Table 7. County records of *C. sexguttata* collected in the United States.

ALABAMA:	Clarke; Lee; Madison; Mobile; Monroe; Randolph; Washington; Winston.
ARKANSAS:	Arkansas; Bradley; Calhoun; Chicot; Clark; Crawford; Franklin; Hemptstead; Jefferson; Johnson; Logan; Lonoke; Madison; Miller; Mississippi; Montgomery; Newton; Pike; Polk; Pope; Saline; Van Buren; Washington; Yell.
CONNECTICUT:	Fairfield; Hartford; Litchfield; New Haven; Tolland.
DELAWARE:	New Castle.
FLORIDA:	Gadsden; Jackson; Jefferson; Leon; Liberty; Madison.
GEORGIA:	Bibb; Chattooga; Cherokee; Clarke; Cobb; Crawford; Decatur; De Kalb; Fulton; Lumpkin; Macon; Madison; Meriwether; Murray; Muscogee; Oglethorpe; Paulding; Pike; Rabun; Randolph; Richmond; Rockdale; Thomas; Towns; Union; Washington; White.
ILLINOIS:	Carrol; Champaign; Clay; Cook; Du Page; Fayette; Lake; La Salle; Macoupin; Ogle; Peoria; Pope; Sangamon; Union; Winnebago.
INDIANA:	Allen; Brown; Cass; Clark; Clay; Crawford; Delaware; Franklin; Fulton; Gibson; Greene; Huntingdon; Jefferson; Knox; Kosciusko; Lagrange; Lawrence; Marion; Monroe; Montgomery; Morgan; Orange; Owen; Parke; Porter; Posey; Tippecanoe; Vigo; Warren.
IOWA:	Allamakee; Benton; Boone; Clarke; Clayton; Davis; Decatur; Delaware; DesMoines; Dickinson; Floyd; Henry; Jackson; Johnson; Jones; Lee; Louisa; Mahaska; Marshall; Muscatine; Polk; Scott; Storey; Union; Van Buren; Wayne.
KANSAS:	Bourbon; Cherokee; Clay; Dickinson; Doniphan; Douglas; Franklin; Leavenworth; Montgomery; Ottawa; Pottawatomie; Reno; Riley; Saline; Sedgewick; Shawnee; Sumner; Wabaunsee; Wilson; Wyandotte.

KENTUCKY:	Bath; Bullit; Cumberland; Edmonson; Franklin; Hardin; Henderson; Jefferson; McCreary; Trigg; Wayne.
LOUISIANA:	Allen; Bienville; Bossier; Caddo; Catahoula; De Soto; East Baton Rouge; East Feliciana; Evangeline; Grant; Jackson; Jefferson Davies; Lafayette; Lincoln; Livingston; Morehouse; Natchitoches; Ouachita; Rapides; Red River; Sabine; St. Tammany; Tangipahoa; Terrebonne; Union; Vernon; Webster; West Baton Rouge; West Feliciana; Winn.
MAINE:	Cumberland; Hancock; Kennebec; Penobscot; Piscataquis; York.
MARYLAND:	Allegany; Ann Arundel; Baltimore; Charles; Garrett; Howard; Montgomery; Prince George; St. Marys.
MASSACHUSETTS:	Barnstable; Berkshire; Franklin; Hampden; Hampshire; Middlesex; Norfolk; Plymouth; Suffolk; Worcester.
MICHIGAN:	Alcona; Allegan; Alpena; Arenac; Barry; Berrien; Calhoun; Cheboygan; Clare; Eaton; Emmet; Genesee; Grand Traverse; Hillsdale; Huron; Ingham; Ionia; Iosco; Isabella; Jackson; Kalamazoo; Kent; Lake; Lapeer; Livingston; Macomb; Manistee; Marquette; Menominee; Midland; Missaukee; Newaygo; Oakland; Ogemaw; Oscoda; Presque Isle; Saginaw; St. Clair; Sanilac; Schoolcraft; Shiawassee; Van Buren; Washtenaw; Wayne.
MINNESOTA:	Anoka; Becker; Blue Earth; Cass; Chisago; Clearwater; Crow Wing; Dakota; Goodhue; Hennepin; Houston; Kandiyohi; Nicollet; Olmsted; Pine; Ramsey; Sherburne; Stearns; Washington; Winona.
MISSISSIPPI:	Adams; Attala; Carrol; Claiborne; Copiah; Franklin; Greene; Harrison; Hinds; Holmes; Lafayette; Leake; Lincoln; Madison; Newton; Oktibbeha; Stone; Tippah; Union.
MISSOURI:	Atchison; Barry; Bates; Boone; Buchanan; Callaway; Cooper; Greene; Howard; Jackson; McDonald; Osage; Pike; St. Charles; St. Louis; Scott; Stone.

NEBRASKA:	Boyd; Cass; Douglas; Lancaster; Nemaha; Nuckolls; Pawnee; Richardson; Sarpy; Saunders; Thurston.
NEW HAMPSHIRE:	Belknap; Carroll; Cheshire; Coos; Grafton; Hillsborough; Merrimack; Rickingham; Strafford; Sullivan.
NEW JERSEY:	Atlantic; Bergen; Burlington; Camden; Essex; Gloucester; Hudson; Hunterdon; Middlesex; Morris; Ocean; Passaic; Somerset; Sussex; Union; Warren.
NEW YORK:	Albany; Broome; Cattaraugus; Chautaugua; Chemung; Chenango; Clinton; Columbia; Delaware; Erie; Essex; Franklin; Fulton; Genesee; Greene; Hamilton; Herkimer; Jefferson; Monroe; Montgomery; Nassau; Niagra; Oneida; Onondaga; Ontario; Orange; Otsego; Rennsselaer; Rockland; St. Lawrence; Saratoga; Schuyler; Suffolk; Sullivan; Tompkins; Ulster; Warren; Washington; Wayne; Westchester; Yates.
NORTH CAROLINA:	Avery; Buncombe; Chatham; Cherokee; Dare; Graham; Haywood; Henderson; Jackson; Macon; McDowell; Mitchell; Moore; Orange; Pender; Swain; Transylvania; Wake.
OHIO:	Ashland; Ashtabula; Athens; Auglaize; Butler; Crawford; Franklin; Guernsey; Hamilton; Hocking; Holmes; Lucas; Montgomery; Portage; Preble; Ross; Scotio; Trumbull.
OKLAHOMA:	Alfalfa; Bryan; Caddo; Carter; Delaware; Lincoln; Marshall; McCurtain; Murray; Osage; Pawnee; Payne; Pushmataha; Tulsa.
PENNSYLVANIA:	Allegheny; Armstrong; Beaver; Blair; Bucks; Center; Chester; Clearfield; Clinton; Columbia; Crawford; Dauphin; Delaware; Fulton; Huntingdon; Lackawana; Lancaster; Lehigh; Mercer; Monroe; Northumberland; Perry; Philadelphia; Pike; Porter; Schuylkill; Somerset; Washington; Wayne; Westmoreland.
RHODE ISLAND:	Kent; Providence; Washington.
SOUTH CAROLINA:	Anderson; Colleton; Florence; Greenville; Oconee; Orangeburg; Pickens; Richland.

TENNESSEE:	Anderson; Blount; Carroll; Chester; Cumberland; Davidson; Decatur; Fayette; Fentress; Franklin; Gibson; Hardeman; Hardin; Haywood; Henderson; Knox; Lake; Lawrence; Madison; McNairy; Montgomery; Rutherford; Sevier; Shelby; Union; Weakley.
TEXAS:	Bosque; Bowie; Cooke; Dallas; Hopkins; Houston; Lee; McLennan; Montague; Nacogdoches; Panola; Parker; Rusk; Shelby; Van Zandt; Wise.
VERMONT:	Addison; Bennington; Caledonia;Chittenden; Lamoille; Orleans; Washington; Windham; Windsor.
VIRGINIA:	Amelia; Arlington; Augusta; Bland; Essex; Fairfax; Fauquier; Giles; Lee; Madison; Montgomery; Nansemond; Nelson; Norfolk; Page; Powhatan; Princess Ann; Prince William; Richmond; Rockingham; Tazewell; Wise.
WEST VIRGINIA:	Greenbrier; Hardy; Marshall; Mercer; Monongallia; Pendleton; Pocahontas; Wyoming.
WISCONSIN:	Chippewa; Dane; Eau Claire; Grant; Iowa; Iron; Jackson; Jefferson; Juneau; Milwaukee; Oconto; Pierce; Polk; Portage; Racine; Richland; Sauk; Shawano; Walworth; Waukesha; Winnebago; Wood.

(1979) checklist of the New Mexico *Cicindela* does not. There are no other records of a New Mexico distribution and the habitat of *C. sexguttata* does not exist there. The record is probably based on a misidentified specimen of the blue *C. punctulata chihuahua* Bates, or a mislabelled specimen of *C. sexguttata*.

Other doubtful records are as follows:

KSU	2 *C. sexguttata* labelled Cobalt, Ont. 19.VII.1907. Although this does not represent a great range extension, it is not in the normal climate/habitat regime.
UG	2 *C. sexguttata* labelled Los Angeles, Calif.
	2 *C. sexguttata* labelled Vancouver, B. C.
UMMZ	3 *C. sexguttata* labelled Phoenix, Ariz. The labels on these specimens are in the same handwriting and have the same date.

The species *Cicindela denikei* Brown n. sp.

Cicindela sexguttata denikei Brown 1934:22. Type locality - Ingolf, Ontario.

Recognition

Described as a subspecies of *C. sexguttata* by Brown (1934), *C. denikei* is a cryptic or sibling species of *C. sexguttata*. Adults of *C. denikei* are larger and more robust than adults of *C. sexguttata*, except for adults of *C. sexguttata* from the central mid-western states, Florida and a few large individuals throughout the range. The colour of *C. denikei* adults is olivaceous green, emerald green, brassy green, or blue to purpulish blue. The genitalia of *C. denikei* are larger and more robust and tend to be more strongly sclerotized. Females of

C. denikei have a lower rate of egg production than females of *C. sexguttata*.

Larvae of *C. denikei* are larger and lighter incolour than those of *C. sexguttata*. The inner surface of the pygopod is lightly sclerotized in *C. sexguttata* and unsclerotized in *C. denikei*. The larval burrow of *C. denikei* is found under stones, with the burrow mouth unexposed.

The habitat of *C. denikei* is the boreal forest of Northwestern Ontario, southeastern Manitoba, and possibly northern Minnesota, compared to the oak-hickory forest habitat of *C. sexguttata*. Populations of *C. denikei* are found on sandy, silty till; whereas *C. sexguttata* occurs on warm, moist loamy soils. Populations of *C. sexguttata* are rare on the Canadian Shield, whereas populations of *C. denikei* are found only on the Canadian Shield. The ranges of the two species are allopatric.

Notes on Synonomy and Taxonomic History.

Brown (1934) described the subspecies *C. s. denikei* from Ingolf, Ontario. He noted that the new subspecies was larger, dull green, had reduced maculation, and occurred in rocky situations. Blackwelder (1939) recognized *C. denikei* as a valid subspecies. A number of authors suggested that *C. denikei* might be a sibling species of *C. sexguttata* (Wallis, 1961; Graves, 1965; Willis, 1968), but none actually gave it specific rank. Leffler (1979, unpub.) assigned specific rank to *C. denikei*. Boyd *et al*. (1982) recognized *C. denikei* as a subspecies of *C. sexguttata*.

Distribution.

Figure 78 is the known range of *C. denikei*. See discussion on distribution of *C. sexguttata*.

Doubtful Distribution records.

Wallis (1961) records *C. sexguttata* from Makinak, Manitoba, although he states that it is probably a misidentification of *C. s. denikei* as the specimen came from a student collection. If valid, this specimen would represent a range extension of 500 km, for a climate where *C. denikei* has not been found before. Unless the record is confirmed, this specimen should be considered as mislabelled as well as misidentified. Also, Wallis doubts a record from Morden, Manitoba as it is "far from the coniferous zone", but he accepts a record from Altona, Manitoba, 32 km from Morden and approximately the same distance from the coniferous zone. These records, and others, seem to have come from the student collection, Department of Entomology, University of Manitoba. Although I borrowed this collection, I did not find these specimens, nor have they been deposited in the CNC. I searched the region west of the White Shell Forest Reserve for *C. denikei*, but did not find the beetles or a suitable habitat. For this reason, the records from Morden, Altona and Sandilands Forest Reserve are considered doubtful.

The species *Cicindela patruela* Dejean

Cicindela patruela Dejean 1825:62. Type locality - Amerique septentrionale. *Cicindela consentanea* Dejean 1825:63. Type locality - Amerique septentrionale. *Cicindela montana* Hentz in litt. (Leng, 1920).

a. *consentanea* Dejean 1825:63. Type locality - Amerique septentrionale.

Recognition.

The species *C. patruela* is well described in the literature. The best description is Leng (1902), but see also Dejean (1825), Gould (1834), Emmons (1854) and Schaupp (1884). Characters distinguishing *C. patruela* from *C. sexguttata* are discussed under recognition of *C. sexguttata*.

Notes on Synonomy and Taxonomic History.

In 1825 Dejean described two new species of tiger beetle from America, *C. patruela* and *C. consentanea*. Gould (1834), Harris (1852) and Emmons (1854) recognized *C. patruela*, but Schaupp (1884) described both *patruela* and *consentanea* as varieties of *C. sexguttata*. Leng (1902) accorded *patruela* species rank and described *consentanea* as a variety of *patruela*. Unfortunately, the variety status of *patruela* was established (Townsend, 1889) and continued to be used (Shelford, 1906). Horn (1915) regarded *patruela* as a subspecies of *C. sexguttata*, and *consentanea* as a form or sport. Leng (1920) recognized *patruela* and *consentanea* as he had in 1902; whereas Horn (1925, 1930; Dawson and Horn, 1928) continued to regard them as in 1915. Rivalier (1954) and Wallis (1961) recognized *patruela* as a species, but did not comment on the status of *consentanea*. Boyd (1973, 1978, and Boyd *et al.*, 1982) recognized *patruela* as a species, and *consentanea* as a subspecies. Hentz described *C. patruela* as *C. montana* in litt. (Horn, 1915; Leng, 1920). Lawton (1976) described a variant of *C. p. patruela*, but did not assign it status or a name.

Geographic variation.

The discriminant analysis of *C. p. patruela* and *C. p. consentanea* indicated that the two populations were not different, and I did not find consistent differences in the genitalia. Nonetheless, I preserve the subspecific status of _C. p. consentanea_. The black colour of _C. p. consentanea_ is present in all individuals, whereas melanism is very rare and sporadic in _C. p. patruela_. The habitat of _C. p. consentanea_ is different from that of _C. p. patruela_. The two subspecies are parapatric, with no apparent zone of intergradation. The fall emergence of teneral adults of _C. p. consentanea_ includes most, if not all, individuals in the population. In _C. p. patruela_ the fall emergence includes only a portion of the population.

The discriminant analysis also indicated two northern populations, one to the northeast and one to the northwest of the range of _C. patruela_. There is no other evidence that these populations are different from the central population (ie., genitalia, habitat, or life history). The difference between the central population and these more northern populations are probably due to a combination of climatic factors and the fact that they are on the periphery of the range.

Distribution.

Figure 26 is the known distribution of _C. patruela_. See discussion of distribution of _C. sexguttata_. County records of _C. patruela_ collected in the United States are listed in Table 8.

Doubtful distribution records are as follows:

UWS — 1 _C. patruela_ labelled Pendelton, Oregon
1 _C. patruela_ labelled Waitsburg, Washington
1 _C. patruela_ labelled Walla Walla, Washington
All 3 of the above records have the same handwriting on the labels.

Table 8. County records of C. patruela collected in the United States.

GEORGIA:	Rabun.
INDIANA:	Brown; Lake; La Porte; Lawrence; Owen; Porter; Starke.
KENTUCKY:	Boone; Bullitt; Henderson; Knox.
MARYLAND:	Baltimore; Montgomery; Prince George.
MASSACHUSETTS:	Plymouth.
MICHIGAN:	Alcona; Berrien; Cheboygan; Chippewa; Crawford; Grand Traverse; Huron; Iosco; Kent; Lake; Marquette; Misaukee; Monroe; Otsego; Ottawa; Presque Isle.
MINNESOTA:	Anoka; Crow Wing; Sherburne; Todd; Wadena.
NEW JERSEY:	Warren.
NEW YORK:	Livingston, Thomkins; Westchester.
NORTH CAROLINA:	Buncombe; Burke; Macon; Wake; Watauga.
OHIO:	Cuyahoga; Hocking; Jackson; Lucas; Muskingum.
PENNSYLVANIA:	Allegheny; Berks; Bucks; Centre; Crawford; Dauphin; Indiana; Juniata; Lancaster; Lehigh; Monroe; Northhampton; Northumberland; Perry; Westmoreland.
RHODE ISLAND:	Kent; Providence; Washington.
SOUTH CAROLINA:	Pickens.
TENNESSEE:	Cumberland.
VIRGINIA:	Augusta; Bath; Lee; Loudoun; Montgomery; Nelson; Rockingham.
WEST VIRGINIA:	Wyoming.
WISCONSIN:	Adams; Bayfield; Clark; Dane; Douglas; Eau Claire; Jackson; Juneau; Monroe; St. Croix; Sauk; Wood.
C. patruela consentanea	
NEW JERSEY:	Atlantic; Burlington; Camden; Cape May; Gloucester; Middlesex; Ocean.
NEW YORK:	Suffolk.

AMNH 1 *C. patruela* labelled Florida.

Phylogeny.

The close relationship of *C. sexguttata* and *C. patruela* was first implied by Gould (1834) when he placed their descriptions adjacent to each other in his Cicindelidae of Massachusetts. Schaupp (1884) felt they were varieties of a single species. Leng (1902) placed the two species in his Sexguttata-Purpurea Group, recognizing only *C. sexguttata* as a species. Horn (1930) did not recognize *C. patruela* as a species, and placed *C. sexguttata* as the only species in his *sexguttata* Group (2), between the *formosa-purpurea-oregona* Group (1) and the *obsoleta-punctulata* Group (3). Rivalier (1954) placed the two species in his Group VII of *Cicindela*. Rivalier's Group VII is similar to Leng's Sexguttata-Purpurea Group (1902); however, Rivalier included *C. formosa* and made it the type species for the group. Wallis (1961) stated that it was not possible to relate *C. sexguttata* and *C. patruela* to any other species of North American *Cicindela*.

Leffler (1979) places *C. sexguttata* and *C. patruela* in his *formosa* group, which is Rivalier's Group VII, except for the assignment of species and subspecies names. Leffler states that the *formosa* group is derived from a common ancestor with the Nearctic *maritima* group (see Freitag, 1965). The *formosa* group then divides into the *formosa*, *decemnotata*, and *purpurea* subgroups. The *sexguttata* subgroup splits off from the *purpurea* subgroup, and *C. patruela* becomes a species separate from the ancestor of *C. sexguttata* and *C. denikei*.

Leffler's (1979) phylogeny of the *formosa* group is mainly correct;

however, his analysis of two character states is probably in error. Leffler states that the female genitalia of the formosa group have no unique external characters and are similar to the generalized members of the maritima group. With the exception of C. formosa, and possibly C. plutonica and C. pugetana members of the formosa group have a scalloped margin of the ventral ridge of the 8th sternum (Figs. 16, 17). This does not exist in the maritima group (Freitag, 1972) or C. scutellaris (Fig. 17g). The character is probably apomorphic, although examination of many more species is required to be certain. If the character is apomorphic it supports Gaumer (1977) who concluded that C. formosa has not been associated with any other lineage of Cicindela for quite some time. It is probable that quite early the formosa subgroup split from an ancestral lineage of the purpurea-decemnotata-sexguttata subgroup.

Leffler (1979) also states that the antennal scape of C. sexguttata, C. denikei, and C. patruela is glabrous, and therefore unique in the formosa group. In these species, the antennal scape is glabrous for 30 to 60% of the examined individuals; others have one to four setae on the scape.

Zoogeography

The zoogeography of Nearctic species of Cicindela is largely unknown. Wickham (1904) examined the effects of glaciation on the Cicindela of the Great Basin region, and Willis (1967) studied the zoogeography of the Cicindela of saline habitats of central United States. The zoogeography of C. formosa and its subspecies was done by Gaumer (1977). The most comprehensive work on the zoogeography of related species is by

Freitag (1965), who worked on the North American species of the maritima group.

Leng (1912) considered the effects of the Wisconsin glaciation on the C. sexguttata species group, and stated that both C. sexguttata and C. patruela were driven south by the glaciers, and followed them north again. Leng also postulated a Georgia refugium for C. p. patruela, and a separate New Jersey refugium for C. p. consentanea.

Speculation on the phylogeny of an insect group must necessarily consider the rate of evolution. Some authors state that many of the extant species evolved in the Pleistocene (Ross, 1953, 1965; Howden, 1969); more recent works indicate that most living species had evolved by the end of the Pliocene (Matthews, 1979; Freitag, 1965). The sexguttata group is so distinct from related groups that an early separation from the main stem is indicated, and within the group there is evidence of recent evolution of species.

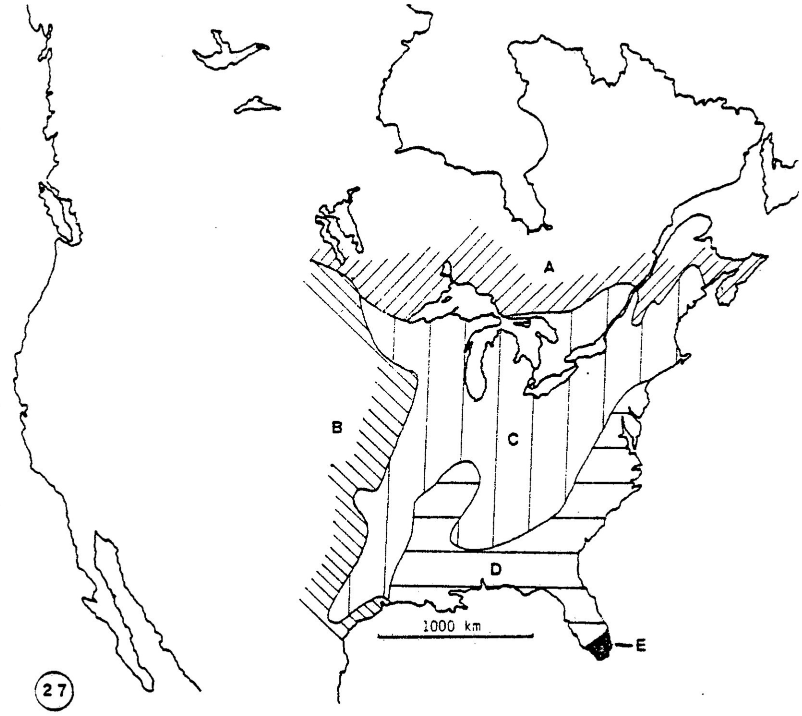
The ancestral stock of the sexguttata group probably split from the purpurea stem some time in the late Miocene. A forest habitat of the type the ancestor would have required was available then (Brown, 1950). In the Pliocene the cooling temperatures (Matthews, 1979) and drier climates (King, 1959) undoubtedly caused certain amounts of habitat disruption and disjunctions. The species C. patruela probably speciated in this period.

During the Pleistocene, North America was repeatedly glaciated causing drastic climatic changes (Butzer, 1964; Matthews, 1979). It effected multiple speciation (Ross, 1965; Howden, 1969), reduction of species area, and southward migration of some species (Ross, 1965).

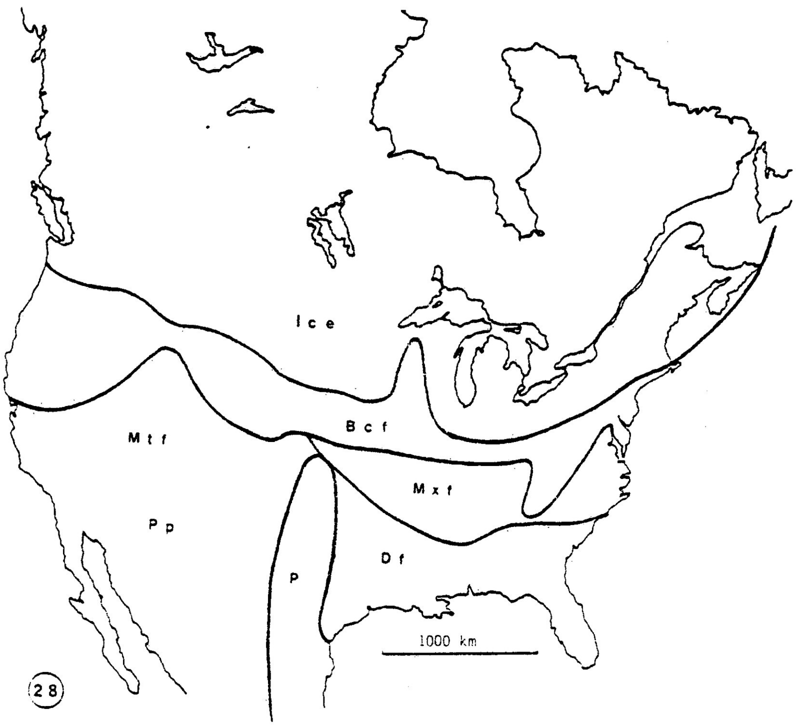
There was no mixing of eastern and western fauna in the south (Dillon, 1956). Speciation occurred south of the ice sheets, on the coasts, or in refugia (Ross, 1965). Undoubtedly, the *sexguttata-denikei* ancestor and *C. patruela* shifted their ranges south during glaciations and north during warm periods. These range fluctuations probably resulted in the creation of numerous subspecies that subsequently became extinct. During the Wisconsin maximum the *sexguttata-denikei* ancestor probably occurred in the deciduous forest in the south, and *C. patruela* in the mixed forest (Fig. 28). The Appalachian mountains split the range of *C. patruela*, with *C. p. consentanea* on the coast and *C. p. patruela* inland. In the warmer period following the Wisconsin glaciation, the species moved north with their habitat (Fig. 27). The two subspecies of *C. patruela* were no longer isolated, and *C. p. patruela*, through competition or genetic swamping, limited *C. p. consentanea* to the Pine Barrens of New Jersey and the tip of Long Island, New York. The *sexguttata-denikei* ancestor spread north and then northwest (Fig. 29). A marginal population pinched off the northwestern tip of the *C. sexguttata-denikei* ancestor range and became *C. denikei*. Because of the recent movement of the hickory forests (Matthews, 1979) and retreat of Lake Agassiz (Morgan and Morgan, 1980), speciation could not have occurred before 5,000 years BP.

Figure 27: The floristic provinces of continental North America. A. Northern Conifer, B. Grassland, C. Eastern Deciduous, D. Coastal Plain, E. West Indian (Redrawn from Gleason and Cronquist, 1964; in Scudder, 1979).

Figure 28: Probable distribution of biomes and ice front during Wisconsin maximum, northern refugia excluded. Bcf. Boreal Coniferous Forest, Mxf. Mixed Forest, Mtf. Montane Forests, Pp, Palouse Prairie, P. Prairie, Df. Deciduous forest. (Redrawn from Ross, 1970; in Lehmkuhl, 1980).

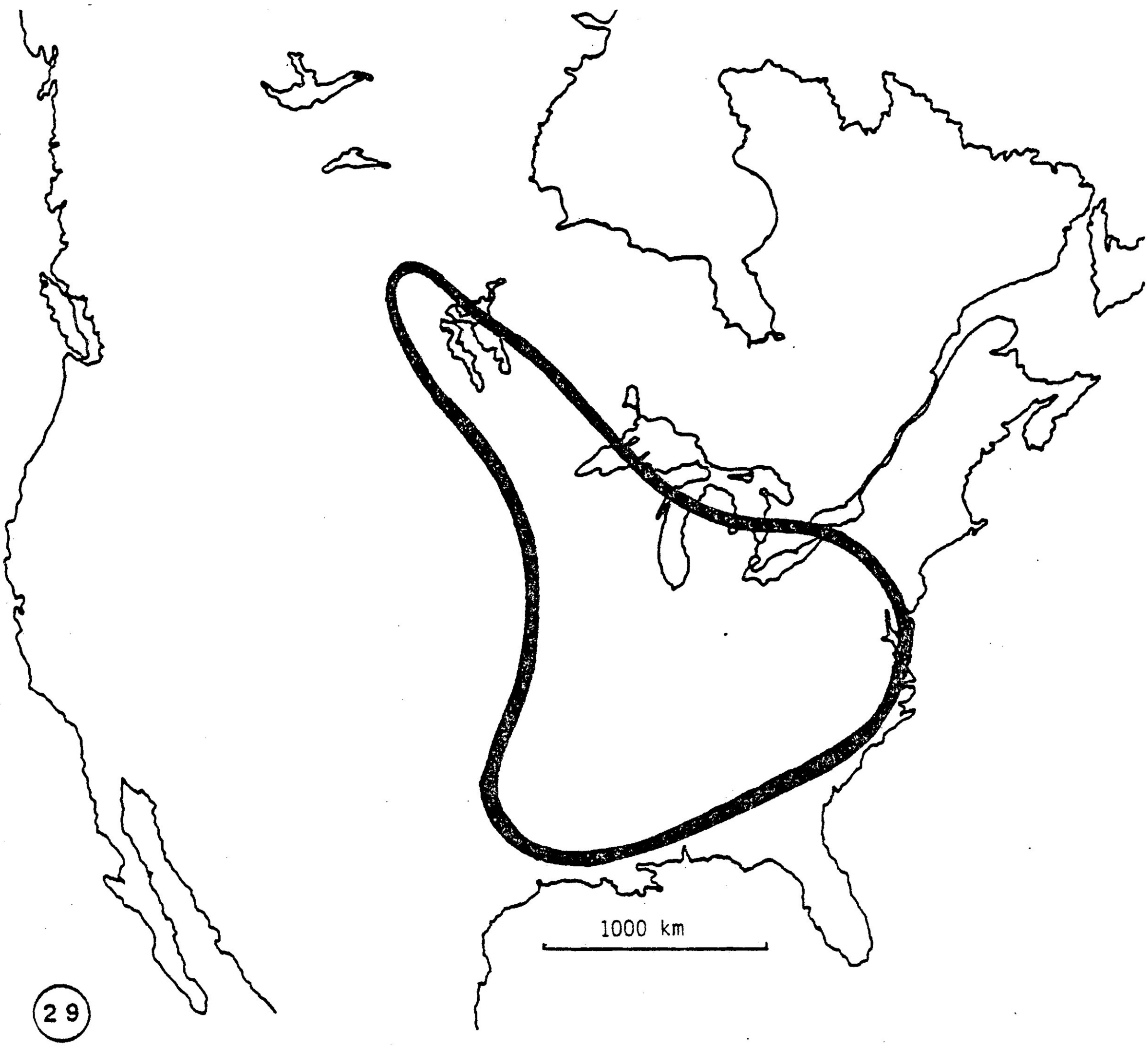


27



28

Figure 29: Generalized distribution of colonizers from the southeast (Modified from Lehmkuhl, 1980).


1000 km
29

Ecology and Behaviour

Seasonality

Adult tiger beetles of temperate North America have two basic seasonal patterns. The peak activity of mature adults occurs during spring or summer, and either may have a fall population consisting of teneral adults (Willis, 1967; Knisley, 1979).

Adults of *C. sexguttata* first appear in March or April and survive until June or mid-July. Some studies indicate that there is a fall population (Graves and Pearson, 1973; Lawton, 1970 a), whereas others state that there is none (Gaumer et al., 1970; Willis, 1970; Boyd, 1978; Knisley, 1979). Adults of *C. patruela* first emerge during April and are active until June. There is a second activity peak in the months of August and September (Graves, 1963). Adults of *C. p. consentanea* are numerous in April and May, uncommon in July, peak again in September, and decline in October (Boyd, 1978).

Collection records of each species are sorted into two week intervals for each state or province. The two week intervals begin on the first and 16th and end on the 15th and last day of the month respectively, thus they are not necessarily 14 days long. In an attempt to prevent bias from large series of specimens, no more than three specimens from a single collection record (i.e. same date, collector, and locality) are used. The number of collections for each interval is expressed as a percentage of the total for the year. The percentages are plotted as seasonality histograms in Figures 30 to 32.

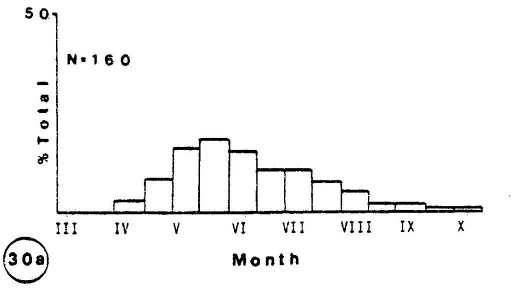
Adults of *C. sexguttata* emerge during the spring with peak activity occurring in late May (Fig. 30a). Some individuals are long-lived, being active into October. Possibly the late fall populations include recently emerged adults, but these individuals are the exception. A comparison of the seasonality of *C. sexguttata* in Pennsylvania with Wisconsin shows little difference between the populations (Figs. 30a, 31a). In Wisconsin, the activity peak also occurs in late May and early June, but it is about a month shorter as is the overall period of activity.

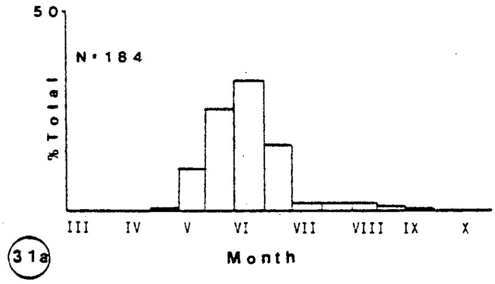
Figure 32a is a histogram for activity of adults of *C. sexguttata* in Ontario. The pattern is about mid-way between the histograms for Pennsylvania (Fig. 30a) and Wisconsin (Fig. 31a). Populations in Texas emerge quickly and form an abrupt early spring peak (Fig. 32b). The pattern of seasonal activity of adults of *C. sexguttata* in Texas is almost identical to that of Ontario, with a two month period of peak activity and an overall period of 17 weeks; however, activity begins about 6 weeks earlier. Perhaps the duration of the Texas activity period is limited by mid to late summer heat and aridity. In Georgia the activity histogram shows two distinct peaks (Fig. 32c). This is typical of populations in the Appalachian Mountains and Coastal Plain. The first and second peaks are respectively the coastal and mountain populations (Fig. 54). As with other populations of adults of *C. sexguttata*, most of the activity occurs in a two month period, with a few long-lived individuals extending the total activity period to about 17 weeks.

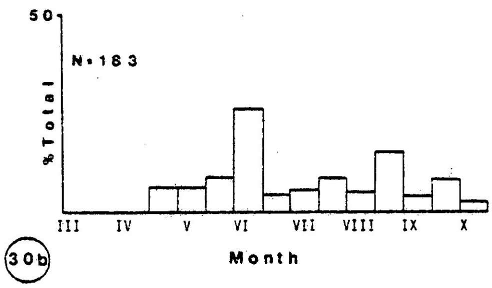
The activity pattern of adults of *C. denikei* is similar to that

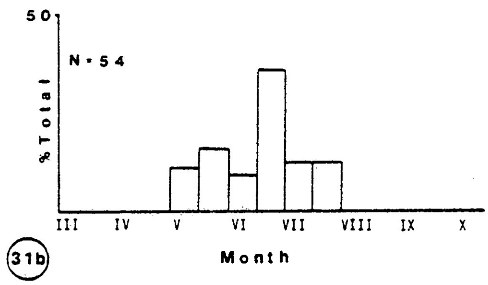
Figure 30: Seasonality histogram of adults of a. _C. sexguttata_ in Pennsylvania, b. _C. patruela_ in Pennsylvania, c. _C. p. consentanea_ in New Jersey.

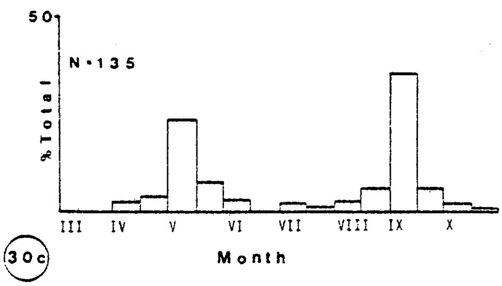
Figure 31: Seasonality histogram of adults of a. _C. sexguttata_, in Wisconsin, b. _C. patruela_ in Wisconsin, c. _C. denikei_.


50
N=160
% Total
III IV V VI VII VIII IX X
Month
30a


50
N=184
% Total
III IV V VI VII VIII IX X
Month
31a


50
N=183
% Total
III IV V VI VII VIII IX X
Month
30b


50
N=54
% Total
III IV V VI VII VIII IX X
Month
31b


50
N=135
% Total
III IV V VI VII VIII IX X
Month
30c

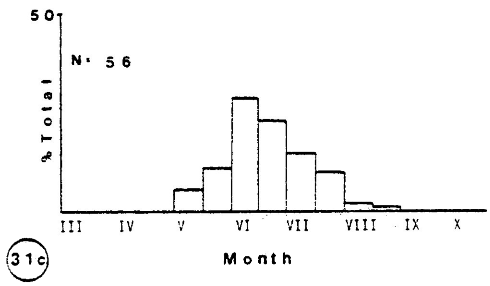
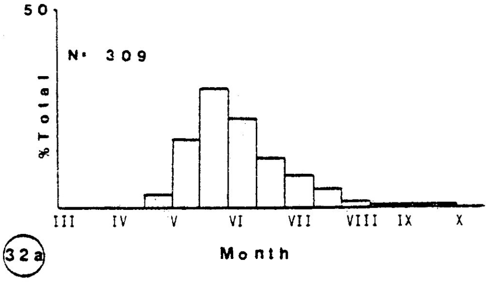
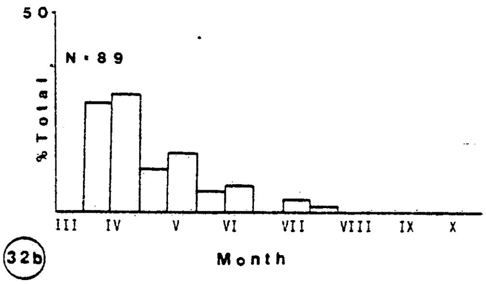

50
N= 56
% Total
III IV V VI VII VIII IX X
Month
31c

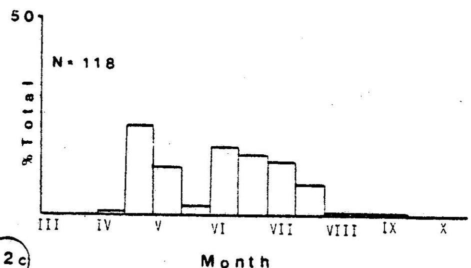
Figure 32: Seasonality histogram of adults of *C. sexguttata* in a. Ontario, b. Texas, c. Georgia.


50
N= 309
% Total
III
IV
V
VI
VII
VIII
IX
X
Month

32a


50
N=89
% Total
III
IV
V
VI
VII
VIII
IX
X
Month

32b


50
N= 118
% Total
III
IV
V
VI
VII
VIII
IX
X
Month

32c

of *C. sexguttata*, although the season is about 8 to 10 weeks shorter (Fig. 31c). The period of peak activity is in June and July, about the same duration as that for *C. sexguttata* in Wisconsin. The large difference in total activity period is due to the few long-lived individuals in *C. sexguttata*.

Adults of *C. patruela* emerge during the spring with peak activity occurring in early June (Fig. 30b). There is a fall population which peaks in late August and continues to mid-October. The two population peaks are not discontinuous and collections from late July contain old spring and early fall emergents.

A comparison of the populations of Pennsylvania and Wisconsin (Figs. 30b, 31b) is difficult because of biased Wisconsin collections. The activity peak in Wisconsin occurs during late June although there is activity from early May. While Figure 31b shows no distinct fall population, examination of records from neighbouring states indicates that a fall population occurs, although slightly earlier and not as strongly as in Pennsylvania. Figure 31b shows the beginning of the fall population in late July.

Activity of adults of *C. p. consentanea* begins in April and continues until the end of October (Fig. 30c).

Two distinct activity peaks occur with beetles absent or rare between mid-June and late July. The second larger activity peak occurs in early September. Examination of the genitalia of the fall specimens showed that they were teneral. Some *C. p. patruela* adults emerge immediately after pupation, and apparently all *C. p. consentanea* do.

Life History

Rearing of both adults and larvae of C. denikei was done to gain information of the life history of the species. Nine larvae of C. denikei were collected between June 17 and 23, 1980. Five were killed and preserved, four third instar larvae were reared in the laboratory, as follows:

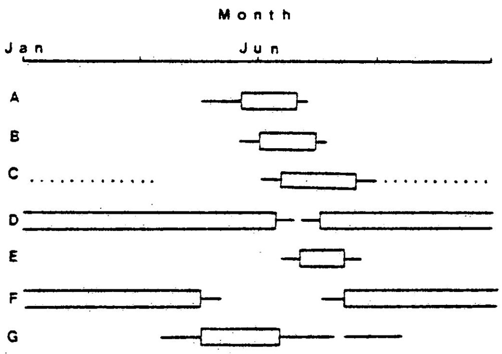
July 10 - 15:	All burrows closed.
July 27:	One larva dead.
July 29 - 31:	Remaining three larvae form pupae.
August 10 - 12:	Pupation, adults do not leave burrow.
August 20:	All are dug up, two are killed and preserved, remaining beetle is reared.
December 21:	Reared adult dies.

On June 26, 1980, 18 adults of C. denikei were brought to the lab. for rearing. All but two died by August 1, when the last two were killed. On July 29, 1981, 32 adult C. denikei were brought to the lab. for rearing. All died by August 17. In both years, mortality was more or less constant.

The complete life cycle for individuals of C. sexguttata (Fig. 33), C. denikei (Fig. 34), C. p. patruela (Fig. 35), and C. p. consentanea (Fig. 36) takes two years to complete. In Figures 33 to 36, open boxes represent the period when the main portion of the population is in the indicated stage of the life cycle, and the lines on each end of the boxes show the total range for that particular life stage. Data for these diagrams are drawn from field work, laboratory studies, collection records, literature on the species studied, principally Shelford (1907, 1908), literature on other species, Criddle (1907, 1910), Hamilton (1925), Willis (1967) and Palmer (1978), some deduction and guesswork. The exact life cycle of these species will remain unclear until rigorous life history investigations are carried out, eg., Palmer (1978). The information presented here is an approximation only.

Life cycles of C. sexguttata, C. denikei, C. p. patruela, and C. p. consentanea are similar and will be discussed as one, with differences noted where they occur. Eggs are laid two to three weeks after the adults first emerge during the spring. The egg (Fig. 33 - 36, line A) takes about 10 to 14 days to hatch into the first instar larva (line B). The first instar larval stage lasts 2 to 4 weeks. The second instar larval stage lasts 4 to 6 weeks (line C), although overwintering by the second instar is a possibility in C. denikei . and in the more northern populations of C. sexguttata because of a relatively short season. The third instar larva is probably the immature stage that overwinters, becoming dormant in early fall and active again in early spring (line D). The pupa forms in late July and the adult emerges in August (line E). Teneral adults of C. denikei and most of C. sexguttata remain in the pupal burrow to overwinter (line F). Many adults of C. patruela and most of C. p. consentanea emerge in the fall and become active for 4 to 6 weeks. Their overwintering site is unknown, but it is assumed that they construct another burrow or seek shelter under stones and bark. In the spring the adults emerge and begin copulating after one to two weeks (line G). Eggs are laid 10 to 14 days later. In relatively long seasons, it is possible that the life cycle is completed in one year.

Figures 33-36: Seasonality of the life stages of 33. C. sexguttata, 34. C. denikei, 35. C. p. patruela 36. C. p. consentanea. Open boxes indicate when the majority of the individuals in the population are in the indicated life stage. A. egg, B. first instar larva, C. second instar larva, D. third instar larva, E. pupa, F. dormant adult, G. active adult. These diagrams are an approximation only.


Month
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A
B
C
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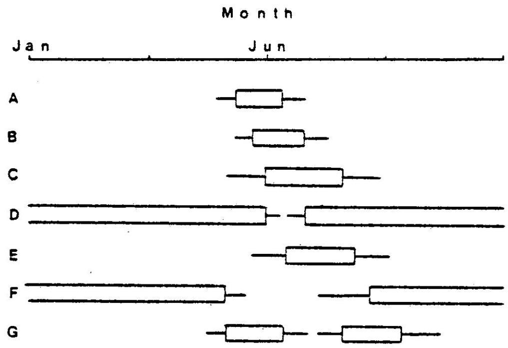
33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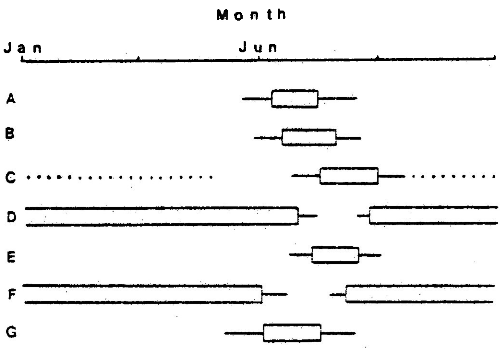
35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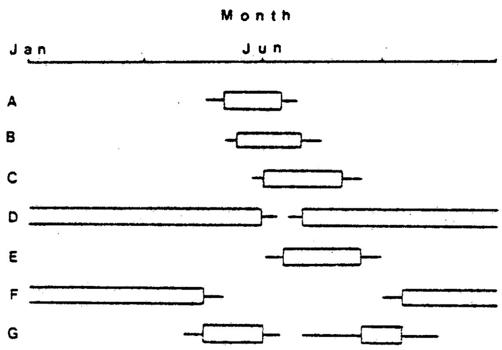
34


Month
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G

36

Soil Associations

The idea that cicindelid distributions are correlated with soil type or condition was first suggested by Shelford (1907). Dawson and Horn (1928) noted that "The segregation of various species (of tiger beetles) and varieties to particular soil types and moisture conditions is rather definite". Experiments on oviposition behaviour of C. purpurea Olivier showed a clear preference for sloped clay sites over sand or humus Shelford (1907). Shelford gave a number of examples of different species of larvae specific to certain soil types. Willis (1967) examined species segregation by soil type and concluded that it did not occur except in some cases, however, he was dealing with the adult stage only. Leffler (1979) showed a high correlation between the length of the second gonapophysis of the female genitalia of various species and the proportions of sand, silt, and clay in the soil of their respective habitats.

The wide distribution of C. sexguttata suggests that it is found on a wide variety of soils. It has been reported on predominantly sandy soils (Lawton, 1974; Wilson, 1978; Freitag and Tropea, 1969), soils that are predominantly clay (Goldsmith, 1916; Lawton, 1970a) and on loamy sand (Glaser, 1976). Although C. patruela is also widely distributed, it is comparatively rare which suggests a narrow range of soil tolerances. The soil associations of any species of tiger beetle are probably due to the temperature and moisture requirements of the larvae (Shelford, 1907; Dunn, 1978).

Distribution maps of C. sexguttata were divided into land resource areas (Figs. 37 to 78). For the United States these resource areas were taken from Agricultural Handbook 296 (1978). For Canada the physiographic regions given in Clayton _et al._, (1977) were used. Information on soil distributions was obtained from publications and maps listed in Appendix III. For this study the Soil Survey Staff (1960; 1967) system of soil classification is used. Conversions were made for maps and publications that used other systems. Soil associations of _C. patruela_ are not presented because of insufficient distribution information.

Appendix I is the alphabetic listing of resource areas showing soil type and abundance of _C. sexguttata_ and _C. denikei_. Different soils within each area are scored for the abundance of beetles. The abundance score is based on the number of collection records relative to the total area of the soil type within a given state and resource area. Scores of abundance have an abbreviation and numerical value as follows: Ab = Absent = 0, R = Rare = 1, F = Few = 2, S = Some = 3, M = Many = 4. The numerical scores are not the frequency of collecting records for a given area, they are subjective scores used to make Table 9 . Definitions of soil names are given in Appendix II. For complete definitions, see Soil Survey Staff (1960, 1967).

Northeastern Region, Figures 37 - 45.

The dominant soils in the Northeast are Haplorthods (Aa, Ar, Csl, Cv, Nm, Nmeu and Sneu). Where there are warm moist Haplorthods such as on the Southern New England Upland (Sneu) and the Connecticut Valley (Cv), _C. sexguttata_ is common. Further north, the soils are cool Haplorthods and the beetles are rare to absent (Aa, Ar, Nm). The Haplorthods

Figures 37-77: The distribution of _C. sexguttata_, _C. p. patruela_, and _C. p. consentanea_ in Canada and the United States. The land resource areas of the United States (Agricultural Handbook 296, 1978) and the physiographic regions of Canada (Clayton et al., 1977) are indicated. Collection records of _C. sexguttata_ are represented by circles where the exact locality is known and squares for county records. The size of the symbol indicates the number of different records from that locality; the small symbol is one collection record, the medium symbol is two different collection records, and the largest symbol is three or more different collection records. Collection records of _C. p. patruela_ are represented by triangles. Collection records of _C. p. consentanea_ are represented by diamonds. Closed symbols indicate records from specimens that I have examined, open symbols represent records taken from the literature.

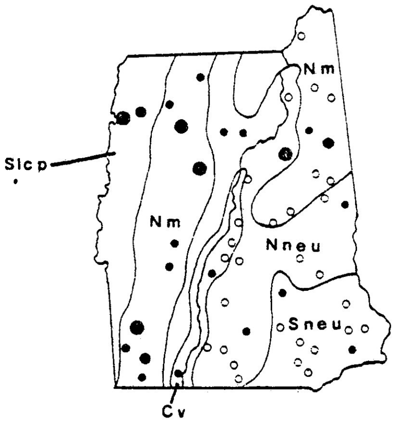
Figure 37: Distribution of _C. sexguttata_ in Vermont and New Hampshire. Cv. Connecticut Valley, Nm. Northern Mountains, Nneu. New England and Eastern New York Upland, northern part, Slcp. St. Lawrence-Champlain Plain, Sneu. New England and Eastern New York upland, southern part.

Figure 38: Distribution of _C. sexguttata_ in Maine. Aa. Aroostook Area, Nm. Northern Mountains, Nneu. New England and Eastern New York Upland, northern part.

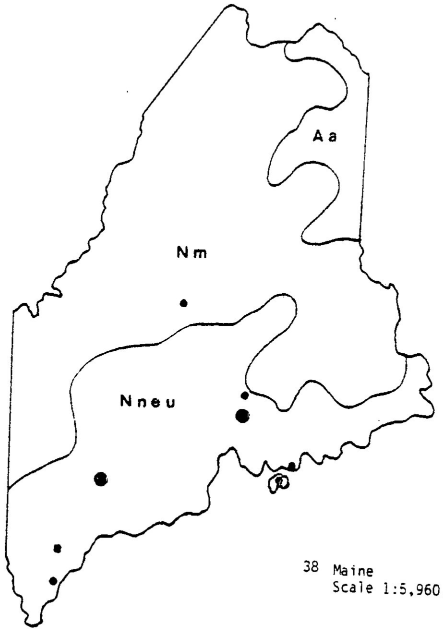
Figure 39: Distribution of _C. sexguttata_ and _C. patruela_ in Massachusetts. Cl. Long Island and Cape Cod Coastal Lowland, Cv. Connecticut Valley, Sneu. New England and Eastern New York Upland, southern part.

Figure 40: Distribution of _C. sexguttata_ in Connecticut. Cv. Connecticut Valley. Sneu. New England and Eastern New York Upland, southern part.

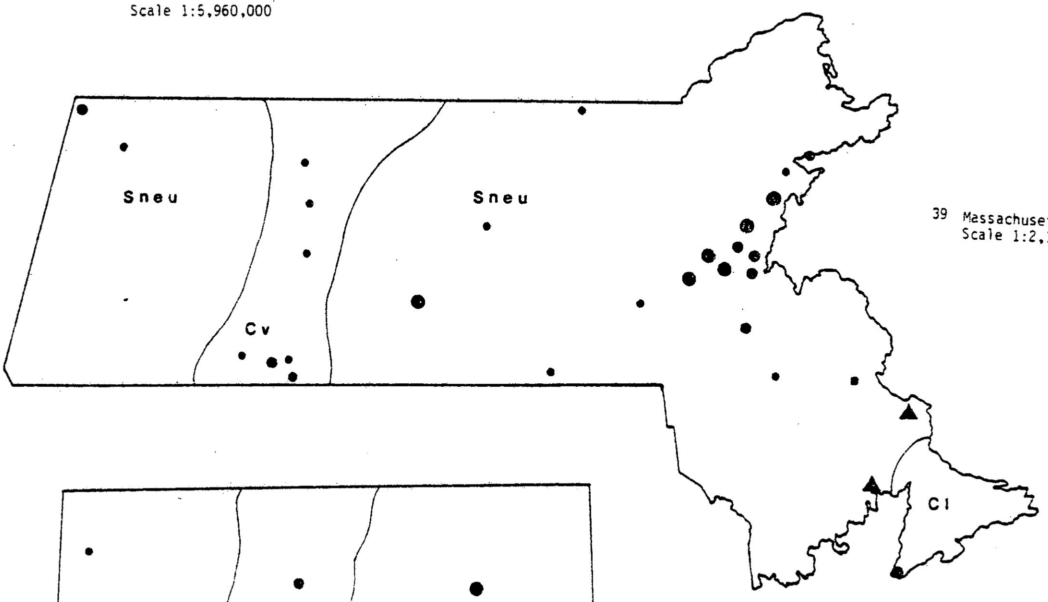
Figure 41: Distribution of _C. sexguttata_ and _C. patruela_ in Rhode Island. Sneu. New England and Eastern New York Upland, southern part.



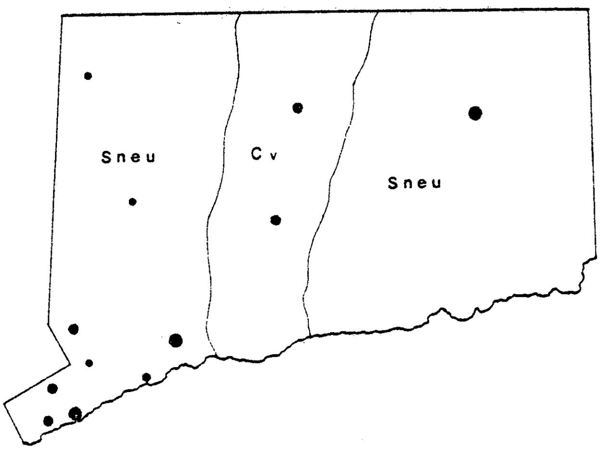
37 Vermont & New Hampshire
Scale 1:5,960,000



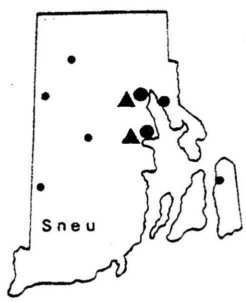
38 Maine
Scale 1:5,960,000



39 Massachusetts
Scale 1:2,104,000



40 Connecticut
Scale 1:2,104,000



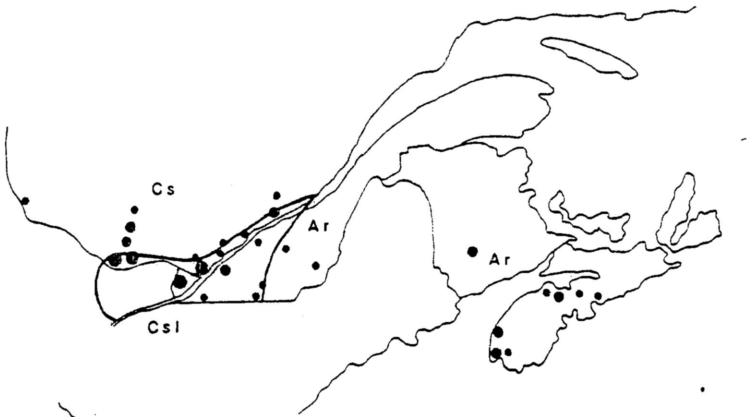
41 Rhode Island
Scale 1:2,104,000

Figure 42: Distribution of C. sexguttata and C. patruela in Ontario. Cs. Canadian Shield, Csl. Central St. Lawrence Lowland, Wsl, Western St. Lawrence Lowland.

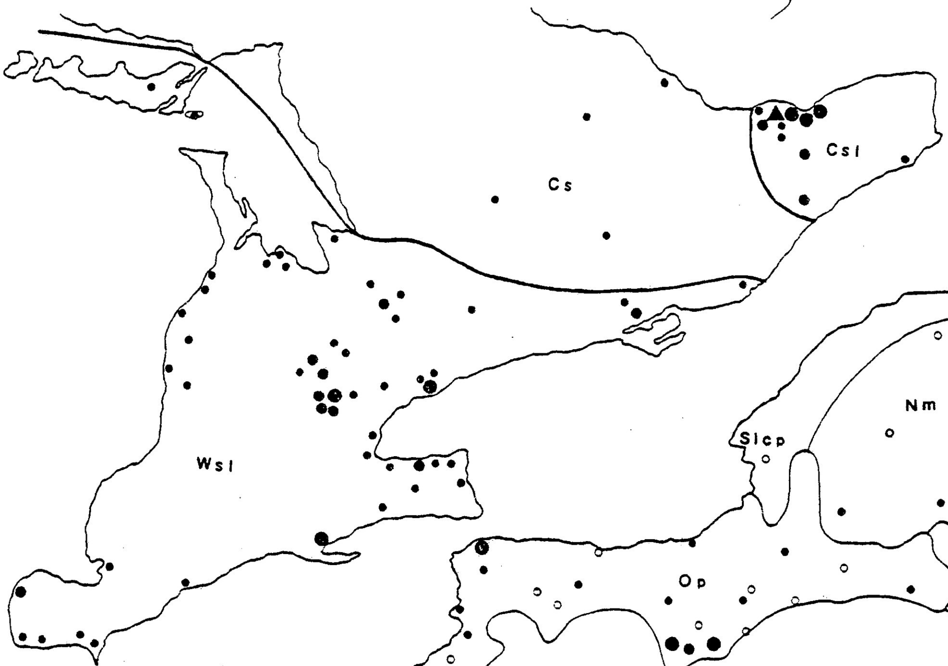
Figure 43: Distribution of C. sexguttata in Quebec, New Brunswick, and Nova Scotia. Cs. Canadian Shield, Csl. Central St. Lawrence Lowland, Ar. Appalachian Region.

Figure 44: Distribution of C. sexguttata in New York. Cl. Long Island and Cape Cod COastal Lowland, Gap. Glaciated Allegheny Plateau and Catskill Mountains, Nm. Northern Mountains, Op. Ontario Plain and Finger Lakes Region, Slcp. St. Lawrence-Champlain Plain, Sneu. New England and Eastern New York Upland, southern part.

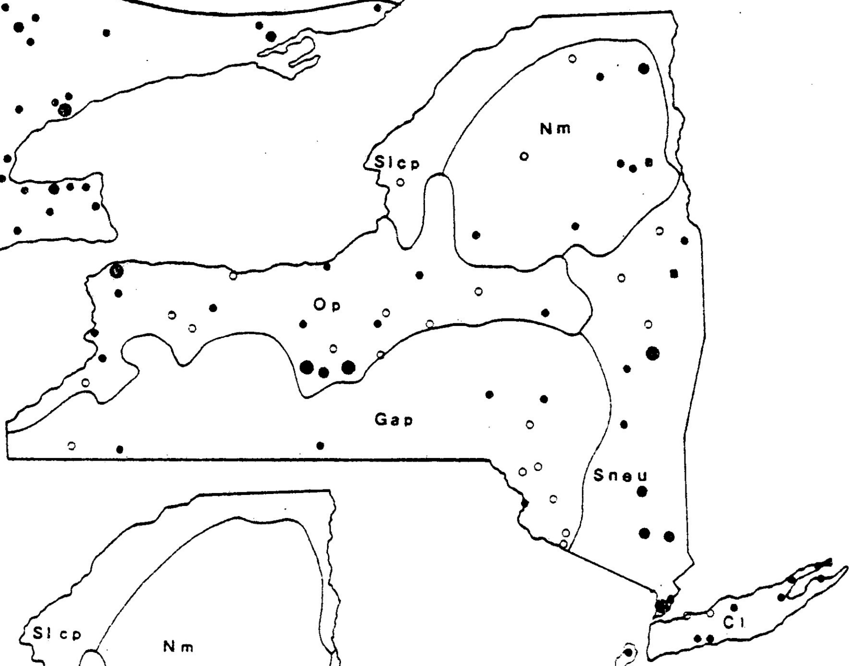
Figure 45: Distribution of C. patruela in New York. Cl. Long Island and Cape Cod Coastal Lowland, Gap. Glaciated Allegheny Plateau and Catskill Mountains, Nm. Northern Mountains, Op. Ontario Plain and Finger Lakes Region, Slcp. St. Lawrence-Champlain Plain, Sneu. New England and Eastern New York Upland, southern part.



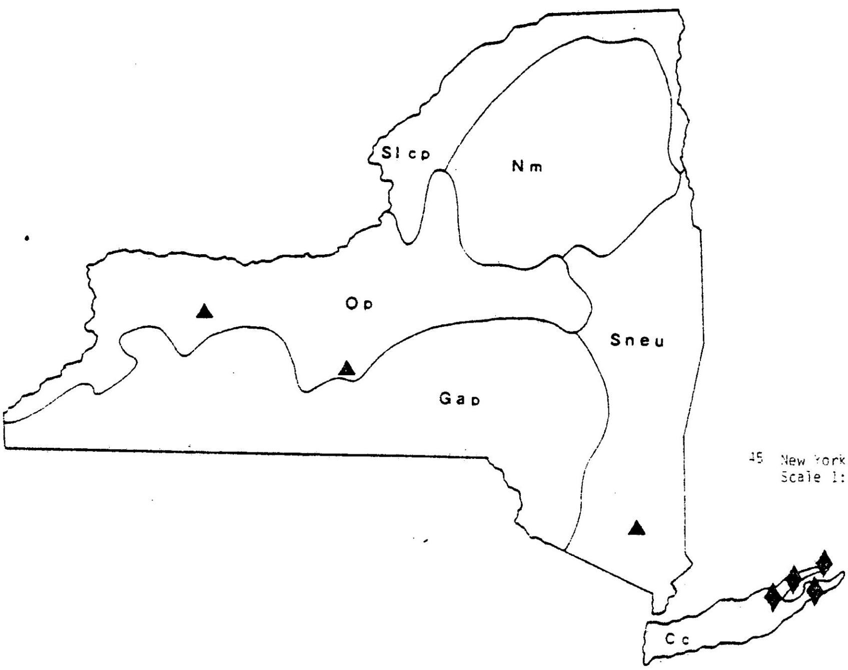
43 Quebec and Maritimes
Scale 1:18,600,000



42 Southern Ontario
Scale 1:5:960,000



44 New York
Scale 1:5,960,000



45 New York
Scale 1:5,960,000

of the Northern Appalachians give way to Inceptisols in the Catskills and on the Allegheny Plateau (Gap). In the Catskills, C. sexguttata is common. The Inceptisols of the Allegheny Plateau are wetter than those in the Catskills, and the beetles are not as common there.

Atlantic Coastal Region, Figures 39, 44 - 57.

Along the Atlantic coast, populations of C. sexguttata are common on the Inceptisols of the Coastal Lowland (Cl) and the Northern Coastal Plain (Ncp). They become less frequent as Udults become the dominant soils are are absent from the Mid-Atlantic Coastal Plain (Macp). Within the Atlantic Coastal Flatwoods (Acf), the beetles are rare, and found only on Histols. Inland on the Southern Coastal Plain (Scp) and Southern Piedmont (Sp), populations of beetles are scattered on Hapludults and Paleudults.

Eastern Central Region, Figures 48 - 55 and 67 - 69.

In the central Appalachians, the beetles are more common on the Udults of the Northern Piedmont (Np) than on the Inceptisols of the mountains (Nar). Further south, the Udults are the dominant soils in the mountains and the beetles occur more frequently in the mountains (Br, Sa) than on the piedmont (Sp). In the far south of the Appalachians, they are common both on the Southern Piedmont (Sp) and in the mountains (Br, Sa) of Georgia, but they are rare to absent in Alabama. West of the central Appalachians, Inceptisols are the dominant soils and populations of beetles are few and scattered (Hrp, Kis, Cpm).

Great Lakes Region, Figures 42, 44, 58, 62, 63, 66.

The beetles are most numerous on the Alfisols of the Ontario

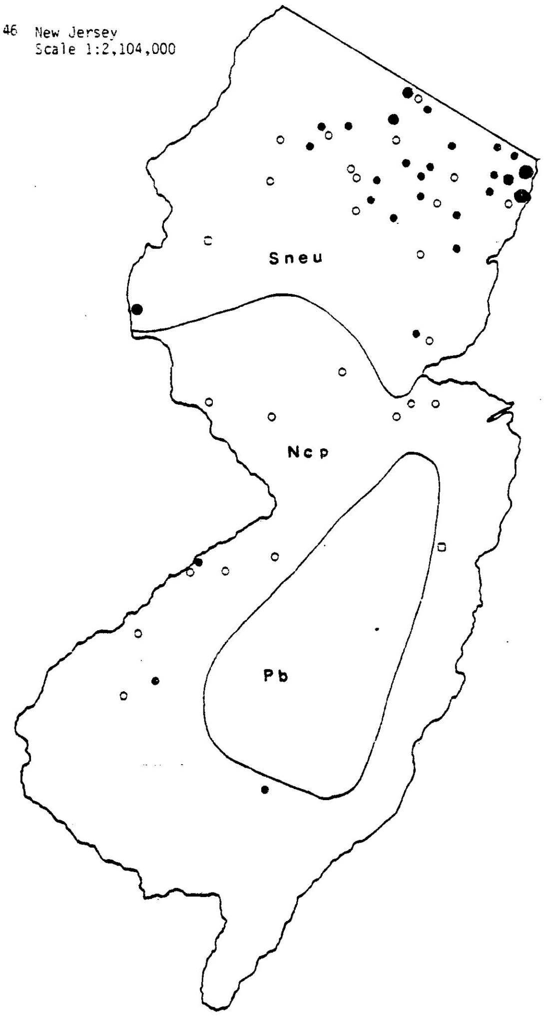
Figure 46: Distribution of *C. sexguttata* in New Jersey. Ncp. Northern Coastal Plain, Pb. Pine Barrens, Sneu. New England and Eastern New York Upland, southern part.

Figure 47: Distribution of *C. p. patruela* and *C. p. consentanea* in New Jersey. Ncp. Northern Coastal Plain, Pb. Pine Barrens, Sneu. New England and Eastern New York Upland, southern part.

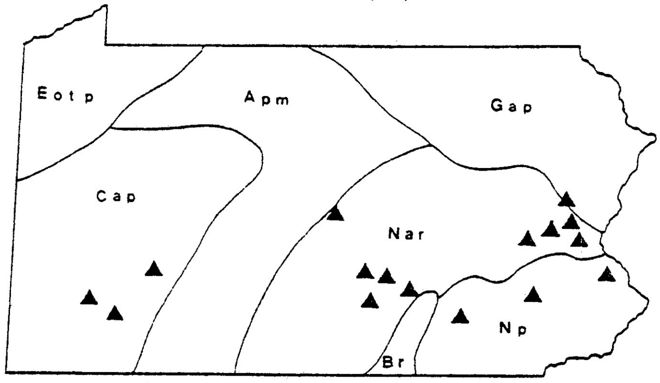
Figure 48: Distribution of *C. sexguttata* in Pennsylvania. Apm. Eastern Allegheny Plateau and Mountains, Br. Blue Ridge, Cap. Central Allegheny Plateau, Eotp. Eastern Ohio Till Plain, Gap. Glaciated Allegheny Plateau and Catskill Mountains, Nar. Northern Appalachian Ridges and Valleys, Np. Northern Piedmont.

Figure 49: Distribution of *C. patruela* in Pennsylvania. Apm. Eastern Allegheny Plateau and Mountains. Br. Blue Ridge, Cap. Central Allegheny Plateau, Eotp. Eastern Ohio Till Plain, Gap. Glaciated Allegheny Plateau and Catskill Mountains. Nar. Northern Appalachian Ridges and Valleys, Np. Northern Piedmont.

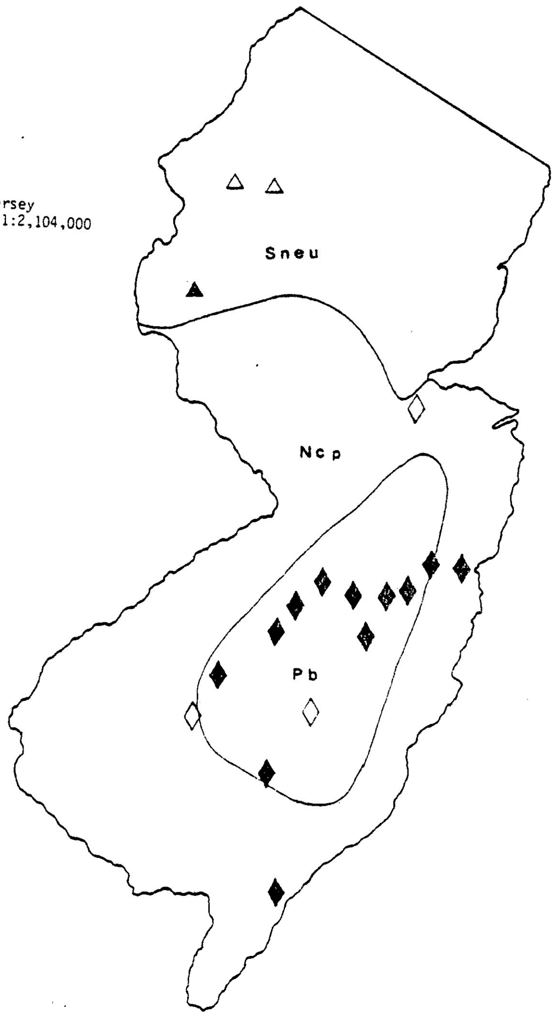
46 New Jersey
Scale 1:2,104,000

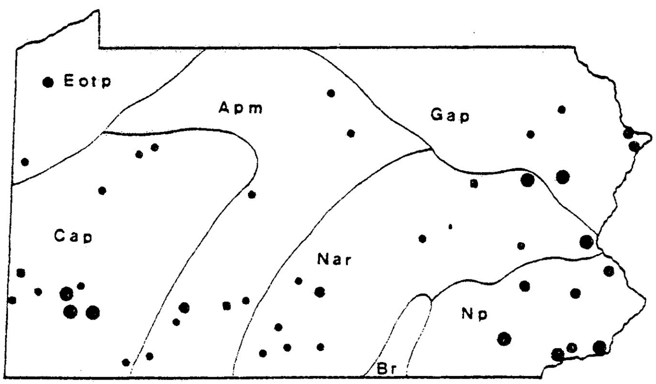


49 Pennsylvania
Scale 1:5,960,000



47 New Jersey
Scale 1:2,104,000





48 Pennsylvania
Scale 1:5,960,000

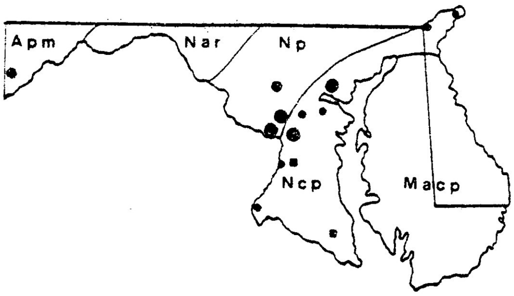
Figure 50: Distribution of *C. sexguttata* in Maryland and Delaware. Apm. Eastern Allegheny Plateau and Mountains, Macp. Mid-Atlantic Coastal Plain, Nar. Northern Appalachian Ridges and Valleys, Ncp. Northern Coastal Plain. Np. Northern Piedmont.

Figure 51: Distribution of *C. sexguttata* and *C. patruela* in Virginia. Acf. Atlantic Coastal Flatwoods, Br. Blue Ridge, Cpm. Cumberland Plateau and Mountains, Nar. Northern Appalachian Ridges and Valleys, Np. Northern Piedmont, Sa. Southern Appalachian Ridges and Valleys, Scp. Southern Coastal Plain, Sp. Southern Piedmont.

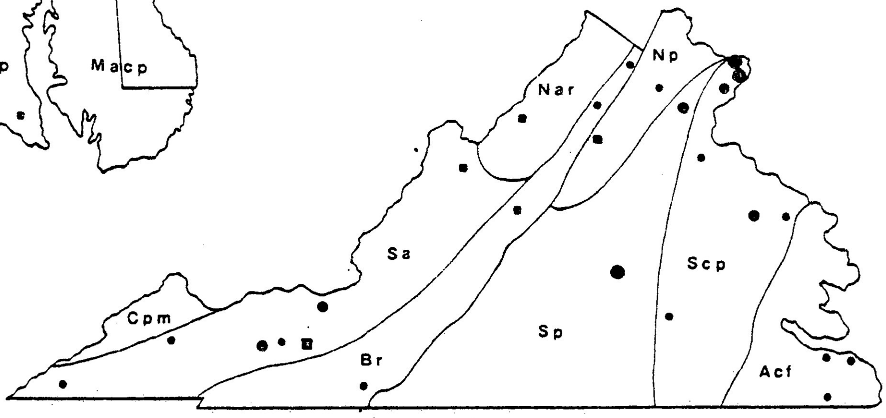
Figure 52: Distribution of *C. patruela* in Maryland. Apm. Eastern Allegheny Plateau and Mountains, Macp. Mid-Atlantic Coastal Plain, Nar. Northern Appalachian Ridges and Valleys, Ncp. Northern Coastal Plain, Np. Northern Piedmont.

Figure 53: Distribution of *C. sexguttata* and *C. patruela* in North Carolina. Acf. Atlantic Coastal Flatwoods, Br. Blue Ridge, Scp. Southern Coastal Plain, Sp. Southern Piedmont.

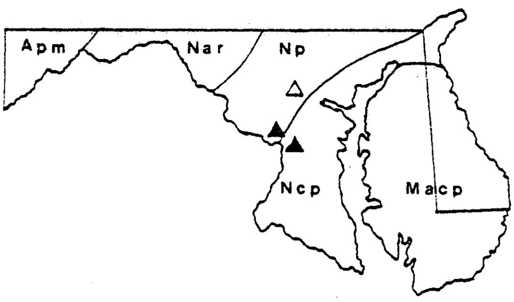
50 Maryland and Delaware
Scale 1:5,960,000



51 Virginia
Scale 1:5,960,000



52 Maryland and Delaware
Scale 1:5,960,000



53 North Carolina
Scale 1:5,960,000

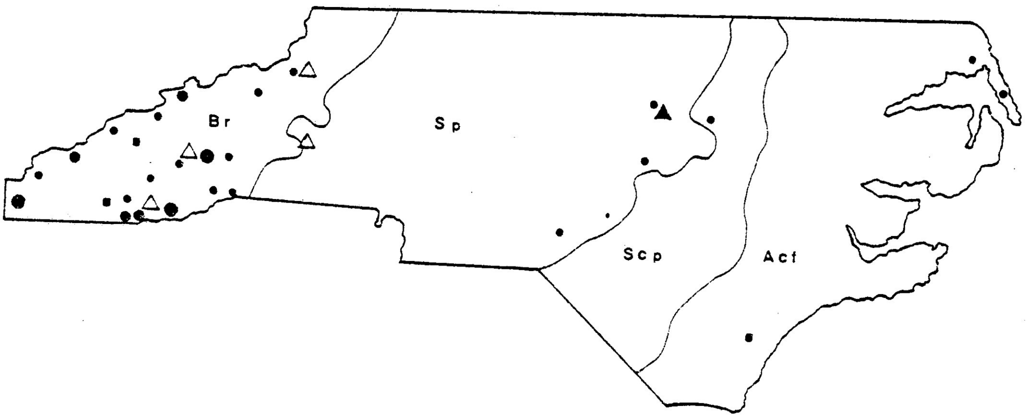


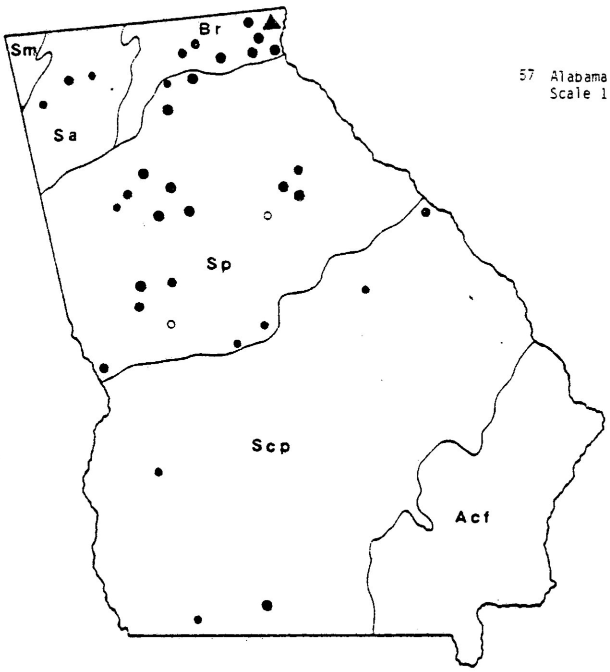
Figure 54: Distribution of C. sexguttata and C. patruela in Georgia. Acf. Atlantic Coastal Flatwoods, Br. Blue Ridge, Sa. Southern Appalachian Ridges and Valleys, Scp. Southern Coastal Plain. Sm. Sand Mountains, Sp. Southern Piedmont.

Figure 55: Distribution of C. sexguttata and C. patruela in South Carolina. Acf. Atlantic COastal Flatwoods, Br. Blue Ridge, Cgsh. Carolina and Georgia Sand Hills, Sp. Southern Piedmont.

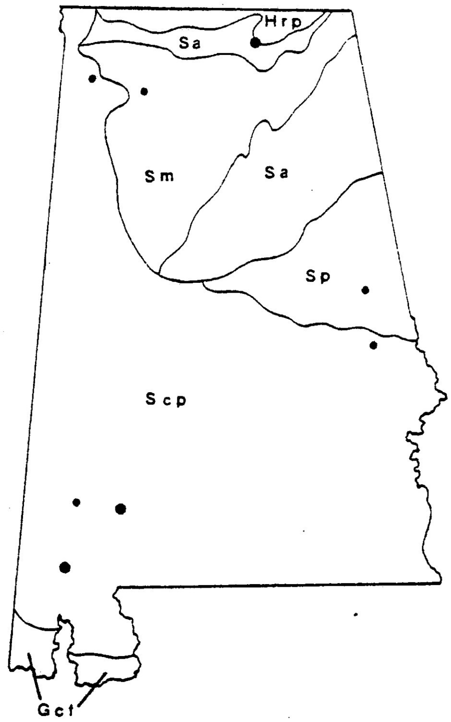
Figure 56: Distribution of C. sexguttata in Northern Florida. Acf. Atlantic Coastal Flatwoods, Fs. Florida Subtropical, Gcf. Gulf Coast Flatwoods, Scp. Southern Coastal Plain.

Figure 57: Distribution of C. sexguttata in Alabama. Gcf. Gulf Coast Flatwoods, Hrp. Highland Rim and Pennyroyal, Sa. Southern Appalachian Ridges and Valleys, Scp. Southern Coastal Plain, Sm. Sand Mountains, Sp. Southern Piedmont.

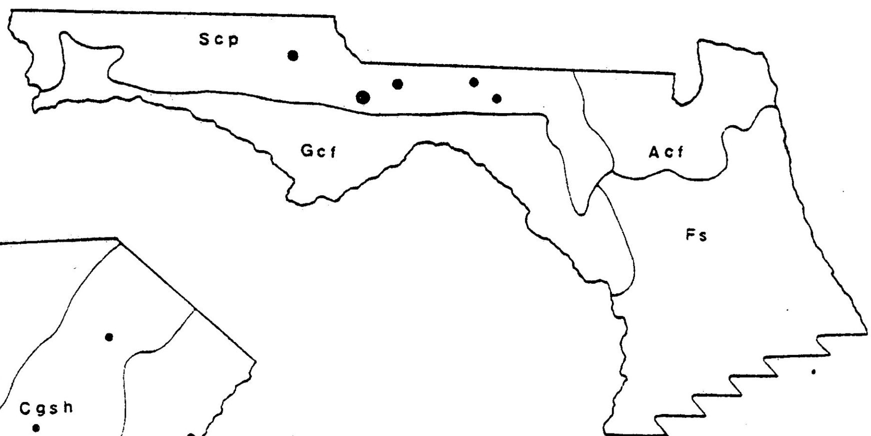
54 Georgia
Scale 1:5,960,000



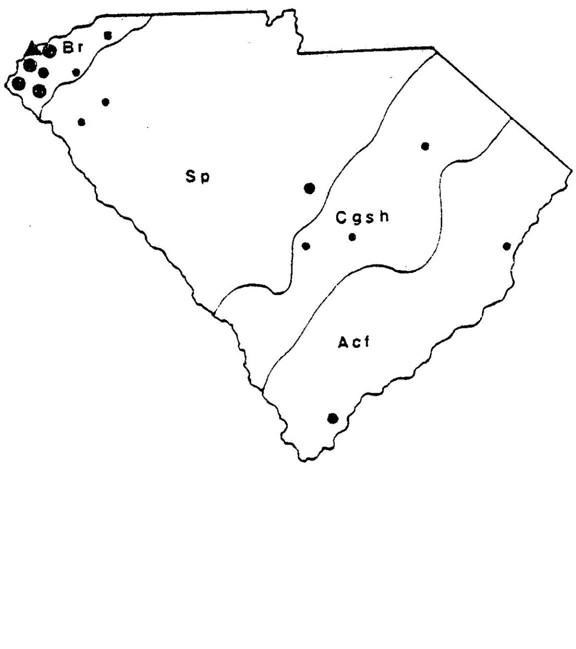
57 Alabama
Scale 1:5,960,000



56 Northern Florida
Scale 1:5960,000



55 South Carolina
Scale 1:5,960,000



Lake Plain (Op) and the Erie-Huron Lake Plain (Hlp). They are also numerous on the Aqualfs and Aquepts of the Erie-Huron Lake Plain (Hlp) and the West St. Lawrence Lowland (Wsl), and on the Alfisols of the drift plains of Michigan (Mdp) and Wisconsin (Wd). Around Lake Superior, cool Orthods are the dominant soil group, and C. sexguttata is rare or entirely absent (Glb, Slp, Ssp).

Northwestern Region, Figures 62 - 63.

Beetle populations are numerous on the Alfisols of the Northern Mississippi Valley (Nmv) and Thin Loess and Till (Tlt) and on the Entisols of the Minnesota and Wisconsin Sandy Outwash (Mso). They are not found on the cool wet Histols to the North (Mgd, Glb), or the dry Mollisols to the West (Rrv, Rtp).

North Central Region, Figures 48, 60 - 66.

The Western Allegheny Plateau (Wap) is dominated by Inceptisols and beetle populations are few and scattered. The beetles are more common on the Alfisols of the Ohio Till Plain (Otp) and Udults in southern Indiana (Kis), but are rarer on the Mollisols of the Heavy Till Plains and Prairies (Htp, Mhtp, Mitp, Mtp). Large populations are found on the Haplaquolls of the Central Mississippi Valley (Cmv).

West Central Region, Figures 70 - 73.

The Haplaquolls along the Missouri River in the Deep Loess Hills (Mdl) support numerous populations of C. sexguttata, as do the moist Mollisols of the Loess Drift Hills (Nkl) and Cherokee Prairies (Cp). A few populations are found on the dry Mollisols of the Central Great

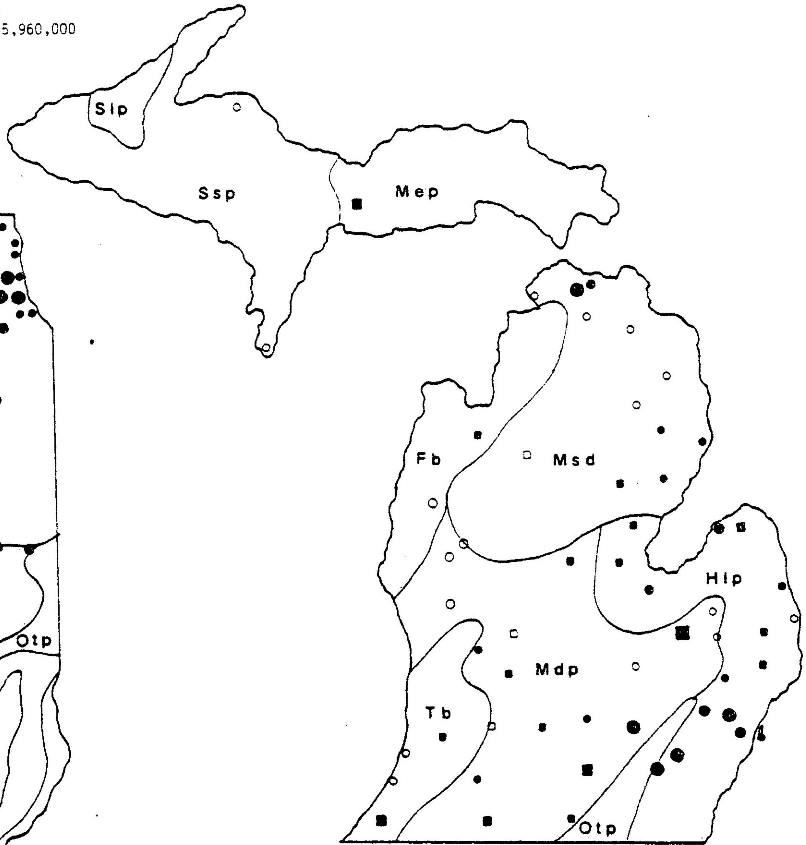
Figure 58: Distribution of *C. sexguttata* in Michigan. Fb. Michigan Fruit Belt, Hlp. Huron Lake Plain, Mdp. Southern Michigan and Northern Indiana Drift Plain, Mep. Michigan Eastern Upper Penninsula Sandy Drift. Msd. Northern Michigan and Wisconsin Sandy Drift. Otp. Indiana and Ohio Till Plain. Slp. Superior Lake Plain, Ssp. Superior Stony and Rocky Loamy Plains, Tb. Southwestern Michigan Fruit and Truck Belt.

Figure 59: Distribution of *C. patruela* in Michigan. Fb. Michigan Fruit Belt, Hlp. Huron Lake Plain, Mdp. Southern Michigan and Northern Indiana Drift Plain, Mep. Michigan Eastern Upper Penninsula Sandy Drift. Msd. Northern Michigan and Wisconsin Sandy Drift. Otp. Indiana and Ohio Till Plain. Slp. Superior Lake Plain, Ssp. Superior Stony and Rocky Loamy Plains, Tb. Southwestern Michigan Fruit and Truck Belt.

Figure 60: Distribution of *C. sexguttata* in Illinois. Idl. Iowa and Illinois Deep Loess and Drift, Itp. Southern Illinois and Indiana Thin Loess and Till Plain, Cc. Central Claypan Areas, Cmv.Central Mississippi Valley Wooded Slopes, Htp. Northern Illinois and Indiana Heavy Till Plain, Otp. Indiana and Ohio Till Plain, Wdp. Southern Wisconsin and Northern Illinois Drift Plain.

Figure 61: Distribution of *C. sexguttata* and *C. patruela* in Indiana. Cmv. Central Mississippi Valley Wooded Slopes, Hrp. Highland Rim and Pennyroyal, Htp. Northern Illinois and Indiana Heavy Till Plain, Itp. Southern Illinois and Indiana Thin Loess and Till Plain, Kis. Kentucky and Indiana Sand Stone, Mdp. Southern Michigan and Northern Indiana Drift Plain, Otp. Indiana and Ohio Till Plain.

58 Michigan
Scale 1:5,960,000



60 Illinois
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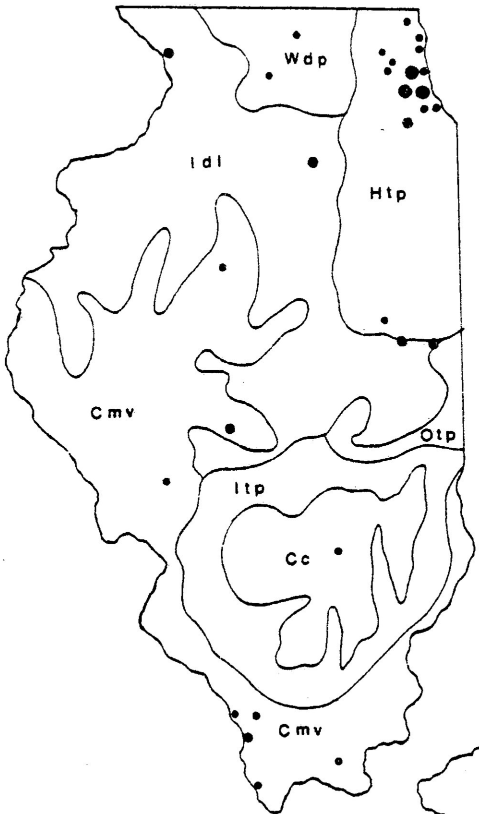

59 Michigan
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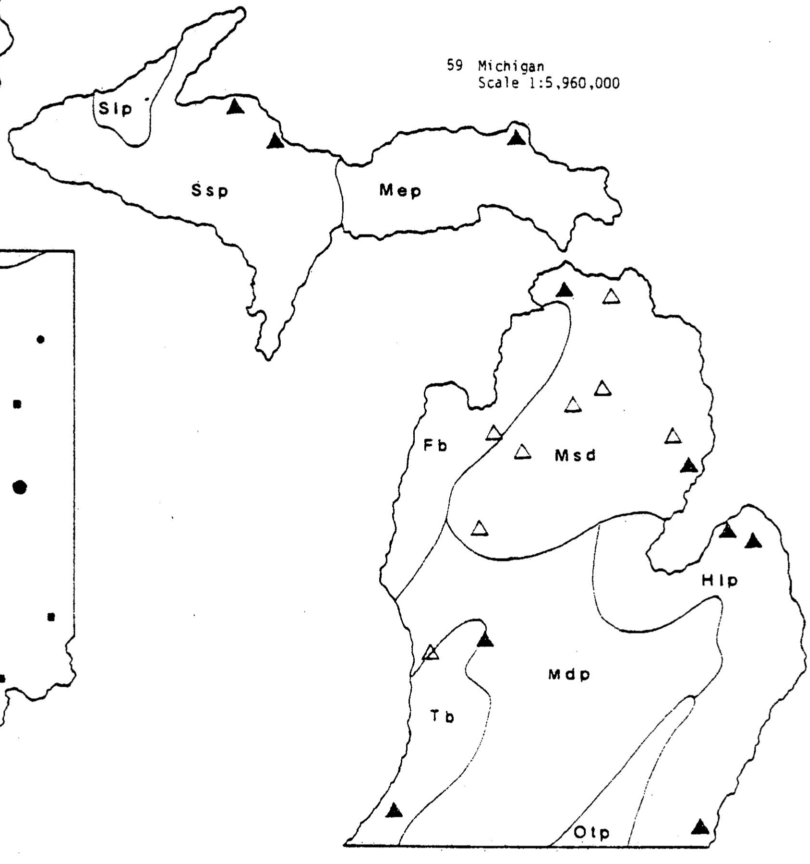


61 Indiana
Scale 1:5,960,000

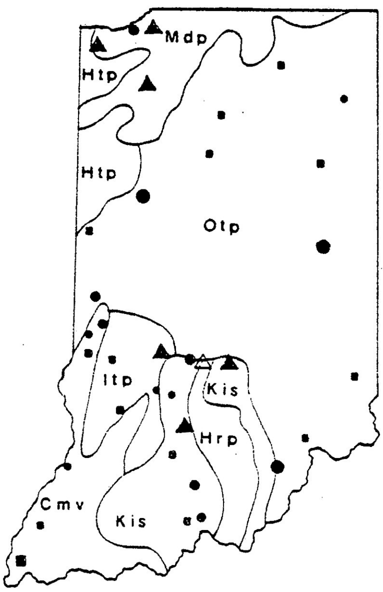


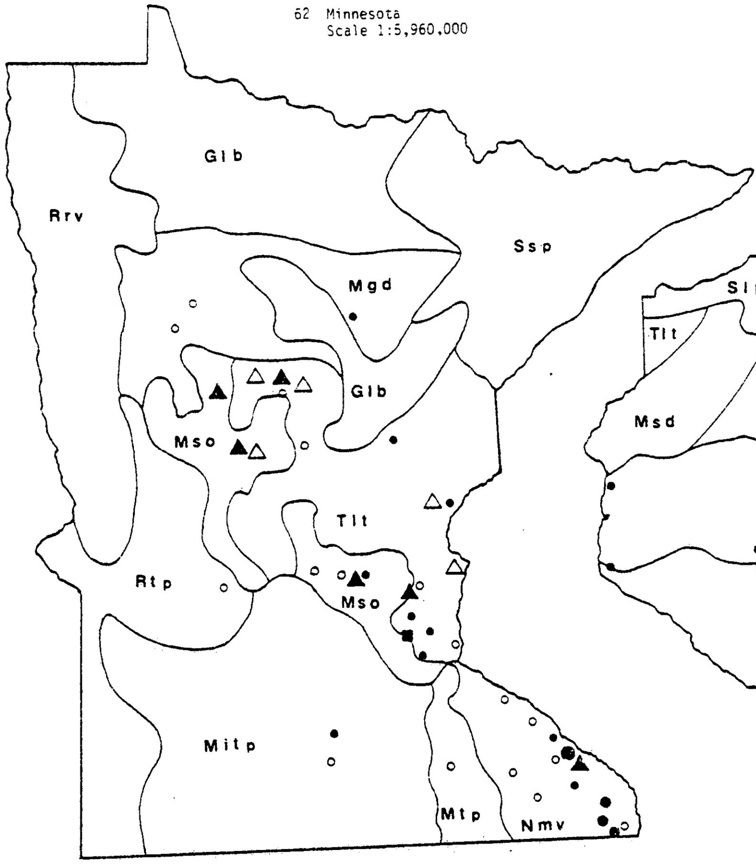
Figure 62: Distribution of *C. sexguttata* and *C. patruela* in Minnesota. Glb. Northern Minnesota Glacial Lake Basins, Mgd. Northern Minnesota Gray Drift, Mso. Wisconsin and Minnesota Sandy Outwash, Mtp. Eastern Iowa and Minnesota Till Prairies, Mitp. Central Iowa and Minnesota Till Prairies, Nmv. Northern Mississippi Valley Loess Hills, Rrv. Red River Valley of the North, Rtp. Rolling Till Prairie, Ssp. Superior Stony and Rocky Loamy Plains, Tlt. Central Wisconsin and Minnesota Thin Loess and Till.

Figure 63: Distribution of *C. sexguttata* in Wisconsin. Msd. Northern Michigan and Wisconsin Sandy Drift, Nmv. Northern Mississippi Valley Loess Hills, Slp. Superior Lake Plain, Ssp. Superior Stony and Rocky Loamy Plains, Tlt. Central Wisconsin and Minnesota Thin Loess and Till, Wd. Northern Wisconsin Drift Plain, Wdp. Southern Wisconsin and Northern Illinois Drift Plain.

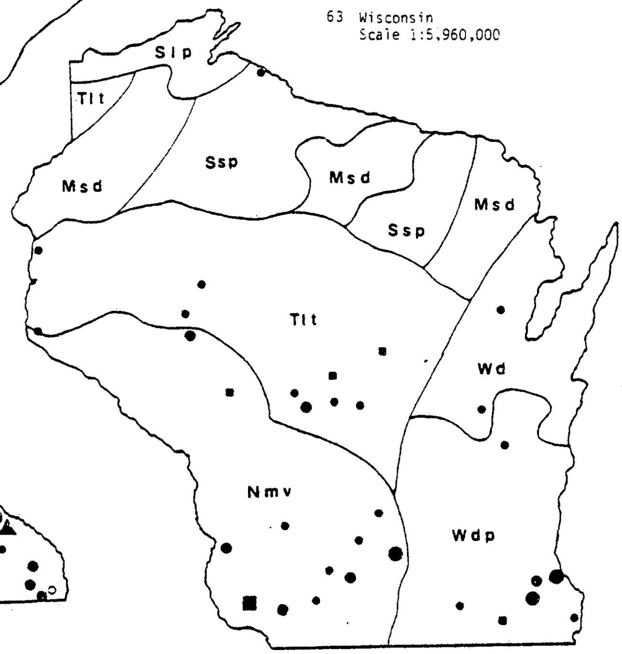
Figure 64: Distribution of *C. sexguttata* in Iowa. Idl. Iowa and Illinois Deep Loess and Drift, Mdl. Iowa and Missouri Deep Loess Hills, Mhtp. Iowa and Missouri Heavy Till Plain, Central Iowa and Minnesota Till Prairies, Mtp. Eastern Iowa and Minnesota Till Prairies. Nmv. Northern Mississippi Valley Loess Hills.

Figure 65: Distribution of *C. patruela* in Wisconsin. Msd. Northern Michigan and Wisconsin Sandy Drift. Nmv. Northern Mississippi Valley Loess Hills, Slp. Superior Lake Plain, Ssp. Superior Stony and Rocky Loamy Plains, Tlt. Central Wisconsin and Minnesota Thin Loess and Till, Wd. Northern Wisconsin Drift Plain, Wdp. Southern Wisconsin and Northern Illinois Drift Plain.

62 Minnesota
Scale 1:5,960,000



63 Wisconsin
Scale 1:5,960,000



65 Wisconsin
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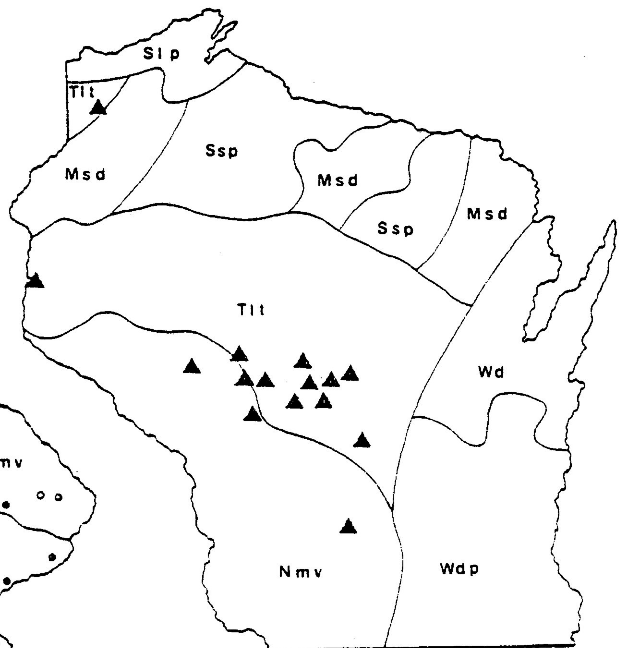

64 Iowa
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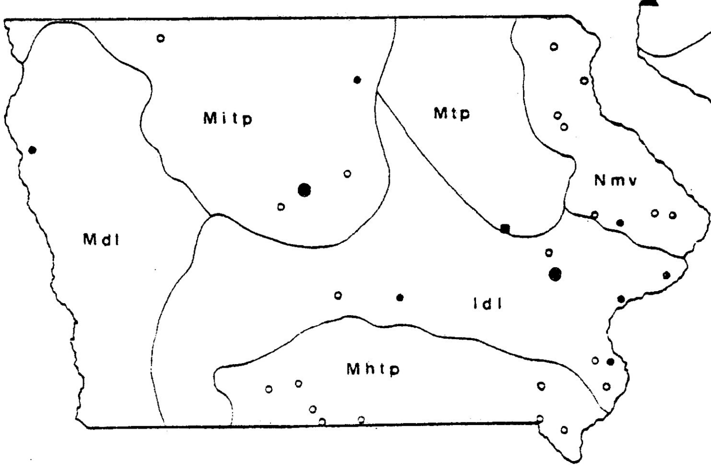


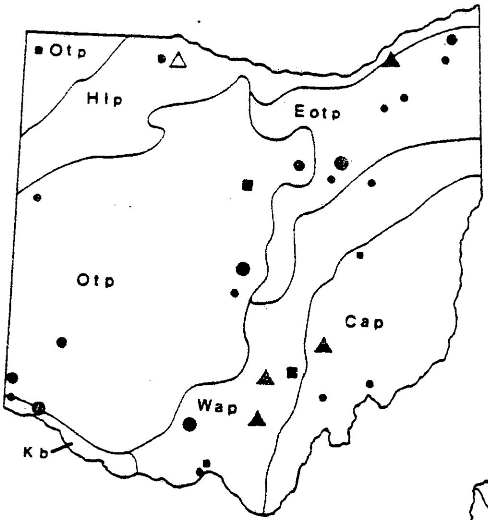
Figure 66: Distribution of *C. sexguttata* and *C. patruela* in Ohio. Cap. Central Allegheny Plateau, Eotp. Eastern Ohio Till Plain, Hlp. Huron Lake Plain, Kb. Kentucky Blue Grass, Otp. Indiana and Ohio Till Plain, Wap. Western Allegheny Plateau.

Figure 67: Distribution of *C. sexguttata* and *C. patruela* in West Virginia. Apm. Eastern Allegheny Plateau and Mountains, Br. Blue Ridge, Cap. Central Allegheny Plateau, Cpm. Cumberland Plateau and Mountains, Nar. Northern Appalachian Ridges and Valleys.

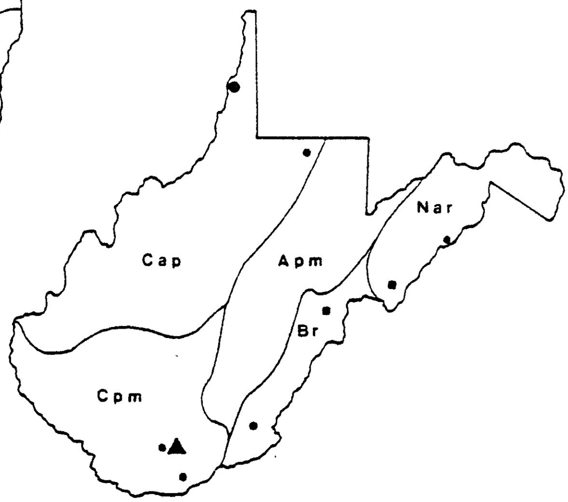
Figure 68: Distribution of *C. sexguttata* in Tennesse. Br. Blue Ridge, Cpm. Cumberland Plateau and Mountains, Hrp. Highland Rim and Pennyroyal, Nb. Nashville Basin, Sa. Southern Appalachian Ridges and Valleys, Scp. Southern Coastal Plain, Smv, Southern Mississippi Valley Alluvium, Smvu. Southern Mississippi Valley Uplands.

Figure 69: Distribution of *C. sexguttata* and *C. patruela* in Kentucky. Cpm. Cumberland Plateau and Mountains, Hrp. Highland Rim and Pennyroyal, Kb. Kentucky Blue Grass, Kis. Kentucky and Indiana Sandstone, Smvu. Southern Mississippi Valley Uplands.

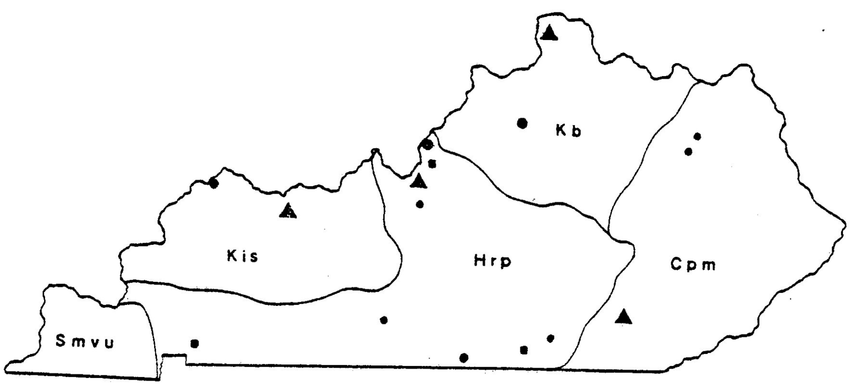
66 Ohio
Scale 1:5,960,000



67 West Virginia
Scale 1:5,960,000



69 Kentucky
Scale 1:5,960,000



68 Tennesse
Scale 1:5,960,000

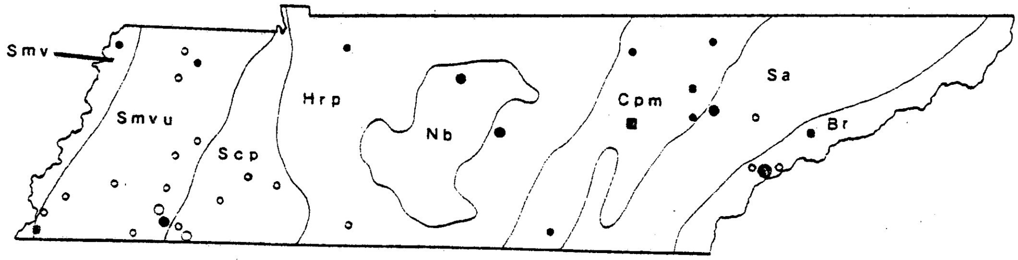
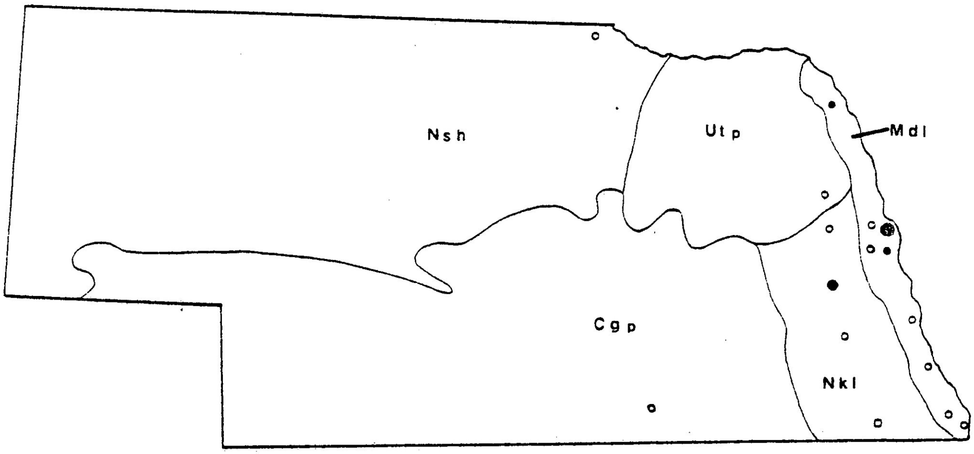


Figure 70: Distribution of C. sexguttata in Nebraska. Cgp. Central Great Plains, Mdl. Iowa and Missouri Deep Loess Hills, Nkl. Nebraska and Kansas Loess Drift Hills, Nsh. Nebraska Sand Hills, Utp. Loess Uplands and Till Prairies.

Figure 71: Distribution of C. sexguttata in Kansas. Bh. Bluestem Hills, Cgp. Central Great Plains, Clp. Central Loess Plains, Cp. Cherokee Prairies, Gsp. Great Bend Sand Plains, Ksh. Central Kansas Sandstone Hills, Mdl. Iowa and Missouri Deep Loess Hills, Nkl. Nebraska and Kansas Loess Drift Hills, Rp. Central Rolling Red Prairie, Rrp. Central Rolling Red Plains.

Figure 72: Distribution of C. sexguttata in Oklahoma. Av. Arkansas Valley and Ridges, Bm. Boston Mountains, Cgp. Central Great Plains, Cp. Cherokee Prairies, Ct. Cross Timbers, Gp. Grand Prairie, Oh. Ozark Highland, Om. Ouichita Mountains, Rp. Central Rolling Red Prairie, Wcp. Western Coastal Plain.

70 Nebraska
Scale 1:5,960,000



71 Kansas
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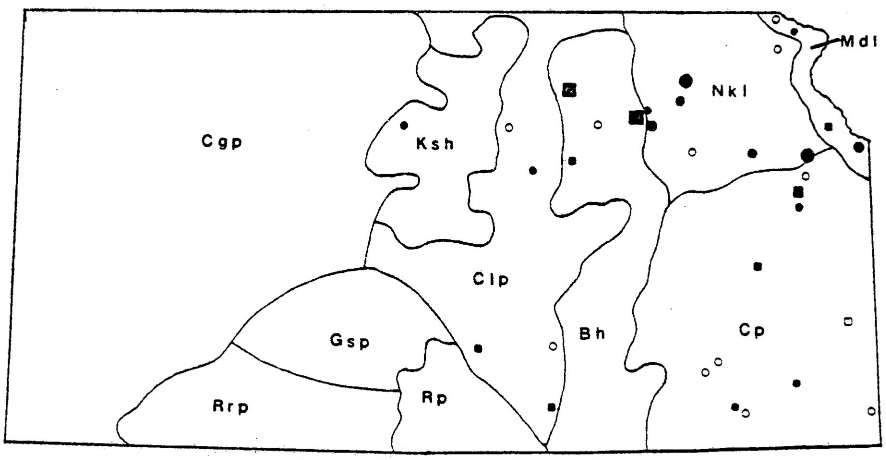
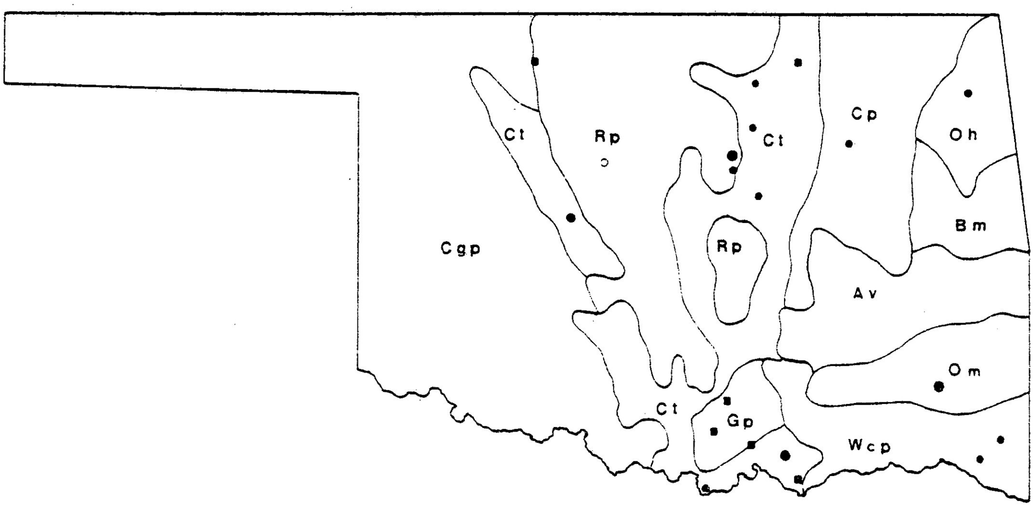


72 Oklahoma
Scale 1:5,960,000



Plains (Cgp) and Nebraska Sand Hills (Nsh), and they are not found west of the 100°W.

Southwestern Region, Figures 72 - 74, 76.

Although C. sexguttata populations are not found in the Ozark Border, (Ob), they are common in the Ozark Highland (oh), Boston Mountains (Bm), Arkansas Valley (Av) and Ouichita Mountains (Om) although they are less common in the west of these regions. These regions are part of a large region of Udults that extend into the Western Coastal Plain (Wcp). A number of beetles are found on the arid soils of the Cross Timbers (Ct) and Texas Blackland Prairie (Tbp). Whether they occur here naturally, or are in some way associated with irrigation by man is unknown.

Gulf Coast Region, Figures 57, 75 - 77.

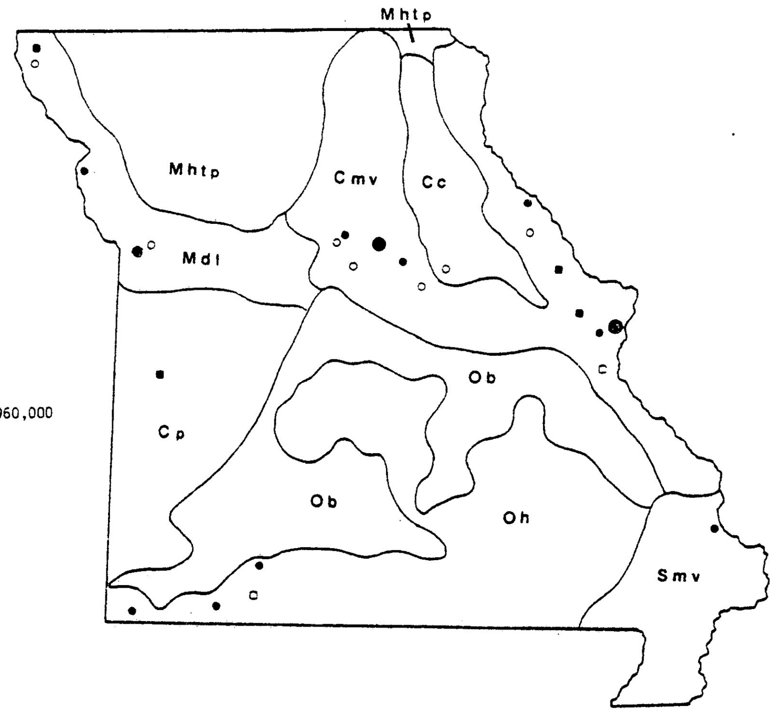
The warm wet soils of the Florida Subtropical region (Fs) and the Gulf Coast Flatwoods (Gcf), Marsh (Gcm) and Prairie (Gcp) are not suitable for C. sexguttata and the beetles are not found there. The wet Inceptisols of the Southern Mississippi Valley (Smv) have only a few scattered populations of beetles, and these are probably associated with the adjacent Southern Mississippi Valley Uplands (Smvu) and Mississippi Blackland Prairie (Bp) which are predominantly Alfisols.

Average abundance scores for different dominant soil types are given in Table 9. The temperature and moisture type of the soils is indicated by the average abundance score. These values are crude representations of relative suitability and should be taken as indicative rather than conclusive. Note that some Haplorthods (ie., Ultic Haplorthods) are actually warm moist soils.

Figure 73: Distribution of C. sexguttata in Missouri. Cc Central Claypan Areas, Cmv. Central Mississippi Valley Wooded Slopes, Cp. Cherokee Prairies, Mdl. Iowa and Missouri Deep Loess Hills, Mhtp. Iowa and Missouri Heavy Till Plain, Ob. Ozark Border, Oh. Ozark Highland. Smv. Southern Mississippi Valley Alluvium.

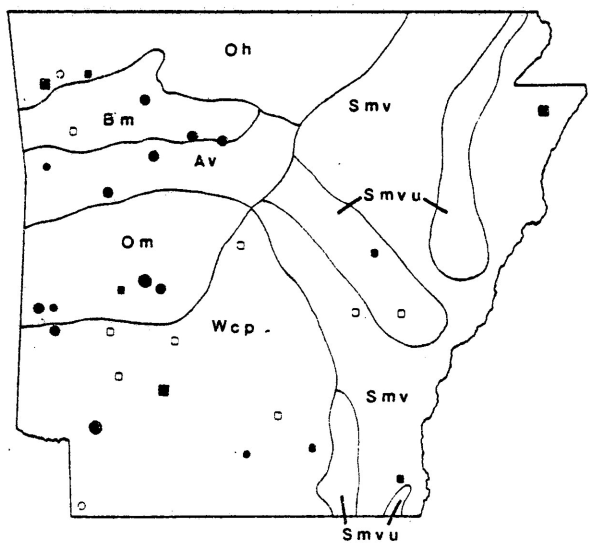
Figure 74: Distribution of C. sexguttata in Arkansas. Av. Arkansas Valley, Bm. Boston Mountains, Oh. Ozark Highland, Om. Ouichita Mountains, Smv. Southern Mississippi Valley Alluvium, Smvu. Southern Mississippi Valley Uplands, Wcp. Western Coastal Plain.

Figure 75: Distribution of C. sexguttata in Mississippi. Bp. Mississippi Blackland Prairie, Gcf. Gulf Coast Flatwoods, Scp. Southern Coastal Plain, Smv. Southern Mississippi Valley Alluvium, Smvu. Southern Mississippi Valley Uplands.



73 Missouri
Scale 1:5,960,000

74 Arkansas
Scale 1:5,960,000



75 Mississippi
Scale 1:5,960,000

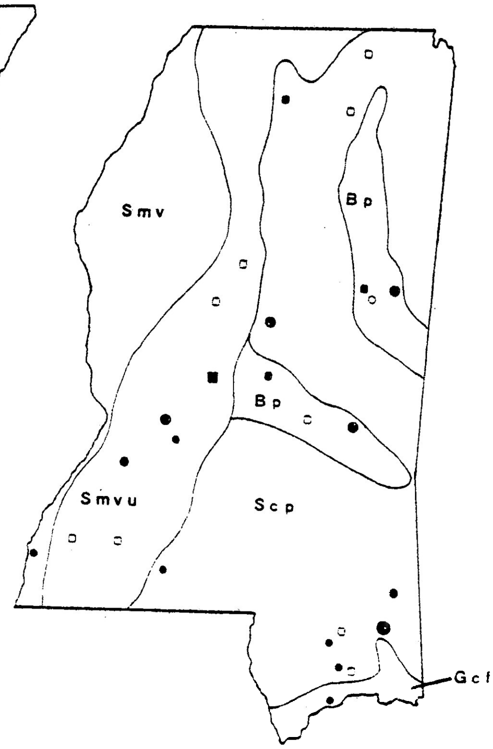
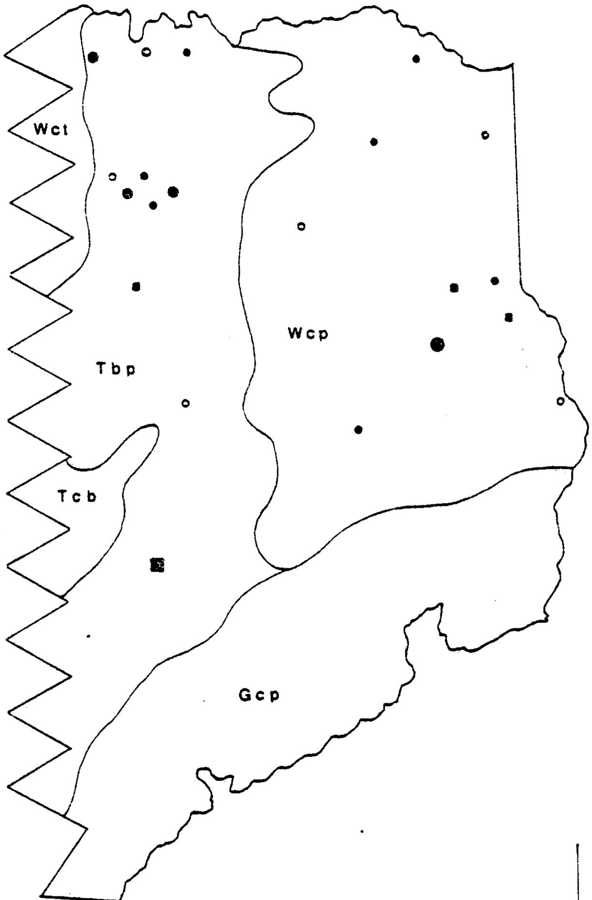


Figure 76: Distribution of C. sexguttata in Texas. Gcp. Gulf Coast Prairies, Tbp. Texas Blackland Prairie, Tcb. Texas Central Basin, Wcp. Western Coastal Plain, Wct, West Cross Timbers.

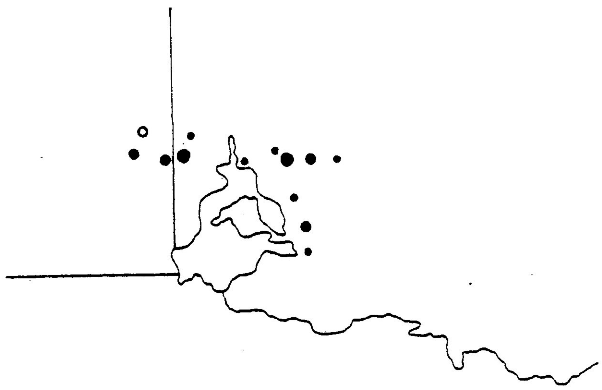
Figure 77: Distribution of C. sexguttata in Louisiana. Gcf. Gulf Coast Flatwoods, Gcm. Gulf Coast Marsh, Scp. Southern Coastal Plain, Smv. Southern Mississippi Valley Alluvium, Smvu. Southern Mississippi Valley Uplands, Wcp. Western Coastal Plain.

Figure 78: Distribution of C. denikei. Solid circles represent collection records from specimens that I have examined, open circle is a collection record from Wallis (1961). The size of the circle indicates the number of collection records from that locality. The small circle is one collection record, the medium circle is two different collection records, the large circle is three or more different collection records.



76 Northeastern Texas
Scale 1:5,960,00

78 Northwestern Ontario, Northern Minnesota, and Southeastern Manitoba
Scale 1:5,960,000



77 Louisiana
Scale 1:5,960,000

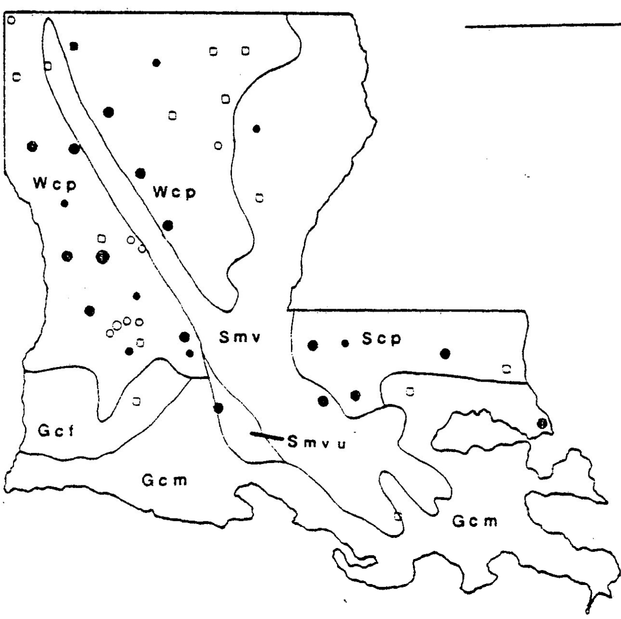


Table 9. Relative abundance of *C. sexguttata* on dominant soil types. The values in the table are averages of the numerical values of the abundance scores given in Appendix 1 calculated for dominant soils only. The values given here are representative of relative suitability and should be considered indicative rather than conclusive. Note that some Haplorthods are actually warm moist soils (ie. Ultic Haplorthods).

	Warm Soils			Cool Soils	
	Moist	Wet	Dry	Moist	Wet
Alfisols					
Udalfs					
Fragiudalfs	1.29				
Hapludalfs	1.59				
Paleudalfs	0.43				
Aqualfs					
Albaqualfs		0.33			
Ochraqualfs		0.33			
Ustalfs			0.5*		
Boralfs				0.43	
Entisols					
Psamments					
Quartzipsamments	0				
Udipsamments	0.75				
Aquents		0.5*			
Orthents			0.5*		
Histols		0.43			
Inceptisols					
Ochrepts					
Dystrochrepts	1.19				
Eutrochrepts	0.14				
Fragiochrepts	1.78				
Ustochrepts			0*		
Aquepts		0.67			
Mollisols					
Udolls					
Argiudolls	1.19				
Hapludolls	0.65				
Aquolls					
Calciaquolls		0*			
Haplaquolls		1.57			
Ustolls					
Arguistolls			0.07		
Haplustolls			0*		
Boralls				0*	
Spodsols					
Aquods		0.20			
Orthods					
Fragiorthods				0*	
Haplorthods				1.64	
Ultisols					
Humults	0*				
Udults					
Fragiudults	0.50				
Hapludults	1.77				
Paleudults	1.28				
Aquults					
Ochraquults		0.18			
Vertisols					
Uderts	0.5*				
Usterts			2*		

* Generated from only one or two observations.

Table 9 indicates that populations of C. sexguttata are most common on warm moist soils. In the table, only three values greater than one are associated with other soils. The value of two for the Usterts is due to the low number of observations (n = 1) for this soil type. The large value of 1.64 for the Haplorthods is misleading as some of these soils are actually warm and moist. The value of 1.57 for Haplaquolls is due to the numerous collecting records from along the Central and Northern Mississippi Valley (Cmv and Nmv) and tributaries of the Mississippi River.

Within the warm moist soils, C. sexguttata is most common on loamy soils. If there is a large proportion of clay (eg., Paleudalfs) or little clay (eg., Hapludolls and Fragiudults) the beetles are rare. The beetles are rare on soils that are high in bases (eg., Calciaquolls and Eutrochrepts), but otherwise tolerate a broad pH range (eg., Alfisols, Haplaquolls, and Fragiochrepts).

The association of distribution and soil type is undoubtedly due to the requirements of the larvae. Loamy warm moist soils provide the temperature and moisture regime necessary for larval growth in C. sexguttata.

The distribution of C. denikei is correlated to Rock land and Cryoboralfs (Appendix I). The larvae are found on silty to sandy till which is often dry.

Habitat

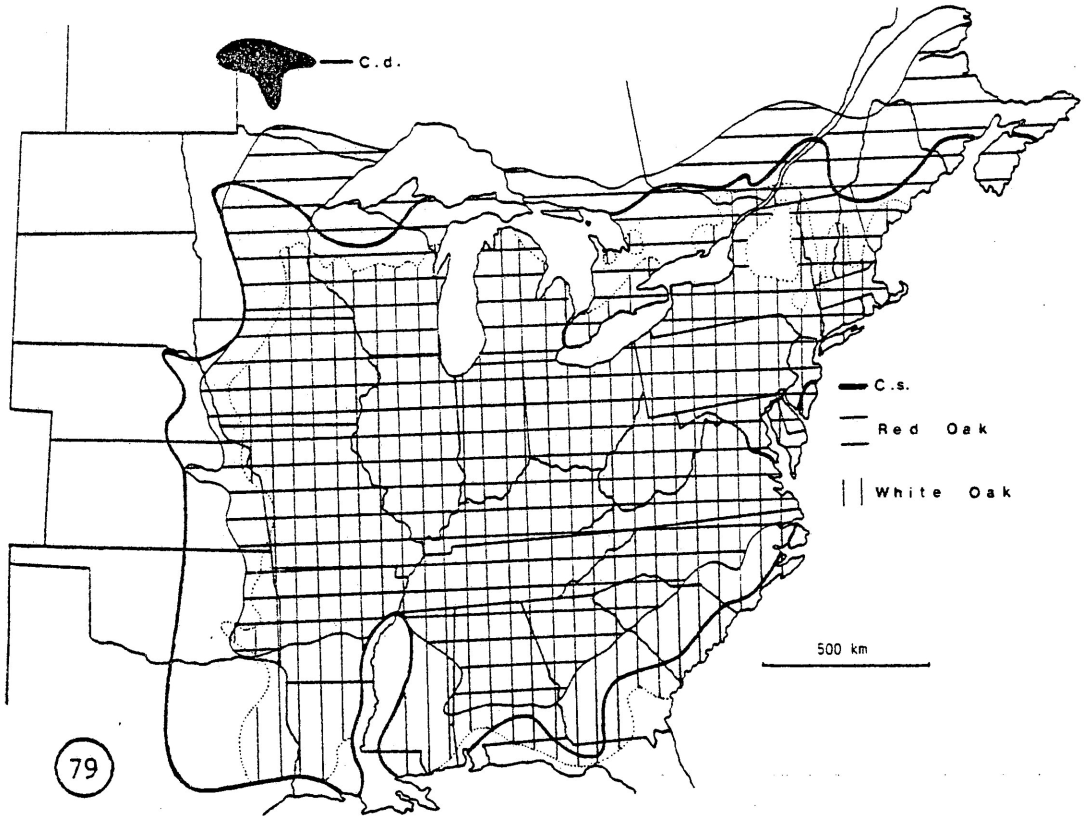
The species C. sexguttata is found in deciduous hardwood forest (eg., Wickham, 1911; Glaser, 1976; Knisely, 1979). The beetles are occasionally found in mixed oak/pine forest (Easton, 1909; Lawton, 1974), but not in pure pine stands (Harris, 1902; Davis 1912). The only in depth examination of C. sexguttata habitat was made by Shelford (1907). He associated the beetles with the White Oak-Red Oak-Hickory forest. The beetles reach dominance during the early stages of this forest and are crowded out when the Beech Maple forest stage begins. The thick humus layer in the Beech Maple forest deprives the beetles of suitable ovi-position sites, although they continue to thrive along paths, roads, blow outs and other open areas.

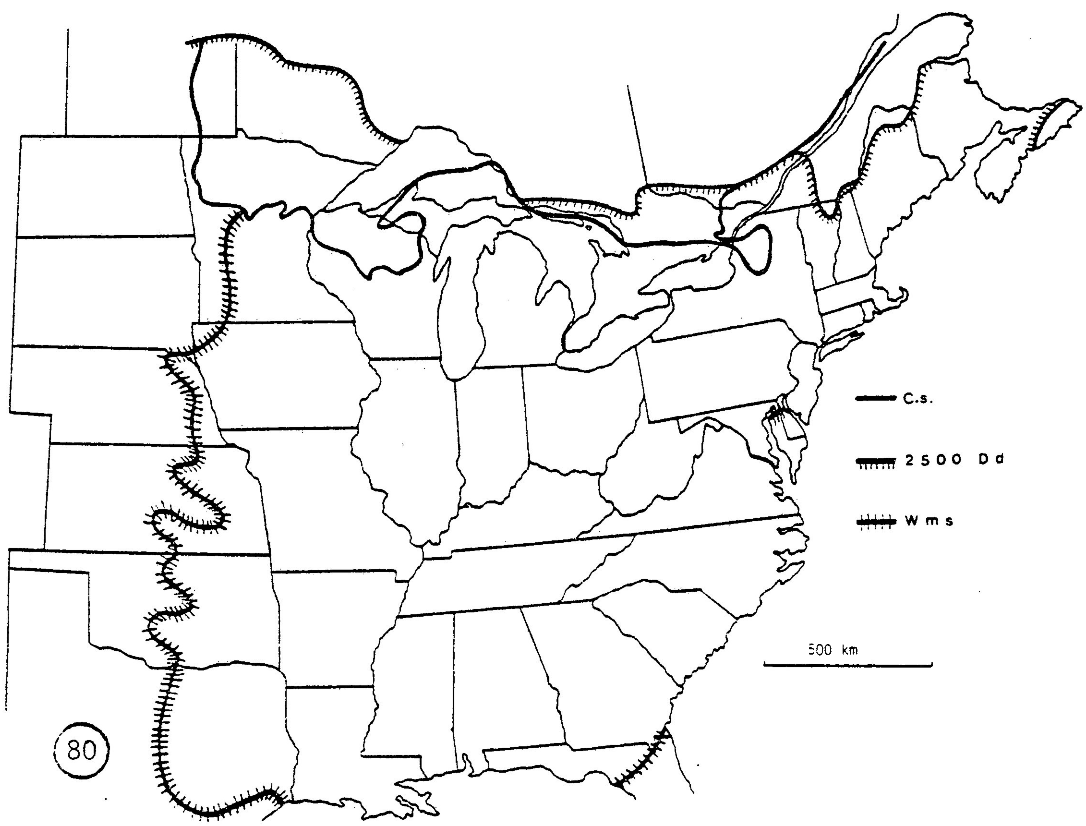
Figure 79 compares the distribution of Red Oak and White Oak with that of C. sexguttata. The distribution of Shag Bark Hickory is approximately described by the overlap of the Red Oak and White Oak distributions. The tiger beetles are not exclusively associated with these three tree species, but they form the habitat in which the beetles are most common. In the west the range of C. sexguttata extends beyond the range of these three species, although the beetles are associated with an Oak Hickory forest associated with river systems (Fowells, 1965). Populations of C. sexguttata are probably associated with the Oak Hickory forest because soil moisture and temperature regimes necessary for larval survival are found within this habitat.

Brown (1934) gives the habitat of C. denikei as "rocky situations" without stating whether it is the same habitat as that for C. sexguttata. Wallis (1961) describes the habitat of C. denikei as being rocky areas in predominantly conifer stands, although he incorrectly describes the

Figure 79: Distribution of C. sexguttata, C. denikei, White Oak and Red Oak. C. s. is C. sexguttata, C. d. is C. denikei.

Figure 80: Factors limiting the distribution of C. sexguttata. C.s. Canadian Shield, 2500 Dd. 2500 degree days isoline, Wms. Limit of warm moist soils.


C.d.
C.s.
Red Oak
White Oak
500 km
79


C.s.
2500 Dd
Wms
500 km
80

physiographic region as the Laurentian Highlands.

The habitat of *C. denikei* is open areas within the boreal forest, in rocky or stoney situations. The eggs are laid and the larvae develop beneath the rocks and stones. Figure 80 shows that *C. denikei* is not associated with the Oak Hickory habitat of its sibling species, *C. sexguttata*.

Populations of *C. p. patruela* are found in mixed coniferous deciduous forest (Fox, 1910; Davis, 1910). The subspecies *C. p. consentanea* is associated with the Pine Barrens of New Jersey, a region of sterile acid soils dominated by Pitch Pine (*Pinus rigida*) (Boyd, 1978).

Limits to distribution

In the absence of gross climatic changes, distributions of *C. sexguttata*, *C. denikei*, and *C. patruela* are probably close to the maximum. The most widely distributed is *C. sexguttata*. To the south and east it is limited by the Gulf of Mexico and the Atlantic Ocean (Fig. 80). It is limited by warm wet soils along the coast, particularly in northern Florida.

In the west, *C. sexguttata* is limited by warm dry soils. Willis (1970) speculated that the beetles would probably be found further west in Kansas along the rivers. This distribution may be possible as the Oak-hickory forest extends further west along the rivers.

Two factors limit the distribution of *C. sexguttata* in the north, climate and soils. As with many species, the Canadian Shield limits the northern distribution of *C. sexguttata* (Graves, 1965; Hicks, 1965).

Scattered populations occur on the Shield, but they are exceptions. The only area where the beetles are abundant on the Shield is in the Gatineau River Valley in Quebec. This is an area of Haplaquept soils that are associated with the river and atypical of the Shield. The other northern limiting factor is the 2500 degree days isoline. Where the isoline extends south of the Canadian Shield, it limits the northern distribution of C. sexguttata (Fig. 80).

To the south C. denikei is limited by soils. The sandy silty till on which it lives was deposited by Lake Agassiz and only extends into Northern Minnesota (Zoltai, 1961, 1968), nor are the same soils found to the east or west. These soils extend farther north than where C. denikei has been found, and possibly C. denikei ranges further north. However, C. denikei is probably limited by the 2500 degree days isoline. During a warming trend, C. sexguttata would still be limited by the Canadian Shield while C. denikei would be able to range further north.

Because the biology of C. p. patruela is poorly understood, speculation about distribution limits is tenuous. The species is confined to the mixed forest and limited by the Atlantic Ocean to the east, dry prairie soils to the west, the border of the true mixed forest to the south, and possibly by climate to the north. The activity period of C. patruela becomes shorter in northern localities (Figs. 30b and 31b), with an earlier fall activity peak. Possibly fall emergence of teneral adults limits C. patruela to areas with a longer season than C. sexguttata. The subspecies, C. patruela consentanea is limited by a specialized habitat.

Adult daily activity

Most adults of Cicindela are diurnal and tend to be active on hot sunny days. Different species have optimal temperature ranges in which peak activity occurs (Payne, 1972; Willis, 1967); activity drops off outside of these ranges. Adult C. sexguttata are unable to fly in the early morning, and are generally torpid when the temperatures are cool (Smyth, 1905; Larochelle, 1978a). Under experimental conditions, adults of C. lepida and C. formosa do not become fully active until the temperature has reached 18°C (Wilson, 1970).

Heat avoidance behaviour has been observed in C. ocellata Klug (Ideker, 1980), C. formosa (Gaumer, 1977) and C. patruela (Clark, pers. com.). Boyd (1978) noted that C. p. consentanea has two daily activity peaks, and that specimens cannot be found during the warmest part of the day. This behaviour has been documented for C. cancellata Dejean as well (Soans and Soans, 1975).

Activity of diurnal adults of Cicindela ceases in the late afternoon to early evening (Moore, 1906; Davis, 1921; Gaumer, 1977). Activity also ceases just prior to thunderstorms or other inclement weather (Willis, 1967; Larochelle 1973a).

Prior to becoming inactive the tiger beetles seek a shelter. Beetles have been found torpid under logs, stones, bark (Larochelle, 1978a) alkali encrustations (Knisley, 1978) and cow chips (Sumlin, 1974). Adult C. cursitans shelter at the edge of, but not under, such debris (Cutler, 1973). Adults of C. sexguttata usually shelter under loose bark (Liebeck, 1890; Smyth, 1907; Graves, 1963; Willis, 1967), but they have also been found under stones and pieces of wood (Larochelle, 1978a).

Other tiger beetles seek shelter by burrowing in the soil, which has been observed in 12 species of Cicindela (Townsend, 1884; Willis, 1967; Larochelle, 1973a; Gaumer, 1977). Knisley (1978) found that although adults of C. willistoni estancia Rumpp shelter under alkali encrustations, some of them construct burrows as well. The digging of adult shelter burrows is described in Willis (1967).

After the beetles are sheltered they become dormant or quiescent. Whether this state constitutes the physiological states of "sleep" or "torper" is not known. The behaviour of the beetles while in this state is discussed by Larochelle (1974b).

Adults of C. denikei are most active on hot, sunny days. Activity begins between 10 and 11 a.m. and ceases between 5 and 7 p.m. Threshold air temperature at the beginning of activity is 18°C. Air temperature when activity ceases is more variable. Other factors such as light intensity and length of activity are probably important as well.

Quiescent adults were not found in the field. In the laboratory terraria, adults sought shelter under pieces of paper and jar lids, where they entered a passive state called "sleep" by Larochelle (1974a). The beetles maintained a typical pattern of diurnal activity in the laboratory. If soil was available, the beetles sometimes constructed an open burrow underneath objects in the terraria. On a number of occasions, all objects were removed from the terraria to determine whether the beetles would seal the burrow. Two sealed burrows were dug under these conditions.

Reproduction

Copulation. Interaction between adult tiger beetles of the same species can be divided into actual or attempted copulation, and "other". The "other" interactions are generally interference type behaviour, attacks, grappling, or rushing at one another (Moore, 1906; Willis, 1967). This interference behaviour does not occur as often in the more gregarious species such as _C. cursitans_ Leconte (Cutler, 1973) or _C. oregona_ Leconte (Maser, 1976), as compared with the solitary adults of _C. sexguttata_ and _C. patruela_.

Copulation requires that male and female come together, which in tiger beetles is a haphazardous process. Usually the more aggressive male approaches a female, but males also attempt to copulate with other males (Willis, 1967), other species of tiger beetle (Fattig, 1951; Larochelle, 1973a), other arthropods (Freitag, pers. com.) and bits of wood of about the right size and shape (Maser, 1976b). Palmer (1976) concluded that copulation encounters were by chance alone, and that there is no evidence of mate attraction behaviours or pheromones in either sex.

Copulation has been described for 22 species of tiger beetle (Mitchell, 1902; Moore, 1906; Shelford, 1908; Goldsmith, 1916; Willis, 1967; Cutler, 1973; Larochelle, 1974a; Maser, 1976; and Freitag et al. 1980). Generally, the male approaches the female in short dashes. He then mounts the dorsum of the female and grasps her between the prothorax and elytra with his mandibles (Willis; 1967). The mandibles of the male fit into the coupling sulci of the female. The shape of the coupling sulci varies from species to species, but is broad in adults of _C. sexguttata_ and _C. patruela_ (Freitag, 1974).

Freitag et al. (1980) described mating in three phases. In the first phase, the adeagus is inserted deep into the female for about 5 seconds. The male's abdomen is curved down towards the female's. The female often shakes her abdomen vigourously during this phase. In the second phase, the abdomen of the male is roughly parallel to the female's and penetration by the adeagus is shallow. The second phase lasts 2 to 3 minutes although it can last longer. In the third phase, the males once again curve their abdomens, more so than in phase one, and deeply insert the adeagus into the abdomen of the female. The three phase copulation by tiger beetles is probably due to interaction between the sclerites of the internal sac of the male and internal genitalia of the female (Freitag et al., 1980).

During copulation, females often shake their abdomens vigourously, and occasionally escape from the male. Also, females may avoid copulation by placing the tip of the abdomen against the substrate (Moore, 1906; Larochelle, 1974a; Willis, 1967).

Although adults of C. denikei are essentially solitary, I noted 18 interactions between adults during the field study. An adult of C. denikei approaches any beetle that enters its visual field unless engaged in feeding or copulation. Usually the two beetles approach one another with short dashes until they are about 5 to 10 cm apart, then one beetle sometimes turns and runs, in which case it is pursued by the other. Pursuit continues until the beetle is caught or takes flight. If neither beetle attempts to flee, the two rush at each other and grapple. Often one beetle attempts to mount the other, if successful,copulation is attempted, regardless of the sex of the other beetle. Usually one of the beetles disengages and takes flight.

Females respond to copulation attempts in two ways. If unreceptive, the female places the tip of her abdomen against the substrate and remains immobile and the male unsuccessfully attempts to insert the aedeagus into the female genitalia. Eventually, the female is released and flies away. The other response by females is to shake the abdomen vigourously, particularly during the early stages of copulation. Occasionally, the male will lose grip of the female and she will flee; otherwise copulation occurs.

Copulation in C. denikei is similar to that of other species of tiger beetle (Willis, 1967; Freitag et al., 1980). Interactions between adults of C. denikei were monitored in the laboratory where it was possible to determine the sex of individuals. Behaviour is similar to that in the field, with some additions. Adults of both sexes approach one another, but when they get within 5 to 10 cm, females tend to turn and flee. If a beetle turns to flee, the other beetle pursues regardless of the sex. In the laboratory, a fleeing beetle often encounters the side of the terrarium and stops. When this occurs, the pursuing beetle stops and begins searching behaviour, which indicates that the beetles probably do not recognize one another without movement.

Adults of C. denikei will attempt to copulate with, flee from, or pursue all other adults within their visual field. This behaviour results in a defended territory that extends to the limit of the adult's vision. Other adults are tolerated within the territory when an adult is copulating or feeding.

Although mate selection in tiger beetles is generally attributed to males (Willis, 1967; Maser 1976b) the female ultimately controls copulation. By placing her abdomen against the substrate, the unreceptive female can ensure that copulation does not occur. The existence of two female responses raises two questions. What factors determine female receptivity? What is the purpose of vigourously shaking the abdomen during copulation?

The receptiveness of the female is probably influenced by factors such as general condition, age, and frequency and time of other copulations. Abdominal shaking probably prevents copulation with undesirable mates. This includes males that are in poor condition because they are diseased or unsuccessful predators, or males of other species whose mandibles do not fit the female's coupling sulci (Freitag, 1974). Vigourous abdominal shaking probably dislodges such undesirable mates. Thus, the behaviour may be a form of sexual selection as well as an isolating mechanism.

Sex Ratios. Adult sex ratios have been examined in four species of *Cicindela*. Townsend (1884) reports a male to female sex ratio of 1.15:1 in *C. tranquebarica* Herbst. The sex ratio of *C. bellissima* Leng is 1:1 (Maser, 1973b). Freitag (1965) examined changes in the sex ratios of *C. oregona* and *C. duodecimguttata* Dejean and found that there are more females than males early in the season, and more males than females late in the season.

The sex ratio of adult *C. sexguttata* from the material examined is 1.25:1 (n = 3,500) males to females. For *C. patruela* adults, it is 1.23:1 (n = 750). Because of behavioural differences, the males are over-represented in collections, particularly as most collecting occurs at the adult foraging site. At a given time, a certain percentage of the females are ovipositing. In many species, the oviposition site is different from the adult foraging site, therefore ovipositing females are not available for sampling by the collector. I have noted that when two adults of C. denikei encounter one another, one is always driven away. If they are of opposite sexes, mating may occur first, but invariably the female leaves the site afterwards. Thus, the males tend to outnumber females in prime open foraging areas, which is where most collecting of tiger beetles occurs. The study of sex ratio is further complicated if it changes over the season, as found by Freitag (1965) for two species of tiger beetle. The above ratios, therefore, probably do not represent the actual adult sex ratio of the species. Determination of actual adult sex ratio will require extensive rearing of larvae or total sampling of several populations.

Oviposition. Ovipositing females of various species of tiger beetle have been observed in the field and in the laboratory (Mitchell, 1902; Moore, 1906; Shelford, 1907, 1908; Goldsmith, 1916; Willis, 1967; Cutler, 1973; Palmer, 1976). The act of oviposition is largely the same in all species studied.

The female seeks a suitable oviposition site by sampling the soil with her antennae, and occasionally her mandibles (Willis, 1967). The female digs an egg hole by everting the ovipositor and inclining the body. The principal digging tools are the gonapophyses. Shelford (1907) suggested that the hairs on the 10th abdominal segment and on the appendages of the 9th are "probably sensitive to the varying degrees of soil moisture and size of soil particles". Frequently the female will dig several holes before ovipositing in one. The oviposition holes are 5 to 10 mm deep and take 5 to 10 minutes to dig. After the egg is laid, the female usually covers the egg burrow with soil, sealing it. The entire process takes about 10 to 12 minutes (Willis, 1967).

The limited mobility of the larvae means that choice of oviposition site is critical to survivorship. Experimental evidence indicates clear preferences by adult females for oviposition sites, which mark the "true index of habitat" (Shelford, 1907). Within their habitat, females of *C. sexguttata* do not lay in the humus proper; instead, they choose bare areas with a little humus (Shelford, 1907). These bare areas may be the result of erosion, uprooted trees, burns, or man's actions.

Oviposition by an adult female *C. denikei* was witnessed in the laboratory. The oviposition behaviour of the female is the same as that in other species of *Cicindela* (see Willis, 1967). In the field, females of *C. denikei* oviposit beneath stones and rocks. No cover was provided for the females in the laboratory, so it is not known how this affects their behaviour.

Fecundity. There have been no detailed studies of the fecundity of tiger beetles. Shelford (1908) observed a female *C. purpurea* Olivier lay about 50 eggs and suggested that this was probably all the eggs that she would lay in her lifetime. Palmer (1976) estimated a lifetime total of about 114 eggs laid per female *Pseudoxychila tarsalis* Bates.

The fecundity of an individual beetle is a product of its life expectancy times the rate of egg production. After a female is ready to begin ovipositing, a number of factors influence the rate at which eggs are laid. I separate these factors into four categories and consider them individually. The importance of each category varies with the species being considered.

I) Location of suitable oviposition sites. Oviposition sites for *C. sexguttata*, *C. denikei*, and probably *C. patruela* are small and scattered; locating suitable sites is probably a major limiting factor for these species. Female *C. repanda* oviposit on the beach where the adults are found (Wilson, 1978), thus the females investment in finding a suitable site is probably minimal; she need only space the eggs to prevent crowding.

II) Time required to lay individual eggs. The time required to dig an egg burrow and lay the egg is roughly 12 minutes (Willis, 1976). The type of soil that the female selects will influence digging time, but overall the time required to lay eggs probably does not severely limit any species.

III) Interference by predators or conspecifics. Palmer (1976) observed that ovipositing females of *Pseudoxychila tarsalis* were often interrupted by conspecifics. Adults of *Cicindela* commonly rush and grapple with conspecifics when they encounter them (eg., Moore 1906) and this behaviour certainly interferes with oviposition.

The frequency of such encounters, while difficult to estimate, is probably low. Many tiger beetles lay their eggs in a microhabitat different from the adult foraging site, reducing the probability of encountering conspecifics. I have noted that feeding and mating adults of *C. denikei* are ignored by conspecifics. Because the feeding beetle is almost motionless, other beetles probably have trouble detecting their presence. Ovipositing females are probably ignored for the same reason.

IV) Physiological limitations. The number of eggs that a female can produce is determined by the amount of energy, in the form of prey, that is available for egg maturation.

One method of estimating the rate at which eggs are laid is to count the number of mature eggs in the abdomen of the female. At a given time, a female would lay only those eggs which are already mature, or almost mature. The eggs take a few days to mature fully (Chapman, 1979); therefore, this number of eggs is the maximum that the female could lay in roughly a two-day period.

I counted the number of mature eggs in 17 mature female *C. sexguttata* and 17 *C. denikei*. The average number of mature eggs per female was 7.7 and 3.7 for *C. sexguttata* and *C. denikei* respectively. Mature females of *C. sexguttata* probably lay from four to eight eggs per day, whereas females of *C. denikei* lay two to four eggs per day (Table 10).

The number of mature eggs found in the females of the two species was compared using a Mann Whitney U test (Table 10). The difference between the means is statistically significant at the 95 and 99% confidence levels. This difference may reflect a number of factors such as age of the individuals and prey availability, but I attempted to control for these variables by using females from a variety of collecting sites and dates. The difference in the means probably reflects a real difference in the fecundity of the two species, which indicates that the bionomics of the two species are different.

Table 10. Number of mature eggs found in abdomens of mature females of C. denikei (n = 17) and C. sexguttata (n = 17). Values given for U statistic, Z statistic, and corrected 2 tailed probability.

	Number of mature eggs																
C. denikei	4	6	6	7	2	2	7	0	3	4	2	0	1	4	4	3	7
C. sexguttata	14	11	8	13	13	9	6	12	3	1	10	6	7	10	1	6	0

	$\bar{X}$	S.D.
C. denikei	3.7	2.3
C. sexguttata	7.7	4.3

Mann Whitney U Test

U = 68.5 Z = -2.63 P = 0.0086

Larval burrow

The first instar larva begins to dig a burrow after completion of sclerotization (Willis, 1967). Willis gives a detailed description of burrowing behaviour, which can be summarized as follows. The larva loosens the soil with its mandibles and carries it to the surface on the head and prothorax. At the surface, the dirt is flicked away from the burrow mouth. Within a species, the burrow depth varies with instar, season, weather, soil moisture and soil type (Willis, 1967).

Different species of Cicindela construct a wide variety of burrow types. In general, most burrows are perpendicular to the soil surface. They extend from a few cm (Willis, 1967) to 1 1/2 m (Criddle, 1910). The mouth of the burrow is perfectly round and usually flush with the surface of the soil. Burrow variations include a funnelled entrance in _C. lepida_ Dejean (Shelford, 1908), pit entrance in _C. formosa_ Say (Gaumer, 1977), turret entrance for _C. willistoni_ Leconte (Knisley and Pearson, 1981), oblique burrow for _C. limbata_ Say (Criddle, 1910), and burrows that extend under rocks and stones in _C. rufiventris hentzi_ Dejean (Wilson, 1970) and _C. marginipennis_ Dejean (Dunn, pers. com.). Burrows and burrowing in various species are discussed in Shelford (1911), MacNamara (1922), Hamilton (1925), Zikan (1929), Dunn (1978), and Palmer (1978).

The larva burrow of _C. sexguttata_ has a round opening that is flush with the soil surface and the burrow extends down perpendicular to the soil surface. The mouth of the burrow is generally exposed although it may be quite close to cover such as fallen leaves or a log. Burrows are found in loamy sand in level areas or on slight slopes.

The larval burrow of _C. denikei_ differs from typical _Cicindela_ burrows in that the mouth of the burrow opens directly beneath stones and rocks. The soil was a silty sandy till with numerous stones and gravel. The larval burrows of _C. denikei_ twisted and turned to avoid these obstructions. Depth of burrows was 8 to 14 cm for second instar larvae and 10 to 20 cm for third instar larvae.

The larval burrow of _C. denikei_ is unique in _Cicindela_. Larvae of _C. rufiventris_ and _C. marginipennis_ extend their burrows underneath stones (Wilson, 1970; and Dunn, pers. com.), but no other _Cicindela_ has the mouth of the burrow open underneath stones. The burrow location of all three species may be designed to avoid extremes of temperature and moisture.

Correct moisture balance is critical to the larvae as they readily desiccate (Shelford, 1908; Wilson, 1967; Palmer, 1978). In many species, the depth of the burrow is increased to avoid high temperatures and drying (Willis, 1967). The habitat of C. denikei makes this tactic difficult. The habitat is subject to high temperatures and periods of extreme aridity. The soil where the larvae are found is mixed with stones and gravel, making digging very difficult, and it is shallow, with bedrock often only a few cm below the surface. The soil is moister and cooler beneath stones, therefore the larva does not need a deep burrow to avoid desiccation. In addition, such a burrow probably reduces the rate of parasitism.

Predation Behaviour.

Foraging. Tiger beetles tend to forage in open places such as meadows, paths, old roads, beaches, river banks, etc., as expected of visual hunters (Pearson and Mury, 1979). Adults of Cicindela are acotopic and have excellent fields of vision. The visual field of C. tranquebarica Herbst covers 70% of the unit sphere with no anterior or posterior blind spots. The beetles have stereoscopic vision anteriorly, posteriorly, dorsally, and ventrally for about 50% of the visual field (Kuster and Evans, 1980). By foraging in an open area, the beetle obtains the maximum benefit from the wide visual field.

Adults of C. sexguttata forage on paths and old roads within the forest (Easton, 1909; Larochelle, 1972a;Glaser, 1976). Lawton (1974) reports an adult of C. sexguttata foraging on a patch of lily pads some distance from shore. Only Shelford (1907) records foraging on fallen logs, however, this behaviour may be more prevalent. Clark (pers. com.)

has evidence that fallen logs may be an important foraging site for C. sexguttata adults. On two occasions, I have seen the beetles on the trunks of standing trees.

Clark (pers. com.) reports adults of C. patruela foraging along dirt trails. Adults of C. p. consentanea also forage in open areas within their habitat (Boyd, 1978).

Working with adults of C. hybrida Linneaus, Swiecimski (1957) reported two kinds of predatory behaviour. The first consists of non-directed wandering through the habitat while sampling objects in the environment. The beetle will eat both live and dead animal matter that is encountered. This scavanging behaviour has also been observed in C. ocellata Klug (Mitchell, 1902), C. punctulata Olivier (Rogers, 1974) and C. repanda Dejean (Wilson, 1978). Wilson (1978) and Clark (pers. com.) studied predation by C. sexguttata and C. patruela. In the laboratory, members of either species rarely ate even freshly killed prey, and scavanging was not observed at all in the field.

The second type of predation described by Swiecimski (1957) is direct attack of mobile prey. In seeking live prey a tiger beetle has the option of actively searching, waiting for prey, or some combination of the two. Adults of C. patruela were found to spend 94% of their foraging time immobile (Clark, pers. com.), indicating that these tiger beetles are ambush predators.

The selection of an ambush site is important for an ambush predator. Good ambush sites will maximize the frequency of prey encounters. Adult C. patruela choose slight elevations that give good fields of vision over the path that is their foraging site. Suitable sites will have a beetle on them, sometimes the same individual, day after day (Clark, pers. com).

Adults of C. denikei forage in open areas. They can be found on paths, old roads, cleared and burned areas, and on the many large pieces of exposed bedrock that occur throughout the habitat. If an adult strikes at a prey and misses, it will then probe the substrate and sample objects in the immediate environment in search of the prey. Otherwise, they were not seen to exhibit scavanging behaviour. Adults of C. denikei, obtain food by direct attack on mobile prey.

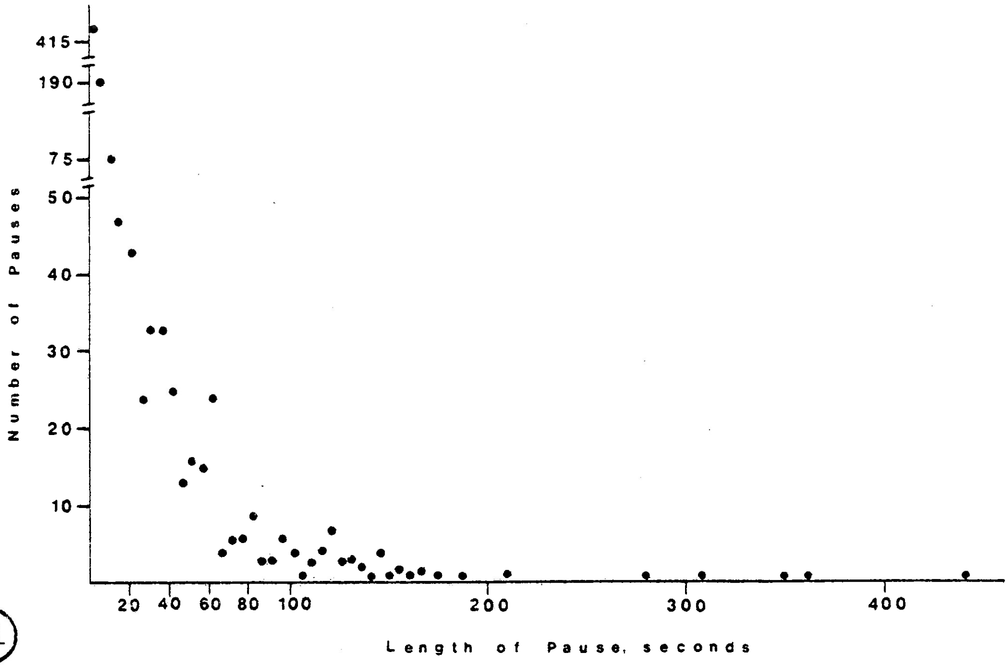
Twenty-six adult C. denikei were observed for 469 minutes, of which 94.7% of their foraging time was spent immobile. Rather than choose a single ambush site, the beetles move from spot to spot, pausing in each from several seconds to several minutes. Figure 81 shows the frequency of the different pauses. There is some indication that individuals have preferences for pause duration, but it is not statistically significant.

About 40% of all pauses are very short, from one to five seconds. As the beetle moves, it makes many short pauses, presumably in search of prey. The other 60% of the pauses range from six seconds to over seven minutes. The average pause duration is 23 seconds; if short pauses are not considered, the average pause duration is 38.4 seconds. Although the beetle is an ambush predator, it frequently changes the ambush site, which suggests that the distribution of prey is not uniform.

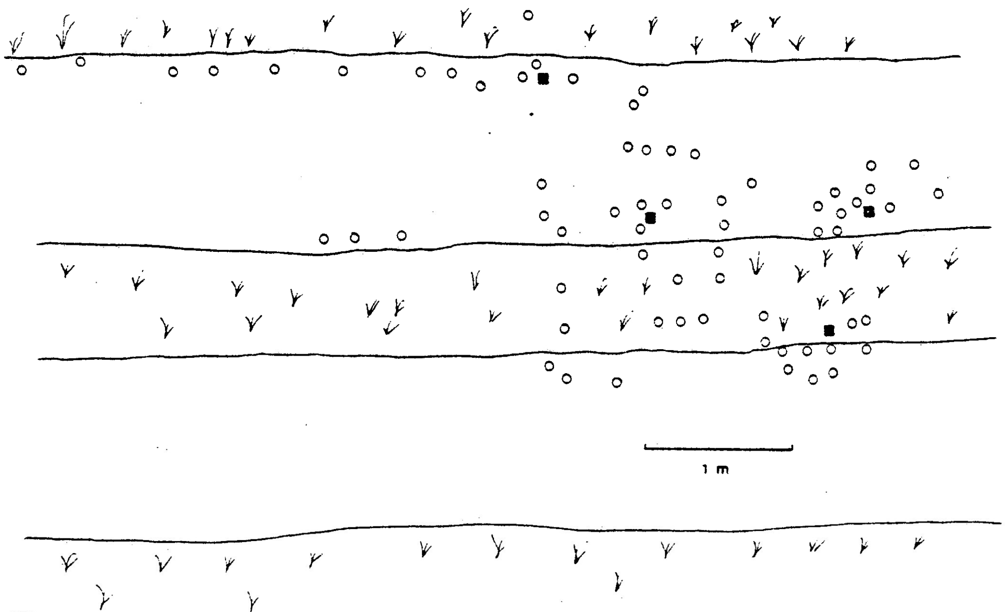
The mean duration of pauses prior to a prey encounter is compared to mean duration after a prey encounter. At least four, and as many as 10 pauses per encounter, five before and five after, were compared. It was

Figure 81: Number of pauses by foraging *C. denikei* plotted as a function of pause duration.

Figure 82: Foraging microhabitat of *C. denikei* and activity of foraging adult. The open circles indicate pauses of greater than 5 seconds duration. Closed squares indicate prey encounters. Vegetation is indicated on sides of road tracks.


415
190
75
50
40
30
20
10
Number of Pauses
20
40
60
80
100
200
300
400
Length of Pause, seconds

81


1 m

82

not possible to use 10 pauses in all cases because of subsequent encounters with prey or conspecifics, which further modified the behaviour, or because the beetle left the study area before pausing five times. Only 22 prey encounters by 14 beetles were suitable for analysis. The two data sets are compared using a Mann Whitney U Test (Table 11).

Table 11. Analysis of effect of prey encounter on pause duration by adults of C. denikei. Group 1 is the pause duration prior to the prey encounter. Group 2 is the pause duration after the prey encounter. The difference in the means is significant at the 95 and 99% confidence levels.

	$\bar{X}$ (sec)	S. D.	n (pauses)
Group 1	13.7	19.42	127
Group 2	31.8	48.80	127

U = 6159 Z = -3.265 P = 0.0011

A beetle modifies its behaviour in the vicinity of an encounter with prey. Following an encounter, the beetle pauses more frequently (Fig. 82) and longer. Analysis of 22 prey encounters by 14 beetles shows an average pause length of 13.7 seconds prior to the encounter and 31.8 seconds after the encounter. The two means were tested with a Mann Whitney U Test and found to be significantly different at the 95 and 99% confidence levels (Table 11). Swiecimski (1957) found that tiger beetles also remember the size and shape of prey and alter their behaviour accordingly.

Many tiger beetle prey escape by becoming immobile (Willis, 1967; Wilson, 1978). By remaining in the vicinity of an encounter, the beetle increases the probability that it will encounter the same prey again. A common food item of tiger beetles is ants (Willis, 1967). The foraging strategy of the beetle is such that it will be successful at locating and exploiting ant colonies. By moving frequently , the beetle will eventually move into the vicinity of a colony. If it encounters an ant, it will tend to remain in the area; the more prey it encounters, the longer it will remain in the area. The foraging strategy of the beetle will result in locating prey concentrations and remaining in the area of the concentration.

While adults of C. denikei are foraging, they move and pause close to the interface between the road and the vegetation. Figure 82 shows the location of long pauses by a single adult as it forages along the road. The movement of the beetle is roughly a connection of the dots. This behaviour is typical of all of the observed beetles. Because they have 360^{o} vision, one would expect the beetles to pause and forage in the middle of the track where there are fewer obstructions to vision. By remaining near the interface, the beetle reduces its effective visual field. It is probable that the reduction in visual field is compensated by an increased rate of prey encounter.

The road where the beetle forages is homogenous and resource-poor, thus arthropod density and diversity is low. In the vegetation where there are more resources, the arthropod densities are higher. Arthropod density and diversity is highest in lush mixed vegetation. If the beetles prey on arthropods that "spill over" from the surrounding vegetation, one would expect them to preferentially forage near lush, mixed vegetation. Table 12 shows the linear density of the beetles along the road expressed as a function of the adjacent vegetation. The linear density is highest where the vegetation is lush and mixed, and correlates with the density of adjacent vegetation. Where the road itself is overgrown, there are few beetles; they do not forage within the vegetation itself. The higher density of beetles near lush vegetation is probably a result of the beetles tending to remain where they encounter more prey.

Table 12. Linear density of beetles per meter of road expressed as a function of the vegetation beside the road. The data base was 92 beetles over 420 meters of road.

Adjacent Vegetation	Beetles per meter of road
Absent	0.062
Sparse	0.171
Intermediate	0.263
Lush	0.354
Lush (mixed)	0.380
Lush (grasses only)	0.267
Road overgrown, Intermediate	0.092

Foraging behaviour by adults of *C. denikei* was also analyzed using behaviour sequence matrices. Table 13 shows absolute frequency of various behaviours in the study. The "run/stop" is the most common type of

Table 13. Behaviour sequence matrix showing absolute frequencies.

		FOLLOWS				
		Pause	Run/Stop	Orient	Move	Run
PRECEDES	Pause		424	229	37	31
	Run/Stop	553	545	143	16	43
	Orient	94	288	10	17	16
	Move	45	9	19		1
	Run	33	28	25	5	34
		725	1294	425	75	125

Table 14. Behaviour sequence matrix showing relative frequencies calculated to show probability of other behaviours following a given behaviour.

		FOLLOWS					
		Pause	Run/Stop	Orient	Move	Run	
PRECEDES	Pause		58.8	31.8	5.1	4.3	-- 100%
	Run/Stop	42.5	42	11	1.2	3.3	-- 100%
	Orient	22	67.8	2.4	4	3.8	-- 100%
	Move	60.8	12.2	25.6		1.4	-- 100%
	Run	26.4	22.4	20	4	27.2	-- 100%

movement. The number of "moves" and "runs" is misleading as most of them are associated with prey conspecific encounters. They are not as frequent during foraging.

From Table 14, it is possible to calculate the distance a beetle moves when it changes the ambush site. The probability of a run/stop being followed by a pause is 0.425, thus for 42.5% of the events, the beetle moves about 13 cm before pausing again. For 82% of the events, the beetle moves 0.25 m or less. The probability that a beetle will move 40 cm or more is less than 0.08. The beetles detect small to medium prey from 8 to 15 cm away, which has been observed in other species (Moore, 1906; Balduf, 1925; Willis, 1967). For 42.5% of the events, the beetle moves a distance roughly equal to the radius of its visual field. The beetle moves a distance equal to or less than the diameter of its visual field 82% of the time that it changes the ambush site. When a beetle changes its ambush site, the new site usually borders on, or includes 50% of the old site. Thus, while foraging, the beetle tends to cover an area systematically and thoroughly.

The probability that an "orient" will be followed by some type of movement is 0.75. Because the beetle has a visual field of 360°, the orient is probably used to point the body in the desired direction of travel. However, 22% of the "orients" are followed by "pause". The "orient" move is usually 90°, which probably serves to change the field of the beetles stereoscopic vision.

Almost 25% of all movement is followed by an "orient", indicating frequent changes in direction of travel. Rather than move down the road consistently in one direction, the beetle follows the vegetation interface on one side of the road, crosses to the middle and follows the interface there. Beetles frequently forage on one track of the road and then move into the vegetation. If they find a suitable foraging area, such as the other track of the road, they forage there. If they do not find a foraging site after moving 50 to 100 cm, they usually return to the road. While in the vegetation, the beetles move quickly with few pauses.

Prey capture and feeding. The size of foraging area is a circle that extends to the limit of the beetle's vision. The radius of the circle has been estimated as 10 to 13 cm for *C. purpurea*, 8 to 13 cm for *C. repanda* (Moore, 1906) and 25 cm for *C. hybrida* (Swiecimski, 1957). The beetles are completely dependent on movement by the prey for detection (Swiecimski, 1957; Willis, 1967; Wilson, 1978). Attacks on prey are divided into four stages (Swiecimski, 1957). They are i) preparation, ii) attack, iii) capture, and iv) consumption.

In preparation for attack, the beetle faces the prey and elevates the front of the body, possibly to center the prey in its stereoscopic visual field. The pursuit and attack on the prey is made with short dashes characteristic of tiger beetle movement.

Capture of the prey occurs when the beetle grasps the prey with its mandibles. Wilson (1978) studied success rates of attacks by tiger beetles and found that they are successful about 50% of the time. He noted that success depended on the type of prey, and that the beetles had a high success rate with ants (Formicidae) and low success with flies (Diptera).

Detailed descriptions of the beetles' consumption of prey, including articulation of the mouth parts, can be found in Balduf (1925), Evans (1965) and Willis (1967). Clark (pers. com.) studied handling time and consumption time in adult C. patruela and found that they average 0.48 and 3.3 min. respectively.

The radius of the beetles' effective visual field varies with the size of the prey. On a flat surface without obstructions large prey, about the same size as the beetle, were seen at a distance of roughly one meter. Small prey, 5 mm or less, are seen at a distance of 10 to 15 cm. As with other tiger beetles adults of C. denikei perceive prey by its movement.

Table 15 lists the frequency of certain events experienced by observed adults of C. denikei. The definition of prey encounters and success rates are not comparable to those of Wilson (1978). In this context, prey encounter is defined as an attempted attack on a prey item, whether it is in striking range or not. The median time between captures of 78 min is comparable to 94.2 min for Arizona grassland species (Pearson and Stemberger, 1980). Table 16 lists capture success rate by prey type. As with adults of C. sexguttata and C. patruela (Wilson, 1978), adults of C. denikei are most successful in attacks on ants (Formicidae) and least successful with flies (Diptera).

Prey capture and consumption by adults of C. denikei occurs as described for other tiger beetles (Balduf, 1925; Swiecimski, 1957; Evans, 1965). Table 17 lists the handling and consumption time for prey captures witnessed. The respective means of 20.5 and 225 seconds are comparable to those for C. patruela, 30 and 200 seconds (Clark, pers. com.).

Table 15. Frequency of events during foraging by adults of *Cicindela denikei*.

Event	Number	Median time between events
Prey Encounter	40	12 min.
Prey Capture	6	78 "
Conspecific Encounter	18	26 "
Mating	3	156 "

Table 16. Number of capture attempts and successful captures of various prey by adults of *Cicindela denikei*. Identifications of prey are tentative as none of them were recovered for identification.

Prey Type	Number of Attempts	Number of Captures
Diptera	13	0
Formicidae	6	3
Sphecidae (?)	5	0
Ichneumonoidea (?)	2	1
Unknown	14	2

Table 17. Amount of time spent by adults of *Cicindela denikei* in handling and consuming captured prey.

Handling time in seconds	Consumption time in seconds
35	287
28	250
7	120
13	344
30	126
10	flew w/prey
$\bar{X}$ = 20.5	$\bar{X}$ = 225

Prey types. Reviews of the prey that *Cicindela* have been observed to capture are Larochelle (1974c, 1977) and Willis (1967). Adults of *Cicindela* should be described as general predators, although "indiscriminant predators" would be a better description. Willis stated that "*Cicindela* eat nearly any arthropod that they can subdue and which occurs in their microhabitat" (p. 195). My observations of *C. denikei* bear this out. Table 16 lists the prey items that I witnessed adult *C. denikei* capture or attempt to capture. Given the opportunity, adults will attack any and all arthropods near them.

Predators of *Cicindela*

The following papers record instances of *Cicindela* captured by other predators; Day (1969), Huber (1980), Larochelle (1972b), Lavigne (1972, 1977), Maser (1973a, 1976a; Nagano (1980), Shook (1979), and Smith (1976). Larochelle (1974d, 1975a, 1975b, 1978b) reviews the vertebrates that prey on tiger beetles. Apparently, adults of *Cicindela* are frequently the prey of a large number of vertebrates and invertebrates; however, they do not constitute a large part of the diet of any predator.

Associated *Cicindela*

Adults of *C. sexguttata* are solitary (Larochelle, 1972a) but some species of *Cicindela* share the same habitat with them in some areas. Associations of *C. sexguttata* with other species seem to be local and inconsistent. Along the borders of the deciduous forest, adults of *C. sexguttata* and *C. punctulata* forage in the same places (Harris, 1891; Lawton, 1970a). Within the forest, proper adults of *C. sexguttata* and

C. rufiventris Dejean can be found together (Lawton, 1970a). Choate (1975) reports sympatric populations of *C. sexguttata* and *C. scutellaris unicolor* Dejean, but he does not indicate whether they were taken in the forest or in the open. Smythe (1907) reports *C. sexguttata* with *C. limbalis* and *C. splendida* Hentz, but notes that the adults of *C. sexguttata* are not plentiful. In northern Michigan, *C. longilabris* Say and *C. patruela* are often associated (Graves, 1963).

I found that populations of *C. sexguttata* usually do not share their habitat with members of other species. Instances of habitat sharing were found, but there was no consistent association with any one species. In Powhottan Co. Virginia, a single adult of *C. unipunctata* Fabricius was collected with *C. sexguttata* adults. In Torreya State Park, Florida, a single third instar larva of *Megacephala* sp. was found in a sand bank adjacent to a loamy clayey forest trail where larvae of *C. sexguttata* were common. On the Vermillion River in Nemaha Co. Kansas, adults of *C. sexguttata* were found with adults of *C. duodecimguttata*. Adults of *C. sexguttata* were common on the banks of the river, on a small gravel island about one meter off shore and in the forest along the river, whereas the larvae were found only in the forest. Adults of *C. duodecimguttata* were common along the banks and on the island, whereas the larvae were found along the banks of the river.

At the pipeline road collecting site east of Kenora, Ontario, specimens of *C. denikei* were collected with *C. longilabris*, *C. tranquebarica*, *C. repanda*, *C. duodecimguttata*, and *C. limbalis*. Adults of *C. repanda* and *C. duodecimguttata* were collected near a low lying swampy area where *C. denikei* adults were not common. Only a few individuals of each of the other species were captured. Adults of both _C. longilabris_ and _C. limbalis_ were more common about 500 m down the road where the vegetation was thicker and the soil moister.

On the Assinaki Nature Trail in Manitoba, _C. denikei_ adults were found with those of _C. longilabris_ and _C. tranquebarica_. At this site, specimens of _C. denikei_ were rare whereas _C. longilabris_ adults were common. Only a few adults of _C. tranquebarica_ were found. About half of the remaining _C. denikei_ sites had adults of other species of _Cicindela_ present. Generally, one or two specimens of either _C. longilabris_ or _C. tranquebarica_ were found. Occasionally, adults of _C. repanda_ or _C. duodecimguttata_ were found with _C. denikei_ adults, but only near open water.

Adults of _C. patruela_ were collected in Todd Co. Minnesota. No other species of _Cicindela_ were found on the path in the forest with _C. patruela_ but adults of _C. scutellaris_ were common where the path ran through a meadow. At a nearby garbage dump, adults of _C. scutellaris_ and _C. formosa_ were common, but adults of _C. patruela_ were not found.

Interspecific Competition.

Considering the broad feeding habits of most species of _Cicindela_ one would expect interspecific competition for the food resource. Most species exhibit habitat preference (Blanchard, 1921; Fox 1910; Willis, 1967) which accounts for a certain amount of spatial segregation, but as noted, many species also share the same habitat.

Spatial partitioning of the microhabitat by a few riparian species was first noted by Shelford (1907). Spatial or temporal partitioning of the microhabitat has since been shown for 22 species of _Cicindela_

(Willis, 1967; Klop,1974; Knisley, 1979). However, cases exist where two or more species do not partition the microhabitat (eg., Johnson, 1979). Pearson and Stemberger (1980) demonstrated that although tiger beetles attack a wide range of prey, their ability to subdue and handle the prey varies with the species of tiger beetle. Mean prey size has been correlated with mandible size of a number of grassland Cicindela in Arizona, suggesting resource partitioning on the basis of capture efficiency (Pearson and Mury, 1979). Pearson (1980) found that Hutchinson ratios existed for the mandible length of a number of tropical forest tiger beetles, suggesting the same method of resource partitioning.

Because individuals of C. sexguttata and C. patruela are usually found alone, they probably do not compete with members of other species. In areas where C. sexguttata and C. patruela are found with members of other species, the microhabitat is subdivided (eg., Goldsmith, 1916) or one of the species is rare (eg. C. unipunctata). Adults of C. sexguttata and C. patruela are occasionally found in the same area, but they have not been found sharing the same foraging site (Leng, 1910; Wallis, 1961; Johnson, pers. com.; Spanton, pers. com.). Adults of C. denikei are sometimes found foraging with adults of other species. This usually occurs in an overlap zone between two different microhabitats with adults of each species being more abundant in their appropriate microhabitat. Alternatively, members of one of the species are rare.

Sympatric life stages of a species may compete for resources. In Cicindela larvae and adults are general predators and intraspecific competition between them is possible. Competition for prey is likely between the third instar larva and the adult, as they are of comparable size. In some species, the larvae and adults are spatially separated (eg., Mitchell, 1902; Shelford, 1907), whereas in other species adults and larvae forage in the same microhabitat (Willis, 1967). Wilson (1978) examined predation in *C. repanda* and postulated that the adult evolved as a less aggressive predator than the larva, consequently, the food resource was partitioned by life stage selection.

Competition has been postulated but not demonstrated for members within the same life stage. In the adult, the limiting resource probably is oviposition sites (Shelford, 1907; Wilson, 1967; Willis, 1967). Larvae are probably food limited (Willis, 1967).

Shelford (1907) observed that adults of *C. sexguttata* oviposit in sites other than their foraging site; therefore, adults do not compete with the larvae for food. The oviposition site is different from the adult foraging site in *C. denikei*. The oviposition site of *C. patruela* is unknown, which suggests that it is different from the adult foraging site.

The solitary nature of all three species suggests that the adults compete with one another for foraging sites. The aggressive nature of the adult beetles produces a defended territory that extends to the limit of their visual field. The foraging strategy of adults of *C. denikei* leads them into areas of higher prey density. By maintaining a defended territory, an adult excludes others from its foraging area. The defended territory probably assures a higher rate of success in prey acquisition and mating, and its existence suggests competition for one or both resources.

Flying and dispersal

Although tiger beetles are strong flyers, they usually fly only to escape danger (eg., Townsend, 1884, 1886; Willis, 1967; Gaumer, 1977). Flying and escape behaviour are described by Willis (1967). Mark and recapture studies of adult tiger beetles have shown that their movement is fairly restricted. Willis (1974) studied adults of *C. togata* Laferte-Senectere and found that the beetles move readily within a habitat patch, up to 18 m in 24 hours, but do not move to new habitat patches even when they are relatively close (5 m). Palmer (1976) observed that adults of *Pseudoxychila tarsalis* also remained close to the habitat patch where they were marked.

The literature on tiger beetles notes that they are reluctant flyers, but this was not borne out by my observations. Of 37 observed flights, less than half could be called escape behaviour (Table 18). By comparison, only three observation sessions ended because the beetle walked out of the study area. Tiger beetles fly more readily than the literature indicates, probably because the accounts of behaviour in the literature are largely anecdotal, casual observations.

Table 18. Circumstances under which adult *C. denikei* were observed to fly.

Beetle - encounters conspecific	15
approached by spider	1
captured prey	1
leaves study area, no apparent reason	14
travels 20-70 cm, no apparent reason	6
	37

The results from the mark recapture study are highly variable. Ten individuals moved over 100 m from the marking site, whereas nine moved less than 20 m. The maximum movement is approximate, based on one individual that had left the study area; no other beetles, marked or unmarked, were found outside the study area.

Table 19. Movement of marked individuals of *C. denikei*.

$\bar{X}$ movement	3.8 m/day
$\bar{X}$ displacement	3.2 m/day
Maximum movement, 1 day	approx. 500 m.
Minimum movement, 1 week	0.0 m.

Although the data base for Table 19 is small, some conclusions can be made from it. Adults of *C. denikei* move freely within the habitat patch, but do not leave it readily. Beetles return to the foraging area soon after leaving if they do not encounter another foraging area. These findings agree with those of Willis (1967) and Palmer (1976). Beetles leave the habitat patch through similar habitat (ie., open road) and not through unsuitable habitat (ie., forest).

Within the habitat patch, the beetles move freely and are capable of moving large distances in a short time. The beetles do not seem to remain in a single foraging site as has been found for some individuals of *C. patruela* (Clark, pers. com.). The data was analyzed for sexual differences, but none were found. The movement patterns of the beetles probably reflect their foraging strategy; if prey items are numerous the beetles are conservative and hardly move at all, whereas if prey items are few, the beetles move frequently.

Impact of Man

C. sexguttata. Most of the eastern hardwood forests have been decimated by man (Eyre, 1968) which has undoubtedly reduced the numbers of C. sexguttata. However, in the Oak Hickory forests that remain, man has created microhabitats by making paths and roads, which probably have brought about larger local populations and greater dispersability. Localized extinctions within disturbed habitats are probably replaced more quickly than extinctions in undisturbed habitats.

C. denikei. At this time, man's impact on the habitat of C. denikei is limited as Northwestern Ontario is largely unsettled. As with C. sexguttata, man has created microhabitats by making logging and pipeline roads.

C. patruela. In some respects, man's impact on C. patruela is probably similar to that of C. sexguttata; however, C. patruela seems to be more sensitive to man's encroachment. Most recent collections of C. patruela are from the northwestern part of its range where man has had less impact on the environment. Of the approximately 900+ specimens of C. patruela examined in this study, only three records from east of Indiana were collected after 1945. Hood (1903) noted that C. patruela had been common around Boston, but that by 1903 it was rare or extinct in that area. The population of C. patruela at Constance Bay, Ontario is now extinct, and no other populations have been found in Canada.

C. p. consentanea. The populations on Long Island are now certainly extinct. Within the Pine Barrens of New Jersey the beetles are still found, although Boyd (1973) notes that they are local and rare. Most of the material that I examined had been collected before 1930. It is likely that this subspecies is also sensitive to man's presence, and that they owe their continued existence to the fact that the Pine Barrens are largely unsuitable for logging, farming, or habitation.

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Appendix 1: Alphabetic listing of resource areas showing soil type and abundance of _C. sexguttata_ and _C. denikei_. Different soils within each area are scored for abundance of beetles. The abundance score is based on the number of collection records relative to the total area of the soil type within a given state and resource area.

Within soil types abundance is indicated as:

Ab = Absent

R = Rare

F = Few

S = Some

M = Many

C. *denikei*

Canadian Shield

Ontario and Manitoba   Figure 78

Rock land plus Cryoboralfs	S
Histols plus Cryoboralfs	R
Cryorthods plus Rock land	Ab

C. *sexguttata*

Aa   Aroostook Area

Maine   Figure 38

Haplorthods plus Fragiorthods	Ab

Acf   Atlantic Coastal Flatwoods

Virginia   Figure 51

Histols	F
Ochraquults plus Glossaqualfs and Paleudults	Ab

North Carolina   Fig. 53

Histols	R
Ochraquults plus Glossaqualfs and Paleudults	Ab
Haplaquods plus Quartzipsamments	Ab

South Carolina Fig 55

Haploquods plus Quartzipsamments	R
Humaquepts plus Hydraquents and Psammaquents	R
Ochraquults plus Hapludults and Paleudults	Ab
Ochraquults plus Quartzipsamments	Ab

Florida Fig. 57

Haplaquods plus Quartzipsamments	Ab
Quartzipsamments	Ab

Georgia Fig. 54

Quartzipsamments plus Ochraquults	Ab
Ochraquults plus Quartzipsamments	Ab

Apm Eastern Allegheny Plateau and Mountains

Pennsylvania Fig. 48

Dystrochrepts plus Hapludalfs and Hapludults	S
Dystrochrepts	R

Maryland Fig. 50

Dystrochrepts plus Hapludalfs and Hapludults	R

West Virginia Fig. 67

Dystrochrepts plus Hapludults and Rock land	Ab

Ar Appalachian Region

Nova Scotia Fig. 43

Haplorthods plus Haplaquepts	S
Haplorthods plus Haplaquepts and Udorthents	F
Haplorthods plus Dystrochrepts	Ab
Cryoboralfs plus Haplorthods	Ab

New Brunswick Fig. 43	
Haplorthods	R
Haplorthods plus Dystrochrepts	Ab
Haplorthods plus Cryaquepts	Ab
Quebec Fig. 43	
Haplorthods plus Cryaquepts	Ab
Haplorthods	Ab
Haplorthods plus Rock land	Ab
Av Arkansas Valley and Ridges	
Arkansas Fig. 74	
Argiudolls plus Albaqualfs and Paleudolls	S
Hapludults plus Hapludalfs and Rock land	S
Oklahoma Fig. 72	
Argiudolls plus Albaqualfs and Paleudolls	Ab
Bh Bluestem Hills	
Kansas Fig. 71	
Hapludolls plus Argiustolls and Argiudolls	F
Bm Boston Mountains	
Arkansas Fig. 74	
Hapludults plus Hapludalfs and Rock land	S
Oklahoma Fig. 72	
Hapludults plus Hapludalfs and Rock land	Ab
Bp Mississippi Blackland Prairie	
Mississippi Fig. 75	
Paleudults plus Fragiudults	F

Chromuderts plus Eutrochrepts	R
Hapludalfs plus Ochraqualfs	F
Br Blue Ridge	
Pennsylvania Fig. 48	
Paleudalfs plus Hapludalfs and Dystrochrepts	Ab
Hapludults	Ab
West Virginia Fig. 67	
Paleudalfs plus Hapludalfs and Dystrochrepts	Ab
Hapludults plus Paleudults	F
Virginia Fig. 51	
Hapludults	F
Hapludults plus Dystrochrepts	F
Tennessee Fig. 68	
Hapludults plus Paleudults	Ab
Hapludults plus Paledults and Dystrochrepts	F
North Carolina Fig. 53	
Hapludults	F
Hapludults plus Dystrochrepts	F
Hapludults plus Paleudults and Dystrochrepts	F
South Carolina Fig. 55	
Hapludults plus Dystrochrepts	M
Georgia Fig. 54	
Hapludults plus Dystrochrepts	M
Cap Central Allegheny Plateau	
Ohio Fig. 66	
Dystrochrepts plus Hapludalfs and Hapludults	F

Pennsylvania Fig. 48	
Dystrochrepts plus Hapludalfs and Hapludults	R
Hapludults	M
West Virginia Fig. 67	
Dystrochrepts plus Hapludalfs and Hapludults	Ab
Hapludults	F
Cc Central Claypan Areas	
Illinois Fig. 60	
Albaqualfs plus Natraqualfs and Fragiudalfs	R
Missouri Fig. 73	
Albaqualfs plus Hapludalfs	R
Cgp Central Great Plains	
Kansas Fig. 71	
Argiustolls plus Paleustolls	Ab
Argiustolls plus Ustipsamments and Ustochrepts	Ab
Nebraska Fig. 70	
Argiustolls	R
Argiustolls plus Ustorthents	Ab
Oklahoma Fig. 72	
Argiustolls plus Paleustolls and Ustorthents	Ab
Argiustolls plus Ustipsamments and Ustochrepts	Ab
Cgsh Carolina and Georgia Sand Hills	
South Carolina Fig. 55	
Paleudults plus Quartzipsamments	F

Georgia Fig. 54

Paleudults plus Quartzipsamments	F

Cl Long Island and Cape Cod Coastal Lowland

Massachusetts Fig. 39

Haplorthods	R

New York Fig. 44

Dystrochrepts	M

Cpm Cumberland Plateau and Mountains

Kentucky Fig. 69

Dystrochrepts plus Rock land and Hapludults	F
Hapludults plus Dystrochrepts and Rock land	Ab

Tennessee Fig. 68

Dystrochrepts plus Rock land and Hapludults	F
Hapludults plus Dystrochrepts and Rock land	F

Cs Canadian Shield

Quebec Fig. 43

Haplaquepts plus Dystrochrepts	S
Haplorthods plus Haplaquepts and Rock land	R
Haplorthods plus Rock land	Ab
Dystrochrepts	Ab

Ontario Fig. 42

Eutrochrepts plus Hapludalfs and Haplorthods	F
Eutrochrepts	R
Haplorthods plus Rock land	Ab

Csl	Central St. Lawrence Lowland	
	Quebec Fig. 43	
	Haplaquepts plus Dystrochrepts	M
	Humaquepts plus Haplaquolls	F
	Cryochrepts	Ab
	Dystrochrepts plus Rock land	Ab
	Ontario Fig. 42	
	Haplaquepts plus Dystrochrepts	M
	Dystrochrepts plus Rock land	F
	Eutrochrepts	R
	Haplorthods plus Rock land	Ab
Ct	Cross Timbers	
	Oklahoma Fig. 72	
	Argiudolls plus Haplaquolls	F
	Hapludolls plus Argiustolls and Argiudolls	F
	Argiustolls plus Ustipsamments and Ustochrepts	Ab
	Ustochrepts plus Haplustaffs	Ab
Cv	Connecticut Valley	
	New Hampshire Fig. 37	
	Haplorthods plus Fragiorthods	S
	Vermont Fig. 37	
	Haplorthods plus Fragiorthods	R
	Massachusetts Fig. 39	
	Haplorthods plus Haplaquepts and Fragiochrepts	S
	Connecticut Fig. 40	
	Haplorthods plus Haplaquepts and Fragiochrepts	S

Eotp Eastern Ohio Till Plain

Ohio Fig. 66

Fragiudalfs plus Ochraqualfs and Fragiaqualfs	S
Hapludalfs plus Ochraqualfs	Ab

Pennsylvania Fig. 48

Hapludalfs plus Ochraqualfs	Ab
Fragiochrepts plus Fragiaquepts and Dystrochrepts	F

Clp Central Loess Plains

Kansas Fig. 71

Hapludolls	R
Hapludolls plus Argiustolls and Argiudolls	R
Argiustolls	Ab

Cmv Central Mississippi Valley Wooded Slopes

Illinois Fig. 60

Haplaquolls plus Udifluevents, Hapludolls and Hapludalfs	F
Hapludalfs plus Argiudolls	R

Indiana Fig. 61

Haplaquolls plus Udifluevents, Hapludolls and Hapludalfs	F
Fragiudalfs plus Hapludalfs	Ab

Missouri Fig. 73

Haplaquolls plus Udifluevents, Hapludolls and Hapludalfs	M
Hapludalfs plus Argiudolls	R

Cp Cherokee Prairies

Kansas Fig. 70

Argiudolls plus Albaqualfs and Paleudolls	F

Argiudolls plus Argiaquolls	F
Missouri Fig. 73	
Argiudolls plus Argiaquolls	R
Albaqualfs plus Argiabolls and Argiudolls	Ab
Cpm Cumberland Plateau and Mountains	
Virginia Fig. 51	
Dystrochrepts plus Rock land and Hapludults	Ab
West Virginia Fig. 67	
Dystrochrepts plus Rock land and Hapludults	Ab
Hapludults plus Paleudults	F
Fb Michigan Fruit Belt	
Michigan Fig. 59	
Haplorthods plus Glossoboralfs	R
Haplorthods plus Glossoboralfs and Udipsamments	Ab
Fs Florida Subtropical	
Florida Fig. 57	
Haplaquods plus Quartzipsamments	Ab
Histols	Ab
Quartzipsamments plus Paleudults	Ab
Gap Glaciated Allegheny Plateau and Catskill Mountains	
New York Fig. 44	
Fragiochrepts plus Dystrochrepts (both stoney)	M
Fragiochrepts plus Fragiaquepts and Dystrochrepts	R
Pennsylvania Fig. 48	
Fragiochrepts plus Dystrochrepts	F

Fragiochrepts plus Fragiaquepts and Dystrochrepts R

Gcf Gulf Coast Flatwoods

Florida Fig. 57

Haplaquods plus Quartzipsamments Ab

Paleudults plus Quartzipsamments Ab

Alabama Fig. 56

Haplaquepts plus Ochraquults, Paleudults and Hapludults Ab

Mississippi Fig. 75

Paleudults plus Fragiudults R

Haplaquepts plus Ochraquults, Paleudults and Hapludults Ab

Haplaquepts plus Psammaquents, Haplaquents and Haplaquods Ab

Louisiana Fig. 77

Ochraquults plus Glossaqualfs and Paleudults R

GCM Gulf Coast Marsh

Louisiana Fig. 77

Ochraquults plus Glossaqualfs and Paleudults R

Haplaquolls plus Udipsamments and Humaquepts Ab

Histosols Ab

Gcp Gulf Coast Prairies

Texas Fig. 76

Haplaquolls plus Udipsamments and Humaquepts Ab

Haplohumults plus Haplumbrepts Ab

Glb Northern Minnesota Glacial Lake Basins

Minnesota Fig. 62

Histosols plus Psammaquents and Haplorthods Ab

Gp Grand Prairie

Oklahoma Fig. 72

Argiudolls plus Albaqualfs and Paleudolls	F

Gsp Great Bend Sand Plains

Kansas Fig. 71

Argiudolls plus Argiustolls, Argiuquolls and Ustipsamments	Ab

Hlp Erie-Huron Lake Plain

Michigan Fig. 58

Haplaquepts plus Haplaquods	S
Hapludalfs plus Haplaquolls and Udipsamments	S
Ochraqualfs plus Haplaquepts and Hapludalfs	R

Ohio Fig. 66

Hapludalfs plus Haplaquolls and Udipsamments	R
Ochraqualfs plus Haplaquepts and Hapludalfs	Ab

Hrp Highland Rim and Pennyroyal

Indiana Fig. 61

Paleudalfs plus Hapludalfs and Dystrochrepts	Ab

Kentucky Fig. 69

Paleudalfs plus Hapludalfs and Dystrocrepts	F
Hapludults	R
Hapludults plus Dystrochrepts and Rock land	Ab
Paleudults plus Hapludults and Fragiudults	R
Dystrochrepts plus Rock land and Hapludults	R

Tennessee Fig. 68

Fragiudults plus Paleudults	Ab

Hapludults plus Dystrochrepts and Rock land	Ab
Hapludults plus Hapludalfs and Rock land	R
Paleudults plus Hapludults and Fragiudults	R
Alabama Fig. 56	
Fragiudults plus Paleudults	Ab
Paleudults plus Hapludults and Fragiudults	Ab

Htp Northern Illinois and Indiana Heavy Till Plain

Illinois Fig. 60	
Hapludalfs plus Hapluquolls	M
Hapludalfs plus Rock land	R
Argiudolls plus Haplaquolls	Ab
Indiana Fig. 61	
Argiudolls plus Haplaquolls	Ab

Idl Iowa and Illinois Deep Loess and Drift

Illinois Fig. 60	
Argiudolls plus Haplaquolls	Ab
Argiudolls plus Hapludalfs and Haplaquolls	Ab
Hapludalfs plus Rock land	F
Iowa Fig. 64	
Argiudolls	R
Haplaquolls plus Udifluevents, Hapludolls and Hapludalfs	S

ITP Southern Illinois and Indiana Thin Loess and Till Plain

Illinois Fig. 60	
Albaqualfs plus Natraqualfs and Fragiudalfs	Ab

Indiana Fig. 61

Fragiudalfs plus Hapludalfs F

Fragiudalfs plus Hapludalfs and Rock land F

Kb Kentucky Bluegrass

Ohio Fig. 66

Hapludalfs plus Paleudalfs, Hapludults and Hapludolls R

Kentucky Fig. 69

Hapludalfs plus Paleudalfs, Hapludults and Hapludolls R

Ks Kentucky and Indiana Sandstone

Indiana Fig. 61

Paleudalfs plus Hapludalfs and Dystrochrepts Ab

Hapludults plus Dystrochrepts and Rock land S

Kentucky Fig. 69

Hapludults plus Dystrochrepts and Rock land R

Fragiudalfs plus Hapludalfs Ab

Ksh Central Kansas Sandstone Hills

Kansas Fig. 71

Hapludolls plus Argiudolls and Argiustolls R

Argiustolls Ab

macp Mid-Atlantic Coastal Plain

Maryland Fig. 50

Ochraquults plus Umbraquults and Tidal Marsh Ab

Delaware Fig. 50

Ochraquults plus Umbraquults and Tidal Marsh Ab

Mdl Iowa and Missouri Deep Loess Hills

Nebraska Fig. 70

Haplaquolls plus Udifluevents, Hapludolls and Hapludalfs	M

Iowa Fig. 64

Haplaquolls plus Udifluevents, Hapludolls and Hapludalfs	R
Hapludolls plus Argiudolls, Udorthents and Hapludalfs	Ab
Hapludolls	Ab

Kansas Fig. 71

Haplaquolls plus Udifluevents, Hapludolls and Hapludalfs	F

Missouri Fig. 73

Haplaquolls plus Udifluevents, Hapludolls and Hapludalfs	F
Hapludolls plus Argiudolls, Udorthents and Hapludalfs	Ab

Mdp Southern Michigan and Northern Indiana Drift Plain

Indiana Fig. 61

Udipsamments plus Hapludalfs and Haplaquolls	R

Mdl Southern Michigan and Northern Illinois Drift Plain

Michigan Fig. 58

Hapludalfs plus Argiudolls	S
Hapludalfs plus Argiuquolls	F
Haplorthods plus Glossoboralfs	R
Haplorthods plus Glossoboralfs and Rock land	Ab

Mep Michigan Eastern Upper Penninsula Sandy Drift

Michigan Fig. 58

Haplorthods plus Glossoboralfs	Ab

Histosols plus Psammaquents and Haplorthods	Ab
Eutroboralfs plus Haplaquepts	Ab
Psammaquents plus Sideraquods and Histols	R

Mgd Northern Michigan Gray Drift

Michigan Fig. 58

Eutroboralfs	R
Udipsamments plus Eutroboralfs and Haploboralls	R

Mhtp Iowa and Missouri Heavy Till Plain

Iowa Fig. 64

Argiudolls plus Argiaquolls and Argiabolls	F

Missouri Fig. 73

Argiudolls plus Argiaquolls and Argiabolls	Ab
Argiudolls	Ab

Mitp Central Iowa and Minnesota Till Prairies

Minnesota Fig. 62

Hapludolls plus Haplaquolls	Ab
Hapludalfs plus Argiudolls	R

Iowa Fig. 64

Hapludolls plus Haplaquolls	F

Msd Northern Michigan and Wisconsin Sandy Drift

Michigan Fig. 58

Glossoboralfs plus Eutroboralfs	F
Haplorthods plus Glossoboralfs	S
Haplorthods plus Glossoboralfs and Udipsamments	Ab

Histosols plus Psammaquents and Haplorthods Ab

Wisconsin Fig. 63

Haplothorods Ab

Mso Minnesota Sandy Outwash

Minnesota Fig. 62

Haploborolls Ab

Eutroboralfs Ab

Udipsamments plus Eutroboralfs and Haploborolls Ab

Udipsamments plus Histols F

Mtp Eastern Iowa and Minnesota Till Prairies

Iowa Fig. 64

Hapludolls plus Haplaquolls Ab

Minnesota Fig. 62

Argiudolls plus Hapludalfs and Haplaquolls R

Nar Northern Appalachian Ridges and Valleys

Pennsylvania Fig. 48

Dystrochrepts plus Paleudalfs and Hapludults S

Paleudalfs plus Hapludalfs and Dystrochrepts Ab

Maryland Fig. 50

Dystrochrepts plus Paleudalfs and Hapludults Ab

Paleudalfs plus Hapludults and Dystrochrepts Ab

West Virginai Fig. 67

Dystrochrepts plus Rock land and Hapludults F

Virginia Fig. 51

Dystrochrepts plus Paleudalfs and Hapludults	Ab
Paleudalfs plus Hapludults and Dystrochrepts	R

Nb Nashville Basin

Tennessee Fig. 68

Paleudalfs plus Hapludults and Rock land	R

Ncp Northern Coastal Plain

Maryland Fig. 50

Hapludults plus Fragiudults	M
Hapludults plus Ochraquults	R

New Jersey Fig. 46

Hapludults plus Ochraquults	S
Ochraquults plus Umbraquults and Tidal Marsh	Ab

Nkl Nebraska and Kansas Loess Drift Hills

Nebraska Fig. 70

Argiudolls plus Argiaquolls	F

Kansas Fig. 71

Argiudolls plus Argiaquolls	S

Nm Northeastern Mountains

Maine Fig. 38

Haplorthods plus Rock land	Ab
Haplorthods plus Fragiorthods	R

New Hampshire Fig. 37

Haplorthods plus Fragiorthods and Rock land	M

Vermont Fig. 37

Haplorthods plus Fragiorthods M

New York Fig. 44

Haplorthods plus Fragiorthods S

Haplorthods plus Fragiorthods and Rock land F

Nmv Northern Mississippi Valley Loess Hills

Minnesota Fig. 62

Hapludalfs plus Rock land M

Wisconsin Fig. 63

Hapludalfs plus Rock land S

Argiudolls plus Hapludalfs and Hapluquolls S

Iowa Fig. 64

Hapludalfs plus Rock land S

Hapludalfs plus Argiudolls F

Nneu New England and Eastern New York Upland, Northern Part

Maine Fig. 38

Haplorthods plus Haplaquepts and Ochraqualfs S

Haplorthods plus Fragiorthods Ab

New Hampshire Fig. 37

Haplorthods plus Fragiorthods M

Vermont Fig. 37

Haplorthods plus Fragiorthods F

Np Northern Piedmont

Pennsylvania Fig. 48

Hapludults plus Dystrochrepts	S
Paleudalfs plus Hapludalfs and Dystrochrepts	R
Maryland Fig. 50	
Hapludults plus Dystrochrepts	S
Paleudalfs plus Hapludalfs and Dystrochrepts	Ab
Virginia Fig. 51	
Hapludults	R
Paleudalfs plus Hapludalfs and Dystrochrepts	R
Nsh Nebraska Sand Hills	
Nebraska Fig. 70	
Hapludolls	R
Arguistolls	Ab
Argiustolls plus Ustipsamments	Ab
Argiustolls plus Ustorthents	Ab
Haplustolls plus Ustorthents	Ab
Ob Ozark Border	
Missouri Fig. 73	
Paleudults plus Fragiudults	Ab
Hapludalfs plus Fragiudalfs	Ab
Oh Ozark Highland	
Oklahoma Fig. 72	
Paleudults plus Fragiudults	R
Missouri Fig. 73	
Paleudults plus Fragiudults	F

Hapludults plus Hapludalfs and Rock land	Ab
Paleudults plus Hapludults and Fragiudults	Ab
Arkansas Fig. 74	
Paleudults plus Fragiudults	S
Hapludults plus Hapludalfs and Rock land	Ab
Om Ouichita Mountains	
Oklahoma Fig. 72	
Hapludults plus Hapludalfs and Dystrochrepts	R
Arkansas Fig. 74	
Hapludults plus Hapludalfs and Dystrochrepts	R
Hapludults	S
Op Ontario Plain and Finger Lakes Region	
New York Fig. 44	
Fragiochrepts plus Fragiaquepts and Dystrochrepts	Ab
Hapludalfs	M
Hapludalfs plus Ochraqualfs	F
Otp Indiana and Ohio Till Plain	
Illinois Fig. 60	
Hapludalfs plus Rock land	R
Indiana Fig. 61	
Hapludalfs	S
Hapludalfs plus Argiaquolls	F
Eutrochrepts	Ab
Fragiudalfs plus Fragiaqualfs and Haplaquepts	Ab

Ohio Fig. 66	
Hapludalfs plus Argiaquolls	S
Michigan Fig. 58	
Hapludalfs plus Argiaquolls	R
Scp Southern Coastal Plain	
Florida Fig. 57	
Paleudults	S
Alabama Fig. 56	
Hapludults	F
Paleudults	Ab
Paleudults plus Ochraquults and Fragiaquults	Ab
Haplaquepts plus Ochraquults, Paleudults and Hapludults	R
Eutrochrepts plus Chromuderts	Ab
Quartzipsamments plus Umbraquults	Ab
Mississippi Fig. 75	
Hapludults	R
Paleudults plus Fragiudults	S
Louisiana Fig. 77	
Paleudults plus Fragiudults	R
Fragiudalfs plus Hapludalfs	S
Slcp St. Lawrence-Champlain Plain	
New York Fig. 44	
Hapludalfs	Ab
Hapludalfs plus Rock land	R
Eutrochrepts plus Dystrochrepts	Ab

Fragiochrepts plus Fragiaquepts and Dystrochrepts	Ab
Fragiorthods	Ab
Haplorthods (sandy)	Ab
Vermont Fig. 37	
Haplorthods plus Fragiorthods	F
Eutrochrepts plus Dystrochrepts	Ab
Hapludalfs plus Rock land	Ab
Pb Pine Barrens	
New Jersey Fig. 46	
Haplorthods plus Quartzipsamments and Hapludults	Ab
Rp Central Rolling Red Prairie	
Kansas Fig. 71	
Argiustolls plus Paleustolls	Ab
Oklahoma Fig. 72	
Argiustolls plus Paleustolls	Ab
Argiustolls plus Paleustolls and Ustorthents	Ab
Ustorthents plus Argiustolls and Argiudolls	R
Rrp Ventral Rolling Red Plains	
Kansas Fig. 71	
Ustorthents plus Argiustolls and Argiudolls	Ab
Rrv Red River Valley of the North	
Minnesota Fig. 62	
Calciaquolls	Ab
Haplaquols plus Calciaquolls	Ab
Haplaquols plus Histols and Haplaquepts	Ab

Rtp Rolling Till Prairie

Minnesota Fig. 62

Haploborolls plus Haplaquolls and Calciaquolls	Ab
Hapludolls plus Eutrochrepts and Udifluevents	Ab

Sa Southern Appalachian Ridges and Valleys

Virginia Fig. 51

Hapludults plus Paleudults	S
Dystrochrepts plus Rock land and Hapludults	Ab
Paleudalfs plus Hapludalfs and Dystrochrepts	Ab

Tennessee Fig. 68

Hapludults plus Paleudults	Ab
Hapludults plus Paleudults and Dystrochrepts	R
Paleudults plus Rhodudults	R
Eutrochrepts	Ab

North Carolina Fig. 53

Paleudults plus Rhodudults	R

Alabama Fig. 56

Paleudults	R
Paleudults plus Rhodudults	Ab

Scp Southern Coastal Plain

Virginia Fig. 51

Hapludults plus Fragiudults	S
Paleudults plus Hapludults	F

Tennessee Fig. 68

Fragiudults plus Plaeudults	Ab

Paleudults plus Fragiudults	S
Paleudults plus Rhodudults	Ab
North Carolina Fig. 53	
Ochraquults plus Glossaqualfs and Paleudults	Ab
Hapludults	R
Paleudults plus Hapludults	Ab
Georgia Fig. 54	
Paleudults	F
Paleudults plus Hapludults	Ab
Paleudults plus Quartzipsamments	Ab
Quartzipsamments plus Paleudults	Ab
Slp Superior Lake Plain	
Michigan Fig. 58	
Eutroboralfs plus Haplaquepts	Ab
Wisconsin Fig. 63	
Eutroboralfs plus Haplaquepts	Ab
Sm Sand Mountain	
Alabama Fig. 56	
Hapludults	R
Dystrochrepts plus Rock land and Hapludults	Ab
Georgia Fig. 54	
Dystrochrepts plus Rock land and Hapludults	Ab
Smv Southern Mississippi Valley Alluvium	
Missouri Fig. 73	
Haplaquolls plus Udifluevents, Hapludolls and Hapludalfs	R

Haplaquepts plus Ochraqualfs, Haplaquolls and Natraqualfs	Ab
Hapludalfs plus Fragiudalfs	Ab
Tennessee Fig. 68	
Haplaquolls plus Udifluevents, Hapludolls and Hapludalfs	R
Haplaquepts plus Ochraqualfs, Halaquolls and Natraqualfs	Ab
Arkansas Fig. 74	
Haplaquepts plus Ochraqualfs, Haplaquolls and Natraqualfs	R
Mississippi Fig. 75	
Haplaquepts plus Ochraqualfs, Haplaquolls and Natraqualfs	R
Ochraqualfs plus Hapludalfs	Ab
Louisiana Fig. 77	
Haplaquepts plus Ochraqualfs, Haplaquolls and Natraqualfs	R

Smvu Southern Mississippi Valley Silty Uplands

Kentucky Fig. 69	
Fragiudalfs plus Hapludalfs	Ab
Hapludalfs plus Fragiudalfs	Ab
Hapludalfs plus Hapludults	Ab
Tennessee Fig. 68	
Fragiudalfs plus Hapludalfs	F
Hapludalfs plus Fragiudalfs	R
Hapludalfs plus Hapludults	S
Arkansas Fig. 74	
Albaqualfs plus Hapludalfs	Ab
Fragiudalfs plus Natraqualfs	Ab
Hapludalfs plus Fragiudalfs	R

Mississippi Fig. 75	
Fragiudalfs	R
Fragiudalfs plus Hapludalfs	F
Hapludalfs plus Fragiudalfs	F
Louisiana Fig. 77	
Fragiudalfs plus Glossaqualfs	R

Sneu New England and Eastern New York Upland, Southern Part

New Hampshire Fig. 37	
Haplorthods plus Fragiorthods	S
Haplorthods plus Haplaquepts and Ochraqualfs	F
Massachusetts Fig. 39	
Haplorthods plus Fragiorthods	M
Eutrochrepts plus Dystrochrepts	R
Rhode Island Fig. 41	
Haplorthods	M
Connecticut Fig. 40	
Haplorthods	M
New York Fig. 44	
Dystrochrepts	F
Dystrochrepts plus Fragiochrepts and Hapludalfs	F
Eutrochrepts plus Dystrochrepts	Ab
Fragiochrepts plus Fragiaquepts and Dystrochrepts	F
New Jersey Fig. 46	
Dystrochrepts plus Fragiochrepts and Hapludalfs	Ab
Dystrochrepts plus Rock land and Hapludults	F

Hapludults	F
Fragiochrepts plus Fragiaquepts and Dystrochrepts	M
Sp Southern Piedmont	
Virginia Fig. 51	
Hapludults	F
North Carolina Fig. 53	
Hapludults	S
Paleudults plus Hapludults	Ab
South Carolina Fig. 55	
Hapludults	R
Paleudults	R
Georgia Fig. 54	
Hapludults	S
Hapludults plus Dystrochrepts	M
Alabama Fig. 56	
Hapludults	R
Paleudults plus Rhodudults	Ab
Dystrochrepts plus Rock land and Hapludults	Ab
Ssp Superior Stoney and Rocky Loamy Plains	
Michigan Fig. 58	
Haplorthods plus Fragiorthods	R
Haplorthods plus Rock land	Ab
Wisconsin Fig. 63	
Haplorthods plus Fragiorthods	R
Minnesota Fig. 62	
Haplorthods plus Rock land	Ab

	Eutroboralfs plus Fragioboralfs	Ab
Tb	Southwestern Michigan Fruit and Truck Belt	
	Michigan Fig. 58	
	Hapludalfs plus Argiudolls	R
	Udipsamments plus Hapludalfs and Haplaquolls	F
Tbp	Texas Blackland Prairie	
	Texas Fig. 76	
	Paleustalfs plus Haplustalfs	F
	Pellusterts plus Chromusterts	F
Tcb	Texas Central Basin	
	Texas Fig. 76	
	Chromusterts plus Paleustalfs	Ab
Tlt	Central Wisconsin and Minnesota Thin Loess and Till	
	Wisconsin Fig. 63	
	Fragiudalfs plus Fragiochrepts	F
	Hapludalfs plus Haplaquolls and Glossoboralfs	F
	Minnesota Fig. 62	
	Hapludalfs plus Haplaquolls and Glossoboralfs	F
	Udipsamments plus Hapludalfs and Haplaquolls	F
Utp	Loess Uplands and Till Prairies	
	Nebraska Fig. 70	
	Ariudolls plus Argiaquolls	R
	Hapludolls	Ab

Hapludolls plus Ustorthents	Ab
Wap Western Allegheny Plateau	
Ohio Fig. 66	
Dystrochrepts plus Hapludalfs and Hapludults	F
Dystrochrepts plus Rock land and Haludults	F
Wcp Western Coastal Plain	
Arkansas Fig. 74	
Fragiudults plus Paleudults	F
Paleudults plus Fragiudults	R
Paleudults plus Hapludults	S
Paleudults plus Paleudalfs, Hapludults and Hapludalfs	F
Hapludolls plus Eutrochrepts and Udifluevents	Ab
Haplaquepts plus Psammaquents, Haplaquents and Haplaquods	Ab
Albaqualfs plus Hapludalfs	Ab
Oklahoma Fig. 72	
Paleudults plus Paleudalfs, Hapludults and Hapludalfs	F
Louisiana Fig. 77	
Paleudults plus Paleudalfs, Hapludults and Hapludalfs	M
Texas Fig. 76	
Paleudults plus Paleudalfs, Hapludults and Hapludalfs	S
Paleudults	F
Paleustalfs plus Haplustalfs	Ab
Wct West Cross Timbers	
Texas Fig. 76	
Haplustolls plus Pellusterts	Ab

Wd Northern Wisconsin Drift Plain

Wisconsin Fig. 63

Haplorthods	Ab
Haplorthods plus Fragiorthods	Ab
Hapludalfs plus Haplaquolls	F

Wdp Southern Wisconsin and Northern Illinois Drift Plain

Wisconsin Fig. 63

Hapludalfs plus Haplaquolls	F
Hapludalfs plus Haplaquolls and Argiudolls	R

Illinois Fig. 60

Hapludalfs plus Haplaquolls and Argiudolls	R
Argiudolls plus Hapludalfs and Haplaquolls	R

Wsl Western St. Lawrence Lowland

Ontario Fig. 42

Hapludalfs plus Dystrochrepts	M
Hapludalfs	S
Haplaquolls	F
Eutrochrepts	R

Appendix II. Explanation of soil names. Definitions are taken from the National Atlas of the United States of America (1970). For more accurate definitions see Soil Survey Staff (1960, 1967).

Alfisols

Soils that are medium to high in bases (base saturation at pH 8.2) and have a gray to brown surface horizon and subsurface horizons of clay accumulation: usually moist but during the warm season of the year some are dry part of the time.

Aqualfs - Seasonally wet Alfisols that have mottles, iron manganese concretions or gray colors.

Albaqualfs - Aqualfs that have a bleached upper horizon and change abruptly in texture into an underlying horizon of clay accumulation.

Fragiaqualfs - Aqualfs that have a dense brittle, but not indurated horizon.

Glossaqualfs - Aqualfs that have tongues of an upper bleached horizon in an underlying horizon of clay accumulation.

Natraqualfs - Aqualfs that have a subsurface horizon of clay accumulation with alkali (sodium).

Ochraqualfs - Aqualfs that change gradually in texture into the underlying horizon.

Boralfs - Alfisols of cool to cold regions.

Eutroboralfs - Boralfs that have a subsurface horizon high in bases and a horizon that is dry for short periods in most years.

Glossoboralfs - Boralfs that are always moist or are low in bases. They usually have tongues of an upper bleached horizon in an underlying subsurface horizon of clay accumulation.

Udalfs - Alfisols that are in temperate to tropical regions. Soils usually moist but during the warm season of the year may be intermittently dry in some horizons for short periods.

Fragiudalfs - Udalfs that have a dense brittle but not indurated horizon usually below a horizon in which clay has accumulated.

Hapludalfs - Udalfs that have a subsurface horizon of clay accumulation that is relatively thin or brownish.

Paleudalfs - Udalfs that have a thick reddish horizon of clay accumulation.

Ustalfs - Alfisols that are in temperate to tropical regions. Soils mostly reddish brown; during the warm season of the year, they are intermittently dry for long periods.

Haplustalfs - Ustalfs that have a subsurface horizon of clay accumulation that is thin or brownish.

Paleustalfs - Ustalfs that have an indurated horizon cemented by carbonates or a horizon having one or both of the following: A thick reddish clay accumulation or a distribution that is clayey in the upper part and abruptly changes in texture into an overlying horizon.

Entisols

Soils that have no pedogenic horizons.

Aquents - Entisols that are either permanently wet or are seasonally wet and that have mottles or gray colors.

Hydraquents - Aquents that are permanently wet, have textures of loamy very fine sand or finer, and offer little resistance to applied weight.

Psammaquents - Aquents that have textures of loamy fine sand or coarser.

Fluevents - Entisols that have organic matter content that decreases irregularly with depth; formed in loamy or clayey alluvial deposits.

Udifluevents - Fluevents that are usually moist.

Orthents - Loamy or clayey Entisols that have a regular decrease in organic matter content with depth.

Ustorthents - Orthents that during the warm season of the year are intermittently dry for long periods.

Psamments - Entisols that have textures of loamy fine sand or coarser.

Quartzipsamments - Psamments that consist almost entirely of minerals highly resistant to weathering, mainly quartz.

Udipsamments - Psamments that contain easily weatherable minerals; they are usually moist in all parts of the soil in most years.

Ustipsamments - Psamments that contain easily weatherable minerals; during the warm season of the year, they are intermittently dry for long periods.

Histolsols

Wet organic (peat and muck) soils; includes soils in which the decomposition of the plant residues ranges from highly decomposed to not decomposed; formed in swamps and marshes.

Inceptisols

Soils that have weakly differentiated horizons; materials in the soil have been altered or removed but have not accumulated. These soils are usually moist, but during the warm season of the year some are dry part of the time.

Aquepts - Seasonally wet Inceptisols that have an organic surface horizon, sodium saturation, mottles, or gray colors.

Fragiaquepts - Aquepts that have a dense brittle, but not indurated horizon.

Haplaquepts - Aquepts that have either a light coloured or thin black surface horizon.

Humaquepts - Aquepts that have an acid dark surface horizon.

Ochrepts - Inceptisols that have formed in materials with crystalline clay minerals, have light coloured surface horizons, and have altered subsurface horizons that have lost mineral materials.

Dystrochrepts - Ochrepts that are usually moist and low in bases and have no free carbonates in the subsurface horizons.

Eutrochrepts - Ochrepts that are usually moist and are either high in bases, have free carbonates in the subsurface horizons, or both.

Fragiochrepts - Ochrepts that have a dense brittle but not indurated horizon.

Mollisols

Soils that have nearly black friable organic-rich surface horizons high in bases; formed mostly in subhumid and semiarid warm to cold climates.

Albolls - Mollisols of flat places and high closed depressions. They have a seasonal perched water table and a nearly black surface horizon underlain by a bleached mottled horizon over a horizon of clay accumulation that has mottles or gray colors.

Agrialbolls - Albolls that have a horizon of clay accumulation without alkali (sodium).

Aquolls - Seasonally wet Mollisols that have a thick nearly black surface horizon and gray subsurface horizons.

Agriaquolls - Aquolls that have a subsurface horizon in which clay has accumulated.

Calciaquolls - Aquolls that have a horizon near the surface in which large amounts of calcium carbonate have accumulated.

Haplaquolls - Aquolls that have horizons in which materials have been altered or removed but no clay or calcium carbonate has accumulated.

Borolls - Mollisols of cool and cold regions. Most Borolls have a black surface horizon.

Haploborolls - Borolls of cool regions. They have no horizons of clay accumulation.

Rendolls - Mollisols with subsurface horizons that have large amounts of calcium carbonate but no accumulation of clay.

Udolls - Mollisols of temperate climates. Udolls are usually moist and have no horizon in which either calcium carbonate or gypsum has accumulated.

Argiudolls - Udolls that have a subsurface horizon in which clay has accumulated.

Hapludolls - Udolls that have horizons from which some materials have been removed or altered but have no subsurface horizon of clay accumulation.

Paleudolls - Udolls that have a thick reddish horizon of clay accumulation.

Ustolls - Mollisols that are mostly in semiarid regions. During the warm season of the year these soils are intermittently dry for a long period or have subsurface horizons in which salts or carbonates have accumulated.

Argiustolls - Ustolls that have a subsurface horizon of clay accumulation that is relatively thin or is brownish.

Haplustolls - Ustolls that have a subsurface horizon that is high in bases but without large accumulations of clay, calcium carbonate, or gypsum.

Oxisols

Soils that are mixtures principally of kaolin, hydrated oxides and quartz and that are low in weatherable minerals.

Spodsols

Soils with low base supply that have in subsurface horizons an accumulation of amorphous materials consisting of organic matter plus compounds of aluminum and usually iron; formed in acid mainly coarse textured materials in humid, and mostly cool or temperate climates.

Aquods - Seasonally wet Spodsols.

Haplaquods - Aquods that have a subsurface horizon that contains dispersed aluminum and organic matter, but only small amounts of free iron oxides.

Sideraquods - Aquods that have an appreciable amount of iron in the subsurface horizons.

Orthods - Spodsols that have a horizon in which organic matter plus compounds of iron and aluminum have accumulated.

Fragiorthods - Orthods that have a dense brittle but not indurated horizon below a horizon that has an accumulation of organic matter and compounds of iron and aluminum.

Haplorthods - Orthods that have a horizon in which organic matter plus compounds of iron and aluminum have accumulated but they have no dense, brittle or indurated horizon.

Ultisols

Soils that are low in bases and have subsurface horizons of clay accumulation; usually moist, but during the warm season of the year some are dry part of the time.

Aquults - Seasonally wet Ultisols that have mottles, iron-manganese concretions, or gray colors.

Ochraquults - Aquults that have either a light colored or thin black surface horizon.

Umbraquults - Aquults that have a thick black surface horizon.

Humults - Ultisols that have a high content of organic matter.

Haplohumults - Humults that either have a subsurface horizon of clay accumulation that is relatively thin, a subsurface horizon having appreciable weatherable minerals, or both.

Udults - Ultisols that are usually moist and that are relatively low in organic matter in the subsurface horizons; formed in humid climates that have short or no dry periods during the year.

Fragiudults - Udults that have a dense brittle but not indurated horizon in or below a horizon in which clay has accumulated.

Hapludults - Udults that have either a subsurface horizon of clay accumulation that is relatively thin, a subsurface horizon having appreciable weatherable minerals, or both.

Paleudults - Udults that have a thick horizon of clay accumulation without appreciable weatherable minerals.

Rhodudults - Udults that have dark red subsurface horizons of clay accumulation.

Vertisols

Clayey soils that have wide, deep cracks when dry; most have distinct wet and dry periods throughout the year.

Uderts - Vertisols that are usually moist. They have wide, deep cracks that usually open and close one or more times per year but do not remain open for more than two months.

Chromuderts - Uderts that have a brownish surface horizon.

Pelluderts - Uderts that have a black or dark grey surface horizon.

Usterts - Vertisols that have wide, deep cracks that usually open and close more than once during the year and remain open intermittently for periods that total more than three months but do not remain open continuously throughout the year.

Chromusterts - Usterts that have a brownish surface horizon.

Pellusterts - Usterts that have a black or dark gray surface horizon.

Appendix III. Maps and publications used in compiling information on soils, arranged alphabetically by state.

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Virginia (Soil) Soil Conservation Service, U.S.D.A. 1979. 52 X 27 cm. coloured.

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