

STRIDULATION AND ITS SIGNIFICANCE IN THE  
WATERBUG GENUS CENOCORIXA

by

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## STRIDULATION AND ITS SIGNIFICANCE IN THE WATERBUG GENUS

CENOCORIXA

## Abstract

Stridulation in the waterbug genus Cenocorixa was studied in the field and experimentally in the laboratory. It was shown that both males and females stridulate. The stridulatory signals, analysed by use of a sound spectrograph, were shown to be species and sex specific, differing in temporal pattern of pulses, pulse rate, pulse structure, and signal length.

It was shown that the annual rhythm of stridulation in both male and female is correlated with sexual maturity. Males will spontaneously stridulate when there is mature sperm in the testes, and this occurs in spring, early summer, and late fall. Females do not stridulate spontaneously, but can be induced to stridulate when they have chorionated eggs in the lateral oviducts, but no sperm in the receptaculum seminis; they are sexually mature only in the spring and early summer.

Stridulation was shown to be important in behavior leading to successful copulation. Male stridulation functions as a calling signal facilitating pair-formation by attracting conspecific females, and as an agonistic signal serving to space out individuals. Males will answer almost any stridulatory signal, but only calls from a conspecific female initiate searching behavior. Receptive females respond to stridulatory stimuli from conspecific males by stridulating, and successful copulations were observed only when preceded



by such signal recognition; female stridulation functions as an agreement signal.

Stridulation serves as a premating isolating mechanism in Cenocorixa. However, it is not the only isolating mechanism, but is reinforced by geographic and ecological isolation in a number of cases.

The Corixidae, since they mostly have only a single stridulatory signal that can function in at least two contexts, are considered to represent a primitive stage in evolution of stridulatory signals: a stage in which functional diversification of signals is just evolving.



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## I. INTRODUCTION

During the past hundred years a considerable literature has accumulated on insect sounds. The early studies on these sounds, however, were only notes on the different sounds produced by various species, and suggestions on the mode of production of these sounds. It is only during the last 30 years that technical apparatus has been developed and thorough investigations on bioacoustics undertaken by physiologists and ethologists. These studies have resulted in a) thorough description of the mechanism of sound production, b) detailed analysis of the signals, and c) playback experiments using previously recorded or artificial signals.

In insects, according to Dumortier (1963 a) three different mechanisms of sound production can be distinguished: 1) Sound production as a byproduct of some other normal activity; e.g. flight sound; 2) Sound production by percussion on the substratum, e.g. the knocking of the Death Watch Beetles (*Anobiidae*); 3) Sound production by a special sound producing apparatus.

The apparatus for sound production is often a very specialized organ, and Dumortier (1963 a) separates the following three classes: a) Sound production by passage of fluid (gas or liquid) across an orifice, e.g. Death's Head Moth (*Acherontia atropos* L.) is said to blow air in and out through its pharynx, producing whistling sounds; b) Sound production by vibration of a membrane (other than wings), e.g. representatives of Homoptera have a membrane



where a special muscle is attached and contractions of this muscle cause the membrane to vibrate; c) Sound production by friction, e.g. crickets (Orthoptera, Gryllodea) make sounds by rubbing certain parts of their wings against each other. Sound production by friction is the most widespread mechanism used in insects. It is often called stridulation and this usage is adopted herein; etymologically, however, this term can be applied to any sound production.

The stridulatory apparatus is composed of two parts: a "pars stridens" (a file, a strigil), a special stridulatory surface with pegs, teeth, or spines, and a "plectrum", a sharp edge, a tooth, or a line of denticulations. The sound is produced by the rubbing of the plectrum on the pars stridens or vice versa. In fact, the distinction of the parts is rather artificial and often it is impossible to say which is which.

Several attempts have been made to classify the biological function of stridulatory signals in insects (e.g. Busnel, 1963; Dumortier, 1963 c; Haskell, 1964; Alexander, 1967). All of these classifications are based primarily on studies on Orthoptera, and some Orthopteran species have several different calls apparently having different functions. However, in most other insects only one or two signals are known, and the function of these signals may be difficult to classify according to the existing classifications.

Functionally, signals which are classified as calling, rival's, or premating songs, may also have an important role in sexual isolation of closely related species. This has been



shown in several cases of vertebrates (e.g. Dilger, 1956; Marler, 1957; Littlejohn and Michaud, 1959; Delco, 1960). Generally these cases fall into the category of premating isolating mechanisms since the males produce species specific signals which attract conspecific females. Females of other species do not respond, and thus pair formation is facilitated by the signals. In insects such studies have been carried out mostly on Orthoptera (e.g. Walker, 1957; Perdeck, 1958; Haskell, 1961; Spooner, 1968).

In the waterbug family Corixidae it has been known for more than 120 years that some species are able to stridulate while completely submerged. The first note on this phenomenon was published by Ball (1846), who made observations on the sounds of Corixa striata (L.) [= Sigara striata (L.)] in England. After this, other notes on stridulation of European Corixidae were published (e.g. Thomson, 1894; Carpenter, 1894; Kirkaldy, 1901), describing the quality of the sound (as it is heard by the human ear), and its apparent mode of production. All these notes concerned the subfamily Corixinae\*, and the mechanism was described incorrectly. Mitis (1936) came closest to the truth by stating that the sound was produced by rubbing certain stridulatory areas of the front femora against the sharp edges of the head about midway between the antennae and labium; the former part being called plectrum and the latter pars stridens. However, usually the

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\* The family Corixidae is taxonomically divided into six subfamilies: Diaprepocorinae, Micronectinae, Stenocorixinae, Cymatiinae, Heterocorixinae, and Corixinae. For more details see Hungerford (1948).



plectrum is a sharp edge, and the pars stridens is the part containing the stridulatory pegs, and thus Mitis' (1936) terminology will be reversed in the present study. [For a more detailed review of the early works describing the method of sound production in Corixidae, see Finke (1968)]

Mitis (1936) compared the sexes of certain Corixinae and found that only the male had stridulatory areas located on the inside of the front femur that contained several rows of short pegs; these pegs were said to be absent from the female. Further, Mitis (1936) observed only males to stridulate, and this has been concluded also in other studies (e.g. Schaller, 1951; Leston and Pringle, 1963). In only two species have possible female calls been reported: Leston (in Haskell, 1957) and Southwood and Leston (1959) claim that both sexes of Arctocorisa germari (Fieb.) stridulate during the mating period, but nothing more is said about the stridulation of this species. Finke (1968) observed some unusual faint signals in cultures of Sigara striata (L.), but was unable to obtain satisfactory recordings. However, she observed that both males and females produced these sounds and the mode of production was by rubbing the hind legs against the fore wings lying above the abdomen. Also Moore (1961) observed and recorded sounds produced in a similar way by males of two species of North American Corixidae, Hesperocorixa atopodonta (Hung.) and Sigara grossolineata Hung.; no movements of the front legs were observed during these stridulations.

Mitis (1936) compared the morphology of the strid-



ulatory areas on the front femora of males of several species. He found that the thickness of the pegs correlate with the loudness of the sounds produced (as judged by the human ear): the thicker the pegs the louder the signal. Further, he found that the subfamily Corixinae contains both stridulating and nonstridulating species, and according to the structure of the pegs on front femora he was able to predict if a species was able to stridulate. A similar comparison of the stridulatory areas was made by Hungerford (1948), who gave a list of 75 western hemisphere species of Corixinae supposed to stridulate although observations of actual stridulation exist for only one of them.

In contrast to the subfamily Corixinae, several species of the genus Micronecta (subfamily Micronectinae) have been observed to stridulate although they do not have stridulatory pegs on the front femora. Mitis (1936) and Southwood and Leston (1959) suggest that they produce the sound by a strigil, an organ located dorsally on the sixth abdominal segment: this organ would be rubbed against the tergum of the fifth segment or against some parts of genitalia. Males of most species of the subfamily Corixinae also have the strigil, but its function seems to be for attaching to the female during copulation (Larsén, 1938).

Corixinae and Micronectinae are the only subfamilies of Corixidae in which stridulating species have been reported so far. Representatives of Cymatiinae (genus Cymatia) are known to be unable to stridulate (Mitis, 1936), and observations on other subfamilies are lacking.



Only three publications exist on audiospectrographic analysis of signals of Corixinae. Moore (1961) gives sound spectrograms of signals produced by Hesperocorixa atopodonta, and from his figure it is possible to see that the stridulation of this species is composed of more or less irregular pulses, the main frequency area of the sound being 7-8 kilocycles per second. Haskell (1961) gives oscillograms of two calls produced by Sigara dorsalis (Leach.). These figures do not give any information on the frequency of the sound, but it can be seen that one of the signals is composed of regularly repeated pulses, while the other one is composed of pulse groups repeated with regular intervals. Finke (1968) gives both spectrograms and oscillograms of the calls of two species, Sigara striata (L.) and Calli-corixa praeusta (Fieb.). In these figures the calls of S. striata appear to be very much like the calls of S. dorsalis in Haskell (1961), while C. praeusta only has one call, this being composed of two parts, each with regularly repeated pulses, but with different pulse rate. The main frequency area for both species in Finke's (1968) study appear to be 3-6 kc/sec, with some higher overtones up to 16 kc/sec and over.

Hagemann (1910) described the tympanal organ of Corixidae located near the wing base on the mesothorax. Schaller (1951) demonstrated in various experiments that acoustic stimuli are received by this organ, although it also might have a function as a hydrostatic pressure indicator.



The function of stridulation in Corixinae has been discussed a number of times. Because it is commonly observed that these insects stridulate during the breeding season (Mitis, 1936; Schaller, 1951; Finke, 1968; Jansson, 1968) and have species specific signals, it is supposed that the song is combined with sexual behavior. Schaller (1951) reports that the song of male S. striata is a courtship song causing females to swim rapidly in small circles, which is an effective mechanism because the males attempt to copulate with any moving object of suitable size. Also Finke (1968) observed an increase in the swimming activity of the females in the presence of the male signals. However, Larsén (1938) and Jansson (1968) did not observe any visible effect of the song of the males upon females. In addition, Larsén (1938) observed males of Corixa dentipes (Thoms.) to stridulate both in early spring and in late fall, and noted that the late fall stridulation is not in connection with breeding. To date, no comprehensive study has been undertaken on the function of stridulation in this group of water bugs.

The aim of the thesis is to obtain a more detailed understanding of stridulation in the Corixinae. The genus Cenocorixa Hungerford was chosen for study because it contains several closely related species which are often difficult to identify according to morphological characters (cf. Appendix I) and which could be predicted to stridulate because they have stridulatory pegs on the front femora. All species in the genus also have their geographic distribution in western



North America (Hungerford, 1948), and both allopatric and sympatric situations can be studied. Two species in particular, C. bifida (Hung.) and C. expleta (Uhler) are abundant in British Columbia, where they occur allopatrically and sympatrically (Scudder, 1969 a; 1969 b), and so they were studied most intensively.



## II. MATERIAL AND METHODS

### 1. Sampling and handling of specimens

The general distribution of the species was determined from published records (Hungerford, 1948; Lansbury, 1960; Scudder, 1969 a), then specific localities to be studied were selected for all the species.

Bugs were collected using a sweep net, and were transported to the laboratory in one gallon thermos jugs about half filled with lake water. In cases when the transportation took several days (from California and Utah) the thermos jugs were carried in styrofoam ice chests containing melting ice; in this way the bugs were kept at about 8-10°C during transportation.

In the laboratory the bugs were transferred to 30x24x10 cm transparent covered plastic trays (henceforth called culture trays) with about 4-5 litres of natural lake water, so that the depth of the water was about 5 cm. Pieces of plastic screen were placed on the bottom of the culture trays to provide support for the bugs while resting. Culture trays were then kept either in a constant temperature cabinet at 5°C until needed, or in the laboratory at a temperature of about 21-24°C (room temperature) for various experiments. Photoperiod in both cases was 16 hours artificial light per day, except in experiments requiring natural light conditions. At 5°C the bugs survived several months without any attention. At room temperature they were fed daily on frozen brine shrimp [Artemia salina (L.), Longlife Fish Food Products, Div. of



Sterno Industries Inc., Harrison, N.J.]. Three of the species studied, C. bifida, C. andersoni, and C. expleta produced three consecutive generations in the laboratory on this diet, and all the other species survived without trouble. Thus this food supply was considered sufficient although the reared specimens always were slightly smaller than the field caught insects (cf. Jansson, 1969).

Owing to the rapid rotting of excess food in the cultures, continuous ventilation was required. This was accomplished by use of air stones run off the air supply to the laboratory.

## 2. Life cycle

In order to investigate how the annual rhythm of stridulation correlates with the life cycle, populations of C. bifida and C. expleta in selected lakes in the Southern Interior Plateau of British Columbia were studied. Samples were taken at 1-3 weeks intervals between May and October 1969. The lakes studied were: A) Chilcotin, Beeche's Prairie area: East Lake (= Racetrack in Scudder, 1969 a; 1969 b), Barnes Lake (= Box 4), and Lake Lye (= Box 20-21); B) Cariboo, Springhouse area: Westwick Lake, Boitano Lake, and Boitano Lake North End; C) Cariboo, Green Timbers Plateau between Clinton and Gang Ranch: Long Lake; D) Kamloops, Lac du Bois area: LB2. The characteristics of the lakes are given in Scudder (1969 a).

Sampling included 10 minutes of tape recording in situ,



a temperature recording, a 10 standard sweep sample (1 standard sweep = about one metre long vigorous back and forth sweep with sweep net at the depth of 20-30 cm, consecutive sweeps were taken by moving slowly parallel to the shore line). Some additional adult corixids were also collected. Sampling was done at the same locality in the lakes each time. Sweep samples were preserved in 70 per cent alcohol, and additional adults were preserved in alcohol or modified alcoholic Bouin's fluid (Ewen, 1962).

In addition to recording the temperature at the time of each sample, air and water temperatures were continuously recorded at Westwick Lake using a Bristol portable two pen recording thermometer model 2T 50L-1A-1B (Bristol Co., Waterbury, Conn.). Continuous records of the temperature in shallow water in all water bodies were also obtained by using Ryan model D-15 waterproof recorders (Ryan Instrument Co., Seattle, Wash.). Conductivity of water samples was recorded monthly with a Radiometer type CDM 2 d conductivity meter (Radiometer Co., Copenhagen, Denmark).

From the standard sweep samples the identity and number of adults and larvae in the different instars were counted and thus the sequence of generations for the species was determined. The adult specimens of various species occurring in the lakes were identified according to Hungerford (1948). The larvae of C. bifida and C. expleta were identified according to Scudder (1966), and the larvae of other species could be separated from Cenocorixa larvae according to some characters common to both adults and larvae (cf. Jansson, 1969),



and a key of Jansson and Scudder (in preparation). In identification of adult specimens from samples taken at a time when two generations overlap, the relative age of the specimens was determined according to their softness and color: old specimens are hard and darkly pigmented while young ones are soft and lightly pigmented.

From preserved adult material the development of gonads was studied in the laboratory; females were examined by opening the abdomen dorsally and observing the presence or absence of chorionated eggs; alcohol preserved males were studied by placing them into distilled water for 6-18 hours and then removing the testes. Testes were then stained by a method using both a solution of natural orcein (10-15 minutes) and synthetic orcein (15-20 minutes) at room temperature (Strickberger, 1962), and finally squashed lightly on a microscope slide with a cover slip. In these preparations the chromatin stained dark purple and the stages of spermatogenesis could easily be identified. The results obtained by using this method were confirmed by making serial sections of testes and seminal vesicles using the material preserved in modified alcoholic Bouin's fluid.

During the summer of 1970 the same sampling methods were applied to populations of C. andersoni and C. blaisdelli at the following localities: A) Washington, Whatcom County, Custer: a golf course pond (C. andersoni); B) British Columbia, Vancouver: semitemporary pond at the corner of 16th Avenue and Wesbrook Crescent; MacCleery Golf Course: artificial pond (C. blaisdelli). However, the annual rhythm



of stridulation was tested in the laboratory rather than in the field because the populations were not very dense. Also the testis squash preparations were made from fresh rather than alcohol preserved material. Temperature recorders could not be used during the summer of 1970, but data on air temperatures at Surrey Municipal Hall weather station, British Columbia, were obtained for comparison with the air temperatures in the interior.

### 3. Stridulation

All recordings were made with a portable/mains tape recorder (Uher 4000 Report-L), type LC-10 hydrophone (Atlantic Research Co., Alexandria, Va.), Ampex 341 and 641 tapes (Ampex Co., Redwood City, Cal.). Tape speed in the tape recorder was always 19 cm per second except in the diel periodicity experiments when 2.4 cm per second speed was used. Battery operation was used only under field conditions. Owing to the faintness of the signals of some Cenocorixa species, maximum input was always used while recording. The signals were analysed on a sound spectrograph type 675 Missilyser (Kay Electric Co., Pine Brook, N.J.). Settings used in the spectrograph while analysing were as follows: input and reproduce VU -1.5 for peaks of the signals, mark level 6.5, shape flat, bandwidth narrow for general figures of the signals and wide for detailed analysis of the pulse structure.



Terminology used in the descriptions of the signals is as follows: (Fig. 1):

Impact: shortest distinguishable element of a signal (can only be seen in the detailed figures of pulse structure). This is not the same as a sound wave, but would appear to be a combination of several sound waves.

Pulse: the emission resulting from the passage of the pars stridens over the plectrum: a complete cycle of the apparatus beginning and ending at the position of rest. This is the common concept of a pulse in bioacoustics, which differs from the physical definition of a pulse.

Pulse interval: the interval between two consecutive pulses.

Pulse structure: arrangement of impacts in a pulse.

Pulse group: a distinct group of pulses within a signal.

Pulse group interval: the interval between two pulse groups. In some signals this is clearly longer than the pulse interval, but in some cases it may be almost equal to a pulse interval. However, in the latter case there is a clear difference between the pulses of the pulse groups and this defines the location of the pulse group interval.

Pulse rate: repetition rate of pulses within a stated time (second).

Pulse group rate: repetition rate of pulse groups within a stated time (second).

Main frequency area: the frequency range at which the amplitude of the sound is strongest (appears as the darkest area in the sound spectrograms).



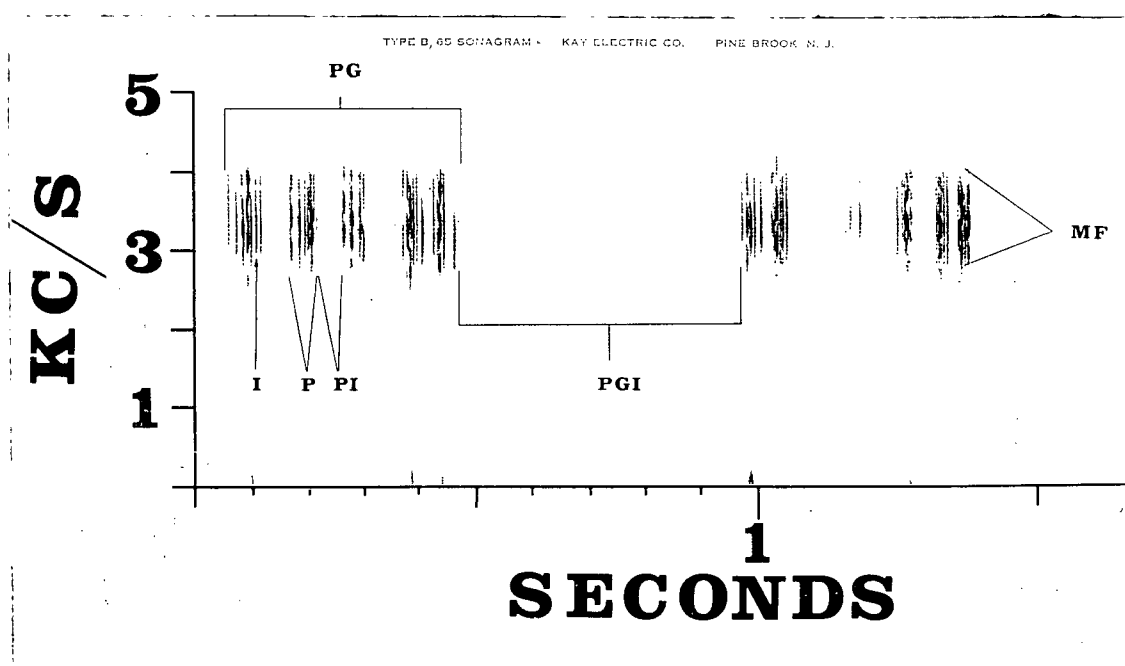


Fig. 1. Terminology used in the descriptions of the stridulatory signals. Abscissa: time (seconds); ordinate: frequency (kilocycles per second); I = impact; P = pulse; PG = pulse group; PGI = pulse group interval; PI = pulse interval; MF = main frequency area.



Temporal pattern of pulses: arrangement of pulses in a complete signal (according to some authors this is also called pulse modulation).

Signal or call: a complete set of pulses or pulse groups.

Recording of the stridulatory signals was made both in natural habitats and in the laboratory. In the laboratory satisfactory recordings could be made, providing that no motors were used in the same room. The bug container was isolated from the general vibrations of the building by placing it on a 5 cm thick foam rubber cushion.

The problem of possible sound changes in laboratory conditions was studied by analysing signals recorded in several different containers. Glass, brick, styrofoam, and several different plastic containers were tried and all had an effect of making one or more frequency areas of the sound stronger than others, or creating harmonics. Wooden trays and some soft plastic trays and paper mugs were found to absorb almost all sounds thus making the signals too faint. The only container where the signals were similar to those recorded in natural conditions was a metal cottage bathtub lined interiorly at the sides and bottom with a 5-10 cm thick layer of fine grain sand and with some larger rocks on the bottom; the best results were obtained when the bugs were sitting on the rock while stridulating. To keep the bugs within the area at which the recording could be done satisfactorily, a fence made of soft plastic screen was used.



The effect of temperature on stridulation was studied by recording in natural conditions, bathtub, and culture trays. It was shown that although the culture trays had some effect on the frequency of the sounds, this did not affect the pulse rate, and the trays could be used for this study. Low temperatures in the laboratory were obtained by placing the trays in a constant temperature cabinet at 5°C for a few hours, and high temperatures were produced by placing a 100 watt lamp above the trays until the temperature was so high that the bugs did not stridulate any more. After these treatments the temperature was allowed to increase or decrease slowly towards room temperature. The bugs were induced to stridulate at desired temperatures by playing back to them certain signals from previous recordings and simultaneously recording all signals with another tape recorder. The loudspeaker used for these playbacks was a Uher earphone protected from wetting by a thin rubber sleeve (condom).

Graphs for the effect of temperature on pulse rate as well as on pulse group rate were plotted and calculated by computer (Biology Data Centre, Institute of Animal Resource Ecology, University of British Columbia).

Stridulatory mechanism and movements involved in the sound production were observed while the bugs responded to playback signals. However, because the movements are relatively fast, satisfactory observations could be made only at low temperatures (10-15°C).

Morphology of the stridulatory apparatus was studied



by a mark 2 A Cambridge Stereoscan electron microscope (Cambridge, England). Specific differences in the structure of the pars stridens and the plectrum apparently correlate with the loudness of the signals of various species (cf. Mitis, 1936). However, no suitable equipment was available for measuring the amplitude of the signals and thus, the study of the morphology of the stridulatory apparatus was restricted to the general structure of the pars stridens and the plectrum.

The diel periodicity of the stridulating activity of some species was investigated in the field. Recordings for five minutes in each hour were carried over 24 hour periods during May and June 1969 at Barnes Lake, Westwick Lake, and LB2. Laboratory observations on diel periodicity of the stridulating activity in all species were carried out during the spring and summer of 1970. In these experiments the bugs were placed in culture trays which had been painted grey on the sides and bottom: in transparent trays the bugs tend to swim for hours against the walls. The trays were kept undisturbed in the laboratory at relatively constant temperature ( $20-24^{\circ}\text{C}$ ) and the bugs were placed in them 24 hours prior to the beginning of each experiment. The light conditions were natural except that the trays never received direct sunlight and the room apparently was always slightly darker than indirect light outdoors: no artificial light was allowed in the room during the tests. Recordings were made by connecting the tape recorder to a time clock set such that there was a recording for five minutes every



hour over the full 24 hour period, and the tests were run for five consecutive days. The hydrophone was placed in the middle of the tray and the tray was positioned on a foam rubber cushion.

#### 4. Behavior

The behavioral role of stridulation was initially studied by observing the bugs in culture trays and in their natural environment in shallow water during the summer of 1969. Experimental tests in the laboratory were carried out during the spring and summer of 1970.

The most detailed analysis of the stridulatory behavior was carried out on C. bifida. The first experiments followed those of Schaller (1951) and Finke (1968) by observing and quantifying all activities of the experimental specimens under various conditions. However, only one or two specimens were tested at one time, in order to avoid possible disturbing effects of large numbers on each other. For this analysis, 200 specimens of C. bifida were taken from Lake Lye in late April 1970 and transported to the laboratory. Because males were stridulating and also copulation attempts were observed, the specimens were thought to be ready for the tests. The following four cultures were set up: 30 males; 20 males and 20 females; 30 females; 1 male. Tests were carried out every second day until the 11th or 13th day, and the test period for each experimental condition was 15 minutes. The experimental conditions were: alone, with



auditory, visual, or chemical stimuli. In order to provide natural auditory stimuli, a small cage was made of plastic screen, and 4-5 specimens from the 30 male culture were placed into this cage which then was placed into the tray with the experimental animals, i.e. the experimental bugs could hear the signals of the specimens in the cage, but could not touch them. For visual stimuli, a small waterproof container of transparent plastic was made and the stimulating specimen was placed into this container which then was introduced to the experimental animals. Also a dead pinned specimen was tried, in this case fixed at the end of a glass rod. Chemical stimulus was provided by keeping two males from the 30 male culture, or two females from the 30 female culture, in a tray for 3-4 hours and removing these specimens just before introducing the experimental animals into the tray.

Results of the experiments were analysed using the Wilcoxon matched-pairs signed-ranks test and Friedman two-way analysis of variance (Siegel, 1956).

When the true response of receptive C. bifida females to conspecific male signals was discovered the basis for further behavioral studies was to keep males and females of every species in separate cultures thus preventing all undesired copulations. The function and the significance of the stridulatory signals was then tested by playing back conspecific male signals to a group of females and the responding females were transferred to another tray. The response of these females was then tested against all



possible Corixidae signals, and finally some males of their own species were introduced into the same tray and copulation behavior was observed. Also the group of females which did not respond to conspecific male signals was observed in the presence of some males. By playing back previously recorded female signals the males were induced to try to copulate, but the unreceptive females adopted a certain release behavior which could then be studied. After these tests both receptive and unreceptive females were preserved in alcohol and their gonad development was examined.

Playback experiments utilising all possible previously recorded signals were also carried out with males of each species of the genus Cenocorixa. In these experiments the stridulatory response of various males was recorded and observations of their moving activities were made.

In the species recognition experiments each signal was played five times to a group of specimens (usually five). When all different signals had been played back five times the whole experiment was repeated five times (thus total playback for each signal was 25 times). When specimens were tested against various signals, the bugs were allowed five seconds in which to answer, for a positive reaction. Another five seconds was allowed to elapse before repeating the playback, but if the test animals stridulated during this latter five second period, the signal was not considered to be a response to the playback, and a further five seconds was allowed to elapse before the next playback. All of these experiments were made at room temperature (21-24°C).



In all playback experiments the loudness of the signals was adjusted to be as natural as possible. The volume of the tape recorder playing the signals back was adjusted by recording with another tape recorder through the hydrophone. These experiments were carried out in the culture trays, using the earphone as a loudspeaker. However, owing to echoes in the trays the experiments on the distance for recognition of signals of the opposite sex were carried out in the sand lined bathtub, using an underwater loudspeaker model MM-2PPS (University Sound Co., Oklahoma City, Okla.). The results of this experiment were confirmed with some of the species by placing males and females in separate small cages made of plastic screen, and observing their responses to each other's signals at various distances. The detailed observations on agonistic behavior between males were also made in the bathtub.



### III. RESULTS

#### 1. Mechanism of sound production and morphology of the stridulatory apparatus

In the genus Cenocorixa both males and females are able to stridulate. Three different mechanisms of sound production were observed: i) By rubbing a series of special stridulatory pegs (*pars stridens*), located anterobasally on the fore femora (Fig. 2), against the edge of the maxillary plate (*plectrum*), located just posteriorly to the dorsolateral corner of the anteclypeus (terminology according to Parsons, 1965; 1966)(Fig. 3). ii) By rubbing the hind legs alternately or together against the folded fore wings lying above the abdomen, or against the ventral side of abdomen and external genitalia. iii) In two species faint stridulatory sounds were recorded at the beginning of successful copulation, but the origin of these sounds could not be detected.

The first category is clearly true signalling in that the movement is made specifically for sound production. The second category seems to belong to sounds produced as a by-product of some activity, the prime action of which is not sound production, but one of cleaning or the like. The third category might be just sound produced as a result of friction between the two specimens, but alternatively it might as well be an important signal for a successful copulation. However, it cannot be classified owing to the fact that the source of the sound is unknown.



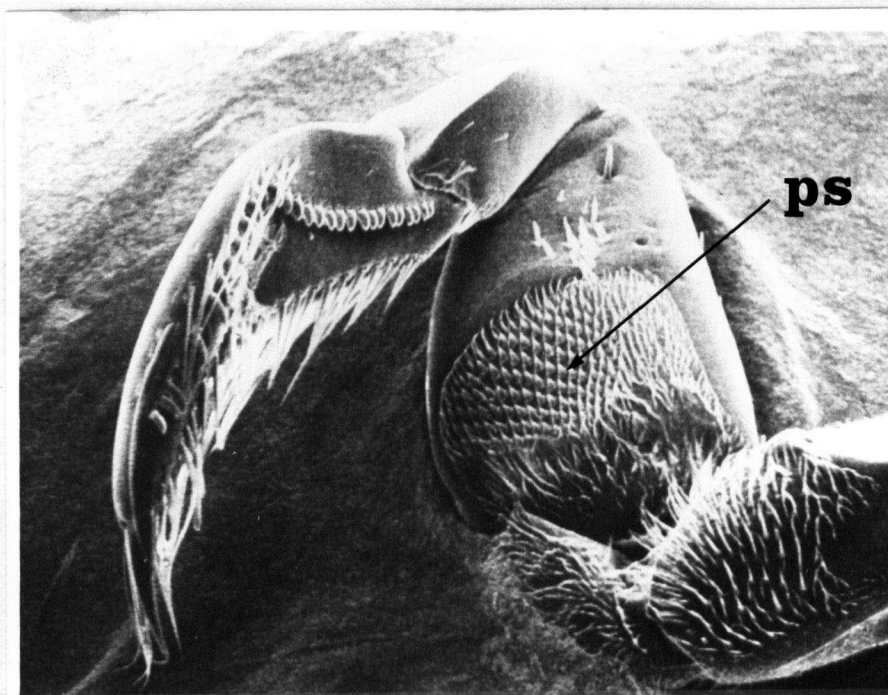


Fig. 2. Stereoscan photograph of the front leg of *C. blaisdelli* male showing the location of the pars stridens (ps). Magnification x100.



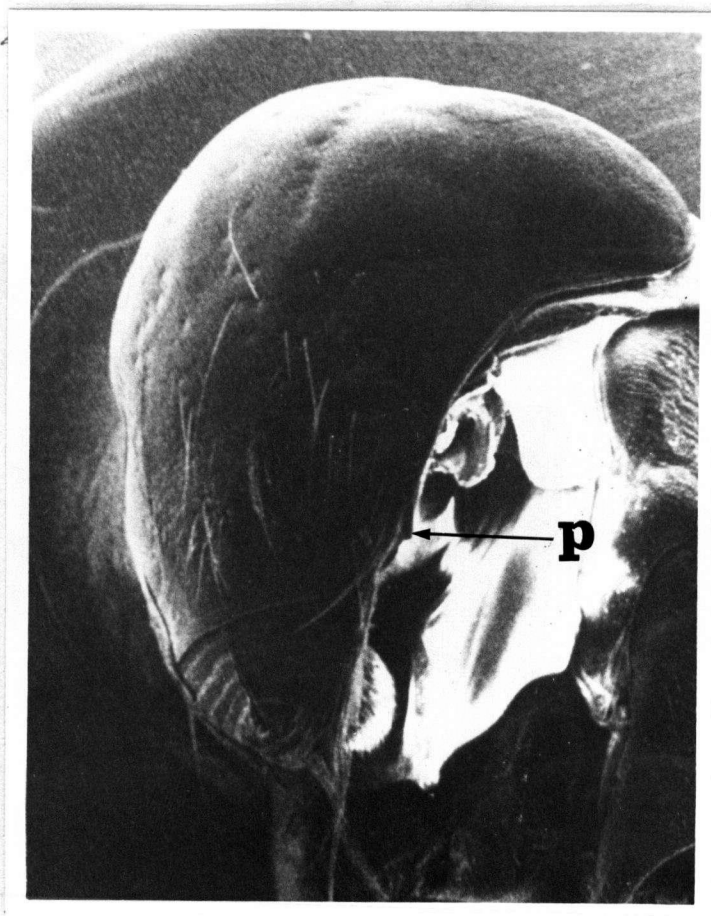


Fig. 3. Stereoscan photograph of the head of C. blaisdelli female showing the location of the plectrum (p). Fronto-lateral view, magnification x50.



The true stridulatory signals in the first category consist of a series of pulses, each pulse being a forward push of one leg. When the leg is moved backwards it does not touch the plectrum. However, usually the other leg is pushed forwards at the same time, i.e. every second pulse is produced by one leg. The alternate movement of the front legs was the only way that both males and females were observed to produce these signals, regardless of the pulse rate or the temporal pattern of pulses in the signals.

The study of the morphology of the stridulatory apparatus showed that generally the males have more pegs and thicker pegs on the pars stridens than the females (Table I, Fig. 4). Also the size of the plectrum is different in the two sexes: the maxillary plate of the males is generally larger than that of the females (Fig. 4).

Although no equipment was available for actual measurement of the loudness of the signals, subjective observations indicate clear differences between the species. In addition, in each species the male call always appears louder than the female call. A correlation is suggested between the loudness of the signals and the thickness of the pegs of the pars stridens. However, the structure of the pars stridens may not be the only factor affecting the amplitude of the sound: the size of the plectrum was also observed to be different in the two sexes.



Table I. Thickness of the pegs of the pars stridens (average from 10 specimens) and comparison of the number of peg rows on the pars stridens (10 specimens) and the number of impacts per pulse (mean  $\pm$  standard error; number of specimens as in Table II). In several species the males are able to produce "slow" and "fast" pulses in their signals: the number of impacts per pulse in these different pulses are indicated by s and f, respectively. \* = no signals recorded. The order of the species is according to data contained in Appendix I.

Species/sex	Pars stridens, thickness of pegs (mm)	Number of peg rows on pars stridens	Number of impacts per pulse
bifida ♂	.0056	15-18	9.04 $\pm$ 0.29
bifida ♀	.0040	8-12	6.64 $\pm$ 0.30
kuiterti ♂	.0046	13-15	s 7.58 $\pm$ 0.18
kuiterti ♀	.0018	6- 9	f 4.35 $\pm$ 0.13
			*
andersoni ♂	.0065	10-13	s 4.56 $\pm$ 0.14
andersoni ♀	.0029	7- 9	f 3.27 $\pm$ 0.08
			1.68 $\pm$ 0.06
utahensis ♂	.0058	10-12	s 5.56 $\pm$ 0.18
utahensis ♀	.0021	7- 8	f 2.88 $\pm$ 0.09
			4.63 $\pm$ 0.14
dakotensis ♂	.0059	11-14	8.08 $\pm$ 0.31
dakotensis ♀	.0029	8-12	5.39 $\pm$ 0.22
blaisdelli ♂	.0081	11-14	s 8.05 $\pm$ 0.24
blaisdelli ♀	.0030	8-12	f 4.82 $\pm$ 0.18
			7.92 $\pm$ 0.23
wileyae ♂	.0062	13-15	s 10.72 $\pm$ 0.35
wileyae ♀	.0033	9-12	f 3.96 $\pm$ 0.14
			6.97 $\pm$ 0.30
expleta ♂	.0093	15-17	6.26 $\pm$ 0.18
expleta ♀	.0050	12-16	7.05 $\pm$ 0.22



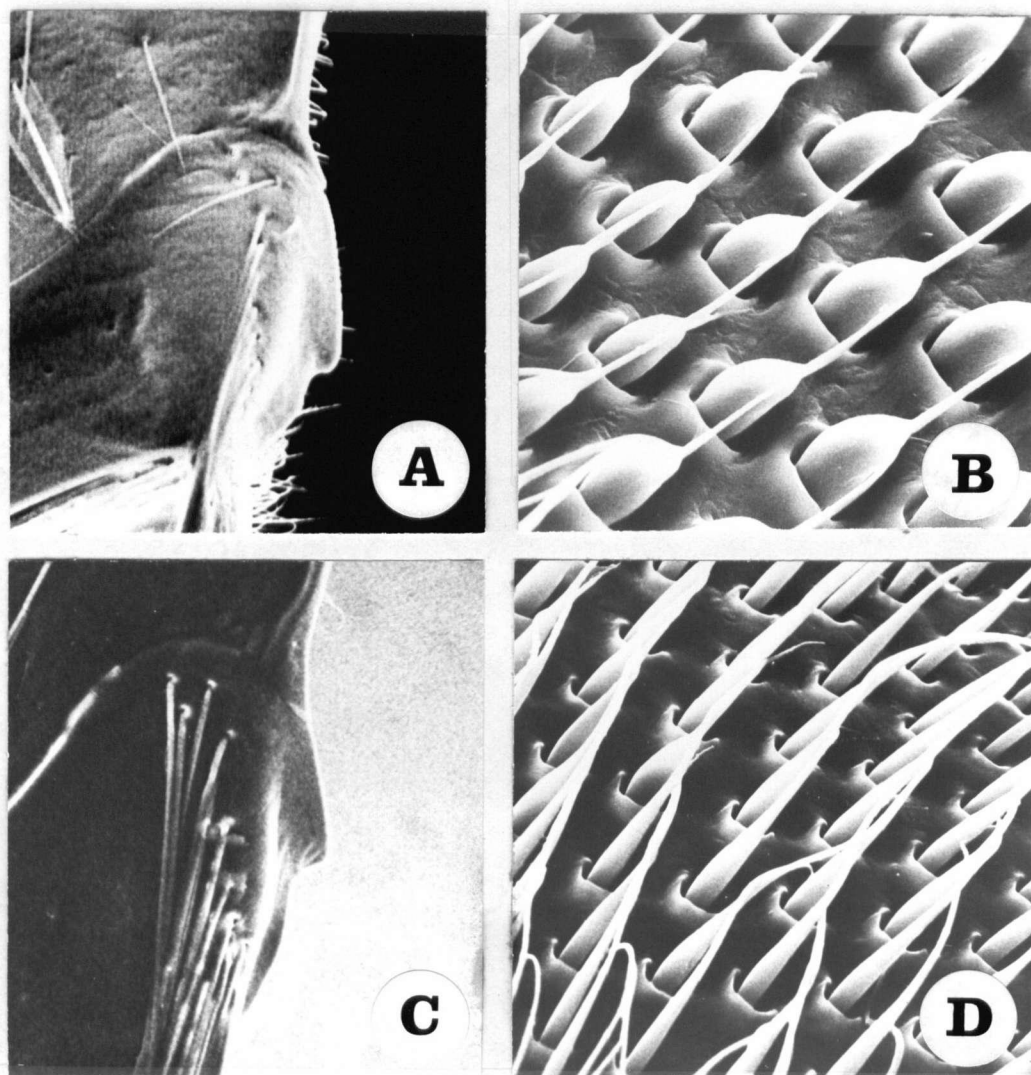


Fig. 4. Stereoscan photographs of the stridulatory apparatus of C. blaisdelli. A = male plectrum; B = male pars stridens, pegs; C = female plectrum; D = female pars stridens, pegs. Magnifications: plectrum x200, pars stridens x1000.



## 2. Audiospectrographic analysis of the stridulatory signals

### a) General

The stridulatory signals of the various species of Cenocorixa are species specific. The most constant character is the temporal pattern of pulses. Further specific differences are found in the structure of pulses, in the pulse rate, and in the signal length. The signals of the two sexes are also different.

Cenocorixa females are able to produce only one kind of signal per species, while in the males of several species the signal is composed of two distinctly different parts. In some cases these parts can be produced separately; these males are thus able to produce two different signals.

In the stridulation the signals are composed of several pulses, and further, each pulse consists of several impacts. Thus the sound is not continuous, but even within the pulses it is built up of short cycles each followed by a short interval. Length of the intervals between two consecutive impacts vary between the species and between different parts of the signals, and in some cases even within a single pulse. It is also affected by temperature: the higher the temperature the shorter the interval. This clearly correlates with the speed used to draw the pars stridens over the plectrum, and thus it is apparent that each impact represents a strike of one peg row of the pars stridens on the plectrum. However, the number of peg rows of the pars stridens is always more than the average number of impacts per pulse (Table I): the bugs do not seem to use the whole pars stridens in producing



the sounds.

Table II records the main frequency areas, average numbers of pulses per signals, and the numbers of pulse groups per signals in the various species. From these data the following generalizations can be made:

i) The frequency of the sound is approximately the same in all species and sexes.

ii) Female signals usually include more pulses per call than comparable male signals and consequently, the duration of the female signals is usually longer than that of the male signals.

iii) The male signals are usually more complicated than the comparable female signals.

Concerning the numbers of individuals used and the numbers of signals analysed for the information in the Table II, it should be noted that recordings were made when a number of individuals was in a culture tray or in the sand lined bathtub, but it is not known how many signals from each individual was analysed. However, each individual was tested prior to the recordings so that all insects were known to be in normal stridulatory condition. This experimental procedure is considered meaningful, since the significance of stridulation concerns more the species than the individuals, i.e. the signals are species specific, but not individually different.



Table II. Numerical characteristics of Cenocorixa signals. Symbols: \* = signal composed of one pulse group (number of pulses per pulse group = number of pulses per signal); ‡ = all pulse groups are similar (subsequent groups = the first group).

Species/sex	Number of specimens present at recording	Number of signals analysed	Main frequency area (kc/sec)	Average number of pulses/signal $\pm$ standard error	Number of pulse groups per signal	Number of pulses per pulse group	
						First group	Subsequent groups
bifida ♂	10	75	3-4.5	$19.57 \pm 0.59$	1	*	*
bifida ♀	5	36	3-4.5	$21.92 \pm 0.87$	1	*	*
kuiterti ♂	10	72	3-4.5	$15.03 \pm 0.56$	2	$11.20 \pm 1.33$	$13.27 \pm 1.11$
andersoni ♂	10	52	3-5	$30.08 \pm 1.36$	2	$9.19 \pm 0.89$	$20.81 \pm 1.33$
andersoni ♀	3	20	4-5	$51.63 \pm 4.13$	$1.75 \pm 0.14$	$28.85 \pm 1.11$	‡
utahensis ♂	3	34	3-5	$85.26 \pm 3.34$	2	$46.50 \pm 3.66$	$38.79 \pm 1.68$
utahensis ♀	2	19	3-5	$100.21 \pm 3.40$	1	*	*
dakotensis ♂	10	52	4-5	$23.83 \pm 0.81$	1	*	*
dakotensis ♀	4	30	3-5	$21.89 \pm 1.85$	1	*	*
blaisdelli ♂	10	37	4-5	$17.75 \pm 1.42$	$5.62 \pm 0.62$	$13.08 \pm 1.24$	$1.00 \pm 0.00$
blaisdelli ♀	4	30	3-5	$28.70 \pm 1.94$	1	*	*
wileyae ♂	10	32	3.5-5	$36.03 \pm 1.07$	$9.25 \pm 0.30$	$9.42 \pm 0.45$	$2.55 \pm 0.03$
wileyae ♀	5	41	3-4	$52.66 \pm 3.71$	1	*	*
expleta ♂	10	38	3-5	$28.05 \pm 1.52$	$6.41 \pm 0.30$	$9.84 \pm 0.72$	$4.47 \pm 0.24$
expleta ♀	3	14	2.5-3.5	$64.43 \pm 8.63$	$8.85 \pm 1.28$	$7.28 \pm 0.48$	‡



b) Description of the signals

C. bifida (Hungerford) (Fig. 5):

Male call: Recorded between 8.0 - 28.8°C. In the experimental conditions no signals were obtained at 7.0°C or below, or at 30.0°C or above. The signal is of simple multipulsate type with clear and even pulse intervals\*.

Female call: Recorded at 21.0 - 24.7°C only, but temperature limits for females to produce signals are probably the same as for males. The signal is very much like that of the male, but with fewer impacts per pulse and much lower amplitude\*.

C. kuiterti Hungerford (Fig. 6):

Male call: Recorded between 15.0 - 28.0°C, but it is probable that the lower limit for stridulation of this species is below 15.0°C. The signal of C. kuiterti male is more complicated than that of C. bifida, and two different pulse groups were observed: i) a group of "slow" pulses which resemble the call of C. bifida, but the pulses follow each other with very short pulse intervals and thus are almost fused together, and ii) a group of "fast" pulses in which the pulses are much shorter than the slow pulses, but follow each other with more or less irregular, but distinct intervals. Structurally the fast pulses include less impacts than the slow ones\*. The signal may be composed of slow pulses alone, or both types together. If it is composed of both types the slow pulses are always in the beginning. The transition from

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\* Numerical data on signals of each species are in Tables I and II.



the slow pulses to the fast ones is usually gradual.

Female call: Never recorded satisfactorily. Occasionally the bugs were observed to perform stridulatory movements with their front legs, but apparently the amplitude of these signals was too low for the equipment used. According to the stridulatory movements the signals probably are of simple multipulsate type.

C. andersoni Hungerford (Fig. 7):

Male call: Recorded between 12.0 - 28.0°C, but the lower limit may be below the observed one. Usually the signal is composed of two pulse groups (like that of C. kuiterti): a slow pulsated beginning and fast pulsated end. Sometimes the first pulse group is produced alone. Pulses of the first group are somewhat irregular and with short intervals, but the pulses of the second group are regular and with distinct intervals. The transition from the slow pulses to the fast ones is abrupt.

Female call: Recorded between 21.5 - 26.2°C, but temperature limits are probably the same for both sexes. The signal is composed of 1-3 simple multipulsate, somewhat irregular pulse groups. The pulse group intervals were always 1-2 seconds and did not seem to be affected by temperature. Pulse intervals are distinct and the number of impacts per pulse in C. andersoni female is less than in any other species.



C. utahensis (Hungerford) (Fig. 8):

Male call: Recorded between 11.7 - 28.0°C. To the human ear this call sounds very much like the call of C. andersoni male, but both the slow and the fast pulse groups are considerably longer in C. utahensis. The spectrogram also shows that the pulses of the slow pulse group are not all similar, but approximately every second pulse is shorter in duration (almost like the pulses of the fast pulse group). In C. utahensis, as in C. andersoni, the slow pulse group may be produced alone. In a complete signal the transition from the slow pulses to the fast ones is abrupt.

Female call: Recorded between 21.5 - 23.4°C, but temperature limits are probably the same as for the opposite sex. The signal is somewhat irregular being a simple multi-pulsate call with distinct pulse intervals.

C. dakotensis (Hungerford) (Fig. 9):

Male call: Recorded between 15.0 - 27.4°C. The signal is composed of gradually changing pulses: at the very beginning the pulses are relatively long and without clear intervals, but towards the end of the signal the pulses become shorter and the pulse intervals become longer. The very first pulses contain more impacts than there are peg rows in the pars stridens: it is probable that these pulses are produced by back and forth movement of the pars stridens so that the stridulatory pegs touch the plectrum when the front leg is drawn backwards and when it is pushed forwards, while in other pulses the sound is produced



only when the leg is pushed forwards.

Female call: Recorded between 20.0 - 24.9°C, but probably produced in same temperature range as the male call. The signal resembles very much the male call, but has almost even pulse rate throughout the signal, and the very first pulses contain less impacts than the subsequent pulses.

C. blaisdelli (Hungerford) (Fig. 10):

Male call: Recorded between 7.0 - 28.8°C. The signal is composed of two different parts, both of which may be produced completely independently from each other, but which usually are produced as follows: a simple multipulsate pulse group with somewhat irregular pulse intervals, followed by single, very fast pulses with considerably long and often irregular intervals. This second part is henceforth considered to be composed of "unipulsated pulse groups" (cf. C. wileyae and C. expleta).

Female call: Recorded between 22.2 - 27.2°C. The signal resembles very much the C. bifida call. However, only part of the C. blaisdelli female call is composed of regularly repeated pulses, part of it being more or less irregular.

Mounting signal (Fig. 11): An odd stridulatory signal was observed always during the first few seconds of a successful copulation. Origin of the sound is unknown. At 22.8°C this signal was composed of six somewhat irregular pulse groups and the whole signal lasted about five seconds (the copulation lasted much longer, but no sounds were



recorded after the first five seconds). The main frequency area seems to be about 3-5 kc/sec (recording made in a culture tray). Pulse rate is about 24 pulses per second at 22.8°C; this is nearly twice the pulse rate of the first pulse group of the normal male call, or a female call.

C. wileyae (Hungerford) (Fig. 12):

Male call: Recorded between 5.4 - 28.2°C. The signal is usually composed of two parts: first a simple multipulse pulse group with slow pulses and short or non-existing pulse intervals, then several very short groups of fast pulses with clear pulse intervals and regular pulse group intervals. Occasionally one part of the signal is produced alone.

Female call: Recorded between 13.6 - 22.9°C, but temperature limits are probably closer to the male limits. The signal is very regular and a simple multipulse call with distinct pulse intervals.

C. expleta (Uhler) (Fig. 13):

Male call: Recorded between 8.0 - 31.0°C. The signal is composed of several pulse groups, the first one being the faintest in amplitude and with the slowest pulse rate, the subsequent pulse groups are louder and with faster pulse rate, i.e. the whole signal accelerates in both amplitude and pulse rate. The pulse intervals are distinct, but sometimes more or less irregular, and the pulse group intervals are somewhat irregular.



Female call: Recorded between 22.4 - 22.8°C only, but temperature limits are probably the same as in the opposite sex. The signal is composed of distinctly separate pulses arranged in several pulse groups, thus resembling the male call. However, the female signal is much lower in amplitude and longer in duration than the male signal, and it does not accelerate in amplitude or in pulse rate.

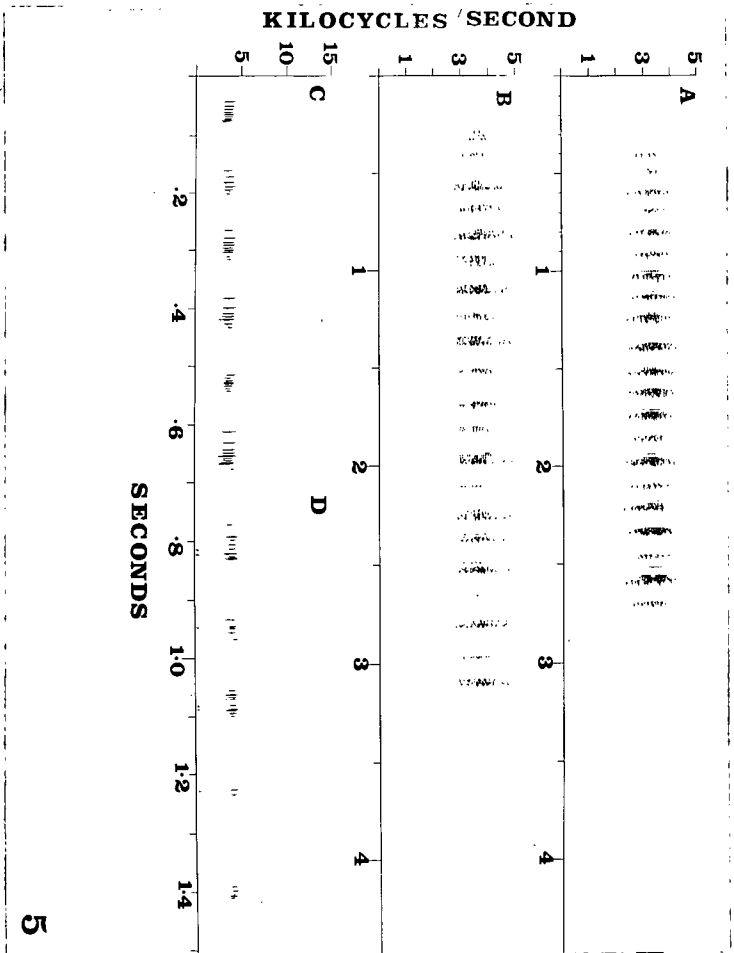
Mounting signal: During the first few seconds of successful copulations some faint stridulatory signals were observed. However, no satisfactory recordings were obtained since the amplitude of these sounds was too low for the equipment used. To the human ear the signals sounded very much like the mounting signals of C. blaisdelli.



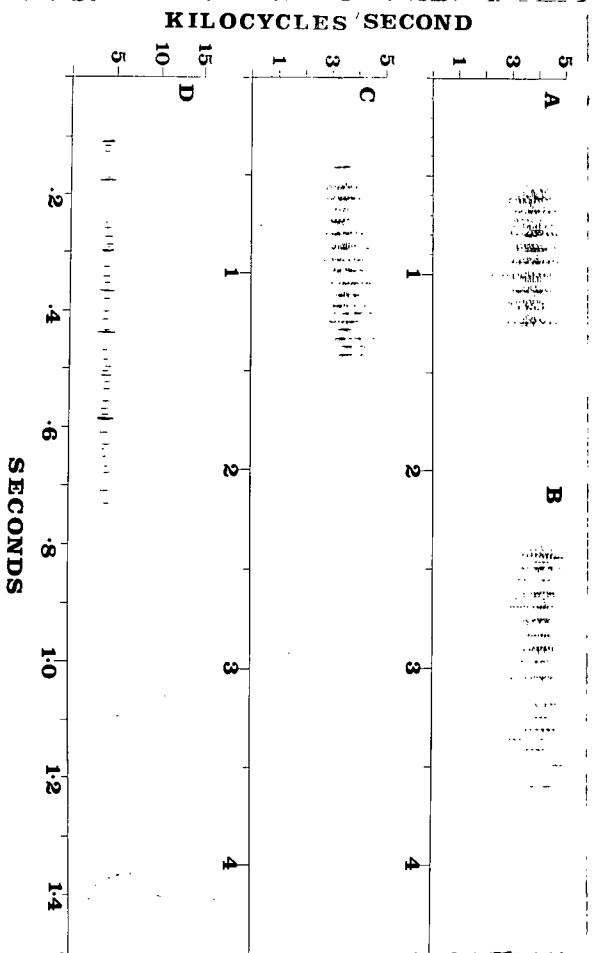
Fig. 5. Sound spectrograms of C. bifida signals. A = male signal; B = female signal; C = details of male signal (pulses 10-15 in A); D = details of female signal (pulses 7-11 in B). Recorded at 21.3°C. Specimens from British Columbia, Chilcotin, Beeche's Prairie, Lake Lye.

Fig. 6. Sound spectrograms of C. kuiterti signals. A = male signal with slow pulses alone; B = complete male signal; C = a male signal with second part dominating; D = details of male signal (pulses of A). Recorded at 21.9°C. Specimens from California, Tuolumne Co., Tioga Pass.





5



6



Fig. 7. Sound spectrograms of C. andersoni signals. A = complete male signal; B = male signal with slow pulses alone; C = female signal; D = details of male signal (from the middle of A); E = details of female signal (from the middle of the first pulse group in C). Recorded at 22.4°C. Specimens from Washington, Whatcom Co., Custer.

Fig. 8. Sound spectrograms of C. utahensis signals. A = complete male signal (a male signal with the slow pulses alone is similar to the first pulse group of the complete signal); B = female signal; C = details of male signal (end of the first and beginning of the second pulse group in A); D = details of female signal (pulses 9-18 of B). Recorded at 22.1°C. Specimens from Alberta, Medicine Hat.



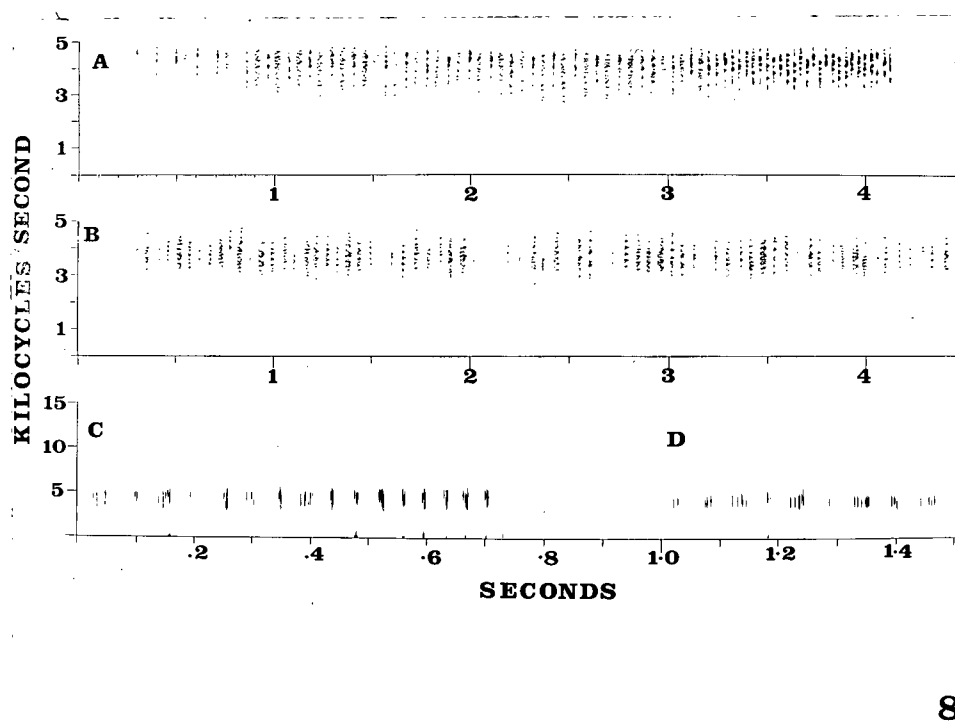
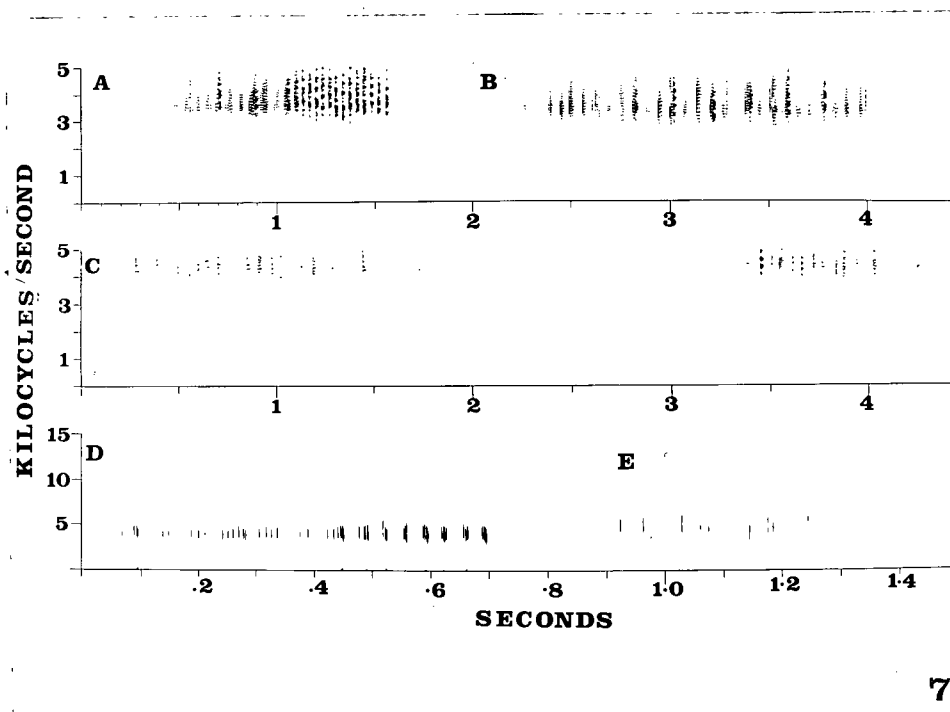
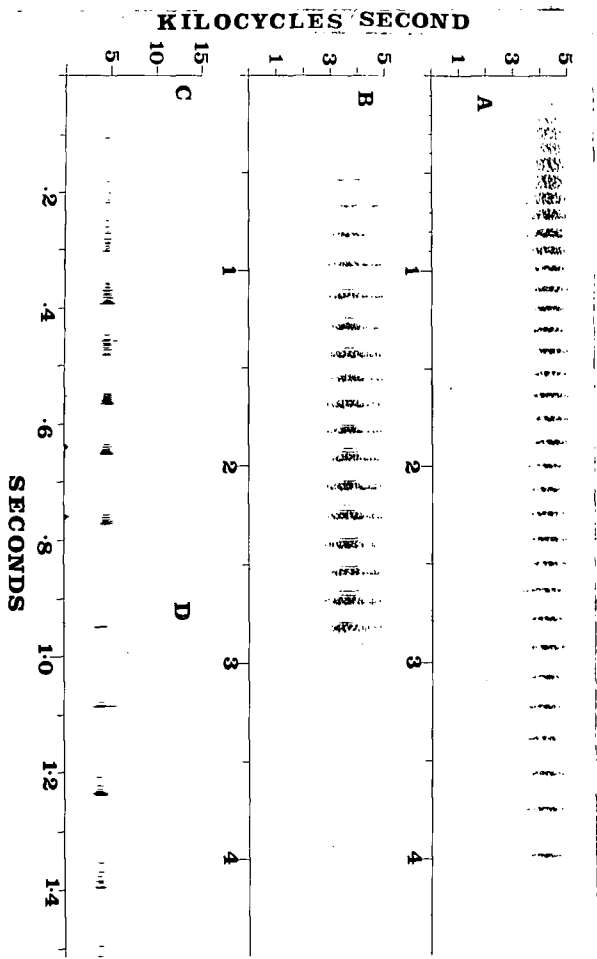




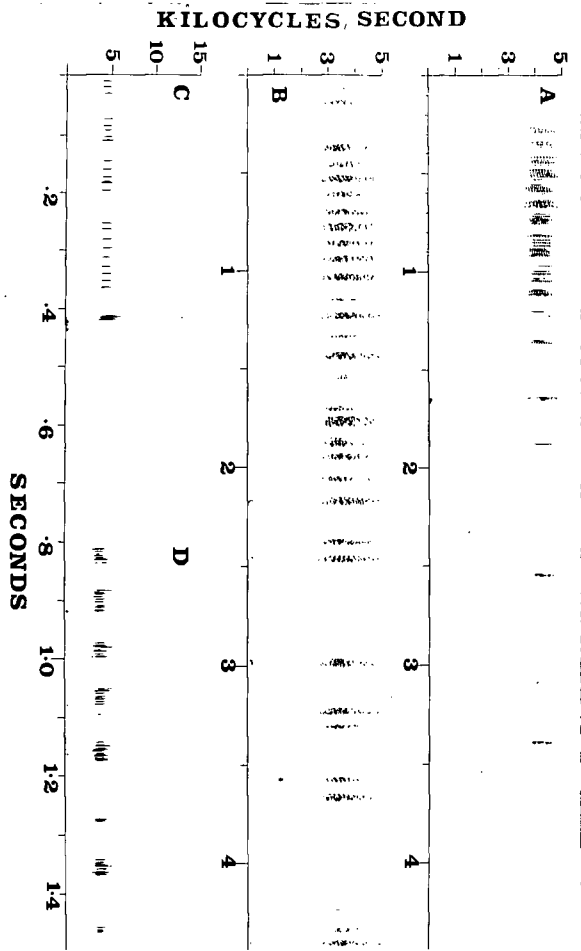
Fig. 9. Sound spectrograms of C. dakotensis signals. A = male signal; B = female signal; C = details of male signal (pulses 4-12 of A); D = details of female signal (pulses 1-3 and 7 of B). Recorded at 21.0 °C. Specimens from Alberta, Brooks.

Fig. 10. Sound spectrograms of C. blaisdelli signals. A = male signal (note the unipulsate 'clicks' after the multipulsate beginning); B = female signal; C = details of male signal (pulses 5-7 of the first pulse group and the first 'click' of A); D = details of female signal (pulses 6-13 of B). Recorded at 22.4 °C. Specimens from British Columbia, Vancouver, Point Grey.





9



10



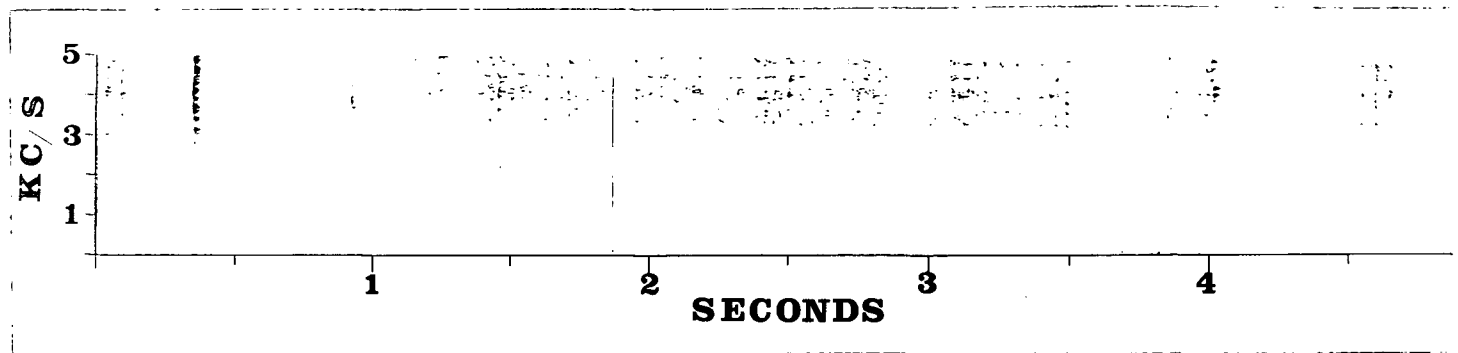


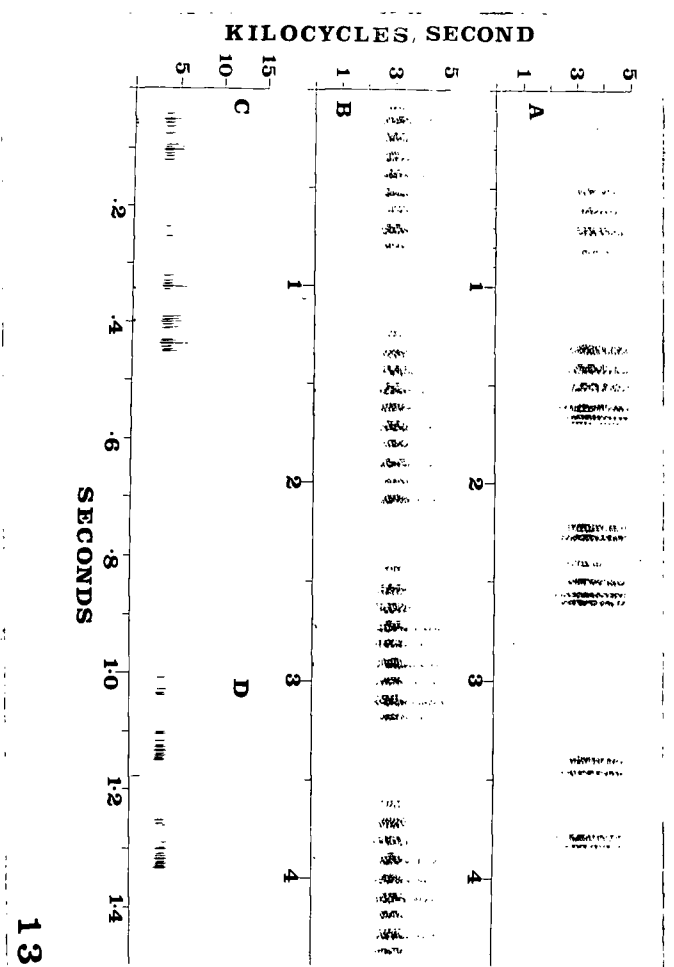
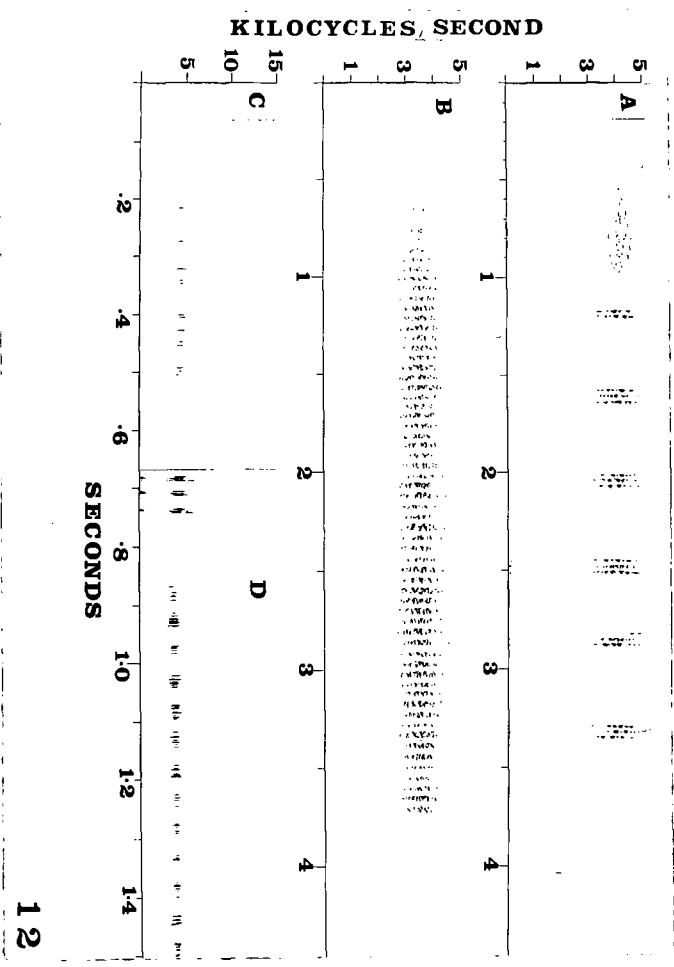
Fig. 11. Sound spectrogram of C. blaisdelli mounting signal. The signal was recorded during the first few seconds of a successful copulation at 22.8 °C. The first two pulses at the left are the last pulses of female signal, then one unipulsate 'click' of the male, and the sounds produced during the copulation begin just before the one second mark. Specimens from British Columbia, Vancouver, Point Grey.



Fig. 12. Sound spectrograms of C. wileyae signals. A = male signal; B = female signal; C = details of male signal (the first and the third pulse group of A); D = details of female signal (part of B from the middle of the signal). Recorded at 21.9 °C. Specimens from California, Lassen Co., Said Lake.

Fig. 13. Sound spectrograms of C. expleta signals. A = male signal; B = female signal (only part of the signal is shown: whole signal included seven pulse groups); C = details of male signal (third pulse group of A); D = details of female signal (the last four pulses of the second pulse group in B). Recorded at 22.3 °C. Specimens from British Columbia, Kamloops (LB2).







c) Effect of temperature on stridulation

In Corixidae, as in all poikilotherms, temperature affects all body activities, including speed of movements; upper and lower limits on the body functions also exist. Since stridulation is produced by movements of the front legs, it is affected by temperature. However, the temporal pattern of pulses and the number of pulses per signal are constant in each species regardless of temperature (except in some cases close to temperature extremes). Thus, the parameters affected by temperature are the duration of the signals and the pulse rate in the signals.

The only species where the change in temperature changed the temporal pattern of pulses was C. utahensis, and this occurred at temperature extremes: above  $27.5^{\circ}\text{C}$  and below  $13.0^{\circ}\text{C}$  the specimens tested were able to produce only slow pulses, i.e. fast stridulation was inhibited. The normal signal of this species is composed of both a slow pulse group and a fast pulse group.

Figs. 14-16 show the average duration of the signals in various species at different temperatures. It is seen that the curve with signal length plotted against temperature has a hyperbolic shape. Departures from this were observed only when stridulation was recorded close to the temperature extremes (Fig. 16: C. wileyae signals at the lowest temperature and C. expleta signals at the highest temperatures).

A graph with increase in pulse rate plotted against temperature forms a straight line (linear regression) (Figs. 17-26). In cases where a signal is composed of pulse groups



the temperature affects both the pulse rate within the pulse groups (Figs. 24 and 26) and the repetition rate of the pulse groups (Figs. 27-29).



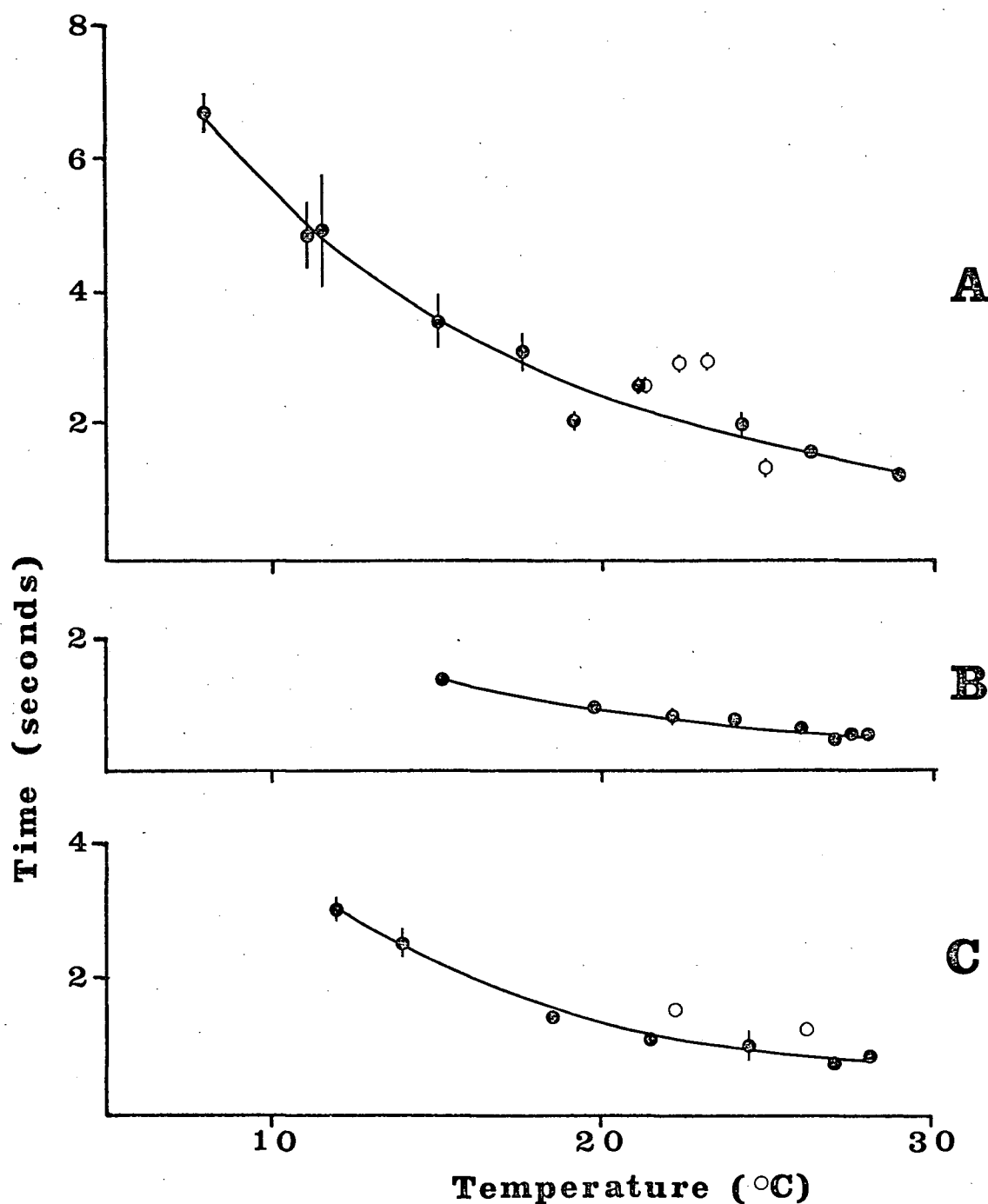


Fig. 14. Effect of temperature on signal duration in *C. bifida* (A), *C. kuiterti* (B), and *C. andersoni* (C). Symbols: closed circles = male signals; open circles = female signals. Standard errors indicated by vertical lines (less than 0.1 second standard error falls within the sign of the symbol used). Curves fitted by eye only on male signals.



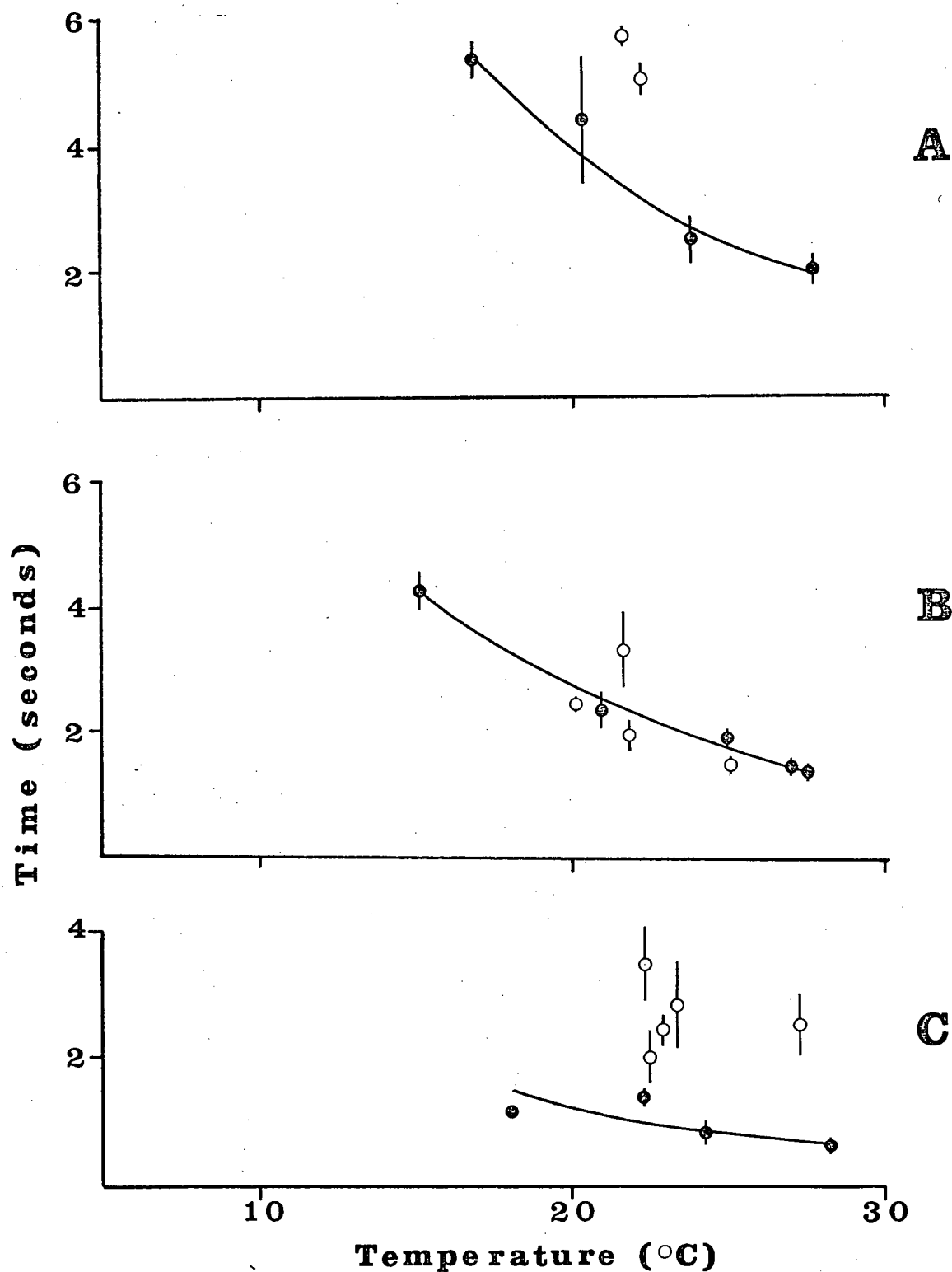
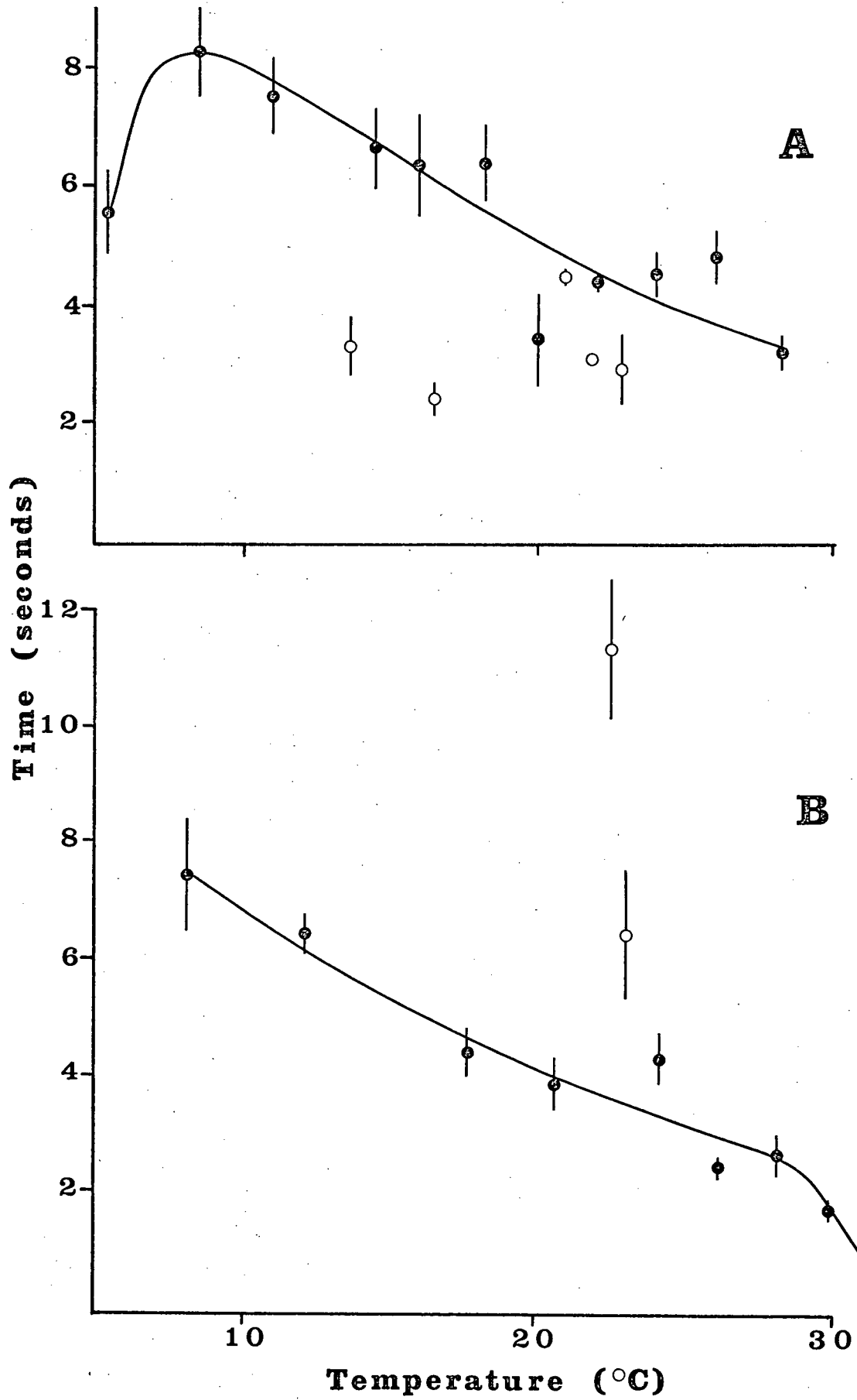


Fig. 15. Effect of temperature on signal duration in *C. utahensis* (A), *C. dakotensis* (B), and *C. blaisdelli* (C). In *C. blaisdelli* male signals only the first pulse group of the signals is concerned. Symbols as in Fig. 14.



Fig. 16. Effect of temperature on signal duration in C. wileyae (A) and C. expleta (B). Symbols as in Fig. 14.







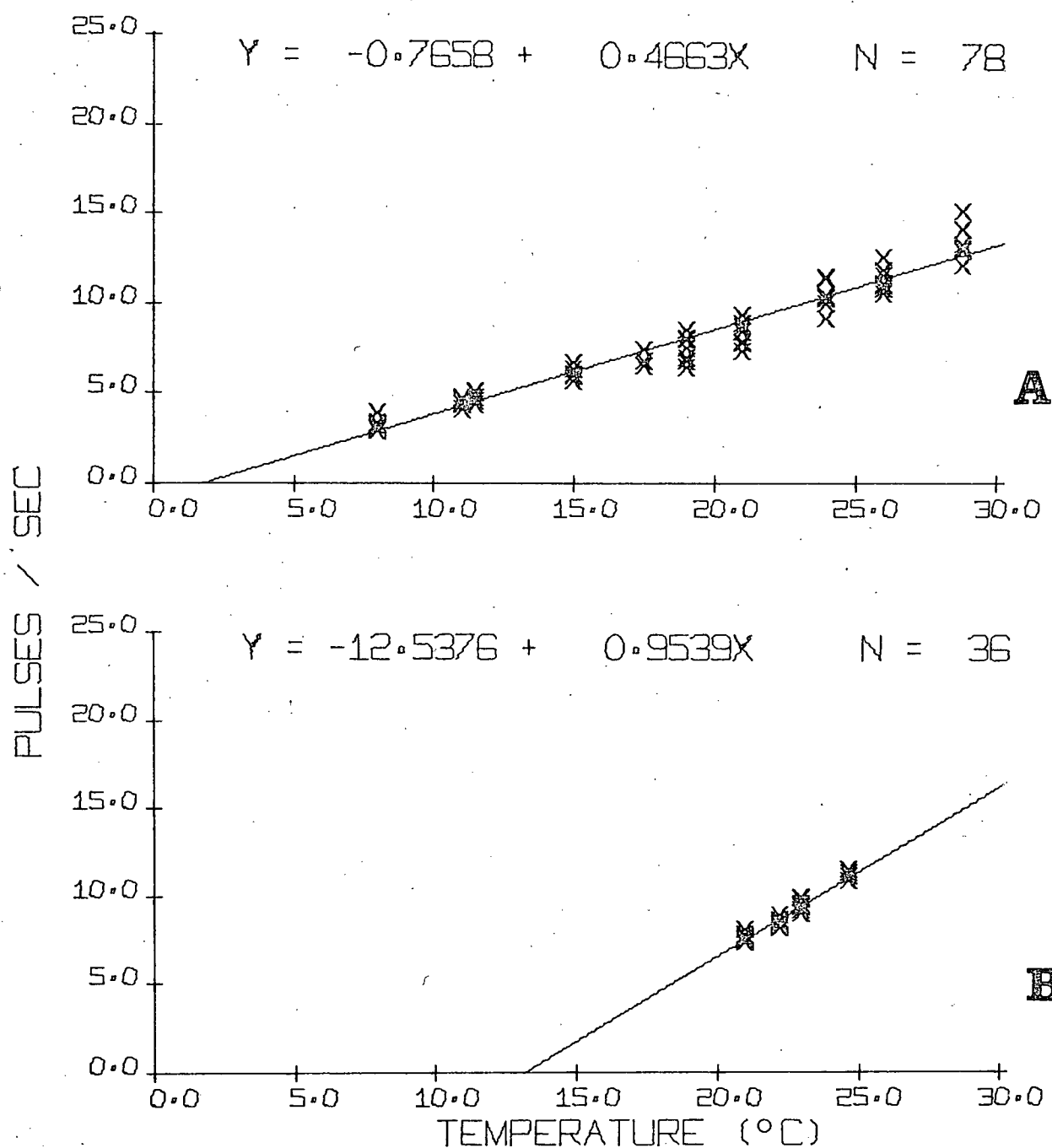


Fig. 17. Effect of temperature on pulse rate in C. bifida signals. A = male signals; B = female signals. Specimens from British Columbia, Chilcotin, Beeche's Prairie, Lake Lye.



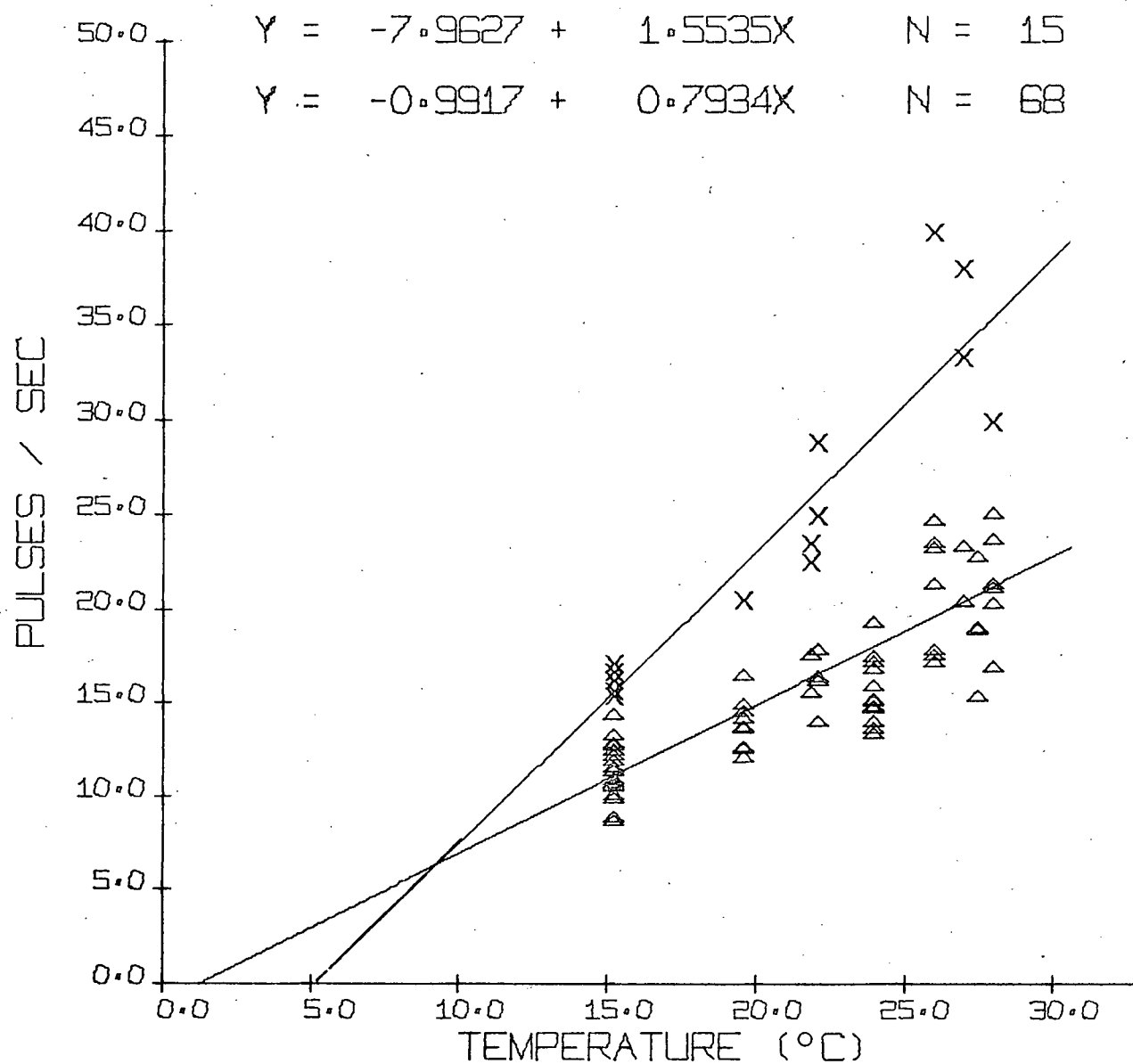


Fig. 18. Effect of temperature on pulse rate in *C. kuiterti* male signals. Symbols: triangle = first pulse group of the signal; X = second pulse group of the signal. Specimens from California, Tuolumne Co., Tioga Pass.



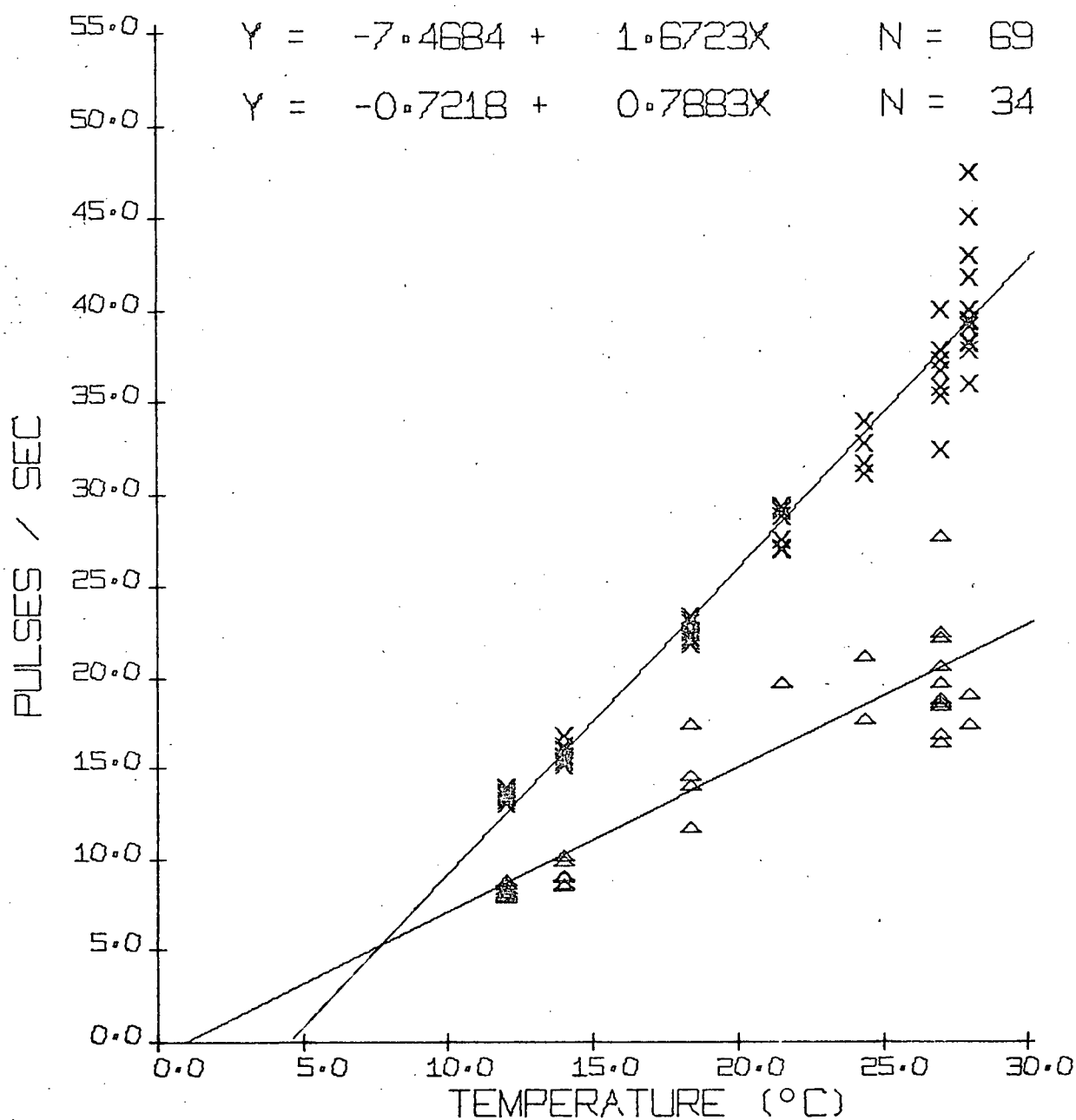


Fig. 19. Effect of temperature on pulse rate in *C. andersoni* male signals. Symbols as in Fig. 18. Specimens from Washington, Whatcom Co., Custer.



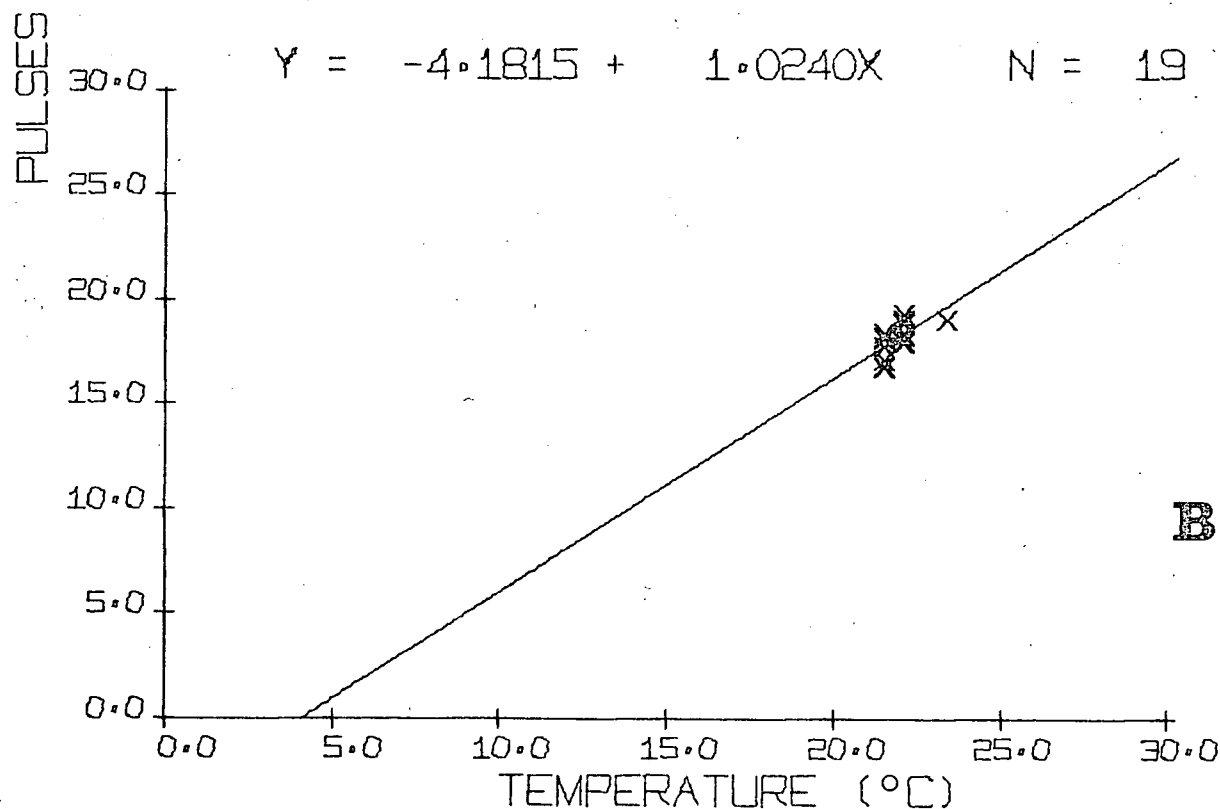
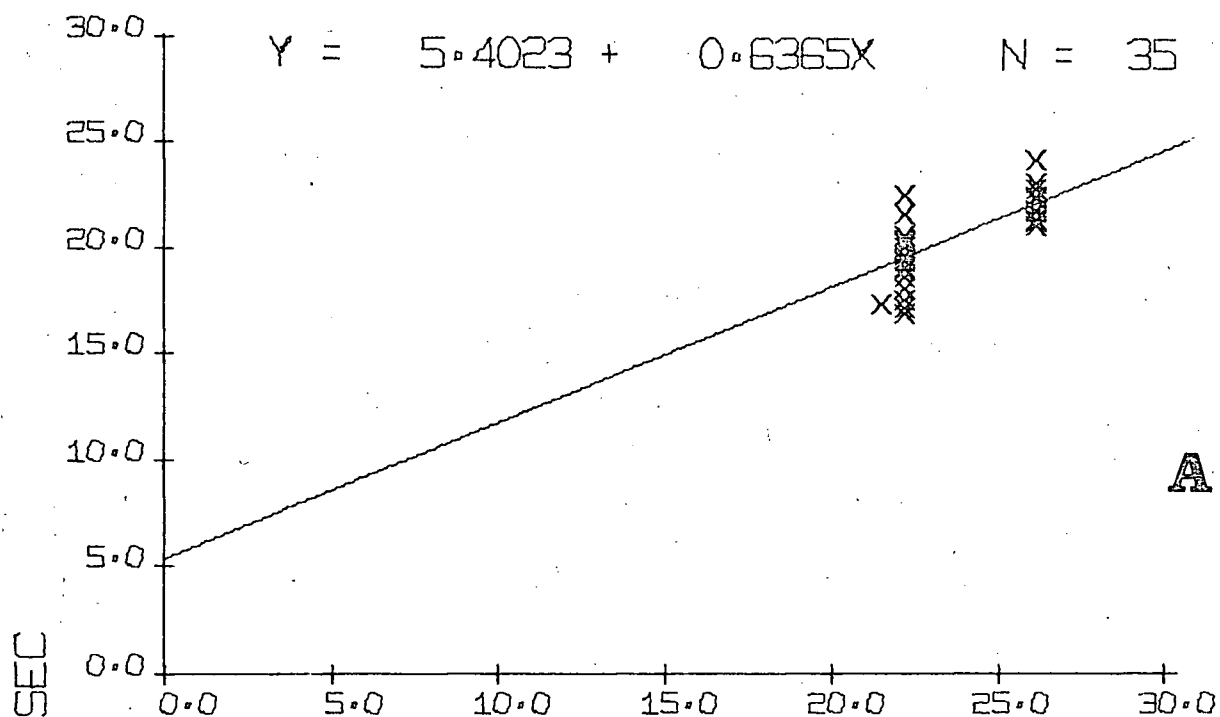


Fig. 20. Effect of temperature on pulse rate in C. andersoni (A) and C. utahensis (B) female signals. Specimens of C. andersoni from Washington, Whatcom Co., Custer and C. utahensis from Alberta, Medicine Hat.



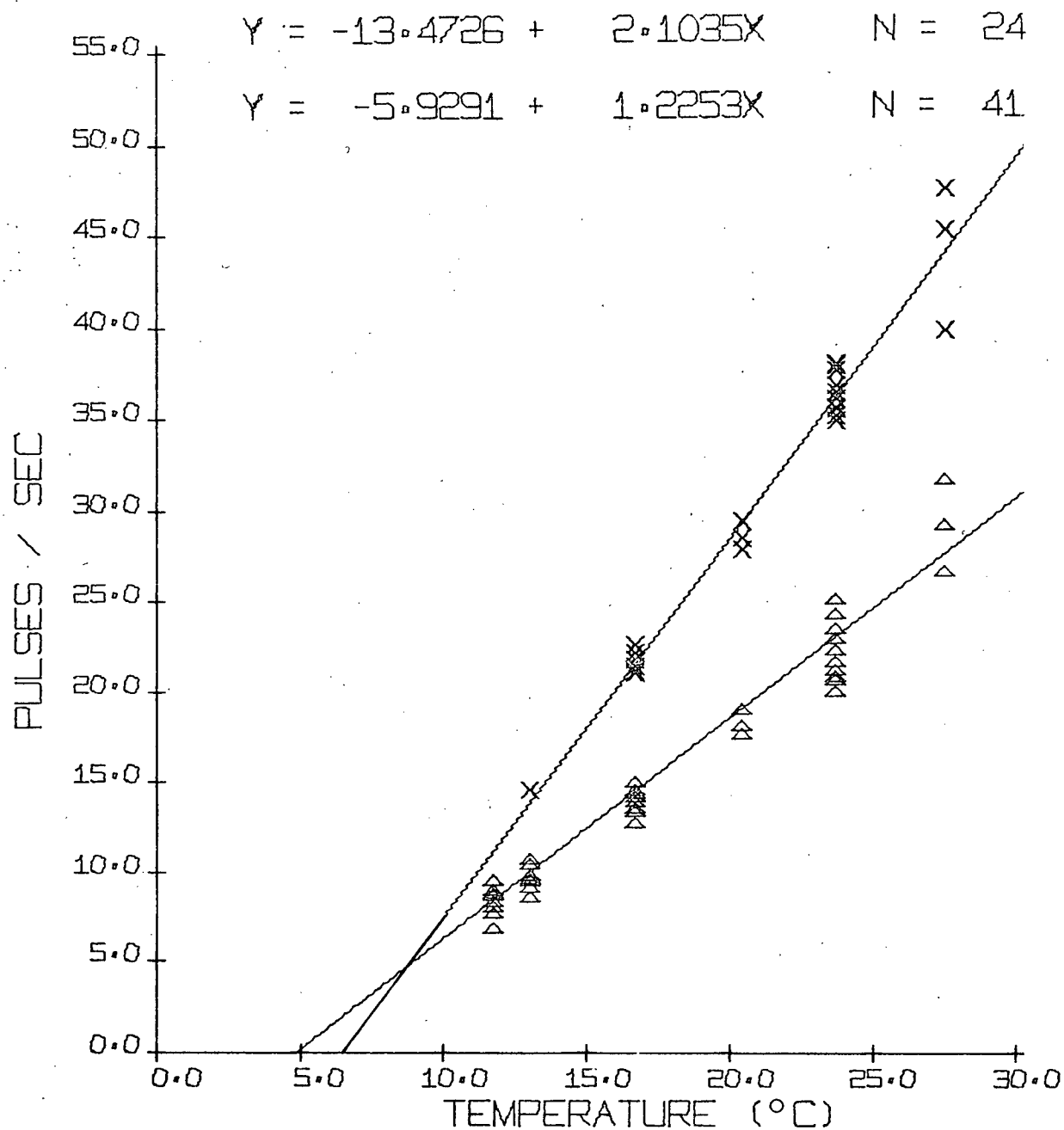


Fig. 21. Effect of temperature on pulse rate in *C. utahensis* male signals. Symbols as in Fig. 18. Specimens from Washington, Franklin Co., Scootenay Reservoir and Mesa..



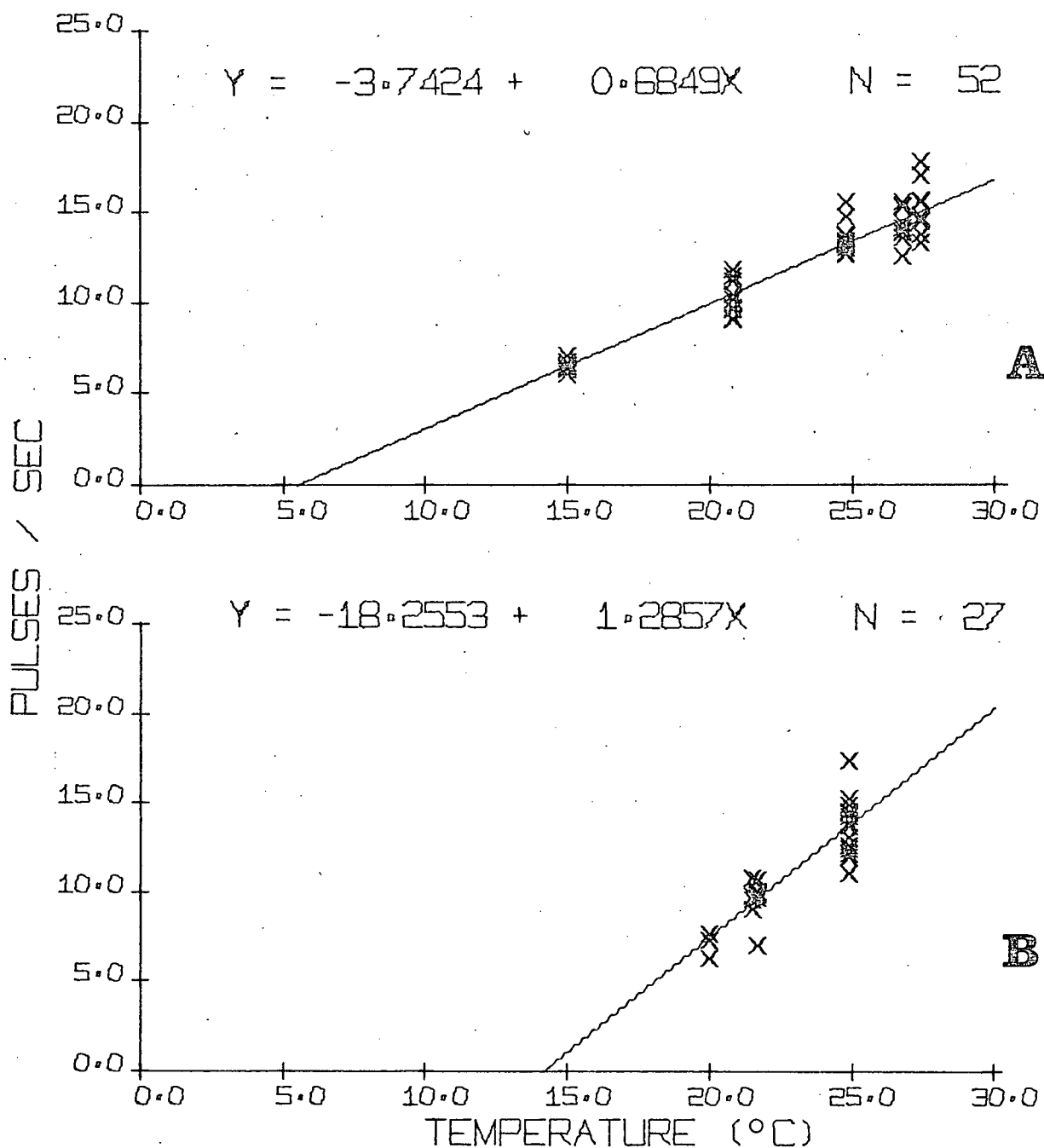


Fig. 22. Effect of temperature on pulse rate in C. dakotensis signals. A = male signals; B = female signals. Specimens from Alberta, Brooks.



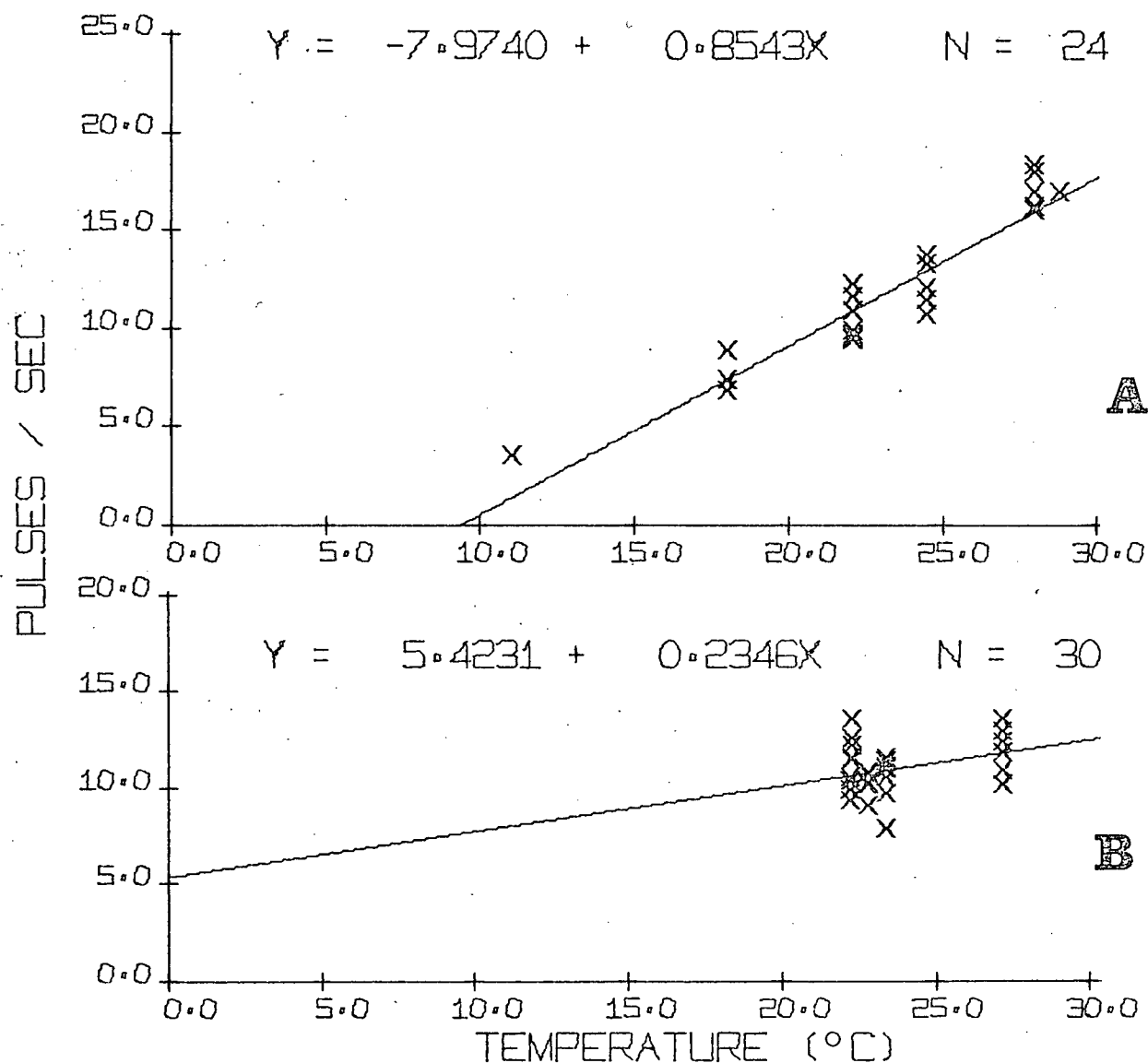


Fig. 23. Effect of temperature on pulse rate in *C. blaisdelli* signals. A = first pulse group of the male signal; B = female signal. Specimens from British Columbia, Vancouver.



$$Y = -0.2068 + 1.7823X \quad N = 69$$

$$Y = 2.9018 + 0.4458X \quad N = 30$$

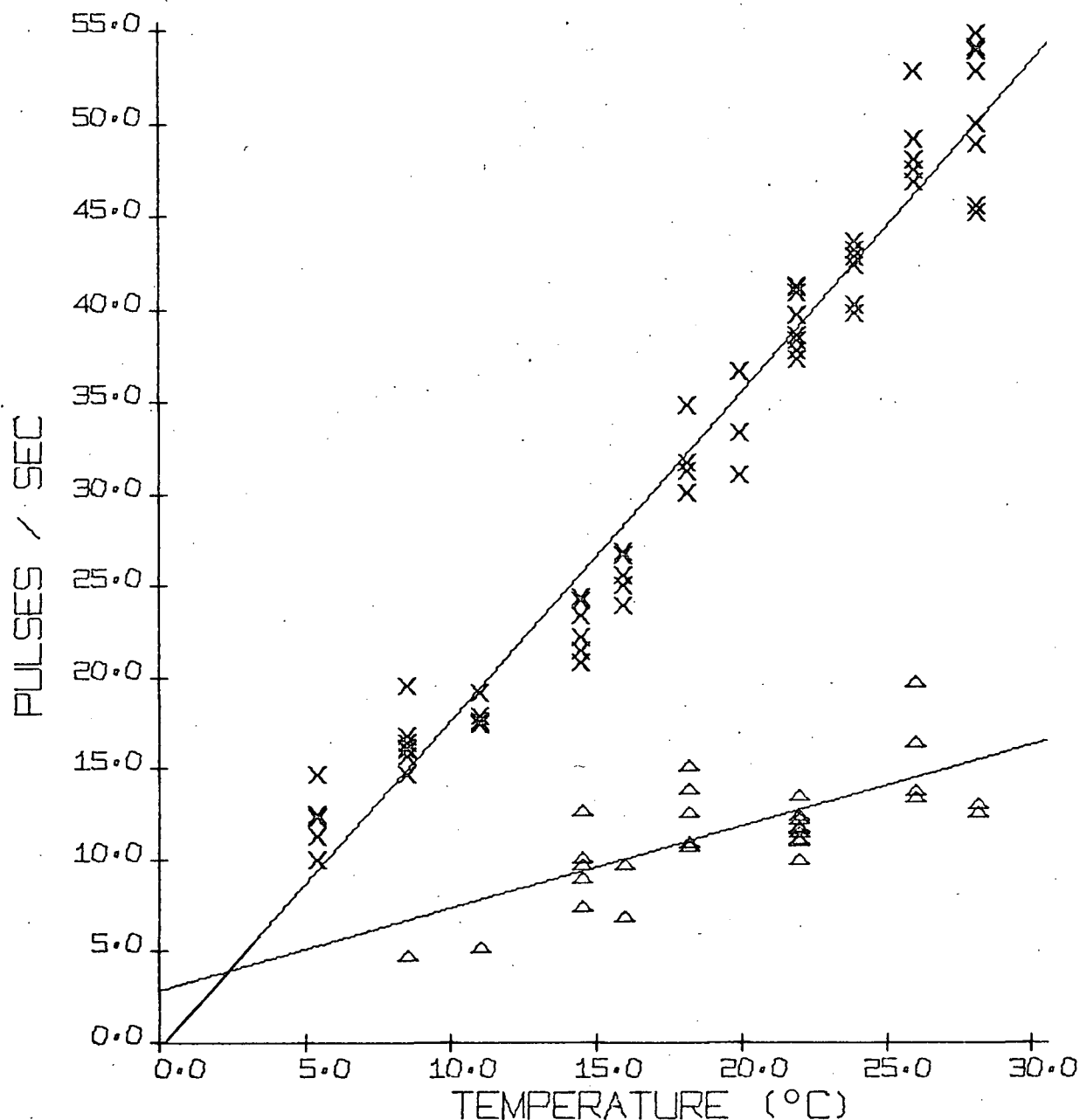


Fig. 24. Effect of temperature on pulse rate in *C. wileyae* male signals. Symbols: triangle = pulse rate within the first pulse group of the signal; X = pulse rate within subsequent pulse groups of the signal. Specimens from California, Lassen Co., Said Lake.



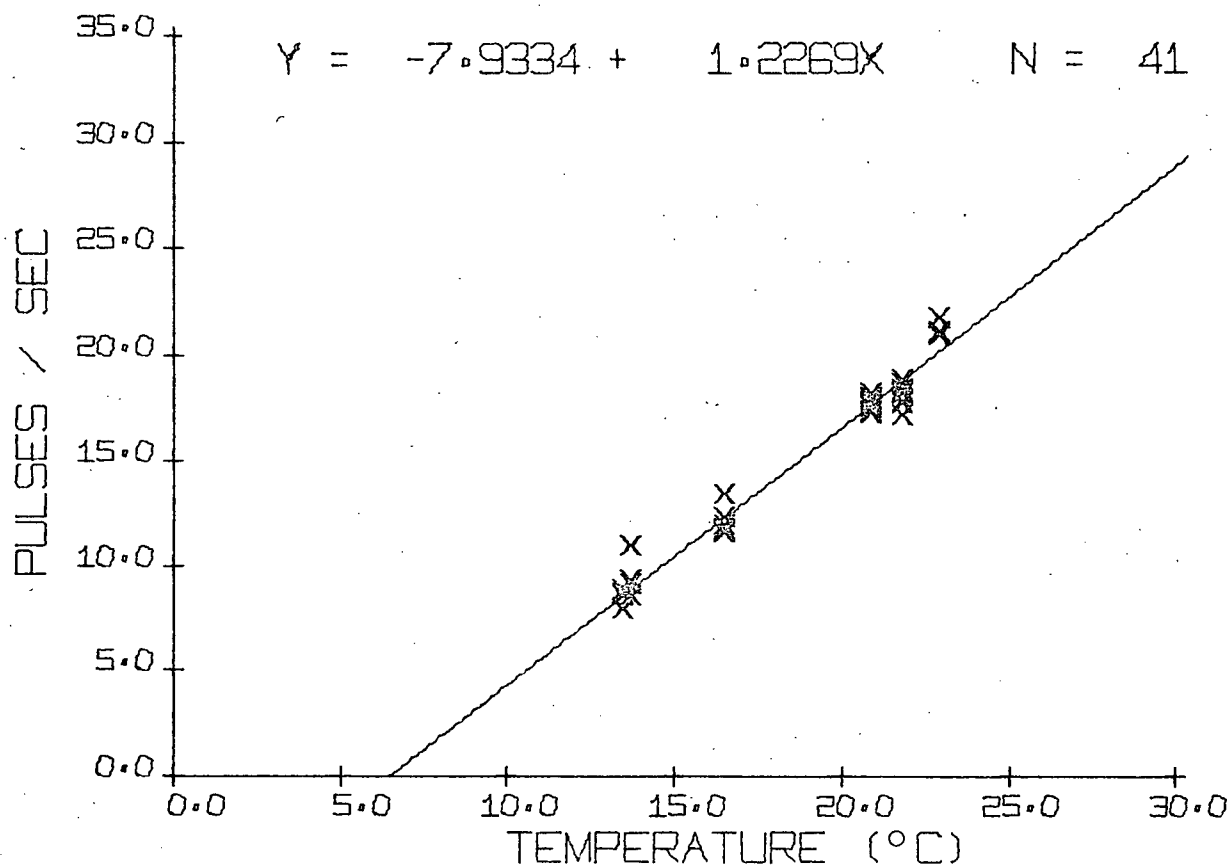


Fig. 25. Effect of temperature on pulse rate in C. wileyae female signals. Specimens from California, Lassen Co., Said Lake.



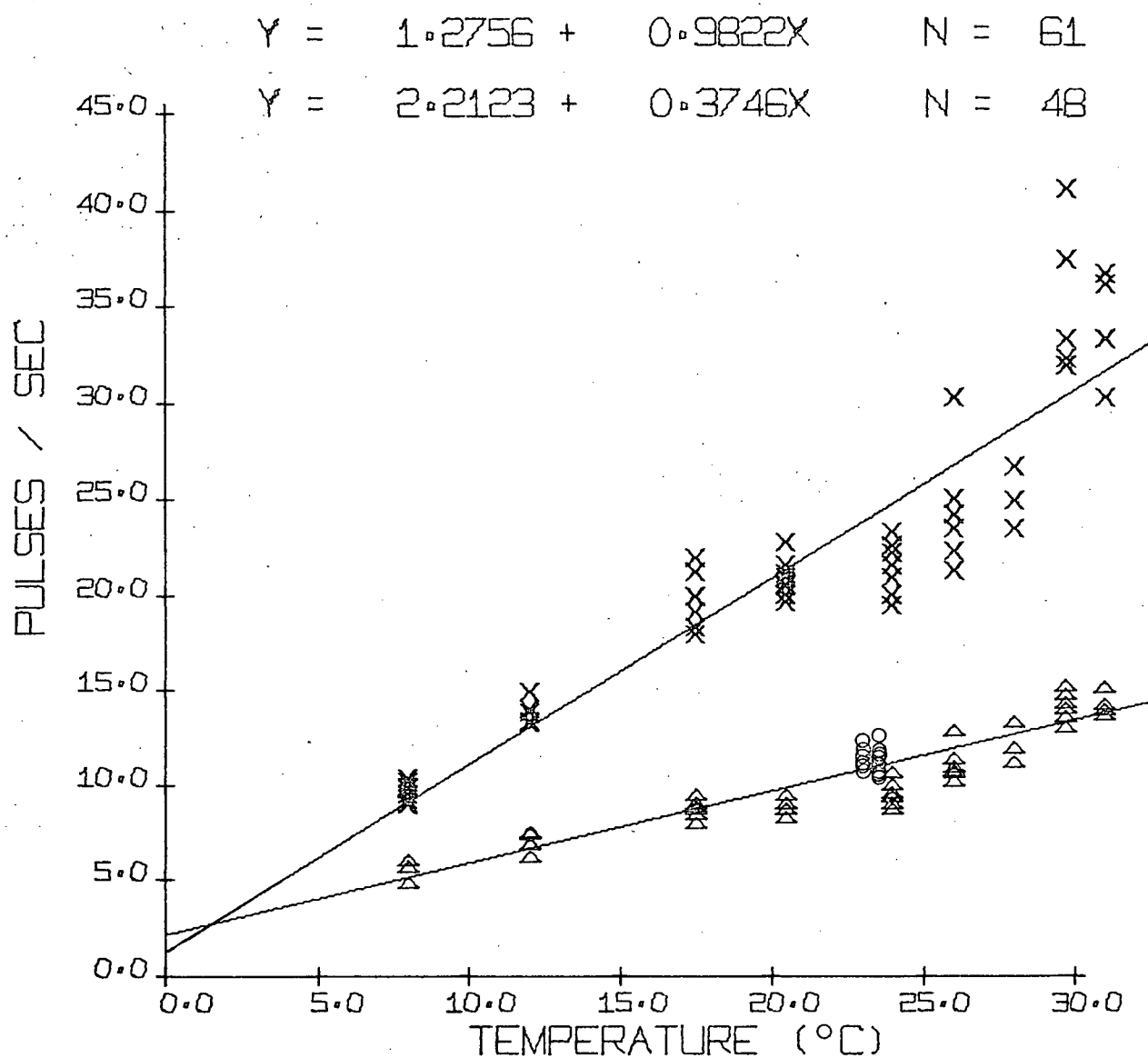


Fig. 26. Effect of temperature on pulse rate in *C. expleta* signals. Symbols as in Fig. 24, but open circle = pulse rate within pulse groups of female signals. Specimens from British Columbia, Kamloops, Lac du Bois area, LB2. Regression lines are calculated for male signals only.



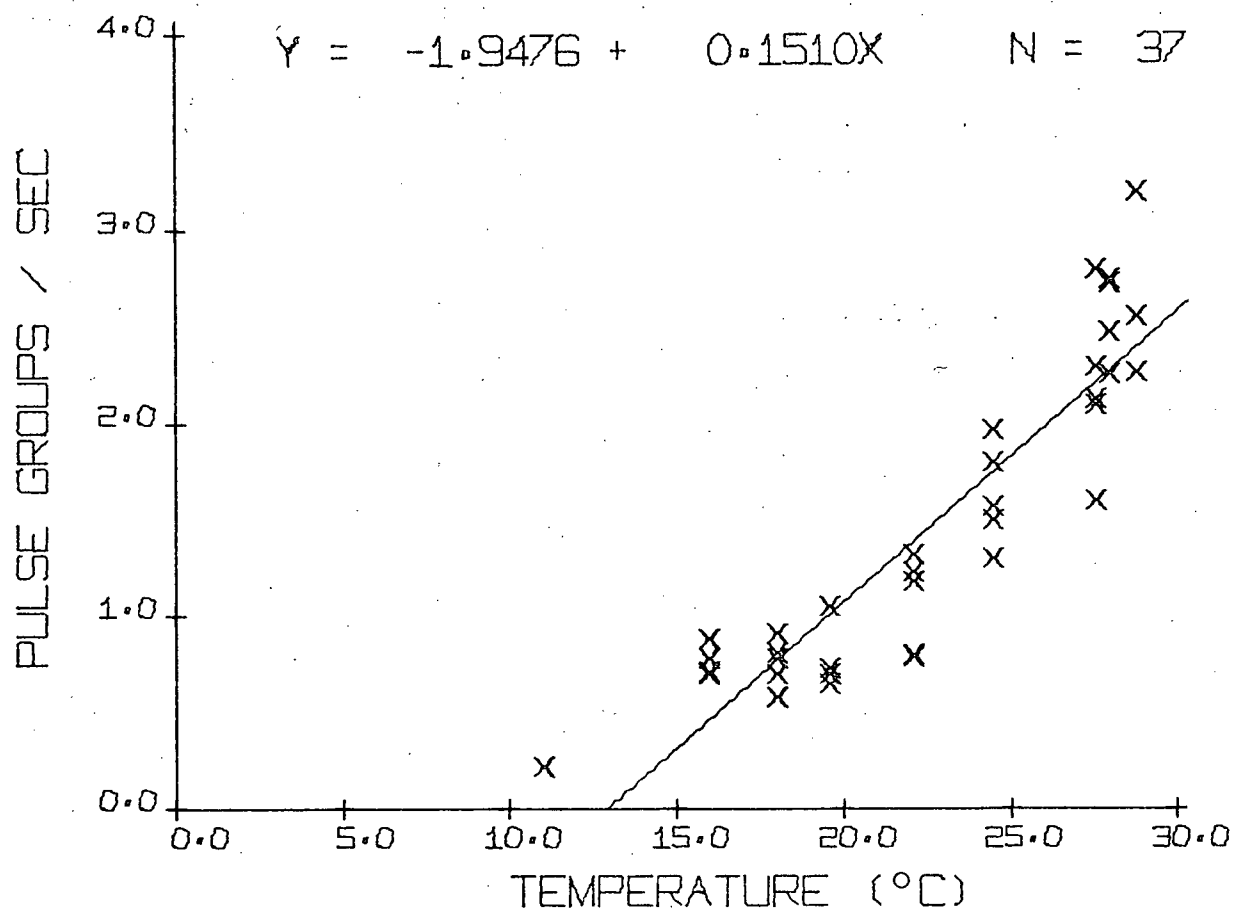


Fig. 27. Effect of temperature on repetiton rate of "uni-pulsate pulse groups" of the second part of the signal in C. blaisdelli male. Same specimens as in Fig. 23 A.



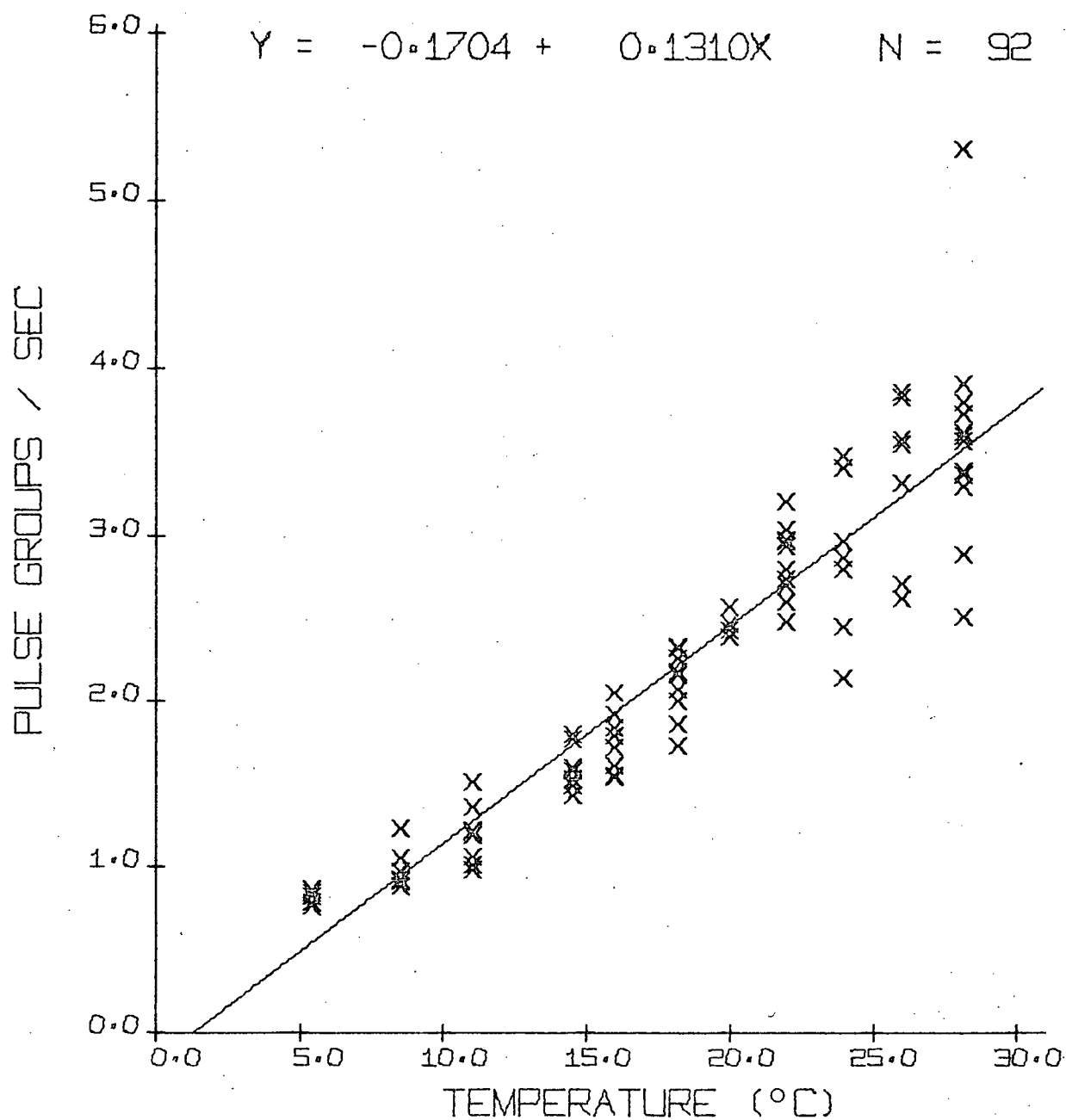


Fig. 28. Effect of temperature on repetition rate of pulse groups of the second part of the signal in C. wileyae male. Same specimens as in Fig. 24.



$$Y = -0.9417 + 0.1622X \quad N = 59$$

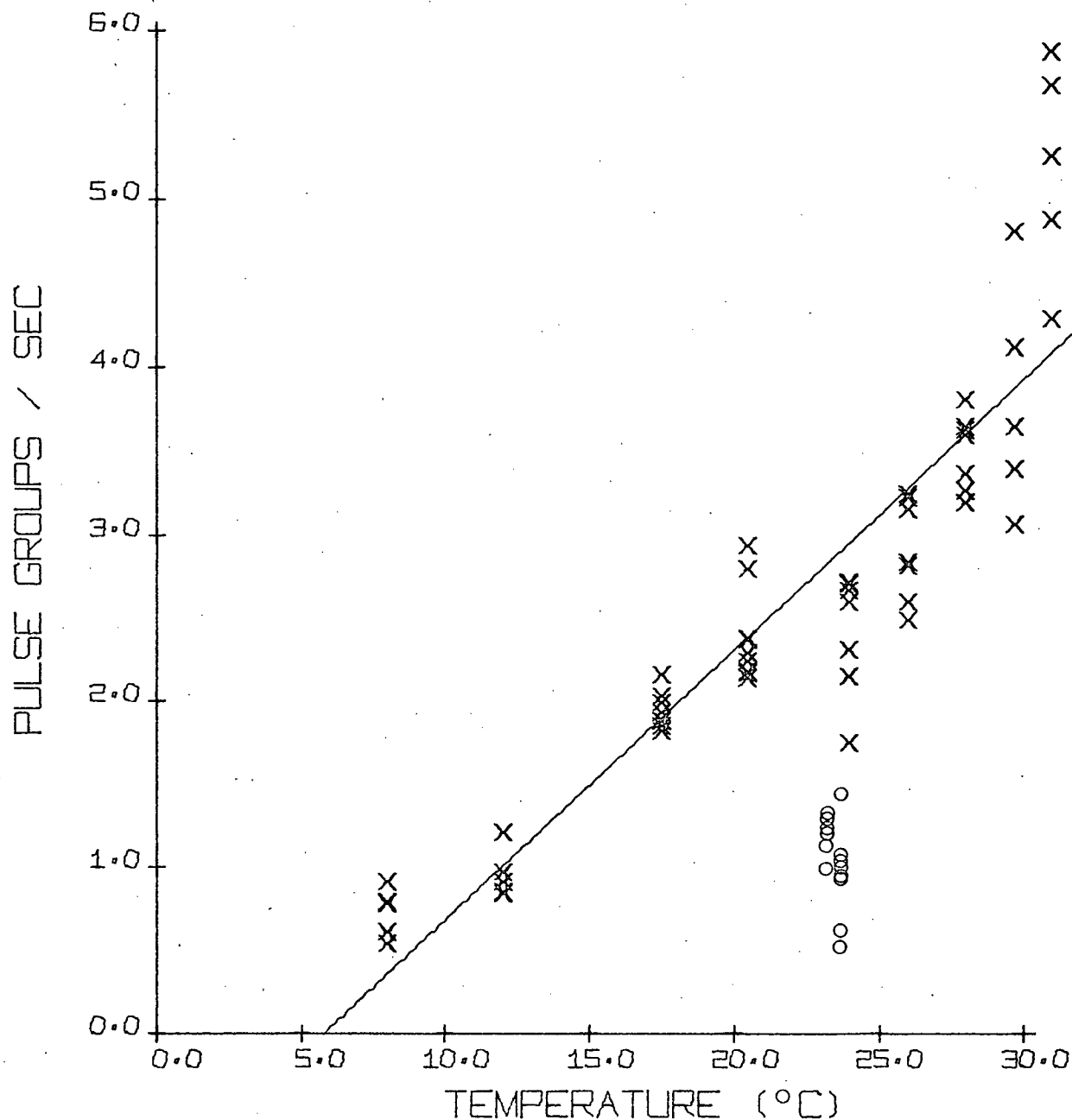


Fig. 29. Effect of temperature on repetition rate of pulse groups of the signals in *C. expleta*. Symbols: X = male signals; o = female signals. Same specimens as in Fig. 26. Regression line is calculated for male signals only.



d) Sounds produced as byproduct of cleaning movements

Two types of very faint sounds were observed to be produced and could be recorded when a specimen was resting on the hydrophone. These were: i) Sounds from simultaneous movements of the hind legs over the costal margins of the fore wings (Fig. 30 A); ii) Sounds produced by alternate movements of the hind legs when rubbed against abdominal venter or external genitalia (Fig. 30 B). These two sounds were recorded from every species and both sexes, and all were similar. The main frequency area in all species was around 3-4 kc/sec and all had approximately the same pulse rate, about 5 pulses per second for simultaneous and 10 pulses per second for alternate movements of the legs at 22°C. The sounds were most frequently produced after a specimen was transferred from one container to another. No annual rhythm was found in the production of these sounds, and they seem to be byproducts of cleaning movements.



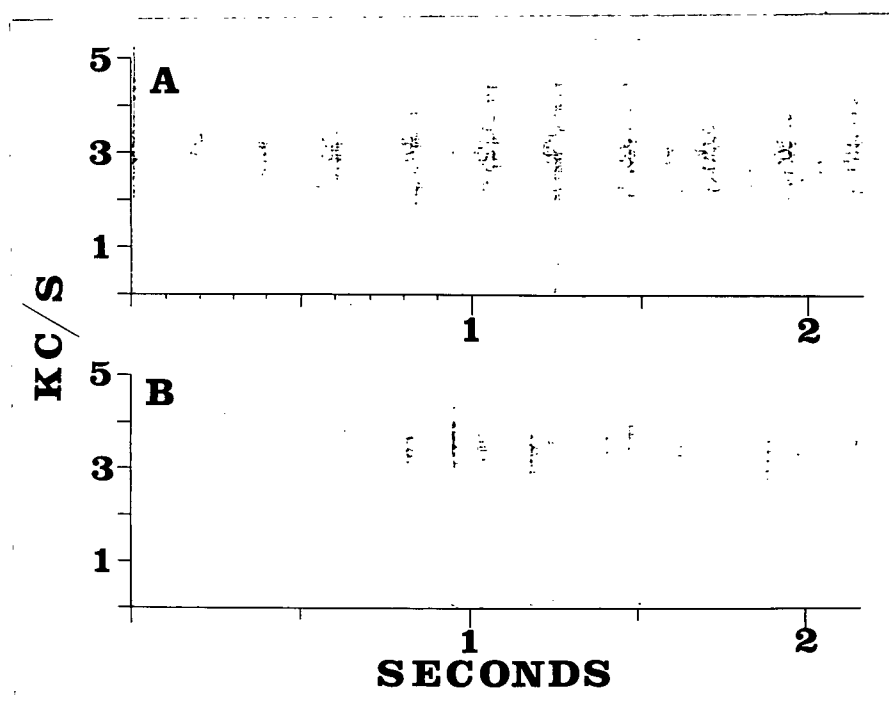


Fig. 30. Sound spectrograms of sounds produced as a byproduct of cleaning movements. A = C. andersoni female, simultaneous movements of the hind legs on fore wings; B = C. bifida male, alternate movements of the hind legs on fore wings. Recorded at 22.8 °C.



### 3. Life cycle, annual rhythm of stridulation, and gonad development

Generally Corixidae have been reported to stridulate during the spring and early summer, or during the breeding season (Mitis, 1936; Schaller, 1951; Leston, 1955; Leston and Pringle, 1963; Finke, 1968). However, in one case stridulation has also been reported during the fall (Larsén, 1938). A detailed study on life cycle of four species of Cenocorixa was undertaken in order to investigate how the annual rhythm of stridulation correlates with the life cycle and sexual maturity in this genus.

#### a) Life cycle

##### i) C. bifida and C. expleta in interior British Columbia.

The life cycle of cenocorixids was studied from standard sweep samples. Fig. 31 A shows the sequence of generations of C. bifida in East Lake, and Fig. 32 A the same species in Long Lake. It can be seen that there were two generations in both localities and in Long Lake, where the sampling was continued until late September, the data shows that adults from the second generation as well as some adults of the first generation did not reproduce, but survived to overwinter. A similar life cycle pattern was observed in C. bifida in all lakes except LB2. C. expleta also showed the same pattern in Barnes Lake and Long Lake (it only occurred in these lakes and in LB2). The life cycle of the two species were in phase from the time of appearance of the first larvae in the spring to the final molting of larvae in the fall.



Fig. 33 A shows the life cycle of C. expleta in the water body LB2. In this lake the species produced three generations: the first summer generation was very short; the second one was longer and part of it overwintered (like part of the first generation in other lakes); the third generation started in September, but was only partially successful. Owing to the low temperatures in late fall, the larval development was prolonged and many of the larvae failed to reach the adult stage before freeze-up: they died during winter. C. bifida in LB2 produced a single generation simultaneously with the first one of C. expleta, and a few larvae of C. bifida were detected before the second generation of C. expleta was completed, but adults of C. bifida were not found later in the summer (until late September when a few, apparently migrating specimens were caught).

Standard sweep samples also showed that the species were not equally abundant in the various lakes. East Lake (Fig. 31 B) had a fairly high number of C. bifida adults in the early spring, but during the summer the number decreased. The number of insects was very high during the larval life of the first generation, but low for the second generation: Westwick Lake (C. bifida) and Boitanø Lake North End (C. bifida) had similar patterns.

In Long Lake (Fig. 32 B) the number of C. bifida adults was very high in the early spring and also at the time of emergence of the new generations. C. expleta also produced two generations in this lake, but the number of specimens caught was very low throughout the summer. In Lake Lye



(C. bifida) and Barnes Lake (C. bifida and C. expleta) the life cycle pattern was similar to that of C. bifida in Long Lake.

In the water body LB2 (Fig. 33 B) there were low numbers of C. expleta specimens during the early spring and the first summer generation, but in the second and third generations the population increased markedly. The number of C. bifida specimens was low both in the early summer and late fall, and none of this species was observed during July and August.

The differences in the life cycle of the species in the various lakes may reflect differences in temperature and productivity of the lakes. Temperature data for each lake as well as the air temperatures at Westwick Lake are presented in Figs. 34-35. In general, the data show few differences in the lake temperatures, with only LB2 appearing on average slightly warmer, and Long Lake a little cooler than the others. No study of the primary productivity was undertaken, but conductivity correlates with productivity (Rawson and Moore, 1944), and differences in this environmental parameter are obvious (Fig. 36).



Fig. 31. Sequence of generations of C. bifida in East Lake according to standard sweep samples in 1969. A = per cent of adult specimens and different larval instars. Symbols: OW = overwintered adults; 1 = first generation adults; 2 = second generation adults; I to V = different larval instars. B = actual number of specimens caught. Symbols: continuous line = adult specimens (generations as in A above); dotted line = larvae.



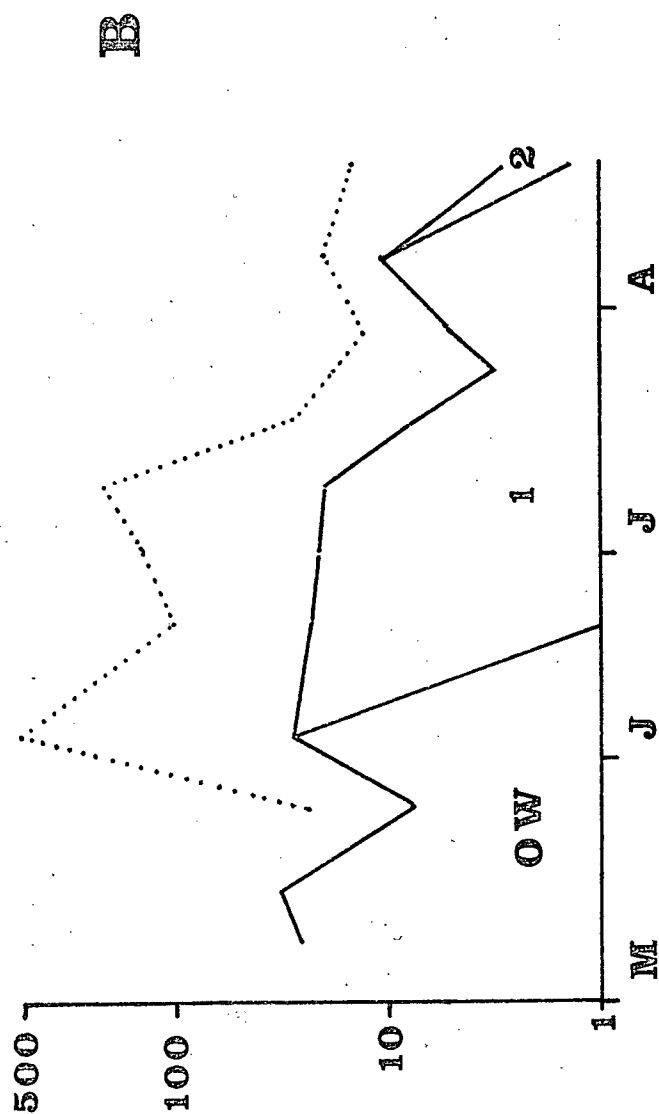
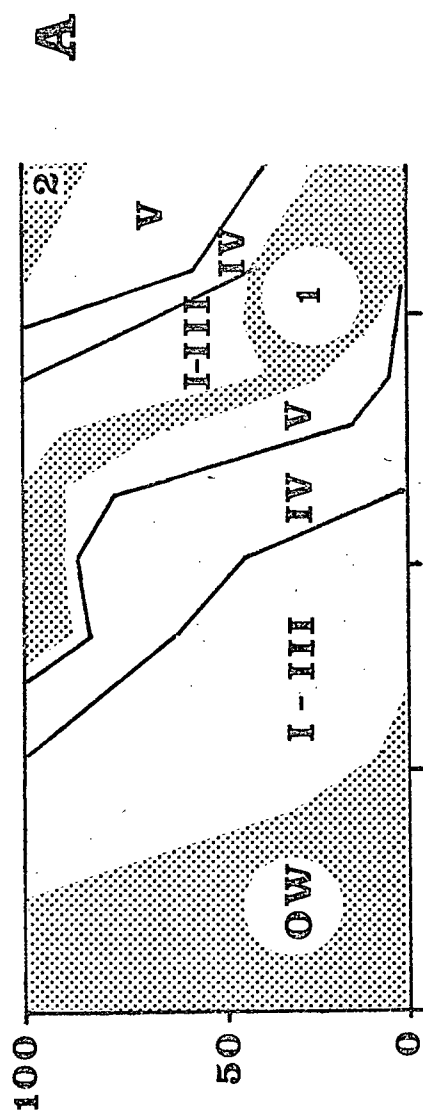




Fig. 32. Sequence of generations of C. bifida in Long Lake according to standard sweep samples in 1969. A = per cent of adult specimens and different larval instars. B = actual number of specimens caught. Symbols as in Fig. 31.



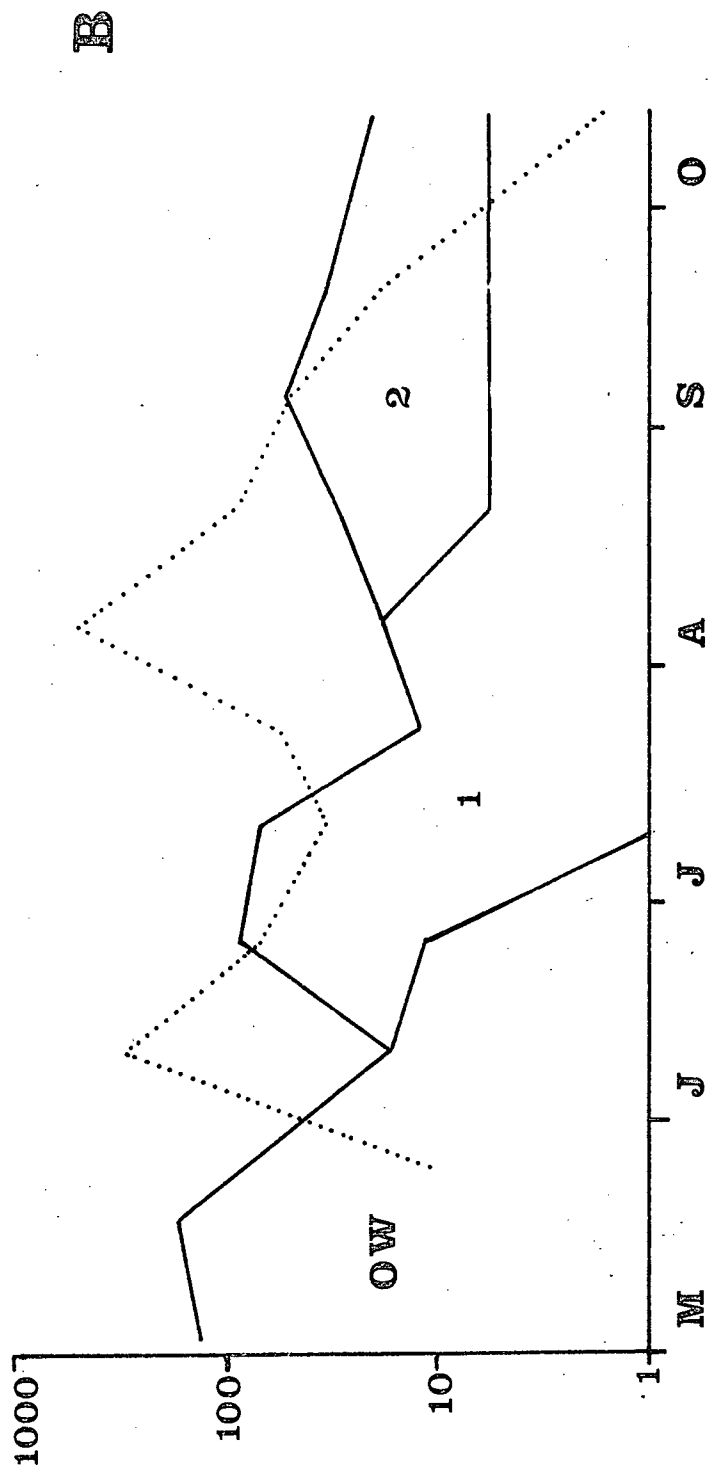
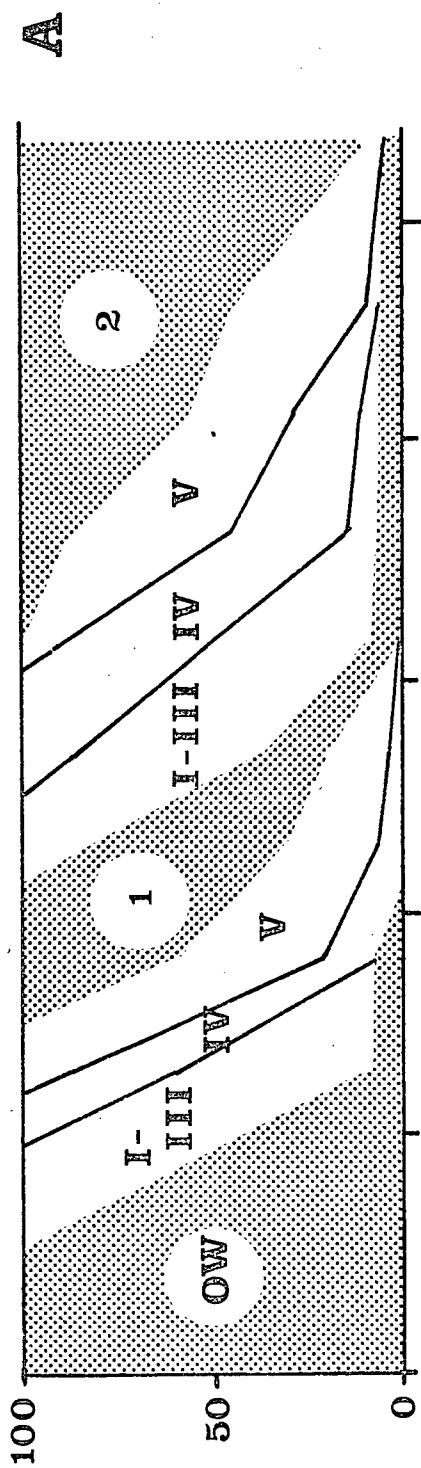




Fig. 33. Sequence of generations of C. expleta in LB2 according to standard sweep samples in 1969. A = per cent of adult specimens and different larval instars. B = actual number of specimens caught. Symbols as in Fig. 31, but 3 = third generation.



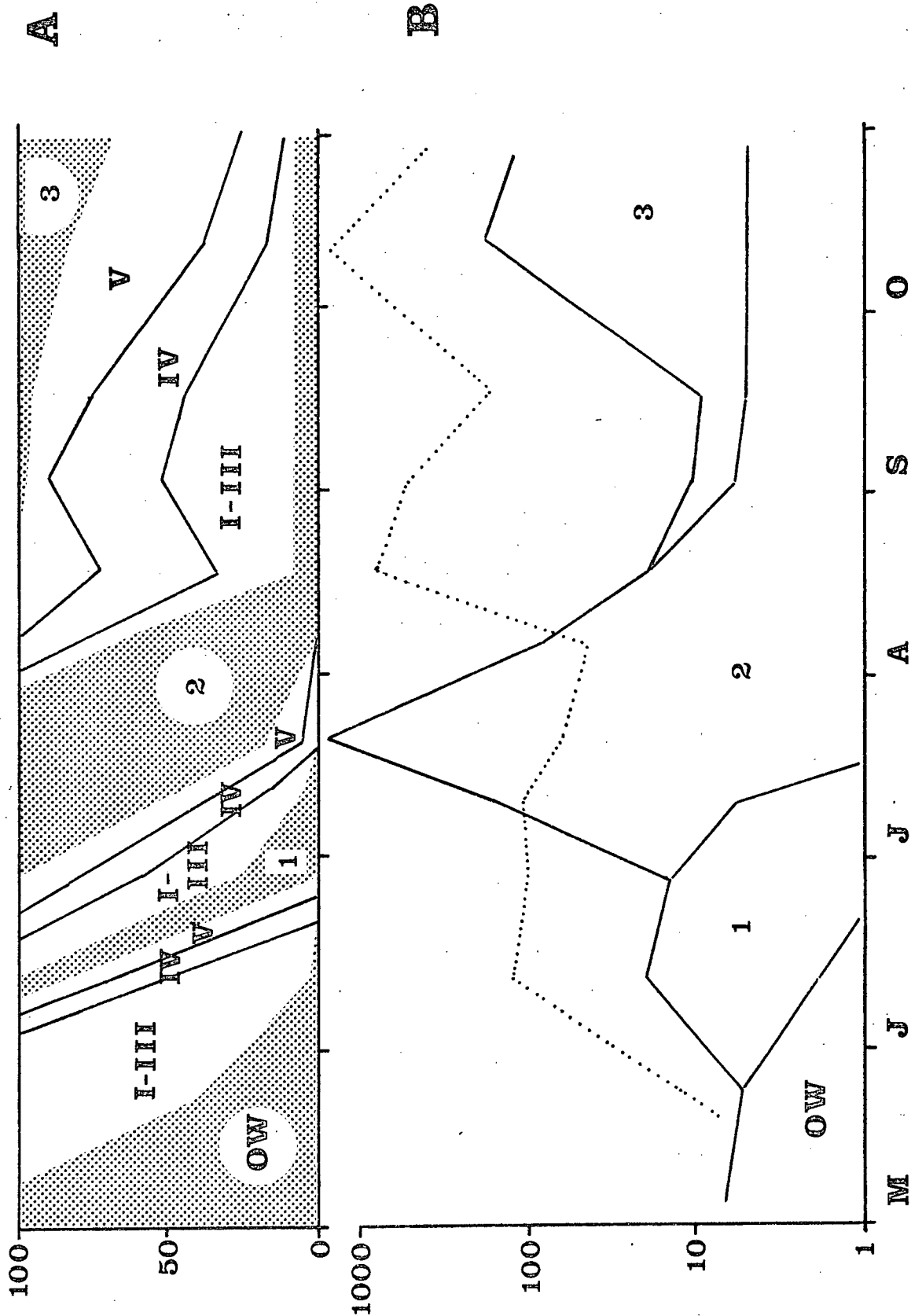




Fig. 34. Daily maximum and minimum temperatures at Westwick Lake and Boitano Lake during the summer of 1969. A = Westwick Lake, air temperature; B = Westwick Lake, shallow water (20 cm); C = Boitano Lake, shallow water (30 cm); D = Boitano Lake North End, shallow water (15 cm).



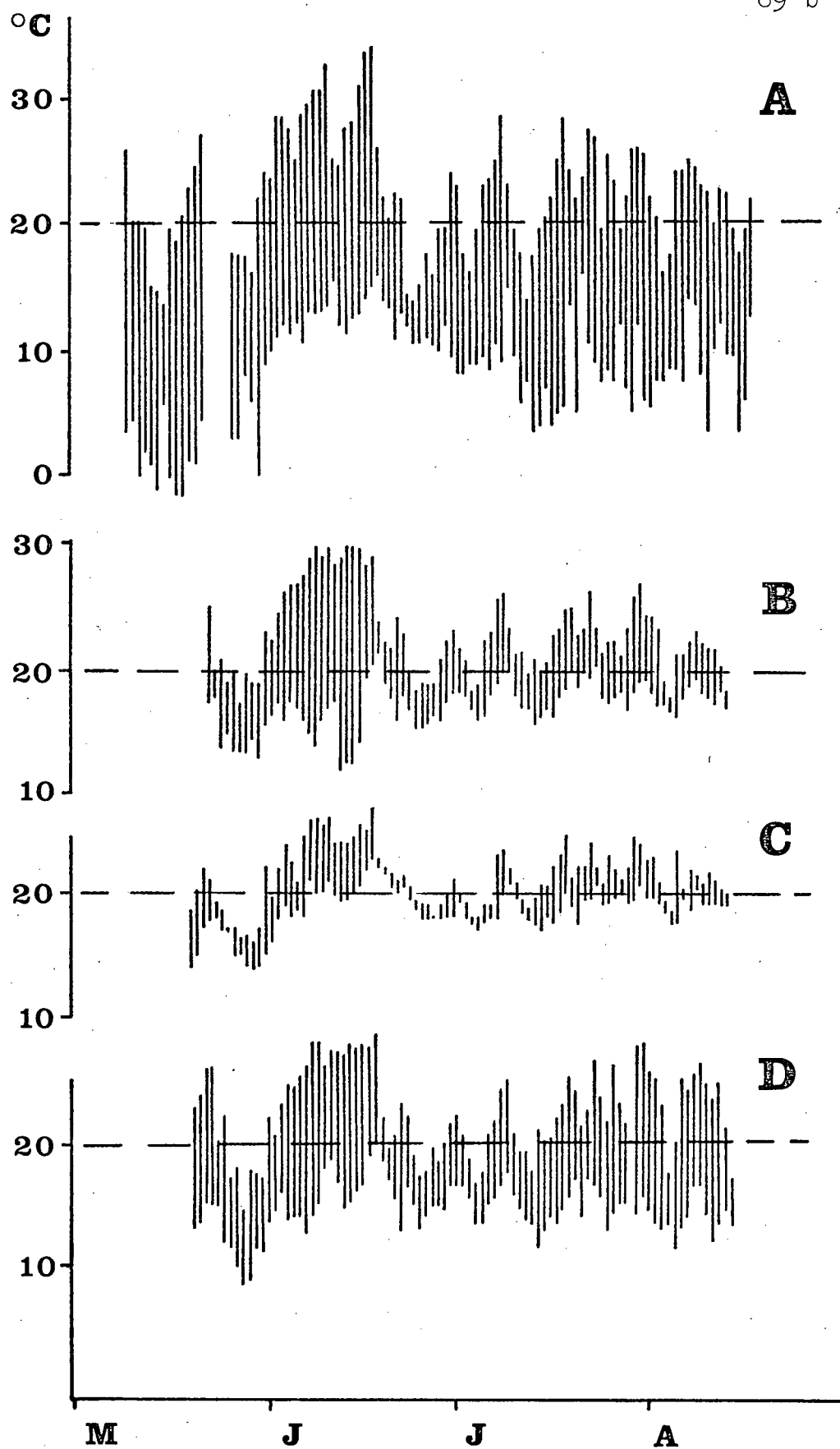




Fig. 35. Daily maximum and minimum temperatures in five lakes in the interior British Columbia during the summer of 1969. A = East Lake (20 cm); B = Lake Lye (30 cm); C = Barnes Lake (25 cm); D = Long Lake (30 cm); E = LB2 (30 cm).



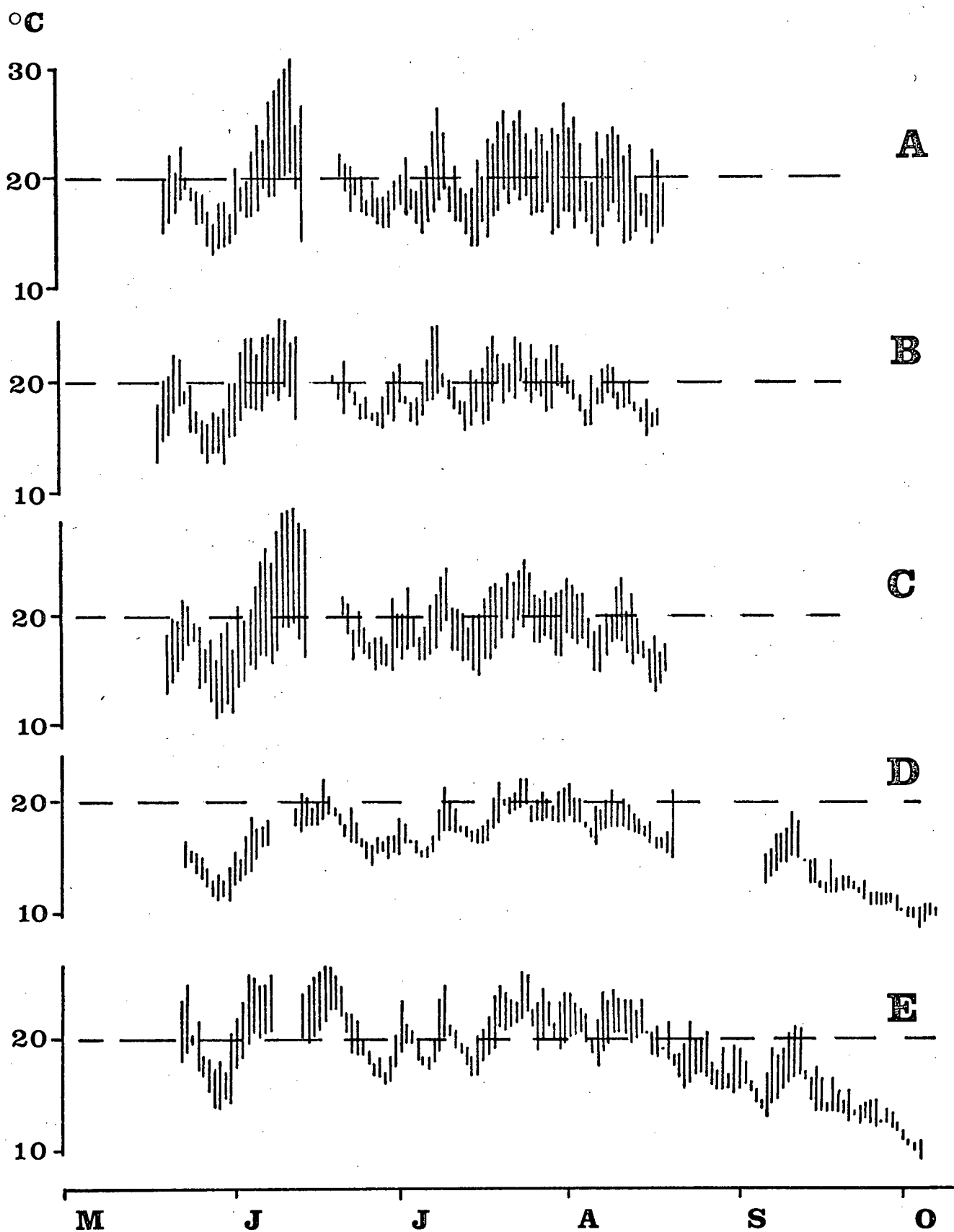


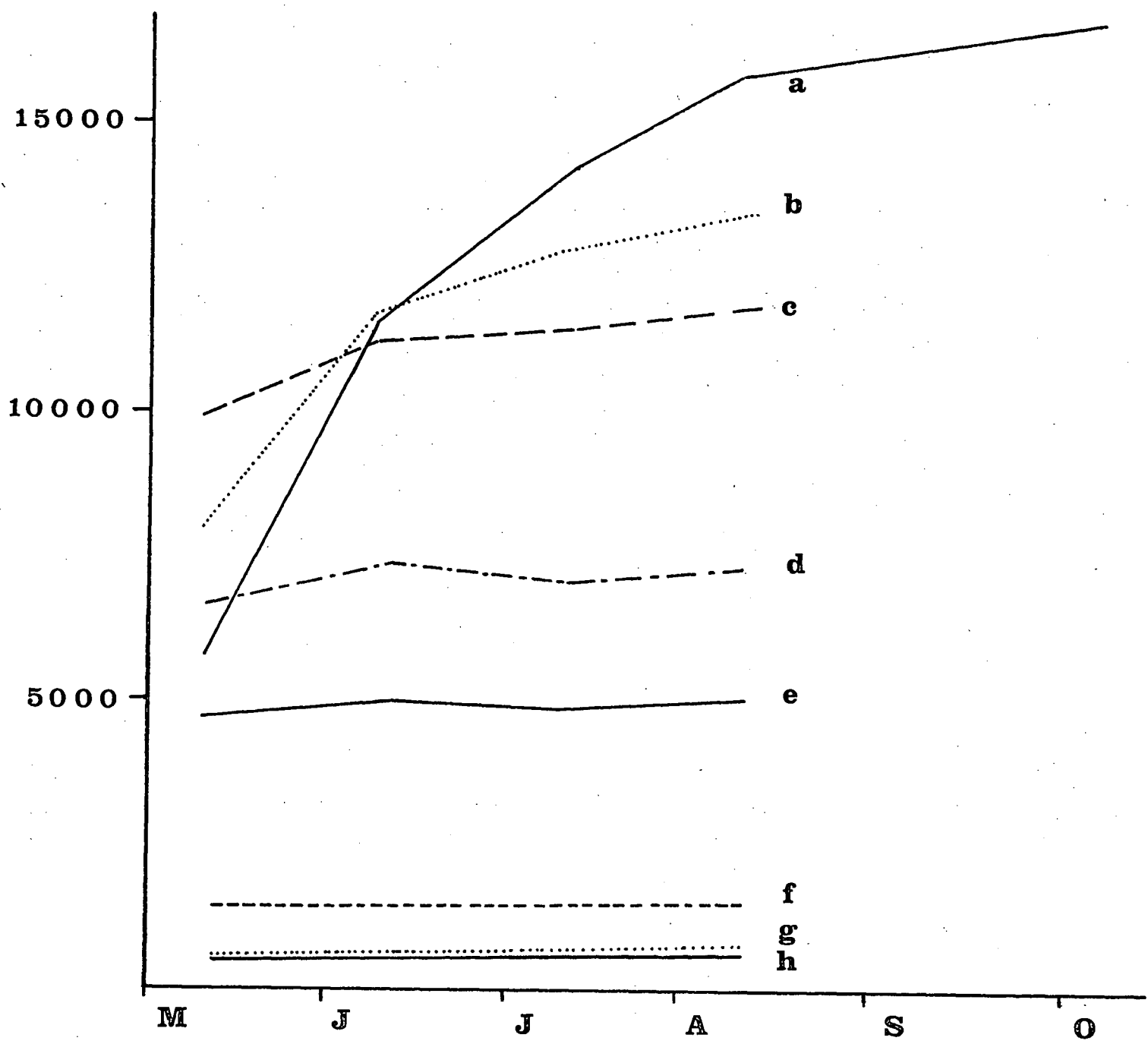


Fig. 36. Specific conductivity of surface water in eight water bodies in the interior British Columbia during the summer of 1969. a = LB2; b = Barnes Lake; c = Long Lake; d = Lake Lye; e = Boitano Lake; f = Westwick Lake; g = East Lake; h = Boitano Lake North End.



71.2

Micromhos/cm at 25°C





ii) C. andersoni and C. blaisdelli, the species of the Pacific Westcoast.

Standard sweep samples showed that there were two generations of C. andersoni in the Custer golf course pond during the summer of 1970 (Fig. 37 A). Overwintered adults were caught until mid April, although a few survived in the pond until mid May. The first generation adults appeared in mid June, and the second generation in early August. The first larvae appeared as early as the beginning of April, much earlier than in the interior species, but the larval development in C. andersoni lasted considerably longer than in the interior species.

The number of insects in the sweep samples throughout the summer was fairly low (Fig. 37 B); the pond apparently has a low productivity (conductivity of the surface water from 260 micromhos/cm at 25°C in April to 485 micromhos/cm at 25°C in October). However, water from the pond was also used for irrigation of the adjacent golf course lawn from June to August, and the sudden decrease in the water level may have affected the population of C. andersoni by destroying eggs and young larvae which typically are found at the very edge of the water body.

Temperature in coastal areas is much more even throughout the year when compared to the interior temperatures. On the coast there was practically no freeze-up during the winter of 1969-1970. However, the summer temperatures are almost the same as in the interior except for some hot periods which last longer in the interior. The early and



mild spring as well as the relatively warm late fall apparently allow much longer breeding and growing periods in the coastal areas. Thus, although the golf course pond was low in productivity, the long summer allowed the completion of the two generations. For comparison with the interior temperature data, Fig. 38 shows air temperature data from Surrey, Surrey Municipal Hall Weather Station, British Columbia (about 25 kilometres north of Custer), during the time when observations on C. andersoni were made.

Life cycle of C. blaisdelli was initially studied in a semitemporary pond in the corner of 16th Avenue and Westbrook Crescent, Vancouver. From October 1969 until May 1970 the species was abundant in the pond. The first larvae were observed on the same day as those of C. andersoni in Custer (late April), and the initial adults of the first generation of C. blaisdelli appeared in early June. However, owing to the temporary nature of the habitat, these adults left the pond in about two weeks as it was drying up. In July and August the species was occasionally found in other temporary ponds, and in a permanent pond at the MacCleery Golf Course, Vancouver. However, the population of this last pond was too scattered to give any information on the sequence of generations, but it is assumed that only two generations of C. blaisdelli were produced during the summer.



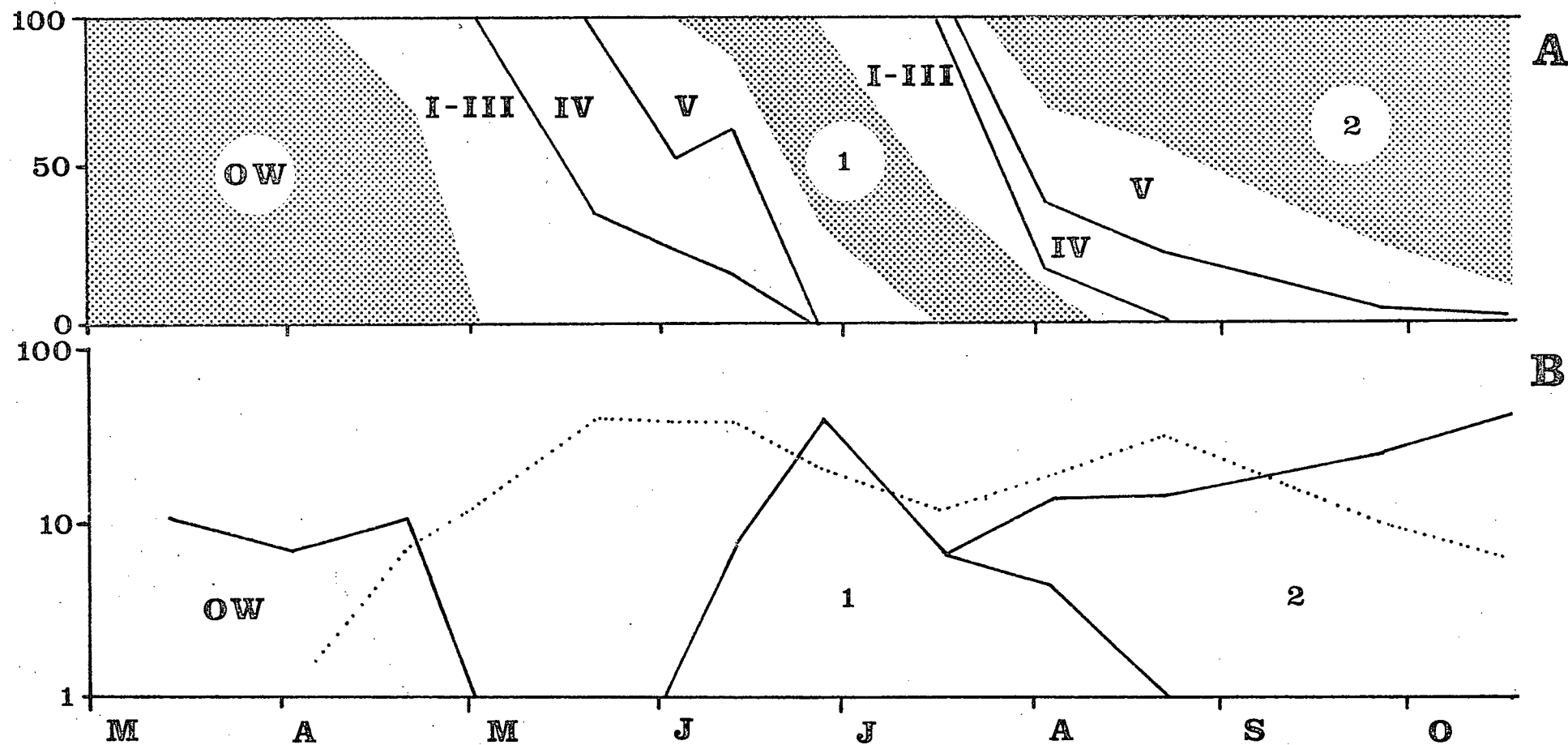
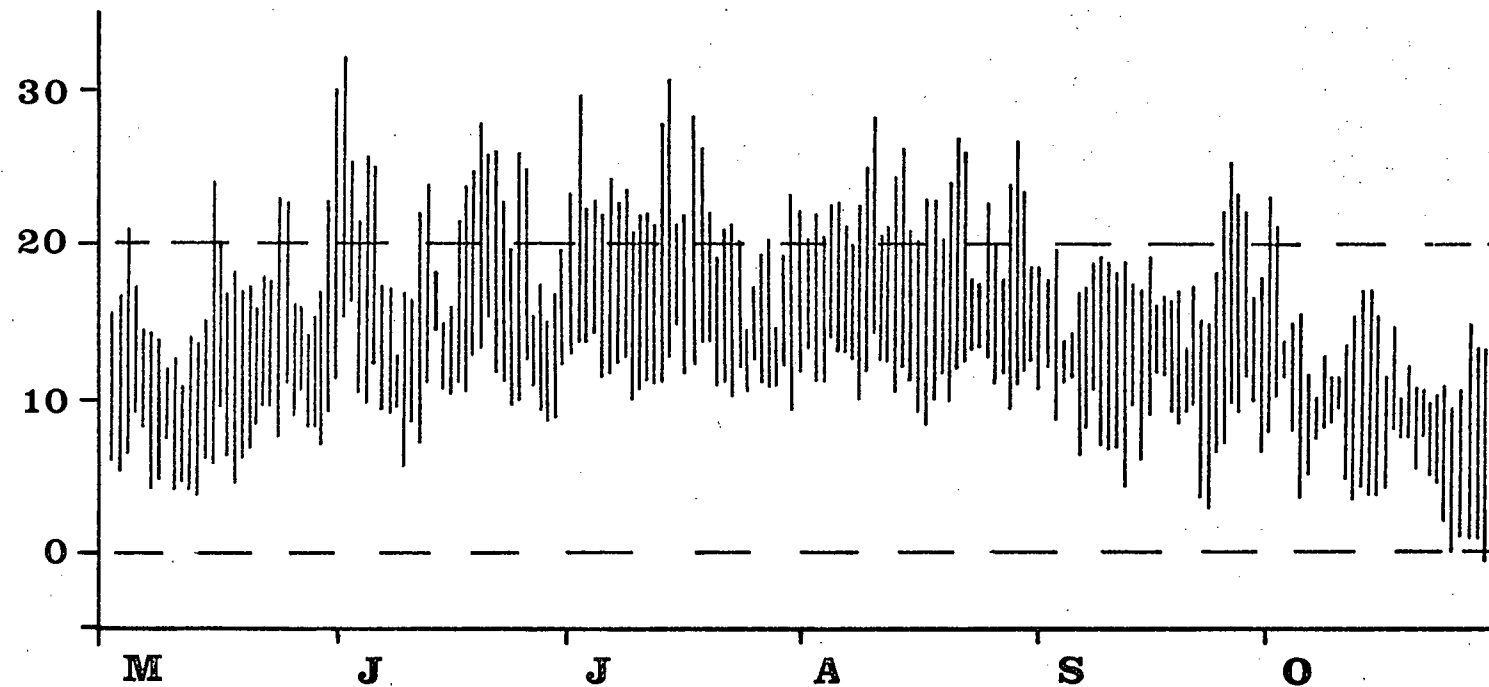
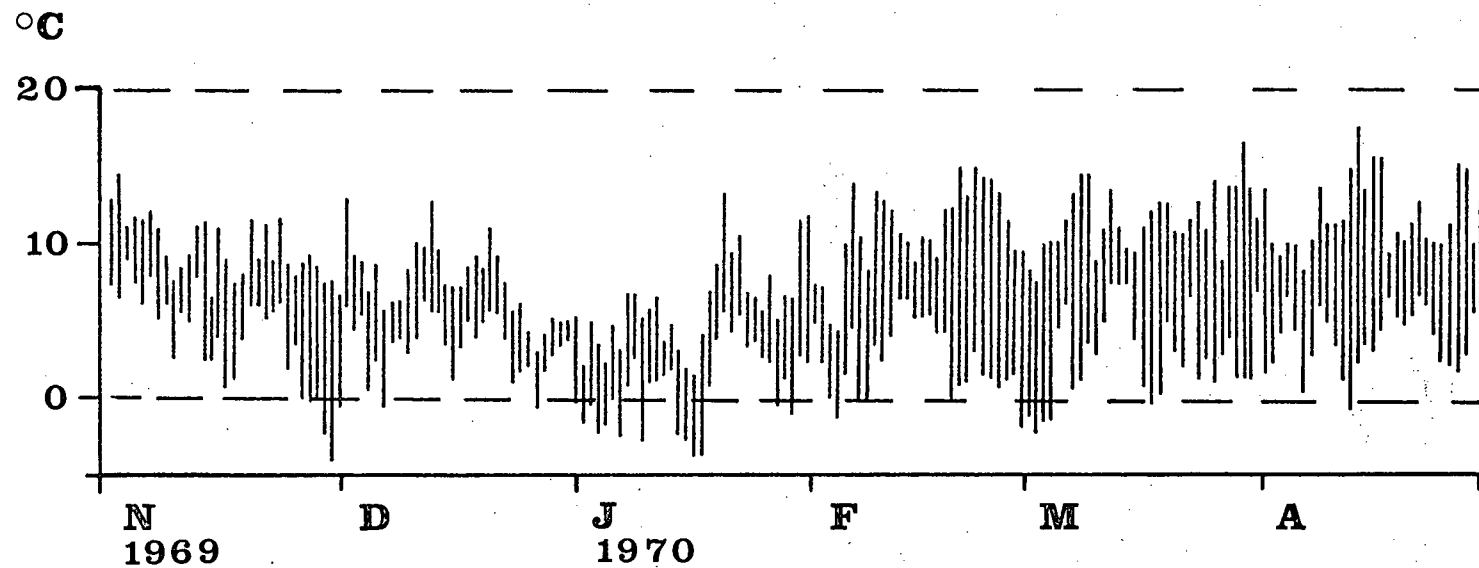


Fig. 37. Sequence of generations of *C. andersoni* in Custer golf course pond according to standard sweep samples in 1970. A = per cent of adult specimens and different larval instars. B = actual number of specimens caught. Further explanations as in Fig. 31.



Fig. 38. Daily maximum and minimum temperatures at Surrey Municipal Hall Weather Station, British Columbia, during the period of November 1969 - October 1970.







## b) Gonad development

### Females:

In the ovarian development the following three stages were distinguished: A) Undeveloped stage, with no recognisable oöcytes (newly emerged females); B) Intermediate stage, with oöcytes recognisable, but no chorionated eggs present (overwintering females); and C) Mature stage, with chorionated eggs present. Fig. 39 shows light microscope photographs of these stages in C. bifida. Because stages A) and B) grade into each other and represent immature ovarian stages, they were grouped together in the final analysis.

### Males:

In spermatogenesis the following stages were recognised: A) Zone of spermatogonia at the tip of the testicular follicles; B) Zone of reduction division, with chromosomes clearly visible; C) Cysts of spermatids in their early developmental stage, while spermatids were still round; D) Cysts of spermatids in their late developmental stage, while spermatids had an oval shape with both ends acutely produced; E) Cysts of mature spermatozoa, while the sperm had fully developed tails. Fig. 40 shows light microscope photographs of the stages of spermatogenesis in C. bifida.

Figs. 41-43 show the presence of mature and immature specimens in East Lake (C. bifida), Long Lake (C. bifida), LB2 (C. expleta), and Custer golf course pond (C. andersoni). The development in the interior area was somewhat different from that in the coastal area, and so the two areas are considered separately below.



Fig. 39. Light microscope photographs of stages of ovarian development in C. bifida. A = newly emerged specimen, ovarian follicles undeveloped; B = late fall specimen, intermediate stage with oocytes, but no chorionated eggs present; C = mature stage, chorionated eggs present (this specimen also demonstrates the stage when the female is receptive: eggs in lateral oviducts). Length of the scale indicator is one millimeter divided into 0.01 mm parts.



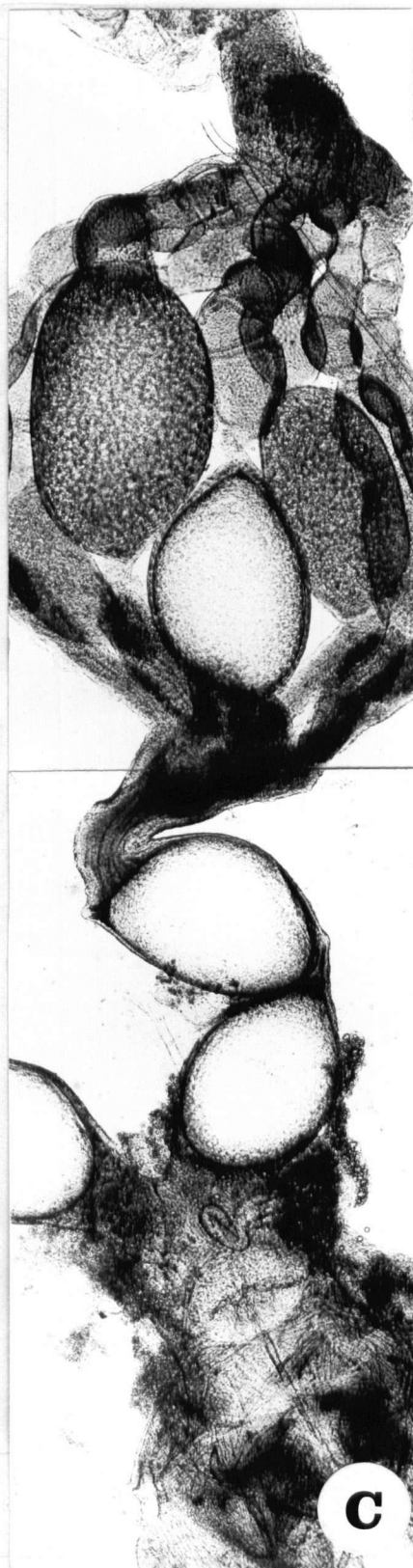
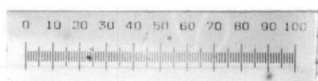
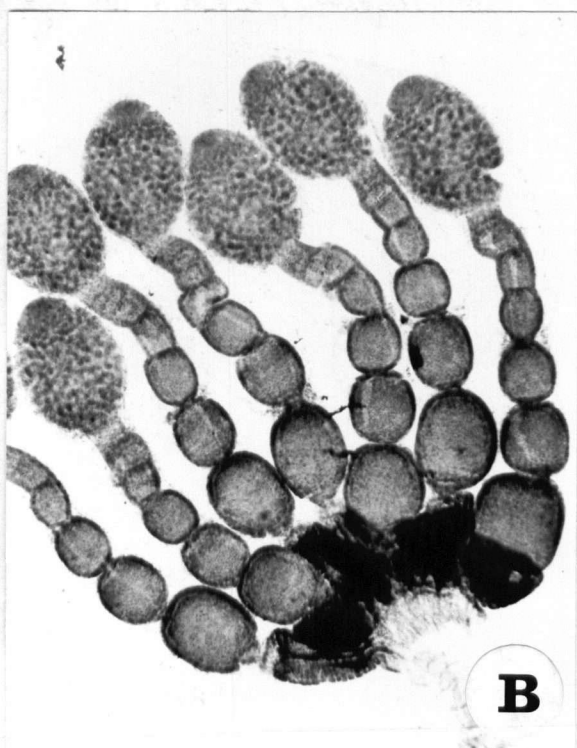
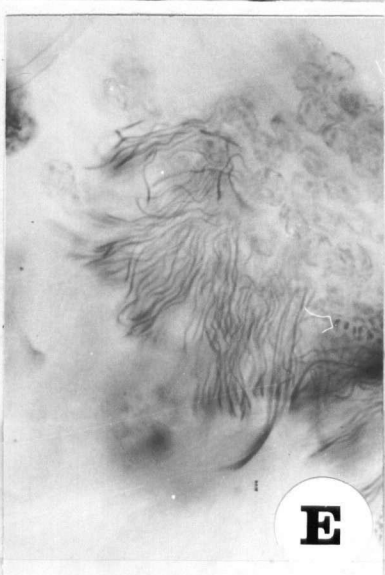
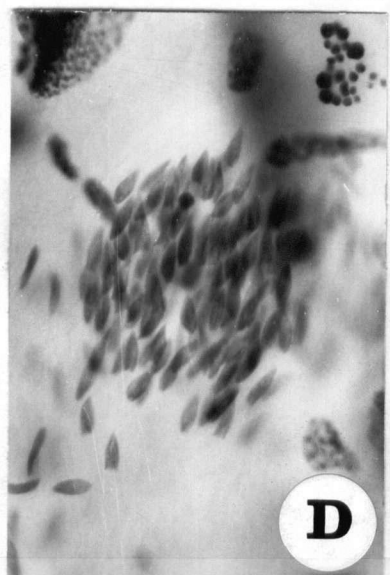
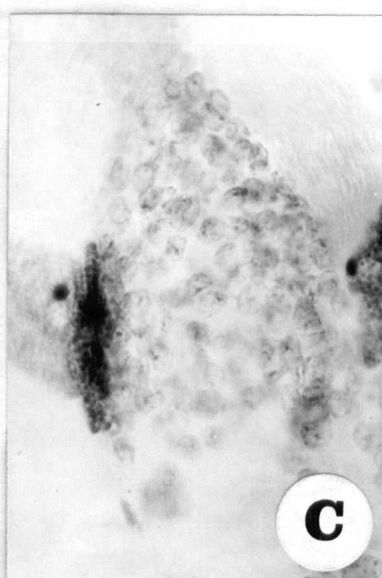
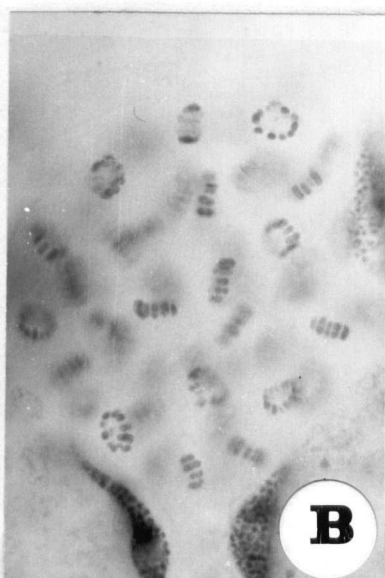
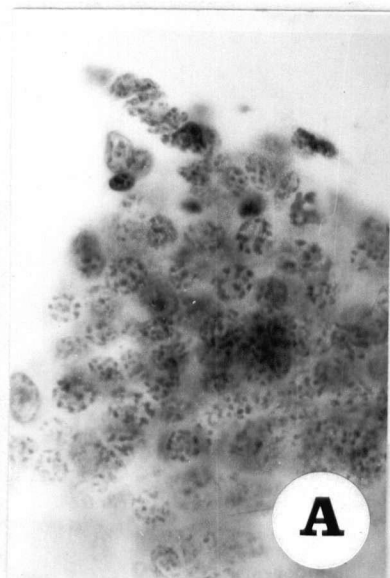




Fig. 40. Light microscope photographs of stages of spermatogenesis in C. bifida. A = zone of spermatogonia at the tip of the testicular follicle; B = a cyst including reduction division; C = cyst of spermatids in their early developmental stage; D = cyst of spermatids in their late developmental stage; E = mature sperm. Length of the scale indicator is 0.1 mm divided into 0.01 mm parts.



[illegible]



Females of the interior species: Samples taken in the spring 1966 by Dr. G. G. E. Scudder from Long Lake showed that on 10 April a few females of C. bifida had one or two chorionated eggs while none of C. expleta females was observed to have eggs; on 18 April most C. bifida females had 10-20 eggs, but C. expleta females were still without eggs; 1 May both species had chorionated eggs present in the ovaries. In the spring of 1969 both species were fully reproductive, with chorionated eggs when field work commenced in early May. Overwintered females were found to have eggs present until the end of the generation: parasitised specimens lacked chorionated eggs in the spring. In LB2 all first generation specimens of both species produced eggs within about a week of emergence, but in all other lakes only the initial part of the first generation of each species had fully developed ovaries; late emerging first generation females remained sexually immature. The second generation of C. expleta in LB2 was observed to be similar to the first one in other lakes, with the initial part producing eggs and the later females remaining sexually immature. All females of the third generation of C. expleta in LB2 as well as the second generation of both C. bifida and C. expleta in other lakes remained immature until the following spring.

In previous studies it has been suggested that the initiation of ovarian arrest in Corixidae depends on photoperiodic effects (Young, 1965; Pajunen, 1970). An experiment set up in late fall of 1970 failed to confirm this. Specimens



of C. bifida were brought to the laboratory from Lake Lye on 8 October and placed in a controlled environment cabinet at 5°C and 6 hours photoperiod. 22 days later, cultures with sex ratio of 1 male : 2 females were set up at room temperature (21-23°C) with 8 hours and 16 hours photoperiod. Development of gonads was studied from samples of 15 females taken at intervals of four days. The first female with chorionated eggs in the ovaries was found on the 12th day at 16 hours photoperiod. On the 16th day two more females at the 16 hours photoperiod possessed chorionated eggs in the ovaries, but also in the 8 hours photoperiod, two females with chorionated eggs were found. The experiment indicates that under these conditions most of the females did not attain sexual maturity within the 16 day test period; differences between the 8 hours and 16 hours photoperiod were not detected.

Males of the interior species: Overwintered males, parasitised or unparasitised, showed mature sperm present in samples taken at the time of ice break-up in 1966, and throughout the spring 1969. Males belonging to the initial part of the first summer generation in all Cariboo and Chilcotin lakes had sperm in the testes immediately on emergence, and sperm was shown to be present in the fifth larval instar that gave rise to these adults. Later, towards the end of the first generation, newly emerged males of both C. bifida and C. expleta were sexually immature, as were all specimens of the second generation. However, in late fall samples some of the older specimens were observed to



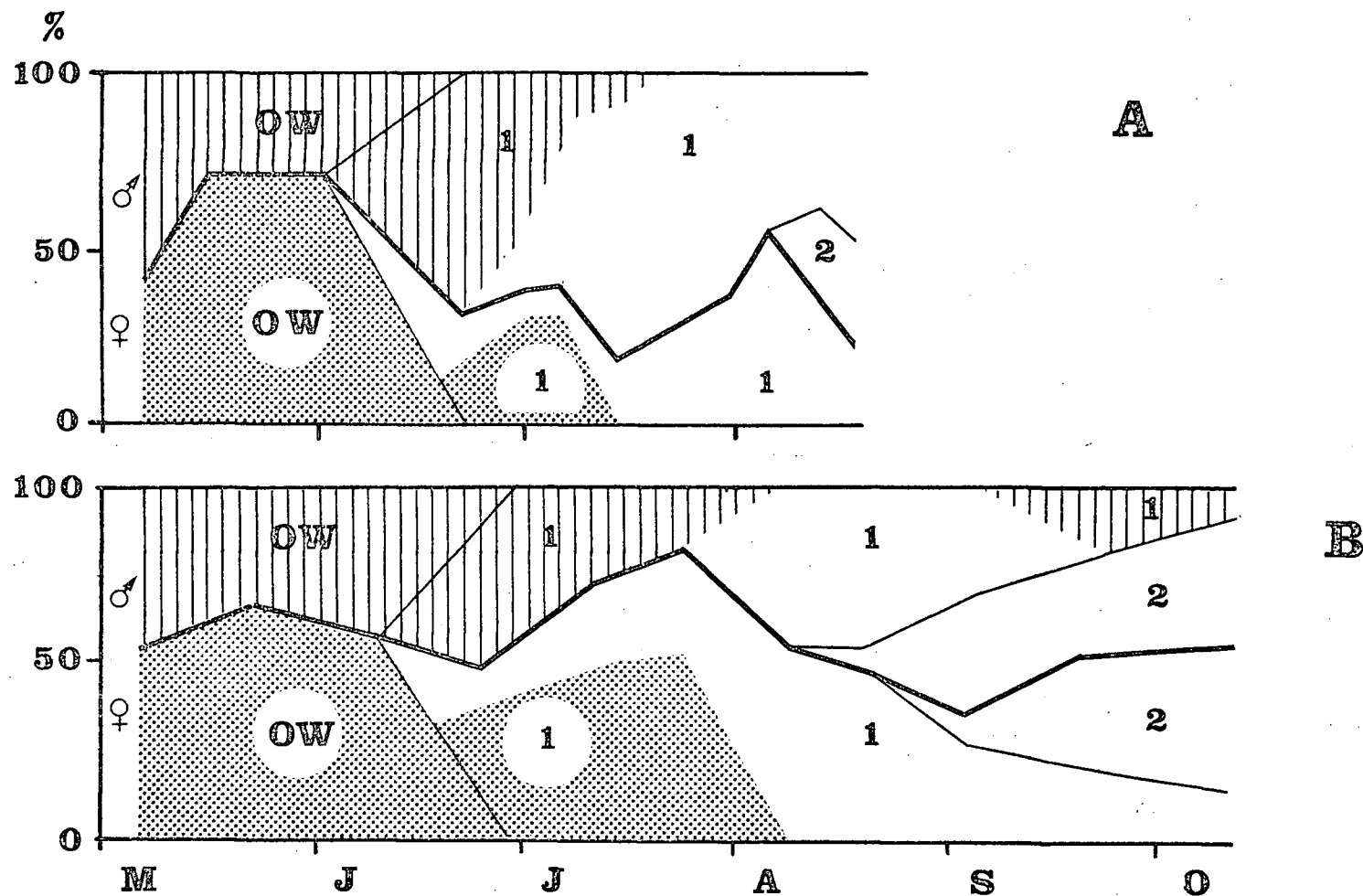


Fig. 41. Presence of sexually mature specimens of *C. bifida* in East Lake (A) and Long Lake (B) in 1969. Symbols: vertical hatching = sexually mature males; stippled = sexually mature females. OW = overwintered specimens; 1 = first generation; 2 = second generation.



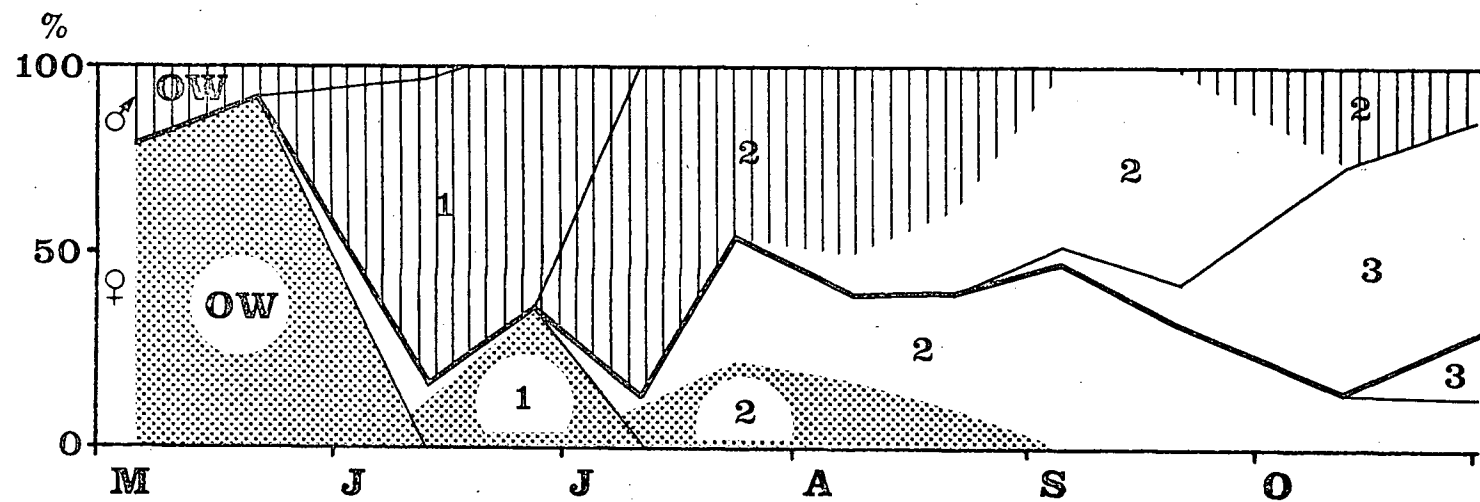


Fig. 42. Presence of sexually mature specimens of *C. expleta* in LB2 in 1969. Symbols as in Fig. 41, but 3 = third generation.



have sperm in the testes. It seems probable that these late fall insects with sperm were first generation specimens from the latter part of that generation.

In the Kamloops area, in the water body LB2, all first generation males had sperm at the time of emergence. The second generation was similar to the first one in other lakes studied, with the initial part having sperm on emergence, but the later part remaining immature. The third generation remained immature, but late fall samples again showed some old specimens with mature sperm in the testes.

Gonad development in coastal species: Study of the gonads in C. andersoni females showed that no chorionated eggs were found in overwintering specimens in late fall (November) or early spring (March). The first specimens with chorionated eggs appeared in early April, and eggs were found until the end of the overwintered generation. Females of the first summer generation had eggs within a week from emergence, and all females (except newly emerged) caught from June to mid August had chorionated eggs. The second generation adults emerging from the beginning of August until late October, did not possess chorionated eggs. These females overwintered, the ovaries developing the following spring.

About one third of males of C. andersoni caught on 21 November 1969 had mature sperm in the testes, and in March 1970 all the males examined had sperm. Males with sperm were found until the overwintered population died off.



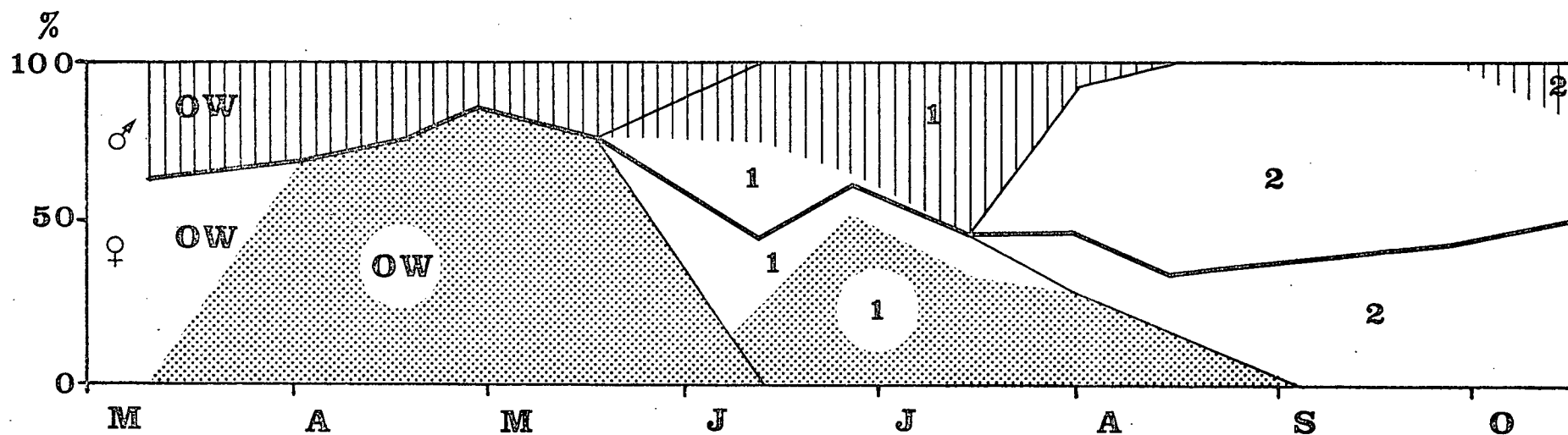


Fig. 43. Presence of sexually mature specimens of *C. andersoni* in Custer golf course pond during the summer of 1970. Symbols as in Fig. 41.



At the beginning of the first summer generation about half of the males had mature sperm on emergence. Later, however, all the first generation males were found to have mature sperm. The second generation males were without sperm on emergence, but samples taken in mid October showed mature sperm in about 20 per cent of the specimens, and also the rest of them showed cysts of spermatids in their late developmental stage.

Scattered observations on the gonad development of C. blaisdelli indicate that overwintered females had chorionated eggs from late March until the end of the generation. The females of the first generation in the temporary pond studied did not have chorionated eggs in the ovaries by the time they left the pond, which seemed to happen within one week from emergence. However, in the laboratory they were observed to develop chorionated eggs in about a week. In the permanent pond of the MacCleery Golf Course, on the other hand, females with chorionated eggs were found until late July.

Overwintering males of C. blaisdelli from all habitats had mature sperm in the testes when observations were started on 15 October 1969, and sperm was present all through the winter and in early spring until the insects died. The first generation males had sperm present on emergence. The last summer specimens with mature sperm were caught on 19 July 1970, and in specimens caught on 9 August no mature sperm could be detected. However, on 4 October 1970, after a very warm period, the temporary pond at 16th Avenue and



Wesbrook Crescent was found to be repopulated, and two thirds of the male specimens had mature sperm in the testes.

The main stages of the gonad cycle were very similar in all four species studied in detail. In general, overwintered females did not possess chorionated eggs until after ice break-up or general increase in temperature in cases where no true winter freeze-up existed. First generation females developed chorionated eggs within about one week of emergence, but in the interior species the later part of this generation remained immature until the following spring. All of the second generation remained immature until the following spring. LB2, with a partial third generation, was an exception from the normal pattern. In males the overwintered generation had mature sperm before ice break-up. Males of the first generation had mature sperm by the last larval instar, but in the interior species the later part of this generation remained immature until late fall. In the interior species the second generation males remained immature during the fall, but matured during winter; in the coastal species the second generation males matured during late fall. In all species the males remaining as immature showed an arrest of spermatogenesis in the stage of cysts of spermatids in their early developmental stage (Fig. 44). In late fall, when development was renewed, old males developed mature sperm (Fig. 45), and also the newly emerged males had spermatogenesis in the stage of cysts of spermatids in their late developmental stage,



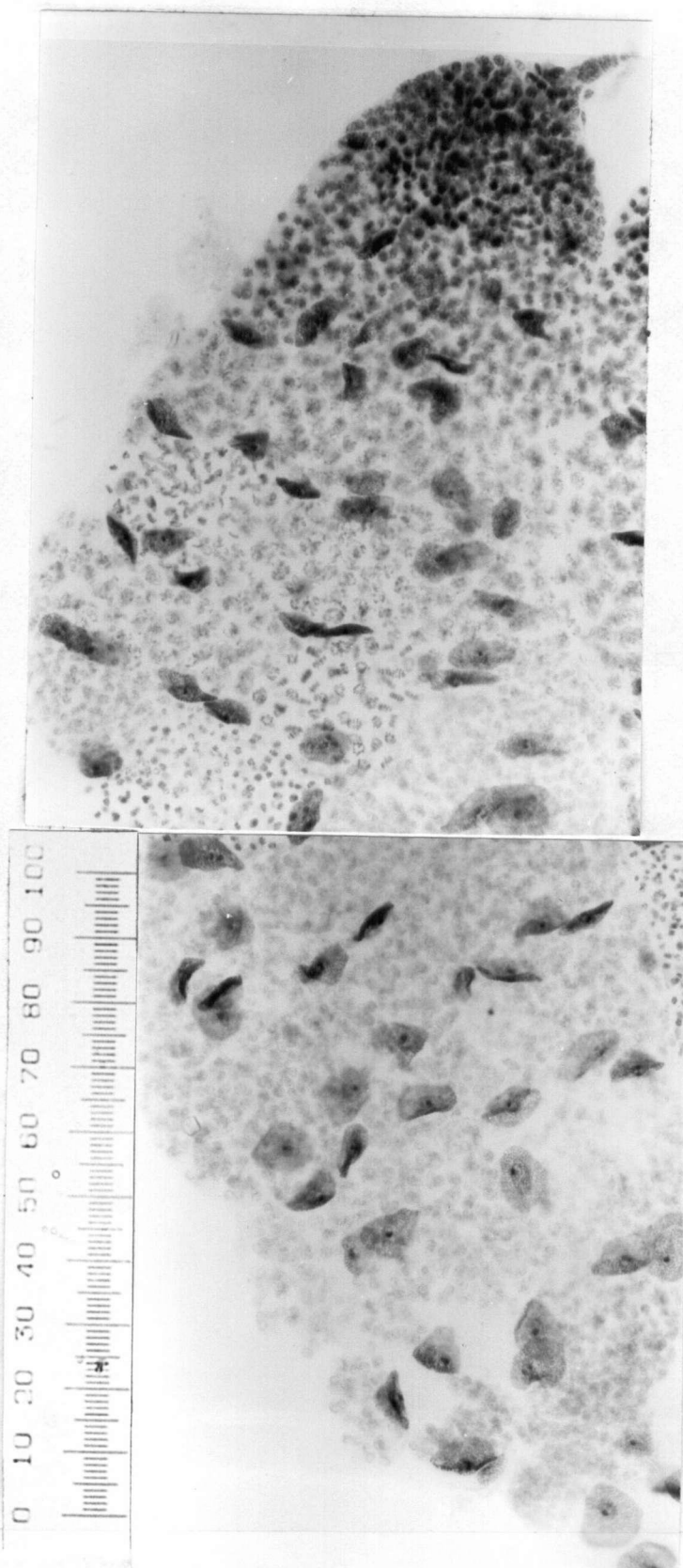


Fig. 44. Light microscope photograph of a follicle from an arrested testis of *C. bifida*. Scale indicator 1 mm, divided into 0.01 mm parts.



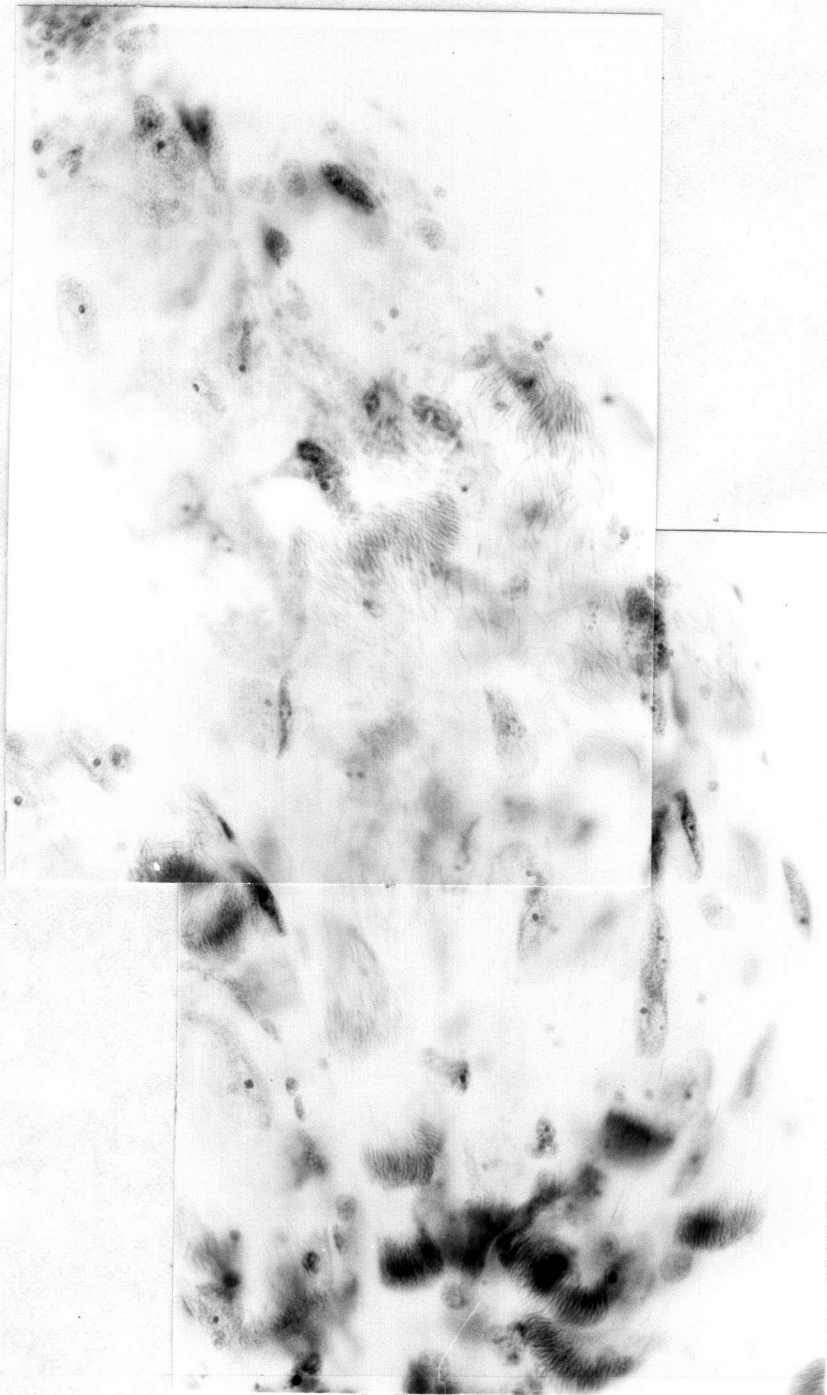


Fig. 45. Light microscope photograph of a follicle from a mature testis of C. bifida. Scale as in Fig. 44.



c) Annual rhythm of stridulation

i) Interior species.

Male and female signals of C. bifida are impossible to separate in field recordings, but those of C. expleta can be distinguished easily. In C. expleta only male signals were observed in the field. Thus, it is assumed that in both species females stridulate so seldom that all signals recorded in the field were produced by males.

The distance at which the equipment used picked up stridulatory signals was measured in Barnes Lake for C. bifida to be about 35 cm and for C. expleta about 60 cm from the hydrophone. Barnes Lake has a fairly hard bottom covered by only a few centimetres of soft detritus. It seems likely that sounds were picked up in hard bottom lakes (Long Lake, LB2) from longer distances than in Barnes Lake, and in soft bottom lakes (Westwick Lake, Boitano Lake, Boitano Lake North End, East Lake, and Lake Lye) from shorter distances than in Barnes Lake. At low population densities field recording is not always successful (as was the case in studies on the coastal species).

Field recordings made in late April 1970 and early May 1969 showed that both interior species were stridulating at this time. Stridulation of C. bifida continued in all lakes (excluding LB2) until the end of June. In LB2 the signals of C. bifida were not observed after early May, which might be owing to the fact that C. expleta was stridulating in this lake so actively that it obscured all other signals. In July, C. bifida signals were no more observed



in Boitano Lake North End, and towards the end of July stridulation also ceased in East Lake, Westwick Lake, and Long Lake, but continued until the end of the first week of August in Lake Lye, Barnes Lake, and Boitano Lake (Fig. 46). C. expleta occurred only in Barnes Lake, Long Lake, and LB2. Stridulation of this species was observed in Long Lake and in Barnes Lake until the end of July, but in LB2 signals were recorded as late as 21 August 1969. (Fig. 46). In September no signals were observed in any lake, and specimens brought into the laboratory did not stridulate.

On 10 October 1969 some specimens of C. bifida from Lake Lye and Long Lake were brought into the laboratory, and some of the males began to stridulate immediately at room temperature. Similar stridulation was observed in specimens of C. bifida brought into the laboratory on 1 November from ponds close to Vernon, British Columbia. It is probable that stridulation would also occur in the field if temperatures allow. Specimens of C. expleta brought into the laboratory on 1 November 1969 from LB2 and a roadside pond near Falkland, British Columbia, began to stridulate after seven days at room temperature.

ii) Coastal species.

Study of the stridulation of the coastal species began in the fall of 1969, and the occurrence of stridulation was tested both in the field and in the laboratory. Only male signals were observed during recordings.

Specimens of both C. andersoni and C. blaisdelli began to stridulate immediately when brought to the laboratory in



mid October 1969, and C. blaisdelli was also observed to stridulate in the field at temperatures of 7-12°C. Recordings were made throughout the year and stridulation was observed in both species until the end of July. Further, C. blaisdelli signals were again detected in the beginning of October, and C. andersoni signals in mid October 1970 (Fig. 46).

Fig. 46 shows that generally the annual rhythm of stridulation in Cenocorixa males in British Columbia is about the same in all species, i.e. they stridulate when they are sexually mature. However, although males begin to stridulate in late fall females do not respond to them until the following spring which is the time of maturation of the females. The main difference between the interior and coastal species is that the relatively high temperatures on the coast enable the species to stridulate much of the winter, while in the interior, the low temperature of the water inhibits stridulation at this time.



Fig. 46. Observed annual rhythm of stridulation and sexual maturity in four species of Cenocorixa.

C. bifida: a = Boitano Lake North End; b = East Lake; c = Westwick Lake; d = Long Lake; e = Barnes Lake; f = Lake Lye; g = Boitano Lake.

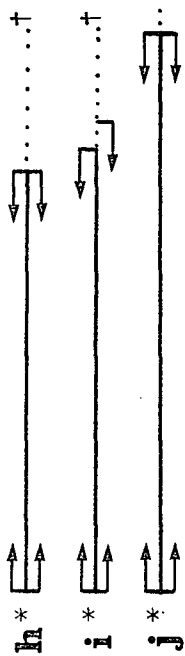
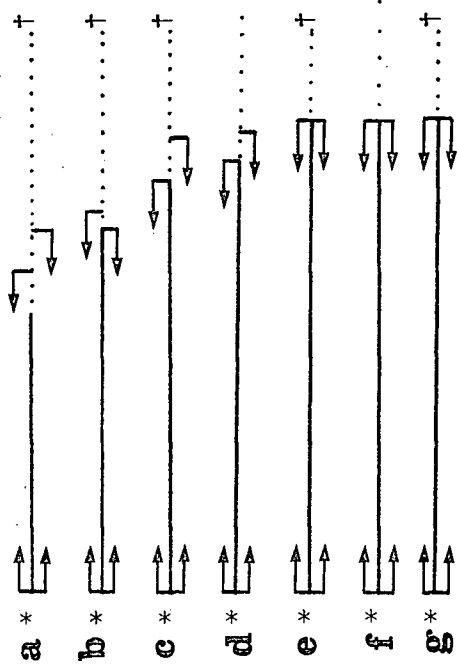
C. expleta: h = Long Lake; i = Barnes Lake; j = LB2.

C. andersoni: k = Custer, golf course pond.

C. blaisdelli: l = Vancouver, 16th Avenue and Wesbrook Crescent pond and MacCleery Golf Course pond.

Symbols: continuous line = stridulation observed; arrows = sexually mature specimens present in samples between the time indicated by the arrows: males above, females below the line; \* = beginning of observations; † = end of observations.





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d) Miscellaneous observations on other species and localities

During the course of the field work, several localities were visited occasionally in order to obtain other species of the genus. At the same time additional comparative data were obtained on life cycles. Information was as follows:

C. bifida: This species was found stridulating and mating in southern Alberta on 21-22 May 1970, but no larvae were detected. On 6 August most of the males were non-stridulating, but a few stridulating ones were also observed and many larvae were collected at the same locality. On 8 July the species was found in northern Utah at 2400 m altitude; copulating pairs and stridulation were observed, and a few IV and V instar larvae were caught also. It seems probable that the life cycle both in southern Alberta and northern Utah is similar to that in interior British Columbia, with two generations per year.

C. kuiterti: The species was found stridulating and mating at 3000 m altitude in Central California (Tioga Pass) on 5-6 July 1970. No larvae were detected. It seems obvious that the species has only one generation per summer owing to the low temperatures at high altitudes.

C. utahensis: The species was found in southern Alberta (sympatrically with C. bifida and C. dakotensis) stridulating and mating on 21-22 May 1970. On 6 August no C. utahensis specimens were detected at this locality. Scattered populations of the species were found in southern and northern Utah on 7-8 July 1970: adult males were stridulating, females had chorionated eggs in ovaries, and also larvae were collected.



In southern Washington both on 10 July and 1 August 1970, one stridulating male specimen was caught. It seems probable that the species has at least two, maybe three generations per year in Utah, but it is not known whether the species breeds successfully in Alberta or Washington.

C. dakotensis: The species was found in southern Alberta on 21-22 May 1970, sympatrically with C. bifida and C. utahensis. Adult males stridulated when brought into the laboratory and females had chorionated eggs in the ovaries. No larvae were detected in the field. On 6 August the species was not found in the same localities.

C. blaisdelli: On 18-20 January 1970, the species was found overwintering in California (San Francisco area and Clam Beach); only adult specimens were observed. Males were stridulating, and females did not have chorionated eggs in the ovaries. The number of generations at these localities is not known.

C. wileyae: In lower altitudes (up to 2000 m) the species was found in early July in California, Oregon, Nevada, and Utah as stridulating adults and various larval instars. On 1 August some stridulating adults were caught in southern Washington. However, in early July at high altitudes (2400 to 3000 m) in California, only adults were detected. It seems possible that the species has two to three generations per year at low altitudes, but only one at high altitudes.

C. expleta: On 29 August 1969 the species was found still stridulating in central Washington (Soap Lake), and also various larval instars were caught. A similar situation



was observed on 6 August 1970 at the same locality. It seems likely that the species has three generations per year in this locality, and the third generation is probably more complete than in LB2 in British Columbia.



#### 4. Diel periodicity of the stridulating activity.

In many studies on European Corixidae it has been observed that the bugs have a diel periodicity in their stridulating activity (cf. Jansson, 1968). In order to investigate the validity of the field recordings which were made usually during daytime in the present study, it was necessary to know the diel periodicity of the stridulating activity of the various species. With C. bifida this was studied in Westwick Lake and Barnes Lake, and with C. expleta in LB2 during the summer of 1969 by recording five minutes every hour over a 24 hour period in situ. The results (Fig. 47) indicate that a difference exists between the two species, although the number of signals obtained for C. bifida was not very large, and in C. expleta it was impossible to count individual signals if more than 100 signals were recorded during the five minute periods. Nevertheless, although signals of both species were recorded at all times of day, C. expleta seemed to have highest stridulating activity at nighttime, while C. bifida was most active during the afternoon.

During the summer of 1970 a laboratory study of the diel periodicity of the stridulating activity was carried out on all species. In these experiments 10 male specimens were placed together in a culture tray and kept under natural light conditions at uniform room temperature over a five day period. Recordings were made for five minutes each hour. The results of these experiments (Figs. 48-51) with comparisons to field recordings were as follows:



C. bifida (Fig. 48 A): During the initial two days of the experiment the species was most active during the day, but subsequently the activity was more generally distributed over the 24 hours. For field recordings see Fig. 47 A-E.

C. kuiterti (Fig. 48 B): In the first two days clear night activity was recorded. The test was interrupted for three days (in order to carry out the tests with C. wileyae), and when continued on the 6th to 8th day, the stridulation occurred both in the day and night. No signals were obtained in field recordings made during the day.

C. andersoni (Fig. 49): Highest activity was recorded every day of the five day test period at dusk. No signals were observed in field recordings made during the day.

C. dakotensis (Fig. 50 A): Clearly nocturnal activity was observed on the five days tested. No signals were obtained in field recordings made during the day.

C. blaisdelli (Fig. 51): Signals were recorded during all hours, but the highest activity was at dusk and the lowest around noon. Signals were also observed in field recordings made during the day and at dusk.

C. wileyae (Fig. 48 C): Records show this to be a fairly inactive species stridulating only from dawn to noon. The test was carried out in two parts (2 + 3 days), because C. kuiterti was tested for three days in the mean time. In field recordings C. wileyae signals were obtained at all hours of the day.

C. expleta (Fig. 50 B): According to the laboratory experiment this species is fairly inactive, stridulating



mostly at nighttime. In the field signals were obtained at all times of the day (Fig. 47 F).

In C. utahensis observations were scattered because at the most only three males were available at any one time. However, this species seemed to have the highest activity at dawn and dusk. No signals were obtained in field recordings made during the day.

In cases when the periodicity in the stridulating activity changed during the test period, it is considered that the first days show a periodicity similar to the natural one. Comparison of the field recordings and the experimental recordings in C. bifida (Figs. 47 A-E and 48 A) support this concept. Jansson (1968) has shown experimentally in a European corixid, Callicorixa producta (Reut.), that the diel periodicity of the stridulating activity is influenced by temperature, although the main factor seems to be light. Thus the final day periodicity in the laboratory was probably not always natural, owing to the even room temperature.



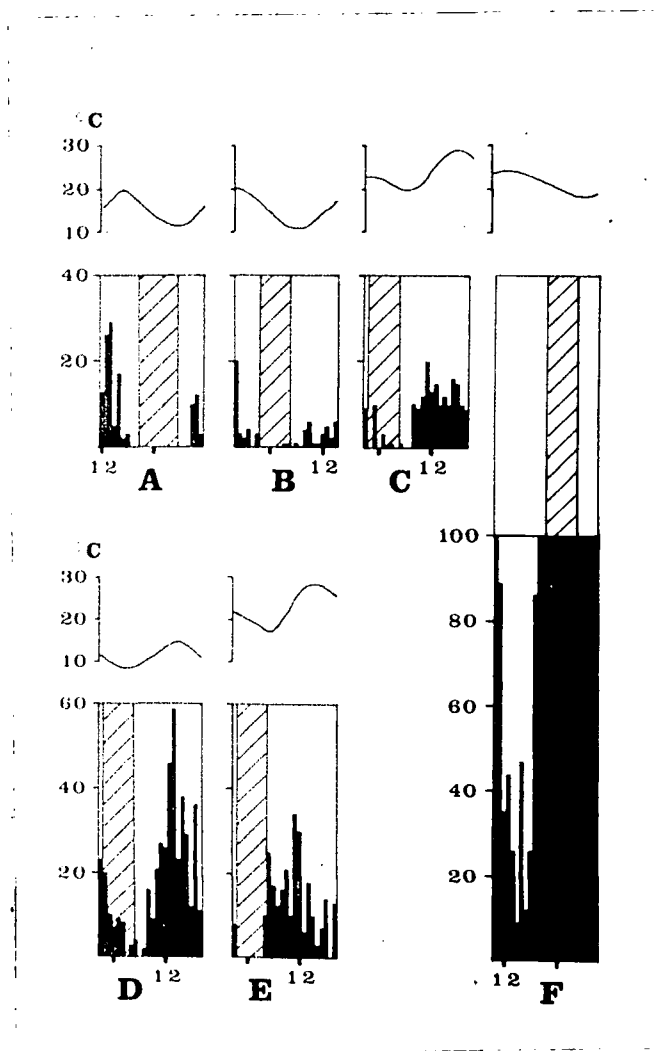


Fig. 47. In situ observations on diel periodicity of the stridulating activity of *C. bifida* and *C. expleta*. *C. bifida*: A = Westwick Lake, 12-13.V.1969; B = Westwick Lake, 25-26.V.1969; C = Westwick Lake, 16-17.VI.1969; D = Barnes Lake, 27-28.V.1969; E = Barnes Lake, 7-8.VI.1969. *C. expleta*: F = LB2, 21-22.V.1969. Ordinate (lower): total number of signals during five minutes (more than 100 signals per five minutes is impossible to count in *C. expleta*), (upper): temperature. Hatching = time between sunset and sunrise.



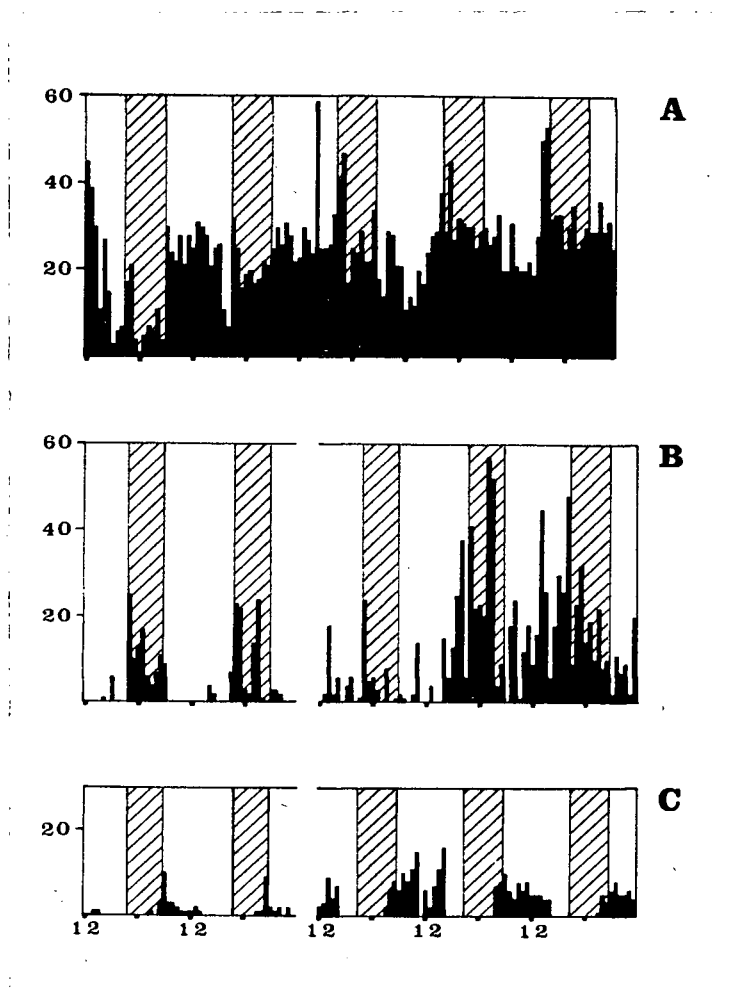


Fig. 48. Laboratory experiments on diel periodicity of the stridulating activity of C. bifida (A), C. kuiterti (B), and C. wileyae (C). Ordinate: total number of signals produced by 10 male specimens in a culture tray during five minutes. Hatching = time between sunset and sunrise (Pacific daylight time). Dates of the experiments: A: 28.IV.-3.V.1970; B: 15-17.VII.1970 and 20-23.VII.1970; C: 17-19.VII.1970 and 23-26.VII.1970.



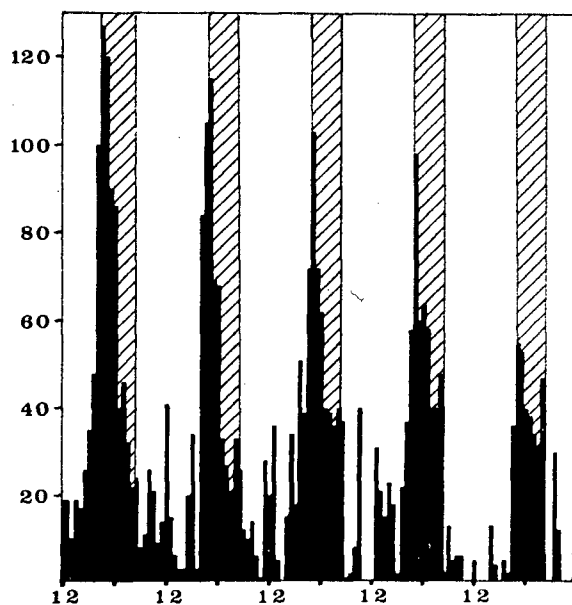


Fig. 49. Laboratory experiment on diel periodicity of the stridulating activity of C. andersoni. Date of the experiment 15-20.VI.1970. Further explanations as in Fig. 48.



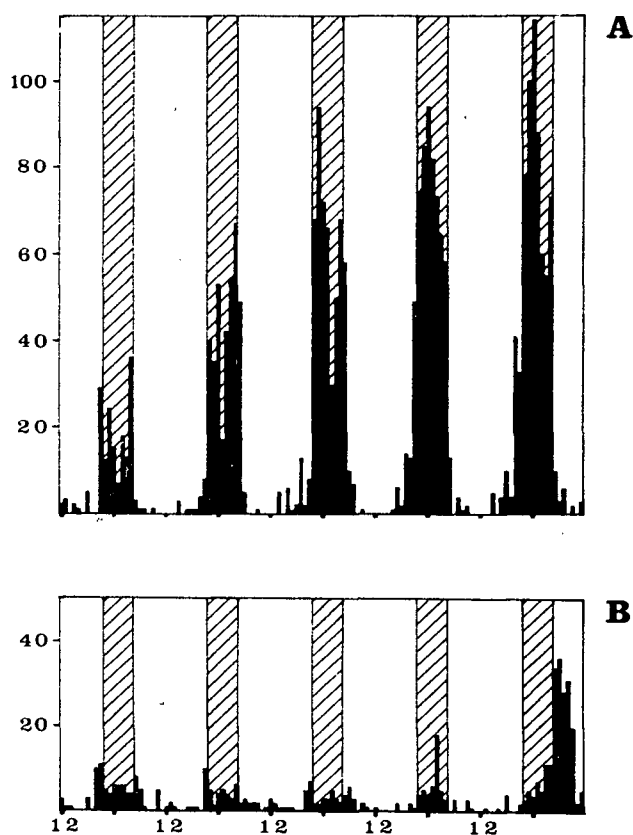


Fig. 50. Laboratory experiments on diel periodicity of the stridulating activity of *C. dakotensis* (A) and *C. expleta* (B). Dates of the experiments: A: 6-11.VI.1970; B: 29.V.-3.VI.1970. Further explanations as in Fig. 48.



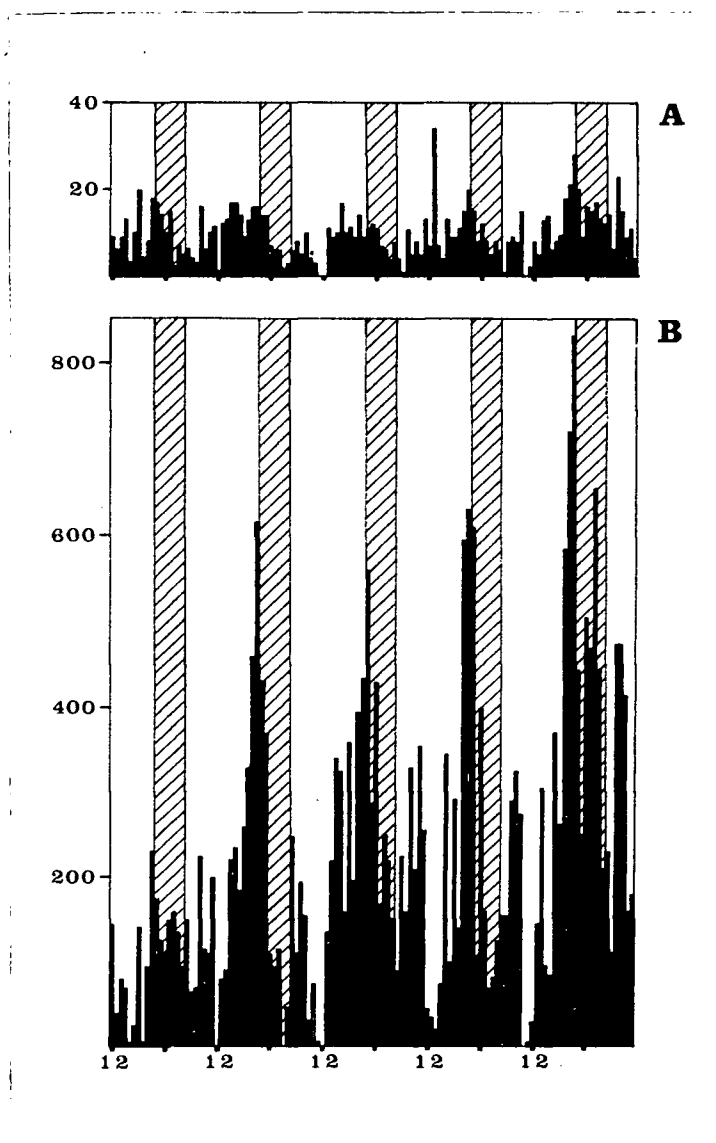


Fig. 51. Laboratory experiment on diel periodicity of the stridulating activity of *C. blaisdelli*. A = total number of the first pulse groups of the signals observed during five minute recordings; B = total number of unipulsate 'clicks' observed. Date of the experiment 21-26.VI.1970. Further explanations as in Fig. 48.



## 5. Behavioral role of stridulation

### a) Male and female response to stridulatory signals and some other stimuli

The tests carried out on the diel periodicity of the stridulating activity provided suitable material for analysing response of males to signals of other males. Fig. 52 represents an example of a four minute recording from each species studied. It can be seen that in most species there is some tendency for the signals to be grouped. It would appear thus that the males respond to signals of other conspecific males by stridulating.

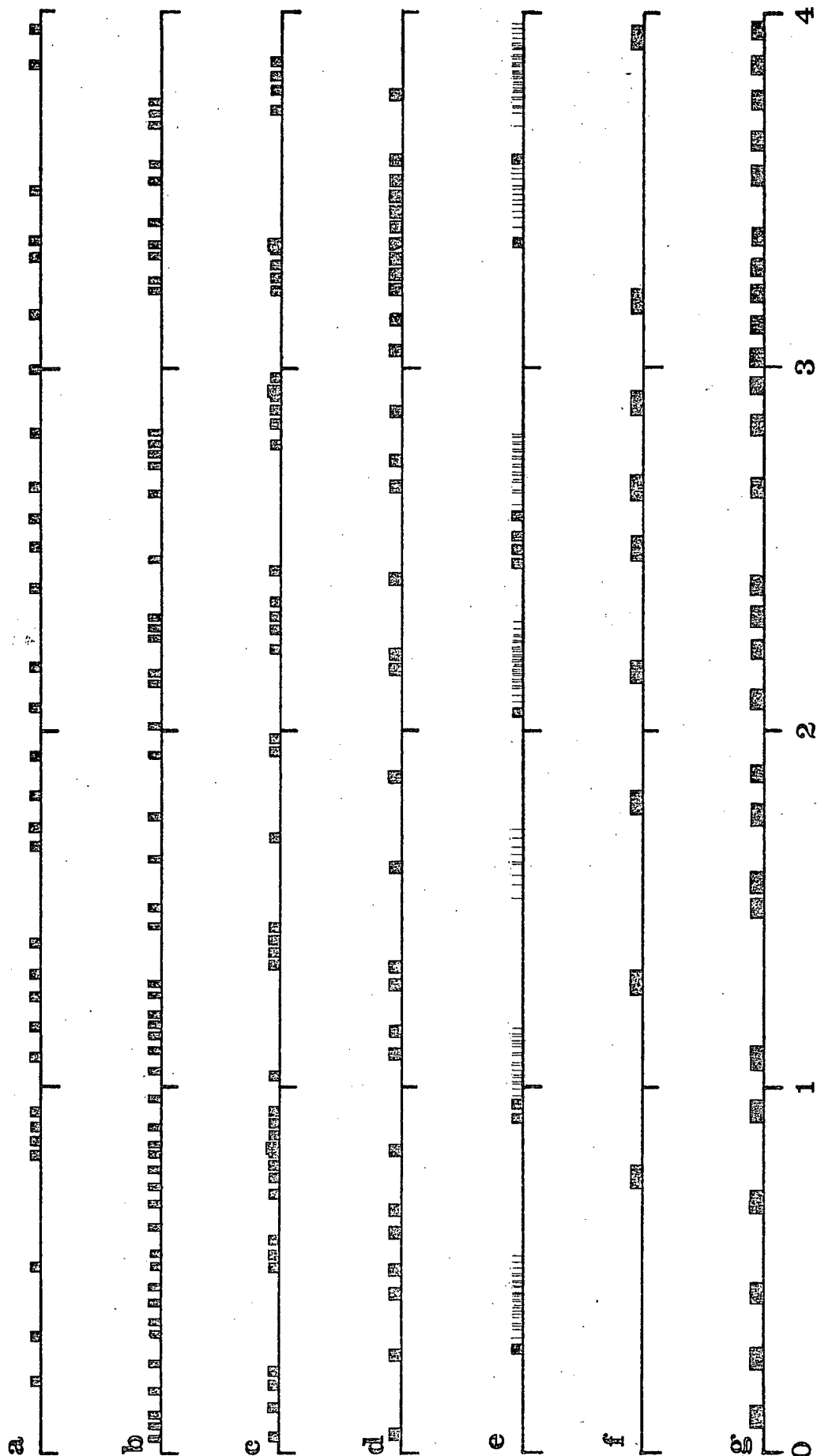
In initial studies in the field and in the laboratory it was frequently observed that when a reproductively active male came close to another specimen, the male produced a few signals, approached the other specimen, and often tried to copulate. On the other hand, sometimes copulation attempts were observed to occur without any introductory signals. If the specimen being approached was a female, the latter often turned away and moved off when the male was stridulating, or if copulation was attempted by clasping the female, the attempt failed owing to a release behavior of the female. However, during the period of April-July, copulating pairs were frequently observed in the field, but initiation of a successful copulation was not observed.

If the specimen being approached was another male, the latter answered the signals of the first male and both stridulated in turn, until one of them nudged the other one away. Alternatively, the male approached simply came and nudged



Fig. 52. Repetition rate of signals produced by 10 male specimens in a sample four minute test period. a = C. bifida; b = C. kuiterti; c = C. andersoni; d = C. dakotensis; e = C. blaisdelli; f = C. wileyae; g = C. expleta. Symbols: each bar represents one signal. Length of bar gives indication of signal length. In C. blaisdelli each thin line represents a unipulsate 'click' and a bar represents a multipulsate first part of a signal.





Time (minutes)



the stridulating one away without stridulatory response. In these interactions the insect that was nudged would usually swim away, and the insect that nudged often showed a chasing reaction and sometimes followed the other specimen for several seconds. In these cases it often nudged the pursued specimen again if this did not swim very far.

The role of stridulation between males was studied in more detail in the laboratory with C. bifida and C. blaisdelli by placing a few specimens into the sand lined bathtub and observing their behavior. In C. bifida it was observed that when two males happened to come close to each other, the sequence of events recorded in the field observations was repeated. However, it was also observed that an auditory stimulus alone could initiate the approach behavior; in this case the approach swimming was a circling movement ending within close range of the stridulating specimen, and then the situation was continued as described in the case of visual stimulus. On the other hand, in C. blaisdelli auditory stimuli were observed to induce the males to stridulate, but it was not observed to initiate any moving activities; only visual stimuli together with auditory stimuli initiated the behavior that would lead to nudging away the other specimen.

Thus it seems likely that the nudging and chasing behavior between males is a kind of agonistic behavior serving to space out individuals: stridulation apparently is often a stimulus important in this context. However, it seemed possible that stridulation also could function



in sex recognition, but there was little to indicate that it would serve as a premating stimulus.

In order to clarify further details in the male and female response to male signals certain laboratory experiments were arranged. These were designed to follow the line of investigations adopted by Schaller (1951) and Finke (1968) whereby all activities of experimental animals were observed and quantified. The species used for these tests was C. bifida.

The experimental animals used were as follows:

- a) One male kept alone during the entire test period (11 days).
- b) One male picked at random from a population of 20 ♂♂ and 20 ♀♀.
- c) Two females picked at random from a population of 30 ♀♀.
- d) Two females picked at random from a population of 20 ♂♂ and 20 ♀♀.

The different test conditions were as follows:

- i) Alone (one male or two females at a time).
- ii) With stridulatory stimuli (4-5 stridulating males isolated in a cage placed into the test container).
- iii) With chemical stimuli: in water previously occupied by two females from the 30 female culture.
- iv) With chemical stimuli: in water previously occupied by two males from the 30 male culture.
- v) With visual stimuli (another specimen isolated in a transparent container, or introducing a dead pinned specimen).
- vi) Back alone in the original tray.



The experiments on chemical stimuli were carried out in order to test possible presence of a pheromone. A clue for this was obtained from an observation on Sigara omani (Hung.) males that showed that these began to stridulate very actively when they were transferred to a tray where females of this species had been kept previously.

The combinations used in the tests were as follows:

Experimental animals	Test conditions
a)	i, ii, iii, (iv), (v), vi,
b)	i, ii, iii, - (v), vi,
c)	i, ii, - (iv), (v), -
d)	i, ii, - (iv), (v), -

Conditions mentioned in brackets were not tested regularly.

Activities studied were classed under six headings:

1) Cleaning, 2) Turning on the spot, 3) Short swimming (swimming bursts that lasted less than five seconds), 4) Long swimming (continuous swimming which lasted more than five seconds), 5) Surface visits (for renewal of air storage), and 6) Stridulation. The stridulatory signals produced by both the experimental animals and the specimens used to provide the test stimuli were recorded.

Experiments on visual stimuli unfortunately did not always work properly because the experimental specimens were frequently greatly disturbed by the placing of the transparent container into the tray. However, in a few successful tests it seemed that females did not respond to the visual stimulus of another specimen, but occasionally



males did in that they were observed to turn towards the specimen in the container, produce a few signals, and finally try to reach the insect inside the container. Also a pinned dry specimen was introduced to the experimental animals, but unnatural movements during this introduction seemed again to be a disturbing factor.

A test for the presence of male odor was carried out only three times for each type of experimental animals. No difference was observed when compared to the situation when no stimuli were present.

Table III shows the results of observations on the behavior of the male specimens of C. bifida under conditions i, ii, iii, and vi above: these results show that in turns on the spot, surface visits, and cleaning there was no significant difference between the test conditions. However, the number of short swims was significantly greater when stridulatory stimuli from other males were present. Long swims, on the other hand, occurred at an equal rate in the case of the male kept alone all the time, but in males kept with females there seems to be a difference between the conditions where the males were alone or with stridulatory stimuli: the males swam more in the latter case. Significant differences were also found in both experimental series in the number of stridulatory signals produced by the experimental animals: the male kept alone all the time stridulated mostly when the female odor was present; however, the males kept with females did not react to the female odor, but reacted to stridulatory stimuli.



Table III. Activities of C. bifida males under various test conditions. Analysis by Friedman two-way analysis of variance. Test conditions as authorised on page 107, 15 minute test periods, each test repeated six times. Explanations:  $\sigma/\varphi$  = mixed culture; \* = value differs significantly from all others; † = significant difference only between the two values marked by this sign (comparison by Wilcoxon matched-pairs ranked-sign test).

Specimen tested	Specific activity	Average number of specific activity per experimental period under test conditions				$\chi_r^2$	Probability of obtaining the result by chance
		i	ii	iii	iv		
$\sigma$ alone	cleaning	0.17	0.83	3.33	1.83	2.35	p < .70
$\sigma$ from $\sigma/\varphi$		2.50	0.83	2.17	1.50	1.35	p < .80
$\sigma$ alone	turns	0.50	0.33	1.00	0.17	1.15	p < .80
$\sigma$ from $\sigma/\varphi$		2.50	4.33	0.17	1.50	0.35	p = .95
$\sigma$ alone	short swims	2.83	11.33*	2.33	2.00	12.05	p < .01
$\sigma$ from $\sigma/\varphi$		6.50	17.33*	4.00	5.83	22.50	p < .001
$\sigma$ alone	long swims	0.00	0.50	0.17	0.00	1.10	p < .80
$\sigma$ from $\sigma/\varphi$		1.67†	5.17†	4.83	3.00	9.77	p < .05
$\sigma$ alone	surfacing	1.17	0.67	2.00	0.83	2.65	p < .50
$\sigma$ from $\sigma/\varphi$		1.50	3.50	4.00	2.50	2.65	p < .50
$\sigma$ alone	stridulation	7.00	14.33	32.17*	5.67	11.35	p < .01
$\sigma$ from $\sigma/\varphi$		0.67	16.83*	4.00	2.83	12.75	p < .01



The results of the tests with females are shown in Table IV (test conditions i and ii). No significant differences could be detected between the test conditions in the amount of cleaning or the number of turns on the spot. However, the females kept isolated from males showed a significant reduction in the number of short and long swims as well as in surface visits when male signals were present. Also the females kept with males showed a significant reduction in the number of long swims and surface visits when stridulatory stimuli were present, but no difference was detected in the number of short swims.

In order to check that there were no differences in the numbers of stridulatory signals produced by insects used to provide the test stimuli, the number of signals produced during each experiment were compared by a Friedman two-way analysis of variance: no significant difference was found. Also the fact that each test was repeated every second day, the entire test period being thus 11 or 13 days, was designed in order to find out if the behavior of the bugs would change during the time under various cultures: no evidence of any change was found.

The foregoing experiments demonstrated that:

- a) Males stridulated spontaneously.
- b) There was an increase in swimming and stridulating activity in males when stimulated by signals of other males.
- c) A male which had been separated from other specimens for some time stridulated actively when in presence of female odor, whereas males maintained with females did not react



Table IV. Activities of C. bifida females under various test conditions. Analysis by Wilcoxon matched-pairs ranked-sign test. Test conditions as authorised on page 107, 15 minute test periods, each test repeated seven times. Explanations: 2♀♀ alone = two females from 30 female culture; 2♀♀/♂ = two females from 20 male and 20 female culture; n.s. = no significant difference between the test conditions.

Specimens tested	Specific activity	Average number of specific activity per experimental period under test condition		Probability of obtaining the result by chance
		i	ii	
2♀♀ alone	cleaning	2.29	3.29	n.s.
2♀♀/♂		3.43	3.14	n.s.
2♀♀ alone	turns	8.86	2.86	n.s.
2♀♀/♂		6.86	2.57	n.s.
2♀♀ alone	short swims	20.14	9.14	p = .01
2♀♀/♂		11.00	10.00	n.s.
2♀♀ alone	long swims	6.86	1.57	p < .05
2♀♀/♂		10.57	3.43	p < .05
2♀♀ alone	surfacings	8.43	4.86	p < .025
2♀♀/♂		7.43	4.86	p < .025



to female odor.

- d) Females responded to male signals by remaining motionless.
- e) Females did not stridulate.

Categories a) and b) above could be explained as an agonistic behavior spacing out the males. However, c) and d) indicate that stridulation might also have something to do with premating behavior. One could hypothesize that a spontaneously stridulating male, after having been apart from females, is induced to call actively by odor of a female in the vicinity. The signals of the male would keep the female stationary, thus giving the male a chance to find the mate according to odor.



b) Mating in C. bifida

Further experiments were carried out in order to check whether the hypothesis on existence of stridulation-odor interaction could be shown to have any role in actual mating of the bugs.

A single female C. bifida from the culture of 30 females kept isolated from males for 20 days, was introduced into the tray of the male kept alone for the previous experiments. Close observation of both insects with continuous tape recording was carried out. At first, both specimens were observed to swim around apparently at random, but after about three minutes the male produced a signal, and immediately afterwards the female, remaining stationary, responded by producing a stridulatory signal. Straight away the male started to swim rapidly in small circles, stopping at intervals to stridulate again. The female remained motionless and answered the male signal each time, but at no time did the female swim in response. The male continued searching, but evidently was not able to orientate directly towards the female (owing to echo in the plastic tray used for the test, see below). Finally, one and a half minutes after the first male signal was recorded, the male located the female and a successful copulation occurred. This copulation lasted about 15 minutes. Half a minute after the copulation was completed the male began to stridulate again, but at this time there was no stridulatory response from the female. Once mated, the female would not respond to a stridulating male for several days. This experiment was repeated several times



with C. bifida with the same result. Even if a copulation was interrupted 2-3 seconds after the genital contact, this was enough for the female not to respond any more to the male stridulation by answering.

The fact that males do orientate according to the female signals could not be studied in the culture trays used for the first mating experiments, evidently because of echoes from the walls. However, in experiments carried out in the sand lined bathtub it was demonstrated that the female signals do serve in orientation of the male: when female signals were played back from tape recordings the males congregated around the loudspeaker and would remain so positioned as long as the playback was continued, trying to find "the female" in the loudspeaker. Also when a receptive female was placed into the bathtub with a stridulating male, the former did not need to answer the male calls more than once when the male swam straight to the female and copulated.

Only females kept isolated from males for at least a week were found to respond to male signals by stridulating. Females from mixed cultures did not stridulate. Such non-stridulating females were often targets for copulation attempts, but these attempts were never observed to be successful. The females, if clasped by males in attempt to copulate, would adopt a release behavior which consists of vigorous swimming, coming up to the water surface, turning almost upside down at the surface, and dislodging the male with the hind legs. In other cases when a stridulating male was close to an unreceptive female, the female swam away



(henceforth called "escape" reaction) or towards it, so that it disturbed the male ("agonistic" reaction). This agonistic behavior in the females was different from the agonistic behavior between two males in that the females did not chase the male after they had nudged the male away. Fig. 53 shows the sequence of events in the successful mating in C. bifida.



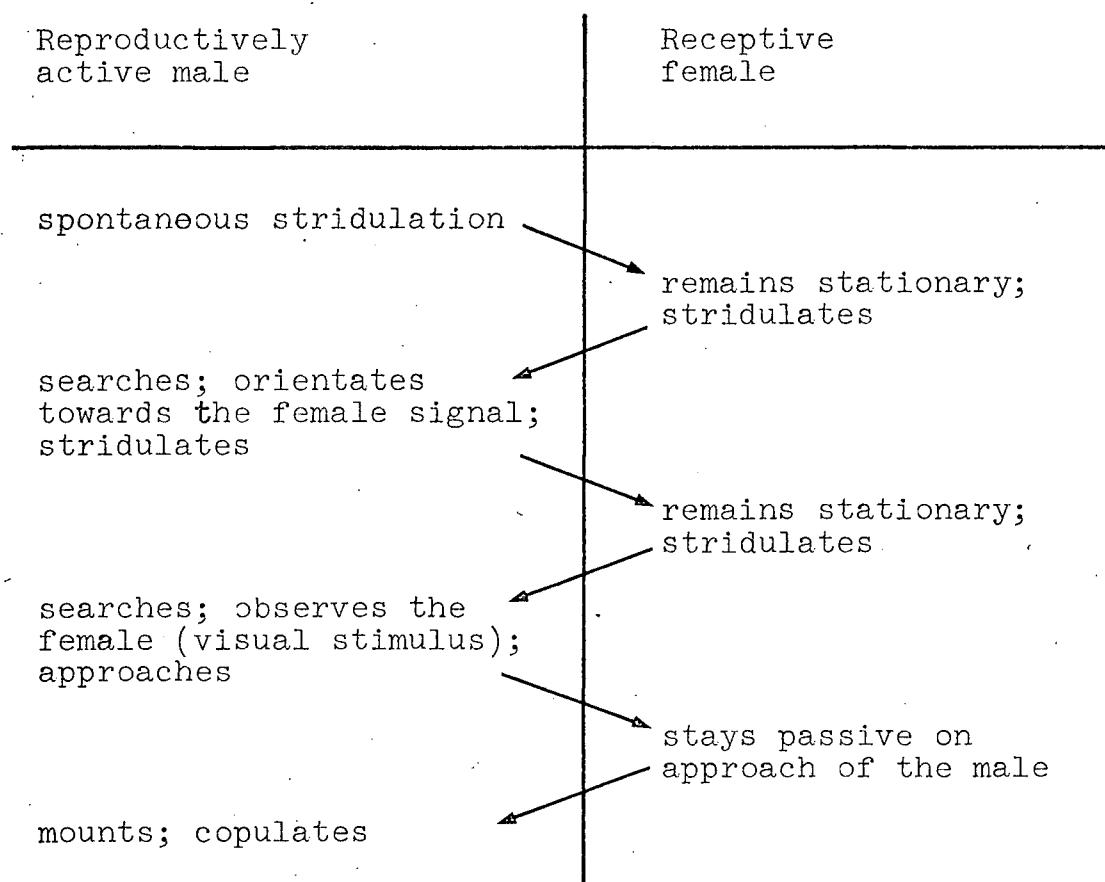


Fig. 53. Diagram on the sequence of events in a successful mating in *C. bifida*.



c) Specific differences in the mating behavior

Experiments on mating were then conducted with all other species. These showed the sequence of events to be much the same in all species.

Experiments carried out in the bathtub were used to determine the distance at which a responsive female answered the signals from a conspecific male, and also the distance at which a male answered the signals of a female. The results of these experiments, which utilized both stridulating specimens and playback from tape recorder through an underwater loudspeaker, are given in Table V.

Some specific differences between the species during their mating behavior were found and are summarised in Table VI for males and in Table VII for females. The stimulus releasing the mating behavior in males seems to be usually both auditory and visual, but in C. dakotensis and C. wileyae it seems to be auditory only: males of all other species were frequently observed to make copulation attempts with unreceptive females. C. wileyae males could be induced to attempt copulation with unreceptive females by placing both sexes in the same container and playing back female signals from a tape. In C. dakotensis the orientation of males seems to be completely dependent upon auditory stimuli because they were never seen to attempt copulation with a non-singing female present in the container, regardless of playbacks: in all such cases they tried to find the source of the female signal. Observations on actual mating in this species were unsuccessful owing to the fact that females were receptive



Table V. Distance for recognition of signals of opposite sex in some Cenocorixa species in sand lined bathtub. Each specimen was tested against 25 signals at each distance shown and positive reactions are shown in per cent of total number of signals tested for each species. No significant differences were found between the individuals of any one species. - = distance not tested.

Species/sex tested	Number of specimens tested	Distances tested (cm)									
		5	7.5	10	15	20	25	30	40	50	60
bifida ♂	2	100	100	0	0	-	-	-	-	-	-
bifida ♀	2	100	-	0	0	-	-	-	-	-	-
utahensis ♂	3	-	-	100	-	100	85	0	-	-	-
blaisdelli ♂	3	100	-	100	0	0	-	-	-	-	-
wileyae ♂	3	-	-	100	-	100	0	0	-	-	-
wileyae ♀	2	100	-	66	0	0	-	-	-	-	-
expleta ♂	2	-	-	100	-	100	-	100	100	54	0



Table VI. Specific differences observed in mating behavior of Cenocorixa males.  
 Explanations: 1) = females receptive only in darkness; 2) = mounting signal  
 observed, origin unknown.

Species	Number of copulations observed		Stimulus releasing mating behavior in males	Response to signals of other males	Mounting process	Remarks
	successful	unsuccess- ful				
bifida	6	35	visual & auditory	agonistic & answer	fast	
kuiterti	0	15	visual & ?	agonistic & answer	fast ?	
andersoni	5	20	auditory & visual	answer & agonistic	fast	
utahensis	2	5	auditory & visual	answer & agonistic	2-step	
dakotensis	0	0	auditory only	answer ?	?	1)
blaisdelli	5	15	auditory & visual	answer	fast	2)
wileyae	6	20	auditory	none	slow	
expleta	5	18	auditory (& visual ?)	none	fast	2)



Table VII. Specific differences observed in mating behavior of Cenocorixa females. Number of copulations as in Table VI. Explanation: 1) = mounting signal of unknown origin observed.

Species	Response to males before copulation or attempt		Response to males during copulation or attempt		Remarks
	receptive ♀♀	unreceptive ♀♀	receptive ♀♀	unreceptive ♀♀	
bifida	answer signals, remain stationary	escape, agonistic or none	passive	vigorous swimming, surfacing, kicking	
kuiterti	answer signals, ?	escape or none	?	vigorous swimming, diving under rocks, kicking	
andersoni	answer signals, remain stationary	none or escape	passive	swimming to surface, kicking	
utahensis	answer signals, remain stationary, (search ?)	none	rub male genitalia with hind legs	vigorous swimming to surface, kicking	
dakotensis	answer signals, but none only in darkness		?	?	
blaisdelli	answer signals, remain stationary	escape or none	passive	press abdomen against bottom, surface, kicking	1)
wileyae	answer signals, remain stationary	none (even when male proceeds to precopula	passive	vigorous swimming and surfacing when genital contact is tried	
expleta	answer signals remain stationary	escape or none	passive	vigorous swimming, surfacing, kicking	1)



(= answered to male signals) only in darkness. However, this is quite natural because the experiments on diel periodicity of the stridulating activity of males showed this species to be nocturnal.

The importance of the female signal in assisting the male to locate the female was also tested by placing several unreceptive females together with one receptive female in the bathtub. In none of these experiments did the male attempt to copulate with the unreceptive females after the receptive one stridulated: immediately after the first answer of the receptive female the male located the female and copulation commenced. Thus, in one experiment three C. blaisdelli females were settled within 1 cm<sup>2</sup> when a male was introduced. The male happened to stop close to the females, and after a while it produced a signal. The receptive female, settled behind two unreceptive ones, stridulated in answer to the male signal. The male immediately oriented towards the group of females. The signal of the receptive female was still continuing when the male passed the two unreceptive females, and without further signals it mounted the receptive female. Thus, it seems obvious that the female signal guided the male directly to the female.

Further, by arranging an experiment with receptive females of C. bifida and C. expleta together, and introducing males of either species, it was observed that only intraspecific copulations occurred.

When the receptive females answered the male call and thus released the searching behavior in males, the female



signal very often started before the male signal was completed: the two signals were partly overlapping. Further, if the male did not produce more than one signal, the female usually repeated its signal two to six times before ceasing to respond. Otherwise females were never observed to stridulate spontaneously. This was checked with three C. bifida and two C. wileyae females over one 24 hour period in each species in a way similar to the experiments on the diel periodicity of the stridulating activity in males, but no signals were obtained.

Usually the female did not search for the male, but remained stationary. Only in one species, C. utahensis, was one female observed to search for the male, but this was in a culture tray, where the male had difficulties in locating the female owing to echoes from the walls. It is probable that the females would not search for males in natural conditions.

Unreceptive females showed agonistic behavior towards stridulating males only in C. bifida: in other species they either swam away (escaped) or showed no special behavior. In C. wileyae the unreceptive females remained passive even when the male mounted them, and release behavior was not shown until the male attempted genital contact. On the other hand, this was a species where the males most often remained in precopula (mounted the female, but did not try genital contact) for a while.

When a male mounted a receptive female, this happened in most species by a very fast movement and genital contact



was obtained almost immediately. However, in C. utahensis the procedure seems to be completed in two steps: the male mounts the female first quite normally, but releases the female immediately and rises a few millimetres above the female, and settles down again. In C. wileyae the procedure is performed slowly and carefully compared to any other species. Usually the male stays in precopula for a few seconds: the male clasps the female with the front legs, but does not immediately initiate genital contact. Similar precopulatory behavior was observed in other species also, but only between a male and an unreceptive female: if the female did not manage to drop the male from the clasping position after the first trial of genital contact, the pair often remained in precopula, but as soon as the male tried further genital contacts, the release behavior of the female was initiated.

During copulation only C. utahensis females showed a special mating activity, by rubbing the genital region of the males with their hind legs. This rubbing was not observed to produce any sounds. Females of all other species seemed to stay passive. However, the origin of the mounting signal observed in C. blaisdelli and C. expleta is unknown, and might be produced by the females. The release behavior of unreceptive females of all species was observed to be generally similar.

Dissection of receptive and unreceptive females showed that the receptive females always had chorionated eggs both in the ovaries and in the lateral oviducts. Unreceptive females which had been kept isolated from males for several



days, did not have any chorionated eggs in the lateral oviducts, and at the most had only a few chorionated eggs in the ovaries: usually the ovaries were obviously immature.



d) Species recognition

A series of playback experiments was undertaken wherein the response of one species was tested against stridulatory signals of the same, and then against signals of all other species. Signals of both males and females were used and active males and receptive females were utilized in order to determine the ability of the specimens to discriminate the signals of their own species, i.e. answer to the right signals. Tables VIII - XI summarise the results of these experiments.

According to table VIII males of C. bifida, C. kuiterti, C. andersoni, C. blaisdelli, and C. wileyae readily answered to the male calls of their own species. C. bifida and especially C. wileyae also answered some other signals, while C. utahensis, C. dakotensis, and C. expleta were not found to respond very much to any signal.

It should be noted that males of certain species sometimes produce a complete signal or the first part of the signal alone, and thus these possibilities were tested separately. Differences were found in the response of males and females to these separate signals. For instance C. utahensis and especially C. andersoni males responded more readily to the first part of the conspecific male signal, while females of the same species required a complete conspecific male signal in order to respond (Tables VIII and X). On the other hand, in C. blaisdelli and C. wileyae both males and females responded more readily to a complete conspecific male signal, and C. kuiterti males equally well



to both types of conspecific male signals. Further, in cases when males of some species responded to signals of other species by stridulating, it was also observed that when mixed cultures with several species were arranged, interspecific agonistic behavior occurred frequently.

Table IX shows the response of the males to various female calls. A response was obtained every time a male was exposed to the call of a conspecific female. Further, males of some of the species also frequently responded to signals from a female of another species. However, observations of the male specimens during these interspecific playback experiments showed that the only signals inducing searching behavior of the males were signals from a conspecific female. In experiments carried out in the sand lined bathtub it was observed that this searching behavior in all species always involved more or less direct movement to the source of the female signal: only if the meeting of the sexes was prevented (by plastic screen or in playback experiments) was swimming in circles observed. In contrast, the agonistic behavior of males always involved a circling swimming movement.

Table X shows the results of experiments testing the response of females to the stridulatory signals of males. In all cases the females responded to signals from a conspecific male. In a few cases involving species pairs occurring allopatrically (C. bifida - C. andersoni, C. dakotensis - C. wileyae) response to a male signals of another species was recorded. In the case of C. bifida females, they answered the first part of a C. andersoni male signal, but did not



respond to a complete signal. On the other hand, C. wileyae females responded every time to C. dakotensis male signals. However, even if these species should occur sympatrically, the results do not necessarily mean a breakdown of the stridulatory isolating mechanism, since the males involved did not search for a mate, although they occasionally answered the wrong female calls (Table IX).

Finally, when female signals were tested against females, only C. expleta responded (Table XI).

Cenocorixa species occur sympatrically with other Corixidae, and where possible, the signals of these other taxa were also tested (for description of the signals of these other taxa, see Appendix II). The tests showed that some Cenocorixa males answered the signals from other Corixidae, but the few females which could be tested did not respond (Table XII). The observed response of Cenocorixa males is apparently in connection with agonistic behavior.

The question of how corixids distinguish the signals of conspecific males or females from signals of other species was not studied in detail in the present work. However, a few observations were made on this phenomenon. In C. andersoni the female call consists of one to three similar pulse groups which are separated from each other by short (1-2 seconds) intervals. When only one pulse group was played back to the males, a searching response was observed only in about 25 per cent of the males, but when a sequence of two or three pulse groups was played back, a searching response in 100 per cent of the tested males was observed. Similarly, C.



expleta males responded to conspecific female signals which are composed of pulse groups, but did not respond to signals composed of continuously repeated pulses which had the same pulse rate as the conspecific female calls. It seems possible that the temporal pattern of pulses is the critical factor in species recognition in Cenocorixa.



Table VIII. Response of Cenocorixa males to playback of male signals. Each species was tested 25 times for each signal. Symbols: 0 = 0-20 per cent response by answering; + = 20-40 per cent response; \* = 40-60 per cent response; \*\* = 60-80 per cent response; \*\*\* = 80-100 per cent response. Single underlining = species sympatric; double underlining = conspecific situation. If two figures appear in the same species entry, the upper one represents the first part of the signal alone used as a stimulus and the lower one a complete signal used as a stimulus.

Species responding	Number of specimens tested	Male signal used as stimulus							
		bifida	kuiterti	andersoni	utahensis	dakotensis	blaisdelli	wileyae	expleta
bifida	5	*** =====	0 0	0 0	0 0	** =	** 0	0 0	*** =
kuiterti	5	0	*** =====	* 0	+ +	0	+ 0	0 0	0
andersoni	5	+	+ 0	*** =====	** *	+ 0	0 0	+ +	0
utahensis	5	0 =	+ 0	0 0	* 0	+ =	0 0	+ 0	0
dakotensis	5	0 =	0 0	0 0	0 0	+ =====	0 0	0 0	0 =
blaisdelli	5	+	* +	+ 0	+ 0	* =	** =====	+ +	* =
wileyae	5	+ =	* **	0 +	*** ***	*** =	0 0	** =====	0
expleta	5	0 =	0 +	0 0	0 0	0 =	0 0	+ 0	0 =====



Table IX. Response of Cenocorixa males to playback of female signals. Explanations as in Table VIII, but - = not tested.

Species responding	Number of specimens tested	Female signal used as stimulus							
		bifida	kuiterti	andersoni	utahensis	dakotensis	blaisdelli	wileyae	expleta
bifida	5	*** ===	-	0	<u>+</u>	<u>+</u>	0	<u>**</u>	<u>+</u>
kuiterti	5	0	<u>-</u> ===	*	0	0	0	<u>0</u>	0
andersoni	5	0	-	*** ===	*	+	<u>0</u>	**	+
utahensis	5	<u>0</u>	-	0	*** ===	<u>0</u>	0	<u>+</u>	0
dakotensis	5	<u>+</u>	-	0	<u>0</u>	*** ===	0	+	<u>+</u>
blaisdelli	5	+	-	<u>0</u>	+	***	*** ===	+	**
wileyae	5	<u>+</u>	<u>-</u>	+	*** ===	***	0	*** ===	0
expleta	5	<u>0</u>	-	0	+	<u>+</u>	0	+	*** ===



Table X. Response of Cenocorixa females to playback of male signals. Explanations as in Table VIII, but - = not tested.

Species responding	Number of specimens tested	Male signal used as stimulus							
		bifida	kuiterti	andersoni	utahensis	dakotensis	blaisdelli	wileyae	expleta
bifida	4	*** ===	+ 0	** +	* 0	0	0 0	0 0	0 0
kuiterti	-	-	==	-	-	-	-	-	-
andersoni	3	0	-	* *** ===	0 0	0	0 0	-	0
utahensis	2	0	-	0 0	0 *** ===	0	0 0	-	0
dakotensis	4	0 0	0 0	0 0	0 0	*** ===	0 0	0 0	0 0
blaisdelli	4	0	-	0 0	0 0	+	* *** ===	-	+
wileyae	5	0 0	0 +	0 0	0 +	***	0 0	* *** ===	*
expleta	3	0 0	0 0	0 0	0 0	+	0 +	0 0	*** ===



Table XI. Response of Cenocorixa females to playback of female signals. Explanations as in Table VIII, but - = not tested.

Species responding	Number of specimens tested	Female signal used as stimulus							
		bifida	kuiterti	andersoni	utahensis	dakotensis	blaisdelli	wileyae	expleta
bifida	4	<u>0</u>	-	0	<u>0</u>	<u>0</u>	0	*	<u>0</u>
kuiterti	-	-	<u>-</u>	-	-	-	-	<u>-</u>	-
andersoni	3	0	-	<u>0</u>	0	0	<u>0</u>	-	0
utahensis	2	<u>0</u>	-	0	<u>+</u>	<u>0</u>	0	<u>-</u>	0
dakotensis	4	<u>0</u>	-	0	<u>0</u>	<u>*</u>	0	0	<u>0</u>
blaisdelli	4	0	-	<u>0</u>	0	+	<u>0</u>	-	+
wileyae	5	<u>0</u>	<u>-</u>	0	<u>+</u>	*	0	<u>+</u>	0
expleta	3	<u>0</u>	-	0	0	<u>0</u>	0	0	<u>***</u>



Table XII. Response of Cenocorixa spp. to playback of signals of sympatric species of other Corixidae. Each species was tested 25 times for each signal. Explanations as in Table VIII, but - = not sympatric, therefore not tested; ‡ = occurs in same general area, but was not found in same water body.

Cenocorixa spp/sex responding	Number of specimens tested	Signals used for stimulus:						
		Callicorixa vulnerata ♂	Callicorixa audeni ♂	Callicorixa tetoni ♂	Sigara omani ♂	Sigara nevadensis ♂	Sigara nevadensis ♀	Corissella tarsalis ♂
bifida ♂	5	0	*	+	-	0‡	0‡	0
bifida ♀	2	0	0	0	-	0‡	0‡	0
kuiterti ♂	10	-	0	-	0	-	-	-
andersoni ♂	5	0	-	-	0	-	-	-
utahensis ♂	3	-	**	+‡	-	0‡	0‡	0
dakotensis ♂	1	-	0	-	-	-	-	0
dakotensis ♀	2	-	0	-	-	-	-	0
blaisdelli ♂	5	*	-	-	***	-	-	-
wileyae ♂	10	-	***	*	***	***‡	***‡	***
wileyae ♀	5	-	0	0	0	0‡	0‡	0
expleta ♂	5	-	0	-	-	-	-	0



## 6. Geographic distribution and notes on ecology and habitats of the species

The species recognition experiments indicate that stridulation serves as an isolating mechanism between the species. However, this isolation may not always be 100 per cent effective. Thus, it would be natural to expect other isolating mechanisms to exist as well. In order to clarify these, the geographic distribution of the species was reviewed, and notes on ecology and habitats were made.

### a) Data on distribution and notes on ecology

Data on general distribution of the species of the genus Cenocorixa are published only in Hungerford (1948). Some additional information can be found in Hungerford (1956), Lansbury (1955; 1960), Sparrow (1966), Brooks and Kelton (1967), and Scudder (1969 a). In the following list, the distributional records are according to Hungerford (1948), and other authors are only mentioned if their records change the range of the species. However, in every case the provinces or states where the species were obtained for the present study are mentioned separately (for more details see Appendix I). Thus the known distribution of the species is as follows:

C. bifida: CANADA: British Columbia, Alberta, Saskatchewan, Manitoba. USA: California\*, Idaho, Utah, Wyoming, Montana, North Dakota, Colorado, Minnesota, Rhode Island\*\*.

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\* Lauck, D.R.‡ (personal communication): The specimens reported from California belong either to C. kuiterti or C. utahensis.

\*\* Rhode Island is way out from the general distributional area of the species and the report is probably a mistake.



Scudder (1969 a) also reports Washington. For the present study the species was obtained from British Columbia, Alberta, and Utah (Fig. 54).

The species seems to occur in freshwater or moderately saline lakes and ponds in the interior plateau and prairies. According to Scudder (1969 a) breeding was observed in water bodies with conductivity from 38.6 to 17688 micromhos/cm at 25°C. The limits for successful breeding during field work of 1969 were observed to be between 50 and 13200 micromhos/cm at 25°C.

C. kuiterti: USA: California, Utah. The latter record (Wasatch Mountains, Duchesne), based on one male and two females (Hungerford, 1948), is probably a mis-identification: the species is often very difficult to separate from C. bifida (cf. Appendix I). I have found C. bifida, but not C. kuiterti in the Wasatch Mountains area. During the present study C. kuiterti was only found at the type locality in California (Fig. 54). This locality is in the high sierra at altitudes of 3300 m, and the species inhabits small freshwater ponds and creeks of a sub-alpine meadow (measured conductivity of the water 60 micromhos/cm at 25°C).

C. andersoni: USA: Washington, Oregon [Hungerford (1956) reports the same States for C. malkini Hungerford, which is a synonym of C. andersoni (cf. Appendix I)]. Lansbury (1960) reported the species from British Columbia, both under its correct name and under the name C. downesi Lansbury, the latter being a synonym of the former (cf. Appendix I). In the present study the species was found in British Columbia



and Washington (Fig. 55).

The species occurs in freshwater ponds (conductivity 485 micromhos/cm or below at 25°C) in the lowland areas between the Pacific coast and the Coast Range mountains.

C. utahensis: CANADA: British Columbia, Alberta, Manitoba. USA: Oregon, California, Idaho, Nevada, Utah, Arizona, New Mexico, Colorado, Texas, Kansas, North Dakota, South Dakota, Iowa. Brooks and Kelton (1967) report also Saskatchewan. In addition to Hungerford (1948), also Lansbury (1960) and Sparrow (1966) report the species from British Columbia. However, in the collections of the University of British Columbia all the specimens identified as C. utahensis from British Columbia belong to C. bifida. It seems that the records of C. utahensis from British Columbia are based on mis-identifications and the species does not occur in this province. In the present study the species was found in Alberta, Washington, and Utah (Fig. 55).

The species was not abundant in any of the studied areas, scattered specimens occurring both in small and large water bodies in the interior plateau and prairies, often in irrigation reservoirs. Conductivity of the water varied between 310 and 1670 micromhos/cm at 25°C.

C. dakotensis: CANADA: North-Western Territories, Alberta, Saskatchewan, Manitoba. USA: Minnesota, Illinois, North Dakota, South Dakota. Lansbury (1955) also reports Iowa. In the present study the species was obtained from Alberta (Fig. 56).

The species was taken in the spring of 1970 in shallow



ponds with conductivity of the water between 1100-1670 micromhos/cm at 25°C. In August 1970 the species had disappeared from these ponds, and conductivity of the water from the pond where the species was most abundant in the spring, had increased from 1420 to 1880 micromhos/cm at 25°C. However, it does not seem likely that the small change in the conductivity could have caused the disappearance of the species because there were several ponds with lower conductivity in the vicinity, but C. dakotensis was not detected.

C. blaisdelli: USA: California. Lansbury (1960) reports the species from British Columbia under the name C. columbiensis Lansbury. For the present study the species was obtained from British Columbia and California (Fig. 56).

The species seems to favor temporary or semipermanent ponds, but is also found in larger, more permanent water bodies and artificial park ponds. The location of every pond where the species was found, was less than two kilometres from the Pacific coastline. However, the water was always fresh (conductivity 215 micromhos/cm or less at 25°C), although at least some of the studied water bodies occasionally must receive salt spray from the ocean. The species was not found in ponds of truly saline environments, but Scudder (unpublished) has experimentally shown that it survives long periods in rather high salinities.

C. wileyae: USA: Washington, Oregon, California, Nevada, Utah, Arizona, New Mexico, Colorado. During the present study the species was obtained from Washington, Oregon, California,



Nevada and Utah (Fig. 57).

The species was found in the high sierra up to altitudes of 3300 m, and in the interior plateau at altitudes beginning at 300 m. Conductivity of the water was usually between 60-300 micromhos/cm at 25°C, but in one location where the species was very abundant, a conductivity of 8500 micromhos/cm at 25°C was measured.

C. expleta: CANADA: Saskatchewan, Manitoba. USA: North Dakota, Colorado. Lansbury (1960) reports the species from British Columbia, and Edmondson (1966) from Washington. In the present study the species was obtained from British Columbia and Washington, with one specimen also from Alberta (Fig. 57).

The species favors higher salinities than any other Cenocorixa species. Scudder (1969 a) reports breeding in lakes with conductivities between 5990-28900 micromhos/cm at 25°C. The data collected during the summer of 1969 showed conductivities between 5720-17540 for the lowest and highest values in LB2 (Fig. 36), but up to 22300 micromhos/cm at 25°C was recorded in Soap Lake, Washington; in all of these lakes breeding was observed to be successful. Occasionally the species was caught in almost freshwater lakes, but these specimens were obviously immigrants because they had a completely black mesonotum and were thus the flying form (Scudder, 1964); no larvae were observed in these lakes.

Sympatric situations between the species are indicated in Tables VIII-XI.



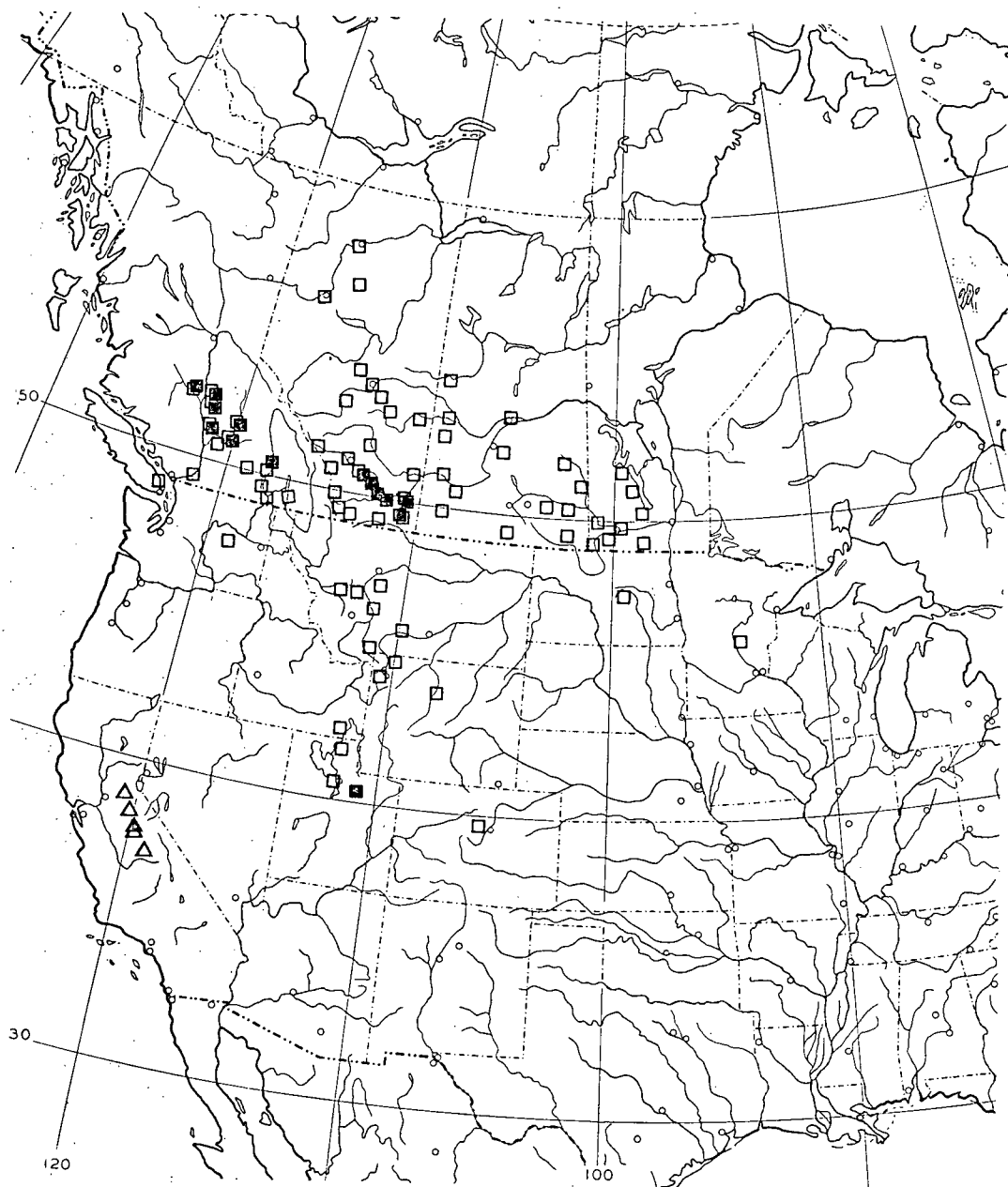


Fig. 54. Known geographic distribution of *C. bifida* (squares) and *C. kuiterti* (triangles). Open figures refer to published records, closed ones represent places where the species were obtained in the present study.



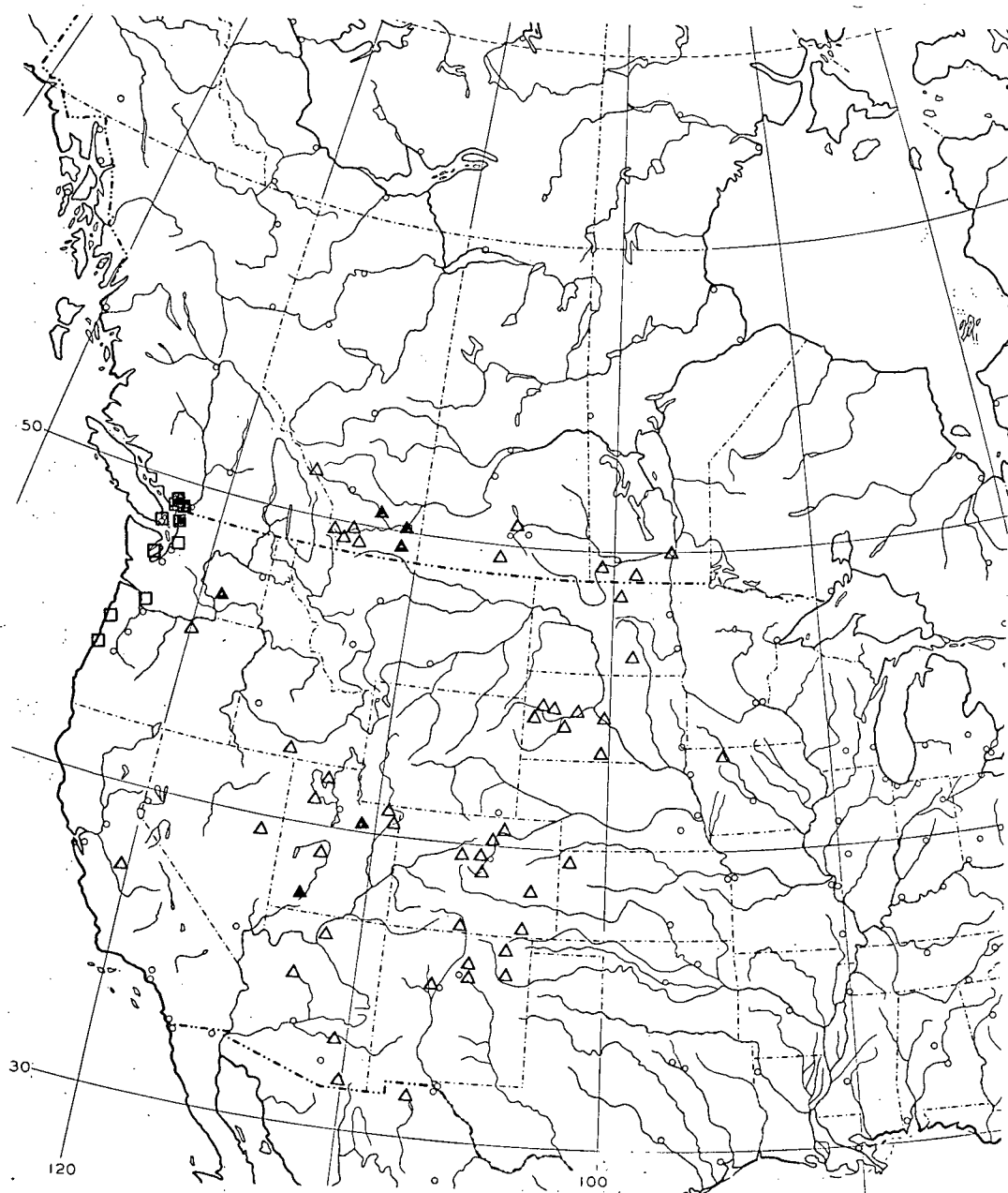


Fig. 55. Known geographic distribution of *C. andersoni* (squares) and *C. utahensis* (triangles). Symbols as in Fig. 54.



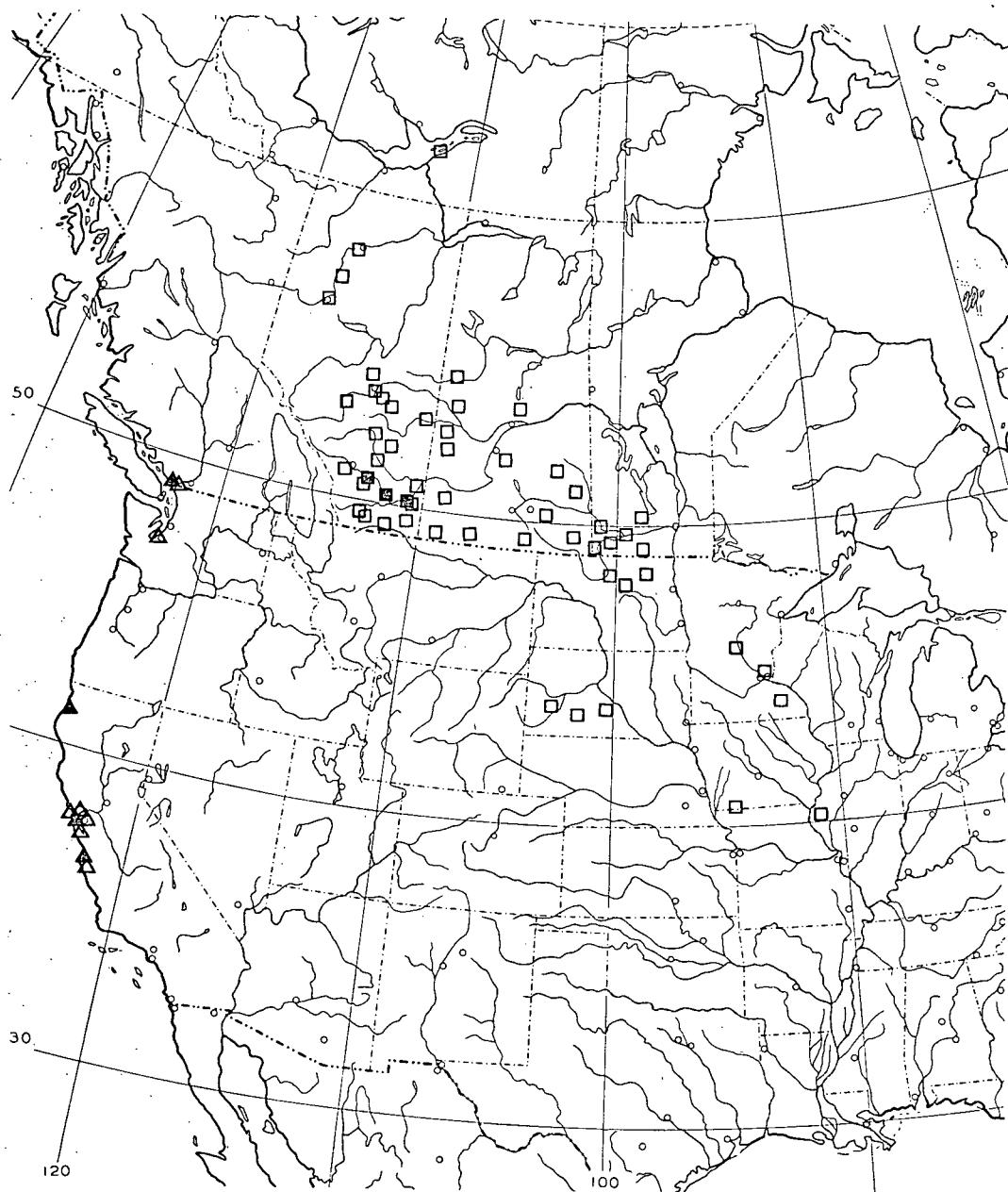


Fig. 56. Known geographic distribution of C. dakotensis (squares) and C. blaisdelli (triangles). Otherwise symbols as in Fig. 54.



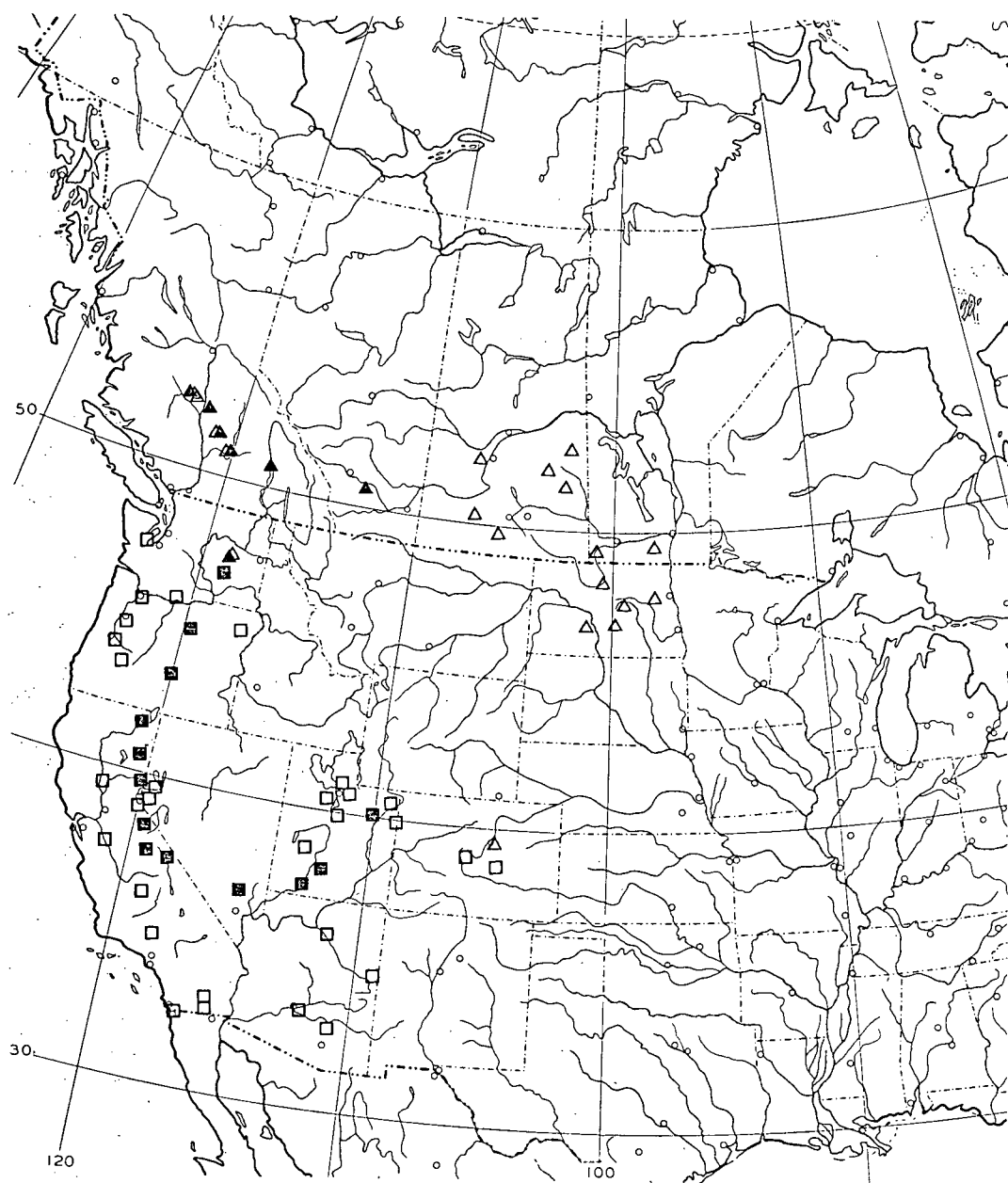


Fig. 57. Known geographic distribution of *C. wileyae* (squares) and *C. expleta* (triangles). Otherwise symbols as in Fig. 54.



b) Notes on ecological isolation in sympatric situations

In cases when two or more Cenocorixa species were found sympatrically, comparative observations were made on the ecology and habitats of the species. Sympatric situations were studied in the following areas:

i) British Columbia, Pacific Westcoast: C. andersoni and C. blaisdelli. These two species do not live continuously in the same ponds because of a partial ecological isolation: C. andersoni occurs mostly in larger, constant water bodies, while C. blaisdelli is mostly found in temporary rainwater ponds and semitemporary pools. Also, while C. andersoni seems to occur on most of the lowland area between the coast and the coastal mountains, C. blaisdelli was only found within 1-2 kilometres of the coastline. Both species are found together only from late fall until spring, i.e. during overwintering. They were not found to breed in the same ponds.

ii) British Columbia, interior plateau: C. bifida and C. expleta. Partial ecological isolation exists between these species since the two are found to breed in different salinity ranges: C. bifida favors only moderately saline waters with conductivities up to 13200 micromhos/cm at 25°C; C. expleta occurs in saline lakes with conductivities between 5700-22300 micromhos/cm at 25°C (upper limit is probably higher). In cases when the species were regularly found in the same lake (Barnes Lake - conductivity 7850 in May, 13200 in August, and Long Lake - conductivity 9800 in May, 11600 in August: Fig. 36), a further difference was observed between the species: C. bifida was found mostly at the very edges of the



water body, inside reed beds, while C. expleta stayed mostly in somewhat deeper water outside reed beds.

iii) Southern Alberta, prairies: C. bifida, C. utahensis, C. dakotensis, and C. expleta. C. expleta does not usually occur with the other species since, as noted above, it favors saline waters. In freshwater habitats studied, with conductivities up to 2080 micromhos/cm at 25°C, one single specimen of C. expleta was found. C. bifida was found in more saline waters than C. utahensis and C. dakotensis, and at conductivities around 2000 micromhos/cm only C. bifida was found. Detailed study of specific differences, however, remain unsolved because the area was visited only twice.

iv) Interior Washington: C. utahensis, C. wileyae, and C. expleta. The three species were not found to occur in the same water bodies, although they occur in the same geographic area, within 60 km radius of each other. Ecologically C. expleta was clearly separated from the two others by high salinity of the habitat (conductivity 22300 micromhos/cm at 25°C), while the other species were found in fresh water. C. wileyae and C. utahensis populations were scattered and no clear evidence of ecological separation could be detected, although they were found in separate ponds.

v) California, high sierra: C. kuiterti and C. wileyae. Both species were found in fresh water (conductivity 60 micromhos/cm at 25°C), but ecologically the ponds inhabited by C. wileyae seemed to be more eutrophic than the ones inhabited by C. kuiterti. The latter species was also found in slowly running water, while C. wileyae was only obtained from



stagnant ponds.

vi) Utah: C. bifida and C. wileyae; C. utahensis and C. wileyae. In Strawberry Reservoir, a few specimens of C. wileyae were found amongst a large number of C. bifida, and in Starvation Reservoir and in southwestern Utah, scattered individuals of C. utahensis and C. wileyae were found together. No habitat differences were detected in the short period of observation; only one visit to this area was possible.



## IV. DISCUSSION

## 1. Mechanism of sound production and analysis of the signals

In all early papers on stridulation of Corixidae (Ball, 1846; Thomson, 1894; Carpenter, 1894; Kirkaldy, 1901) the main question was the mechanism of sound production in one European species, Sigara striata (L.), and it was described incorrectly. The stridulatory signal of S. striata is very close to the signal of C. wileyae\*, [for sound spectrograms of the signal of S. striata see Finke (1968)], with a simple multipulsate first part and a very loud second part composed of regular pulse groups.

Mitis (1936) described the mechanism of stridulation in S. striata as follows: stridulatory pegs on the front femora are rubbed against sharp edges of the head about midway between the labium and the antennae. The first part of the signal is produced by alternating, the second part by simultaneous movements of the front legs: this explanation was also supported by Finke (1968). However, in Cenocorixa the plectrum is the maxillary plate, located posterior to the dorsolateral corner of the anteclypeus (terminology according to Parsons, 1965; 1966). According to specimens in the collections of Dr. G. G. E. Scudder, S. dorsalis (Leach.), which is very closely related to S. striata, and which also has a very similar stridulatory signal (Haskell, 1961), has a maxillary plate similar to the plectrum of Cenocorixa. This apparently functions as the plectrum also in the genus Sigara (as well

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\* Information of S. striata signals based mostly on my own unpublished recordings made in Finland and Sweden.



as in other stridulating European Corixinae).

Another difference between observations on European Corixinae and Cenocorixa is that only alternating movements of the front legs were observed during stridulation of the latter. According to spectrograms of signals of S. striata (Finke, 1968; Jansson, unpublished) it seems unlikely that S. striata utilises simultaneous movements of the front legs: detailed spectrograms do not show any doubling of impacts. Further, Finke (1968) also claims that Callicorixa praeusta (Fieb.), another European species, produces the first part of its signal by alternating and the second part by simultaneous movements of the front legs. The signal of this species (Finke, 1968; Jansson, unpublished) is very much like the signals of some other Callicorixa species [C. producta (Reut.) in Europe, C. audeni Hungfd. in North America], and also resembles very much the signals of Cenocorixa andersoni and C. utahensis, and I have not observed any simultaneous movements of the front legs during stridulation of these species. In fact, I have filmed the stridulation of Callicorixa producta (unpublished) with a high speed camera, and the film shows only alternating movements of the front legs.

In the genus Micronecta (Micronectinae), the mechanism of stridulation is believed to be associated with the abdominal strigil (Mitis, 1936; Southwood and Leston, 1959). Most species of Corixinae also have a strigil, but it seems to function for attachment to the female during copulation (Larsén, 1938). In two of the species studied in the present



work, C. blaisdelli and C. expleta, faint stridulatory signals were observed during the first few seconds of successful copulations. The mode of production of these sounds was not detected, but a possibility exists that the strigil would have a role in production of these sounds: placing the strigil into its proper position could produce these sounds.

Detailed spectrograms on the structure of the pulses in stridulatory signals of Corixidae have not been published previously. However, several studies on Orthoptera (c.f. Haskell, 1961; Dumortier, 1963 b) have shown that each impact of a pulse is equivalent to one strike of one tooth of the pars stridens on the plectrum (when one pulse is defined as a completed movement of the stridulatory apparatus, which is the usual definition in bioacoustical studies; this being incorrect in physical terms). The difference between the pars stridens in Orthoptera and Corixidae is that Orthopterans usually have one single row of teeth or denticles while Corixidae have several rows of stridulatory pegs. However, it seems very likely that each impact in the detailed analysis of the signals of Cenocorixa is produced by one peg row.

Mitis (1936) found a correlation between the thickness of the stridulatory pegs and the loudness of the signals of different species. In the present study, observations on the two sexes of each species suggest that the structure of the plectrum could also affect the amplitude of the signals.

The signals of Cenocorixa were found to be species specific. Similarly, in previous publications (Mitis, 1936;



Leston, 1955) signals of various corixids have been found to be species specific, but owing to insufficient technical apparatus the exact differences were not shown until in Finke's (1968) paper. In this paper, Finke (1968) published sound spectrograms and oscillograms of signals of Sigara striata and Callicorixa praeusta, and the differences between the species appear to be in the temporal pattern of pulses and the pulse repetition rate. The main frequency area of the sound in both species is approximately the same as in Cenocorixa (3-5 kc/sec), but Finke (1968) obtained also some higher overtones ("Oberwelle" in German) at 6-10 and 9-15 kc/sec and over. This seems to be an artifact, because I was able to make similar overtones by overloading reproduce power of the spectrograph (Fig. 58).

The difficulty in analysing signals with short pulses is that the indicator meter of the spectrograph does not have time to show the true reproduce amplitude of the peaks of the very short impulses and so accidental overloading is not detected [c.f. Andrieu (1963): measuring the sonic level]. The fact that overtones are artifacts was demonstrated by filtering some signals with a sound and vibration analyser type 1554 A (General Radio Co., Mass., U.S.A.), so that only the higher frequencies at 11-15 kc/sec were allowed through, and then analysing the filtered sound. The result showed no sounds at these frequencies, and in this experiment both the input and reproduce level could be much higher than with normal signal, because the possibility of overloading effects of the lower frequencies was eliminated.



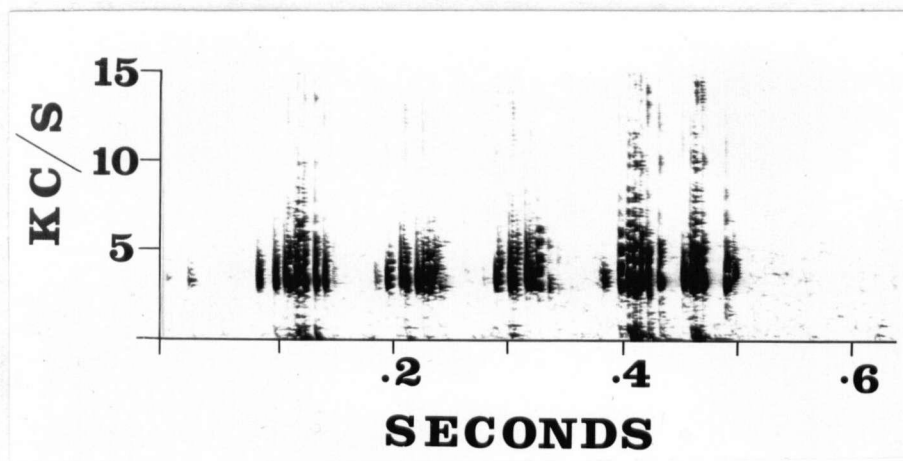


Fig. 58. Example of artifacts created by improper analysis of a Cenocorixa signal: sound spectrogram of one pulse group of a C. expleta male signal analysed by overloading reproduce power of the spectrograph (readings of the VU-meter at peaks of the signal were 0, mark level 7). All sounds appearing above 6 kc/sec are artifacts. Note that the first three pulses are fainter in amplitude than the last two: the stronger the sound, the more artifacts are created.



Finke (1968) may also have obtained overtones because she recorded the signals in a styrofoam container. In comparing signals recorded in a styrofoam container to recordings made under natural conditions, I found styrofoam to change the frequency pattern of Cenocorixa signals.

Temperature was not usually observed to have an effect on the temporal pattern of pulses of Cenocorixa signals, but it clearly affects the pulse rate and, when applicable, the pulse group rate, as well as the signal length. Finke (1968) has also published some data on temperature effect on stridulation of Sigara striata, but this was on duration of pulse groups and pulse group intervals. Thus, actual observations on pulse rates of Corixidae other than Cenocorixa species, are lacking.

Walker (1962) has studied the effect of temperature on signals of several species of crickets. He states that temperature affects the pulse rate of cricket signals in a uniform way and the following generalisations were made: i) rate of change in pulse rate with temperature is constant; ii) the higher the pulse rate at a given temperature, the greater the rate of change; iii) if regression lines are extrapolated downward, they tend to converge at 4°C and 0 pulses per second.

Generally these rules also seem to fit in Cenocorixa signals. Figs. 17-26 show that a graph where pulse rate is plotted against temperature forms a straight line, but as Walker (1962) further states for crickets, if a deviation from a linear relationship is found it will be at the extremes



of temperature; pulse rates of Cenocorixa seem to be slightly higher than expected at low temperatures. Fig. 59 summarises the regression lines of Cenocorixa males, and this shows that the regression lines for the species with high pulse rate are generally the steepest. However, Fig. 59 also shows that the regression lines of Cenocorixa do not converge at 4°C and 0 pulse per second, but most of them (8 out of 13) seem to converge at about 9°C and 6 pulses per second.

Regression lines for female signals were also calculated in most species, but owing to the small temperature range studied the lines are probably somewhat biased. In C. wileyae females, when more observations were made in different temperatures, the regression line is very close to the general lines of the males. This would probably have been the case also in females of other species if more material had been available.

Signal duration plotted against temperature was shown to be non-linear in Cenocorixa (Figs. 22-24). In any signal it can be shown that if the change in the pulse rate with temperature is constant (= linear regression), and the number of pulses in the signal is constant, the duration of the signal does not change linearly when the temperature changes. As an example the pulse rate of C. bifida male has a regression line of  $Y = -0.766 + 0.466X$ . Pulse rates at 10°C, 20°C, and 30°C on this regression line are 3.9, 8.6, and 13.2 pulses per second, respectively, and average number of pulses per signal was observed to be 19.60 for the species. From these values, expected signal durations in the above



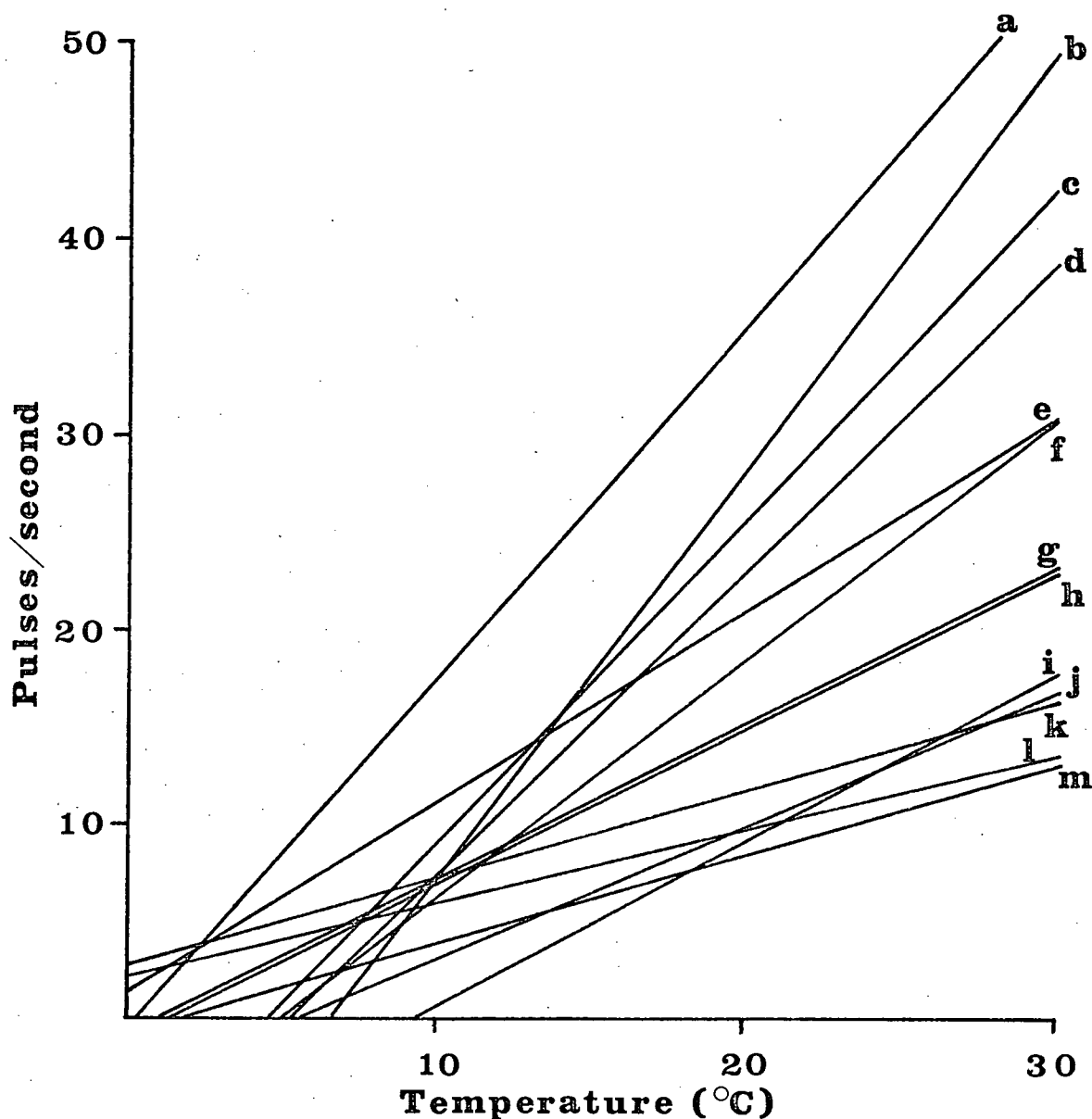


Fig. 59. Summary of the regression lines of temperature effect on pulse rate in *Cenocorixa* male signals. a = *C. wileyae* fast pulse rate; b = *C. utahensis* fast pulse rate; c = *C. andersoni* fast pulse rate; d = *C. kuiterti* fast pulse rate; e = *C. expleta* fast pulse rate; f = *C. utahensis* slow pulse rate; g = *C. andersoni* slow pulse rate; h = *C. kuiterti* slow pulse rate; i = *C. blaisdelli* first part pulse rate; j = *C. dakotensis*; k = *C. expleta* slow pulse rate; l = *C. wileyae* first part pulse rate; m = *C. bifida*.



temperatures can be calculated, and values of 5.0, 2.3, and 1.5 seconds are obtained. Fig. 60 A shows that these expected values form a curve which is very close to the curve obtained from the actual observations on signal duration in C. bifida. Thus, since the actual curve does not depart significantly from the calculated values, it shows that the number of pulses per signal (and apparently the temporal pattern of pulses as well) is constant and independent of temperature.

In Fig. 60 B signal duration graphs from actual observations of all other Cenocorixa males are summarised, and it is seen that the general pattern follows that of C. bifida; specific differences are apparently owing to differences in the pulse rate and average number of pulses per signal. Dumortier (1963 b) has a similar observation on signal duration of Ephippiger provincialis (Yers.) (Orthoptera, Tettigonioidea): signal duration follows a curve of hyperbolic shape.

Moore (1961) published sound spectrograms of signal produced by a North American corixid, Hesperocorixa atopodonta (Hungfd.). The main frequency area of these signals is 7-8 kc/sec, which is clearly higher than in any Cenocorixa signal. However, Moore kept the bugs in a fingerbowl and recording was done by microphone protected from wetting by a fish swimbladder; these factors possibly changed the frequency of the sounds. Further, Moore (1961) states that the pulse rate in these signals is about 200 pulses per second, but this apparently means the impact rate within the pulses [if the pulse is defined according to Dumortier (1963 c)]



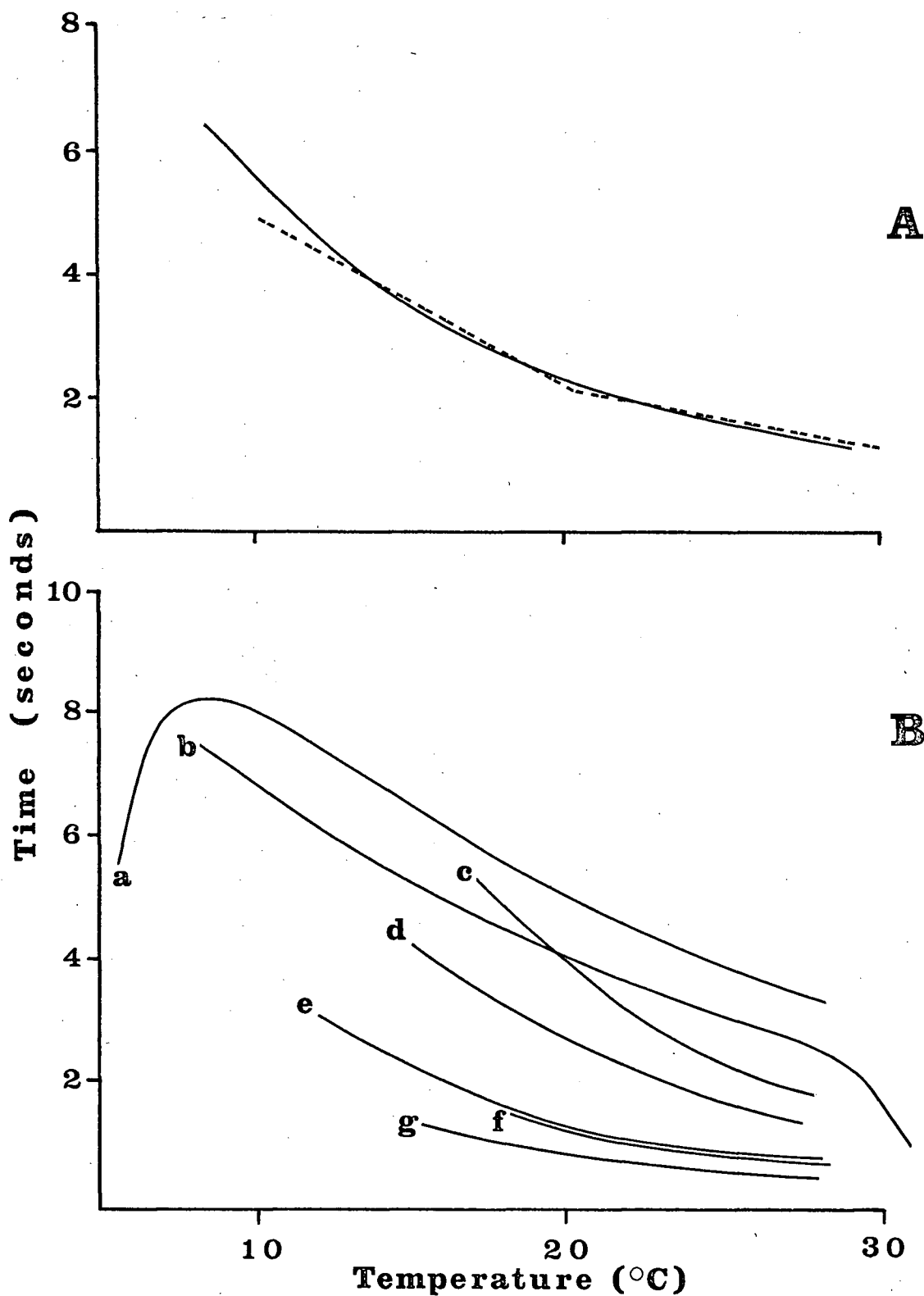


Fig. 60. Summary of temperature effect on signal duration in *Cenocorixa* males. A: *C. bifida*; continuous line = observed curve; broken line = expected curve (for more explanations see text). B: observed curves; a = *C. wileyae*; b = *C. expleta*; c = *C. utahensis*; d = *C. dakotensis*; e = *C. andersoni*; f = *C. blaisdelli* (first part of the signal only); g = *C. kuiterti*.



and the common concept in bioacoustics].

The signals Moore (1961) observed were produced by a male specimen, and they did not have any apparent effect on other specimens (females) in the vicinity. Moore observed further, that the sound was produced by rubbing the hind tibiae and tarsi along the back of the specimen. Another species, Sigara grossolineata Hungfd., was observed to stridulate in a similar way. This mechanism of sound production was also observed by Finke (1968) in studies on Sigara striata, and in this case both males and females produced these sounds, but they were too faint for satisfactory recording.

In the present study all Cenocorixa species were observed to produce these sounds in two ways: i) alternate movements of hind legs, ii) simultaneous movements of hind legs. A spectrogram of these sounds is shown in Fig. 30. No species specificity was observed and playback experiments utilising these sounds did not initiate any response of males or females. The bugs were observed to produce these sounds at any time of the year. These sounds appear to be a result of cleaning movements and are not true stridulatory signals. The movements are apparently made to clean and rearrange the lateral abdominal hairs that are important in maintaining the air bubble between the wings and the abdominal dorsum for respiration (Popham, 1960; Parsons, 1970).

Leston and Pringle (1963) adhere to the old concept that the use of paler pegs in possible stridulatory mechanism has not been disproven. They refer to species which have not been observed to stridulate, and suggest that the signals of



these species might be too faint to be recorded. In fact it is true that all species of Corixidae can often be observed to rub their palae against each other or the rostrum. However, this seems to be nothing more than a kind of cleaning activity, and sounds produced in this way would probably be far too faint to have any significance in the behavior of the bugs, especially when much more intensive sounds, produced by the rubbing of the hind legs, appear to be side-products of cleaning movements and without behavioral significance.

In Cenocorixa the use of palar pegs in stridulation is impossible since only the males have these pegs, yet both males and females stridulate. In similar genera, the palar pegs of the males are used for clasping the female during copulation (Popham, 1961): the pegs are placed under the curved longitudinal ridge of the lateral flange on the female hemielytron; the two sexes are thus firmly attached to one another, and are able to swim while in copula.



## 2. Life cycle, sexual maturation, and stridulation

Detailed study on life cycle of four species was carried out in order to find out how stridulation correlates with sexual maturity in the genus Cenocorixa. The study showed that in the interior of British Columbia both C. bifida and C. expleta commonly have a partial second generation per summer. However, in favourable circumstances a complete second generation and even a partial third generation can be produced, as was shown of C. expleta in the water body LB2. The failure of C. bifida to produce more than one generation in LB2 was apparently owing to increasing salinity which during June and July killed larvae of the second generation.

Hungerford (1948) states that in general North American Corixidae produce one or two generations per summer, depending on temperature. Larsén (1938), Crisp (1962), and Young (1965) have studied the life cycles of several European Corixidae, and some species have been observed to have only one generation while others apparently produce a partial second generation. Similarly, Pajunen and Jansson (1969) and Pajunen (1970) observed a partial second generation in two species of corixids living in rock pools in the archipelago of southern Finland. However, neither a completed second generation (as in C. andersoni in the Pacific Westcoast) nor a partial third generation (C. expleta in LB2) have been reported previously. By comparing the temperature data on the lakes studied during the present work (Figs. 34-35), it can be seen that LB2 generally had a slightly higher temper-



ature than other lakes. Thus the partial third generation in C. expleta occurred in the warmest lake.

Prior to the present work no detailed study of the sequence of generations based on the phenology of the different larval instars has been published. Apparently this is because the five larval instars are commonly found together in the lakes throughout the summer, and the larvae belonging to separate generations may be difficult to separate. The lack of identification keys for larvae also has not been conducive to such studies. In the present work, however, it was possible to identify the larvae following Scudder (1966), and changes in the relative numbers of different larval instars in the samples were considered to be a reliable indicator in placing the larvae into proper generations. The sequence of generations was also followed by studying the gonad development, the method used in previous studies on life cycles, but the larval study made more accurate statements possible.

The study of the ovaries in Cenocorixa showed that overwintered females become sexually mature soon after ice break-up in the interior of British Columbia, while at the coast maturity is reached in March. In addition, C. bifida and C. expleta were observed to fly actively in early May 1969, and C. blaisdelli was found to fly throughout the summer of 1970, when they were breeding. In contrast, rock pool species of southern Finland have a short dispersal period before attaining sexual maturity (Pajunen and Jansson, 1969). On the other hand, Young (1965) observed maturation of



females in some species to occur before break-up in England.

Sexual maturation of females of the initial part of the first generation in Cenocorixa was observed to take about one week. Similarly, Pajunen (1970) observed young females of Callicorixa producta (Reut.) and Arctocorisa carinata (C. Sahlb.) to have chorionated eggs within a period of 10-14 days. The later part of the first generation in Cenocorixa was observed to remain sexually immature in the interior of British Columbia. Both Young (1965) and Pajunen (1970), who made similar observations, explained this in connection with photoperiod. According to Young (1965) there is no diapause in the ovarian development because adult females were observed to mature and lay eggs in the laboratory at all times of the year when under experimental conditions of 16 hours photoperiod and temperatures of 12-32°C. Further, he states that the control of the initial development of the ovaries probably depends on photoperiodic effect. However, some of his own results are inconsistent with this suggestion: He noticed for example in Sigara scotti (Fieb.), living in a lake with wide shallow areas, that when the water level dropped some pools were formed along the lake: the first adults of the first summer generation emerged more than two weeks earlier in these pools than in the lake itself. Further, he observed that in none of the specimens in the pools did ovarian maturation take place, whereas in the main lake in early July it did! In this case at least, photoperiod could not have anything to do with the difference in the ovarian development.

According to Pajunen (1970) arrested ovarian development



appears in early July, which is near the middle of the summer in southern Finland. Further, he states that this arrest depends on photoperiod and that the adaptive value of ovarian arrest in this particular case must lie in the limitation of population size: high reproductive capacity of corixids would boost the density of the populations beyond the levels of food resources in the rock pool environment.

The results of the present study showed differences between the lakes in the interior of British Columbia in the timing of the arrest in ovarian development, but this cannot reflect differences in the photoperiod: all lakes were within a relatively small geographic area, some of them only 1-2 kilometres from each other. Further, the lake where mature females were observed latest (LB2), was about 100 km further south than the others, and thus had a shorter photoperiod than the others throughout the summer. Additional information in support of this contention was obtained from Soap Lake, which is located in Washington, about 500 km south from the main study area. Here C. expleta was found to be breeding as late as 29 August 1969, and so here again the photoperiod is shorter than in the Cariboo-Chilcotin area of British Columbia. Further, the experiment carried out with C. bifida on 8 and 16 hours photoperiod, showed that although not every female, at least some of the females in both short and long photoperiod became sexually mature at the same time in laboratory conditions, and thus independently of the photoperiod.

When differences observed in the field study in the timing of the arrest in ovarian development are compared



with the productivity of the lakes, a clear correlation between the two is found: in low productivity lakes all females were found to show ovarian developmental arrest in early July, while in high productivity lakes reproductive females were observed until the end of July. In lakes with very high productivity, reproductive females were observed as late as end of August. It is known that starving insects do not develop eggs (cf. Johansson, 1958; 1964), and thus in low productivity lakes it seems probable that there is a shortage of food. However, the exact food utilised in these low productivity lakes is unknown.

In the high productivity lakes both C. bifida and C. expleta feed on Diaptomus sicilis Forbes (Scudder, personal comm.), a copepod that is absent from the low productivity lakes (Scudder, 1969 b). Zwart (1965) suggests that almost any form of small living animal would be adequate food supply for corixids generally, but at least in some cases plankton animals seem to be preferred. It is most likely in the Sigara scotti studied by Young (1965), that the specimens in the pools cut off from the main lake, did not have an adequate food supply, and so remained sexually immature, whereas those in the main lake were not short of food. Although Pajunen (1970) states that ovarian arrest prevents overpopulation in rock pools, it is possible that because rock pools are not very productive water bodies, that it is the insufficient amount of food that limits the size of populations by cutting off the development of the ovaries.

Thus, the present study suggests that photoperiod is not



the critical factor in the ovarian developmental arrest in the genus Cenocorixa. However, because the time of the arrest in the high productivity lakes does not coincide with any drop in the availability of copepods, the lack of food may not be the only environmental factor involved. The temperature records for the lakes show that the arrest is not correlated with an obvious decrease in temperature: temperature does not start to drop significantly until late September. Ovarian development is probably influenced by several factors. Food supply, temperature, and photoperiod are factors that may be important in some instances, but this aspect needs further investigations.

Sexual maturation of Cenocorixa males was observed to follow generally the same pattern as the maturation of the females, but with the following differences: newly emerged males of the initial part of the first generation were sexually mature at the time of emergence, and at least some of the overwintering males reached sexual maturity in late fall, rather than early spring. Larsén (1938) studied sexual maturation of corixids in Sweden, and observed mature sperm in the testes generally during spring, but in one species, Corixa dentipes Thoms., he also detected sperm in the testes in September. On the other hand, Young (1965) states that sperm is formed during summer and autumn in the overwintering males, stored in the seminal vesicles until spring, and the testes are inactive in the spring! Also Pajunen (1970) claims that sperm was found in the seminal vesicles of the late summer specimens at the time when ovarian development in



females was already arrested.

Neither Young (1965) nor Pajunen (1970) explain the methods they adopted in investigating the presence of sperm in the seminal vesicles. However, with the squashing method used in most of the present study, it was not possible to observe sperm in the seminal vesicles because in Corixidae this organ is surrounded by a thick layer of connective tissue: if sperm exists in the seminal vesicle it will appear very similar to the fibres of the surrounding connective tissue, and cannot be distinguished. Also in the testes themselves there are some structures which appear very much like mature sperm and some practice is needed to distinguish the presence of mature sperm. However, the results obtained with the squashing method were checked by making serial sections of the testes. Thus, although the seminal vesicles could not be studied in squash preparations, it was shown that if the testicular follicles did not contain spermatids at their late developmental stage (Fig. 40 D), the seminal vesicles did not contain any sperm, and so the specimen was sexually immature.

In mature individuals all of the stages of spermatogenesis were clearly visible in the follicles in the initial part of the first summer generation and late fall insects. In the overwintered specimens it often was observed that mature sperm could not be detected in the testes, but could be found in the seminal vesicles in the serial sections. However, the presence of very large numbers of developing cysts with all other stages of spermatogenesis indicate that the testes were by no means inactive as stated by Young (1965).



It would be more natural to assume that the developing cysts filled the follicles and simply pushed the mature sperm into the seminal vesicles. This is also supported by the fact that sometimes the sperm appeared to be still in bundles in the seminal vesicles in the serial sections. Further, specimens studied in late summer, at the time of ovarian arrest in females, showed that the testicular follicles were filled with cysts in stages of meiotic division and with spermatids in their early developmental stage (Fig. 44), but no further stages were found. At this time, therefore, spermatogenesis was also arrested.

The reason for the arrest of spermatogenesis is not easily explained. It occurred simultaneously with the arrest of oögenesis in females in various lakes. In general, however, insufficient nourishment in male insects does not usually prevent sexual maturity, but merely reduces the size of the testes (Johansson, 1964). However, Geer (1967) and Geer and Newburgh (1970) have shown with Drosophila melanogaster that the development of mature sperm is dependent upon dietary factors. Thus, it may be that the reasons for the arrest of spermatogenesis are the same as for the arrest of oögenesis, and at least partly owing to diet deficiencies. It is not known why the males become sexually mature in late fall while females remain sexually immature.

Almost all previous studies on stridulation of Corixidae state that signals are produced only during the breeding season, i.e. spring and early summer (Mitis, 1936; Schaller, 1951; Leston, 1955; Southwood and Leston, 1959; Leston and



Pringle, 1963; Finke, 1968). The only previous publication mentioning stridulation during the fall is Larsén (1938): Corixa dentipes was observed to stridulate in September (Larsén also detected sperm in the testes of this species at the same time). In the present study it was shown that the stridulation of Cenocorixa males correlates with sexual maturity. Thus, males of Corixidae will stridulate outside of the breeding season.

In some other insects stridulation has been reported several months before actual mating. For instance Van Tassel (1965) reports beetles of the genus Berosus (Hydrophilidae) to stridulate when brought into the laboratory in January. The presence of mature sperm was not investigated in that study, but because the author reports the males to have attempted copulation at the time that they stridulated, they probably were sexually mature. Females, however, obviously reached sexual maturity several months later because successful copulations were not observed until May.

The fact that stridulation in Cenocorixa males is correlated with sexual maturity, was also shown with specimens taken into the laboratory in late fall. Such males stridulated and made attempts at copulation, but females always rejected the males at this time. Two to three weeks later some of the females reached sexual maturity, apparently because the room temperature was high enough to allow this, and the food supply (frozen brine shrimps) was sufficient. At this time the males were accepted and copulations were successful. The fact that no copulations occur normally in



late fall in the natural environments was demonstrated by taking female insects from the field and keeping them at room temperature without males: some of the females matured in about three weeks and laid eggs, but no larvae hatched from these eggs and no embryonic development was detected. The females seem not to have mated and thus they do not store sperm over winter in the receptaculum seminis. Storing sperm over winter in the receptaculum seminis is a common phenomenon in temperate social Hymenoptera (Richards, 1961).

The question of how sexual maturity in Cenocorixa males induces these bugs to stridulate was not investigated in the present study. However, there have been attempts to study this previously in other insects. Haskell (1960), for instance, reports that castrated males of grasshoppers (Orthoptera, Truxalinae) stridulate, perform courtship display, and copulate. According to this, actual presence of sperm is not necessary in these grasshoppers.

The annual rhythm of stridulation in Cenocorixa females could not be studied in the field. However, behavioral experiments showed that only females with chorionated eggs in the lateral oviducts responded to the male signals by answering, providing that they had not mated recently. Thus, the stridulation of females correlates both with sexual maturity and a "need" for a mate.

The question of what changes the behavior of a receptive female to an unreceptive one was not studied in detail in the present work. However, it was noticed that the receptive females always had chorionated eggs in the lateral ovi-



ducts, and no embryonic development occurred in the eggs laid by these females. Mating changed the females from receptive to unreceptive, and eggs laid by these females developed normally and larvae hatched. It was also observed that interrupted copulations (allowed to last only 1-2 seconds) were enough to make the females unreceptive. Whether or not sperm was transferred in these copulations was not studied. The stimulus for females to be unreceptive could thus be chemical, tactile, or both.

It has been shown that the females of certain grasshoppers (Haskell, 1960) and katydids (Spooner, 1964) seem to be receptive to males in a way similar to Cenocorixa females: a mated female is not receptive until after several ovipositions. Haskell (1960) claims that the presence of sperm in the receptaculum seminis has a chemical effect upon the female. However, it should be noted that sperm or accessory gland material or both do not always have to be located in the receptaculum seminis to be chemically effective. Davey (1958) has shown that the spermatophore in Rhodnius (Hemiptera, Heteroptera, Reduviidae) induces rhythmic contractions of the bursa copulatrix, and in Drosophila the walls of the vagina secrete fluid of an insemination reaction (Patterson, 1946; Lee, 1950) soon after coitus and this may start before copulation is completed (Patterson and Stone, 1952). Insect genitalia have sense organs which are important in mating (Scudder, 1971) and the function of these could be sufficient to terminate the response of the female. Spooner (1964) claims that in katydids the presence of eggs in the



ovaries determines the positive response of females: as soon as the eggs move to the lateral oviducts the response is inhibited. In contrast, in Cenocorixa the presence of eggs in the lateral oviducts seems to be essential for receptiveness.



### 3. Stridulatory behavior

Observations on the stridulatory behavior of Cenocorixa males indicate that stridulation commences spontaneously, providing the males are sexually mature. In general classifications of the function of insect signals (Dumortier, 1963 c; Alexander, 1967; 1968) this would be classified as a calling signal, and its function would be to facilitate pair-formation by attracting conspecific females. The experiments confirmed that this is the case in Cenocorixa. However, experiments also showed that signals of males would often stimulate other males to stridulate. Differences were detected between the species in their readiness to answer various signals. When conspecific male signals were used (Fig. 52, Table VIII), some, but not all Cenocorixa species readily answered these signals. Further, in cases when certain species are able to produce two different calls (first part of the call alone or complete signal), the males answered the slow pulsated first part more readily than a complete signal (e.g. C. andersoni: Table VIII).

Both spontaneous and sound evoked stridulation has been observed in male Corixidae previously (Schaller, 1951; Leston, 1955; Leston and Pringle, 1963; Finke, 1968), and the signals have been classified mostly as calling signals. Further, a very commonly held concept is that a courtship signal as distinct from a calling signal also exists: Mitis (1936) observed in Sigara striata, that a male observing a female, started stridulating very actively with shortened intervals and longer signals. Also Leston (1955), Southwood and Leston



(1959), and Leston and Pringle (1963) claim that a courtship signal has been observed in corixids, but they do not explain the difference between the signals belonging to the calling or courtship categories. Haskell (1961) states that male corixids can generally produce two signals, and it is suggested that one is a calling signal, the other a courtship signal, although this has yet to be confirmed.

In the present study it was frequently observed that as well as stridulatory signals, a visual stimulus from a male, female, or specimen of another species induced Cenocorixa males to stridulate. No difference was detected in the structure of these response signals except in cases when the response signal was only a part of the normal call or calling signal, which often, but not always happened in C. andersoni, C. utahensis, and C. blaisdelli. According to the definition of a courtship signal [Dumortier (1963 c): a display of the male, set off by a stimulus from the female], this induced signal is not a courtship signal.

Leston and Pringle (1963) state that the calling signal of corixids may include rivalry or territorial function. Further, when movements of C. bifida males were compared in the situations where the males were alone or exposed to a stridulatory stimulus, it was shown that significantly more swimming (especially short range swimming) occurred when stridulatory signals were present. In observations on males of C. bifida and C. blaisdelli it was found that stridulation was often followed by nudging and chasing behavior which serves to space out individuals. This suggests that the strid-



ulation in Cenocorixa functions as an agonistic signal. Similarly, Leston and Pringle (1963) report that Sigara dorsalis (Leach.) males, stridulating alternately, move towards each other until their heads come together, and one of them finally nudges the other one away. In C. bifida and C. blaisdelli, if the specimens were within visual range of each other, they did not move towards each other during the signalling which preceded the nudging.

In Cenocorixa, the signals produced in agonistic situations, did not usually differ structurally from spontaneously produced calling signals, although their function apparently is different. In contrast, Orthopterans have a more highly developed acoustic communicating system often with structurally different signals for different purposes (Dumortier, 1963 c). However, the function of the agonistic signals of Cenocorixa males seems to be the same as the function of a rival's song in Dumortier's (1963 c) classification: an emission produced, usually alternately, by two individuals a short distance from each other, denoting the so-called rivalry or territorial behavior.

In C. bifida, when a stridulating male was within a few centimetres of an unreceptive female, apparently approaching the latter, the female was observed to swim away from the calling male (escape) or disturb the male by swimming towards it (agonistic behavior). A receptive female, on the other hand, within the range of the sound of the calling male, would stay motionless and stridulate in answer to the male call. In other words, a receptive female produced an agreement



signal [according to classification of Dumortier (1963 c)]. Males were observed to orientate directly to the female according to this agreement signal. No true courtship display was observed in any species of Cenocorixa.

In the mating experiments carried out in the culture trays, it was found that the males could not orient to and locate the females on their agreement song owing to echoes from the walls of the trays. In these cases the males swam very fast in small circles and produced signals which were different from "normal" calling signals: the pulse rate in these signals was more irregular than in the calling signals, and the duration of the signals was short, but the signals were repeated more frequently than normally. In several species these signals were produced while the males were swimming (normally signals are only produced while the specimens are resting on the bottom). However, it was observed that the females did not answer these unusual calls. The next female signal occurred only after the male produced a "normal" signal again. Thus these unusual male signals are not courtship signals, but signals created by an unnatural situation.

Males of C. andersoni and C. utahensis can produce either a complete signal or the first part of the signal alone. It was found that males often respond to the first part of the signal more readily than to the complete signal, while receptive females will respond to only the complete signals and not parts of them (Tables VIII and X). This suggests that the complete signal, which is the calling song, is used to attract females, while the incomplete signal seems



to have the function of an agonistic signal. On the other hand, C. blaidelli and C. wileyae males produce the two parts of the signals often independently from each other, and both females and males seem to respond only to a complete signal or only to the last part of the signal: the differentiation of the functions of the signals does not seem to be clear in these two species. In the European Sigara dorsalis, Haskell (1961) suggests that one signal could be a calling song, the other a courtship song, but according to the observations in Cenocorixa they function as a calling song and an agonistic song. However, working on Sigara striata, which has signals almost similar to the signals of S. dorsalis, Finke (1968) could not detect any difference in the functions of the two calls.

In Cenocorixa stimuli for a successful copulation seem to be i) calling signal of the male, and ii) agreement signal of the female. In orienting to the receptive female from a great distance, males of all species depend on auditory stimuli, but at close range visual stimuli seem to be important in most species. However, C. dakotensis does not seem to orient to visual stimuli at all, but only to auditory stimuli. This is understandable since C. dakotensis is the only species which was never observed to stridulate spontaneously during daytime.

Schaller (1951) claims that the response of females of Sigara striata to a male song is to swim rapidly in small circles, and thus, since the male will try to copulate with any moving object of suitable size, mating is initiated, i.e.



the movement of the female attracts the male. However, Finke (1968), also worked on S. striata, observed no increase in short range swimming of females in response to male calls, but a difference in long range swimming of the females was observed ("Aufschwimmen, längere Bewegungen im Aquarium"): the swimming activity of females increased when the male signals were played. It seems to me that in both cases (Schaller, 1951; Finke, 1968) the reaction of the females of S. striata was not a premating response, but an escape reaction of unreceptive females.

During the present study it was frequently observed that not only females, but also males of Cenocorixa would swim in small circles in culture trays when stimulated by male signals from specimens close by (orientation was impossible owing to echoes). This often attracted other Corixidae and led to copulation attempts between two males or males and females of different species or even different genera! However, even when the male and female were of the same species, the attempt at copulation, without the preceding agreement signal of the female, was unsuccessful.

It is recalled that in Cenocorixa the reaction of unreceptive females placed with caged stridulating males was for the females to remain motionless, the males not being able to get into close proximity to the females. On the other hand, unreceptive females placed so that the stridulating males could come into contact with them, did not stay still, but escaped. Schaller's (1951) experiments were carried out in glass aquaria and in these I have noticed plenty of echoes,



as indeed Schaller (1951) also reported. Females under such conditions would not be able to orientate away from the male because the sound would appear to come from everywhere. In Finke's (1968) study the females of S. striata used were collected in early spring, and then kept in constant temperature cabinet at 4°C until early May when the experiments were carried out. While this is the time that mating occurs in the natural habitat, experiments with Cenocorixa demonstrated that females kept at 4°C would not attain sexual maturity. Thus the female specimens used by Finke (1968) were probably sexually immature, and the swimming observed, was probably an escape reaction.

A morphological study of females of several European species (collections of Dr. G. G. E. Scudder: Corixa dentipes, Sigara dorsalis, Arctocorisa germari, Callicorixa praeusta) showed that a plectrum and pars stridens existssinthese. In previous studies (Mitis, 1936; Schaller, 1951; Finke, 1968) females are reported to lack the stridulatory apparatus. It is true that this apparatus in the females of the European species studied is less developed than the apparatus of the males, and for instance the S. dorsalis male has about 12 rows of well developed pegs in the pars stridens, while the female only has about seven rows of these pegs and they are not as strongly thickened as in the male. A similar tendency to have less developed stridulatory apparatus was found in Cenocorixa females when compared totthe males (cf. Table I, Fig. 4). However, there is no doubt that the females of the European species studied are able to stridulate. This is also



supported by Southwood and Leston (1959) who state that both sexes of Arctocorisa germari stridulate during the breeding season, although nothing is said about how this is connected with breeding. Further, during the present study, stridulatory signals of both sexes of Sigara nevadensis Walley were recorded (cf. Appendix II), and their function was observed to be the same as the function of the signals in Cenocorixa.

Crisp (1962) has described the mating in Arctocorisa germari and notes that the male detects the female when the latter is swimming by. The male then chases the female and mounts the female while the pair is swimming, and then the pair comes up to the surface where copulation occurs. Thus the occurrence of copulations in the natural habitats is easily observed (Crisp, 1962). In Cenocorixa, a similar sequence of events was frequently observed, but in this genus it only occurred between an active male and an unrecptive female: the pair came to the surface because of the release behavior of the female. In a successful copulation in Cenocorixa the pair never comes up to the surface during the initiation of copulation, but if the copulation lasts a long time, the pair may occasionally come to the surface to renew its air supply.

In a few previous studies on European corixids it had been noted that the song of males does not seem to have any visible effect upon the females (Mitis, 1936; Larsén, 1938; Jansson, 1968). However, in all of these studies both sexes apparently were kept all the time in the same container, and thus, if the species are like Cenocorixa species, most females



in such cultures would be mated immediately when they become receptive, and most of the time the females would be unreceptive.

In the experiments carried out with C. bifida, an interesting difference between different males was obtained in the presence of female odor: the male kept isolated from all other specimens readily stridulated in the presence of female odor, but the males picked up randomly from a mixed male-female culture did not show any increased stridulating activity. The males from the mixed culture did not react to the odor of females, perhaps because the experimental situation did not differ in this regard from the conditions in their culture tray. However, for the male kept isolated from all other specimens, the female odor clearly was a stimulus to stridulation (male odor did not have any effect). In this experiment only one specimen was tested, but because similar observations on the effect of female odor have been made on Sigara omani (Hungfd.) (Jansson, unpublished), the results are considered reliable.

The only references to pheromones in Corixidae is in the study of Pinder and Staddon (1965 a; 1965 b), which shows that trans-4-oxohex-2-enal is secreted from the metathoracic glands of both Sigara falleni (Fieb.) and Corixa dentipes (Thoms.). The metathoracic stink glands, as well as the larval dorsal abdominal glands have been studied anatomically and histologically in various Corixidae (Brindley, 1929; Betten, 1943), and the function of the secretion, like that in land bugs (Remold, 1962), has been suggested to be protective.



The fact that the secretion is not species or sex specific supports this concept (Pinder and Staddon, 1965 a). However, Benwitz (1956) has described additional glands, located in all three pairs of legs of Corixidae, the secretion and function of which are unknown.

It is possible that some other pheromone occurs in Corixidae and acts as a sexual attractant. Alternatively, the defensive secretion may under certain circumstances have a subsidiary function, namely that of sexual attraction. However, in Cenocorixa the method using acoustic stimuli is very effective and the importance of pheromones has not been elucidated. On the other hand, several non-stridulating species of Corixidae exist, and the mating behavior of these species is completely unknown. In these the role of stridulation might be replaced by pheromones. Butenandt (1955) has identified trans-hex-2-enyl-acetate in Lethocerus indicus (Lepelletier and Serville), another water bug (Belostomatidae), and because this chemical is sex specific, occurring in males only, it is suggested to function as a sex attractant.



#### 4. Evolutionary significance of stridulation in the genus Cenocorixa

Sound production in insects is advantageous if the sounds are produced in connection with sexual behavior and can guide pair-formation (Haskell, 1961). Acoustic communication in Orthoptera and its significance in pair-formation has been discussed a number of times (cf. Alexander, 1967; 1968). However, only in a few cases has it been shown experimentally that the signals actually function as a pre-mating isolating mechanism so that the females are attracted by signals of conspecific males, but do not respond to male signals of other species (Walker, 1957; Perdeck, 1958; Haskell, 1958; 1961).

The behavioral experiments carried out during the present study showed that both males and females of Cenocorixa are usually able to discriminate the signals of the opposite sex of conspecific specimens from the signals of all other species. By comparing the signals of various species it is obvious that the frequency of the sound cannot have any role in the species/sex recognition. This has also been observed in various other insects (cf. Haskell, 1961). Walker (1957) suggests that the key character in species recognition of tree crickets (Orthoptera, Gryllidae, Oecanthinae) is the pulse rate. However, Haskell (1961) does not agree with this because individual variation in the pulse rate is quite large, and the pulse rates of various species often overlap.

Haskell (1961) claims that the key character is pulse modulation (= temporal pattern of pulses in a signal), this



being very constant and species specific character in Orthopteran signals. Bennet-Clark and Ewing (1969), on the other hand, claim that pulse interval is the critical parameter in the courtship song of Drosophila melanogaster, but because the signals of this fly are composed of pulses, each of which include only one impact, the pulse interval could refer to pulse rate as well as to the temporal pattern of pulses.

In Cenocorixa, owing to intraspecific variation, the pulse rates of various species (Figs. 17-26) seem to overlap much more than those of tree crickets (Walker, 1957), although the regression lines of the species are more or less different. However, the temporal pattern of pulses in Cenocorixa is always constant and species specific, thus supporting Haskell's (1961) concept this being the key character. On the other hand, the loudness of the signals vary greatly between the species (according to subjective observations), and the structure of pulses (arrangement of impacts in a pulse) and the number of impacts per pulse are usually more or less specific; these factors might also have an important role in species discrimination. A thorough study involving electrophysiological recordings is required, but was outside the aims of the present thesis. The Corixidae have auditory organs in the thorax (Hagemann, 1910; Schaller, 1951), but it is not known what difficulties would arise if recording with electrodes connected to the nerves is tried.

Haskell (1961) has discussed whether the stridulation alone is important in species recognition in grasshoppers, or if it works together with some other factor or factors.



Experiments with Orthoptera have demonstrated that often visual and chemical stimuli may accompany stridulation and play important roles in the mating behavior. In the present study it was also observed that visual stimulus apparently is important in most species in close range approach, but species discrimination seems to be solely on the basis of the auditory stimulus.

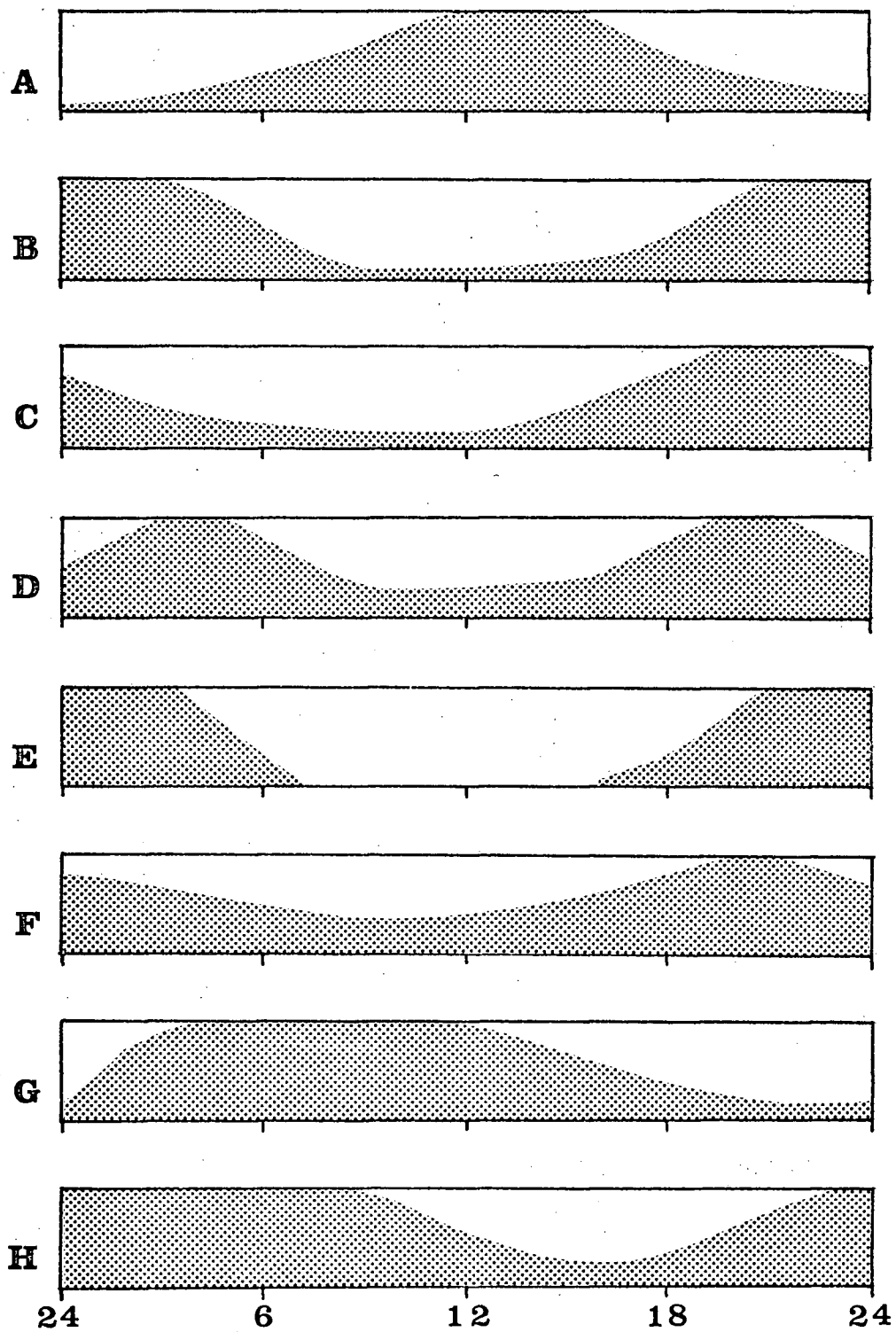
In addition to the characteristic differences in the structure of the stridulatory signals, temporal differences in the stridulating activity of the species were also observed. This again is similar to Orthopterans, with some species stridulating in day time, others at night time (Dumortier, 1963 c). Fig. 61 summarises the diel periodicity of the stridulating activity of all Cenocorixa species as indicated both by laboratory experiments and field observations. There is evidently a partial temporal isolation in the stridulating activity, and in one pair of sympatric species (C. bifida - C. expleta) this difference was also observed in the natural habitats.

Cenocorixa does not rely completely, however, on the stridulation behavior for species isolation, although this would appear to constitute the main isolating mechanism in sympatric situations. It is reinforced by differences in geographic distribution and habitat preference. The study of the geographic distribution of the species indicates some geographic isolation (Figs. 54-57), but owing to the difficulties in identification of Cenocorixa species (cf. Appendix I), the published records certainly include some mis-



Fig. 61. Summary of the diel periodicity of the stridulating activity of Cenocorixa males. Explanations: abscissa = time of day; stippled area expresses the relative activity in stridulation. A = C. bifida; B = C. kuiterti; C = C. andersoni; D = C. utahensis; E = C. dakotensis; F = C. blaisdelli; G = C. wileyae; H = C. expleta.







identifications, and some minor modifications to the recorded distributions and range can be expected in the future.

In cases when two or more Cenocorixa species are observed sympatrically, ecological differences are usually observed. Scudder (1969 a; 1969 b) has reported a partial ecological isolation between C. bifida and C. expleta since they inhabit different ranges of salinity. This information was confirmed during the present study, but another partial ecological isolation between the two species was detected in cases when salinity allows the two to occur in same lake: C. bifida inhabits the very edges of the lakes inside reed beds, while C. expleta prefers slightly deeper water outside reed beds. Partial ecological isolations were also detected between other Cenocorixa pairs: C. andersoni in permanent ponds, C. blaisdelli in temporary pools; C. kuiterti in slowly running or oligotrophic waters, C. wileyae in stagnant, more eutrophic waters.

In Table XIII I have collected together estimates on the effectiveness of various isolating mechanisms between the species of Cenocorixa in the light of the present study. The form of the table is similar to that of Moore (1949) for isolation of a group of frogs in the northeast of North America. However, geographic isolation in my table is only very roughly estimated because the detailed distributions of the species are unknown. Ecological isolation is according to my observations or is the potentially expected value. Seasonal isolation does not exist between Cenocorixa species, and is always 0. Temporal isolation in diel periodicity of the strid-



ulating activity is estimated from laboratory experiments and actual observations in natural environments; stridulatory isolation is taken directly from playback experiments (Table X).

From the Table XIII it can be seen that the two strongest isolating mechanisms are geographic isolation and stridulatory isolation. In several cases they are both 100 per cent effective, but it should be noted that especially when geographic isolation is not complete, the stridulatory one is. On the other hand the only case when stridulatory isolation seems to fail altogether, happens in C. wileyae females which answer C. dakotensis male calls every time. However, C. dakotensis males do not answer the signals of C. wileyae females very actively (Table IX), and no searching behavior was observed in C. dakotensis males when stimulated with C. wileyae female signals. In addition, these two species have a firm geographic isolation: C. dakotensis occupies the northern plains east of the Rocky Mountains while C. wileyae has its distribution mostly between the Rocky Mountains and the Coast Range.



Table XIII. Estimates of the magnitude of different isolating mechanisms in Cenocorixa. G = geographic isolation; E = ecological isolation; S = stridulatory isolation; T = temporal isolation in stridulation.

Males		bifida	kuiterti	andersoni	utahensis	dakotensis	blaisdelli	wileyae	expleta
Females									
bifida	G		100	100	10	40	100	90	30
	E		50	50	50	50	50	0	30
	S		90	60	80	100	100	100	100
	T		80	80	60	90	40	50	60
kuiterti	G	100		100	0	100	100	0	100
	E	0		0	0	0	0	0	100
	S	-		-	-	-	-	-	-
	T	80		0	0	10	0	40	10
andersoni	G	100	100		100	100	50	100	100
	E	0	0		0	0	75	0	100
	S	100	-		100	100	100	-	100
	T	80	0		0	10	0	50	10
utahensis	G	50	95	100		60	100	50	60
	E	0	0	0		0	0	0	90
	S	100	-	100		100	100	-	100
	T	60	0	10		30	10	40	0
dakotensis	G	20	100	100	40		100	100	60
	E	0	0	0	0		0	0	90
	S	100	100	100	100		100	100	100
	T	90	0	10	10		0	50	0
blaisdelli	G	100	100	60	100	100		100	100
	E	0	0	75	0	0		0	100
	S	100	-	100	100	80		-	80
	T	50	0	0	0	30		20	0
wileyae	G	90	95	100	10	100	100		95
	E	0	50	0	0	0	0		70
	S	100	90	100	90	0	100		60
	T	70	30	30	0	50	40		20
expleta	G	0	100	100	10	30	100	95	
	E	30	100	100	90	90	100	70	
	S	100	100	100	100	80	90	100	
	T	50	0	0	0	30	0	20	



## 5. Evolution and stridulation in Corixidae

In general in evolution it is the more complicated forms that are the most advanced ones (Rensch, 1959). If this concept is applied to the structure of the stridulatory signals of Cenocorixa males, an order can be obtained as shown in Fig. 62. Certainly the genus can be divided into two subgroups according to the structure of male signals:

- 1) Signals composed of an uninterrupted sequence of pulses; the bifida group (C. bifida, C. kuiterti, C. andersoni, C. utahensis, and C. dakotensis) and
- 2) Signals composed of distinctly separate groups of pulses; the wileyae group (C. blaisdelli, C. wileyae, and C. expleta). This subdivision of the genus coincides with a division that exists in morphological characters. The wileyae group in body form is more slender than the bifida group, and the right paramere of the male genitalia in the latter group is bifurcate (except in C. andersoni), while in the wileyae group it is not bifurcate. In C. andersoni the non-bifurcate form of the paramere might be a secondary modification.

The general geographic distribution of the genus suggests a western origin in areas south of the Pleistocene glaciation. However, the evolution could have been pre or post Pleistocene or partly both. If more detailed speculation of evolution of the genus is desired, my suggestion, based on zoogeography, morphology, and stridulation differences, would be as follows:

The ancestors of the genus were something like present day C. bifida. At some time this ancestral form was split



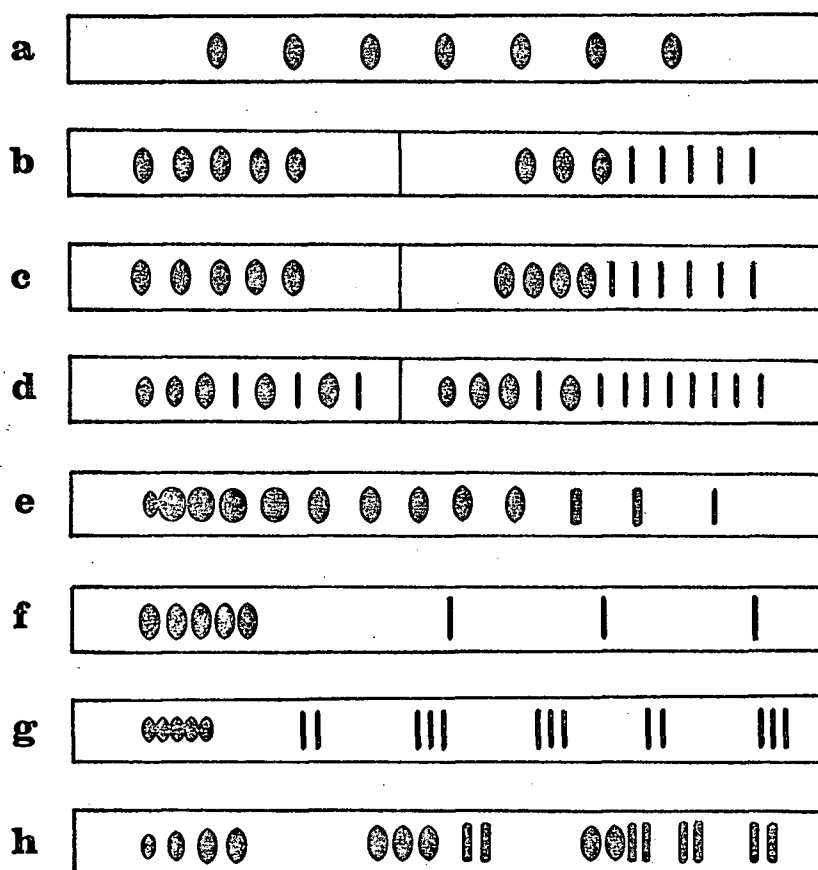


Fig. 62. Diagram of suggested increasing complexity of signals of Cenocorixa males. The simplest type is at the top. a = C. bifida; b = C. kuiterti; c = C. andersoni; d = C. utahensis; e = C. dakotensis; f = C. blaisdelli; g = C. wileyae; h = C. expleta. Explanations: in each signal one bar represents one pulse; width of the bar indicates relative duration of the pulse, height of the bar relative loudness of the pulse. Pulse arrangement shows the temporal pattern of the signals. In some species first part of the signal can be produced alone and in these two separate signals are indicated (b, c, and d).



into two: bifida group and wileyae group. The bifida group migrated in different directions: i) Northwards in the western side of the Rocky Mountains, giving rise to C. bifida in the interior plateau; ii) Northwards in the eastern side of the Rocky Mountains: C. dakotensis; iii) Southwest to the high areas on mountains: C. kuiterti; iv) Northwest to the Pacific Westcoast: C. andersoni; v) Eastwards over the Rocky Mountains: C. utahensis. Meanwhile, the wileyae group gave rise to C. blaisdelli after crossing the Coast Range to the Pacific Coast in south, and C. expleta after migrating over the Rocky Mountains. This hypothetical evolution is summarised in Fig. 63, and present day geographic distribution can be derived from the hypothesis by allowing C. bifida to cross over the Rocky Mountains somewhere in Wyoming - Idaho to the northern plains, and C. utahensis and C. expleta the other way back to the interior plateau between the Rocky Mountains and the Coast Range.

The function of the Rocky Mountains as an isolating barrier is suggested by observations on geographic variation in the signals of C. bifida (Jansson, to be published): A slight difference was detected between the populations of British Columbia and Alberta, and the population in northern Utah possesses an intermediate signal compared to the northern populations. Also some slight morphological differences between these populations were detected (cf. Appendix I). These observations do not affect the results of the present study, but show that the two northern populations could evolve apart if the apparent connection through Wyoming - Idaho breaks.



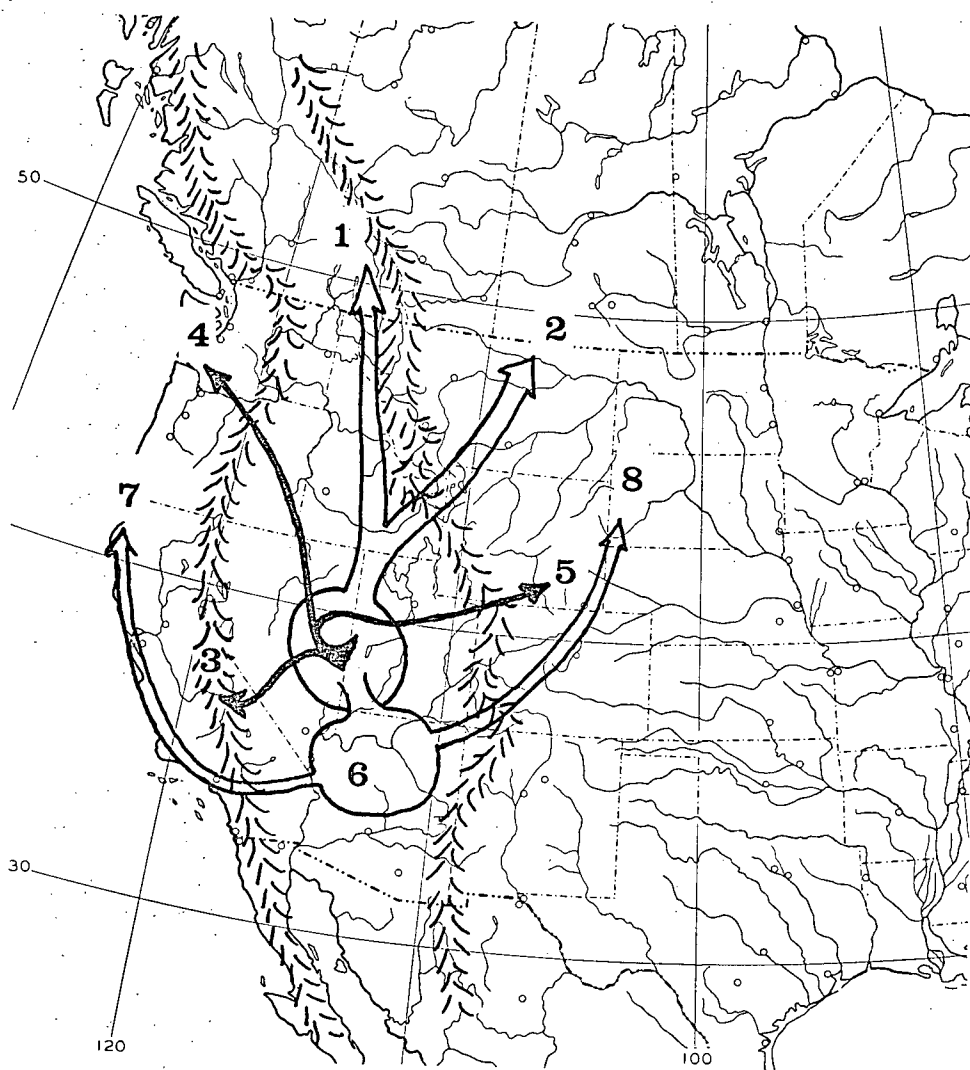


Fig. 63. Suggested evolution of Cenocorixa species. Based on geographic distribution, general morphology, and stridulation. 1 = C. bifida; 2 = C. dakotensis; 3 = C. kuiterti; 4 = C. andersoni; 5 = C. utahensis; 6 = C. wileyae; 7 = C. blaisdelli; 8 = C. expleta.



Divergence in the animal kingdom is thought to take place by geographic isolation and evolution of effective isolating mechanisms (Mayr, 1963). Premating isolating mechanisms are usually considered the most effective because they prevent waste of the sexual products. Thus, premating isolating mechanisms, not surprisingly, are the predominant isolating mechanisms between closely related species that occur sympatrically (e.g. Blair, 1955; Brown, 1965; Hagen, 1967; Licht, 1969; Liley, 1966; Spieth, 1947; Wasserman, 1957). In insects which produce sound, acoustic signals are suggested to be one of the commonest premating isolating mechanisms (e.g. Alexander, 1967; 1968; Alexander and Moore, 1962; Bennet-Clark and Ewing, 1969; Haskell, 1961; Perdeck, 1958; Roth and Hartman, 1967; Spooner, 1964; 1968; Van Tassel, 1965; Waldon, 1964; Walker, 1957).

Evolution of such sound based premating isolating mechanism is an interesting problem, and Alexander (1962) suggests that in Orthoptera, the first cricket apparently was already a specialized stridulator. He further suggests that the function of stridulation in ancient crickets was linked with courtship behavior, and that the other functions of stridulation in living crickets have evolved from this courtship song. According to Alexander (1962) this concept is supported by the fact that courtship in crickets that have lost the ability to stridulate, includes lifting of the wings. Wing lifting associated with courtship is observed in Blattaria (Roth and Willis, 1952; Roth and Hartman, 1967), and is evidently a primitive behavior in Orthopteroids (Alexander,



1964), and thus in this taxon there is a good basis for the evolution of sound production as an addition to these wing lifting movements. The function of the initial courtship was restricted to short distance attraction, and in Orthoptera, when attraction from longer distances evolved, this courtship song gave rise to a calling song, and when acoustical behavior became more complicated, other categories of songs evolved from these pre-existing ones (Alexander, 1962).

Various stridulatory mechanisms exist in both terrestrial and aquatic Hemiptera, but these mechanisms are far too different to have had a common origin. Aquatic Hemiptera are secondarily adapted to aquatic environment, and there is some evidence that they all descended from a common ancestor (China, 1955). However, in aquatic Hemiptera, there are again several stridulatory mechanisms (Dumortier, 1963 a), and since these are quite different, it is apparent that stridulation in these aquatic bugs has evolved independently several times.

The family Corixidae is taxonomically subdivided into six subfamilies. It is not known if any stridulatory apparatus or song exist in the subfamilies Diaprepocorinae and Stenocorinae. The Cymatiinae (genus Cymatia) do not seem to have any stridulatory organ, and no sounds have been recorded. European Micronectinae (genus Micronecta) are known to stridulate (Mitis, 1936; Southwood and Leston, 1959), and the mechanism is probably by use of the abdominal strigil (Mitis, 1936). However, American Micronectinae (genus Tenagobia) are said to lack this abdominal strigil (Hungerford, 1948). In



the Heterocorixinae records on stridulation are lacking, but according to the drawings in Hungerford (1948) all species have a well developed abdominal strigil in males, and specialised pegs are located at the posterior edge of the fifth abdominal tergum just anterior to the strigil: it is possible that stridulatory signals are produced with this apparatus, and thus utilise an apparatus similar to that in the European Micronectinae.

Corixinae seems to be the only subfamily possessing a stridulatory mechanism that involves stridulatory pegs of the front femora and the maxillary plate. However, stridulation is not universal in Corixinae: several genera of this subfamily are not able to stridulate, and it is not known whether they represent an advanced group that has lost the stridulatory apparatus, or a primitive group that have not evolved it. The existence of various different stridulatory mechanisms in Corixidae, nevertheless, suggest that stridulation is not a plesiomorphic character, but rather an apomorphic one (Hennig, 1966), one that has evolved after separation of the subfamilies. The non-stridulating genera of Corixinae are thus postulated never to have had a stridulatory ability.

Since Corixinae do not have a distinct courtship display, it is not likely that the stridulatory behavior has evolved in the way suggested in Orthoptera by Alexander (1962). An alternative evolution must be suggested, and ritualization of "comfort" movements seems to be a possibility. Such ritualization is well documented in vertebrates (e.g. Huxley,



1914), but seems to be a possibility in invertebrates as well: waving display of fiddler crabs (genus Uca) (Crane, 1966).

In the Corixinae, each pair of legs has been adapted to serve a different primary function: the fore legs for feeding, the middle legs for clinging, and the hind legs for swimming. However, these legs also have important subsidiary functions.

It will be recalled that the various species of Cenocorixa will frequently rub the hind legs along the costal margin of the hemielytra. This movement, which was often observed after the insects had been handled, undoubtedly is aimed at rearranging the lateral abdominal hairs that are very important in maintaining the air bubble between the wings and the abdominal dorsum for respiration (Popham, 1960; Parsons, 1970). While this is clearly a "comfort" movement, it is also a movement that produces sounds which have been interpreted by some authors as stridulation (Moore, 1961; Finke, 1968). In Cenocorixa it was shown that such sounds do indeed have certain characteristics that are required in a stridulatory signal; but all species were observed to produce a comparable sound. At present they do not seem to serve as stridulatory signals in Cenocorixa. However, true stridulatory signals could easily evolve from this.

Similarly, the front legs, although used and highly modified for feeding, also are used in cleaning movements, especially movements across the labium for "preening" the long sensory setae that are located at its tip (Lo and Acton,



1969). Such movements could well have been the precursor of the present day stridulatory movements in Cenocorixa and other stridulating Corixinae.

Any two parts of an exoskeleton can be rubbed together to produce a noise, and so these movements could easily have become ritualised and the parts modified. Another modification in the thoracic tracheal system could have led to the evolution of the sound receiving tympanum.

In a similar manner, movements of the sclerotized parts of the abdomen during defecation or mating or both could produce sounds which likewise could have been selected in European Micronectinae. A parallel evolution is also suggested in Heterocorixinae.

It was noted in Cenocorixa that in most species there is only a single type of signal in each sex. In contrast to this, the Orthoptera have frequently several different types of song that appear to be specialised for precise functions. Thus, in Orthoptera there are distinct and different calling, courtship, rival's, etc. songs.

In Cenocorixa the various experiments undertaken suggest that in some species (C. bifida, C. dakotensis, C. expleta) the same signal can function as a calling song and agonistic song. In some other species (C. blaisdelli, C. wileyae) part of their "normal" signal can be produced separately, but no obvious function of this part could be detected. Further, in two species (C. andersoni and C. utahensis) part of their "normal" call seemed to have a different function (agonistic song) from that of the "normal" call (calling song).



It would appear that here we have evidence of the incipient evolution of stridulatory diversity towards a more complex acoustical communication system. Agonistic signals seem to be evolving from a calling signal, i.e. a double stridulatory signal is evolving from a single pre-existing one. The Corixinae, and in particular the genus Cenocorixa, can be considered on the evolutionary threshold of stridulatory diversification.



## V. SUMMARY

1. In the genus Cenocorixa both males and females produce species and sex specific stridulatory signals: the sound is produced by rubbing specialized stridulatory pegs, located anterobasally on the front femora (pars stridens), against the edge of the maxillary plate (plectrum). A correlation seems to exist between the loudness of signals and morphology of the stridulatory apparatus.

2. Specific differences in the signals were found in the temporal pattern of pulses, pulse rate, structure of pulses, and signal length. Change in temperature affects the pulse rate and, when applicable, the pulse group repetition rate, but not usually the temporal pattern of pulses.

3. Annual rhythm of stridulation is correlated with sexual maturity. In males spontaneous stridulation commences when mature sperm occurs in the testes: in the spring, early summer, and in late fall. In areas where no freeze-up exists, the males stridulate throughout the winter. In females spontaneous stridulation was never observed, but induced stridulation commences when chorionated eggs are found in the lateral oviducts and apparently no sperm exists in the receptaculum seminis. Sexual maturity in females is only reached in the spring and early summer.

4. Behaviorally the stridulation of males seems to function both as a calling signal and as an agonistic signal. The female signal can be classified as an agreement signal for it is only produced by receptive females and after a stridulatory stimulus from the male. Recently mated females do



not stridulate and do not accept males attempting copulation.

5. In most species the males answer almost any stridulatory stimuli, but only the signals of conspecific females initiate searching behavior in the males. Females do not respond to male signals of other species, but the response to conspecific male signals is to stay stationary and answer by stridulating.

6. Stridulation functions as a premating isolating mechanism in the genus studied, but does not constitute the whole isolating mechanism. It is reinforced by geographic, and ecological isolation in a number of cases.

7. It is suggested that the stridulatory movements in Corixidae have arisen by ritualization of comfort movements.

8. The Corixidae are considered to represent a stage in evolution at which diversification of stridulatory signals is evolving from a single pre-existing one. At the present time, most species have a single male call that can function in at least two contexts.



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## APPENDIX I

SYSTEMATIC NOTES AND NEW SYNONYMY IN THE GENUS CENOCORIXA

Hungerford (1948) in his revision of the Corixidae of the western hemisphere, erected a new genus Cenocorixa in which he placed nine species. Subsequently, Hungerford (1956) described a new species and more recently, Lansbury (1960) has described three additional species in the genus. At the present time, Cenocorixa thus contains 13 described species.

In the present study it was discovered that there are only eight distinct species in the genus; several of the previously described species must be relegated to synonymy. In addition, while the published descriptions of the species are in general adequate, the published figures on specific differences are not very accurate and the key in Hungerford (1948) is somewhat unreliable, since the characters utilised are often rather variable.

This Appendix thus revises the valid species, gives the new synonymy, and presents a revised key to males of the genus. A key to females of the genus is in preparation.

Cenocorixa bifida (Hungerford)

Arctocorixa bifida Hungerford 1926, Can. Ent. 58: 268.

Cenocorixa bifida, Hungerford 1948, Univ. Kansas Sci. Bull. 32: 569; redescription.

SYN. NOV. Cenocorixa hungerfordi Lansbury 1960, Proc. ent. Soc. B. C. 57: 36.

Cenocorixa bifida, Brooks and Kelton 1967, Mem. Ent.



Soc. Canada 51: 24; redescription.

Considerable geographic and intraspecific variation was observed in this species. The description of the species by Hungerford (1948) must be ammended as follows:

The peg row of the male pala is clearly broken in specimens from Alberta (as stated by Hungerford, 1948), but in specimens from northern Utah it is not so clearly broken, and it is usually unbroken in specimens from British Columbia (Fig. 68).

The right paramere is not quite as in the drawing in Hungerford (1948), and the shape of the more proximal projection varies from roundish in Alberta and Utah specimens to sharp in British Columbia specimens (Figs. 71 and 72): also the shape of the strigil varies slightly. Dorsal view of the posterior abdominal terga is shown in Fig. 64.

Lansbury (1960) described this species under the name C. hungerfordi from British Columbia, but apparently he was not aware of the existing variation. I have cross mated specimens from Alberta and British Columbia (to be published) and despite the differences between the populations, the experiment showed that cross breeding was successful (at the moment the cultures are in the F<sub>3</sub> generation).

~~Type material~~ examined:

Holotype ♂, allotype ♀, and 1♂ (paratype): Lost Lake, Alberta, Canada. (The paratype male studied belongs to C. utahensis) [Univ. Kansas]. 4 ♂♂ and 8 ♀♀ of C. hungerfordi Lansb., Kamloops, British Columbia [U.B.C.].

Additional material: Canada, British Columbia, Chilcotin,



Beeche's Prairie; Kamloops, Lac du Bois area (LB2); Alberta, Brooks. USA: Utah, Wasatch Co., Strawberry Reservoir.

Cenocorixa kuiterti Hungerford

Cenocorixa kuiterti Hungerford 1948, Univ. Kansas  
Sci. Bull. 32:571.

The tergum of the middle lobe of the seventh abdominal segment dorsally does not have a distinct tuft of hairs as shown in Hungerford (1948), but only a few short hairs appear (Fig. 64).

The arrangement of the paler pegs is shown in Fig. 69, and some variation of the shape of the right paramere in Fig. 73.

Material examined: USA: California, Tuolumne Co., Tioga Pass (type locality).

Cenocorixa andersoni Hungerford

Cenocorixa andersoni Hungerford 1948, Univ. Kansas  
Sci. Bull. 32, 573.

SYN. NOV. Cenocorixa malkini Hungerford 1956, J. Kansas ent.  
Soc. 29: 39.

SYN. NOV. Cenocorixa downesi Lansbury 1960, Proc. ent. Soc.  
B. C. 57: 40.

The original description of Hungerford (1948) must be amended as follows:

Male abdomen dorsally has the median lobe of the tergum 7 more or less distinctly separated from the left lobe by a break, which is sometimes clearly seen, but may also be almost



non-existing. However, the two lobes are "tied" together with a tuft of hairs originating from the left lobe; the species thus has two hair tufts, a caudal longitudinal and a transverse one. (Fig. 65). The size of the transverse tuft is somewhat variable and the size of the break between the lobes is proportional to the size of the tuft.

The last segment of the hind leg (tarsus 2) is sometimes dark brown, but sometimes the whole leg is light brown.

Arrangement of the pegs of pala is shown in Fig. 69, and some intraspecific variation of the right paramere is shown in Figs. 71 and 73.

Hungerford (1956) described this species under the name C. malkini apparently because he had not noticed the variation in the color of the tarsus 2; the specimens on which the original C. andersoni description was based, do not have a dark brown tarsus 2, while all C. malkini type specimens I have seen, have dark brown tarsus 2. However, the color of the tarsus 2 seems to depend on the color of the bottom of the pond or lake: in lakes with dark bottom tarsus 2 is dark brown, but in pale bottom lakes it is light\*. Lansbury (1960) based his description of C. downesi on only one male specimen. He noticed the existence of the transverse hair tuft, but because the tip of the median lobe of tergum VII is broken off, the specimen does not have any

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\* For the effect of color of the bottom of lakes on Corixidae, see: Popham, E.J. 1941. The variation in colour of certain species of Arctocorisa (Hemiptera, Corixidae) and its significance. Proc. Zool. Soc. Lond. 111 (A): 135-172.



caudal hair tuft: Lansbury (1960) evidently did not notice that the specimen was broken.

Type material examined:

Holotype ♂, 1 ♀ (paratype): Washington, Kalama River; 1 ♂ (paratype): Oregon, Florence [Univ. Kansas]. C. malkini: Holotype ♂, allotype ♀, 7 ♂♂ and 1 ♀ (paratypes): Washington, Chase Lake, Snohomish Co. [Univ. Kansas, and Calif. Acad. Sci.]. 1 ♂ (paratype): Oregon, Florence [Univ. Kansas]. C. downesi: holotype ♂: British Columbia, Vancouver.

Additional material: Canada: British Columbia, Spectacle Lake, Vancouver Island [Calif. Acad. Sci., coll. J. Simpson]; Vancouver, Stanley Park; White Rock, roadside pond; Abbotsford, Trout Hatchery pond (coll. J. Ryan). USA: Washington, Whatcom Co., Custer.

Cenocorixa utahensis (Hungerford)

Arctocorixa utahensis Hungerford 1925, Bull.

Brooklyn Ent. Soc. 20: 22.

Cenocorixa utahensis, Hungerford 1948, Univ. Kansas Sci. Bull. 32: 580; redescription.

Cenocorixa utahensis, Brooks and Kelton 1967, Mem. Ent. Soc. Canada 51: 25; redescription.

The material studied agreed with the description in Hungerford (1948). However, the drawing on the right paramere in Hungerford (1948) is slightly misleading, and variation in the shape of this is shown in Figs. 71 and 74. Dorsal view of posterior abdominal terga is shown in Fig. 65, and arrangement of the palmar pegs in Fig. 69.



Type material examined:

Holotype ♂, allotype ♀, 2 ♂♂ 3 ♀♀ (paratypes): Utah, Emery Co., [Univ. Kansas].

Additional material: Canada, Alberta, Gleichen; Brooks; Medicine Hat. USA: Washington, Franklin Co., Mesa; Franklin Co., Kootenay Reservoir; Utah, Garfield Co., Hatch; Duchesne Co., Starvation Reservoir;

Cenocorixa dakotensis (Hungerford)

Arctocorixa dakotensis Hungerford 1928, Can. Ent. 60: 229.

Cenocorixa dakotensis, Hungerford 1948, Univ. Kansas Sci. Bull. 32: 567; redescription.

Cenocorixa dakotensis, Brooks and Kelton 1967, Mem. Ent. Soc. Canada 51: 23; (redescription).

The material studied agreed with the description in Hungerford (1948), except that some variation in the shape of the right paramere was observed, and is shown in Figs. 71 and 74. Dorsal view of posterior abdominal terga in male is shown in Fig. 66, and arrangement of palmar pegs in Fig. 69.

Material studied: Canada, Alberta, Gleiche; Brooks; Medicine Hat.

Cenocorixa blaisdelli (Hungerford)

Arctocorixa blaisdelli Hungerford 1930, Pan-Pacif. Ent. 7: 26.

Sigara blaisdelli, Jaczewski 1931, Arch. Hydrobiol. 23: 511.



Cenocorixa blaisdelli, Hungerford 1948, Univ.  
Kansas Sci. Bull. 32: 574; redescription.

SYN. NOV. Cenocorixa columbiensis Lansbury 1960, Proc.  
ent. Soc. B. C. 57: 38.

Hungerford's (1948) description should be amended to state that the seventh abdominal tergum of males has three caudal projections (Fig. 66); the right paramere is as shown in Figs. 71 and 74. Arrangement of palpal pegs is shown in Fig. 70.

Lansbury (1960) described this species from British Columbia under the name C. columbiensis. He also gave drawings, which, however, do not agree with his type specimens. He apparently did not recognise the specimens as C. blaisdelli (Hungerford), because Hungerford (1948) records the latter only from California. However, Hungerford (1948) gives a reference to Jaczewski (1931), and in the latter the species is recorded from Washington. Apparently the species occurs all along the coast from British Columbia to California, although no record from Oregon has been published. Specimens from British Columbia and California do not show any apparent geographic variation.

Type material examined:

3 ♂♂ (paratypes): Vine Hill, Contra Costa Co., California [Univ. Kansas]; 2 ♂♂ 1 ♀ (paratypes): Berkeley, California [Calif. Acad. Sci.] (one of the male paratypes has a female Corisella decolor (Uhler) mounted on the same pin). C. columbiensis Lansb.: holotype ♂, allotype ♀, 5 ♂♂ 5 ♀♀ (paratypes): Pond, Univ. Brit. Col., British Columbia [U.B.C.].



Additional material: Canada, British Columbia, Vancouver, Stanley Park; U.B.C. area. USA: California, San Mateo Co., San Francisco; Humboldt Co., Calm Beach.

Cenocorixa wileyae (Hungerford)

Arctocorixa wileyae Hungerford 1926, Can. Ent.  
58: 271.

Cenocorixa wileyae, Hungerford 1948, Univ. Kansas  
Sci. Bull. 32: 578; redescription.

The shape of the right paramere is as in Figs. 71 and 75, and not as shown in Hungerford (1948). Dorsal view of posterior abdominal terga of male is shown in Fig. 67, arrangement of paler pegs in Fig. 70.

Material studied: USA: Washington, Franklin Co., O'Sullivan dam area; Oregon, Sherman Co., Kent; Deschutes Co., La Pine; California, Modoc Co., Newell; Lassen Co., Said Lake; Doyle; Alpine Co., Monitor Pass; Mono Co. and Tuolumne Co., Tioga Pass; Mono Co., Black Lake; Nevada, Nye Co., Railroad Valley; Utah, Garfield Co., Hatch; Duchesne Co., Starvation Res.; Wasatch Co., Strawberry Res.,

Cenocorixa expleta (Uhler)

Corisa expleta Uhler 1895, (in) Gillette, C. P.  
and Baker, C. F.: Hemiptera of Colorado, Colorado  
Agr. Exp. St. Bull. 31, Tech. ser. 1: 63.

Arctocorisa expleta, Kirkaldy and Torre-Bueno  
1909, Proc. Ent. Soc. Wash. 10: 195.

Cenocorixa expleta, Hungerford 1948, Univ. Kansas



Sci. Bull. 32: 576; redescription.

Cenocorixa expleta, Brooks and Kelton 1967, Mem.

Ent. Soc. Canada 51: 24; redescription.

No major differences were detected between the redescription of Hungerford (1948) and the material studied. Slight variation was observed in the shape of the right paramere (Figs. 71 and 75). Dorsal view of male abdomen is shown in Fig. 67 and male pala is shown in Fig. 70.

Material studied: Canada, British Columbia, Kamloops area (LB2); Okanagan Valley, Falkland. USA, Washington, Grant Co., Soap Lake.

Sigara nevadensis (Walley)

Arctocorixa nevadensis Walley 1936, Can. Ent.  
68: 58.

Sigara (Vermicorixa) nevadensis, Hungerford 1948,  
Univ. Kansas Sci. Bull. 32: 704; redescription.

SYN. NOV. Cenocorixa sorenseni Hungerford 1948, Univ.  
Kansas Sci. Bull. 32: 565.

In addition to the Cenocorixa species above, Hungerford (1948) described C. sorenseni in his monograph from material collected from Brigham, Utah. However, in the general description of the genus Cenocorixa, Hungerford (1948) was forced to make an exception in C. sorenseni females: the last ventral abdominal segment is incised at tip in all other species. In addition, C. sorenseni appears to be clearly smaller than other species of the genus, and the median longitudinal carina of the pronotum is very short. Also the claval pattern is



different from other Cenocorixa species: in C. sorensoni the transverse pale lines are enlarged in the middle of the clavus while in all other species the lines are vermiculate, but not enlarged. Also the male pala in C. sorensoni has a ridge in the middle, which does not appear in any other Cenocorixa species. All these "exceptions" would place C. sorensoni in the genus Sigara. Indeed the species is placed in this genus in Hungerford (1948) under the name S. nevadensis, although the original description placed it in the genus Arctocorixa (Walley, 1936).

The descriptions and figures of S. nevadensis and C. sorensoni in Hungerford (1948) are very similar and no additional description or figure is needed. Some intraspecific variation was found in the shape of the right paramere: the thickness of the distal projection varies slightly.

Type material examined: Holotype ♂, allotype ♀, 4 ♂♂ 7 ♀♀ (paratypes): Humboldt River, Nevada [Am. Mus. Nat. Hist.], 1 ♂ 1 ♀ (paratypes): as above [Univ. Kansas]. C. sorensoni: holotype ♂, allotype ♀, 5 ♂♂ (paratypes): Utah, Brigham [Univ. Kansas], 2 ♂♂ 2 ♀♀ (paratypes): as above [Utah State Univ.].

Additional material: Utah, Box Elder Co., Bear River.

Identification of Cenocorixa species is difficult and some practice is needed for correct results. In males the identification has to be based mostly on the structure of the abdominal dorsum (7th segment), and the shape of the right paramere. Females are more difficult, and no suitable key



is available so far. A key for the males is as follows:

- 1 (2) Pala with the peg row sharply curved (Fig. 70 b)....  
.....C. wileyae
- 2 (1) Pala with the peg row not sharply curved.....3
- 3 (4) Pala with spinose tumescence at base (Fig. 70 c)....  
..... C. expleta
- 4 (3) Pala without a tumescence at the base.....5
- 5 (8) Right paramere not bifurcate.....6
- 6 (7) Seventh abdominal tergum dorsally with a caudal and  
transverse tuft of hairs (Fig. 65 A)..... C. andersoni
- 7 (6) Seventh abdominal tergum dorsally with only caudal  
tuft of hairs (Fig. 66 B).....C. blaisdelli
- 8 (5) Right paramere bifurcate.....9
- 9 (10) Hind leg with the last segment (tarsus 2) entirely  
black or dark brown, right paramere with the proximal  
projection much thinner than the distal projection  
(Fig. 71 e).....C. dakotensis
- 10 (9) Combination of characters not as above.....11
- 11 (12) Median lobe of the 7th abdominal tergum dorsally  
without a hair tuft, at most a few short hairs  
appear (Fig. 64 B), distal projection of the right  
paramere irregularly curved at the tip (Fig. 71 b),  
proximal projection roundish.....C. kuiterti
- 12 (11) Combination of characters not as above.....13
- 13 (14) Posterior pegs of hind femur in 2-3 rows or in a  
clump, their number more than 12, palmar pegs often  
in a broken or almost broken row.....C. bifida

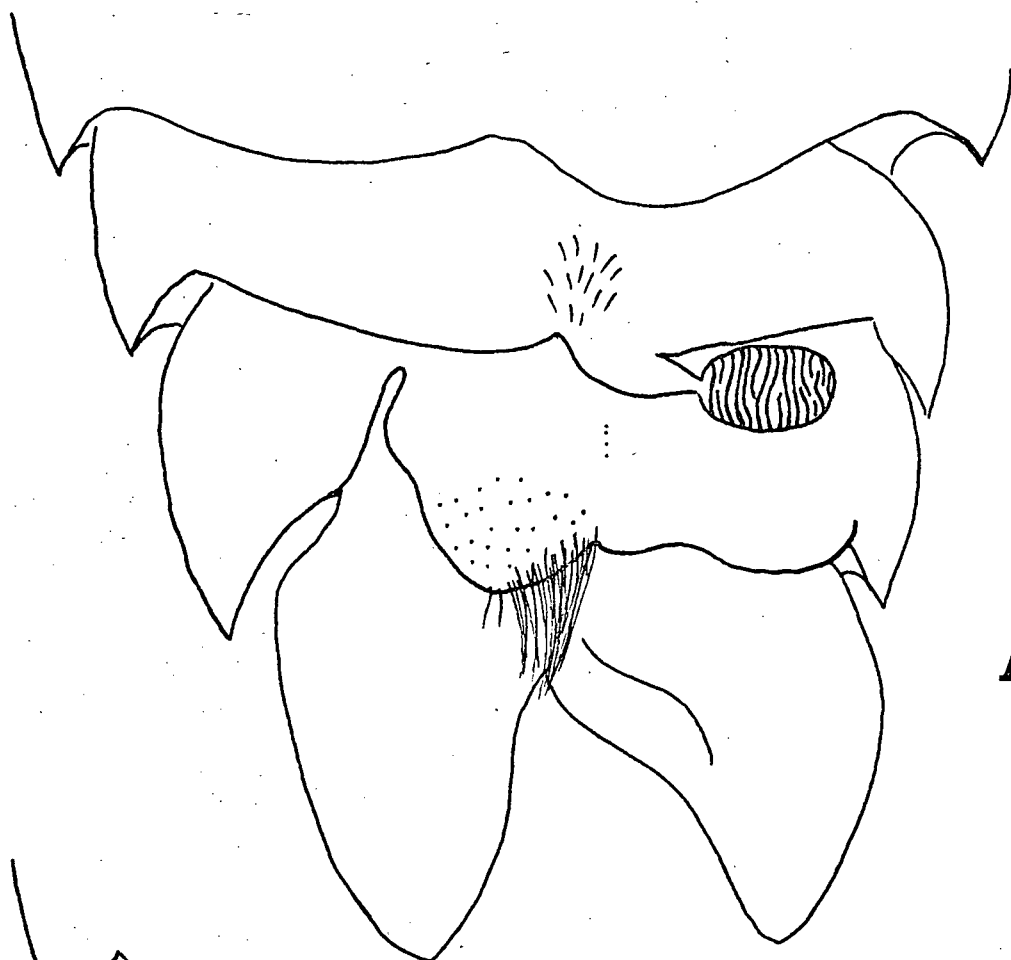


- 14 (13) Posterior pegs of hind femur usually in one  
row, their number less than 12, palmar pegs in  
a regular row.....C. utahensis

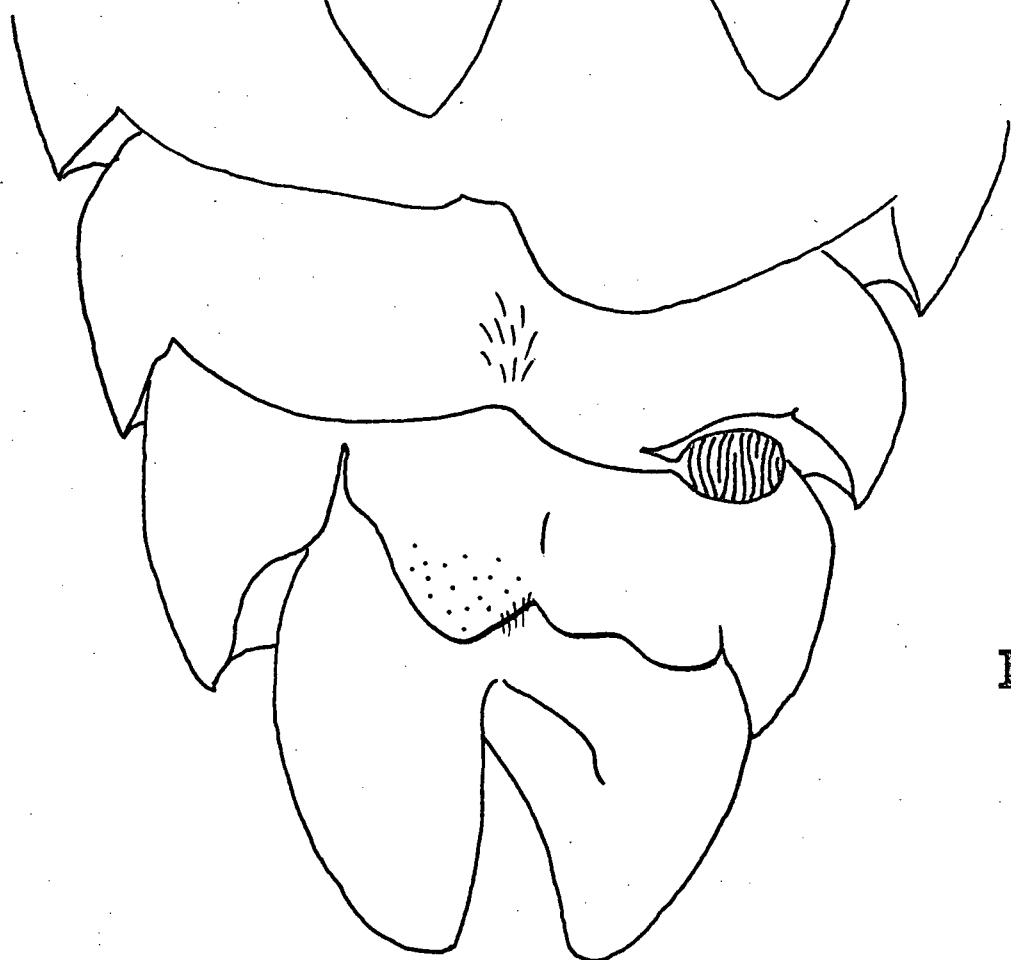


Fig. 64. Dorsal view of posterior abdominal terga of male in C. bifida (A) and C. kuiterti (B).





**A**

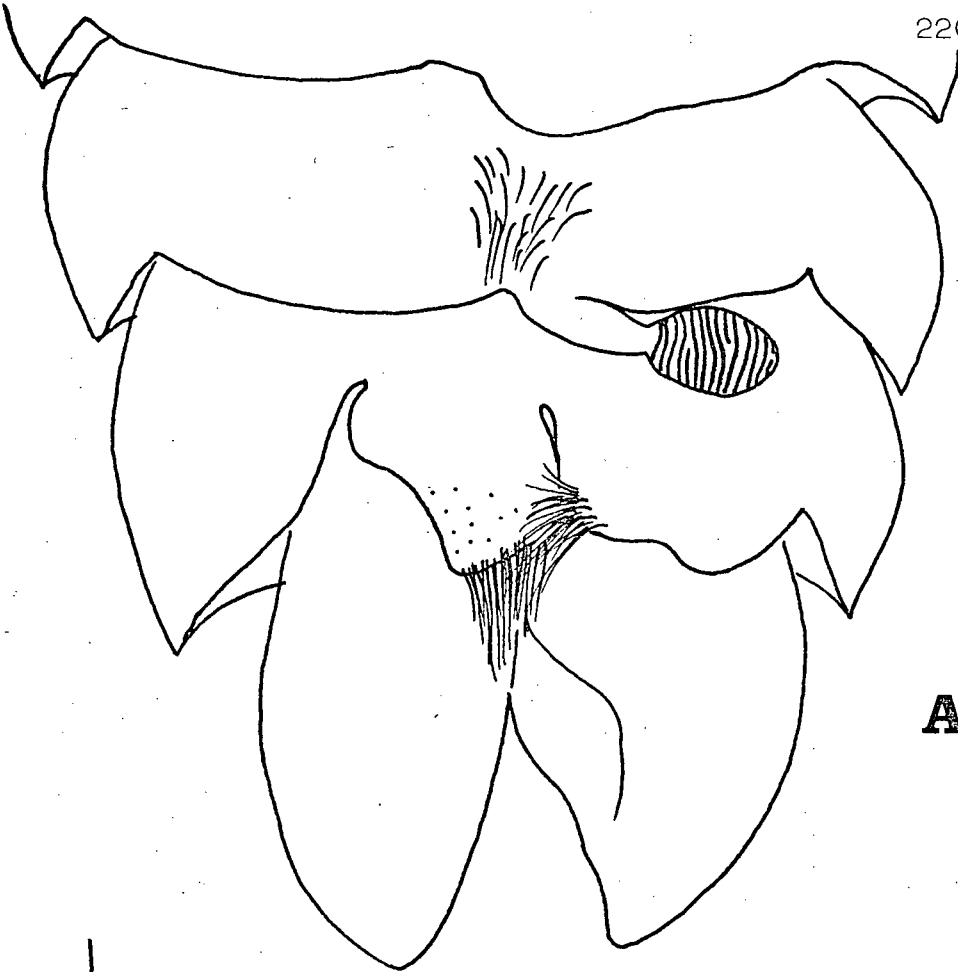


**B**

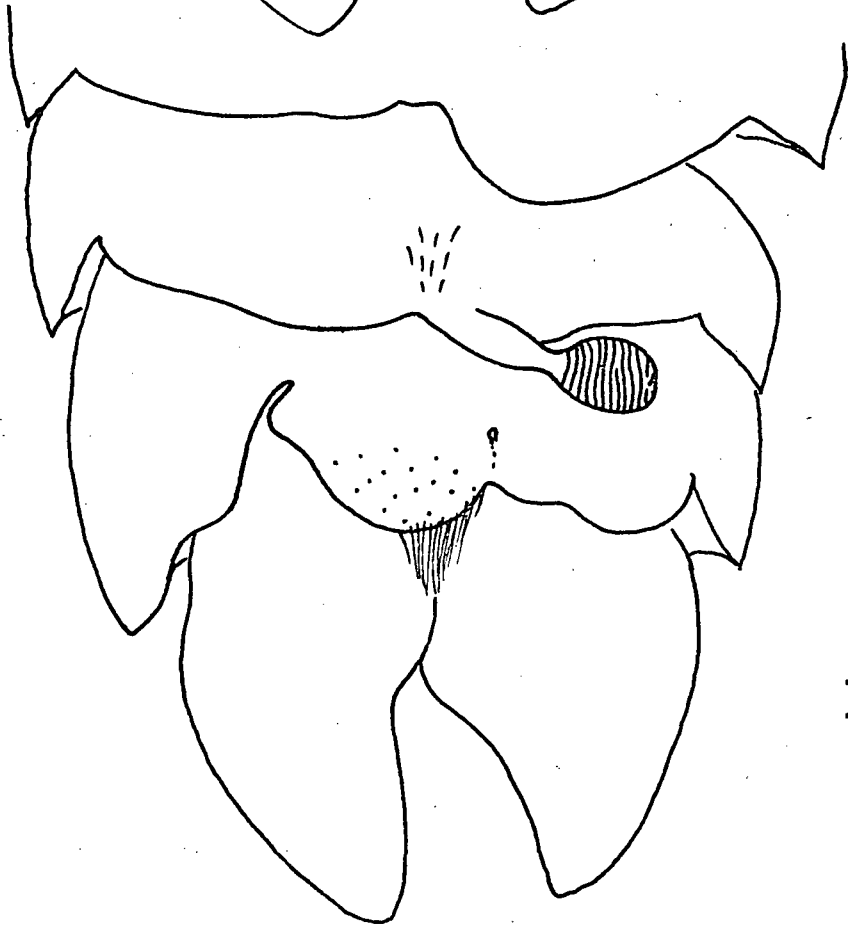


Fig. 65. Dorsal view of posterior abdominal terga of male in C. andersoni (A) and C. utahensis.





**A**

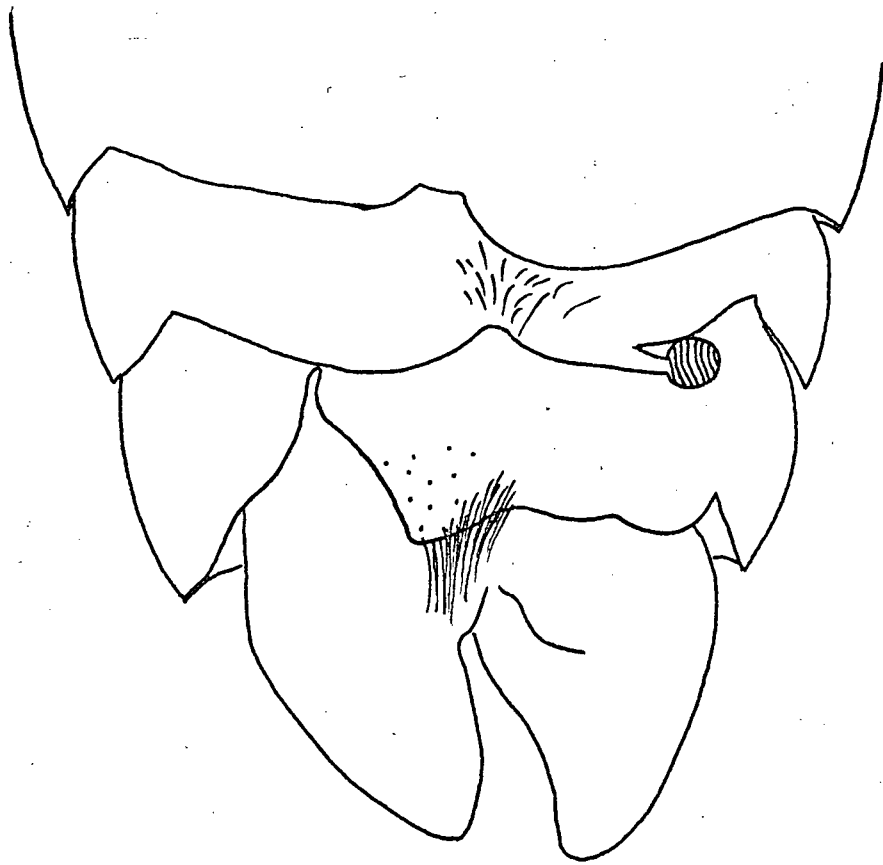


**B**

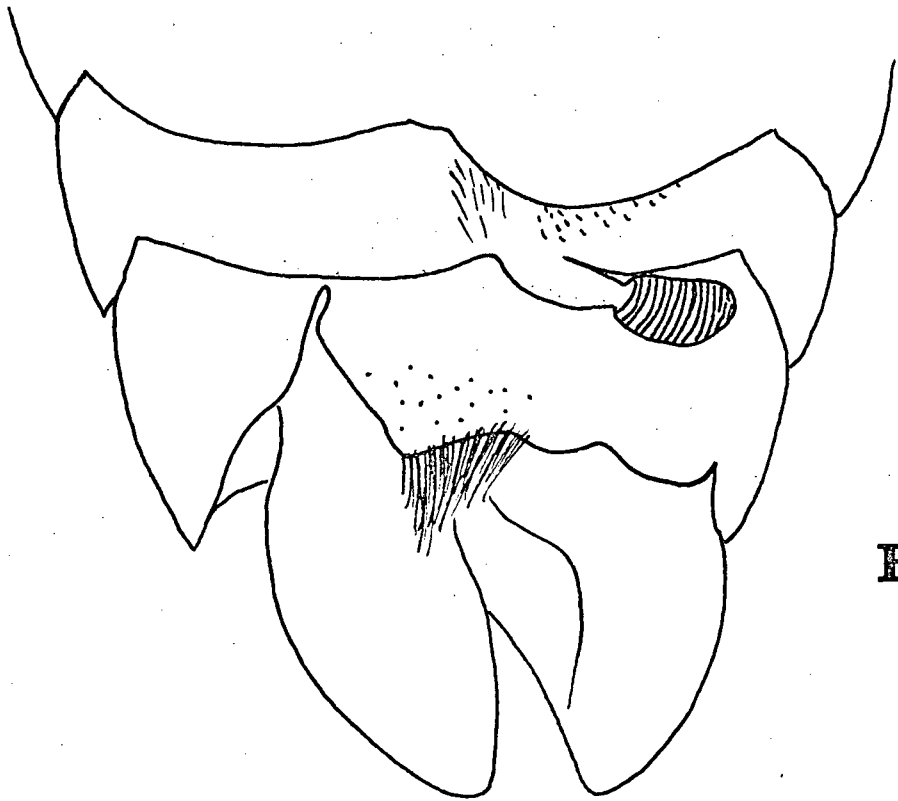


Fig. 66. Dorsal view of posterior abdominal terga of male in C. dakotensis (A) and C. blaisdelli (B).





**A**

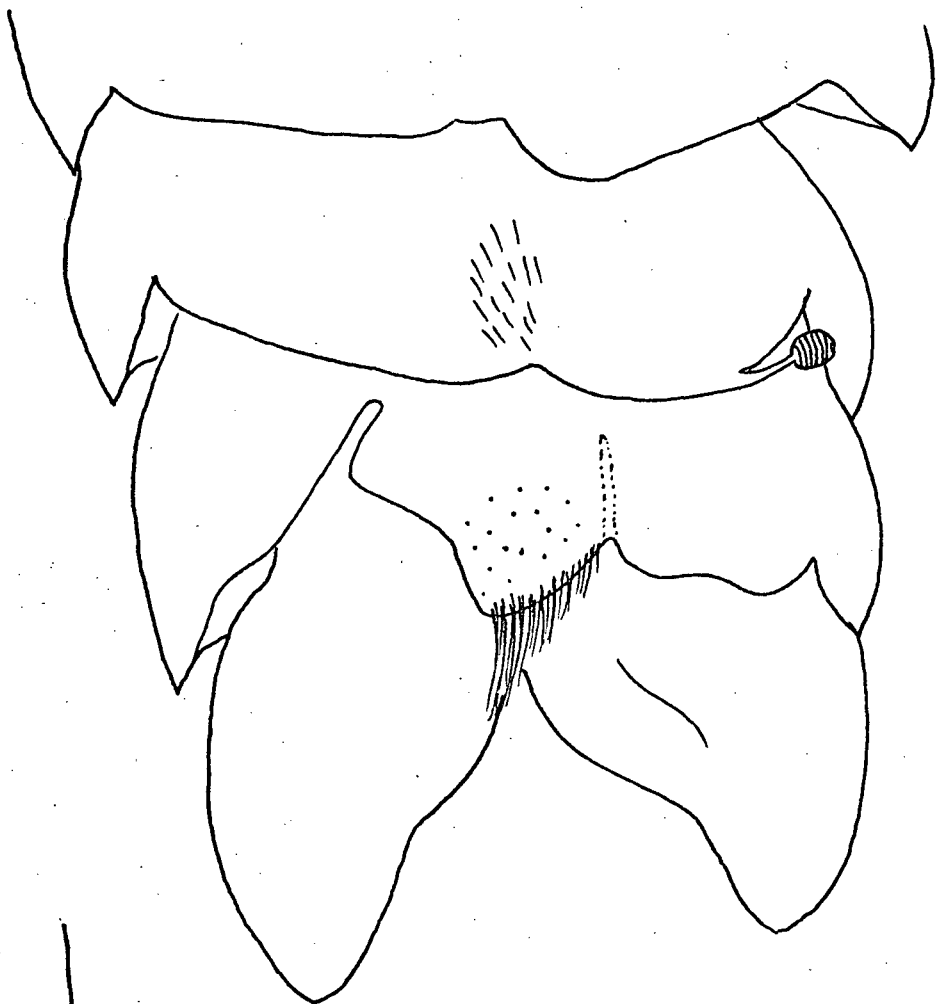


**B**

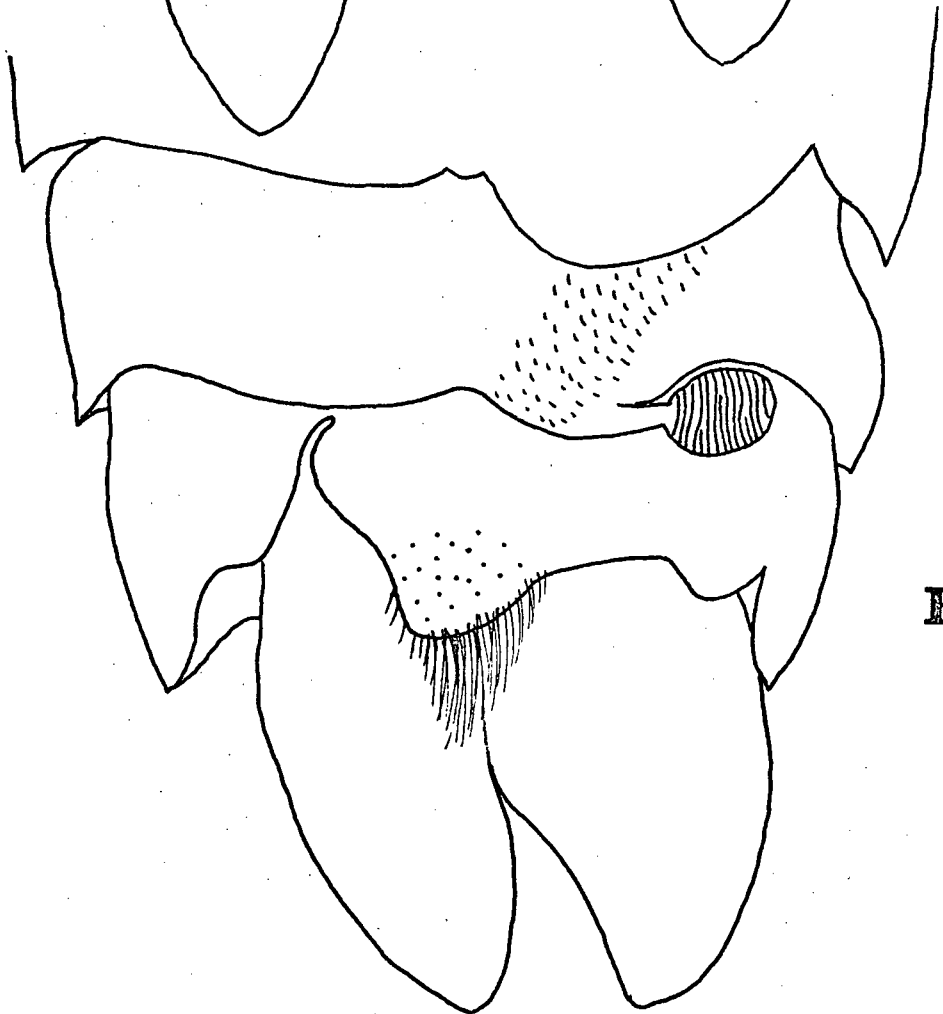


Fig. 67. Dorsal view of posterior abdominal terga of male in C. wileyae (A) and C. expleta (B).





**A**



**B**



Fig. 68. Intraspecific variation in arrangement of paler  
pegs in C. bifida. Specimens from Alberta (a), Utah (b),  
and British Columbia (c, d).



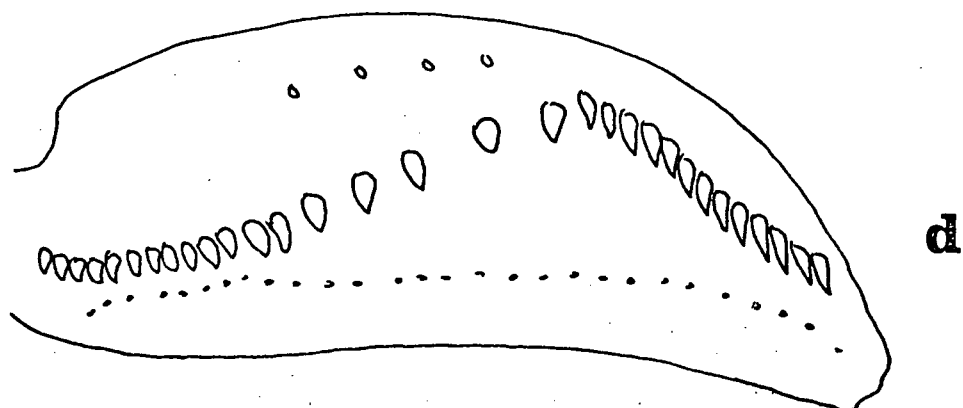
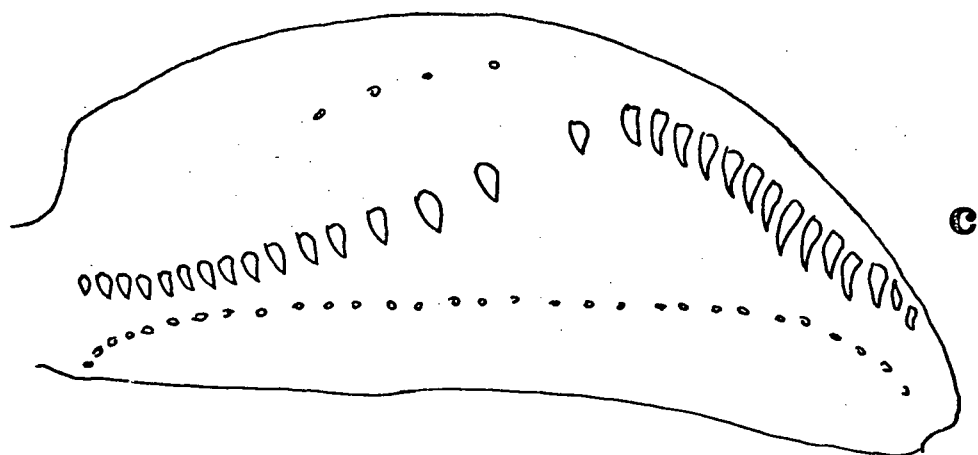
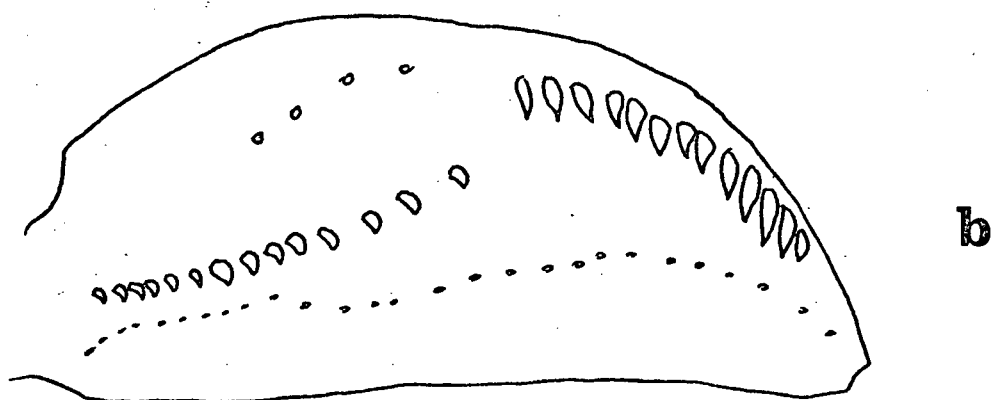
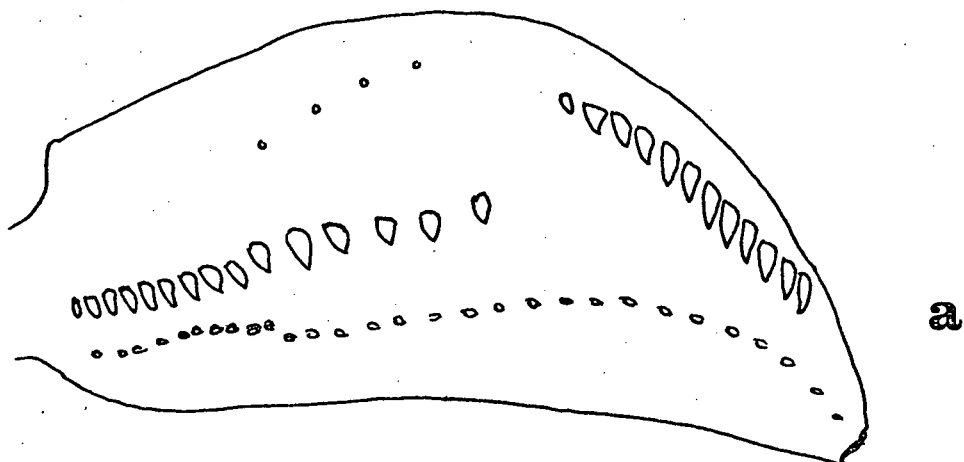




Fig. 69. Arrangement of palmar pegs in C. kuiterti (a),  
C. andersoni (b), C. utahensis (c), and C. dakotensis  
(d).



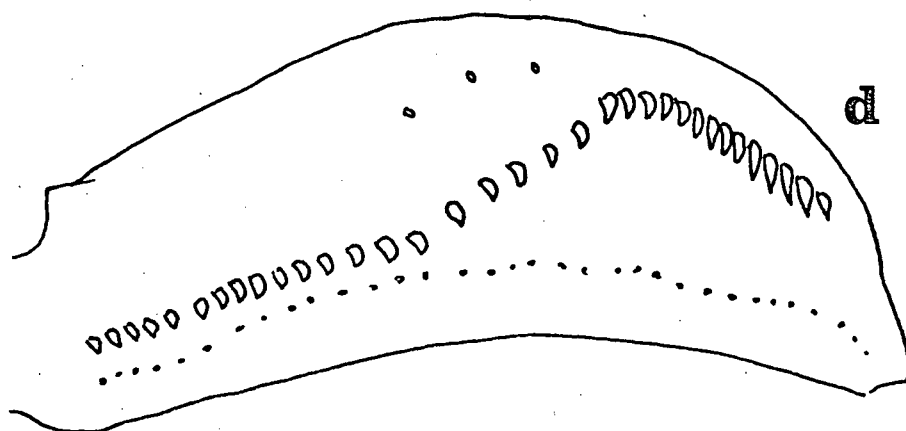
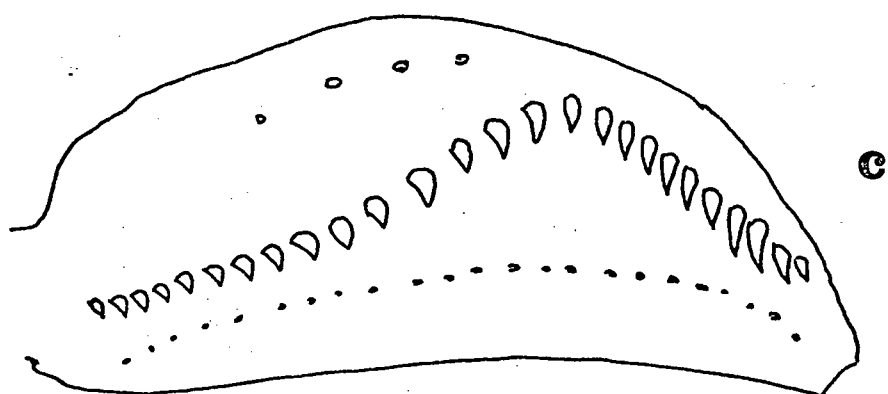
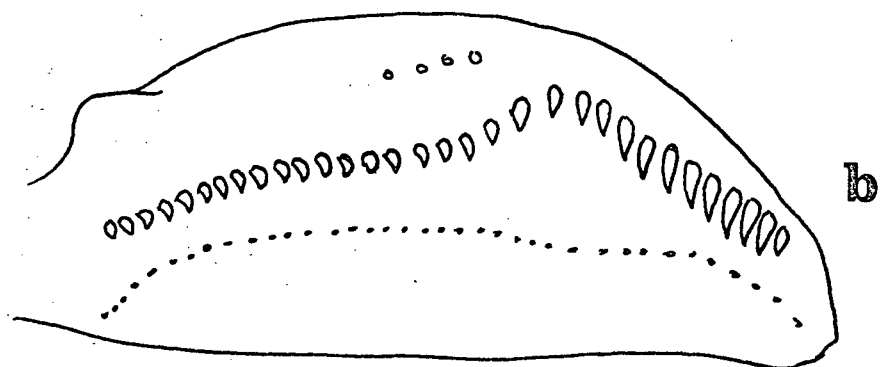
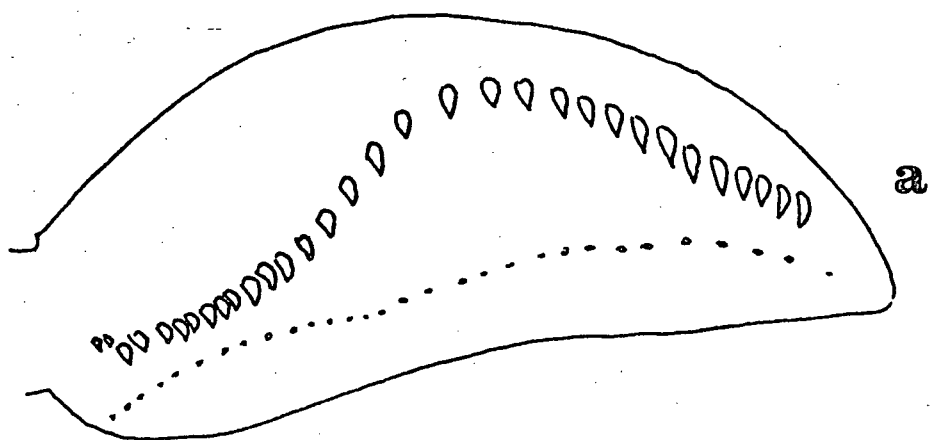




Fig. 70. Arrangement of palmar pegs in C. blaisdelli (a), C. wileyae (b), and C. expleta (c).



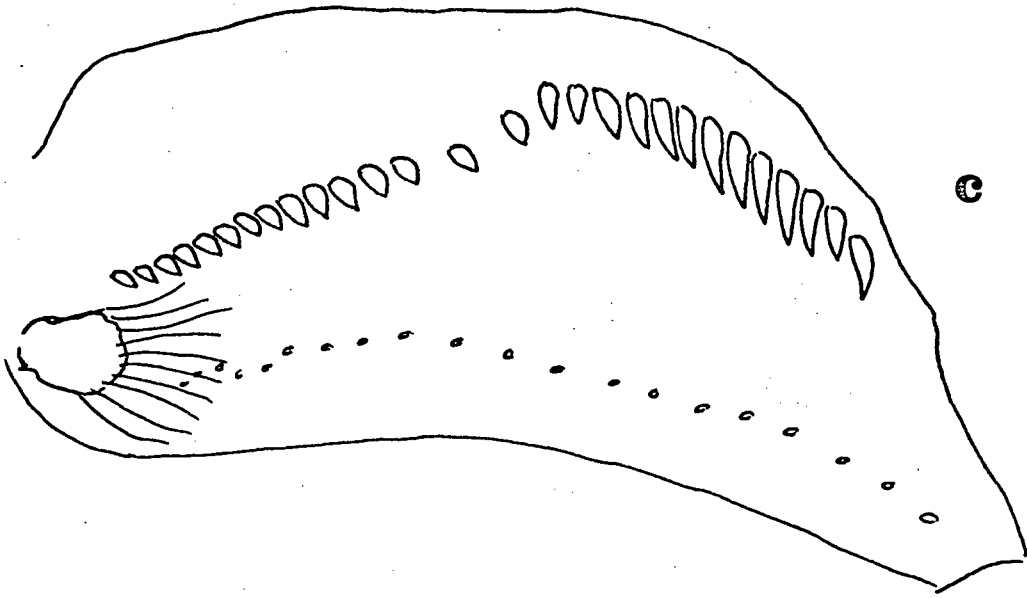
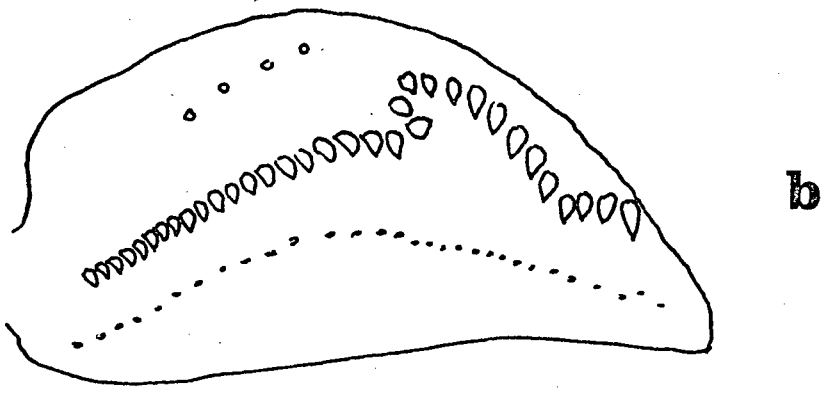
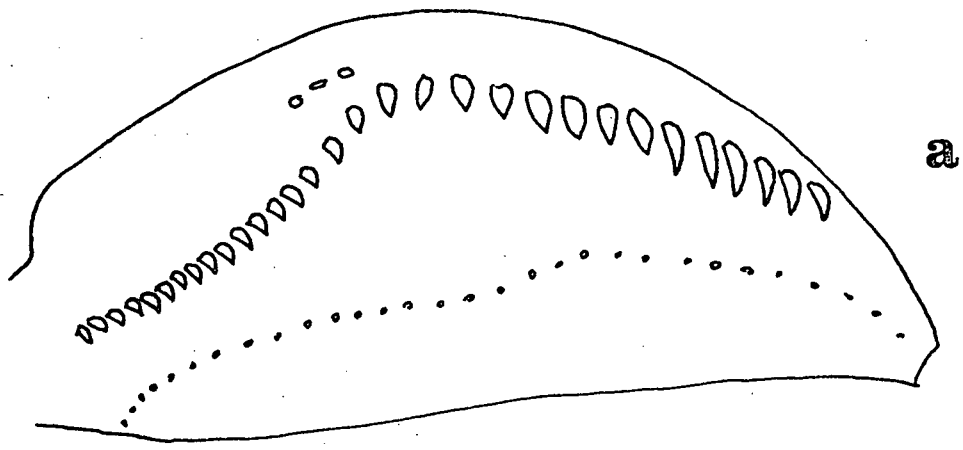




Fig. 71. Typical shapes of the right parameres in Cenocorixa species. a = C. bifida; b = C. kuiterti; c = C. andersoni; d = C. utahensis; e = C. dakotensis; f = C. blaisdelli; g = C. wileyae; h = C. expleta.



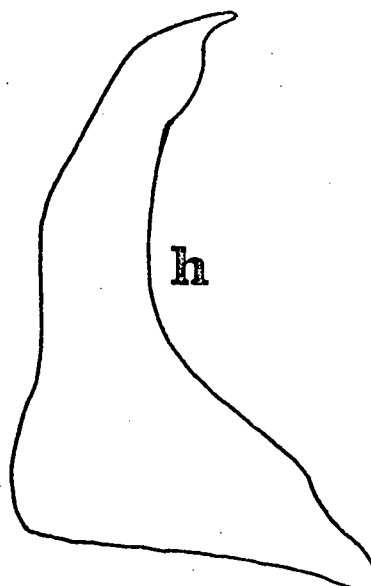
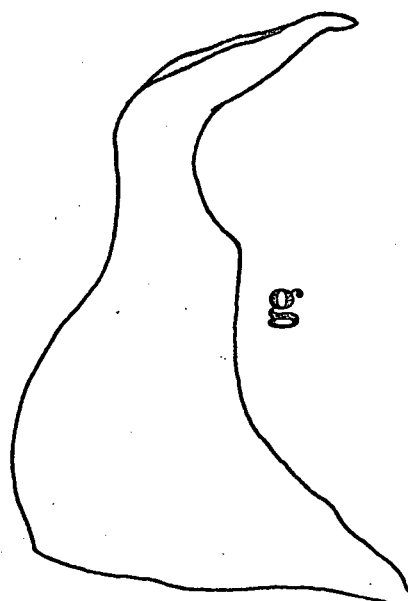
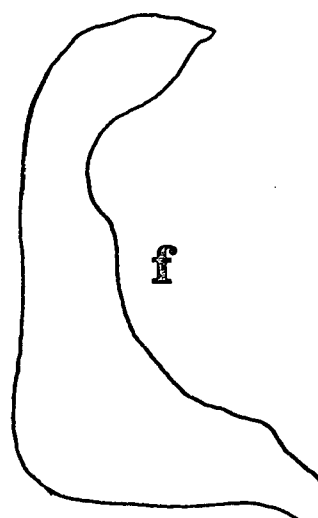
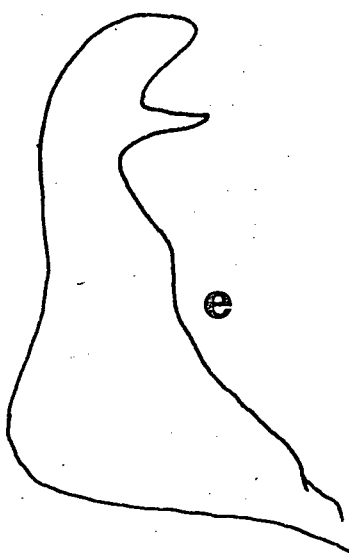
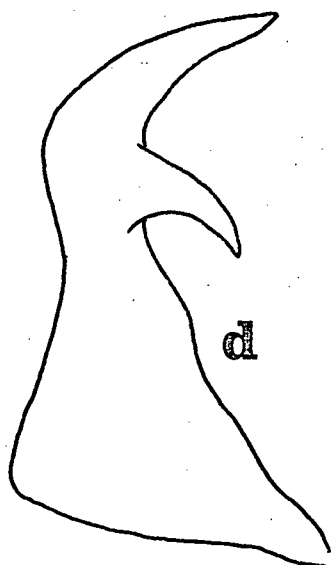
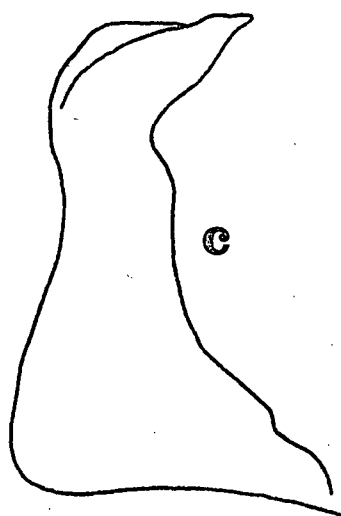
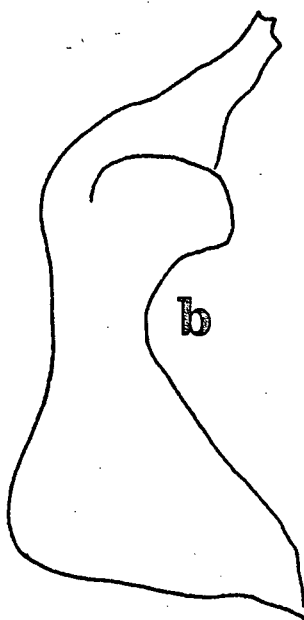
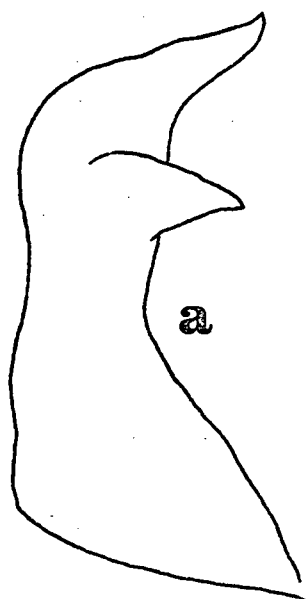




Fig. 72. Intraspecific variation in shape of right paramere in C. bifida. Specimens from British Columbia, Chilcotin, Beeche's Prairie, Lake Lye (a-d); British Columbia, Cariboo, Long Lake (e-h); Utah, Wasatch Co., Strawberry Reservoir (i-j); Alberta, Brooks (k-l).



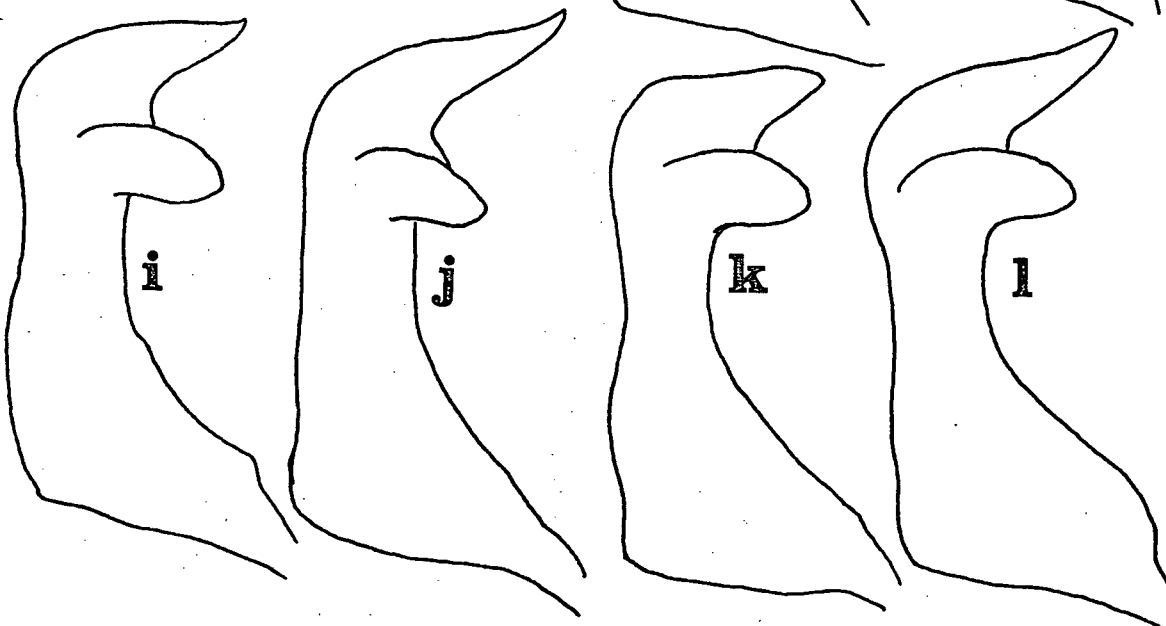
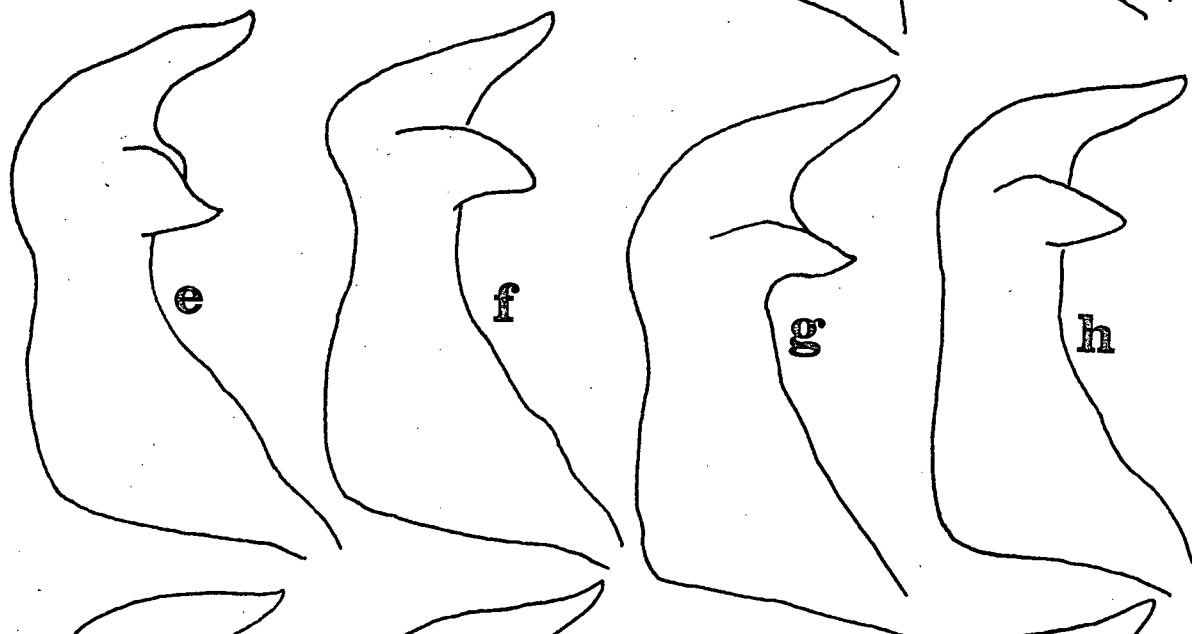
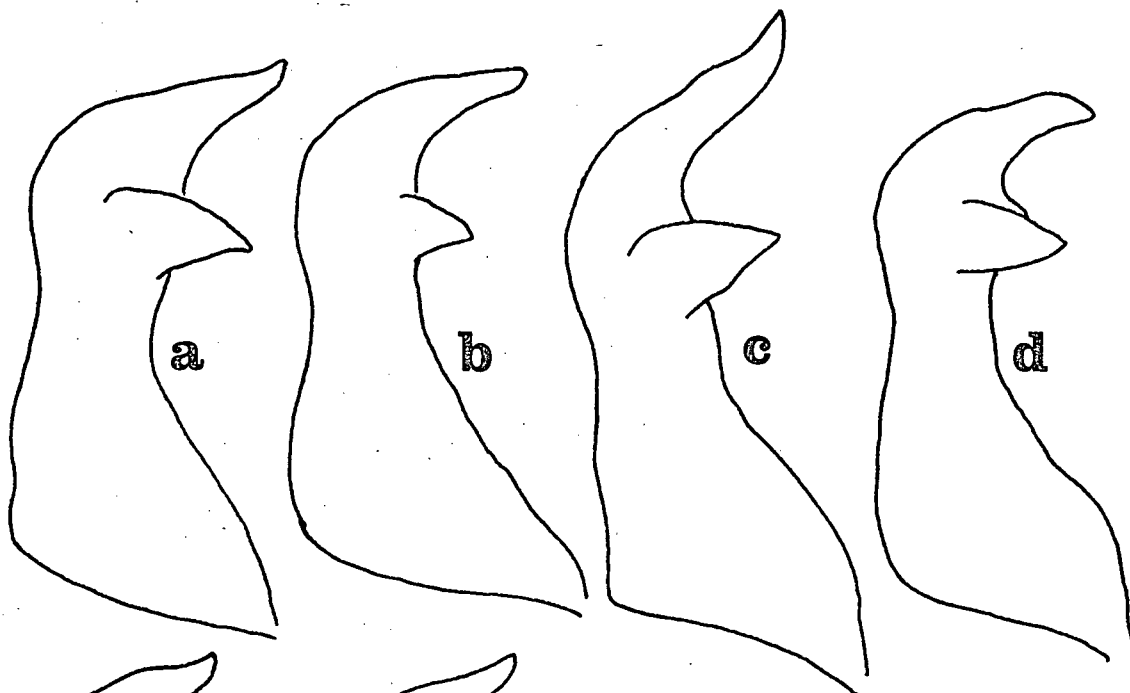




Fig. 73. Intraspecific variation in shape of right paramere of C. kuiterti (a-d) (specimens from: California, Tuolumne Co., Tioga Pass) and C. andersoni (e-l) (specimens from: Washington, Whatcom Co., Custer).



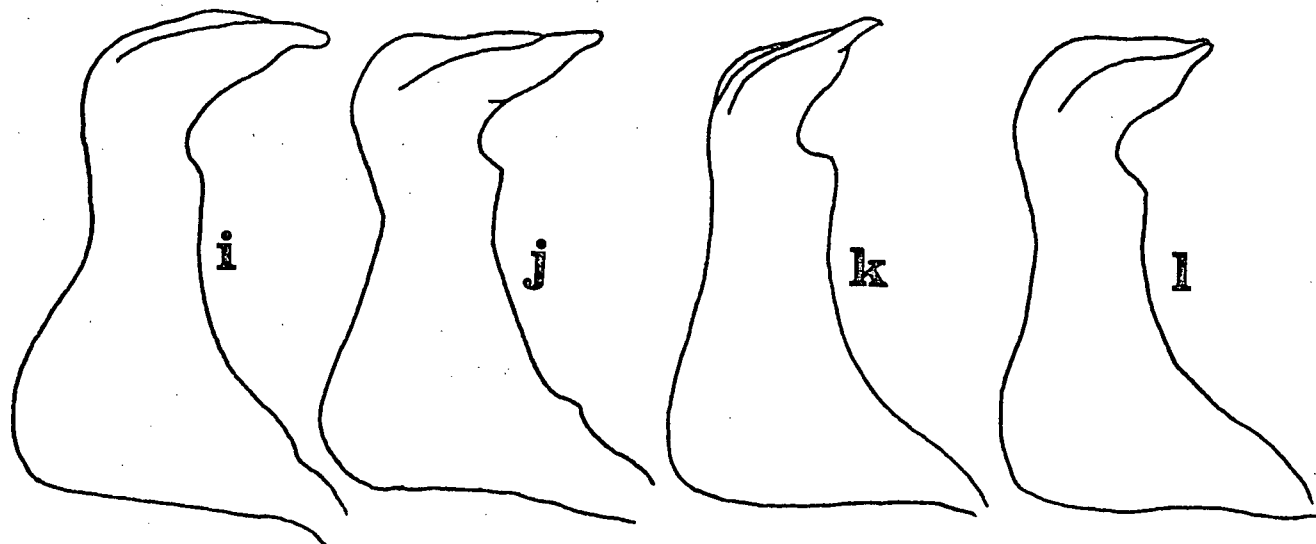
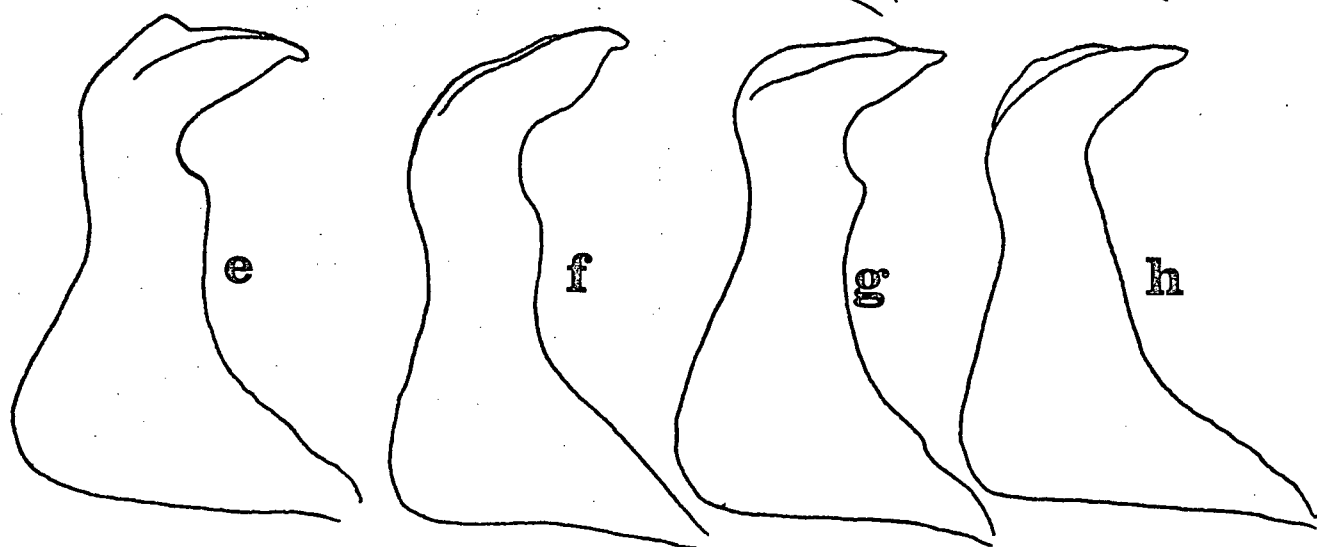
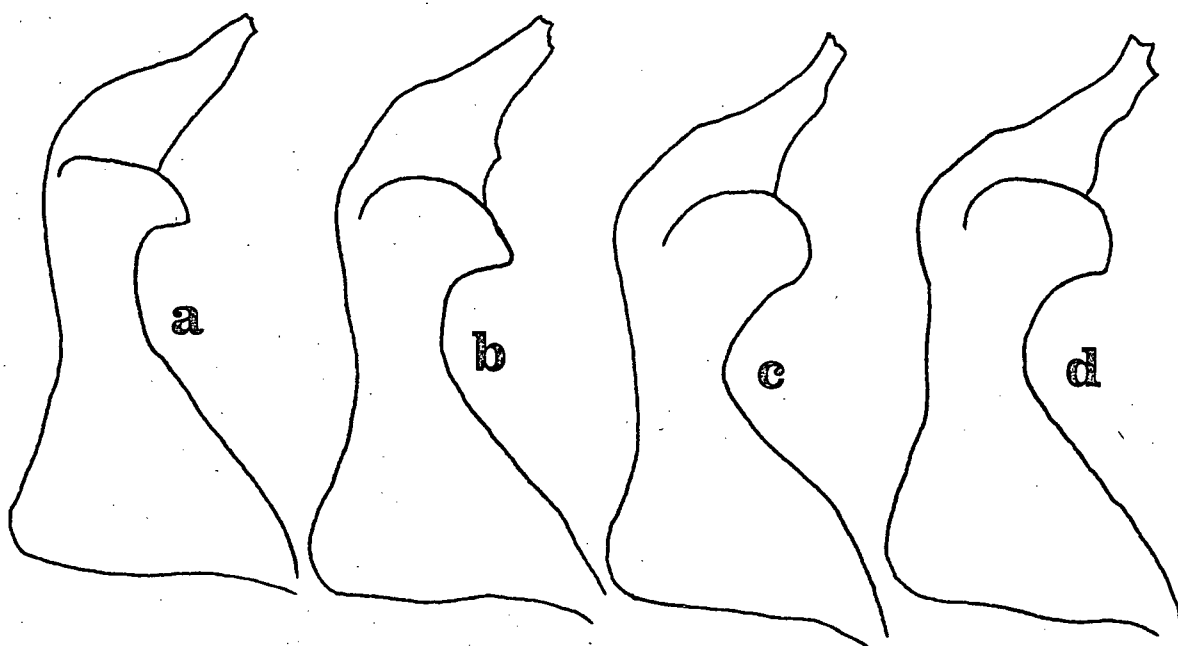




Fig. 74. Intraspecific variation in shape of right paramere in C. utahensis (a-d) (specimens from: a = Alberta, Gleichen; b-c = Alberta, Medicine Hat; d = Washington, Franklin Co., Scootenay Reservoir), C. dakotensis (e-h) (specimens from: Alberta, Brooks), and C. blaisdelli (i-l) (specimens from: i-k = British Columbia, Vancouver; l = California, Humboldt Co., Clam Beach).



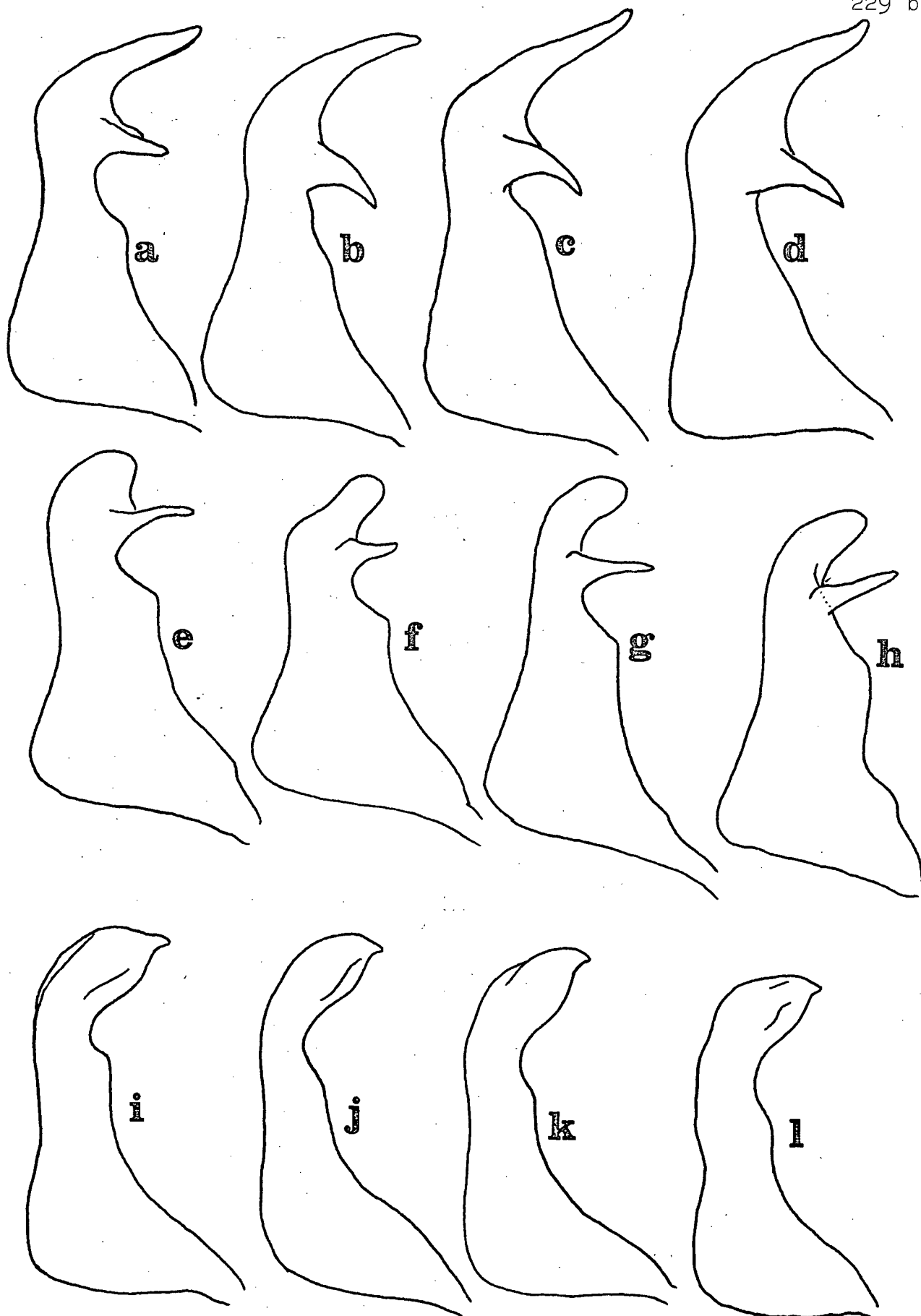
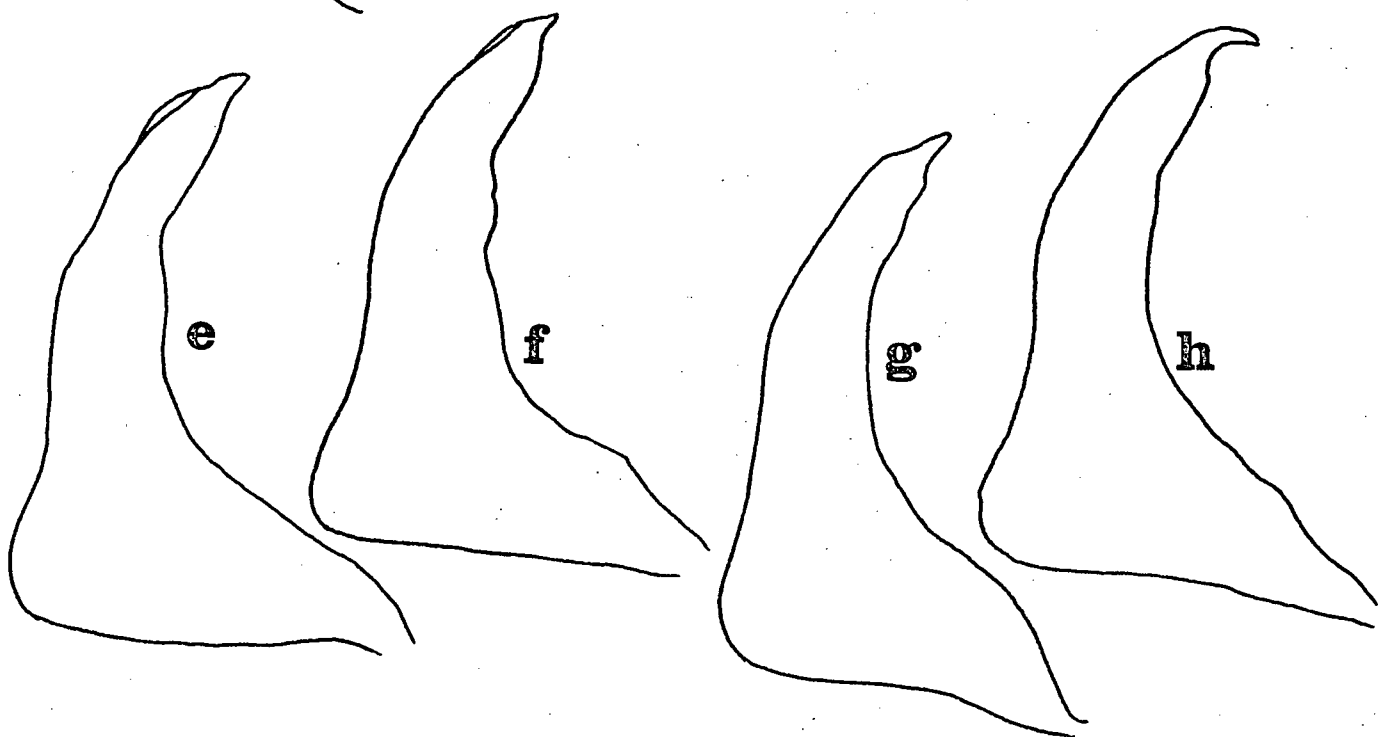
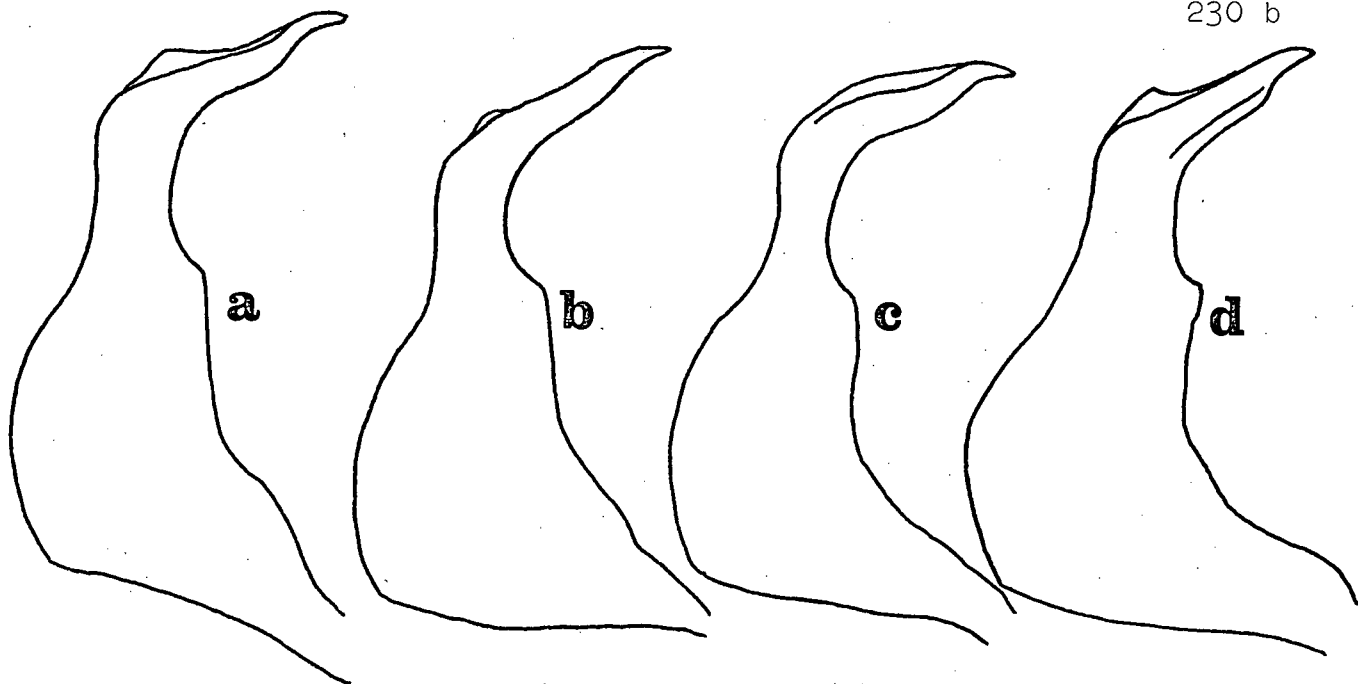




Fig. 75. Intraspecific variation in shape of right paramere in C. wileyae (a-d) (specimens from: California, Lassen Co., Said Lake) and C. expleta (e-h) (specimens from: British Columbia, Kamloops area, LB2).







## APPENDIX II

AUDIOSPECTROGRAPHIC ANALYSIS OF THE STRIDULATORY SIGNALS  
OF SOME NORTH AMERICAN CORIXIDAE FOUND SYMPATRIC WITH  
CENOCORIXA

Various genera and species of Corixidae were found sympatric with Cenocorixa during the present study. Since some of these other species were observed to stridulate, the signals of these were recorded and used in playback experiments with Cenocorixa (see Table XII, page 134). Analysis of the signals of the other taxa showed that these calls are species specific and different from Cenocorixa calls. The localities where other stridulating Corixidae were found sympatric with Cenocorixa, and the signals of these taxa are as follows:

Corisella tarsalis (Fieber)

Sympatric situations were: C. bifida, Alberta; C. utahensis, Alberta, Utah; C. dakotensis, Alberta; C. wileyae, California, Nevada, Utah; C. expleta, Alberta.

Male call: (Fig. 76 A): Recorded at 24.0°C. Basically a simple multipulsate signal. However, the signals are usually produced in a sequence of 3-10 short calls, each lasting approximately 0.5-2 seconds at 24°C. The first calls are usually shorter than the later ones. Pulse rate at the given temperature is about 60 pulses per second. Main frequency area of the sound is 3-5 kc/sec.

Female call was not obtained.



Genus Callicorixa

The signals of all Callicorixa species obtained were found to be basically of the same type with two parts: faint slow beginning which accelerates to a louder and faster ending. Main frequency area in all signals recorded was 3-5 kc/sec. Only male calls were obtained.

C. vulnerata (Uhler). Sympatric situations were: C. bifida, British Columbia; C. andersoni, British Columbia, Washington; C. blaisdelli, British Columbia, California.

Male call (Fig. 76 B): Recorded at 23.2°C. Both parts of the call are relatively short and of simple multipulsate type with distinct pulse intervals. Duration of the first part at 23.2°C was about 0.7 seconds and the second part about 0.3 seconds. The first part consists of somewhat irregular pulses. Pulse rate of the first part was about 12 and the second part about 28 pulses per second at the given temperature,

C. audeni Hungerford. Sympatric situations were: C. bifida, British Columbia, Alberta; C. kuiterti, California; C. utahensis, Alberta; C. dakotensis, Alberta; C. wileyae, California; C. expleta, British Columbia, Alberta.

Male call (Fig. 77 A): Recorded at 22.5°C. C. audeni call is much longer in duration than that of C. vulnerata: the first part lasts about 1.5 seconds and the second part about 1.0 seconds at 22.5°C. Pulse rates at the given temperature for the first and the second parts are about 20 and 30 pulses per second, respectively.

C. tetoni Hungerford. Sympatric situations were: C. bifida, Utah; C. utahensis, Utah (not in the same lake, but in



the same geographic area); C. wileyae, Utah.

Male call (Fig. 77 B): Recorded at 22.0°C. Only one satisfactory recording made. According to this the first part of the call is very faint and nothing can be stated about its length. The second part of the call is of typical Callicorixa signal form. Duration of the second part is about 0.5 seconds and the pulse rate about 34 pulses per second at 22.0°C.

#### Genus Sigara

Several species of the genus were found sympatric with Cenocorixa, but only two of these species were observed to stridulate.

S. omani (Hungerford). Sympatric situations were: C. kuiterti, California; C. andersoni, British Columbia, Washington; C. blaisdelli, British Columbia; C. wileyae, California.

Male call (Fig. 78 A): Recorded at 21.2°C. Simple multipulsate call with slightly fainter beginning than the end and with very short, almost non-existing pulse intervals. Duration of the signal is about 1.5 seconds and pulse rate about 24 pulses per second at the given temperature. Main frequency area is about 4-5 kc/sec. Only male call was obtained for the species.

S. nevadensis (Walley). Sympatric situations were: C. bifida, Utah; C. utahensis, Utah; C. wileyae, Utah. However, S. nevadensis did not occur in the same lakes with any of the mentioned Cenocorixa species, but was found in the same geo-



graphic area.

Male call (Fig. 78 B): Recorded at 22.2°C. Very much like the call of S. omani, with slightly fainter beginning than the end, but in S. nevadensis call the pulse intervals are distinct. Duration of the signal was about 1.5 seconds and pulse rate about 22 pulses per second at the given temperature. Main frequency area of the sound is 4-5 kc/sec.

Female call (Fig. 78 C): Recorded at 21.0°C. A simple multipulsate signal which is much fainter than the male signal. Pulse intervals are distinct, but some irregularities occur. Duration of the signal was about 2.5 seconds and pulse rate about 16 pulses per second at the given temperature. Main frequency area of the sound is 4-5 kc/sec.

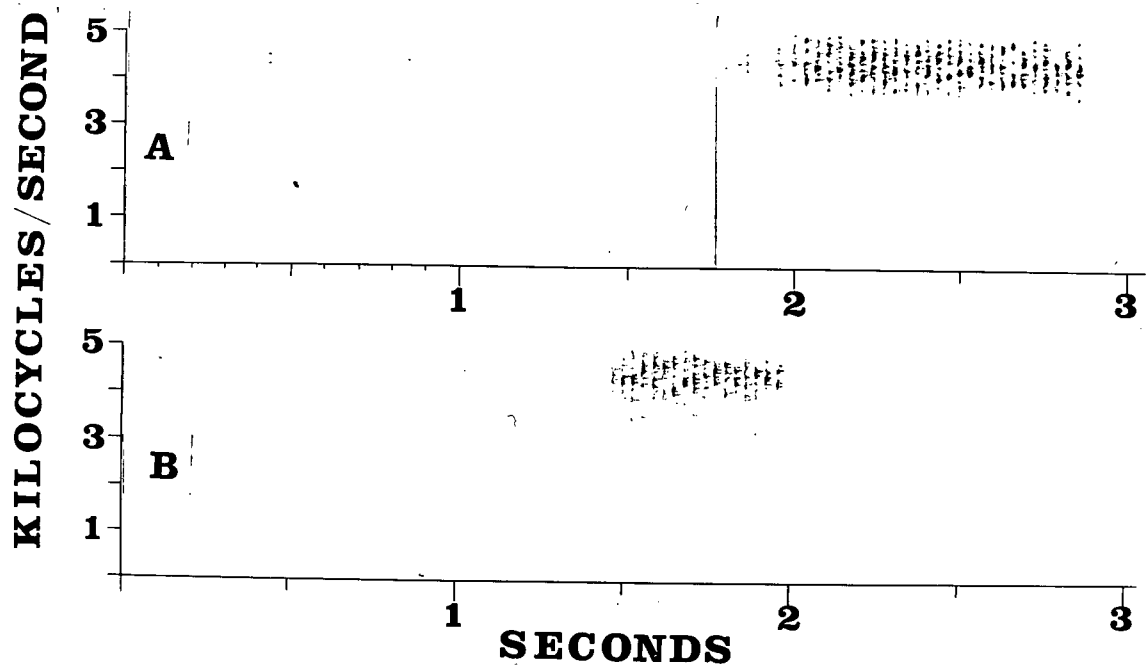
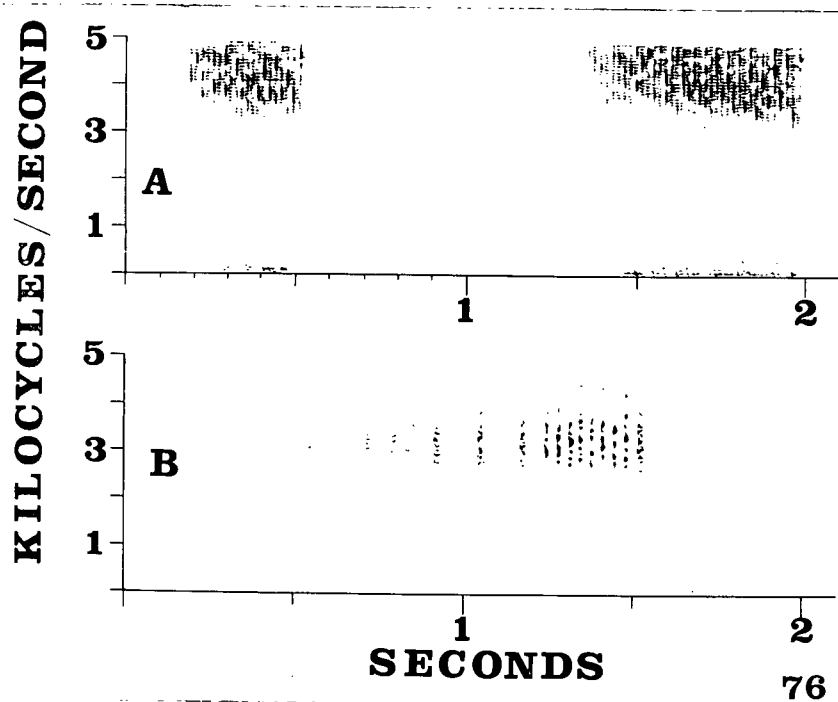
The function of the male and female signals in S. nevadensis was observed to be to facilitate pair formation, i.e. the function of the signals seems to be the same as in the genus Cenocorixa.



Fig. 76. Sound spectrograms of the male calls of Corisella tarsalis (A) and Callicorixa vulnerata (B). C. tarsalis signal recorded at 24.0°C, specimen from: Utah, Box Elder Co., Bear River. C. vulnerata signal recorded at 23.2°C, specimen from: British Columbia, Vancouver.

Fig. 77. Sound spectrograms of the male calls of Callicorixa audeni (A) and C. tetoni (B). C. audeni signal recorded at 22.5°C, specimen from: Alberta, Brooks. C. tetoni signal recorded at 22.0°C, specimen from: Utah, Wasatch Co., Strawberry Reservoir.







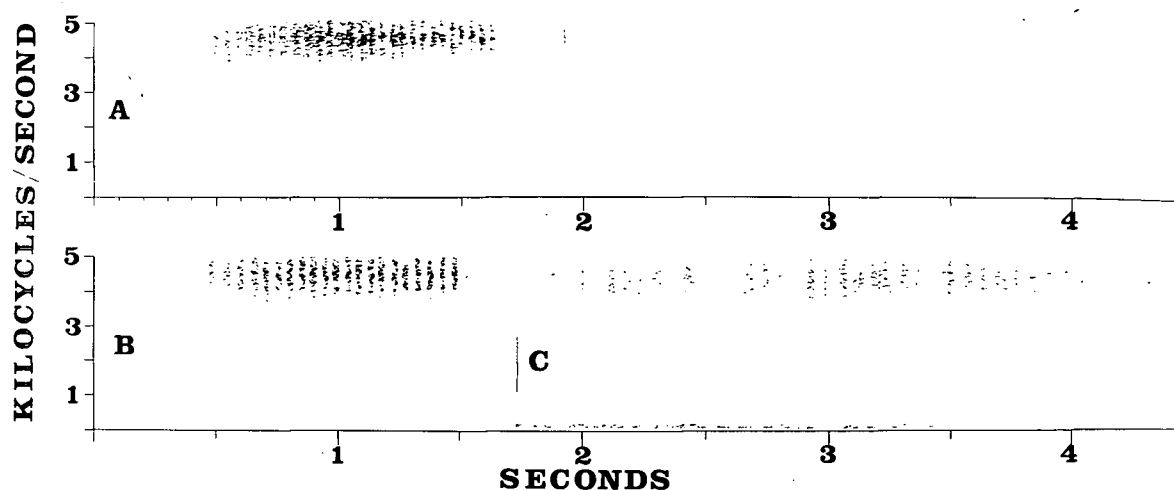


Fig. 78. Sound spectrograms of the signals of Sigara omani (A) and S. nevadensis (B = male call, C = female call). S. omani signal recorded at 21.2°C, specimen from: Washington, Whatcom Co., Custer. S. nevadensis signals recorded at 22.2°C (male) and 21.0°C (female), specimens from: Utah, Box Elder Co., Bear River.