Preliminary investigation into the bioacoustics of *Cicindela* spp. (Coleoptera: Cicindelidae)

by

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ABSTRACT

Initial investigations into bioacoustics of Cicindela spp. (Cicindelidae: Coleoptera) were designed to establish the systematic usefulness of acoustic variables, the possibility of auditory communication, and lay foundations for future studies of acoustic behaviour of the family.

Groups were statistically compared using variables derived from photomicrographs of plectra as well as oscillograms and frequency spectrograms of recorded stridulations.

The noise-like character of tiger beetle stridulations necessitated a new method of comparing stridulation frequency spectra averages: discrete frequencies from the peak-pick procedure of a Nicolet 100n mini-analyzer were compared.

The plectrum consists of a field of posteriorly oriented spines located ventrally at the elytral apex. Plectra characters show trends towards sexual dimorphism and are related to body size and habitat. Among plectra/elytra characters, plectrum field size and shape show the most promise as taxonomic characters.

Stridulations, produced by a two-stroke cycle, consist of 1 to 9 low intensity buzzes (modes), signal mean 49.0 dB at 3 cm (audio range), with an average duration of 0.65 seconds. Cicindelids emit signals of broadband frequency, between approximately 20 Hz and 50 kHz, with significant energy in both audio and ultrasonic ranges.

Although stridulations, for the most part, showed no sexual differentiation, species differences were quite apparent. Signal

timing and amplitude parameters were based on body size, plectrum structure, phylogeny, and habitat. Stridulation frequency was based on phylogeny and may be related to specific stridulatory behaviour and structure of the pars stridens. Acoustic characters appear to show limited promise as useful taxonomic characters.

Temperature at stridulation does not appear to affect stridulatory rates. Evidence suggests that stridulatatory behavior is linked to specific optimal temperatures.

Tiger beetles stridulate spontaneously or when subjected to heated, lighted, or crowded conditions. In contrast to most coleopterans, tiger beetles do not stridulate in response to mechanical stimulation, a behavior associated with a disturbance function. This togther with a relatively ordered stridulatory structure, and initial behavioral observations suggest a territorial and/or calling function of cicindelid stridulations.

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1.00 INTRODUCTION

1.10 General

Many arthropod classes, and most insect orders, produce auditory signals. These sounds are produced by various means, which are: (1) tapping part of the body against the substrate, (2) vibrating a membrane (timbal), (3) expelling gases or fluids through a body orifice, or (4) rubbing together parts of the body. The last of these methods, termed 'stridulation', is the most common method of insect sound production.

Stridulatory sounds are generally used as a means of intraspecific or interspecific communication. Although some sounds that are produced are incidental, the term 'stridulation' in conventional bioacoustic literature implies a means of communication among conspecific individuals.

This study is a preliminary investigation into the bioacoustics of tiger beetles, in particular species of the genus Cicindela (Coleoptera:Cicindelidae).

1.20 Stridulatory organs

The existence of stridulatory organs for many genera of Coleoptera has been documented. Although such is the case for Carabidae (closely related to and often grouped with Cicindelidae) few observations have been recorded for Cicindelidae (Table 1).

Freitag and Lee (1972) found a file (pars stridens) on the dorsal side of the costal vein of the wings of the following carabid genera: Bembidion, Calosoma, Chlaenius, Colliuris,

Galerita and Pterostichus. These are not included in Table 1 because the authors did not indicate whether a complete stridulatory organ was observed.

Gahan (1900) noted that "Wherever any part of the external surface of the body is subjected to the friction of an adjoining part by movements of the insect, there, in some species or other, these organs are almost sure to be found". This is especially true for Coleoptera. The great variety of coleopteran stridulatory organ positions, even among members of the same genus, has led some authors to believe that such organs are recent evolutionary developments (Arrow, 1942; Alexander et al., 1963; Dumortier, 1963a; and Alexander, 1967).

As observed by Haskell (1961) stridulatory organs are remarkably uniform among beetle groups, and they are frictional mechanisms of the simplest type. The structure consists of a file (pars stridens), composed of a number of parallel ridges, and a scraper (plectrum), composed of one or a number of 'pegs' or 'spiny projections'. The scraper is rubbed against the file (or vice-versa).

The 'type' of stridulatory organ found in Coleoptera is denoted by its location. Dumortier (1963a) used a two part name for such mechanisms (or methods). The first part of the name denotes the location of the pars stridens, the last part, denotes the location of the plectrum. Some of the more common coleopteran stridulatory organs are the: cranio-prothoracic, prosterno-mesosternal, pronotal-femoral, mesonoto-pronotal,

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Coleoptera, among these, some Carabidae: Stenolophus mixtus, Amara familiaris, Agonum marginatum, Loricera pilicornis and Elaphrus cupreus (has both elytro-abdominal and alary-elytral mechanisms) (Forsythe, 1979). Some members of the Erotylidae, Endomychidae, and Dytiscidae also have analogous mechanisms (Haskell, 1961; Dumortier, 1963a).

The seemingly simple designation of stridulatory mechanisms is ambiguous and often disagreed upon, as in the case of the alary-elytral mechanism of Cicindela species. Upon observing stridulations of C. repanda, C. fulgida, and C. nevadica, Willis (1967) believed that the sounds were produced by irregularities where the elytra meet. He found no such irregularities, even when viewing the elytra at 80X power. Larson and Pritchard (1974) implied that the alary-elytral "costal architecture" of Adephaga was ineffective in sound production, as they believed that sounds were produced simply by "...whirling the wings beneath the elytra." Hammond (1979) was not convinced that there had been any documented case of an elytral-wing stridulatory mechanism. He believed that spines located beneath the elytra of many beetles were, or at least one time were, 'wing binding patches' used to help fold and hold the wings while the beetle was not flying. All of these disagreements are based primarily on speculation and at this time none can deny that such structures are used to produce sounds.

1.30 Sounds

Insect sounds are described by several physical parameters, namely: frequency spectra; sound pressure level (loudness); and temporal structure (structure in time). Recent investigations into coleopteran bioacoustics have included analyses of these parameters. Sound differences, especially, in temporal structure, are perceived by insect species and are useful for species and sex recognition. Such sound characters are also useful taxonomically.

Early investigators of Coleoptera described sounds produced by insects as buzzing, rustling or rasping noises. The sounds are prevalent throughout the order. These sounds are generally of low intensity, the loudest reported being 60 -62 dB at 1 cm (Alexander et al., 1963). (All sound pressure levels given in decibels have a standard reference value of 20 micropascals.)

Carabid species studied to date produce relatively faint signals with extremely broad frequency ranges, that is, from the audible to the ultrasonic (above 20 kHz). Elaphrus riparius and E. cupreus produce sounds up to 55 kHz at 60 dB and 56 dB at 0.5 cm respectively (Bauer, 1973). Carabus irregularis produces sounds up to 70 kHz at 54-59 dB at 1.0 cm (Bauer, 1975). Cychrus caraboides produces sounds of unknown intensity up to 80 kHz.

Stridulation has been described for Cicindela fulgida, C. nevadica, C. repanda, (Willis, 1967), C. duodecimguttata, C. tranquebarica and others (Freitag and Lee, 1972). The sound was described as an interrupted or continuous 'buzz' lasting about 1

second (Willis, 1967; Freitag and Lee, 1972). Carabids such as Stenolophus mixtus, Amara familiaris, and Agonum marginatum produce similar sounds (Forsythe, 1979). Some Erotylidae and Endomychidae produce faint buzzes lasting up to one minute, using an analogous alary-elytral mechanism (Dumortier, 1963a).

The alary-elytral sound producing mechanism is typified by the slight raising of the elytra and the rapid movement of the flight wings beneath the elytra. This has been observed for Cicindela (Freitag and Lee, 1972) and some Carabidae (Forsythe, 1979).

1.40 Behaviour

There has been some general speculation as to the purpose of coleopteran stridulation. Frings and Frings (1971) stated that, "The presence of stridulatory organs suggests that the sounds produced are significant in the lives of beetles...". Darwin (1874), used an analogy of other sound-producing Arthropoda to conclude that the evolution of stridulation in Coleoptera was sexually selected. Gahan (1900), denied that a reproductive purpose was the only possibility, when it was found that the larvae of some Coleoptera, such as Lucanidae, were known to stridulate. Arrow (1942), among others, argued that beetle stridulation was incidental. He believed that beetles derive some benefit from exercise or experience some form of pleasure when stridulating.

It is now generally known that some Coleoptera use sound production as a means of communication. The stridulatory signals

produced may be used in defense, protection, reproduction, aggressive interactions and/or other situations. A general overview of the various functions of coleopteran stridulation are listed below:

a) Reproduction: Courtship sounds have been described for beetles of many families, for example, Cerambycidae (Michelsen, 1966), Curculionidae (Mampe and Neunzig, 1966; Selander and Jansson, 1977), Dytiscidae (Ryker, 1976), Hydrophilidae (Van Tassel, 1965; Ryker, 1972), Passalidae (Schuster and Schuster, 1971; Schuster, 1975, 1983), Scolytidae (Barr, 1969; Rudinsky and Michael, 1973; Ryker, 1976; Vernoff and Rudinsky, 1980), Tenebrionidae (Eisner et al., 1974; Zachariassen, 1977), Tentyriidae (Tschinkel and Doyen, 1976), and Trogidae (Alexander et al., 1963). The sounds produced are often divided into premating, copulatory and post-mating categories. Each of these categories is represented by a typical stridulation, which is different from others. Sympatric species that live in very close proximity, for example, those in the family Scolytidae may use these signals as reproductive isolating mechanisms (Barr, 1969).

Mampe and Neunzig (1966) were the only researchers to give experimental evidence of sexual attraction by stridulation (Curculionidae). They found that either sex could attract the other by stridulating, while stridulating members of the same sex had little effect on each other.

Rudinsky and Michael (1973) found that males of Dendroctonus pseudotsugae (Scolytidae) produced 'attractant chirps' which

were elicited by female frass or female aggregative pheromones. Stridulation in relation to reproduction might be useful in communicating information which would take more energy by other means.

b) Aggregation: Calling stridulatory behaviour has been reported in some Dytiscidae (Ryker, 1976) and Passalidae (Alexander et al., 1963; Schuster, 1983). Such signals may serve as reproductive isolating mechanisms with sympatric species that do not live in close proximity. Stridulation serves to aggregate conspecific sexes so as to increase frequency of sexual contact.

c) Aggression: Aggressive stridulation has been observed in Passalidae (Gray, 1946; Alexander et al., 1963; Schuster, 1983), Scolytidae (Vernoff and Rudinsky, 1980) and Dytiscidae (Ryker, 1976). The signal is usually more intense than other signals produced by the animal and all cases of aggressive interaction are intraspecific.

d) Disturbance or stress: Disturbance stridulations are produced in response to stress. Most researchers believe that these signals may play some part in the defense and protection of Coleoptera.

Disturbance stridulations are the most prevalent stridulatory signals produced by Coleoptera. Sounds produced in response to stress have been observed in: Carabidae (Marshall, 1832; Larochelle, 1976; Bauer, 1973, 1975; Claridge, 1974; Masters, 1979; Forsythe, 1980), Cerambycidae (Dumortier, 1963c; Miller, 1971; Finn et al., 1972), Chrysomelidae (Kogan et al.,

1970), Curculionidae (Gibson, 1967; Webb et al., 1980), Dytiscidae (Alexander et al., 1967; Dumortier, 1963c; Buchler et al., 1981; Schuster, 1983), Scolytidae (Rudinsky and Michael, 1973).

Generally disturbance stridulation can be elicited by molesting a beetle in ways such as, blowing on the subject, squeezing the subject between fingers or tweezers, tapping or probing the subject, and so on. Reactions in response to crowding or exposure to bright light have been observed for the carabid, Amara familiaris. This species does not stridulate when physically molested (Forsythe, 1979).

It has been suggested that stridulation, in response to physical molestation in natural conditions, may deter the attack of predators and allow a possible escape. When some specimens of Tropisternus spp. (Dytiscidae) and Omophron labiatus (Carabidae) were given to wolf spiders, under field conditions, it was found that the spiders persisted longer when attacking 'silenced' beetles (Masters, 1979). Crows were more hesitant in attacking and took longer to kill and eat stridulating passalid beetles (Buchler et al., 1981). Elaphrus riparius also significantly deterred the attack of Common Sand Pipers (Bauer, 1976). There was no measure of the intrinsic value of the disturbance stridulations in these encounters as these were associated with a noxious secretion from the pygidial glands (Claridge, 1974).

Some members of the genus Berosus (Hydrophilidae) stridulate spontaneously when encountering other individuals of the same

species or when feeding. Van Tassel (1965) labelled such stridulations as "distress" or "stress" sounds although she could not determine their exact function. Some members of Elaphrus (Carabidae) (Bauer, 1973), and Amara familiaris (Forsythe, 1980) stridulated under similar conditions. Both Bauer and Forsythe attributed these stridulations to agonistic behaviour among members of their own species.

Disturbance stridulation may also have an intraspecific alarm function. In one case, Greene (1976), after blowing on a specimen of Scaphinotus sp., found that it stridulated and ran, after which, a second specimen concealed under a leaf 20 cm away immediately exhibited the same behaviour.

Dumortier (1963c) suggested that disturbance stridulations were a 'reflex cry' which served to displace nervous energy. This of course, should not imply that such a 'reflex cry' could not serve another purpose.

e) Mimicry: Lane and Rothschild (1965) suggested that the stridulations and behaviour of disturbed Necrophorus investigator (Silphidae) were similar to the sounds and behaviour of a stunned Bumble-Bee (Bombus). Although the evidence is not experimentally conclusive, this is the only reported case of sound mimicry within Insecta.

Carabids appear to stridulate only when physically molested or exposed to bright light. Freitag and Lee (1972) suggested that the stridulations of adult Cicindela serve as "warning", "aggressive" or "distress" sounds. "Stridulation might also play

a role in the sexual activity and behaviour of tiger beetles" (Freitag and Lee, 1972). There has been no demonstration as to the stridulatory function(s) of Cicindelidae.

1.50 Sound reception

Because beetles respond to sounds they must have some way of receiving these sounds. Analysis of sound receiving organs for Coleoptera has largely been ignored and proof as to their existence is mostly circumstantial (Frings and Frings, 1971).

Some members of Cicindelidae are the only coleopterans reported to have tympanic organs; organs specifically designed to receive relatively long range air-borne sounds. These organs, first described as coleopteran hearing organs by Spangler (1988), consisted of tympana, bilaterally situated on the first abdominal tergum directly beneath the elytra. Spangler (1988) reported morphologically analogous structures for 7 species of Cicindela and 2 species of Megacephala. Structures of similar description, originally proposed to be resonating chambers by Freitag and Lee (1972), were observed for C. tranquebarica (Freitag and Lee, 1972).

Spangler (1988) found that several Cicindela species responded to sounds of ultrasonic frequency. He suggested that reception of sounds during flight enabled some tiger beetle species to avoid noise producing predators such as bats. Megacephala fulgida, which has tympanic organs (Spangler, 1988), and M. brasilensis have also been reported to respond to sounds.

These species exhibit nocturnal phonotactic behaviour to synthesized broadcast calls of mole crickets (Fowler, 1987).

1.60 Objectives

Based on current knowledge of cicindelid stridulatory sound production I performed studies of an exploratory nature. The objectives were as follows:

(1) Investigate the possible morphological differences between the plectra of various cicindelid species.

(2) Investigate possible differences of sounds produced among some species and both sexes of tiger beetles by revealing statistically valid differences based on a number of physical acoustic parameters.

(3) Investigate the effect of temperature on tiger beetle sound production.

(4) Derive biological significance for sound similarities and differences among the taxa studied.

2.00 MATERIALS AND METHODS

2.10 Specimens

Seven species of Cicindela were studied. Adults of Cicindela repanda, C. duodecimguttata, C. tranquebarica, and C. longilabris were collected in Thunder Bay and Stanley (26 km west of Thunder Bay), Ontario. More adults of C. repanda, C. duodecimguttata, C. punctulata and C. sexguttata were collected in the Boyd Conservation Area, 10 km north of Toronto, Ontario. In addition, pinned specimens of C. denikei, collected 32 km east of Kenora, Ontario, were obtained from the collections of Michael Kaulbars (Lakehead University).

2.20 Care and handling of specimens

Beetles were captured with a standard insect net and were transferred to 50 ml vials. The contents of 12 vials, usually 3-4 specimens per vial, were immediately placed in 20 gallon aquaria in the laboratory.

Floors of the aquaria were lined with 5-10 cm of sand. Foliage, consisting of tree branches and crumpled paper, were provided to reduce chances of beetles sighting and cannibalizing each other. No attempt was made to simulate natural temperature cycles or photoperiod. Temperature was maintained at about 20° C.

Water was provided in shallow petri dishes and by moistening the sand at one end of each aquarium. Beetles were fed a daily diet of insects and worms, supplemented by fresh ground beef.

2.30 Measurements of elytra, plectra fields and spines

Pinned or preserved specimens, males and females, two of each for seven species, were used in studies of the plectrum. Specimens were gently boiled in 70% ethanol to clean the tissues. The whole right elytron was removed from each specimen and the highest point on the dorsal side of each elytron was affixed with silver paint to an SEM stage. The elytra were inspected for any extraneous material which was then removed with a soft brush and air propellant.

The outline of each elytron was drawn onto 225 by 280 mm overhead projector transparencies with the aid of a Wild M5 dissecting microscope and attached drawing tube. The drawings were made at 25X magnification and appropriate scales were included with each.

After drawings were made, elytra were sputter coated with gold for examination under a Cambridge Stereoscan 600 scanning electron microscope. Photomicrographs were taken with an attached 35 mm camera using Kodak Plus-X pan film 5062, ASA 125.

Photomicrographs consisted of: (1) a whole view of the plectrum, with the apex pointing to the top of the screen (50X magnification), (2) a whole view of the plectrum, with its apex pointing to the screen bottom (50X magnification), (3) a 60° angle (approximately the maximum angle allowed by the SEM) from normal, focusing on the approximate centre of the plectrum from the inside margin of the elytron (2000X magnification), and (4) a 60° angle from normal, focusing on the approximate centre of the

plectrum from the apex of the elytron with the inside margin facing to the right of the screen (2000X magnification).

One photonegative for each representative view of each elytron was selected, developed, and enlarged on Illford 203 by 254 mm paper.

Plectrum perimeters and magnification scales for each photomicrograph of views (1) and (2) were traced onto 225 by 280 mm overhead projector transparencies. Endpoints for spine lengths and spine base widths of three sample spines were traced for each photomicrograph of views (3) and (4). Magnification scales were also included.

Plectrum perimeters were determined by tracing the area between the spiny field and the surrounding ventral elytron. This junction was usually sharply demarcated on photomicrographs at 50X magnification.

Plectrum spines, chosen from photomicrograph type (3), were those which provided a relatively unobstructed view of their bases and apices. Three spines per plectrum were chosen. Endpoints were determined by placing a point at the apex and at each side of the base, where the outline of the spine appeared to be parallel with the foundation of the elytron. Base width was determined by measuring the distance between the basal endpoints (baseline) and height was determined by measuring the distance between the apex and the point which bisected the base line (Fig. 1).

Elytra and plectra areas, as well as, plectra spine heights and base widths were determined with the use of an Apple II microcomputer in conjunction with an Apple II Graphics Tablet. The graphics tablet consisted of a grid of fine wires set beneath a mylar plastic sheet. A special pen produced a signal on the grid at the point of contact between the pen and the grid and the accumulated signal data were fed into the microcomputer.

The microcomputer was calibrated by taping each transparency between the tablet grid and the mylar sheet and then contacting the endpoints of the traced micrograph scales with the signal pen. Plectrum areas were determined by tracing the entire perimeter of the plectrum from an arbitrary point on the perimeter line. The microcomputer then calculated the area in calibrated units. Plectrum spine widths and heights were determined by using the signal pen to contact the endpoints of the respective distances. The microcomputer then calculated the calibrated linear distances between the endpoints. The average measure of three tracings per item were recorded.

2.40 Statistical analysis of elytra, plectra fields and spines

The following variables were compared among species:

(1) absolute area of plectrum (PA)

(2) absolute area of elytron (EA)

(3) relative area of plectrum as percentage area of elytron (PPE)

(4) spine length-average of 3 spines per plectrum (SL)

(5) spine base width-average of 3 spines per plectrum (SW)

(6) spine length to width ratio-SL divided by SW (LWR)

Species with sexes grouped together were compared using parametric and Kruskal-Wallis oneway analysis of variance procedures ($P< 0.05$) for each variable. When significant differences among species variable means were discovered, specific differences were determined using Duncan's multiple ranges test ($P< 0.05$).

The above statistical procedures were executed with the use of Statistical Program for the Social Sciences ($SPSS^X$), Release 2.2, on a Dec Microvax-I (VMS/V4.5) microcomputer.

Further elaboration of species relationships on combined plectrum/elytron variables was done by: counting numbers of species associations for each on Duncan's ranges test; ranking each paired species association by number of variables related, in case of ties, proximity or range of associated variable means; and using the rank to determine a percentage relationship between species pairs. All possible associations between a single species and all other species added to 100%.

2.50 Sound recording

Sounds of specimens were recorded usually on the same day of capture, or at least within two days, in an acoustically insulated chamber, between the times of 1200 and 1600 hours. Outside sounds were attenuated by approximately 50 dB SPL (sound pressure level).

Using the equipment outlined in Figure 2 single specimens were placed on a bed of dry sand under a fibre-glass mesh cylinder, 5 cm in diameter by 5 cm in height, and stridulations

were elicited by heating the beetle with the aid of an 250 watt infra-red brooding lamp placed directly overhead at a distance of approximately 50 cm from the sand surface.

A Bruel and Kjaer Type 4133 12.7 mm condenser microphone with a frequency response from 4 Hz to 40 Hz ± 2 dB and sensitivity of 12.5 mV/Pa, was placed at a 45 degree angle directly above one edge of the mesh cylinder. The microphone was linked to a Bruel and Kjaer Type 2203 sound level meter, which was set for an unweighted linear fast response at a 50 dB SPL range. A Krohn-Hite Model 3202 filter was connected in-line between the sound level meter and tape recorder to help increase the signal to noise ratio of recorded stridulations. The low and high passes on the filter were set at 40 Hz and 40 kHz respectively.

Stridulations were recorded on Ampex Precision Magnetic Tape (6.4 mm) in a Racal Recorders Store 4DS instrumentation tape recorder. The recorder and filter were placed outside the recording chamber to help lower ambient noise level during recording. The recorder was operated by remote-control from within the chamber. Tape was recorded at 76 cm per second. Only channels 2 and 4 were used so as to prevent cross-talk between adjacent channels.

The temperature of the substrate was measured with a standard mercury thermometer which was placed on the sand surface next to the mesh cylinder.

The substrate temperature at the time of initial recording was kept as close to 25° C as possible. The recorder was started and the heat lamp turned on as soon as the specimen was placed in the testing area. Substrate temperature and tape footage were recorded once a stridulation was observed.

Recently recorded specimens were placed in separate jars for approximately 15 to 30 minutes until another trial could be performed. Sets of 5 individuals were recorded in turn until a maximum of 5 trials were completed for each individual. Individuals that did not stridulate were removed after a 5 minute period for later retesting.

Ten or more males and females for each of seven species were recorded. After testing, specimens were killed by sodium cyanide and preserved in a 70% ethanol solution.

2.60 Recording data analysis

a. Oscillograms

Stridulatory signals for six species were used in oscillogram analysis. Two signals per individual, three individuals per sex, were processed for C. repanda, C. duodecimguttata, C. punctulata, C. tranquebarica, and C. sexguttata. Two signals per individual, one male and two females, were processed for C. longilabris.

Specimens were selected by numbering individuals by sex and species from 1 to ...n , then by drawing cards from a deck of number coded playing cards until the desired random complement of samples were chosen. Stridulatory signals recorded for single

individuals were chosen in a similar manner.

Oscillograms were made with the aid of a kymograph camera, Grass Instruments model C4N, in conjunction with a Textronix Type 564B oscilloscope. The kymograph was set to run Kodak Linagraph 1930 paper, at 250 mm/sec with audio tape running at 95.2 mm/sec. The oscilloscope was set for no sweep with an amplitude of 1 volt/division. The resulting oscillogram records displayed information at 32X slower than real-time, 3.125 msec/cm, with amplitude calibrated at 42.0 dB RMS for ± 1 mm from zero crossing.

All oscillograms were laid out flat on laboratory benches and temporal variables were measured to the nearest 0.5 mm with a high quality 30 cm plastic ruler. Each of 66 stridulations were wholly measured for a number of variables (Figure 3): duration of the major pulse train (MaPT) and the minor pulse train (MiPT) where MaPT had the more powerful pulse train in the typical two-stroke cycle, duration of the major pulse train period (MPP), absolute pulse train period (APP), overall signal length (OSL); maximum amplitude of the most powerful pulse in the major pulse train (MaAMP), and maximum amplitude of the most powerful pulse in the minor pulse train (MiAMP).

Other terms used to describe stridulatory oscillograms are: pulse train group (PTG), a single MaPT and MiPT; mode, two or more PTGs; postmajor silent interval (PmaSI), silent period which follows a MaPT and postminor silent interval (PmiSI), silent period which follows a MiPT (Fig. 3). These terms are variations

of those used by Morris and Walker (1976).

Since some signal elements (eg. MaPT, MiPT, ...) were variable and sometimes difficult to distinguish from extraneous sounds, the values of some measurements were based on subjective judgements. Care was taken to make measurements as consistent as possible.

Oscillograms were calibrated for sound pressure level (SPL) by : (1) rerecording a small segment of a recorded stridulation with a Uher 4000 Report IC tape recorder (R_1); (2) again recording R_1 by playback through the Uher speaker with the main experimental recording apparatus (Uher speaker 3 cm from the condenser microphone) (R_2); (3) playing the R_2 segments with alterations in R_1 by adjusting amplifier gain to the playback speaker, until the maximum amplitudes of the original and R_2 segments were matched (oscilloscope signals compared); and (4) equating the maximum amplitude on the original oscillogram segment to the matching maximum sound pressure level produced by R_1 (sound level meter set to impulse). Calibrations were limited by the frequency response of the Uher speaker (audio range).

b. Frequency spectrograms

Stridulatory signals for five species were examined using frequency spectrograms. Two signals per individual for three individuals per sex were processed for C. repanda, C. duodecimguttata, C. punctulata, C. tranquebarica, and C. sexguttata. The recorded signals used were the same as those used for corresponding species in the oscillogram analysis.

Frequency spectrograms were generated with the use of a fast Fourier transform (FFT) real-time computing spectrum analyzer (Nicolet Scientific Corporation 100n mini-analyzer). The FFT analyzer digitizes a finite portion of an analog signal, 1024 discrete points, in the time domain to a frequency spectrum, expressed in dB RMS, at frequency. Tape speed at analysis was approximately 23.8 mm/sec., which shifted observed frequencies to 32X less than their actual values. The analyzer was set for a 5 Hz to 2 kHz frequency range (X32=160 Hz to 64 kHz actual) with a corresponding 0.2 second time(data) window. The frequency spectrograms were unweighted and calibrated for 100 mV/dB.

Since stridulatory signals exhibited a large range in peak sound pressure level, analyzer sensitivity had to be set according to the most intense signal component. Sensitivities were set according to four discrete signal peaks: 200 mV, 600 mV, 2 V, and 6 V.

Data collection for frequency spectrograms was initiated via a trigger. The trigger was released when the first half of a positive pulse in a pulse train had sufficient energy to reach the triggering threshold. Triggering threshold was automatically set with analyzer sensitivity.

Hanning (Peterson, 1980) a tapered weighting system for time windows (form of a raised cosine arch in the time domain) was used for all FFT signal sampling. Hanning has the effect of reducing the relative importance of data on the outside borders

of the time window, thereby reducing interference from signal components other than those desired in the sample.

Segments of each stridulation underwent a frequency spectrogram averaging procedure. Segments were selected from several relatively uniform pulse train groups that were within a 40% portion of the signal's duration, either side of the signal's centre (80% total). Running averages were made of frequency spectrograms for up to 256 usable pulse trains. Usable pulse trains consisted of those which had enough capacity to release the sampler trigger.

Average stridulatory waveforms underwent a peak pick procedure. The Nicolet mini-analyzer used a 21 peak pick out of a possible 400 point spread. Adjacent peaks were picked only if there was a minimum of a 3-point interval between them. Peaks were listed by SPL (dB RMS) with frequency (Hz) by ascending order of frequency.

Estimation of fundamental frequency was determined by counting the number of pulses in a pulse train and dividing by the pulse train duration. Two values for each of a major and minor pulse train were averaged per signal. Pulse trains were selected from a uniform signal section and only one signal was selected for each species.

2.70 Statistical analysis of stridulations

a. Sample levels and tests

Statistical operations were performed at five specific levels of analysis. These were:

(1) LEVEL A-overall variable data combined.

(2) LEVEL B-signal (single stridulations) data analyzed

(3) LEVEL I-individual signal averages compared within sexes

(4) LEVEL II-sex signal averages compared within species

(5) LEVEL III-species signal averages compared

All analyses were based on 'signals', which used mean variable values for each individual stridulation.

The following tests were performed at LEVELS:

A. Descriptive statistics.

B. Kolmogorov-Smirnov one-sample test for uniform distributions using the observed variable ranges. Used on oscillogram data only.

I. Kruskal-Wallis H test (nonparametric oneway ANOVA).

II. Descriptive statistics. Oneway ANOVA supported by the Mann-Whitney U test. Homogeneity of variance test, Bartlett-Box F, used as diagnostic for oneway ANOVA.

III. Descriptive statistics. Oneway ANOVA with homogeneity of variance test (Bartlett-Box F) and Duncan's ranges test. Kruskal-Wallis H test.

All significance levels reported in the analysis of stridulations were based on two-tailed tests at 0.05 level of significance.

Statistical procedures were executed with the use of the Statistical Program for the Social Sciences (SPSS^{X}), Release 2.2, on a Dec Microvax-I (VMS/V4.5) computer.

Further elaboration of species relationships on combined variables was done by: counting numbers of species associations on Duncan's ranges test; ranking each species association by number of variables related, in case of ties, proximity or range of associated variable means and then rank to determine a percentage relationship between pairs (all possible associations between a single species and all other species adding to 100%. Oscillogram and frequency variables were treated separately.

b. Oscillogram statistical variables

All oscillogram variables, including MaPT, MiPT, MPP, APP, OSD, MaAMP, MiAMP (Fig. 3), and D were used in the statistical breakdown and comparison of stridulatory signals. Signal density (D) for each signal was determined by the calculation:

$$D=\frac{(MaPT_1+...+MaPT_n)+(MiPT_1+...+MiPT_n)}{OSL}$$

and is equivalent to the proportion of the signal occupied by sounds produced by specific stridulatory movements.

Estimates of overall maximum, minimum, and mean sound pressure levels were determined by combining mean MaAMP and MiAMP values.

c. Frequency spectrogram statistical variables

Four variables were used to quantify average frequency spectrograms (FS). These were: (1) median frequency (MEFRQ), 11th frequency of 21 peak-pick, (2) frequency range (RANGE), range of peak-pick values, (3) highest peak-pick frequency (HIFRQ) and (4) lowest peak-pick frequency (LOFRQ).

Statistical operations were performed on data produced by peak pick procedures on 60 frequency spectrogram averages (FS).

Variables derived directly from FS peak pick data were used for the statistical testing of frequency spectrograms. These were: peak pick median (MEFRQ), range (RANGE), maximum (HIFRQ), and minimum (LOFRQ).

2.80 Temperature analysis

Temperatures for all 327 observed stridulations were utilized in determining means and associated statistics for males and females of six species.

Temperatures for analyzed stridulations were correlated with all other average signal variables. Both Pearson's product-moment correlations and Spearman's rho correlations were used in temperature analysis. Both correlation tests used a two-tailed test with a significance level of 0.05.

3.00 RESULTS

3.10 Plectrum Morphology

3.11 Description

a. General morphology

General aspects of plectrum morphology are consistent throughout the variety of the studied cicindelid species. The plectrum consists of a field of slightly curved sharply pointed spines oriented toward the posterior of the elytron (Fig. 4a). Spines project from posterior edges (points) of hexagonal plates which compose the ventral aspect of the elytron (Fig. 4b). Spines decrease in size towards the anterior edge of the plectrum and eventually take the form of relatively small rounded projections which are found throughout the dorsal side of the elytron.

Plectrum fields (areas) occupy a triangular shaped region at the extreme apex of the elytron (Fig. 5a). The region is distinguished by: an anterior ridge, which separates the field from the remainder of the elytron, and a relatively flat profile (Fig. 5b). The fields have crenulated outlines which follow the boundaries of inside and outside margins and 'anterior ridge' Fig. 6a-n). Field boundaries are separated from outside margins of the elytron by undifferentiated regions of hexagonal plates. Pit-like depressions found throughout the ventral elytron are also found within the bounds of the plectrum field.

b. Species

Mean plectra areas (mm^2) range from 0.45 (SD 0.098) to 0.99 (SD 0.351) for C. punctulata and C. longilabris respectively with a difference of 54.5% (Tables 2 and 6). Mean elytra areas range (mm^2) from 14.75 (SD 1.545) for C. repanda to 23.25 (SD 3.682) for both C. longilabris and C. sexguttata, a difference of 36.6%. Mean relative plectrum areas (%) range from 2.22 (SD 0.144) for C. sexguttata to 4.27 (SD 0.523) for C. repanda and differ by 48.0%.

Spine variables exhibit smaller ranges than plectra/elytra area variables. Spine lengths (μm) range from 17.15 (SD 2.984) for C. sexguttata to 22.06 (SD 2.437) for C. repanda. Spine widths (μm) range from 5.87 (SD 0.890) to 8.60 (SD 0.544) for C. sexguttata and C. repanda respectively. Spine length to width ratios range from 2.39 (SD 0.382) for C. denikei to 3.18 (SD 0.419) for C. longilabris. Differences are 22.3, 31.7 and 24.8% for variables SL, SW and LWR respectively.

3.12 Coefficients of variation for plectra/elytra variables.. Level III

Coefficients of variation range from 3.2% for the mean plectrum area of C. duodecimguttata to 35.5% for the mean plectrum area of C. longilabris (Table 3; Figures 7a-b). The overall mean coefficient of variation for plectrum morphological variables is 13.2% (SD 6.11%, n=42).

Of the 42 coefficients, 4 exceed 20%: PA and PPE for both C. punctulata and C. longilabris (Table 3; Figures 7a-b). Variables

EA, SL and SW show most consistently low values; ranging from 4.7 to 17.8%, with respective means of 11.05, 11.9 and 11.4%. LWR exhibits consistently high coefficients; ranging from 12.1 to 19.0% with a mean value of 15.4%. PA and PPE show the least consistent coefficients; ranging from 3.3 to 35.5%, with means of 16.0 and 13.5% respectively.

3.13 Analyses

a. Sexes

Sample size per sex was insufficient for statistical analysis at the 0.05 level of probability.

Consideration of sex differences by variable means shows some consistency through species groups (Table 4). Sex differences on elytra areas (EA) shows the most consistent trend: females exhibit larger elytra areas than males for all species. This trend is exemplified by males having a larger portion of the elytron covered by the plectrum field (PPE), 6 out of 7 species, and males having larger plectrum fields (PA), 4 species. Examination of the length to width ratio (LWR) on spines find that males have larger values than females for 5 species.

Shapes of plectrum fields are very similar for both sexes of each species (Figs. 6a-n).

b. Species

Two statistical tests are used to determine the existence of species differences on the basis of plectra/elytra variables. These are: parametric oneway analysis of variance and Kruskal-

Wallis oneway analysis of variance (non-parametric). Both procedures test the hypotheses:

H_0:species means are not different on the tested variable.

H_1:at least one species mean is different on the tested variable.

Both statistical procedures reject H_0 for variables PA, EA, PPE and SW, and accept H_0 for LWR at 0.05 significance level (Tables 5a-b). Species differences are not significant for SL by parametric oneway ANOVA. The opposite result is true by Kruskal-Wallis oneway ANOVA (Chi-square=12.28, P >0.05).

Duncan's multiple ranges procedure is used to test associations between species on the basis of mean values for separate variables (Table 6). Homogeneous subsets denote subsets of groups, whose highest and lowest means do not significantly differ (P <0.05).

Plectrum/elytron variables can be separated into two groups according to the relative strength of separation between adjacent subsets. Variables PA, EA and PPE show at least one complete separation of subsets (no subset overlap at the point of separation). Cicindela longilabris and C. tranquebarica form a subset which exhibit larger plectra areas than the other species. Cicindela repanda, C. punctulata and C. duodecimguttata have relatively small elytra areas and form one of two subsets for the variable. Cicindela repanda, C. tranquebarica and C. longilabris occupy a subset which shows greater plectra coverage of elytra

than the remainder of species tested. Homogeneous subsets for variables SL, SW and LWR are less distinctly separated. Cicindela sexguttata and C.denikei form a subset which shows the smallest mean spine lengths; C. sexguttata associates only with C. denikei while C. denikei also associates with C. punctulata and C. duodecimguttata. The remainder of the species are not significantly different on this variable. Only two significant species differences exist for SW. Cicindela repanda, which has the greatest mean spine width separates from C. sexguttata and C. longilabris, which exhibit the smallest mean spine widths. The only significant difference for LWR is between C. longilabris, having the largest ratio, and C. denikei, having the smallest.

Some species occupy similar positions according to the magnitude of their means on a number of variables (Table 6). Cicindela longilabris and C. repanda occupy various positions of the largest mean values, C. longilabris for PA, EA and LWR and C. repanda for PPE, SL and SW. Cicindela tranquebarica exhibits second to largest values for PA, PPE, SL and LWR. Cicindela duodecimguttata occupies position of the fifth magnitude for PA, EA and LWR. Cicindela sexguttata shows the smallest values for PPE, SL and SW.

Species association by variable, ranges from a maximum of 6 to a minimum of 2 for 6 plectrum/elytron variables (Table 7; Figures 8a-g). Cicindela tranquebarica and C. longilabris, are not significantly different for all 6 variables and rank 21 (maximum 21) for relative strength of association. Cicindela

denikei and C. longilabris are the least associated species with 2 variables associated and a rank of 1.

Species relationships are also represented by the proportion related pairs take within a single species (Table 7; Figures 8a-g). For the strongest species association C. tranquebarica accounts for 40.4% of the total associations of C. longilabris whereas C. longilabris accounts for 32.3% of the total associations of C. tranquebarica. The weakest association shows that C. denikei accounts for 1.9% of the total associations of C. longilabris; C. longilabris accounts for 1.4% of the associations of C. denikei.

Cicindela duodecimguttata and C. punctulata are the least independent species, each having a cumulative rank percentage of 16.8%, based on the cumulative total of each species rank as a percentage of all ranked associations (Figure 9). Cicindela sexguttata is the most independent species having a cumulative rank percentage of 10.7%.

Shapes of plectrum fields are generally distinguishable among species. Cicindela sexguttata and C. denikei show the only distinct similarities (Figures 6g-j).

3.20 Oscillograms

3.21 Description

a. Level A..Overall

Most signals observed conform to a basic pattern. The signal begins with either one pulse train group (PTG) or a relatively short duration mode, between 2 and 7 PTGs. Stridulations consist

of 1 to 9 modes, the most typical having 4 (n=65). Signal termination tends to be abrupt relative to signal initiation as short duration mode endings are apparent in only few signal terminations.

Stridulations consistently begin with a MaPT and may end with either a MaPT or MiPT.

Amplitude (MaAMP and MiAMP) variation is apparent in most signals, more so in signals of shorter duration. Maximum amplitudes are usually smaller near the beginning of a signal than near the end. Intramodal amplitude variation is low with the exception of the first one or two modes.

Stridulations last an average of 0.65 seconds (SD 0.42 seconds) (Table 8). Maximum and minimum durations are 2.42 and 0.15 seconds respectively. Estimates of average signal sound pressure levels give 49.0 (SD 44.4) dB RMS at 3 cm (SPL in audio frequency range). Maximum and minimum SPLs are 59.3 and 37.3 dB RMS at 3 cm. MiPTs are approximately 15% longer in duration than MaPTs. Signal average MaAMPs are approximately 64% greater than MiAMPs. MPP is approximately 54% longer in duration than APP.

Intermodal MPPs and APPs are not used in statistical analysis and are omitted in the calculations performed on regular (intramodal) pulse periods. The overall average (n=185) intermodal MPP is 119.1 (SD 74.66) msec. Maximum and minimum values are 446.6 and 18.2 msec respectively. The average intermodal APP (n=168) is 50.7 (SD 35.96) msec. Maximum and minimum values are 171.6 and 1.9 msec respectively.

Intermodal MPPs and APPs are approximately 11.0 and 10.1 times longer than their intramodal counterparts.

Average signal density is 0.27 (SD 0.151). Signal maximum and minimum densities are 0.75 and 0.05 respectively.

Manipulation of above values give respective means of 8.3, 2.2 and 2.5 msec for variables PTG, PmaSI and PmiSI.

b. Level III..Species

Descriptive statistics for species are based on combined sex data. Sample sizes are 12 except for C. repanda, n=11 and C. longilabris, n=6.

Average MaPTs range from 2.3 msec for C. punctulata to 3.6 msec for C. tranquebarica, a 36.1% difference (Table 9a). MiPTs range from 2.8 to 4.1 msec, a difference of 31.7%, for C. repanda and C. tranquebarica. Mean MPPs from 8.8 msec for C. longilabris to 12.8 msec for C.sexguttata differ by 31.3%. APPs are close to half the corresponding range value for MPP, ranging from 3.9 msec for C. punctulata to 6.1 msec for C. sexguttata. The difference is 36.1%. OSL ranges from 443.4 to 1071.4 msec, a 58.6% difference between C. tranquebarica and C. duodecimguttata. D ranges from 0.15 for C. sexguttata to 0.39 for C. repanda and differs by 61.5%.

MaAMP ranges from 2.5 mm (50.0 dB RMS) for C. punctulata to 5.1 mm (56.3 dB RMS) for C. sexguttata, the latter value approximately twice the former (51.0% difference=6.3 dB RMS) (Table 9b). Maximum and minimum values for MiAMP are slightly less than half the corresponding MaAMP values. The range is 0.9

mm (40.7 dB RMS) to 2.0 mm (48.2 dB RMS) for C. repanda and C. sexguttata respectively. The difference is 55.0%.

3.22 Coefficients of variation

Coefficients of variation range from 12.8% for the mean MPP of C. duodecimguttata to 69.3% for the mean MaAMP of C. repanda (Table 10; Figures 10a-b). The overall mean coefficient of variation is 33.9% (SD 16.31%, n=48).

Variables can be divided into two groups on the basis of the relative magnitudes of coefficients: group A includes MaPT, MiPT, MPP and APP (Figure 10a) and group B includes OSL, D, MaAMP and MiAMP (Figure 10b).

Group A variable means range from 17.3 (SD 3.3)% for MPP to 22.8 (SD 5.1)% for APP (for variable coefficient means n=6). The mean APP of C. sexguttata exhibits the largest coefficient at 31.6% while the mean MPP of C. duodecimguttata exhibits the smallest at 12.8%.

Group B variable means range from 39.0 (SD 10.6)% for D to 52.3 (SD 9.7)% for MiAMP and are roughly double the range for Group A. The mean MaAMP of C. repanda shows the largest coefficient at 69.3% while the OSL of C. longilabris shows the minimum at 20.0%.

3.23 Statistical Analyses

a. Level B..Single stridulations

Oscillogram variables for each signal are tested for uniform distributions using the observed variable ranges. Kolmogorov-Smirnov goodness of fit test tests the hypotheses:

H_0: The signal variable does not follow a uniform distribution.

H_1: The signal variable follows a uniform distribution.

Variable uniformity by numbers of uniform signals, ranges from 41.5% for MaAMP to 56.9% for MPP , mean, approximately 52% (Table 11).

Counts of uniform variables give 14 out of 65 signals with all 6 variables uniform. The average number of MaPTs per signal is 103.9 (SD 54.19). There are 8 signals with no variables uniform and these have an average of 11.5 (SD 5.23) MaPTs. Stridulations with at least 3 uniform variables number 36.

b. Level I..Comparison of individuals

Individuals within sexes of five species (sample sizes for C. longilabris too small for oneway procedure) were compared using Kruskal-Wallis Oneway ANOVA. The test hypotheses are:

H_0: Variable means by individual within a single sex and species do not differ.

H_1: At least one variable mean by individual within a single sex and species differs.

All individuals within sexes and species show no significant difference at the 0.05 level of significance.

c. Level II..Comparison of sexes

Two tests are used to determine existing species differences. These are parametric oneway ANOVA and the Mann-Whitney U test. Both tests test the hypotheses:

H_0: Sexes are not different on the tested variable averages.

H_1: Sexes are different on the tested variable averages.

Significant differences are found for 5 out of 48 sex comparisons evaluated by oneway ANOVA (Table 12a). Significant differences are found for 3 out of 48 sex comparisons evaluated by the Mann-Whitney U Test (Table 12b).

Of the five sex differences reported by parametric tests, three are supported by the non-parametric Mann-Whitney U. These are: MiPT of C. repanda, OSL of C. tranquebarica and MaAMP of C. sexguttata. The MPP of C. punctulata and APP of C. sexguttata show sex differences by parametric oneway ANOVA only.

For each difference confirmed by both analysis of variance tests, female exceed male variable means (Tables 13a-b). Respective mean MiPT for male and female C. repanda are 2.3 (SD 0.52) and 3.2 (SD 0.27) msec, a difference of 28.1%. Mean sex OSL of C. tranquebarica differs by 47.9% with respective means of 303.6 (SD 82.19) and 583.1 (SD 248.25) msec for males and females. Sexes of C. sexguttata differ by 36.5% on MaAMP with respective means of 54.1 (SD 44.31) and 58.0 (SD 45.62) dB for males and females.

Diagnostic homogeneity of variance tests reveal 6 of 48 comparisons are too variable for the valid use of parametric ANOVA tests (Table 12a). Questions of validity are mitigated by positive support from corresponding associations by the Mann-Whitney U test.

d. Level III..Comparison of species

Two tests are used to determine species differences on the basis of oscillogram variables. These are parametric oneway ANOVA and Kruskal-Wallis oneway ANOVA. Both procedures test the hypotheses:

H_0: Species are not different on the tested variable mean.

H_1: At least one species is different on the tested variable mean.

In all cases for both types of test the null hypothesis is rejected in favour of the alternative: at least one species is significantly different on each oscillogram variable (Tables 14a-b).

Diagnostic tests reveal that sample variances for MaPT, APP, OSL and MiAMP are significantly heterogeneous. Variable OSL has the largest sample variance, Hartley's F max (maximum/minimum variance) equals 23.88.

Most species comparisons by variable split into two ranges (Tables 15a-b). The only exception to this is three subsets for MaPT. Cicindela tranquebarica has the longest duration MaPT and forms a single subset. Cicindela punctulata has the smallest duration MaPT and forms a range which separates only from C. sexguttata and C. tranquebarica.

C. tranquebarica has the longest duration MiPT and forms a single subset which separates from the remainder of the species.

C. sexguttata has the longest mean duration for both MPP and APP. It shares a range with C. trangebarica while the remainder of the species form the other range for both variables.

C. duodecimguttata exhibits the longest duration mean OSL and separates from all other species except C. repanda. Cicindela repanda shares both mean ranges for OSL.

C. repanda, C. duodecimguttata and C. punctulata form a range which shows the greatest mean signal densities. Cicindela punctulata shares both ranges for this variable.

C. sexguttata has the greatest mean SPL and forms its own subset for both MaAMP and MiAMP. The remaining species form a single range for these variables.

Some patterns are indicated by the position of species on some variable ranges. Cicindela sexguttata occupies the position of largest value for 4 of 8 variables: MPP, APP, MaAMP and MiAMP. This species also occupies second position for MaPT. Cicindela tranquebarica has the largest mean values for MaPT and MiPT as well as second to largest values for MPP and APP. Cicindela duodecimguttata occupies fourth position for variables MaPT, MPP, APP and MiAMP. Cicindela punctulata has the smallest values for MaPT, APP and MaAMP as well as second to smallest values for MPP, OSL and MiAMP. Cicindela repanda and C. longilabris show no distinct patterns by the position of magnitude of mean variable values.

Species association by Duncan's homogeneous subsets ranges from a maximum of 8 to a minimum of 2 out of 8 possible associated variables (Table 16; Figures 11a-f).

Three species pairs occupy similar ranges for all oscillogram variables and rank highest in rank of association (highest rank is 15). These pairs are, in descending order of rank: C. repanda and C. duodecimguttata, C. longilabris and C. punctulata, and C. repanda and C. punctulata.

Two species pairs share only 2 homogeneous subsets each and rank lowest in relative strength of relationship. These are, in ascending order of rank: C. duodecimguttata and C. sexguttata, and C. duodecimguttata and C. tranquebarica.

For the strongest species association, C. repanda accounts for 37.5% of the total species associations of C. duodecimguttata (Table 16). Cicindela duodecimguttata accounts for 32.6% of the total species associations of C. repanda. Cicindela duodecimguttata is also part of the weakest species relationship and accounts for 3.8% of all associations exhibited by C. sexguttata. Cicindela sexguttata accounts for 2.5% of the total species relationships of C. duodecimguttata.

Comparisons of percentage associations within species finds that C. longilabris has the most even distribution with 4 to 8 variables associated and ranks 7 to 14 (Fig 11f). Cicindela duodecimguttata has the most skewed distribution which ranges from the lowest to the highest rank of association (Fig 11b).

With the exception of C. longilabris other, within species, comparisons show relatively high associations with 2 or 3 other species and relatively low ranked associations with the remainder.

The proportion of total mean variable associations by species are shown in Figure 12. Cicindela longilabris and C. punctulata each represent 20.8% of total associations. Cicindela sexguttata accounts for 10.8% of total species associations, approximately half the highest percentage.

3.24 Qualitative observations

Representative middle portions of oscillograms are culled from relatively uniform segments of the signal within 25% of the signal length either side of the middle (Figures 13a-h).

Visual observations of oscillograms reveal a high degree of variation through every level of sample analysis. Notable examples of variations are:

1) While most pulse trains exhibit slow attacks (and a slow decays) some exhibit fast attacks. Female C. punctulata (Figure 13c), shows a fast attack and slow decay. This is evident over large segments of two signals analyzed for the individual.

2) Most major pulse trains in a pulse train group are composed of much higher amplitude pulses than in corresponding minor pulse trains. Male C. repanda (Figure 13g) female C. longilabris (Figure 13f), are examples of exceptions.

3) While most pulse trains are surrounded by silent intervals some such intervals are not distinguishable. Female C. repanda

(Figure 13a) shows pairs of pulse trains with no intervening post minor pulse train interval.

No group traits are distinguishable on the basis of visual examination of the most consistent portions of oscillograms.

Oscillograms were also compared at the point of initiation of stridulation (Figures 14a-f). A stridulation initiation of C. longilabris, shows transients (Dumortier, 1963b) which are evident for at least one signal of every recorded individual of the species (Figure 14a). Other groups show more typical signal initiations: small duration modes comprised of 1 or more pulse train groups with no transients.

3.30 Frequency spectrograms

3.31 Description

a. Level A..Overall

Frequency spectrogram averages (FS) consist of average frequency spectra of 4 to 16 pulse trains with analyzed signal running at 32 times slower than real time. Frequencies indicated on FS figures must be multiplied by 32 to give actual frequencies.

Most FS occupy an actual band width between 160 Hz and 40 kHz (Figures 15a-e). Frequencies below 160 Hz are not sampled by the analyzer. Frequencies extending beyond 40 kHz are affected by rapid fall-off of microphone sensitivity and cut-off frequency of the in-line filter. The greatest portion of signal energy occupies the observed bandwidth but some frequencies may extend beyond 40 kHz for some species.

Examination of all frequency spectrograms reveals a significant depression in power at about 27200 Hz. This is attributed to an aberration in equipment function.

Tiger beetle stridulations are not completely periodic (Figure 16). Many pulse trains, especially MaPTs, are composed of complex waves which undergo frequency modulation.

Fundamental frequencies are not easily discernible because of the non-periodic components of the signal; however, approximately 87% of all FS show dominant frequencies (highest peaks) between 640 and 12800 Hz. Fundamental frequencies estimated from oscillograms give an average frequency band of 11701-12423 Hz.

Mean peak-pick data range from low frequency (LOFRQ), 1859 (SD 750.4) Hz, to high frequency (HIFRQ), 19785 (SD 8209.4) Hz (Table 17). The mean range (RANGE) is 17926 (SD 7889.5) Hz. Median frequency (MEFRQ) is 10160 (SD 3778.1) Hz and ranges from 5280 to 20800 Hz. The lowest and highest peaks picked are 640 and 40160 Hz respectively.

b. Level III..Species

Descriptive statistics for species are based on combined sex data. Sample sizes for species are n=12 except for C. punctulata and C. repanda which each have sample sizes of n=11.

The positions of lowest and highest values for all analyzed frequency variables are occupied by C. tranquebarica and C. sexguttata respectively.

Average MEFRQs range from 7333 Hz to 12613 Hz, a difference of 41.9%. Mean peak-pick RANGE range from 12480 to 23460 Hz (Table 18). The maximum difference between the values is 47.2%. HIFRQ shows minimum and maximum values of 13693 and 26267 Hz. The difference between these values, 47.9%, is very close to the corresponding difference for RANGE. LOFRQ has a maximum mean range difference of 53.8%. Low and high means are 1213 and 2627 Hz.

Fundamental frequency bands estimated from selected oscillograms range from 9989-10822 Hz for C. tranquebarica to 13382-13993 Hz for C. sexguttata (Table 19). The frequency band for C. longilabris, 13231-13691 Hz, is slightly lower than that of C. sexguttata.

Rank order of species on the basis of estimated frequency bands agree with the order seen for MEFRQ, RANGE and HIFRQ.

Frequency estimates for successive pulse trains reveal some frequency differences between MaPT and MiPT in most cases.

3.32 Coefficients of variation

Coefficients of variation range from 17.5% for HIFRQ of C. tranquebarica to 49.2% for RANGE of C. repanda (Table 20; Figure 17). The overall mean coefficient is 32.6% (SD 8.11%, n=20).

Variable mean coefficients are approximately uniform ranging from 31.4 (SD 7.03)% for MEFRQ to 33.8 (SD 9.91)% for RANGE (for variable coefficient means n=5).

3.33 Statistical analyses

a. Level I..Comparison of individuals

Individuals within sexes of all species were compared using Kruskal-Wallis oneway ANOVA. The test hypotheses are:

H_0: Individuals within a single sex and species do not differ on the variable mean.

H_1: At least one individual differs by variable mean(s) within a single sex and species.

The null hypothesis is accepted in every case at a 95% probability. Individual specimens within single sexes and species show consistent WA on the basis of frequency variables.

b. Level II..Comparison of sexes

Both parametric oneway ANOVA and Mann-Whitney U tests are used to test for significant differences between sexes within species. The hypotheses tested are:

H_0: Males and females within a single species do not differ on the frequency variable mean.

H_1: Sexes within a single species are different on the frequency variable mean.

Both tests reject H_0 for the same 4 species and variables of 20 comparisons (Tables 21a-b).

Significant sex differences are seen for LOFRQ of C. repanda and MEFRQ, RANGE, and HIFRQ of C. sexguttata (Table 22).

Cicindela repanda males exceed females by 25.8% in LOFRQ means; and C. sexguttata females exceed males from 29.9 to 32.9% for means of MEFRQ, RANGE, and HIFRQ.

c. Level III..Comparison of species

Both parametric oneway ANOVA and Kruskal-Wallis oneway ANOVA tests are used to test for species differences on the basis of mean frequency variables. The tested hypotheses are:

H_0: Species do not differ on the frequency variable mean.

H_1: At least one species differs on the frequency variable mean.

Significant species differences are shown for all frequency variables (Tables 23a-b). There are no contradictions between parametric and nonparametric tests.

Diagnostics for the parametric test reveal that variables RANGE and HIFRQ are significantly heterogeneous.

Most homogeneous subsets for frequency variables show a high degree of overlapping (Table 24). The only discrete subset is occupied by C. sexguttata which has the highest mean frequency for LOFRQ. Cicindela tranquebarica has lowest mean frequency for LOFRQ and significantly differs from all other species except C. duodecimguttata. Cicindela duodecimguttata also shares a subset with C. punctulata and C. repanda.

Cicindela sexguttata has the highest mean HIFRQ and does not significantly differ from C. repanda. Cicindela repanda also shares a subset with C. duodecimguttata. Cicindela tranquebarica,

C. punctulata and C. duodecimguttata do not differ on mean HIFRQ at the 0.05 level.

C. sexguttata has the largest mean RANGE and is significantly different from C. punctulata and C. tranquebarica on the variable. Cicindela tranquebarica has the smallest mean RANGE and differs from C. repanda and C. sexguttata.

C. sexguttata has the highest mean MEFRQ and differs from C. punctulata and C. tranquebarica. Cicindela tranquebarica has the lowest mean MEFRQ and occupies a subset with C. punctulata.

Most species hold a consistent position by rank magnitude of value for each frequency variable. The only exception to this is between HIFRQ and LOFRQ where positions of C. punctulata and C. duodecimguttata are reversed.

Species associations on Duncan's ranges, range from 4 to 0 associated variables (Table 25; Figures 18a-e). Two species pairs show no significant difference on all 4 frequency variables. These are, in descending order of rank: C. duodecimguttata and C. punctulata; and C. duodecimguttata and C. repanda. Three species pairs are not associated on any frequency variable. These are: C. tranquebarica and C. sexguttata; C. repanda and C. sexguttata; and C. punctulata and C. sexguttata.

Percent association values (Table 25) show that, for the strongest association, C. punctulata accounts for 43.7% of the total associations of C. duodecimguttata and C. duodecimguttata accounts for 50.0 % of the observed relationships of C. punctulata. Cicindela duodecimguttata also displays the weakest

species association (two associated variables) and accounts for 16.7% of the relationships of C. sexguttata. Cicindela sexguttata assumes 6.2% of the total associations of C. duodecimguttata.

Comparison among species relationships shows a difference between the number of species associations. Both C. tranquebarica and C. sexguttata show relationships with only two other species. Cicindela sexguttata associates almost entirely (83.3%) with C. repanda. Cicindela repanda and C. punctulata are each related to three other species. Cicindela repanda shows no association with C. tranquebarica. Cicindela punctulata shows no association with C. sexguttata. Cicindela duodecimguttata exhibits both the two strongest and two weakest associations with all other species analyzed for frequencies.

Cicindela duodecimguttata, C. repanda and C. punctulata each account for approximately 25% of species associations by cumulative rank (Figure 19). Both C. sexguttata and C. tranquebarica each represent 10.7% of total associations.

3.40 Temperature

3.41 Description

Table 26 gives descriptive statistics for substrate temperatures recorded at stridulation for each sex of six species used in signal analyses. Minimum and maximum recorded temperatures are 24.0° and 51.0° C respectively. Mean temperatures range from 35.0 (SD 3.58)° C (n=31) for male C. duodecimguttata to 45.0 (SD 4.00)° C (n=31) for male C.

punctulata. Overall mean temperature at stridulation is 38.7 (SD 2.86)° C (n=12).

Sex differences are small, the largest being 2.9° C (6.4%) for C. punctulata.

Species mean temperatures are evenly spaced within the range. A maximum difference of 17.9% is observed for C. duodecimguttata, mean temperature approximately 35.8° C, and C. punctulata, mean temperature approximately 43.5° C.

3.42 Statistical analyses

Variables, MPP, OSL, MiAMP and LOFRQ are significantly correlated with temperature by at least one correlation test (Table 27). Of the four variables, only MPP and OSL are supported by both tests. The remaining two associations are not bivariate normal so their reported correlations cannot be considered to be significant.

Temperature is most strongly correlated with signal length. Correlation coefficients are r=-.37 and rho=-.26. Major pulse train period shows approximately half the strength of correlation as does OSL. Correlation coefficients for MPP are r=-.26 and rho=-.26.

Examination of scattergram plots reveal no linear or exponential temperature/signal variable relationships at the overall (Level A) and species (Level III) levels.

4.00 DISCUSSION

4.10 Plectrum morphology

a. Sexual distinctions

While statistical comparisons of cicindelid sexes using plectra/elytra variables were not performed, trends toward some sex differences were apparent. These results are suprising considering that investigations of stridulatory apparatus structure of most coleopteran and all carabid groups reveal no significant sex differences.

The trends are mostly a consequence of females being larger than males, an established sexual dimorphism among Cicindelidae (Freitag, pers. comm.). In the bioacoustical context, the only ecological value of such differences are those manifested in stridulations produced by each sex with regard to communication between sexes. Analysis of stridulations either help confirm or refute the claim to plectra/elytra sex differences. In any case, it is not known whether the exhibited morphological variations between sexes are sufficient to produce differences in stridulations.

b. Species distinctions

There are definite species differences on the basis of plectra/elytra characters. Characters dealing with the absolute and relative sizes of plectrum fields are the most powerful in distinguishing species. These characters have ranges where the largest are roughly twice the smallest mean species values and the average coefficient of variation is about 1/5 standard

deviation (13.5% actual). Shapes of plectrum fields are also useful species distinguishing features.

Plectra/elytra characters are more consistent for sympatric than closely taxonomically related species. Sympatric groups: C. tranquebarica with C. longilabris and C. repanda with C. duodecimguttata show among the strongest relationships. Cicindela tranquebarica and C. longilabris have the overall strongest relationship with no statistical differences on any variable, the only distinguishing character being the shape of their plectrum fields. Cicindela repanda and C. duodecimguttata are also closely related taxonomically (Wallis, 1961; Rivalier, 1954) and show somewhat less strength of association.

Cicindela denikei and C. sexguttata form allopatric populations and are considered to be either subspecies of a single species (Wallis, 1961) or sister species (Kaulbars, 1982). This, the strongest taxonomic relationship, ranks well behind relationships between some distantly related pairs of species.

Implications are that the habitat of a cicindelid species is the more important factor in determination of the morphology of plectrum structure. In this regard environment supersedes genetic relationship (phylogeny), and its importance might be evident in differences of sounds produced by each species.

Analysis of plectra/elytra variables as useful taxonomic characters are mixed. Plectra/elytra characters reflect some established phylogenetic relationships while providing means of separating relatively closely related species. Closely related

species C. repanda and C. duodecimguttata show no significant differences on 5 out of 6 variables and rank 18 out of 21 on overall species pair association. These species can be separated by PPE, shape of plectrum field (Figs. 6c and f), and strength of relationship to other species. Considering percentage association within species, C. repanda is most closely associated with C. duodecimguttata while C. duodecimguttata shows a slightly higher percentage association with C. punctulata and C. denikei than to C. repanda. Cicindela sexguttata and C. denikei are related on 4 variables, rank 15/21 on strength of pair relationships, and have very similar plectrum field shapes. They significantly differ on PPE, SW and varying relationships to other species. Within species, Cicindela sexguttata is most highly associated with C. denikei while C. denikei shows a stronger relationship to C. duodecimguttata (5/6 variables associated; rank 19/21) than to C. sexguttata. These data tend to support Kaulbars (1982) in maintaining C. denikei and C. sexguttata as separate but closely related species.

Relationships based on plectra variables, in some cases, confuse the established taxonomy of Cicindela. Cicindela punctulata shows ambiguous taxonomic distinction. Based on male genitalia this species is placed as a remotely related group among the species examined (Rivalier, 1954; Wallis, 1961). Cicindela punctulata is relatively highly related to all other species on the basis of plectra/elytra variables. For example, C. punctulata and C. duodecimguttata are only distinguished by

shapes of plectrum fields and some variation in relationships to other species. Species separations for C. punctulata are highly related to comparative sizes: it is most related to smaller species, C. duodecimguttata, C. repanda and least related to larger species C. longilabris and C. tranquebarica.

Considering the discriminatory power and relative ease of data collection, among these variables study of plectrum field size and shape appear to show the most promise in adding to the systematic knowledge of Cicindela.

Sizes of plectra areas correspond with sizes of elytra areas and adult bodies. Exceptions to this order are evident for C. repanda and C. sexguttata which have relatively large and small plectra areas respectively. These differences are reflected in the mean PPE, for which C. repanda has the highest and C. sexguttata has the lowest value. Such deviations from the norm might indicate the effects of selective pressures which are somehow a consequence of specific habitats. This might be more fully understood if a plectrum comparison is made among closely related taxa of these two species.

Variables derived from spines show less power in distinguishing species, the largest having a 31.7% difference between minimum and maximum values for spine width. Coefficients of variation for these variables are all under 20%.

Sizes of spines are not as closely related to the relative sizes of species. Spine lengths (SL) show little relationship and spine widths (SW) tend to show an inverse relationship to species

size, but length to width ratio (LWR) of spines shows an approximate direct relationship with species size. Larger species tend to have relatively thin spines in relation to length. One obvious exception to this order is shown by C. denikei which has the smallest LWR while having among the largest elytra area (EA).

Species differ as to the degree of overall development of the plectrum. Development is indicated by magnitude of plectrum components. Cicindela repanda exhibits the most developed plectrum with maximum values for PPE, SL, and SW. Cicindela sexguttata has the least developed plectrum with minimum values for PPE, SL, and SW.

Plectrum development shows strong relations to the loudness of stridulations. The maximal amplitude pulses of the major and minor pulse trains ranks species close to the order observed for elytra areas.

Relationships between the magnitude of plectra/elytra variables and loudness of stridulations may be explained in three ways:

1) Sizes of beetles, inferred from elytra areas, determines the loudness of pulse trains. Larger species employ larger vibrating structures for stridulation, more air is displaced, and louder sounds result.

2) Width of spines determines loudness of pulse trains. Narrow structure facilitates increased bending of spines which might impart greater elastic energy to the pars stridens upon rebound, thereby increasing the amplitude of vibration.

3) Varying combinations of both (1) and (2) are operating.

C. sexguttata and C. repanda show the greatest differences regarding overall plectrum development (by PPE, SL, SW) and show approximately inverse species rank position for maximal amplitude pulses on both the minor and major pulse trains. Cicindela sexguttata has the least developed plectrum and produces the loudest stridulations. This may be attributed to the relatively narrow spines and large overall body size. The reverse case may apply for C. repanda.

Although the extent of the effect of the plectrum field on stridulation is not known, the presence of any effect supports claims of the existence of an alary-elytral stridulatory organ. This contradicts the views of Hammond (1979) who discounts all such structures to working or vestigial wing-binding patches.

4.20 Sound structure

a. Oscillograms

i. Sexual distinctions

The demonstrated consistency of oscillogram parameters between individual specimens within sexes and species establishes a strong base for group comparisons at higher levels.

Sex differences with regard to timing and amplitude of stridulations have not been reported for any related family, such as Carabidae, studied to date (Bauer 1973, 1975; Claridge, 1974). This appears to be the case for Cicindela. Sexes are statistically similar on the basis of oscillogram variables used in this study. The small number of reported differences, 3 out of

48 comparisons, show no consistencies by variable or species, and so, must be attributed to chance.

Lack of sex differentiation on the basis of oscillogram variables implies that information of a sexually isolating nature is not transmitted by using the measured aspects of the signal. This leads to one of three conclusions:

1) Communication between sexes is coded in an aspect of the stridulation that was not measured, for example, mode duration.

2) Communication between sexes is coded by frequency (see Section 4.2b.)

3) Sound/vibration is not used in sexual communication.

ii. Species distinctions

Species differences appear on all eight oscillogram variables. The most powerful discriminatory variables are those concerned with the temporal structure of the signal, MaPT, MiPT, MPP, APP, OSL, and D. Maximum mean species differences regularly exceed, by 7-17%, the corresponding coefficients of variation.

Species associations with regard to the timing and loudness of the stridulation are based on one or more of these factors:

1) Species are directly or inversely related by comparative body sizes.

2) Species are genetically related.

3) Species are sympatric and are related by environment.

Size is the most important factor in determining species associations in that the greatest proportion of species show their strongest relationships to species of similar size.

Cicindela longilabris is distinguished by its anomalous inverse size relationship.

The relatively close phylogenetic relationship of C. repanda and C. duodecimguttata, related on all 8 variables with strongest rank of association, far exceeds the strength of the sympatric relationship of C. tranquebarica and C. longilabris, related on 4 variables, rank 8/15. Both pairs of species are also closely related by size.

Temporal and amplitude structures of tiger beetle stridulations may be exclusively related to body size. Studies on more sympatric and taxonomically closely related species must be done to establish the basis of observed sound differences.

The taxonomic value of the measured oscillogram variables is questionable though promising in part. The phylogenetically related species Cicindela repanda and C. duodecimguttata, cannot be separated, and the taxonomically remotest species, C. punctulata, shows relatively strong associations with every other species. Body size and plectrum field shape appear to be better taxonomic characters than any measured oscillogram variable.

Stridulations recorded for ground beetles take the form of variations on one of two signal types:

1) Type I signals are composed of internally non-differentiated modes. This type of mode corresponds to one complete stridulatory movement (eg. Cychrus).

2) Type II signals have modes composed of pulse trains or pulse train groups. Modes correspond to sequences of complete

stridulatory movements. Each complete stridulatory movement consists of an initial stroke to a point furthest from point of origin and a return stroke back to the original position. Sounds are produced for both initial and return strokes, a two-stroke cycle (pulse trains grouped within modes) or initial strokes only (pulse trains not grouped within modes).

Most carabids and cicindelids produce Type II signals with the exception of Type I signal produced by Cychrus caraboides (Claridge, 1974). The two stroke cycle of Cicindela consists of a power stroke (MaPT) and a return stroke (MiPT).

For the most part, analyzed temporal parameters of carabid stridulations may easily be distinguished from those of Cicindela species used in this study. Pulse train durations range from approximately 35 ms for Omophron labiatum (Masters, 1980) to 200 msec for Elaphrus cupreus (Bauer, 1973). Absolute pulse periods for O. labiatum have a modal value of approximately 200 ms. These values are at least ten times larger than corresponding measures for Cicindela. Other temporal measures show similar magnitude differences.

Cursory recordings of C. sedecimpunctata made by Spangler (1988) revealed modes of variable duration composed of 0.5-1.0 msec pulse trains. Pulse trains for this species are about 3-6 times smaller than average values of the current study group. Stridulations of C. sedecimpunctata needs further investigation before adequate comparisons between it and other cicindelids can be made.

Carabids and cicindelids exhibit similar sound pressure levels. Carabus irregularis produces sound pressure levels of 54-59 dB at 1.0 cm (Bauer, 1975). Elaphrus cupreus and E. riparius produce respective SPL of 54 and 60 dB at 0.5 cm (Bauer, 1973). These levels fall within the range produced by Cicindela, 37.3-59.3 dB at 3.0 cm (audio frequency range).

Carabidae and Cicindelidae exhibit similiar characteristics with regard to gross temporal structure of stridulations. Signals are a number of modes, heard by the human ear as distinct buzzes, or a single continuous mode, one buzz. Cychrus caraboides produce 5 to 10, 70 msec modes, per signal (Claridge, 1974; Forsythe, 1979). Amara familiaris, Agonum marginatum, and Stenolophus mixtus produce continuous signals lasting about 3 seconds (Forsythe, 1979). Cicindelidae produce continuous signals as well as signals consisting of 2-9 modes. Cicindelid stridulations last an average of 0.65 seconds.

Cicindela sounds analyzed in this study closely resemble stress sounds analyzed by Webb et al. (1980) for Conotrachelus nenuphar (Coleoptera: Curculionidae). Sounds for both groups are distinguished by:

1) Two stroke cycles.

2) Pulse trains composed of individual pulses, where each pulse is elicited by contact of the plectrum over one tooth of the file.

3) 'Highly patterned' structure as a result of the uniformity of basic signal parameters.

Signal uniformity for Cicindela is confirmed by significant statistical uniformity for moderate to long duration stridulations and relatively low coefficients of variation for finer signal components, MaPT, MiPT, MPP, and APP. Mean coefficients for these variables are below 24.4 % and compare with the typically regular stridulation parameters of crickets, less than 20% (Masters, 1980). Masters (1980) performed the only analysis of uniformity for Carabidae: MaPT and MiPT for O. labiatum between 29% and 215%.

Regularity of stridulations are important for two reasons: (1) consistency of signals among individual insects may have aposematic value (Webb et al., 1980; Lane and Rothschild, 1965); and (2) uniformity reinforces redundancy in signal transmission which serves to overcome environmental constraints of sound transmission between emitter and receiver (Moles, 1963).

The unique initiations for 4 out of 6 stridulations of C. longilabris are characterized by the emission of transients. Transients were defined by Busnel (1963) as a "...quick rise from intensity zero to maximum intensity or reversed." Busnel (1963) determined that transients were effective in eliciting a phonoresponse from the grasshopper, Chorthippus brunneus. The existence of transients in stridulations of C. longilabris implies that the species may have achieved a higher level of signal communicatory function than the other studied species.

Specific habitats may also play a role in determining signal structure. Cicindela sexguttata emits signals of statistically

higher sound pressure levels than other analyzed species, approximately 34% greater than closest ranked species. Cicindela sexguttata responds to its highly vegetated habitat by producing a stridulation that is able to overcome the attenuating effects of vegetation and maintain an effective signal range. Other species, which occupy more open areas, have less need for louder signals, but they need longer signals. Cicindela duodecimguttata and C. repanda respond to their relatively open habitat by producing longer, redundant signals, which are more able to convey information in places open to sound interference by wind.

b. Frequency spectrograms

i. Sexual distinctions

Frequency variations between sexes and species are firmly based on the demonstrated consistency of frequency measurements between individuals of the same sex and species.

Since all four frequency variables used in this study are highly redundant, as shown by relative similarity of species rank position and character variability, valid significant differences between groups are more likely to occur on more than one variable.

Sex frequency differences have not been demonstrated for closely related groups (Carabidae) and communication through variations in frequency components has not been shown for Coleoptera.

Sex differences on the basis of frequency has been statistically proven for 2 out of 5 species studied. Only the

three variable differences observed for C. sexguttata can be considered valid. If tiger beetles are able to perceive some aspect of frequency structure, sex differences observed for C. sexguttata may be a specific adaptation to a highly vegetated environment where other senses, such as vision and chemoreception, are less efficient in receiving signals emitted by members of the opposite sex.

ii. Species distinctions

Although frequency variables are highly redundant, various combinations of species differences are observed for each variable. The variables have roughly equivalent discriminatory powers with maximum species differences exceeding corresponding coefficients of variation by 10-21%.

Unlike plectra/elytra morphology and oscillogram structure, sound frequency does not appear to be related to body size. Frequency, then, may be more a function of specific stridulatory behaviour (tooth impact rate) or morphology of the pars stridens (tooth spacing). Because behaviour is considered a superior taxonomic character (Mayr, 1969), frequency variables might be powerful tools for determining taxonomic relationships.

In this case, the only close taxonomic and sympatric species relationship, between C. repanda and C. duodecimguttata, is well represented taxonomically as the second highest ranking association. However, like species associations on plectra/elytra and oscillogram variables, the taxonomically remotest species, C. punctulata shows a high degree of association to other species,

which includes the strongest overall association (with C. duodecimguttata). Cicindela punctulata and C. duodecimguttata can only be separated by specific relationships, by frequency variables, to other species.

Further work on taxonomically and sympatrically related cicindelid species must be done to determine the taxonomic usefulness of stridulation frequency variables.

Cicindelid frequency spectrograms are manifestations of a moderately non-periodic, low Q (Michelsen and Nocke, 1974), non-resonant sound emitting system. Carrier (fundamental) frequency is determined by varying tooth strike rates; broad frequency range is determined by a non-resonant system (Michelsen and Nocke, 1974).

Frequency spectrums of Cicindela show little difference among its own species and related Carabidae. Survey of the literature find bandwidths of significant energy falling within 4 Hz and 70 kHz. Elaphrus spp. emit signals of broad bandwidth up to 55 kHz (Bauer, 1973). Cicindela sedecimpunctata emits sound energy up to approximately 50 kHz (Spangler, 1988). The absolute spectral bandwidth for the current group is not known. Considering related species it is assumed that the low end of the spectrum reaches at least 20 Hz and it is highly probable most tiger beetle signals do not extend beyond 50 kHz since many observed spectrums taper off well before 40 kHz.

The fundamental frequency of observed stridulations is higher than most reported values for Coleoptera. Forsythe (1979)

recorded a value of 1600 Hz for A. familiaris (Carabidae). Webb et al. (1980) found that C. nenuphar (Curculionidae) used a 500-1500 Hz carrier frequency. Spangler (1988) recorded a fundamental frequency of 3.1 kHz for C. sedecimpunctata. In contrast, the study group stridulates at an average fundamental frequency of about 12 kHz. The observed difference of magnitude, in this regard, is generally consistent with similar differences observed for oscillogram temporal measurements. This is due to one of three possibilities:

1) Teeth of pars stridens are closer together which increases tooth impact rate.

2) Cicindela species recorded in this study perform relatively rapid, high velocity stridulatory movements.

3) Combination of 1 and 2.

Variations in velocity of stridulatory movements and/or tooth spacing on the pars stridens are responsible for observed frequency modulation. Acceleration and deceleration at the beginning and end of a stroke accounts for most of the frequency modulation in a pulse train. Frequency modulation between major and minor pulse trains are manifestations of relative variations in stridulatory velocity.

4.30 Effects of temperature

Stridulatory rates of many insects show a direct relationship to temperature. Such correlations, when they occur, generally best fit a linear relationship (Walker, 1975).

Stridulatory rates for tested Cicindela species act independently of temperature over the ranges analyzed (24-51 C). Correlation tests and scattergrams reveal very little or no linear or exponential relationship between temperature and any measured stridulation variable. The only notable trend is that r and rho values for each correlation are negative. This means that temperature exerts some effect on stridulatory rates, but far less than the effects documented for most other arthropod species.

The observed species differences on average stridulation temperature suggests similarly ranked stridulatory activity temperature thresholds. This might be an adaptation to specific environment, for example, C. punctulata, the species occupying the most southern and warmest range (Wallis, 1961), initiates stridulations at the highest average recorded temperature. This indicates that species acoustic behaviour might be linked to certain optimal temperatures.

4.40 Behaviour

In contrast to most related species, Cicindela species do not stridulate in response to mechanical stimulation. Stridulation is stimulated in the laboratory by subjecting specimens to sudden heated, lighted or crowded conditions. Amara familiaris is the only other species reported to respond exclusively to similar conditions (Forsythe, 1979). This suggests that tiger beetles do not use sounds to deter the attack of

predators. Deterrent stridulation is generally thought to occur when an insect is molested by a predator.

Spontaneous stridulation is observed for tested Cicindela species in their natural habitats. Stridulation occurs most frequently just after a beetle has landed after flight. Stridulation also occurs during times of feeding, walking, and resting. In one case, a male was observed to stridulate in the mating position (Schincariol pers. comm.). Similar behaviour has not been reported for any related species.

In light of the observed stridulatory behaviour and relative physical sophistication of tiger beetle signals, I suggest that Cicindela spp. are able to use stridulation in intraspecific communicative contexts.

Stridulatory behaviourial purpose in the context of this study is limited to two possibilities:

1) Agonistic behaviour: Stridulation aids tiger beetles in establishing territory by announcing their presence in a specific area. Such a signal is often given when beetles arrive at a new place after flight landings. Evidence of territoriality for these species is observed when beetles attack each other when in a confined, crowded area.

2) Aggregation: Tiger beetles increase the frequency of sexual contacts by calling conspecifics beyond the range of vision. This is especially important for species such as C. sexguttata which live in vegetated environments where visual perception is relatively limited.

Evidence brought forth in this study does not deny the possibility of sexual communication by stridulation. Recordings of spontaneous stridulations are needed to establish such a possibility.

5.00 CONCLUSION

5.10 General

Cicindelid plectra consist of fields of posteriorly oriented spines located ventrally on the elytral apices. Some plectra characters show trends towards sexual dimorphism, although such has not been statistically confirmed. Plectra/elytra characters, especially those dealing with sizes and shapes of plectrum fields, may be useful as taxonomic characters.

Sounds produced by tiger beetles are consistent among individuals of a species, but are not consistent among species. Species stridulatory differences are based on signal parameters which are in turn based on variation in relative adult body size, plectrum structure, taxonomy, habitat, and behaviour.

Stridulation based parameters are successful in confirming established taxonomic relationships, but, at the same time, show strong relationships that do not exist on the basis of other, more traditional, taxonomic characters. This, together with the considerable labour involved in collecting and analyzing sound data, denies the taxonomic usefulness of stridulatory sound characters.

The irregular ,'noise like', stridulations produced by carabid beetles have generally been assigned a disturbance function, of possible use in the deterrence of predators. In contrast, the more sophisticated, uniform signals produced by Cicindela spp., in addition to the presence of airborne sound detectors for some species, makes them well equipped to

communicate intraspecifically. Field observations support the hypothesis that stridulations are used in agonistic and/or calling behaviour.

Tiger beetle stridulations seem to operate independently of physiological temperature dependent controls, and so, appear to be under control of a behaviourial feedback mechanism.

5.20 Problems and future studies

Some interpretations made in this study are inconclusive. This is due to two basic problems. These are:

1) Numbers of taxonomically and sympatrically related species are insufficient to draw firm conclusions as to the role of genetics and environment in cicindelid sound production.

2) Stridulations elicited under laboratory conditions are very far removed from those which naturally stimulate stridulation. Since these novel conditions might stimulate novel reactions, stridulations analyzed in this investigation, can not be directly attributed to respective species as regards intraspecific communication.

In order to eradicate these problems, future studies should incorporate a greater range of taxonomically and sympatrically related species, and all efforts should be made to record spontaneous stridulations under more natural conditions.

Considering the low signal intensities produced, and the difficulty in approaching cicindelids, it is impracticable to attempt recording in the wild. Recordings of spontaneous stridulations in the laboratory may be attempted by placing a

number of conspecific beetles in a relatively large, more naturally lighted area, within an acoustically insulated room. Individual test sample numbers should coincide with the mean densities of specimens in the wild. Stridulations may be transduced by placing a sensitive omnidirectional microphone over the test area. The tested beetles should be isolated from the researcher so as to further simulate natural conditions.

Further investigations into acoustically related morphology, physiology, and behaviour may be done using tests such as:

1) Quantitative morphological analysis of the pars stridens with regard to species and sex differences.

2) Investigations of stridulatory movements using high-speed photography in order to substantiate claims to the existence of functional alary-elytral stridulatory mechanisms.

3) Experiments in the field or laboratory where beetles are subjected to synthesized or recorded stridulations in order to determine the existence of phonoresponsive behaviour.

4) Recording specimen contacts using various combinations of sex, species, stridulating, and stridulating disabled specimens (Mampe and Neunzig, 1966).

5) Look for presence of sound receivers on stridulating species, other than those reported by Spangler (1988), and determine if such structures are responsive to stridulatory sounds.

Further investigations into the bioacoustics of Cicindelidae might provide more information on acoustic signalling systems beyond those which are attributed a, most primitive, disturbance

function.

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Table 1. Cicindelid and carabid genera known to possess stridulatory organs.

a) Cicindelidae	(1) Cicindela (Freitag and Lee, 1972)
	(2) Chiloxia (Horn, 1908, 1910, 1915)
	(3) Mantica (Horn, 1908, 1910, 1915)
	(4) Mantichora (Horn, 1908, 1910, 1915)
	(5) Oxychila (Gahan, 1900; Arrow, 1942)
b) Carabidae	(1) Agonum (Forsythe, 1979)
	(2) Amara (Forsythe, 1979)
	(3) Blethisa (Dudich, 1921; Lindroth, 1954; Claridge, 1974)
	(4) Cychrus (Marshall, 1832; Joutel, 1904; Dudich, 1921; Claridge, 1974)
	(5) Diachila (Lindroth, 1954)
	(6) Elaphrus (Gahan, 1900; Dudich, 1921; Lindroth, 1954; Bauer, 1973; Larochelle, 1976; Forsythe, 1978)
	(7) Graphipterus (Dudich, 1921)
	(8) Harpalus (Horn, 1886; Dudich, 1921,
	(9) Loricera (Forsythe, 1979)
	(10) Omophron (Chittenden, 1889; Benschoter and Cook, 1956; Larochelle, 1976)
	(11) Platyderus (Dudich, 1921)
	(12) Scaphinotus (Dudich, 1921; Larochelle, 1976)
	(13) Siagona (Dudich, 1921)
	(14) Saphaenoderus (Dudich, 1921; Larochelle, 1976)
	(15) Stenolopus (Forsythe, 1979)

Table 2. Species means and species inclusive descriptive statistics for plectrum/elytron variables.

SPECIES	VARIABLE MEANS					
	PA (mm^2)	EA (mm^2)	PPE (%)	SL (μm)	SW (μm)	LWR (SL/SW)
DENI.	0.71	22.81	3.12	17.69	7.50	2.39
PUNC.	0.45	15.76	2.87	21.21	7.55	2.85
SEXG.	0.51	23.25	2.22	17.15	5.87	2.94
TRAN.	0.97	23.20	4.23	21.83	7.28	3.06
REPA.	0.63	14.75	4.27	22.06	8.60	2.57
LONG.	0.99	23.25	4.22	21.68	6.81	3.18
DUOD.	0.59	17.91	3.32	21.48	7.54	2.84
mean	0.69	20.13	3.46	20.44	7.31	2.83
SD	0.197	3.567	0.741	1.933	0.769	0.253
max.	0.99	23.25	4.27	22.06	8.60	3.18
min.	0.45	14.75	2.22	17.15	5.87	2.39
range	0.54	8.50	2.05	4.91	2.73	0.79

n=4.

Table 3. Coefficients of variation for plectrum/elytron variables.

SPECIES	VARIABLES (SD/mean x 100%)					
	PA	EA	PPE	SL	SW	LWR
DENI.	13.5	5.0	14.9	8.3	15.9	16.0
PUNC.	21.9	8.3	20.8	12.5	12.1	19.0
SEXG.	10.9	15.8	6.5	17.4	15.2	18.9
TRAN.	12.6	16.9	8.5	6.4	17.8	16.4
REPA.	14.6	10.5	12.3	11.0	6.4	12.1
LONG.	35.5	15.8	25.6	12.8	7.3	13.2
DUOD.	3.2	4.9	6.3	14.6	4.7	12.4
mean	16.0	11.0	13.5	11.9	11.4	15.4
SD	9.43	4.82	6.84	3.43	4.82	2.71
max.	35.5	16.9	25.6	17.4	17.8	19.0
min.	3.2	4.9	6.3	6.4	4.7	12.1
range	32.2	12.0	19.2	11.0	13.1	7.0

n=4.

Table 4. Sex means and standard deviations for plectrum/elytron variables.

SPECIES	SEX	VARIABLES						
		PA_2 (mm^2)	EA_2 (mm^2)	PPE (%)	SL (μm)	SW (μm)	LWR (SL/SW)	
REPA.	MALE	0.64	13.84	4.60	21.58	9.02	2.39	mean
		0.071	0.262	0.445	2.157	0.163	0.282	SD
	FEMALE	0.62	15.66	3.93	22.54	8.17	2.75	
		0.141	1.945	0.417	3.500	0.417	0.288	
DUOD.	MALE	0.60	17.51	3.43	18.92	7.29	2.60	
		0.028	0.552	0.269	1.775	0.361	0.372	
	FEMALE	0.59	18.32	3.22	24.03	7.79	3.08	
		0.014	1.167	0.127	0.488	0.014	0.057	
PUNC.	MALE	0.50	15.19	3.29	20.80	6.85	3.05	
		0.134	1.351	0.580	2.333	0.424	0.530	
	FEMALE	0.40	16.33	2.46	21.61	8.25	2.64	
		0.000	1.414	0.212	3.854	0.601	0.659	
TRAN.	MALE	0.88	21.37	4.18	22.34	7.01	3.25	
		0.035	3.486	0.516	2.086	1.810	0.544	
	FEMALE	1.06	25.03	4.26	21.32	7.55	2.86	
		0.113	4.568	0.332	0.742	1.209	0.557	
SEXG.	MALE	0.47	20.13	2.33	18.68	6.16	3.08	
		0.028	0.410	0.092	1.612	1.407	0.442	
	FEMALE	0.55	26.38	2.10	15.63	5.58	2.81	
		0.035	1.202	0.035	3.854	0.240	0.812	
LONG.	MALE	0.78	20.13	3.88	23.35	7.17	3.25	
		0.304	0.410	1.442	1.252	0.134	0.114	
	FEMALE	1.21	26.38	4.56	20.00	6.45	3.12	
		0.311	1.202	0.969	3.189	0.438	0.707	
DENI.	MALE	0.78	22.36	3.51	17.95	6.94	2.61	
		0.049	1.761	0.057	2.001	1.513	0.282	
	FEMALE	0.63	23.26	2.73	17.43	8.07	2.18	
		0.049	0.226	0.184	1.471	0.849	0.412	

n=2.

Table 5a. F ratios and significance levels for plectrum/elytron variables: species comparisons.

VARIABLES	PA	EA	PPE	SL	SW	LWR
F RATIO	7.60	8.52	8.13	2.81	3.56	1.50
SIG. (P)	<0.05	<0.05	<0.05	<0.05	<0.05	>0.05

N=28/ n=4.
d.f.=6,21.

Table 5b. Chi-square values and significance levels (Kruskal-Wallis oneway ANOVA) for plectrum/elytron variables: species comparisons.

VARIABLES	PA	EA	PPE	SL	SW	LWR
CHI-SQUARE	18.60	20.99	19.73	12.28	13.16	7.97
SIG. (P)	<0.05	<0.05	<0.05	>0.05	<0.05	>0.05

N=28/ n=4.
d.f.=6.

Table 6. Homogeneous species subsets for plectrum/elytron variables.

PLECTRA AREAS (mm^2)

PUNC.	SEXG.	DUOD.	REPA.	DENE.	TRAN.	LONG.	
0.45	0.51	0.59	0.63	0.71	0.97	0.99	mean
0.098	0.055	0.019	0.092	0.095	0.122	0.351	SD

ELYTRA AREAS (mm^2)

REPA.	PUNC.	DUOD.	DENE.	TRAN.	SEXG.	LONG.
14.75	15.76	17.91	22.81	23.20	23.25	23.25
1.545	1.305	0.881	1.147	3.931	3.682	3.682

PLECTRA PERCENTAGE AREAS OF ELYTRA (%)

SEXG.	PUNC.	DENE.	DUOD.	LONG.	TRAN.	REPA.
2.22	2.87	3.12	3.32	4.22	4.23	4.27
0.144	0.597	0.463	0.210	1.078	0.357	0.523

SPINE LENGTHS (μm)

SEXG.	DENE.	PUNC.	DUOD.	LONG.	TRAN.	REPA.
17.15	17.69	21.21	21.48	21.68	21.83	22.06
2.984	1.465	2.643	3.135	2.766	1.407	2.437

SPINE WIDTHS (μm)

SEXG.	LONG.	TRAN.	DENE.	DUOD.	PUNC.	REPA.
5.87	6.81	7.28	7.50	7.54	7.55	8.60
0.890	0.495	1.295	1.195	0.353	0.915	0.544

SPINE LENGTH TO WIDTH RATIO

DENE.	REPA.	DUOD.	PUNC.	SEXG.	TRAN.	LONG.
2.39	2.57	2.84	2.85	2.94	3.06	3.18
0.382	0.310	0.353	0.542	0.544	0.502	0.419

n=4.

═══ homogeneous subsets (Duncan's ranges test, P <0.05).

Table 7. Species pair associations for plectrum/elytron variables.

REPA. WITH SPP.	NUMBER OF ASSOC. (x /6)	RANK OF ASSOC. (y /21)	PERCENT ASSOC. (%)
DUOD.	5	18	25.7
PUNC.	5	17	24.3
TRAN.	4	16	22.9
DENI.	3	11	15.7
LONG.	3	6	8.6
SEXG.	2	2	2.9

DUOD. WITH SPP.	NUMBER OF ASSOC. (x /6)	RANK OF ASSOC. (y /21)	PERCENT ASSOC. (%)
PUNC	6	20	26.0
DENI.	5	19	24.7
REPA.	5	18	23.4
TRAN.	3	10	13.0
LONG.	3	7	9.1
SEXG.	2	3	3.9

PUNC. WITH SPP.	NUMBER OF ASSOC. (x /6)	RANK OF ASSOC. (y /21)	PERCENT ASSOC. (%)
DUOD.	6	20	26.0
REPA.	5	17	22.1
DENI.	4	14	18.2
SEXG.	3	13	16.9
TRAN.	3	8	10.4
LONG.	3	5	6.5

TRAN. WITH SPP.	NUMBER OF ASSOC. (x /6)	RANK OF ASSOC. (y /21)	PERCENT ASSOC. (%)
LONG.	6	21	32.3
REPA.	4	16	24.6
DENI.	3	9	13.8
PUNC.	3	8	12.3
DUOD.	3	7	10.8
SEXG.	2	4	6.2

SEXG. WITH SPP.	NUMBER OF ASSOC. (x /6)	RANK OF ASSOC. (y /21)	PERCENT ASSOC. (%)
DENI.	4	15	30.6
PUNC.	3	13	26.5
LONG.	3	12	24.5
TRAN.	2	4	8.2
DUOD.	2	3	6.1
REPA.	2	2	4.1

LONG. WITH SPP.	NUMBER OF ASSOC. (x /6)	RANK OF ASSOC. (y /21)	PERCENT ASSOC. (%)
TRAN.	6	21	40.4
SEXG.	3	12	23.1
DUOD.	3	7	13.5
REPA.	3	6	11.5
PUNC.	3	5	9.6
DENI.	2	1	1.9

DENI. WITH SPP.	NUMBER OF ASSOC. (x /6)	RANK OF ASSOC. (y /21)	PERCENT ASSOC. (%)
DUOD.	5	19	27.5
SEXG.	4	15	21.7
PUNC.	4	14	20.3
REPA.	3	11	15.9
TRAN.	3	9	13.0
LONG.	2	1	1.4

Table 8. Species inclusive descriptive statistics for oscillogram variables.

	VARIABLES									
	MaPT (msec.)	MiPT (msec.)	MPP (msec.)	APP (msec.)	OSL (msec.)	D	MaAMP (mm)	MaAMP (dB)	MiAMP (mm)	MiAMP (dB)
mean	2.8	3.3	10.8	5.0	653.3	0.27	3.3	52.4	1.2	43.6
SD	0.71	0.91	2.45	1.51	423.36	0.151	1.85	47.38	0.79	39.99
SE	0.09	0.11	0.30	0.19	52.51	0.019	0.23	29.27	0.10	22.04
max.	5.5	5.4	16.7	10.0	2422.8	0.75	8.9	61.0	5.8	57.2
min.	1.7	1.7	6.4	2.4	152.8	0.05	1.0	41.9	0.2	28.5
range	3.7	3.6	10.3	7.6	2270.0	0.70	8.0	60.1	5.6	57.0

N=65.
dB re. 0.0002 dynes/cm^2

Table 9a. Species descriptive statistics for temporal oscillogram variables.

SPECIES		VARIABLES					
		MaPT (msec.)	MiPT (msec.)	MPP (msec.)	APP (msec.)	OSL (msec.)	D
REPA.	mean	2.5	2.8	10.4	4.6	786.4	0.39
	SD	0.50	0.59	1.65	1.10	332.93	0.214
	SE	0.15	0.18	0.50	0.33	100.38	0.064
	max.	3.3	3.6	13.3	6.4	1367.9	0.75
	min.	1.7	1.9	8.4	2.4	379.8	0.11
	range	1.6	1.7	4.9	4.0	988.1	0.64
DUOD.	mean	2.7	3.2	10.1	4.5	1071.4	0.36
	SD	0.58	0.85	1.29	0.79	678.97	0.167
	SE	0.17	0.24	0.37	0.23	196.00	0.048
	max.	4.2	4.9	11.7	5.9	2422.8	0.69
	min.	2.0	2.2	8.0	3.4	230.7	0.09
	range	2.2	2.8	3.6	2.5	2192.2	0.60
PUNC.	mean	2.3	3.2	8.9	3.9	451.2	0.28
	SD	0.35	0.98	2.04	1.02	224.80	0.126
	SE	0.10	0.28	0.59	0.30	64.89	0.036
	max.	3.2	5.4	12.8	5.5	952.2	0.63
	min.	1.9	1.7	6.4	2.8	152.8	0.15
	range	1.4	3.6	6.3	2.8	799.4	0.48

Table 9a. continued.

SPECIES		VARIABLES					
		MaPT (msec.)	MiPT (msec.)	MPP (msec.)	APP (msec.)	OSL (msec.)	D
TRAN.	mean	3.6	4.1	12.7	6.1	443.4	0.21
	SD	0.94	1.03	2.06	1.28	228.90	0.051
	SE	0.27	0.30	0.59	0.37	66.08	0.015
	max.	5.5	5.4	15.6	7.9	1015.6	0.29
	min.	2.0	1.8	9.5	3.5	171.8	0.14
	range	3.4	3.6	6.1	4.3	843.7	0.15
SEXG.	mean	2.9	3.1	12.8	6.1	505.0	0.15
	SD	0.50	0.67	2.58	1.93	208.24	0.050
	SE	0.14	0.19	0.74	0.56	60.11	0.014
	max.	3.8	4.2	16.7	10.0	1064.7	0.25
	min.	2.1	2.2	8.9	3.4	291.4	0.05
	range	1.7	2.0	7.8	6.6	773.4	0.20
LONG.	mean	2.9	3.3	8.8	4.1	693.7	0.23
	SD	0.43	0.71	1.42	0.69	138.94	0.069
	SE	0.17	0.29	0.58	0.28	56.72	0.028
	max.	3.6	4.4	10.5	5.1	825.9	0.36
	min.	2.5	2.7	6.9	3.3	476.6	0.18
	range	1.1	1.7	3.6	1.8	349.3	0.18

n=12 except for REPA.: n=11 and LONG.: n=6.

Table 9b. Species descriptive statistics for SPL related oscillogram variables.

SPECIES		VARIABLES			
		MaAMP		MiAMP	
		(mm)	(dB rms)	(mm)	(dB rms)
REPA.	mean	2.7	50.6	0.9	40.7
	SD	1.87	47.45	0.53	36.46
	SE	0.56	37.03	0.16	26.01
	max.	7.1	59.0	2.1	48.4
	min.	1.3	44.2	0.2	28.1
	range	5.8	57.3	1.9	47.4
DUOD.	mean	3.5	53.0	1.0	41.9
	SD	1.66	46.43	0.39	33.86
	SE	0.48	35.64	0.11	23.10
	max.	7.4	59.4	1.9	47.4
	min.	1.7	46.5	0.5	36.2
	range	5.7	57.2	1.4	44.7

Table 9b. continued.

SPECIES		VARIABLES			
		MaAMP		MiAMP	
		(mm)	(dB rms)	(mm)	(dB rms)
PUNC.	mean	2.5	44.9	0.9	41.4
	SD	1.59	46.08	0.54	36.62
	SE	0.46	35.29	0.16	25.84
	max.	6.7	58.5	1.7	46.8
	min.	1.0	41.7	0.2	28.5
	range	5.7	57.2	1.5	45.7
TRAN.	mean	2.8	50.9	1.1	42.7
	SD	1.57	45.93	0.43	34.69
	SE	0.45	35.14	0.12	23.90
	max.	6.4	58.1	1.6	46.3
	min.	1.1	42.9	0.4	33.2
	range	5.3	56.5	1.3	44.1
SEXG.	mean	5.1	56.3	2.0	48.2
	SD	1.79	47.07	1.25	43.98
	SE	0.52	36.29	0.36	33.19
	max.	8.9	61.0	5.8	57.2
	min.	2.9	51.1	1.1	43.1
	range	6.0	57.7	4.6	55.3
LONG.	mean	2.7	50.7	1.2	43.8
	SD	0.92	41.34	0.65	38.27
	SE	0.38	33.56	0.26	30.50
	max.	3.8	53.6	2.0	47.9
	min.	1.4	44.7	0.3	31.0
	range	2.4	49.7	1.7	46.5

n=12 except for REPA.: n=11 and LONG.: n=6.
dB re. 0.0002 dynes/cm^2

Table 10. Coefficients or variation for oscillogram variables.

SPECIES	VARIABLES (SD/mean x 100%)							
	MaPT	MiPT	MPP	APP	OSL	D	MaAMP	MiAMP
REPA.	20.0	21.1	15.9	23.9	42.3	54.9	69.3	58.9
DUOD.	21.5	26.6	12.8	17.6	66.5	46.4	47.4	39.0
PUNC.	15.2	30.6	22.9	26.2	49.8	45.0	63.6	60.0
TRAN.	26.1	25.1	16.2	21.0	51.6	24.3	56.1	39.1
SEXG.	17.2	21.6	20.2	31.6	41.2	33.3	35.1	62.5
LONG.	14.8	21.5	16.1	16.8	20.0	30.0	34.1	54.2
mean	19.1	24.4	17.3	22.8	45.3	39.0	50.9	52.3
SD	3.92	3.44	3.29	5.12	13.98	10.58	13.35	9.67
max.	26.1	30.6	22.9	31.6	66.5	54.9	69.3	62.5
min.	14.8	21.1	12.8	16.8	20.0	24.3	34.1	39.0
range	11.3	9.6	10.1	14.8	46.4	30.6	35.2	23.5

n=12 except for REPA.: n=11 and LONG.: n=6.

Table 11. Overall uniformity of oscillogram variables.

VARIABLES	MaPT	MiPT	MPP	APP	MaAMP	MiAMP
NUM./65	31	35	37	36	27	35
X/100%	47.7	53.8	56.9	55.4	41.5	53.8

N=65.

Table 12a. F ratios and significance levels for oscillogram variables: sex comparisons.

SPECIES		VARIABLES							
		MaPT	MiPT	MPP	APP	OSL	D	MaAMP	MiAMP
REPA.	F RATIO	0.3634	12.8701	1.7021	3.9491	0.0461	4.8823	4.5005	0.1268
	SIG. (P)	>0.05	<0.05	>0.05	>0.05	>0.05	>0.05	>0.05*	>0.05
DUOD.	F RATIO	0.3644	0.3633	1.6133	1.5959	0.0494	0.6686	0.0932	0.0001
	SIG. (P)	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
PUNC.	F RATIO	0.3525	1.018	5.1528	0.3245	0.8099	0.5466	3.4865	4.6890
	SIG. (P)	>0.05	>0.05	<0.05	>0.05	>0.05*	>0.05	>0.05	>0.05
TRAN.	F RATIO	1.0077	0.5093	3.0848	0.6886	6.8567	4.6262	2.3636	2.2613
	SIG. (P)	>0.05	>0.05	>0.05	>0.05	<0.05*	>0.05	>0.05	>0.05

Table 12a. continued.

SPECIES		VARIABLES							
		MaPT	MiPT	MPP	APP	OSL	D	MaAMP	MiAMP
SEXG.	F RATIO	3.6115	2.5555	4.3591	5.0481	1.0967	0.3807	7.6061	1.5485
	SIG. (P)	>0.05	>0.05	>0.05	<0.05	>0.05	>0.05	<0.05	>0.05*
LONG.	F RATIO	0.5296	2.2623	0.2297	0.2738	0.1711	0.9922	0.0646	0.3501
	SIG. (P)	>0.05*	>0.05*	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05

$n_M=n_F=6$ except for REPA.: $n_M=5$ and LONG.: $n_M=2$, $n_F=4$.
d.f.=1,10 except REPA.: d.f.=1,9 and LONG.: d.f.=1,4.
* significantly heterogeneous

Table 12b. U values and significance levels (Mann-Whitney U test): sex comparisons.)

SPECIES		VARIABLES							
		MaPT	MiPT	MPP	APP	OSL	D	MaAMP	MiAMP
REPA.	U	12.0	2.0	7.0	5.0	14.0	4.5	6.0	15.0
	SIG. (P)	>0.05	<0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
DUOD.	U	18.0	15.0	11.0	10.0	14.0	12.0	13.0	15.0
	SIG. (P)	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
PUNC.	U	18.0	10.0	6.0	14.0	12.0	16.5	6.0	6.0
	SIG. (P)	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
TRAN.	U	11.0	10.0	9.0	14.0	4.0	6.0	11.0	10.0
	SIG. (P)	>0.05	>0.05	>0.05	>0.05	<0.05	>0.05	>0.05	>0.05
SEXG.	U	7.0	7.0	6.0	7.0	12.0	12.5	4.0	11.0
	SIG. (P)	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	<0.05	>0.05
LONG.	U	4.0	0.0	3.0	3.0	4.0	2.0	4.0	2.0
	SIG. (P)	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05

$n_M=n_F=6$ except for REPA.: $n_M=5$ and LONG.: $n_M=2$, $n_F=4$.

Table 13a. Sex descriptive statistics for temporal oscillogram variables.

SPECIES		VARIABLES											
		MaPT		MiPT		MPP		APP		OSL		D	
		(msec.)		(msec.)		(msec.)		(msec.)		(msec.)			
		male	female	male	female	male	female	male	female	male	female	male	female
REPA.	mean	2.4	2.6	2.3	3.2	11.1	9.9	5.3	4.1	761.5	807.1	0.25	0.50
	SD	0.29	0.64	0.52	0.27	1.27	1.81	0.90	1.02	332.42	363.53	0.139	0.209
	SE	0.13	0.26	0.23	0.11	0.57	0.79	0.40	0.42	148.66	148.41	0.062	0.085
	max.	2.8	3.3	3.1	3.6	12.8	13.3	6.4	5.2	1110.9	1367.9	0.46	0.75
	min.	2.0	1.7	1.9	2.8	9.6	8.4	4.0	2.4	438.7	379.8	0.11	0.18
	range	0.8	1.6	1.3	0.7	3.2	4.8	2.4	2.8	672.1	988.1	0.35	0.57
DUOD.	mean	2.6	2.8	3.0	3.3	9.6	10.6	4.2	4.7	1117.0	1025.9	0.40	0.32
	SD	0.29	0.80	0.62	1.07	1.40	1.10	0.80	0.73	602.17	804.12	0.119	0.208
	SE	0.12	0.33	0.25	0.44	0.57	0.45	0.33	0.30	245.83	328.28	0.049	0.085
	max.	3.0	4.2	3.8	4.9	11.5	11.7	5.3	5.9	2262.2	2422.8	0.53	0.69
	min.	2.2	2.0	2.2	2.2	8.0	8.6	3.4	3.8	566.9	230.7	0.24	0.09
	range	0.8	2.2	1.6	2.8	3.5	3.0	1.9	2.2	1695.3	2192.2	0.29	0.60
PUNC.	mean	2.2	2.4	3.4	2.9	10.1	7.8	4.1	3.7	392.3	510.1	0.25	0.31
	SD	0.27	0.44	1.01	0.96	2.16	1.19	1.06	1.05	82.03	310.03	0.061	0.172
	SE	0.11	0.18	0.41	0.39	0.88	0.49	0.43	0.43	33.49	126.57	0.025	0.070
	max.	2.6	3.2	5.4	4.4	12.8	9.3	5.4	5.5	450.6	952.2	0.36	0.63
	min.	1.9	2.0	2.6	1.7	7.6	6.4	3.0	2.8	243.9	152.8	0.20	0.15
	range	0.7	1.2	2.7	2.7	5.2	2.8	2.5	2.8	206.7	799.4	0.16	0.48
TRAN.	mean	3.3	3.8	3.9	4.3	11.7	13.6	5.8	6.4	303.6	583.1	0.24	0.19
	SD	0.50	1.23	0.55	1.38	2.29	1.36	1.60	0.89	82.19	248.25	0.050	0.038
	SE	0.20	0.50	0.22	0.56	0.94	0.56	0.65	0.36	33.55	101.35	0.020	0.015
	max.	4.2	5.5	4.7	5.4	15.3	15.6	7.9	7.5	384.2	1015.6	0.29	0.24
	min.	2.9	2.0	3.3	1.8	9.5	12.0	3.5	4.9	171.8	342.2	0.15	0.14
	range	1.3	3.4	1.4	3.6	5.9	3.6	4.3	2.6	212.4	673.4	0.14	0.10
SEXG.	mean	2.7	3.2	2.8	3.4	11.4	14.1	5.1	7.2	442.3	567.7	0.16	0.14
	SD	0.46	0.44	0.56	0.68	2.07	2.43	1.57	1.72	151.90	250.79	0.031	0.066
	SE	0.19	0.18	0.23	0.28	0.85	0.99	0.64	0.70	62.01	102.38	0.013	0.027
	max.	3.2	3.8	3.4	4.2	14.3	16.7	7.0	10.0	712.6	1064.7	0.20	0.25
	min.	2.1	2.5	2.2	2.5	8.9	10.9	3.4	5.6	291.4	394.5	0.12	0.05
	range	1.1	1.3	1.2	1.7	5.4	5.8	3.6	4.4	421.1	670.2	0.08	0.20
LONG.	mean	2.7	3.0	2.7	3.5	8.4	9.0	3.8	4.2	730.0	675.5	0.20	0.26
	SD	0.01	0.52	0.02	0.73	0.66	1.74	0.61	0.78	49.50	173.32	0.021	0.079
	SE	0.01	0.26	0.02	0.36	0.47	0.87	0.43	0.39	35.00	86.66	0.015	0.040
	max.	2.7	3.6	2.7	4.4	8.8	10.5	4.3	5.1	765.0	825.9	0.21	0.36
	min.	2.7	2.5	2.7	2.8	7.9	6.9	3.4	3.3	695.0	476.6	0.18	0.18
	range	0.0	1.1	0.0	1.7	0.9	3.6	0.9	1.8	70.0	349.3	0.03	0.18

$n_M=n_F=6$ except for REPA.: $n_M=5$ and LONG.: $n_M=2$, $n_F=4$.

Table 13b. Sex descriptive statistics for SPL related oscillogram variables.

SPECIES	VARIABLES							
	MaAMP				MiAMP			
	male		female		male		female	
	(mm)	(dB rms)	(mm)	(dB rms)	(mm)	(dB rms)	(mm)	(dB rms)
REPA. mean	1.6	46.1	3.6	53.2	0.9	41.1	0.8	40.1
SD	0.32	32.14	2.14	48.64	0.70	38.94	0.39	33.86
SE	0.14	24.96	0.87	40.83	0.31	31.86	0.16	26.12
max.	2.0	48.1	7.1	59.1	2.1	48.5	1.3	44.3
min.	1.3	44.3	1.3	44.3	0.3	31.6	0.2	28.1
range	0.7	38.9	5.8	57.3	1.8	47.1	1.1	42.9
DUOD. mean	3.7	53.4	3.4	52.7	1.0	42.0	1.0	42.0
SD	1.04	42.38	2.22	48.96	0.23	29.27	0.53	36.52
SE	0.43	34.71	0.91	41.22	0.09	21.12	0.22	28.88
max.	5.0	56.0	7.4	59.4	1.3	44.3	1.9	47.6
min.	2.3	49.3	1.7	46.6	0.8	40.1	0.5	36.0
range	2.7	50.7	5.7	57.2	0.5	36.0	1.4	45.0
PUNC. mean	1.7	46.6	3.3	52.4	0.6	37.6	1.2	43.6
SD	1.05	42.46	1.74	46.85	0.50	36.02	0.42	34.50
SE	0.43	34.71	0.71	39.06	0.21	28.48	0.17	26.64
max.	3.6	53.2	6.7	58.6	1.6	46.1	1.7	46.6
min.	1.0	42.0	1.7	46.6	0.2	28.1	0.5	36.0
range	2.7	50.7	4.9	55.8	1.4	45.0	1.2	43.6
TRAN. mean	2.1	48.5	3.4	52.7	0.9	41.1	1.3	44.3
SD	0.80	40.10	1.93	47.75	0.42	34.50	0.39	33.86
SE	0.33	32.41	0.79	39.99	0.17	26.64	0.16	26.12
max.	3.2	52.1	6.4	58.2	1.6	46.1	1.6	46.1
min.	1.1	42.9	1.4	45.0	0.4	34.1	0.6	37.6
range	2.1	48.5	5.0	56.0	1.2	43.6	1.0	42.0
SEXG. mean	4.0	54.1	6.3	58.0	1.6	46.1	2.5	50.0
SD	1.30	44.31	1.51	45.62	0.47	35.48	1.66	46.44
SE	0.53	36.52	0.62	37.88	0.19	27.61	0.68	38.69
max.	6.3	58.0	8.9	61.0	2.4	49.6	5.8	57.3
min.	2.9	51.3	4.5	55.1	1.1	42.9	1.3	44.3
range	3.5	52.9	4.4	54.9	1.3	44.3	4.5	55.1
LONG. mean	2.6	50.3	2.8	51.0	1.5	45.6	1.1	42.9
SD	1.70	46.64	0.66	38.43	0.71	39.06	0.69	38.81
SE	1.20	43.62	0.33	32.41	0.50	36.02	0.35	32.92
max.	3.8	53.6	3.4	52.7	2.0	48.1	1.9	47.6
min.	1.4	45.0	2.0	48.1	1.0	42.0	0.3	31.6
range	2.4	49.6	1.4	45.0	1.0	42.0	1.6	46.1

$n_M=n_F=6$ except for REPA.: $n_M=5$ and LONG.: $n_M=2$, $n_F=4$.
dB re. 0.0002 dynes/cm^2

Table 14a. F ratios and significance levels for oscillogram variables: species comparisons.

VARIABLES	MaPT	MiPT	MPP	APP	OSL	D	MaAMP	MiAMP
F RATIO	6.48	3.39	8.61	6.90	5.37	5.20	4.33	4.59
SIG. (P)	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05

N=65/ n=12 except for REPA.: n=11 and LONG.:n=6.
d.f.=5,59.

Table 14b. Chi-square values and significance levels (Kruskal-Wallis oneway ANOVA) for oscillogram variables: species comparisons.

VARIABLES	MaPT	MiPT	MPP	APP	OSL	D	MaAMP	MiAMP
CHI-SQUARE	22.35	12.88	26.58	22.33	22.09	21.09	16.82	17.84
SIGNIFICANCE (P)	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05

N=65/ n=12 except for REPA.: n=11 and LONG.:n=6.
d.f.=5.

Table 15a. Homogeneous species subsets for temporal oscillogram variables.

DURATION OF MAJOR PULSE TRAIN (msec)						
PUNC.	REPA.	DUOD.	LONG.	SEXG.	TRAN.	
2.3	2.5	2.7	2.9	2.9	3.6	mean
0.35	0.50	0.58	0.43	0.50	0.94	SD

DURATION OF MINOR PULSE TRAIN (msec)						
REPA.	SEXG.	PUNC.	DUOD.	LONG.	TRAN.	
2.8	3.1	3.2	3.2	3.3	4.1	
0.59	0.67	0.98	0.85	0.71	1.03	

DURATION OF MAJOR PULSE TRAIN PERIOD (msec)					
LONG.	PUNC.	DUOD.	REPA.	TRAN.	SEXG.
8.8	8.9	10.1	10.4	12.7	12.8
1.42	2.04	1.29	1.65	2.06	2.58

DURATION OF ABSOLUTE PULSE TRAIN PERIOD (msec)					
PUNC.	LONG.	DUOD.	REPA.	TRAN.	SEXG.
3.9	4.1	4.5	4.6	6.1	6.1
1.02	0.69	0.79	1.10	1.28	1.93

OVERALL SIGNAL LENGTH (msec)					
TRAN.	PUNC.	SEXG.	LONG.	REPA.	DUOD.
443.4	451.2	505.0	693.7	786.4	1071.4
228.90	224.80	208.24	138.94	332.93	678.97

SIGNAL DENSITY					
SEXG.	TRAN.	LONG.	PUNC.	DUOD.	REPA.
0.15	0.21	0.23	0.28	0.36	0.39
0.050	0.051	0.069	0.126	0.167	0.214

n=12 except for REPA.: n=11 and LONG.: n=6
═══ homogeneous subsets (Duncan's ranges test, P <0.05).

Table 15b. Homogeneous species subsets for SPL related oscillogram variables.

SOUND PRESSURE LEVEL FOR MAJOR PULSE TRAIN					
PUNC.	REPA.	LONG.	TRAN.	DUOD.	SEXG.
			mm		
2.5	2.7	2.7	2.8	3.5	5.1 mean
1.59	1.87	0.92	1.57	1.66	1.79 SD
			dB RMS at 3 cm		
50.0	50.6	50.7	50.9	53.0	56.3 mean
46.08	47.45	41.34	45.93	46.43	47.07 SD
SOUND PRESSURE LEVEL FOR MINOR PULSE TRAIN					
REPA.	PUNC.	DUOD.	TRAN.	LONG.	SEXG.
			mm		
0.9	0.9	1.0	1.1	1.2	2.0
0.53	0.54	0.39	0.43	0.65	1.25
			dB RMS at 3 cm		
40.7	41.4	41.9	42.7	43.8	48.2
36.46	36.62	33.86	34.69	38.27	43.98

n=12 except for REPA.: n=11 and LONG.: n=6
═══ homogeneous subsets (Duncan's ranges test, P <0.05).

Table 16. Species pair associations for oscillogram variables.

REPA. WITH SPP.	NUMBER OF ASSOC. (x /8)	RANK OF ASSOC. (y /15)	PERCENT ASSOC. (%)	DUOD. WITH SPP.	NUMBER OF ASSOC. (x /8)	RANK OF ASSOC. (y /15)	PERCENT ASSOC. (%)	PUNC. WITH SPP.	NUMBER OF ASSOC. (x /8)	RANK OF ASSOC. (y /15)	PERCENT ASSOC. (%)
DUOD.	8	15	32.6	PUNC	7	12	30.0	DUOD.	7	12	24.0
PUNC.	8	13	28.3	REPA.	8	15	37.5	REPA.	8	13	26.0
TRAN.	3	3	6.5	TRAN.	2	2	5.0	SEXG.	3	5	10.0
LONG.	7	11	23.9	LONG.	6	10	25.0	TRAN.	4	6	12.0
SEXG.	3	4	8.7	SEXG.	2	1	2.5	LONG.	8	14	28.0
TRAN. WITH SPP.	NUMBER OF ASSOC. (x /8)	RANK OF ASSOC. (y /15)	PERCENT ASSOC. (%)	SEXG. WITH SPP.	NUMBER OF ASSOC. (x /8)	RANK OF ASSOC. (y /15)	PERCENT ASSOC. (%)	LONG. WITH SPP.	NUMBER OF ASSOC. (x /8)	RANK OF ASSOC. (y /15)	PERCENT ASSOC. (%)
LONG.	4	8	28.6	PUNC.	3	5	19.2	TRAN.	4	8	16.0
REPA.	3	3	10.7	LONG.	4	7	26.9	SEXG.	4	7	14.0
PUNC.	4	6	21.4	TRAN.	4	9	34.6	DUOD.	6	10	20.0
DUOD.	2	2	7.1	DUOD.	2	1	3.8	REPA.	7	11	22.0
SEXG.	4	9	32.1	REPA.	3	4	15.4	PUNC.	8	14	28.0

Table 17. Species inclusive descriptive statistics for frequency variables.

VARIABLES	MEFRQ (Hz)	RANGE (Hz)	HIFRQ (Hz)	LOFRQ (Hz)
mean	10160	17926	19785	1859
SD	3778.1	7889.5	8209.4	750.4
SE	496.1	1035.9	1078.0	98.5
max.	20800	37760	40160	4320
min.	5280	8640	9920	640
range	15520	29120	30240	3680

N=58.

Table 18. Species descriptive statistics for frequency variables.

SPECIES		VARIABLES			
		MEFRQ (Hz)	RANGE (Hz)	HIFRQ (Hz)	LOFRQ (Hz)
REPA.	mean	10967	20931	22938	2007
	SD	3888	10292	10322	503
	SE	1172	3103	3112	152
	max.	20800	37760	40160	2720
	min.	6240	9280	10720	1440
	range	14560	28480	29440	1280
DUOD.	mean	10560	17720	19373	1653
	SD	4387	6856	7100	530
	SE	1266	1979	2050	153
	max.	20160	29280	31040	2400
	min.	6880	11520	13280	800
	range	13280	17760	17760	1600
PUNC.	mean	9324	5752	16655	1804
	SD	2558	1734	5841	599
	SE	771	1734	1761	181
	max.	13440	30080	32000	3360
	min.	5760	8640	9920	1120
	range	7680	21440	22080	2240
TRAN.	mean	7333	12480	13693	1213
	SD	1527	2395	2400	508
	SE	441	691	693	147
	max.	10240	17600	18240	1920
	min.	5280	9280	10080	640
	range	4960	8320	8160	1280

Table 18. continued.

SPECIES	VARIABLES			
	MEFRQ (Hz)	RANGE (Hz)	HIFRQ (Hz)	LOFRQ (Hz)
SEXG. mean	12613	23640	26267	2627
SD	3986	7544	7677	809
SE	1151	2178	2216	233
max.	20000	31840	35200	4320
min.	7840	10240	12640	1760
range	12160	21600	22560	2560

n=12 except for REPA. and PUNC.: n=11.

Table 19. Estimated fundamental frequency bands from selected oscillograms.

SPECIES	FREQ. RANGE MaPT (Hz)	FREQ. RANGE MiPT (Hz)	FREQ. RANGE COMBINED (Hz)
REPA.	12552 -13913	12108 -12973	12330 -13443
DUOD.	10847 -11390	10666 -11228	10757 -11309
PUNC.	9796 -10448	11243 -12108	10520 -11278
TRAN.	9600 -10400	10378 -11243	9989 -10822
SEXG.	13963 -14546	12800 -13440	13382 -13993
LONG.	14546 -15127	11915 -12255	13231 -13691
mean	11884 -12637	11518 -12208	11701 -12423

Table 20. Coefficients of variation for frequency variables.

SPECIES	VARIABLES (SD/mean x 100%)			
	MEFRQ	RANGE	HIFRQ	LOFRQ
REPA.	35.5	49.2	45.0	25.0
DUOD.	41.5	38.7	36.6	32.1
PUNC.	27.4	30.2	35.1	33.2
TRAN.	20.8	19.2	17.5	41.9
SEXG.	31.6	31.9	29.2	30.8
mean	31.4	33.8	32.7	32.6
s.d.	7.03	9.91	9.12	5.44
max.	41.5	49.2	45.0	41.9
min.	20.8	19.2	17.5	25.0
range	20.7	30.0	27.5	16.9

n=12 except for REPA. and PUNC.: n=11.

Table 21a. F ratios and significance levels for frequency variables: sex comparisons.

SPECIES		VARIABLES			
		MEFRQ	RANGE	HIFRQ	LOFRQ
REPA.	F RATIO	1.3125	2.2378	2.6284	5.8009
	SIG. (P)	>0.05	>0.05	>0.05	<0.05
DUOD.	F RATIO	0.0490	0.0842	0.1093	0.4624
	SIG. (P)	>0.05	>0.05	>0.05	>0.05
PUNC.	F RATIO	0.5855	0.8147	0.6216	0.8156
	SIG. (P)	>0.05	>0.05	>0.05	>0.05
TRAN.	F RATIO	0.1213	0.1664	0.0572	0.6480
	SIG. (P)	>0.05	>0.05	>0.05	>0.05
SEXG.	F RATIO	7.3086	7.0959	6.4995	0.0268
	SIG. (P)	<0.05	<0.05	<0.05	>0.05

$n_M=n_F=6$ except for REPA.: $n_M=5$ and PUNC.: $n_F=5$.
d.f.=1,10 except for REPA. and PUNC.: d.f.=1,9.

Table 21b. U values and significance levels (Mann-Whitney U test) for frequency variables: sex comparisons.

SPECIES		VARIABLES			
		MEFRQ	RANGE	HIFRQ	LOFRQ
REPA.	U	10.5	8.0	6.0	4.5
	SIG. (P)	>0.05	>0.05	>0.05	<0.05
DUOD.	U	13.0	15.0	17.5	13.0
	SIG. (P)	>0.05	>0.05	>0.05	>0.05
PUNC.	U	10.0	12.0	12.0	13.0
	SIG. (P)	>0.05	>0.05	>0.05	>0.05
TRAN.	U	14.5	17.5	18.0	13.5
	SIG. (P)	>0.05	>0.05	>0.05	>0.05
SEXG.	U	4.0	4.5	5.0	17.5
	SIG. (P)	<0.05	<0.05	<0.05	>0.05

$n_M=n_F=6$ except for REPA.: $n_M=5$ and PUNC.: $n_F=5$.

Table 22. Sex descriptive statistics for frequency variables.

SPECIES		VARIABLES							
		MEFRQ (Hz)		RANGE (Hz)		HIFRQ (Hz)		LOFRQ (Hz)	
		male	female	male	female	male	female	male	female
REPA.	mean	12416	9760	25728	16933	28064	18667	2336	1733
	SD	4980	2558	11509	7982	11339	7879	368	446
	SE	4980	1044	5147	3259	5071	3217	165	182
	max.	20800	13920	37760	13920	40160	32960	2720	2560
	min.	8160	6240	12640	9280	15360	10720	1760	1440
	range	12640	7680	25120	22240	24800	22240	960	1120
DUOD.	mean	10267	10853	18320	17120	20080	18667	1760	1547
	SD	4245	4911	8020	6184	8188	6531	392	661
	SE	1733	2005	3274	2525	3343	2666	160	270
	max.	16320	20160	29280	27520	31040	29760	2400	2400
	min.	6880	7200	11520	12320	13280	13440	1280	800
	range	9440	12960	17760	15200	17760	16320	1120	1600
PUNC.	mean	8773	9984	16293	13120	17947	15104	1653	1984
	SD	1716	3418	7217	3277	7298	3632	374	805
	SE	700	1530	2946	1466	2979	1624	153	360
	max.	10720	13440	30080	17440	32000	19200	2080	1280
	min.	5760	5920	9600	8640	11040	9920	1120	3360
	range	4960	7520	20480	8800	20960	9280	960	2080

Table 22. continued.

SPECIES		VARIABLES							
		MEFRQ (Hz)		RANGE (Hz)		HIFRQ (Hz)		LOFRQ (Hz)	
		male	female	male	female	male	female	male	female
TRAN.	mean	7493	7173	12773	12187	13867	13520	1093	1333
	SD	1262	1864	2953	1921	2692	2314	468	560
	SE	515	761	1205	784	1099	945	191	229
	max.	9280	10240	17600	14720	18240	16640	1920	1920
	min.	5920	5280	10400	9280	11520	10080	640	640
	range	3360	4960	7200	5440	6720	6560	1280	1280
SEXG.	mean	10133	15093	18987	28293	21653	30880	2667	2587
	SD	2881	3449	7832	3449	8077	3654	1035	602
	SE	1176	1408	3198	1408	3297	1492	423	246
	max.	14560	20000	28480	31840	32800	35200	4320	3360
	min.	7840	10880	10240	23040	12640	24960	1760	1920
	range	6720	9120	18240	8800	20160	10240	2560	1440

$n_M=n_F=6$ except for REPA.: $n_M=5$ and PUNC.: $n_F=5$.

Table 23a. F ratios and significance levels for frequency variables: species comparisons.

VARIABLES	MEFRQ	RANGE	HIFRQ	LOFRQ
F RATIO	3.8963	4.856	5.7933	8.8564
SIG. (P)	<0.05	<0.05*	<0.05*	<0.05

N=58/ n=12 except for REPA. and PUNC.: n=11.
d.f.=4,53.
* significantly heterogeneous.

Table 23b. Chi-square values and significance levels (Kruskal-Wallis oneway ANOVA) for frequency variables: species comparisons.

VARIABLES	MEFRQ	RANGE	HIFRQ	LOFRQ
CHI-SQUARE	14.83	13.16	16.06	21.81
SIG. (P)	<0.05	<0.05	<0.05	<0.05

N=58/ n=12 except for REPA. and PUNC.: n=11.
d.f.=4.

Table 24. Homogeneous species subsets for frequency variables.

MEFRQ
MEDIAN FREQUENCY (Hz)

TRAN.	PUNC.	DUOD.	REPA.	SEXG.	
7333	9324	10560	10967	12613	mean
1527	2558	4387	3888	3986	SD

RANGE
FREQUENCY RANGE (Hz)

TRAN.	PUNC.	DUOD.	REPA.	SEXG.
12480	14851	17720	20931	23640
2395	5752	6856	10292	7544

HIFRQ
HIGHEST FREQUENCY (Hz)

TRAN.	PUNC.	DUOD.	REPA.	SEXG.
13693	16655	19373	22938	26267
2400	5841	7100	10322	7677

LOFRQ
LOWEST FREQUENCY (Hz)

TRAN.	DUOD.	PUNC.	REPA.	SEXG.
1213	1653	1804	2007	2627
508	530	599	503	809

n=12 except for REPA. and PUNC.: n=11.
═══ homogeneous subsets (Duncan's ranges test, P <0.05).

Table 25. Species pair associations for frequency variables.

REPA. WITH SPP.	NUMBER OF ASSOC. (x/4)	RANK OF ASSOC. (y/7)	PERCENT ASSOC. (%)	DUOD. WITH SPP.	NUMBER OF ASSOC. (x/4)	RANK OF ASSOC. (y/7)	PERCENT ASSOC. (%)	PUNC. WITH SPP.	NUMBER OF ASSOC. (x/4)	RANK OF ASSOC. (y/7)	PERCENT ASSOC. (%)
DUOD.	4	6	42.9	PUNC.	4	7	43.7	DUOD.	4	7	50.0
SEXG.	3	5	35.7	REPA.	4	6	37.5	TRAN.	3	4	28.6
PUNC.	3	3	21.4	TRAN.	3	2	12.5	REPA.	3	3	21.4
TRAN.	0	0	0.0	SEXG.	2	1	6.2	SEXG.	0	0	0.0

TRAN. WITH SPP.	NUMBER OF ASSOC. (x/4)	RANK OF ASSOC. (y/7)	PERCENT ASSOC. (%)	SEXG. WITH SPP.	NUMBER OF ASSOC. (x/4)	RANK OF ASSOC. (y/7)	PERCENT ASSOC. (%)
PUNC.	3	4	66.7	REPA.	3	5	83.3
DUOD.	3	2	33.3	DUOD.	2	1	16.7
REPA.	0	0	0.0	PUNC.	0	0	0.0
SEXG.	0	0	0.0	TRAN.	0	0	0.0

Table 26. Substrate temperature at stridulation.

SPECIES		TEMPERATURE (° C) male		female	
REPA.	mean	36.9	n=34	36.7	n=33
	SD	3.11		3.12	
	SE	0.53		0.54	
	max.	45.0		41.0	
	min.	29.0		28.0	
	range	16.0		13.0	
DUOD.	mean	35.0	n=31	36.6	n=30
	SD	3.58		2.69	
	SE	0.64		0.49	
	max.	43.0		42.0	
	min.	26.0		31.0	
	range	17.0		11.0	
PUNC.	mean	45.0	n=31	42.1	n=30
	SD	4.00		2.52	
	SE	0.72		0.46	
	max.	51.0		46.0	
	min.	36.0		33.0	
	range	15.0		13.0	
TRAN.	mean	38.7	n=31	37.1	n=41
	SD	3.79		3.93	
	SE	0.68		0.61	
	max.	45.0		45.0	
	min.	32.0		28.0	
	range	13.0		17.0	
SEXG.	mean	38.0	n=25	37.5	n=11
	SD	4.04		5.54	
	SE	0.81		1.67	
	max.	42.0		44.0	
	min.	24.0		28.0	
	range	18.0		16.0	
LONG.	mean	41.7	n=10	39.1	n=20
	SD	3.86		3.58	
	SE	1.22		0.80	
	max.	47.0		44.0	
	min.	35.0		33.0	
	range	12.0		11.0	

Table 27. Temperature with signal variable correlations.

VARIABLES	PEARSON'S R	SIG. (P)		SPEARMAN'S RHO	SIG. (P)
MaPT+	-0.09	>0.05		-0.08	>0.05
MiPT+	-0.12	>0.05		-0.14	>0.05
MPP+	-0.26	<0.05	*	-0.26	<0.05
APP+	-0.17	>0.05		-0.21	>0.05
OSL+	-0.37	<0.05	*	-0.26	<0.05
SD+	-0.14	>0.05		-0.21	>0.05
MaAMP+	-0.24	>0.05		-0.15	>0.05
MiAMP+	-0.33	<0.05	*	-0.09	>0.05
MEFRQ^	-0.14	>0.05		-0.06	>0.05
RANGE^	-0.09	>0.05		-0.03	>0.05
HIFRQ^	-0.12	>0.05		-0.06	>0.05
LOFRQ^	-0.33	<0.05	*	-0.19	>0.05

* at least one correlation significant at P <0.05.
+ N=65
^ N=58

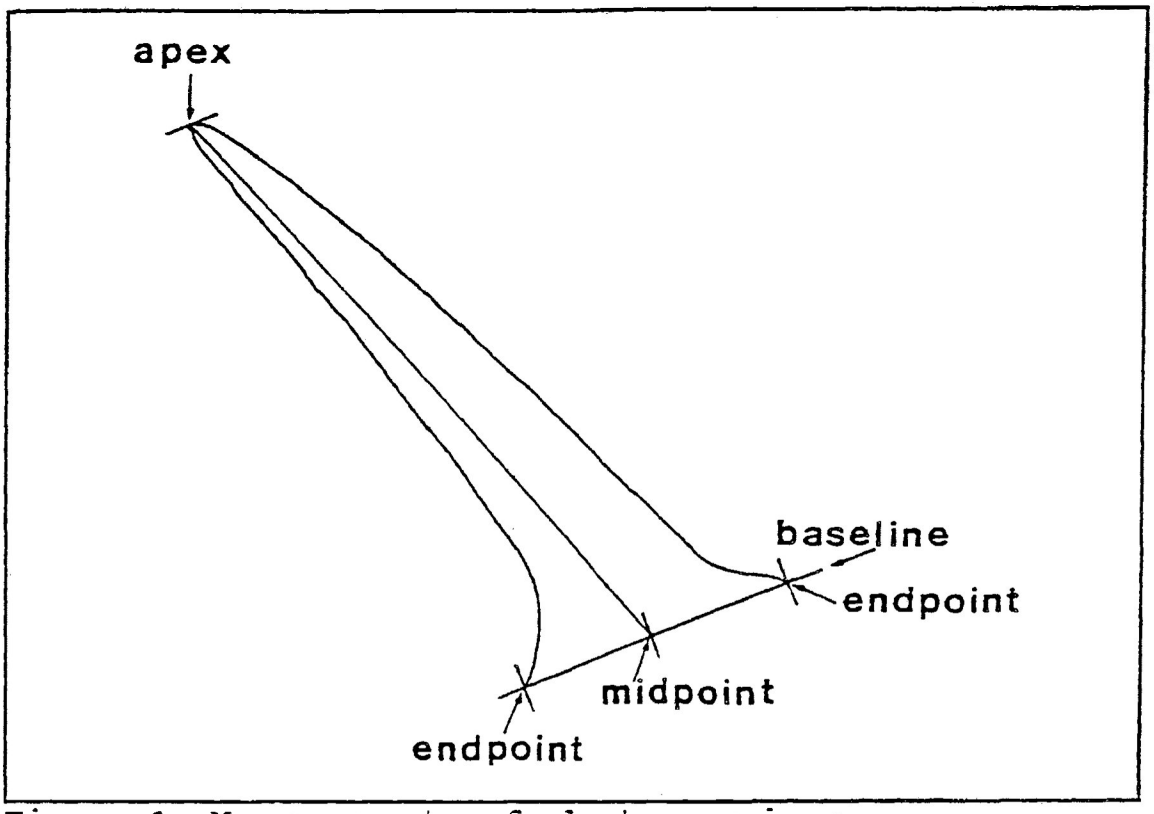


Figure 1. Measurements of plectrum spines.

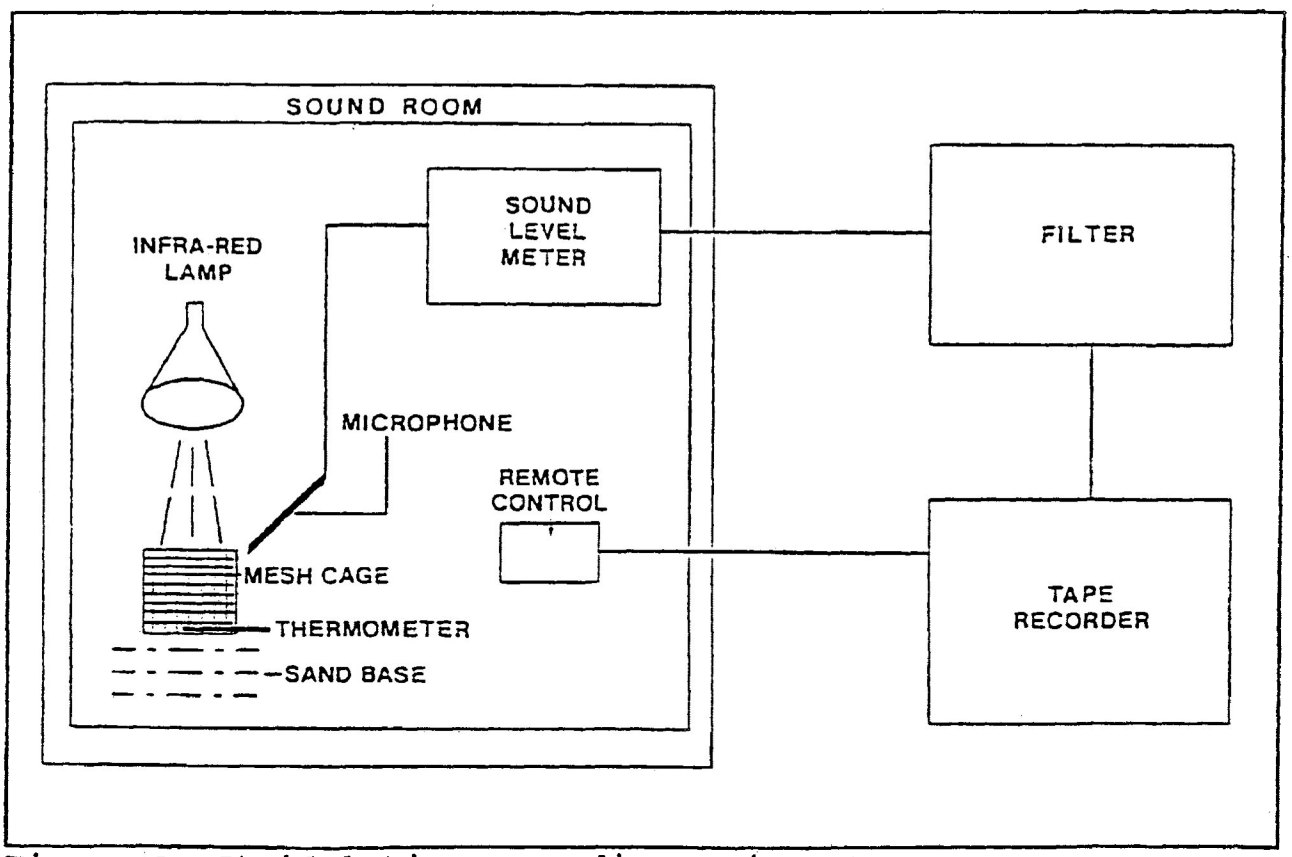


Figure 2. Stridulation recording equipment.

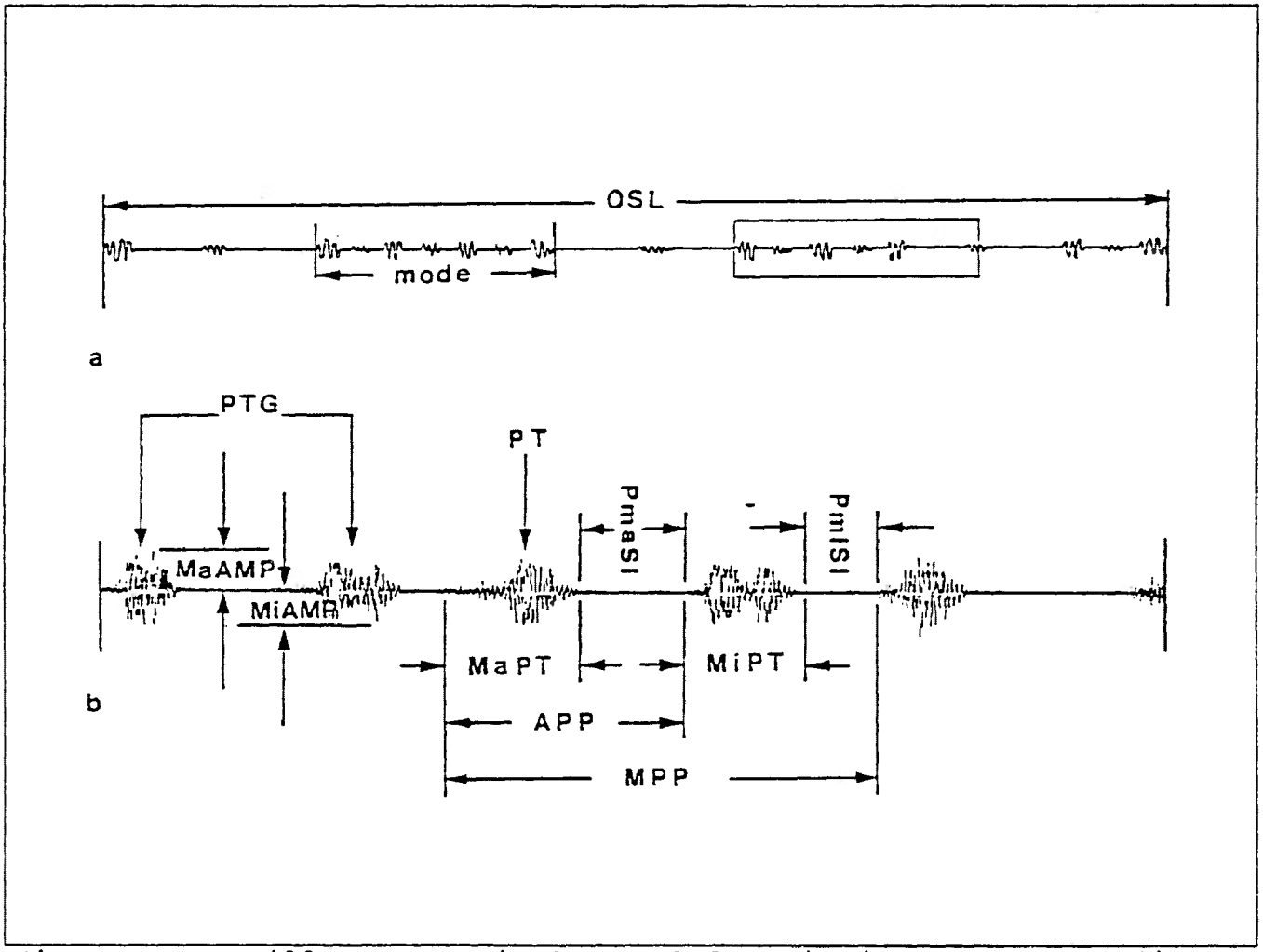


Figure 3. Oscillogram variables and descriptive terms. a, diagram of an entire 4 mode stridulation; b, portion of oscillogram representing boxed-in area in Fig. 3a.

Abbreviations: APP, absolute pulse train period; MaAMP, major pulse train maximum amplitude; MaPT, major pulse train duration; MiAMP, minor pulse train maximum amplitude; MiPT, minor pulse train duration; MPP, major pulse train period; OSL, overall signal length; PmaSI, post major silent interval; PmiSI, post minor silent interval; PT, pulse train; PTG, pulse train group.

Figure 4a. Low angle profile of plectrum spines. Bar scale=20μ.

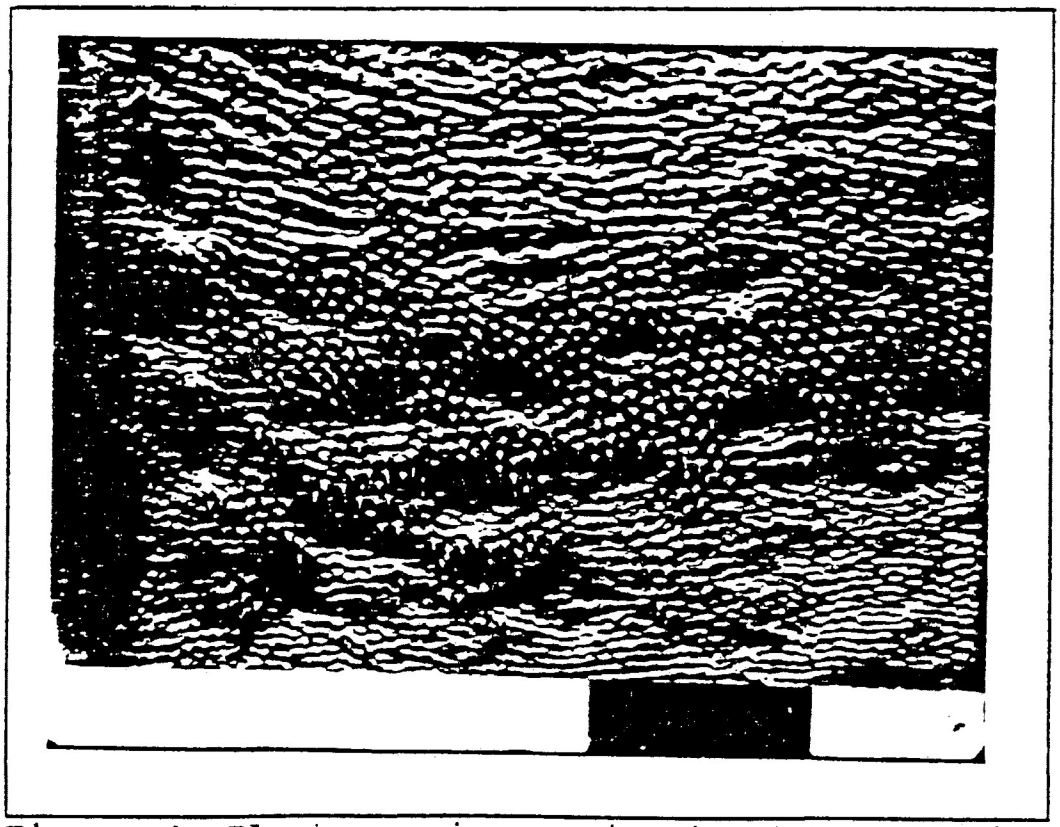


Figure 4b. Plectrum spines projecting from posterior apices of hexagonal plates. Bar scale=200μ.

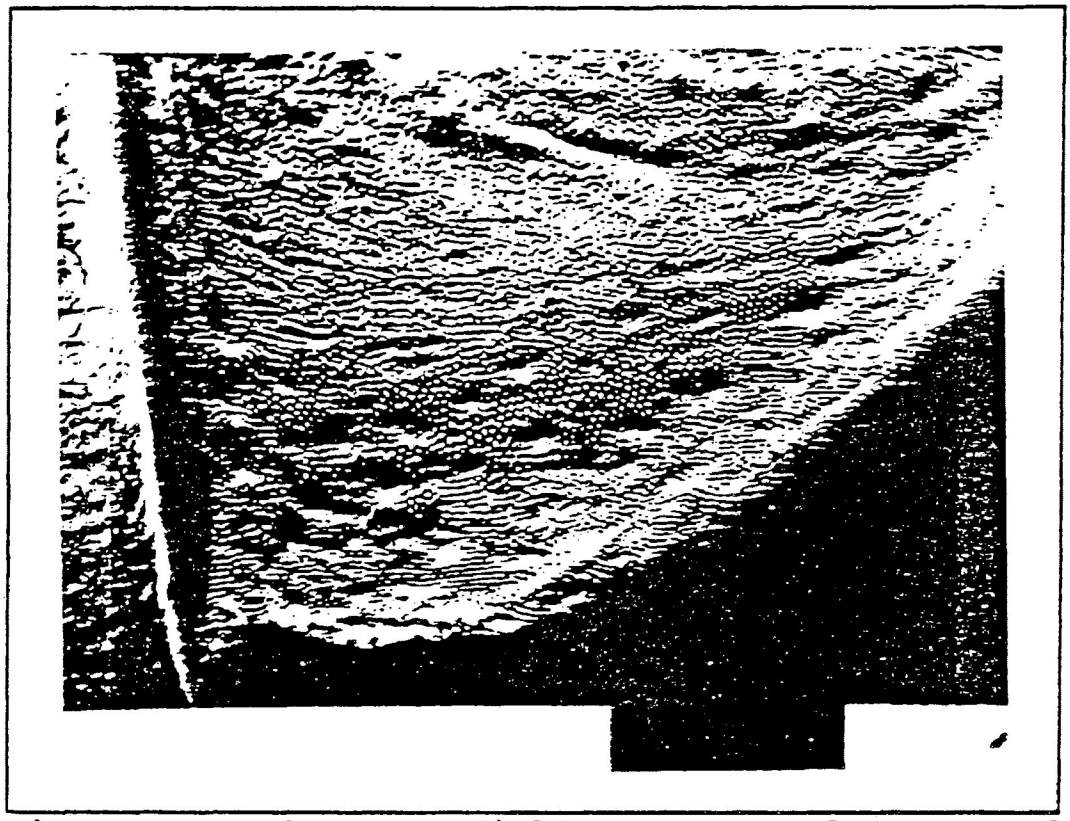


Figure 5a. Plectrum field on ventral apex of elytron. Bar scale=400μ.

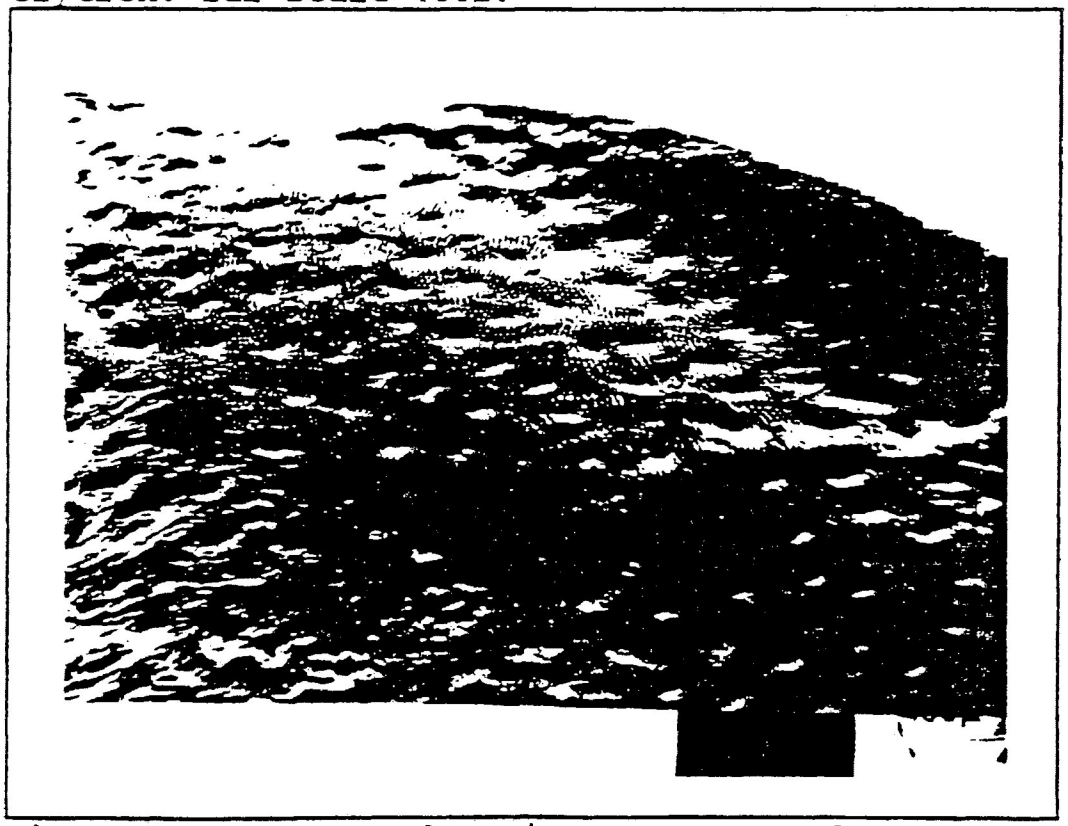


Figure 5b. Low angle view of ventral apex of elytron. Arrow indicates anterior ridge. Bar scale=400μ.

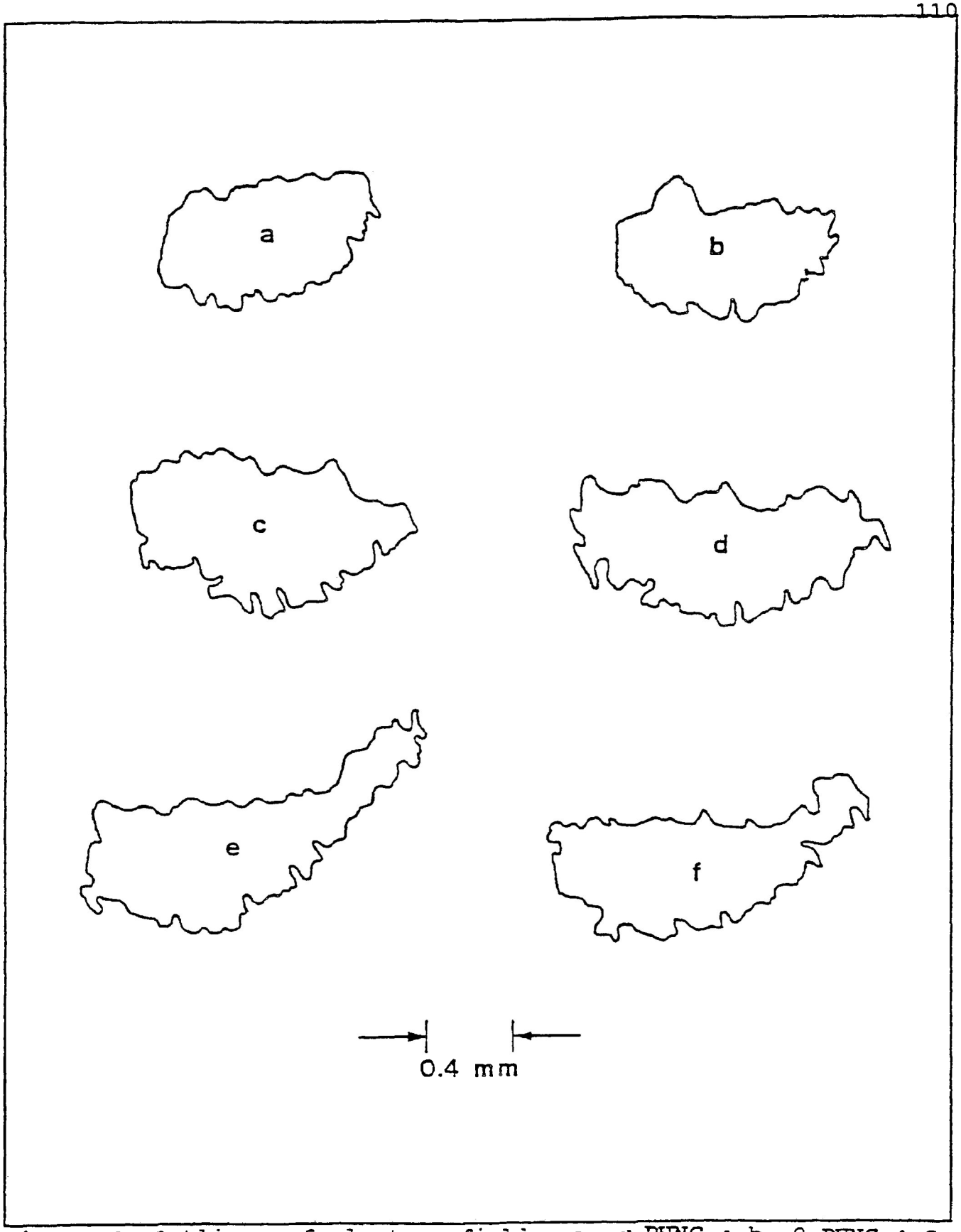


Figure 6. Outlines of plectrum fields. a, ♂ PUNC.; b, ♀ PUNC.; c, ♂ DUOD.; d, ♀ DUOD.; e, ♂ REPA.; f, ♀ REPA..

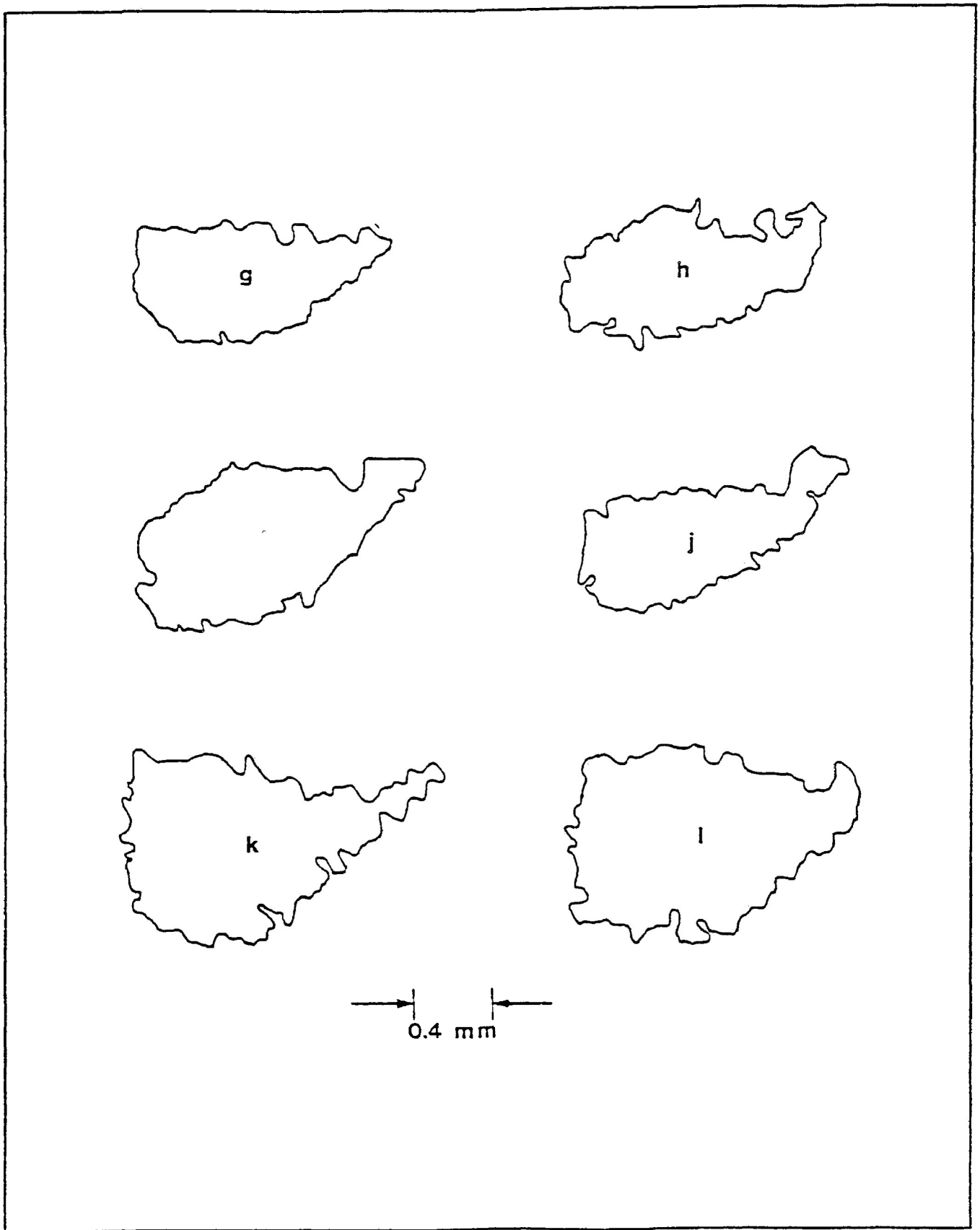


Figure 6 (continued). Outlines of plectrum fields. g, ♂ SEXG.; h, ♀ SEXG.; i, ♂ DENI.; j, ♀ DENI.; k, ♂ TRAN.; l, ♀ TRAN..

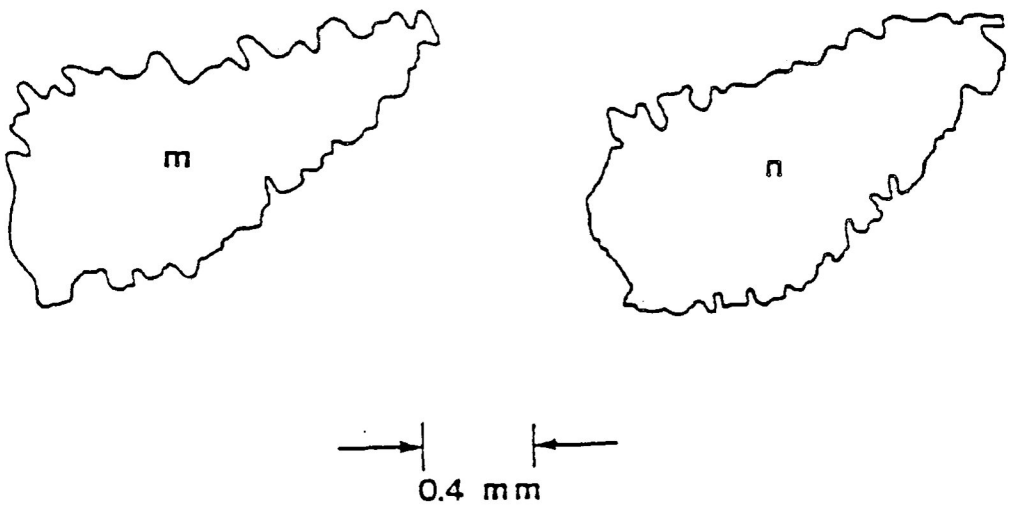


Figure 6 (continued). Outlines of plectrum fields. m, ♂ LONG.; n, ♀ LONG..

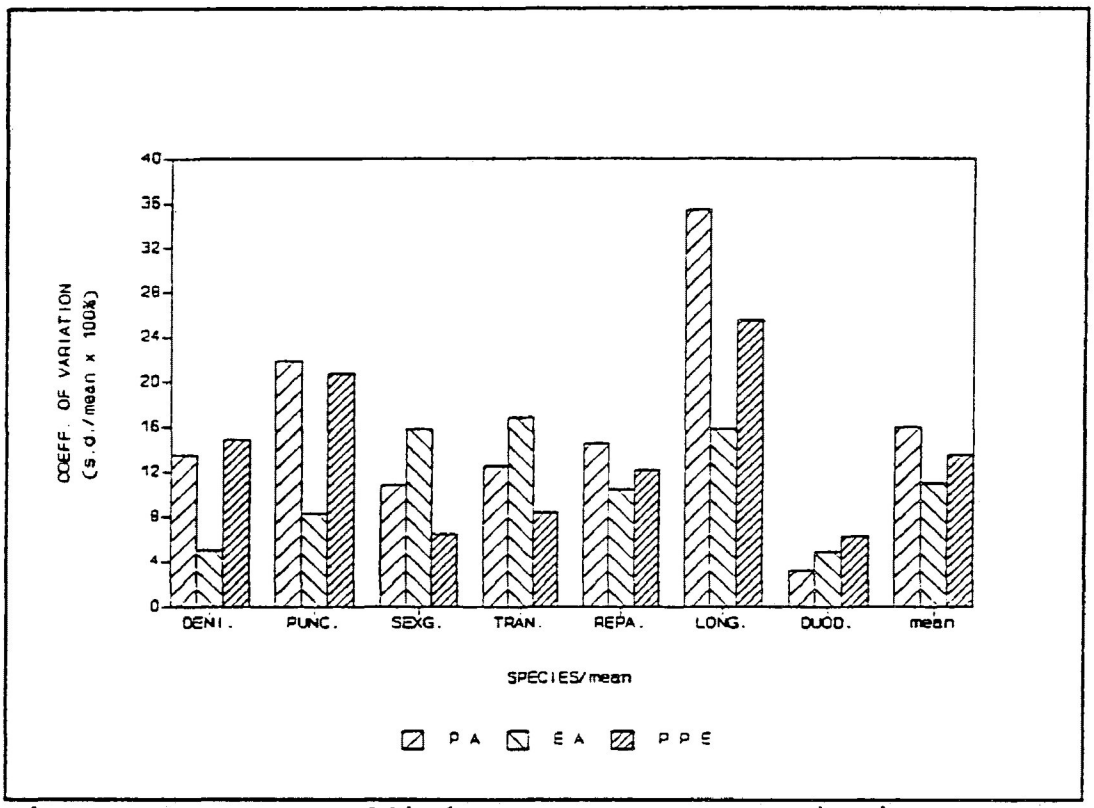


Figure 7a. Coefficients of variation for plectrum/elytron variables (small values).

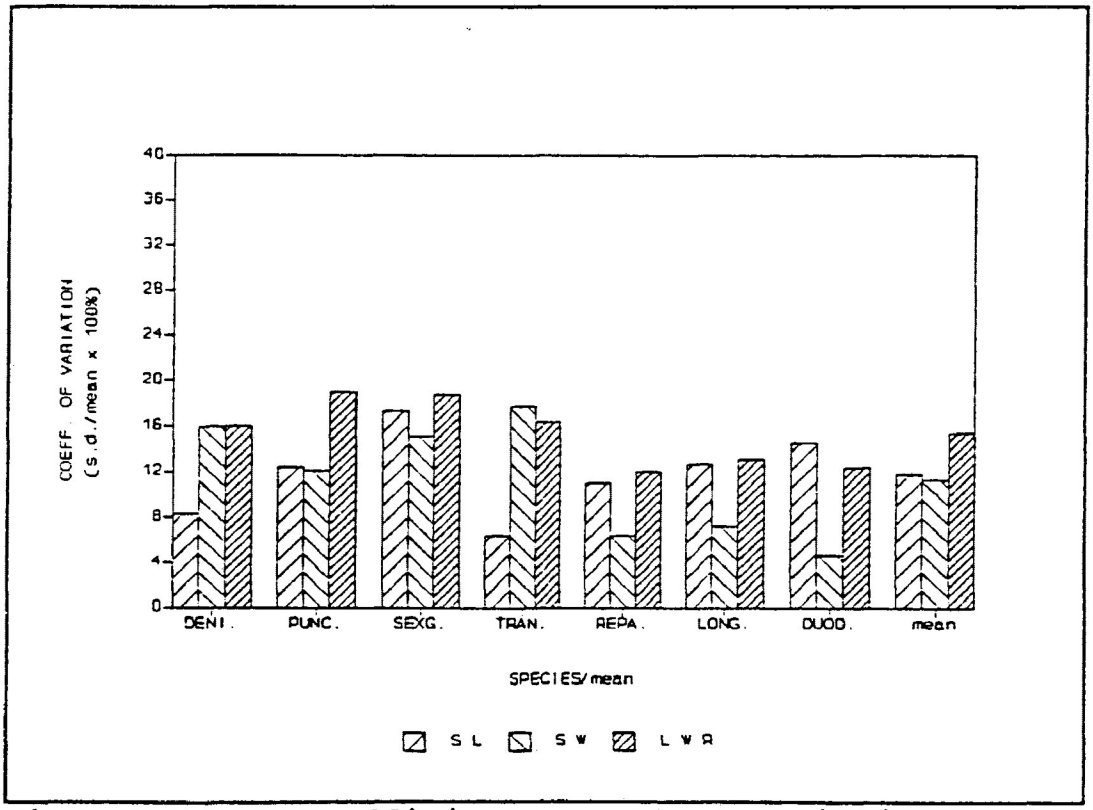
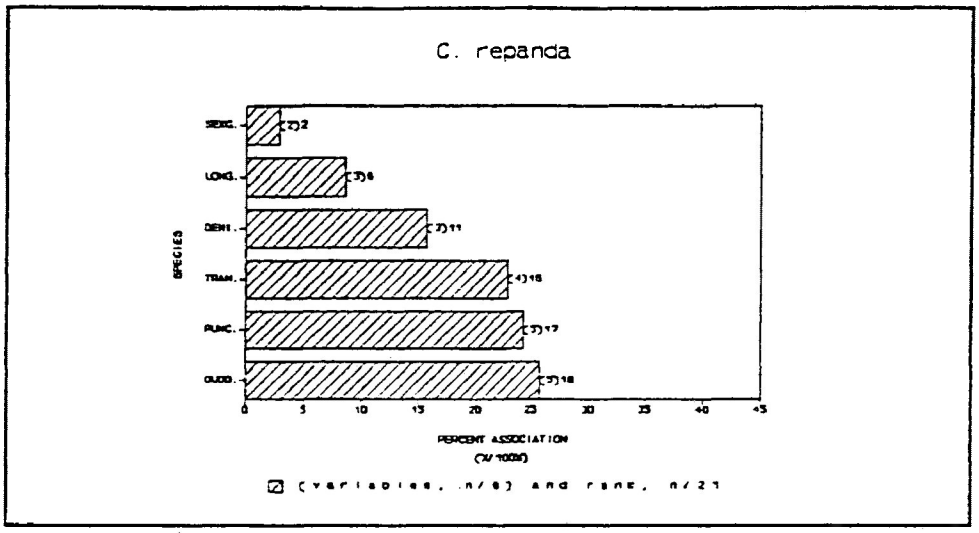
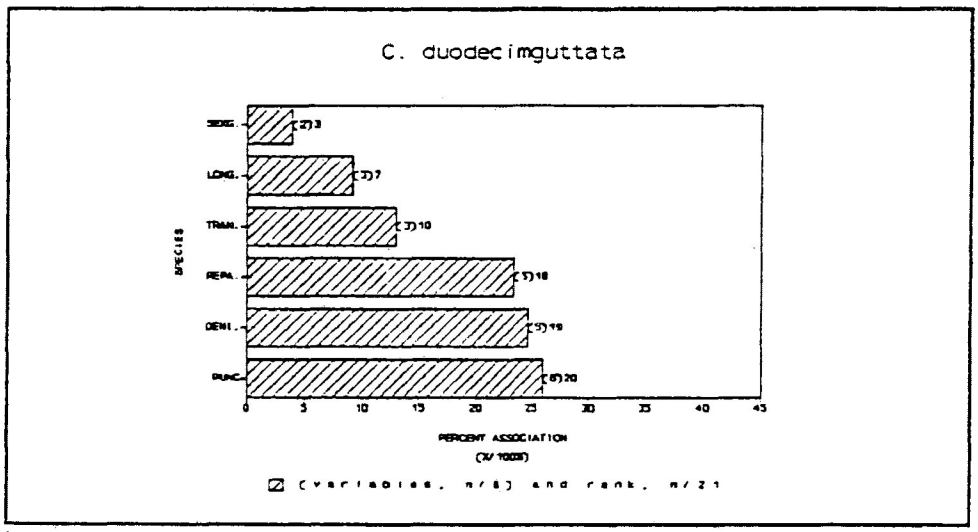


Figure 7b. Coefficients of variation for plectrum/elytron variables (large values).



a.



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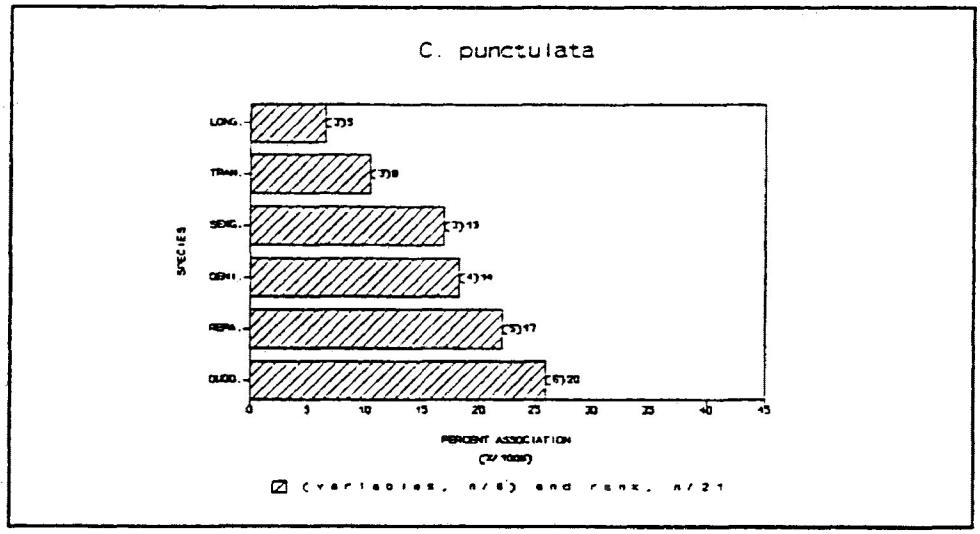
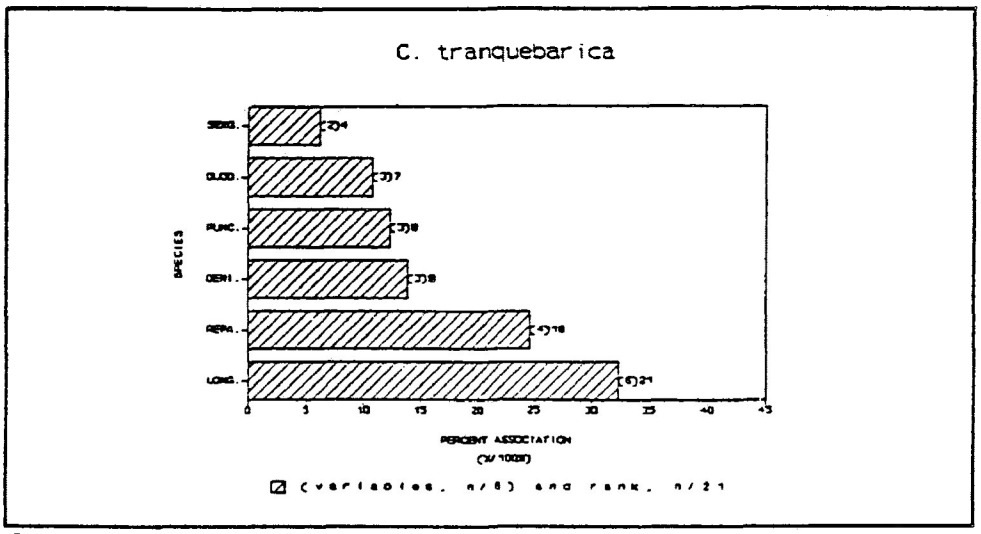
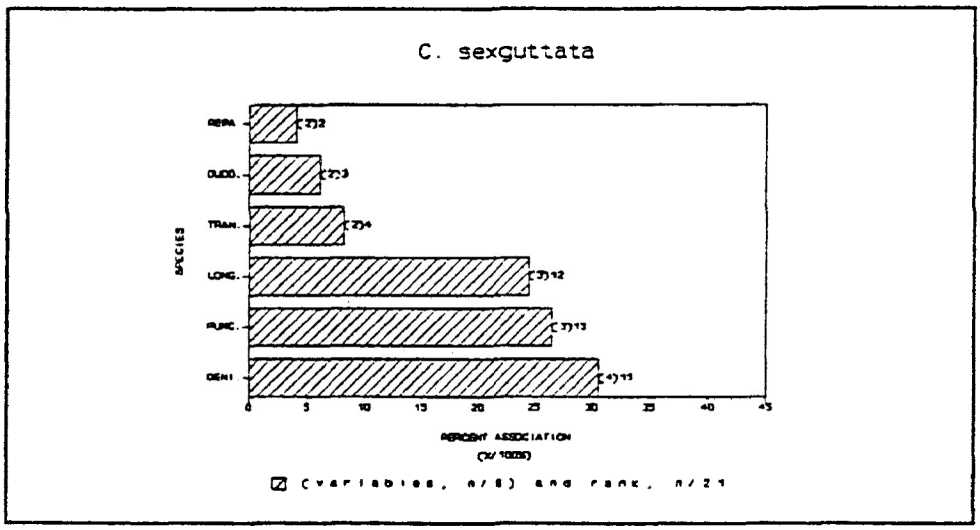


c.

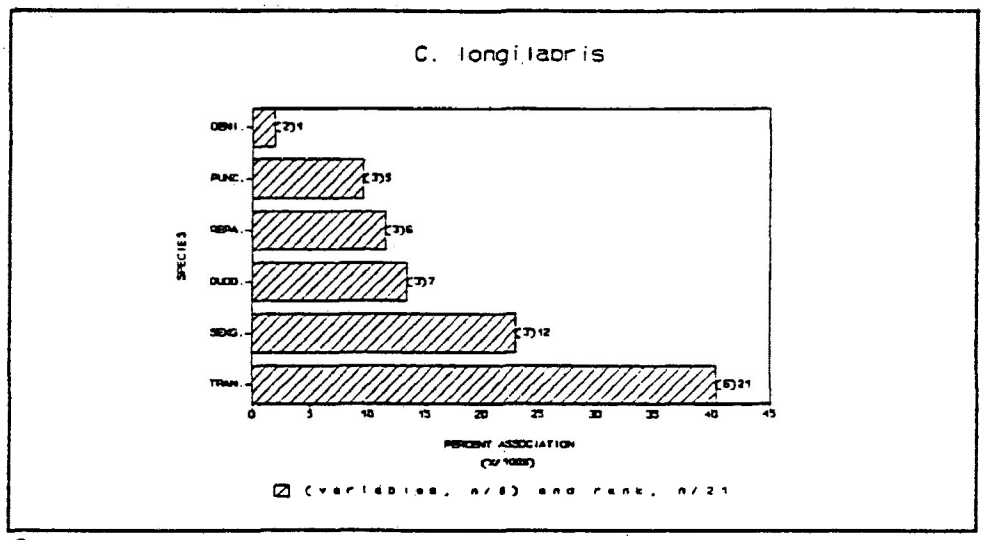
Figure 8. Species pair associations for plectrum/elytron variables.



d.

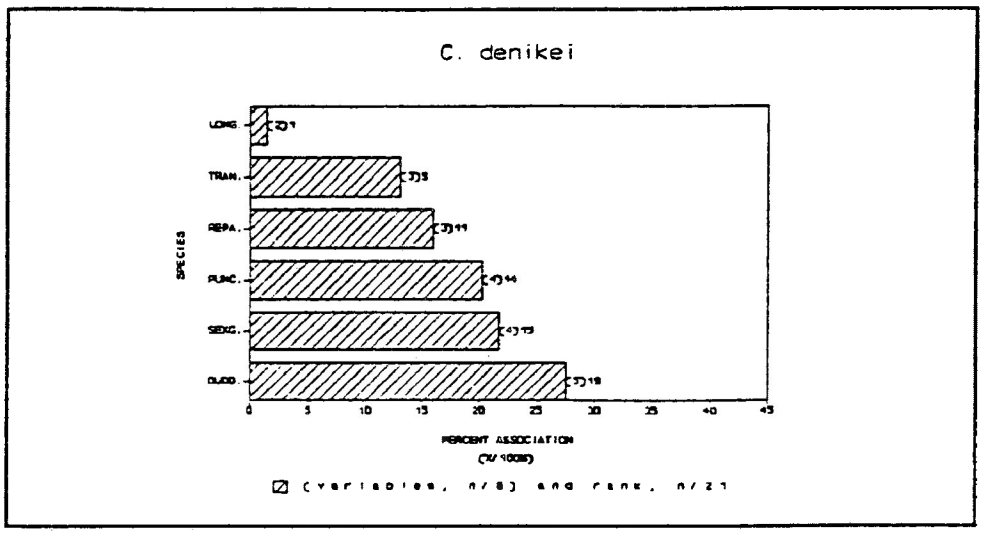


e.



f.

Figure 8 (continued) Species pair associations for plectrum/elytron variables.



g.

Figure 8 (continued). Species pair associations for plectrum/elytron variables.

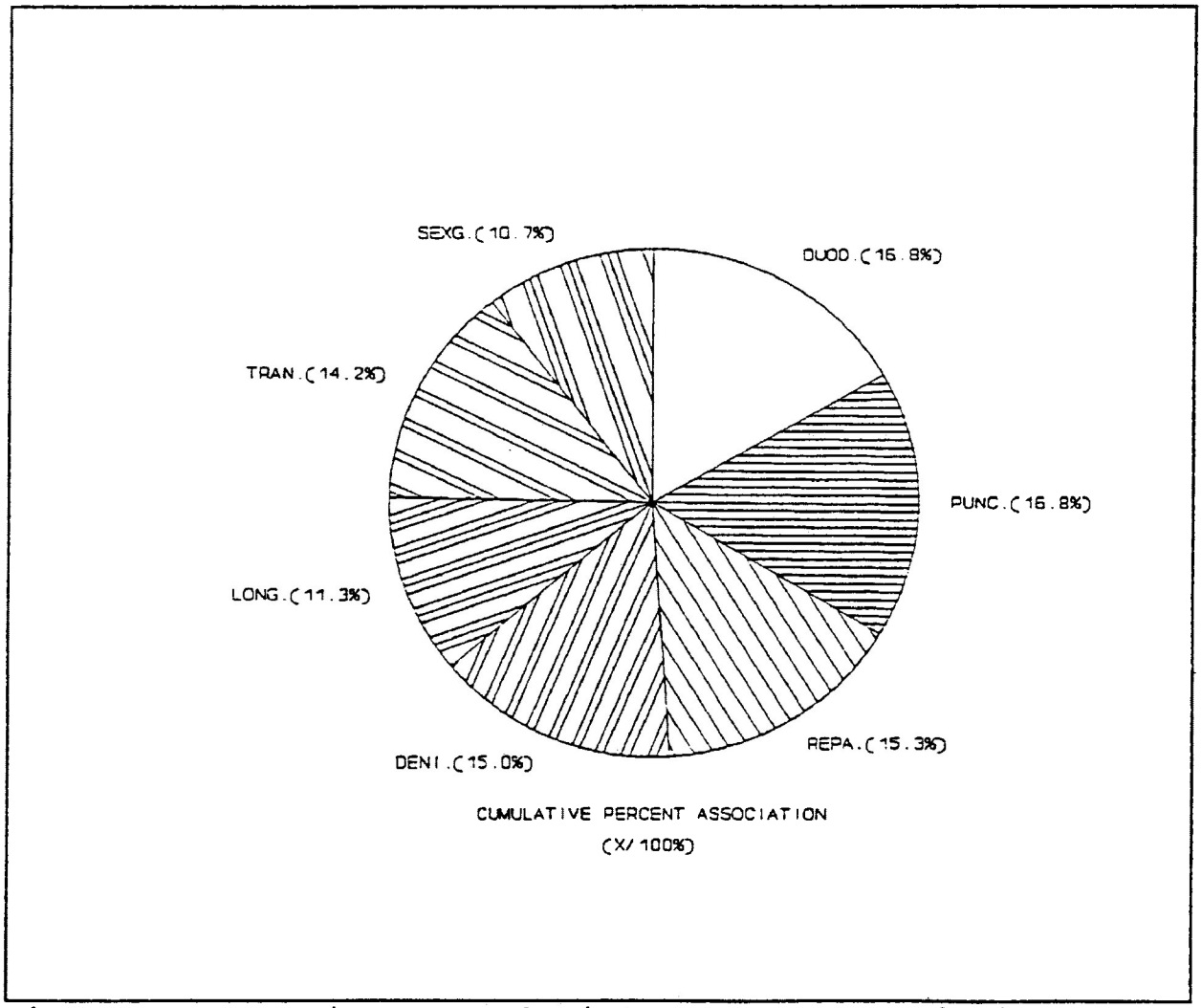


Figure 9. Species cumulative rank associations for plectrum/elytron variables.

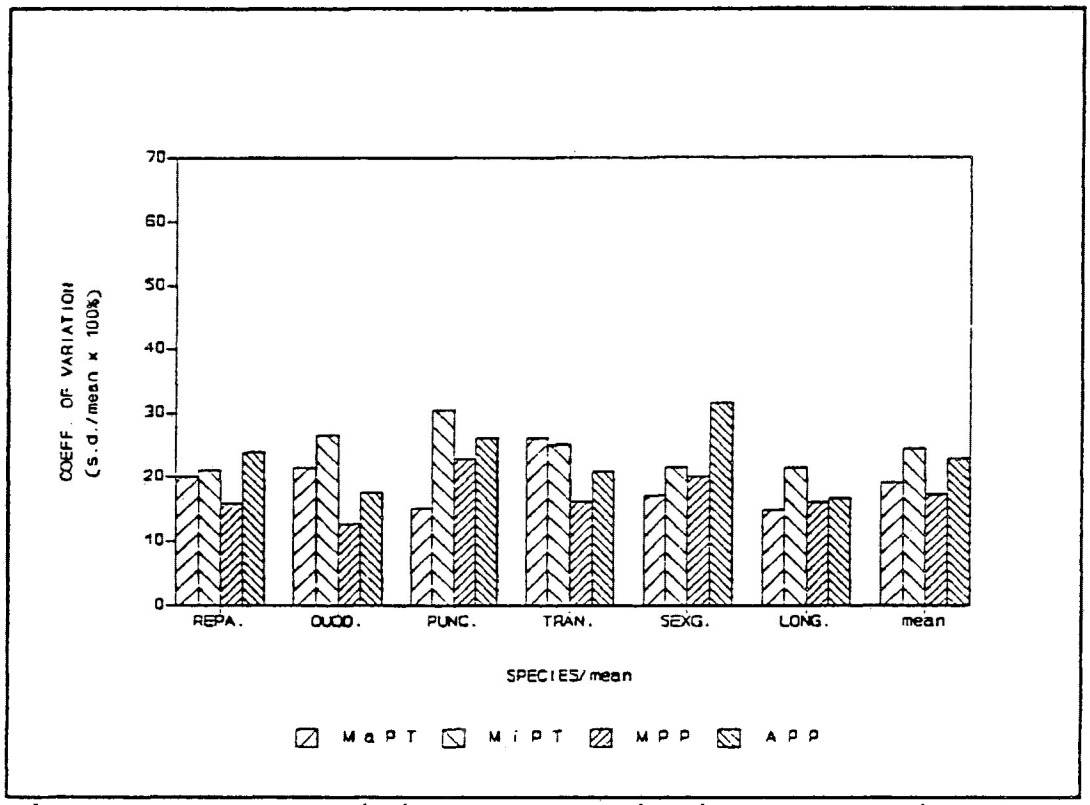


Figure 10a. Coefficients of variation for oscillogram variables (small values).

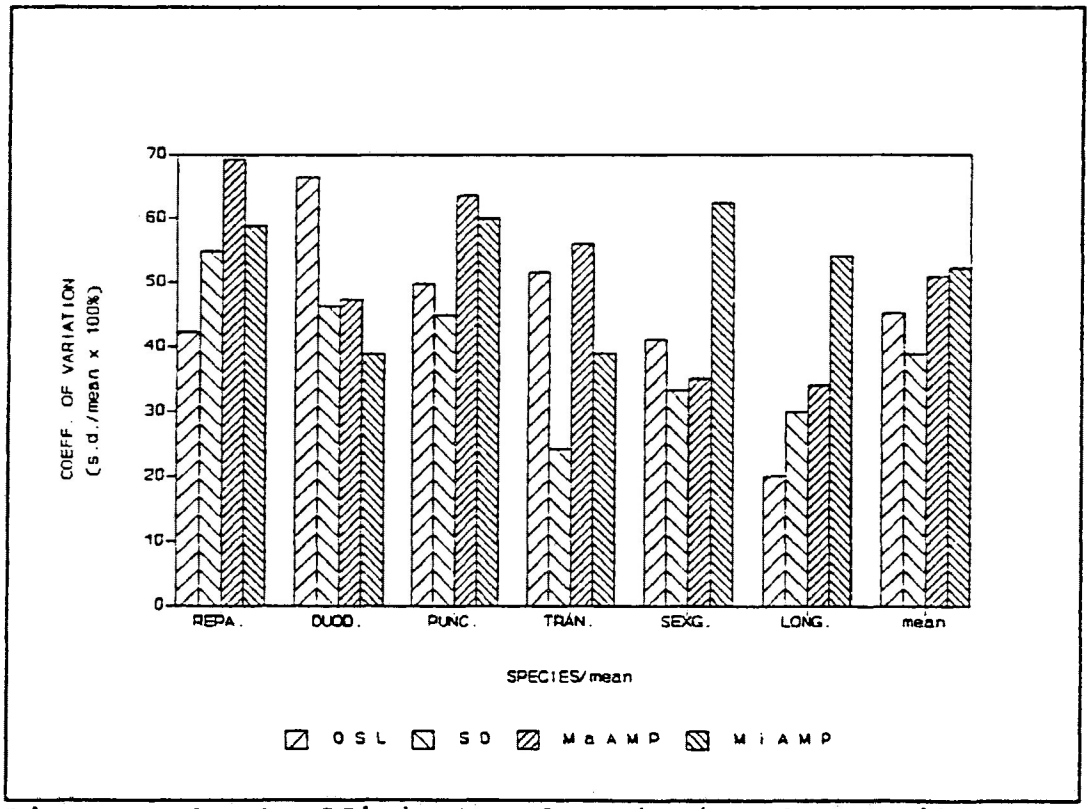
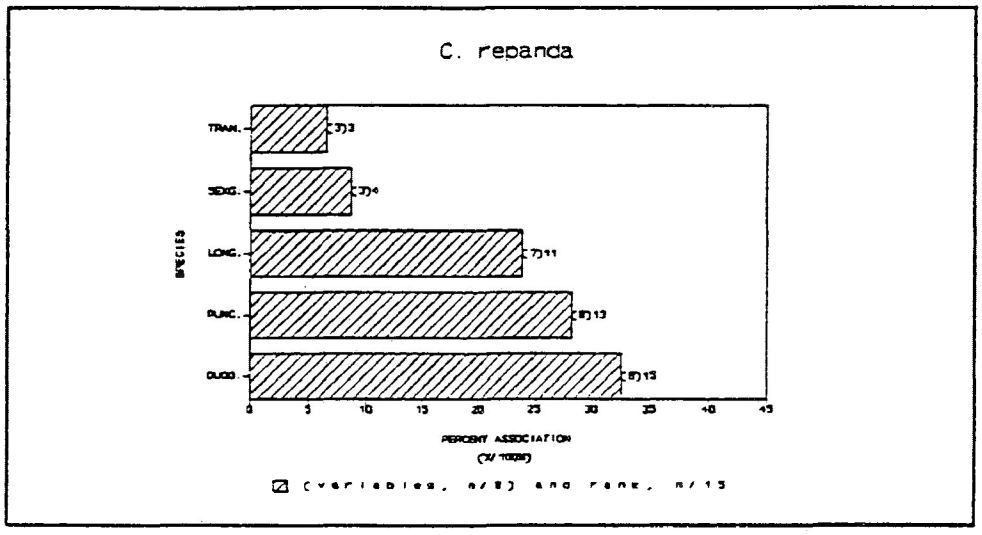
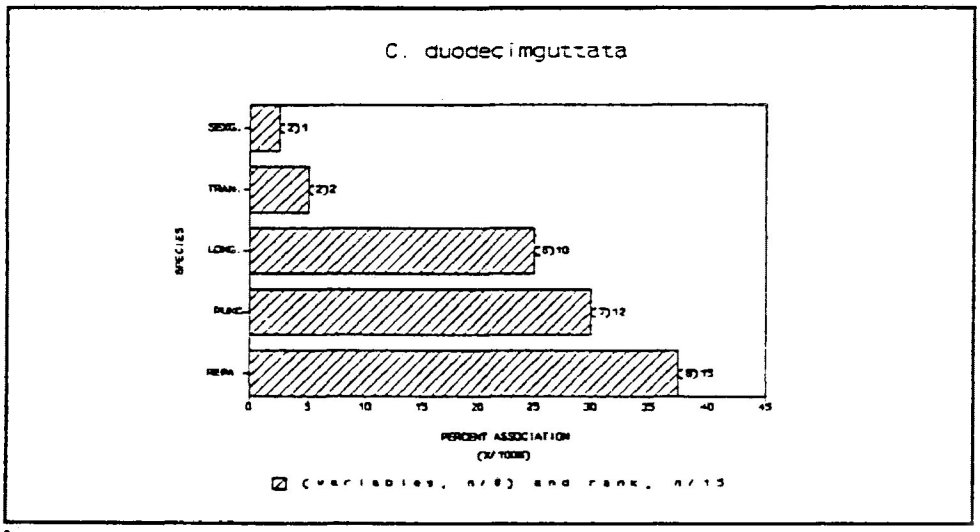


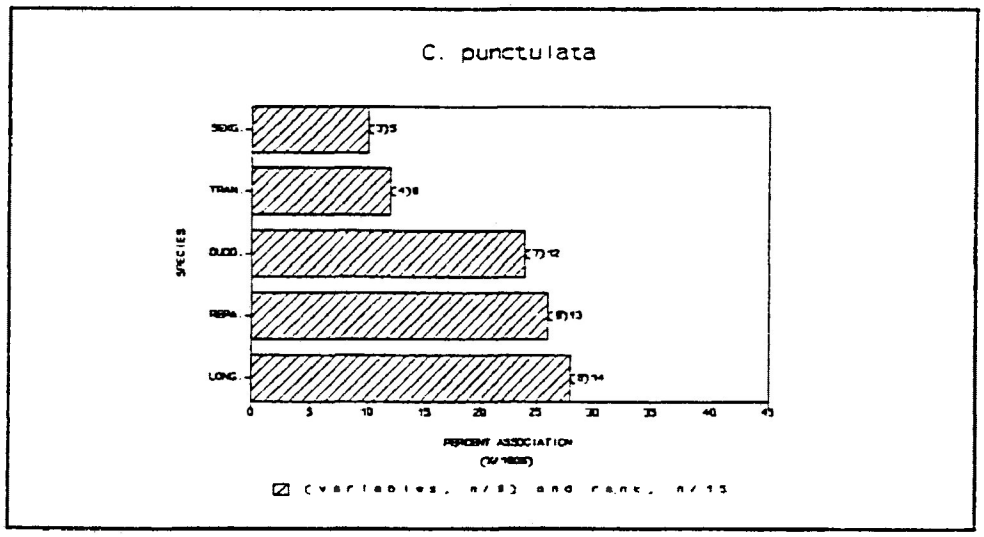
Figure 10b. Coefficients of variation for oscillogram variables (large values).



a.

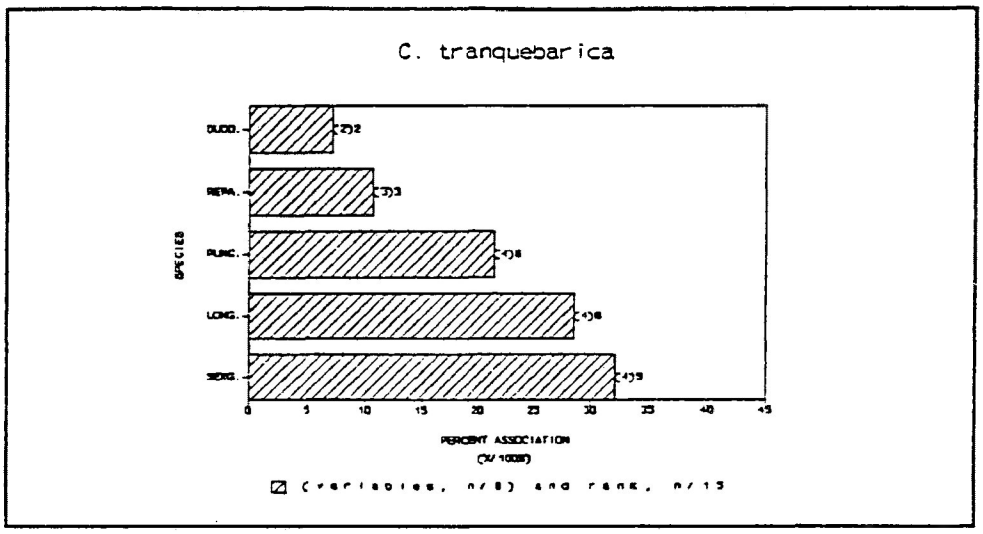


b.

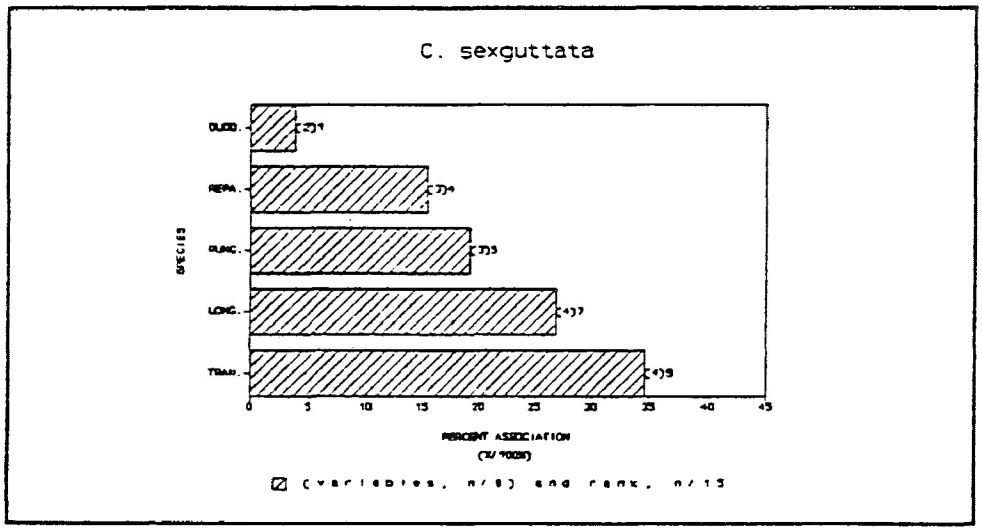


c.

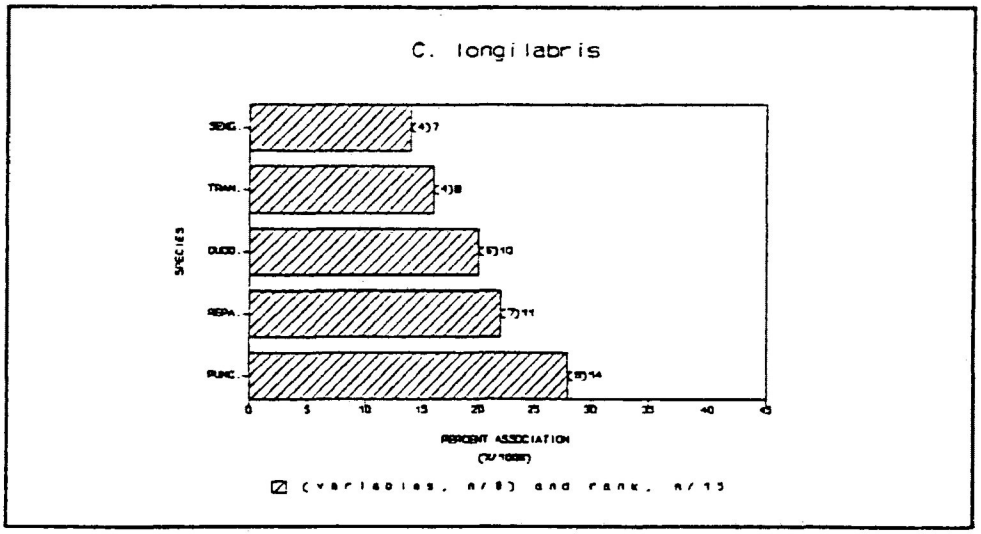
Figure 11. Species pair associations for oscillogram variables.



d.



e.



f.

Figure 11 (continued). Species pair associations for oscillogram variables.

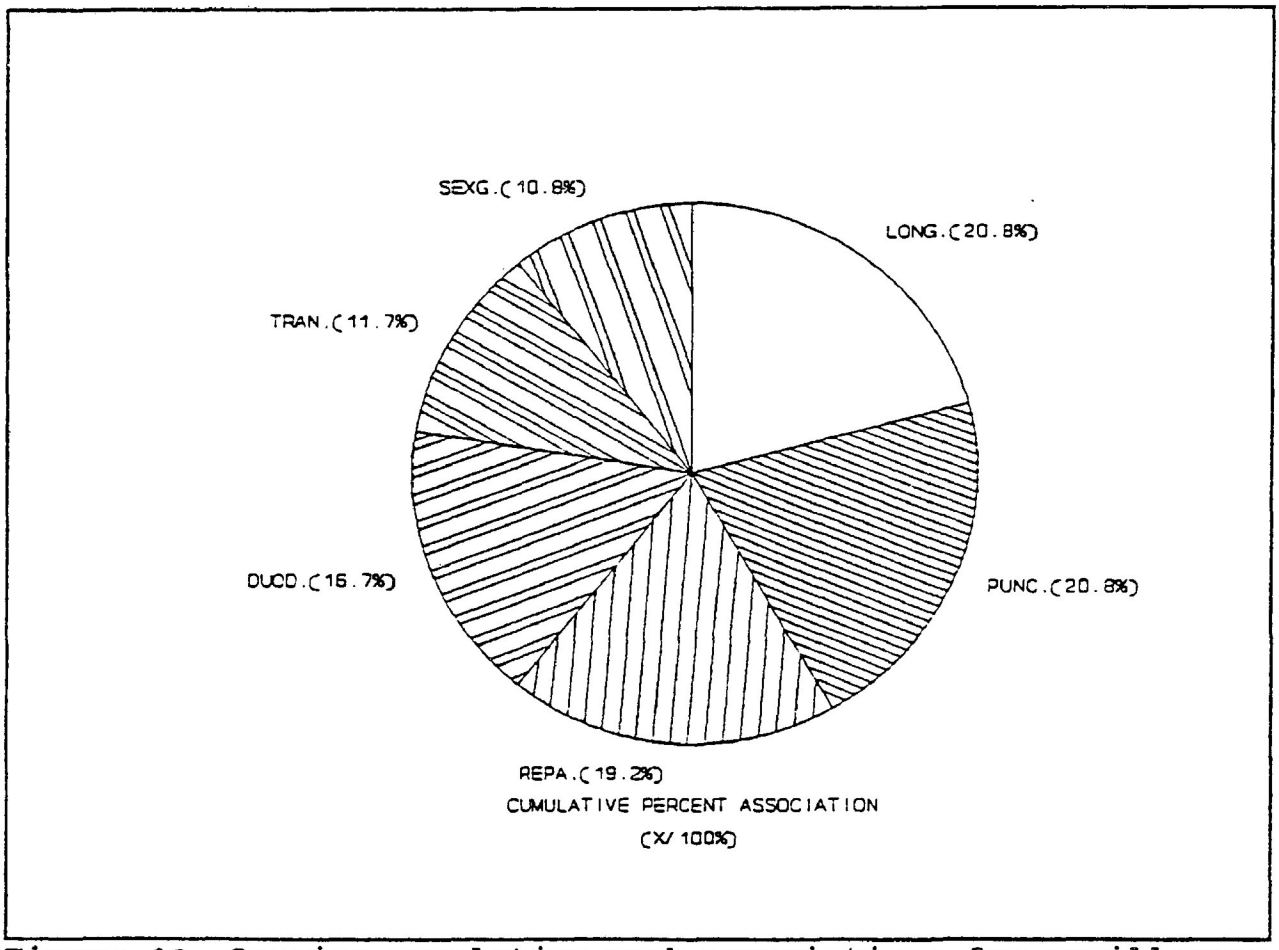


Figure 12. Species cumulative rank associations for oscillogram variables.

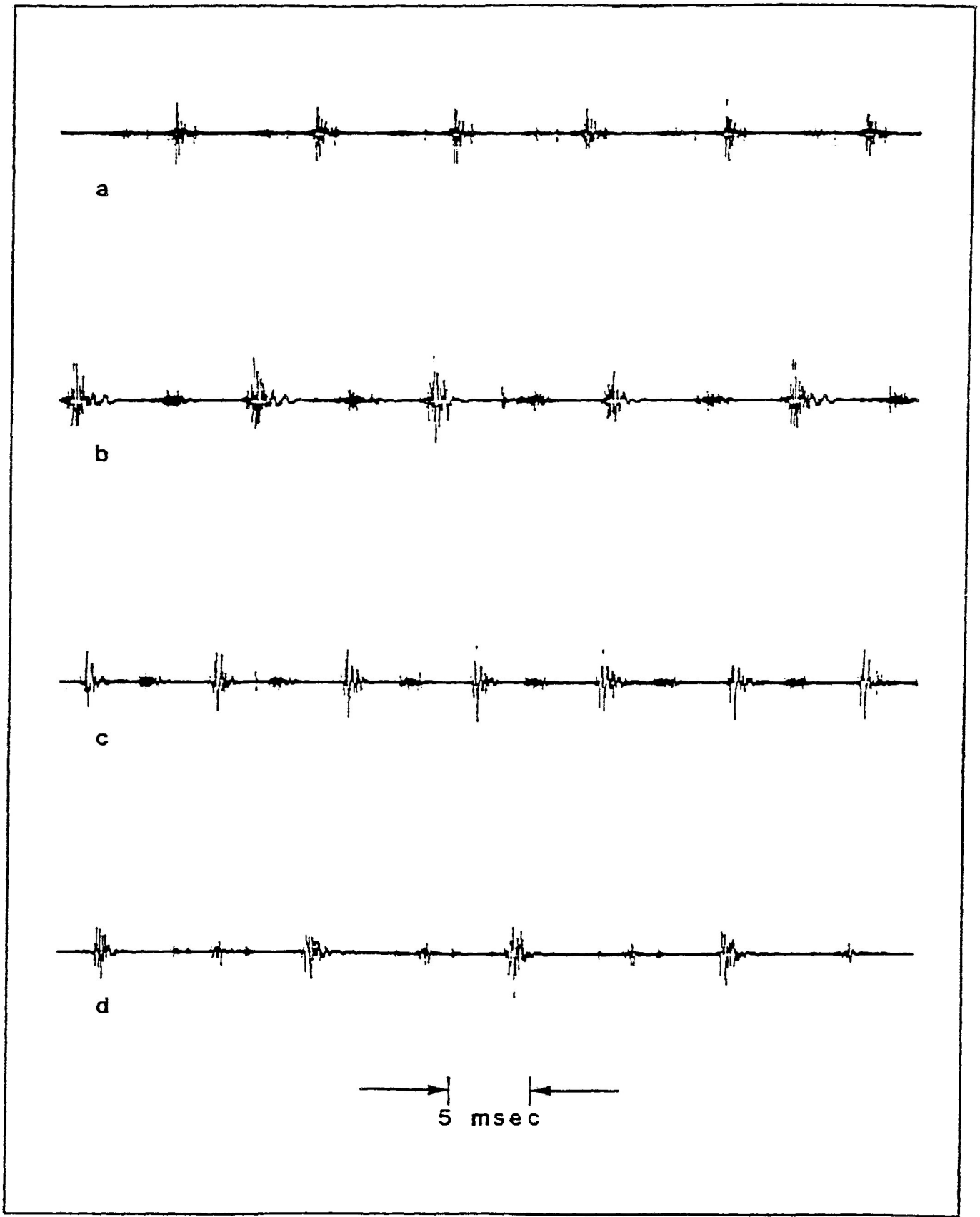


Figure 13. Middle segments of selected oscillograms. a, ♀ REPA. (40°C); b, ♀ DUOD. (40°C); c, ♀ PUNC. (40°C); d, ♀ TRAN. (40°C).

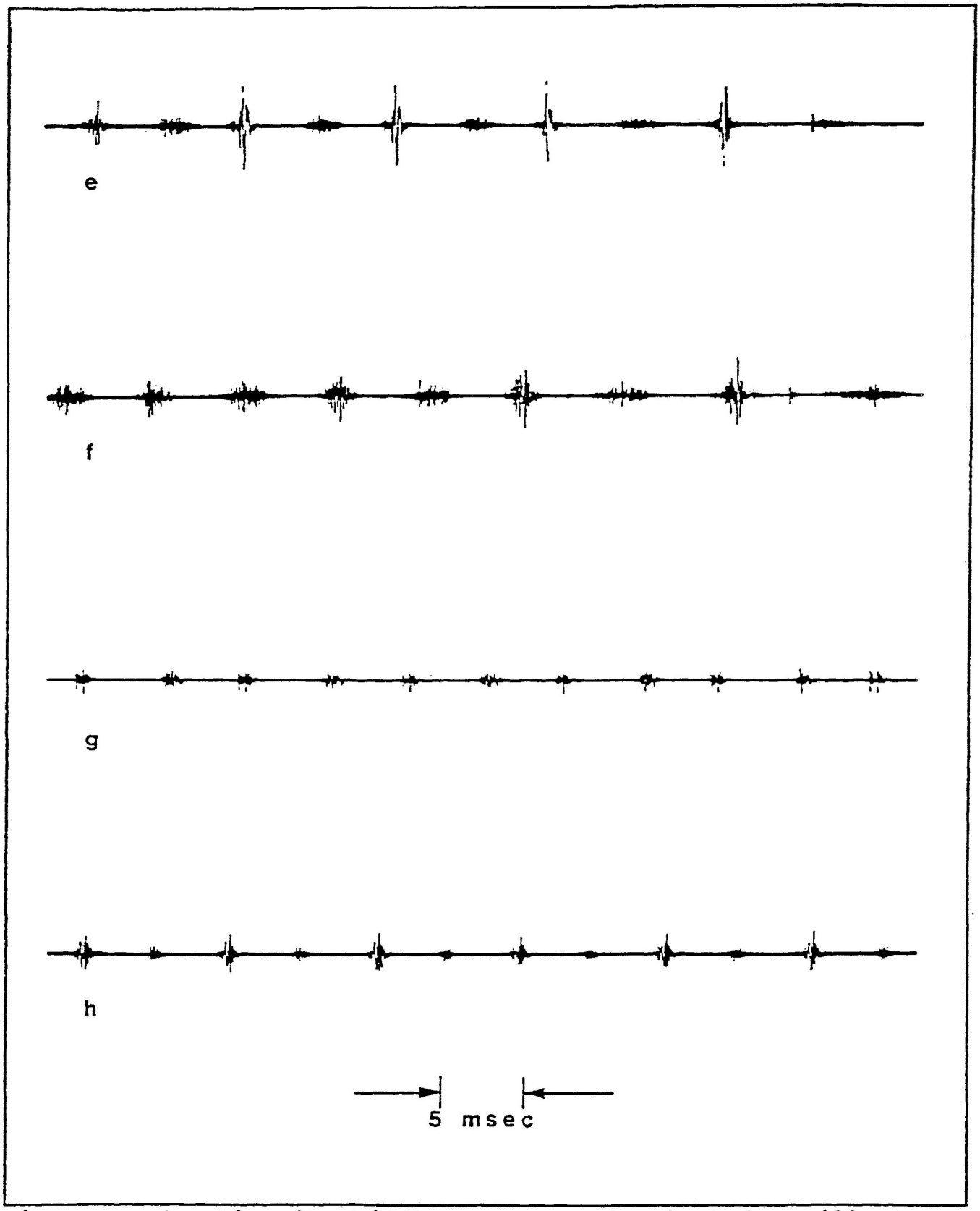


Figure 13 (continued). Middle segments of selected oscillograms. e, ♀ SEXG. (40°C); f, ♀ LONG. (40°C); g, ♂ REPA. (40°C); h, ♂ DUOD. (40°C).

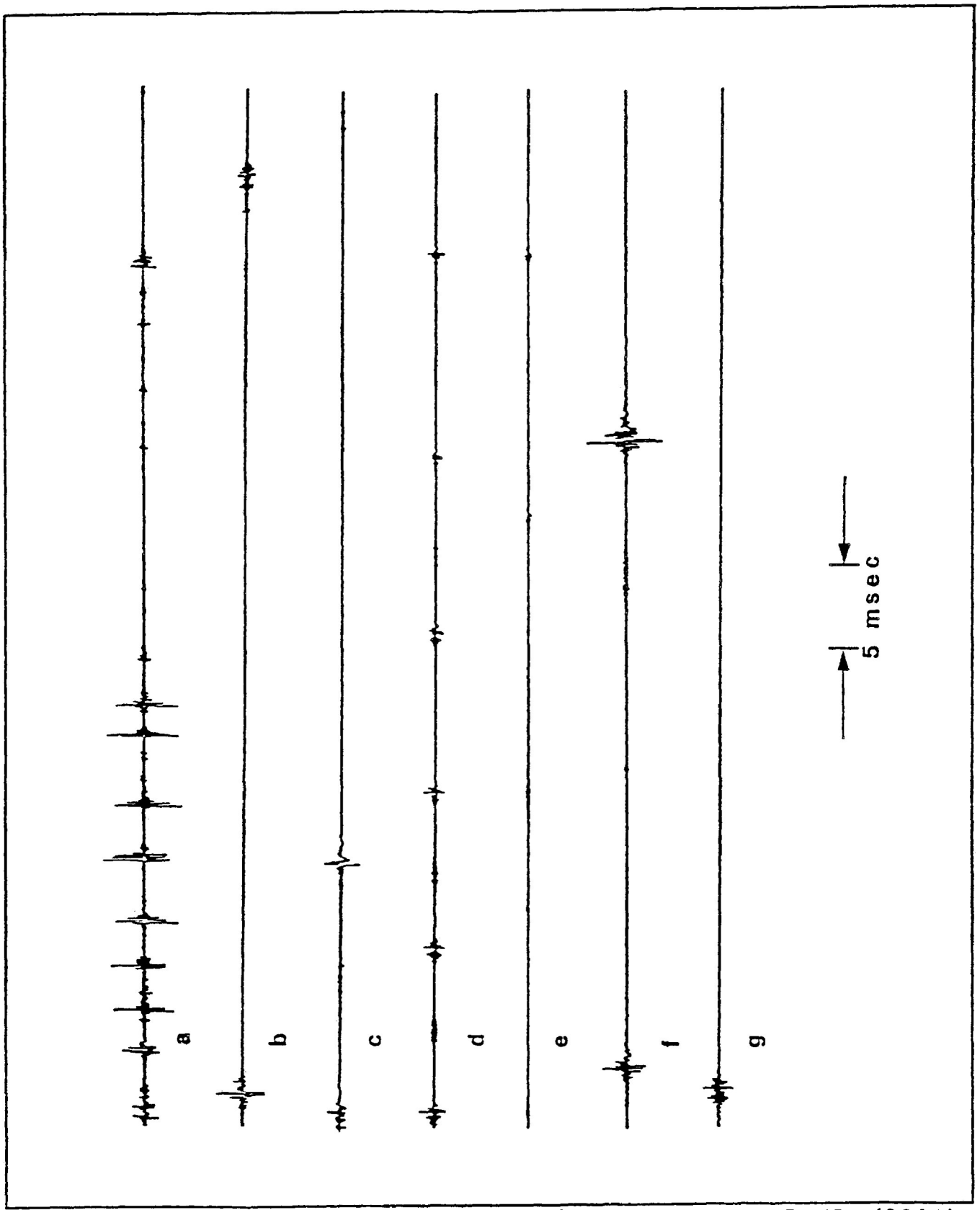
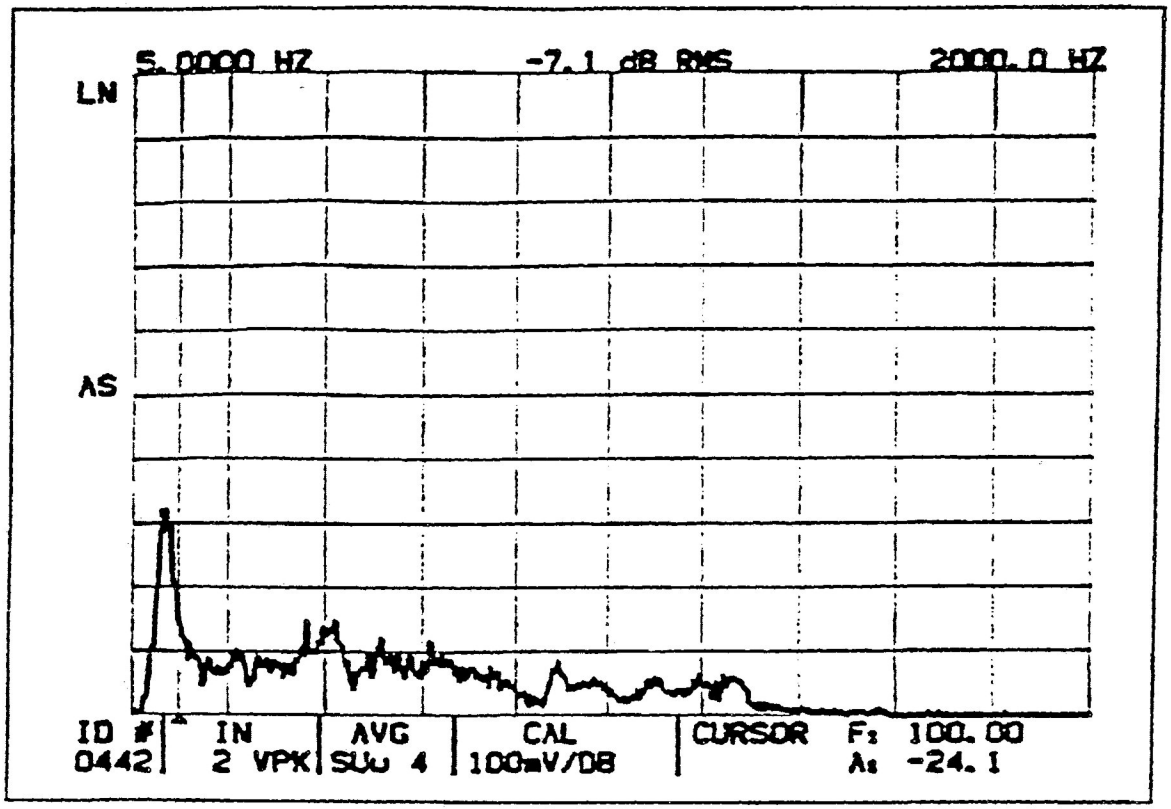
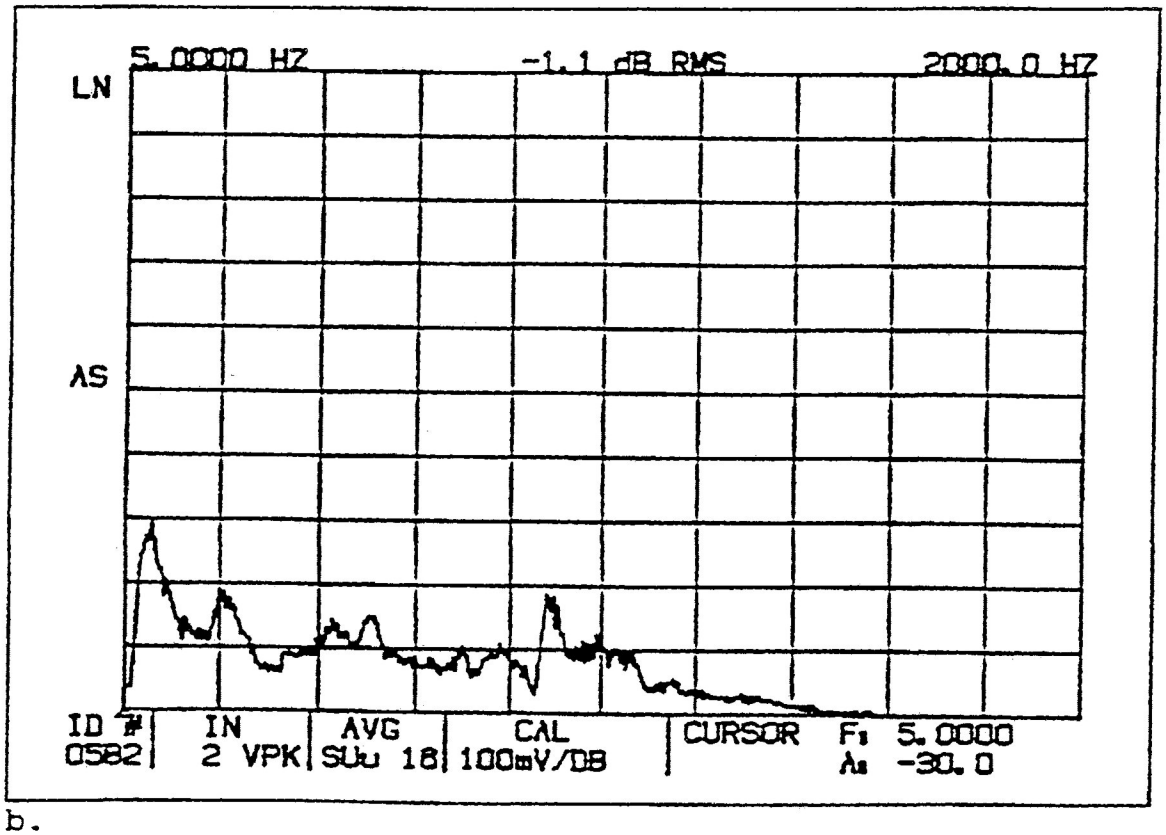


Figure 14. Initiations of selected oscillograms. a, ♂ LONG. (38°C); b, ♀ LONG. (44°C); c, ♂ REPA. (40°C); d, ♂ DUOD. (38°C); e, ♂ PUNC. (47°C); f, ♂ TRAN. (38°C); g, ♂ SEXG. (40°C).

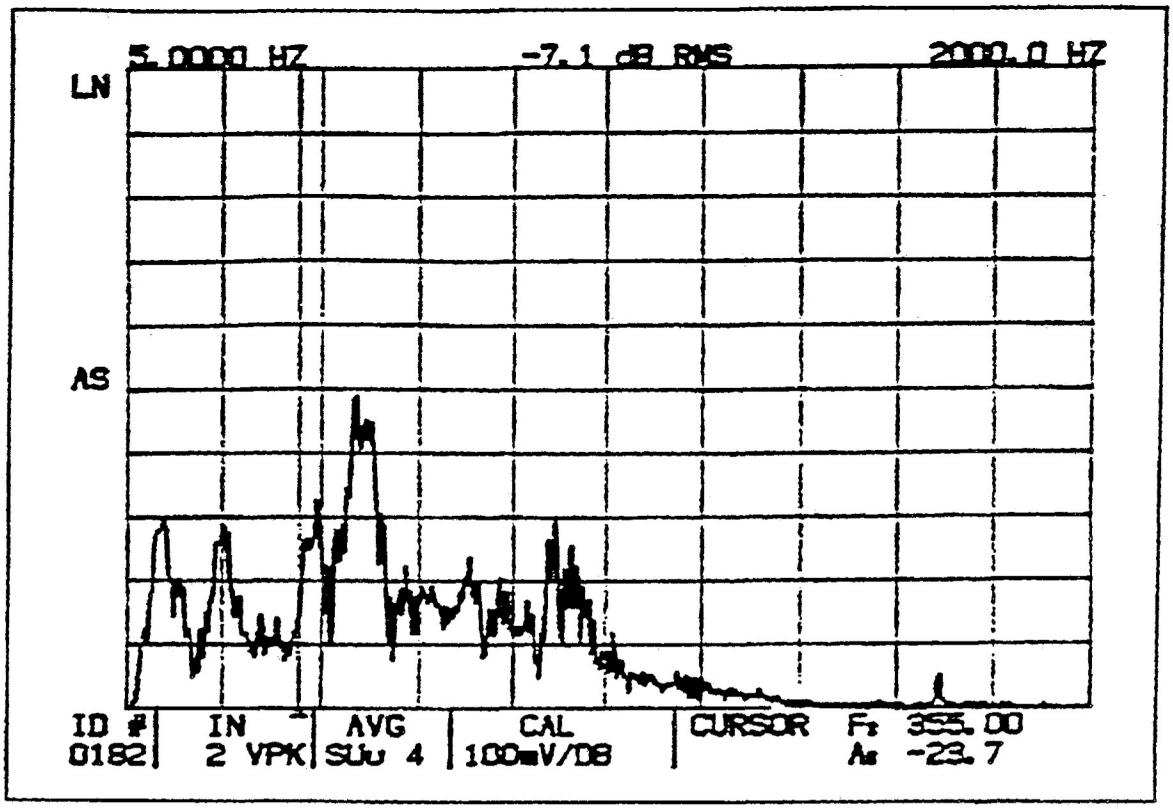


a.

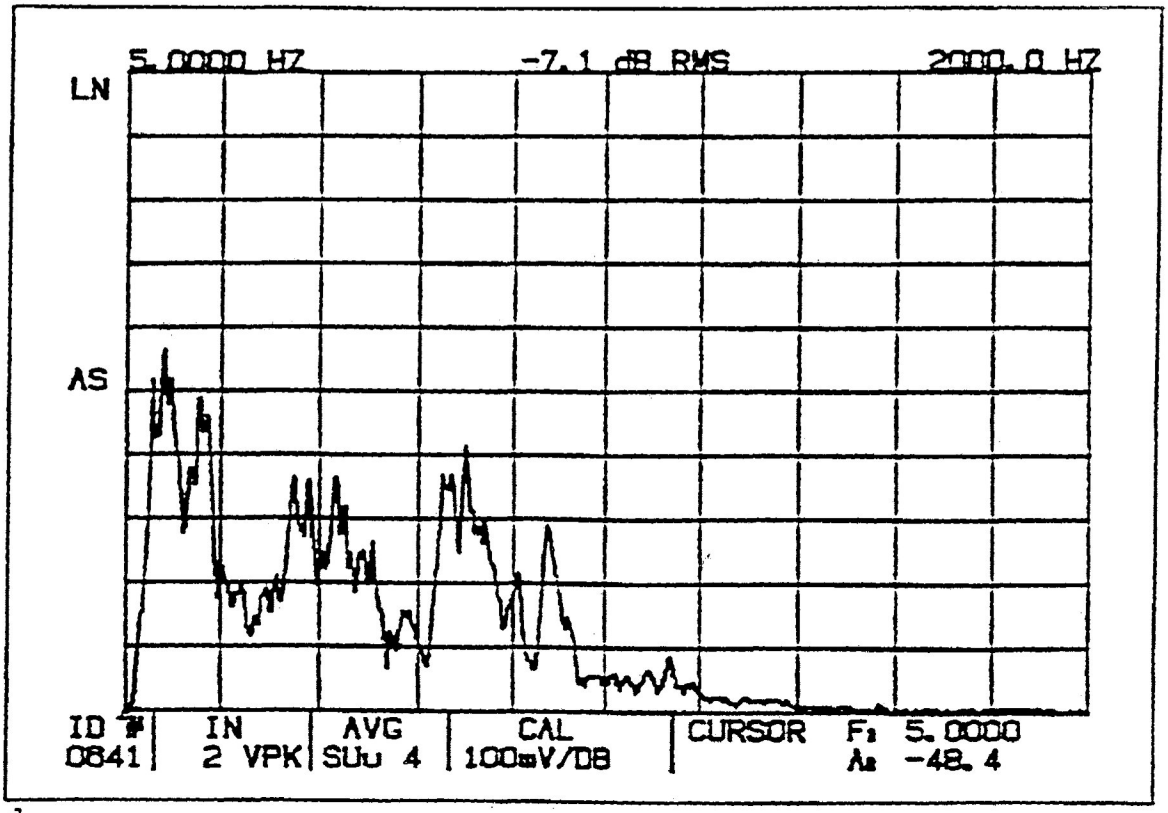


b.

Figure 15. Selected frequency spectrogram averages. a, ♂ REPA. (35°C); b, ♂ DUOD. (36°C).

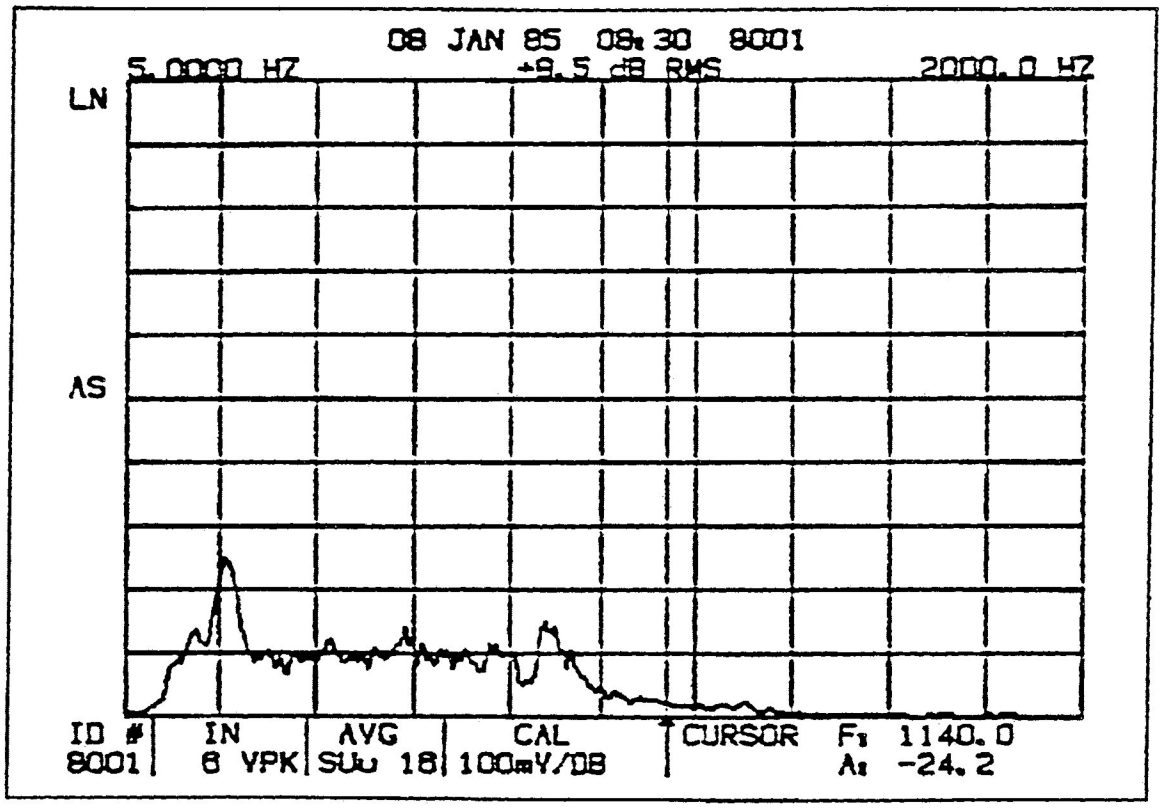


c.



d.

Figure 15 (continued). Selected frequency spectrogram averages. c, ♂ PUNC. (44°C); d, ♂ TRAN. (36°C).



e.

Figure 15 (continued). Selected frequency spectrogram averages. e, ♂ SEXG. (38°C).

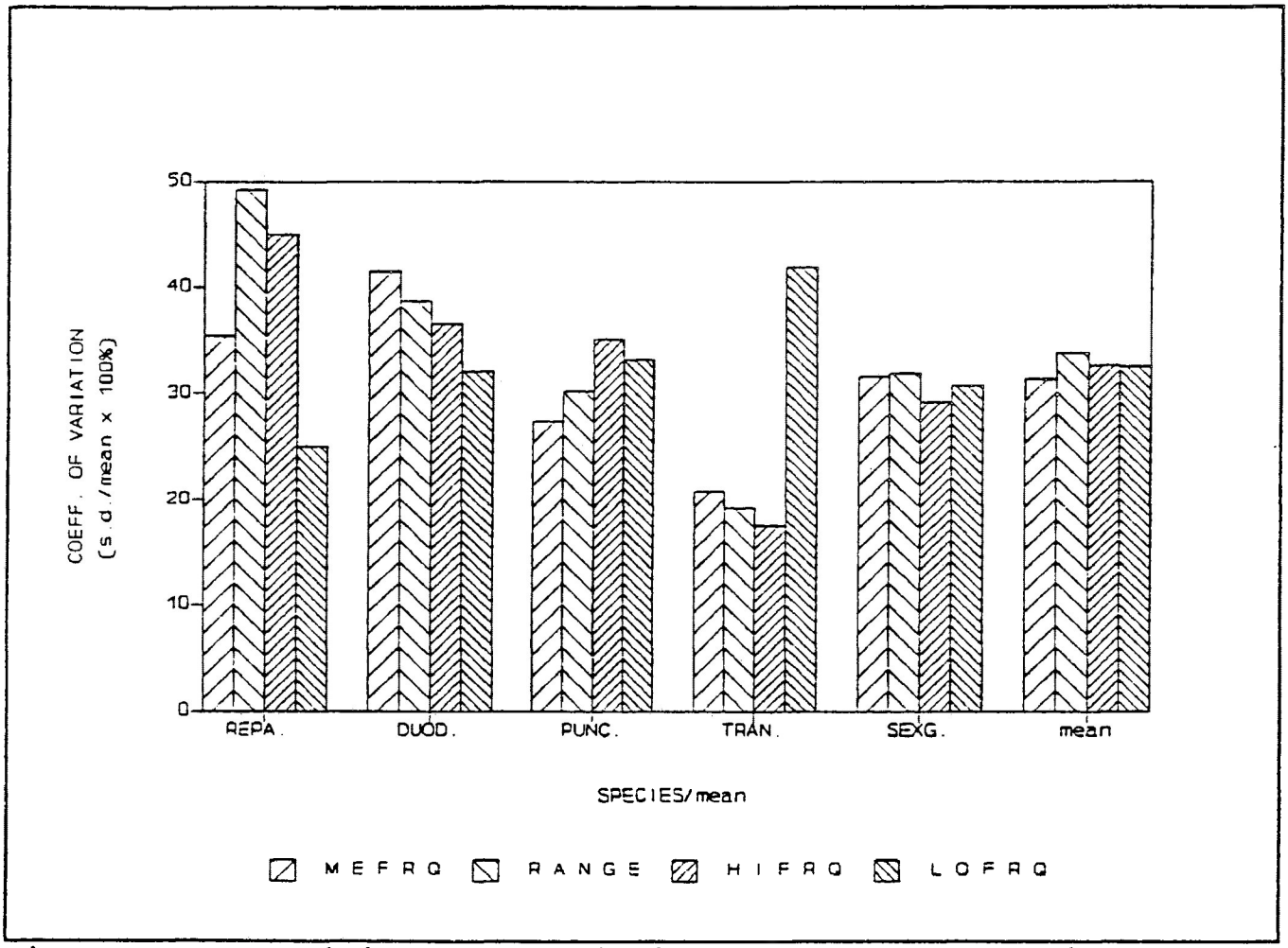
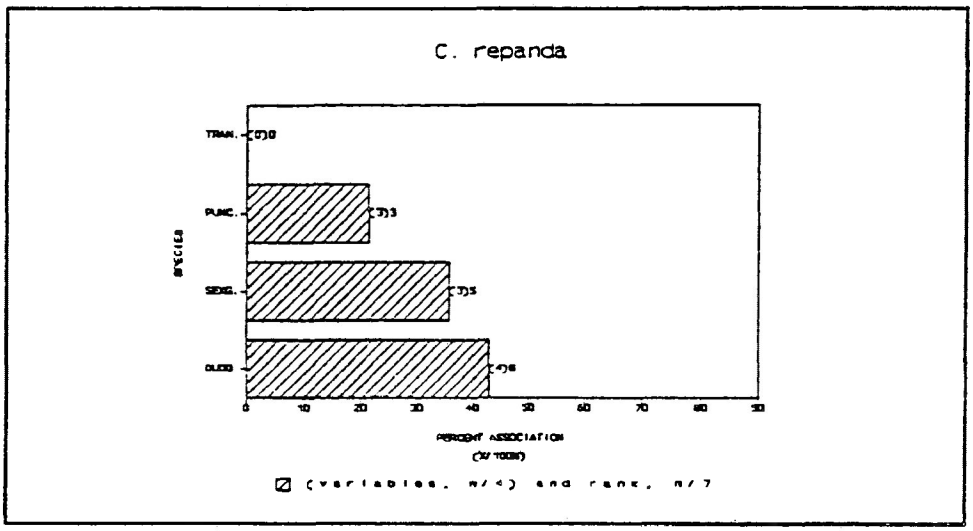
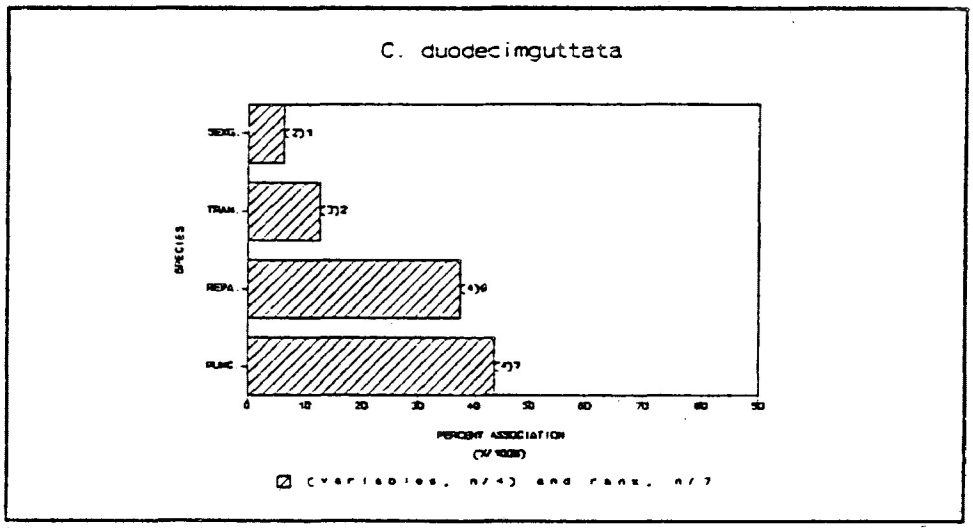


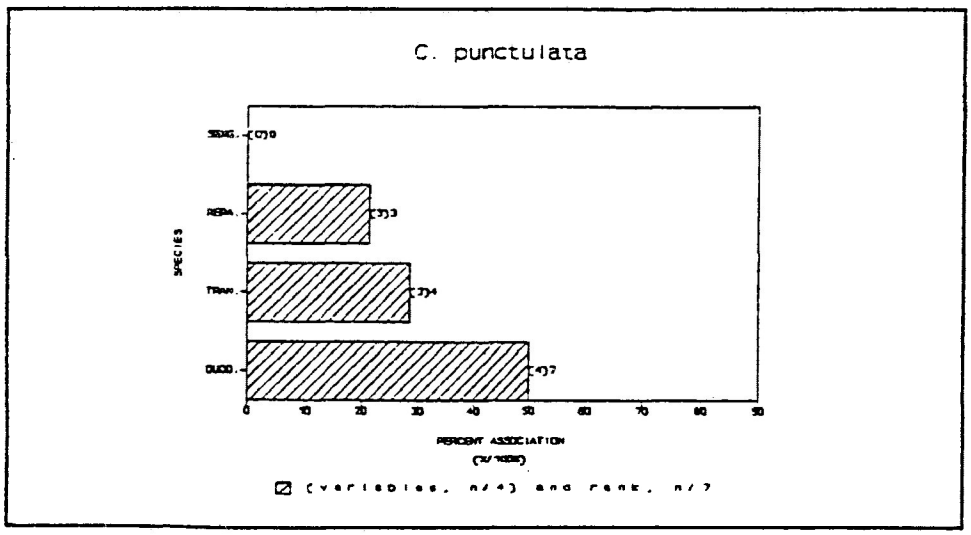
Figure 17. Coefficients of variation for frequency variables.



a.

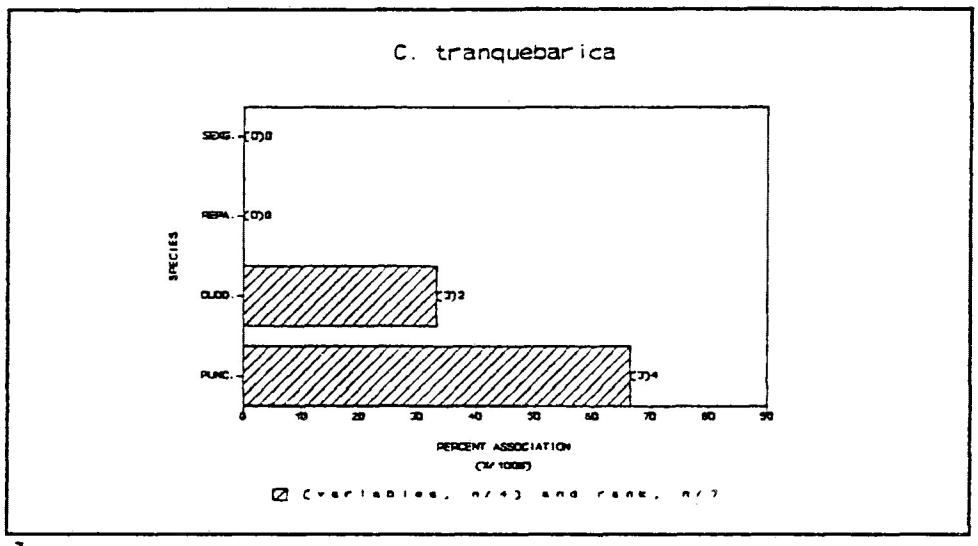


b.

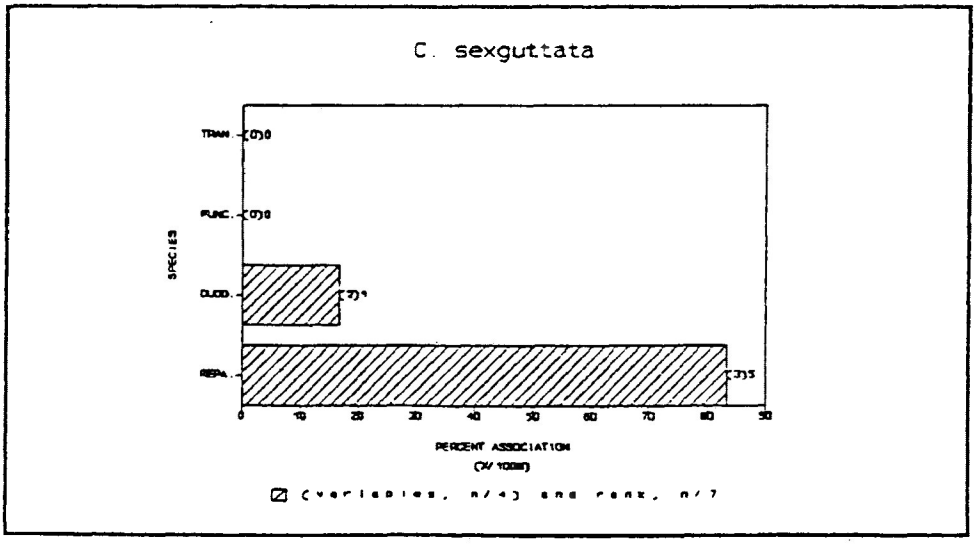


c.

Figure 18. Species pair associations for frequency variables.



d.



e.

Figure 18 (continued). Species pair associations for frequency variables.

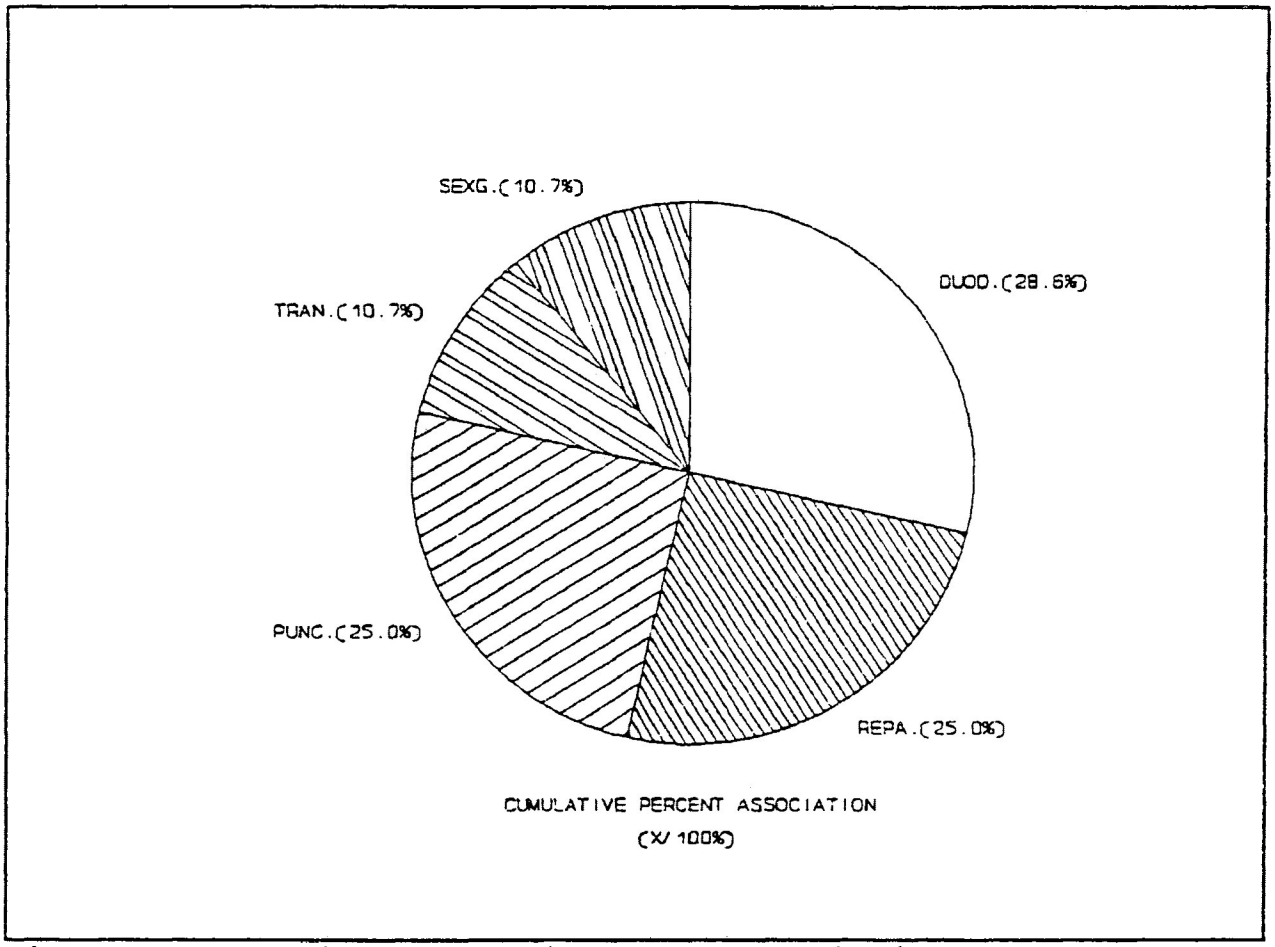


Figure 19. Species cumulative rank associations for frequency variables.