#### O P U S C U L A E N T O M O L O G I C A SUPPLEMENTUM X

# INSECT DRUMMERS

A STUDY ON THE MORPHOLOGY AND FUNCTION OF THE SOUND-PRODUCING ORGAN OF SWEDISH HOMOPTERA AUCHENORRHYNCHA

WITH NOTES ON THEIR SOUND-PRODUCTION

BY.

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WITH 13 PLATES, 12 TABLES AND 1 TEXT-FIGURE

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## Acknowledgements

The present dissertation could not have been written without the direct or indirect co-operation of various persons or without the support of a number of institutions. I am happy to seize this opportunity of here conveying to them all my sincere thanks.

To all my University teachers during my years as a student at Lund I wish in the first place to express my respectful gratitude. Several of them have not only been of the utmost importance for my studies but have also greatly influenced my personal development both as scientist and human being.

The late Professor N. A. Kemner directed my training in entomology during my time at Lund. It was he, too, who interested me in the study of the Hemiptera, especially our Swedish Auchenorrhyncha. Professor Kemner's intense enthusiasm for entomology as a science exerted an extremely stimulating influence on me as well as on so many other of his students. Without this influence my studies might have taken a different direction. I have reason to be most grateful to Professor Kemner for his unfailing readiness to give me active assistance in word and deed. During my time as assistant at the Entomological Museum the relationship between Professor Kemner and myself changed to one of firm personal friendship, which I shall always recall with great joy and deep gratitude.

It has been my inestimable privilege of having as my teachers in zoology Professor Bertil Hanström, Professor Torsten Gislén and Docent Gustap Thulin. If with such teachers I have not become a good zoologist then the fault is entirely mine. To Professor Hanström and Professor Gislén it is besides my pleasant duty to proffer my sincere thanks for the work they have expended on reading the manuscript of the present dissertation and for their good advice and valuable, positive criticism in this connection.

Several colleagues and fellow-workers at the Zoological Institute in Lund and particularly at the Entomological Museum have exerted an influence on me which I value most highly. Here I will mention only Docent KJELL ANDER, whose lively and self-sacrificing interest in the science of entomology has aroused my intense admiration and whose contribution as scientist has seemed to me a noble example. I feel glad about the friendship he has always shown me and thank him for much good advice.

During 1938 my investigations into the sound-producing organ of the Auchenorrhyncha were mainly carried on at the Chemical Institute in Lund, where accommodation was made available to me for which I am indebted to Professors L. Smith and H. Bodforss.

After leaving Lund in 1940 I have continued my investigations at the Swedish Institute of Plant Protection, where I have been employed since that date. I owe a debt of gratitude to the Director of that Institute, Dr. Th.

LINDFORS, for having been allowed, in my spare time, to use the rooms and technical resources of the Institute for my research. For friendly interest, encouragement and help in various connections I wish to thank the head of the Department of Zoology of the Institute, Mr. O. Ahlberg, Fil. Lic. For their constant helpfulness and much good advice I am indebted to my colleagues, Mr. B. Tunblad, Fil. Mag., and Dr. Daniel Lihnell.

I am under an obligation to Professor Fritz Buchthal of Copenhagen for his extreme readiness to acquaint me with valuable information by letter. It was also a great advantage to be able to discuss certain problems personally with Dr. O. Sotavalta of Helsinki. I am also indebted for the same reason to Professor Anders Biberg formerly of the Royal Academy of Music in Stockholm. Dr. C. E. Pemberton of the Experiment Station of the Hawaiian Sugar Planters' Association in Honolulu has helped me very much by lending me Kirkaldy's publication referred to below. Dr. P. W. Oman of the National Museum in Washington has procured for me alcoholic material of Magicicada septendecim, which has enabled me to compare directly the tymbal apparatus of this cicada with that of the small Swedish Auchenorrhyncha.

For technical recommendations and directions and practical assistance I am greatly indebted to Dr. Fredlund of the A.-B. Elektrolux laboratories in Stockholm and to Mr. Ake Janzon, civil engineer, Djursholm.

To the Royal Board of Swedish Telegraphs, which through Mr. C. T. Lindström, chief engineering clerk, placed a radiograph at my disposal during the summer of 1947, I beg to offer my respectful thanks for the same. A.-B. Radiotjänst (The Swedish Broadcasting Corporation) has rendered me assistance in making gramophone records of the calls of some species of Auchenorrhyncha, for which I beg to thank this institution and my friend Mr. Nils Linnman, Fil. Kand. Recording has also been done by the firm of Westin & Co. of Stockholm, and for his interested co-operation I should like to express my thanks to Mr. Erik Johnson, Director of Music. Soundfilms have been made by the two engineers, Mr. Lennart Hamberg and Mr. Artur Waldersten, whom I wish to thank for their invaluable help.

A special acknowledgement is due to Mr. Gunnar Cronhage, engineer, of A.-B. Elektrolux, who in his leisure time, without remuneration, constructed the amplifier that 1 used in my investigations, and a microphone. I have found these tangible evidences of his skill of very great use.

The English manuscript of this dissertation has been read and revised from the linguistic point of view by Miss Kathleen Pain, B. A., Fil. Kand., Lidingö. I wish to thank her for her scrupulous care and the interest she has shown in this work. I am also much indebted to Mr. Stig Asberg, the artist, who created the drawing on the cover of this paper.

Grants for my investigations have been made by the Royal Physiographical Society in Lund, the Royal Academy of Science, the Helge Axelson Johnson Foundation and the Swedish Natural Science Research Council. For these funds I beg to express my respectful thanks to each of these societies and institutions.

Finally, I will express my heartfelt thanks to my beloved parents, the author K. G. Ossiannilsson, Fil. Kand., and his wife Naëmi Ossiannilsson, Fil. Kand., née Arnman. Up to matriculation they were my only teachers. Although both my parents when studying at the universities of Lund and Uppsala respectively devoted themselves to the humanities, they have from

the beginning in every possible way promoted and encouraged my scientific interests. At the same time they have awakened in me and maintained an interest in other forms of civilized culture, which I regard as a priceless gift. By considerable financial sacrifices my parents have themselves defrayed most of the costs of my University education and have thus made it possible. For all that they have done for mc I am deeply and sincerely grateful.

# Introduction

The instrument producing the famous "song" or noise of the mainly exotic cicadas, or the species of the family *Cicadidae*, has been described and reproduced by many authors, among these scientists such as Berlese and Snodgrass. No doubt it may be maintained that this organ has been very well investigated regarding structure, morphology and function.

Just as well as this organ is known, just as slight is the attention that has been shown to the sound-producing organ of the remaining Homoptera Auchenorrhyncha. We are aware of the fact, however, that a sound-producing organ of some kind exists in certain forms. On this matter, WEBER (1930) -- having given an account of the stridulation of certain Cicadidae (Tettigades and other genera) - makes only the following communication (p. 81): "Im übrigen scheinen die Zikaden sowohl wie die auderen Homopteren, mit Ausnahme einiger Kleinzikaden (nach Kirkaldy 1907), kein Stridulationsvermögen zu besitzen." It is worthy of remark that WEBER defines "stridulation" as a sound-production by an apparatus consisting of a "pars stridens" and a "plectrum". Thus, the tymbal apparatus of cicadas is not a stridulatory organ in this sense of the word. The "Kleinzikaden" alluded to, on the other hand, are regarded as possessing a true stridulatory apparatus. In "Lehrbuch der Entomologie" (1933), too, Weber makes clear that the "Trommelorgan" in his opinion is peculiar to the Cicadidae, while "gewisse Kleinzikaden" possess a stridulatory apparatus in the sense above precised.

In IMMS (1925), p. 336, we read the following:

"Among Homoptera, the sound-producing organs of the Cicadidae are complex structures peculiar to the family, and situated one on either side of the ventral aspect of the base of the abdomen . . . The remaining Auchenorrhyncha are usually regarded as being silent, but Kirkaldy (1907) states that several leaf-hoppers possess the power of stridulation."

In Schröder's "Handbuch der Entomologie", Band I, Prochnow (1912) gives an account of the sound-organs of cicadas and their function but mentions nothing whatever about any sound-production in the remaining Auchenorrhyncha.

In Part III of Schröder's "Handbuch", Handlinsch (1925) divides the suborder Cicadariae into the family Cicadidae with "Zirporgan" and, on the other hand, the remaining families without this organ.

In the standard works above cited, thus, no information on the sound-production or on the sound-producing organ of auchenorrhynchous *Homoptera* other than the *Cicadidae* is presented, except the reference to KIRKALDY 1907.

As the paper of Kirkaldy above cited was published in a periodical not available in this country, the passage treating of the sound-production of leaf-hoppers (pp. 7—8) is here reproduced in extenso:

#### "RIOLOGIC NOTES.

#### Stridulation.

In my first memoir (p. 285) it was stated that though Perkinsiella saccharicida had often been heard to stridulate distinctly, by the Entomologists of this Station, researches on the phenomenon had not yet been made.

On his return from Fiji, Mr. Muir handed me the following notes, upon which it is scarcely necessary to enlarge:

"One hot, still morning, when collecting in Fiji, my attention was attracted to a small palm, from which a distinct noise of insects stridulating proceeded. I found the underside of the leaves covered with hundreds of a small red leafhopper (Muiria stridula Pl. 20 figs. 10—13). Their tegmina and wings were erected above the back and occasionally gave one or two rapid movements; sometimes the abdomen was jerked up and down. I recognized it as similar to one I had taken in Natal some years ago, in which the wings were exceedingly small and used entirely as stridulating organs. Upon examination I found the wings in the present species were likewise used for that purpose. The tegmina are about 6 mill. long, whilst the wings are only half a millimetre, the anal lobe being larger than the rest of the wing, thickened and corrugated on the hind margin of the upper side.

"The costal margin is turned over and catches into a fold along the margin of the tegmina; by this means it moves with the tegmina. The corrugated surface is opposed to the anterior angles of the abdomen where there are several white bristles situated.

"In another, (*Proutista moesta* Pl. 20 figs. 8—9) from Java, the tegmina are about  $5^{-1}/_2$  mill, long and the wings 3 mill., the anal area larger in proportion to the rest of the wing and corrugated on the upper side.

"In another (Pyrrhoneura saccharicida Pl. 20 figs. 6-7), from Fiji, the tegmina are about 4 mill, long and the wings 3 mill, the broad edge of the anal area being corrugated. The corrugations thin out gradually on each side, and one can see that they are only a prolongation and intensification of the minute corrugations that border the hind margin of the wing from the end of the costal margin to the base of the wing.

"In another (*Lycicen inthurni*, Pl. 20 figs. 3—5), from Fiji, the proportional size of the tegmina to the wings is more normal, about  $7^{-1}/_2$  to  $5^{-1}/_2$ , and the anal areas of the latter are normal, bearing a strongly corrugated patch near the basal edge.

"Upon examining the anal area of the wing of Perkinsiella saccharicida, an enlarging of the corrugation along the basal portion of the edge can be seen. I am in doubt if this could be the means by which they produce the sound."

I have examined a considerable amount of material and find the stridulatory area developed as follows:

In most of the Derbidae and in some Asiracidae, this structure is present, in both sexes. I cannot find it in any other Auchenorhynchi, nor in those Asiracids in which the wings are rudimentary.

Since my last memoir, Froggati has published "Australian Insects" (1907), in which there are short biologic notes on several Homoptera."

I have not been able to find any account of any special investigations on the sound-producing organ of the Auchenorrhyncha (except the Cicadidae) in the literature. In taxonomic or faunistic papers on the Auchenorrhyncha, a pair of intraabdominal apodemes observed by the authors in certain typhlocybids is sometimes mentioned. Some function for sound-production is often ascribed to these apodemes. For example, GIARD (1889, pp. 709—710) mentions their presence in Typhlocyba and conjectures that they are homologous with the sound-producing apparatus of male cicadas. He erroneously states

that they arise from the first abdominal segment, however. He describes their reduction in specimens parasitized by *Ateleneura spuria* (Dipt.) and *Aphelopus melaleucus* (Hym.).

The form of these apodemes is used by Poos (1933), Paoli (1930, 1931, 1932, 1936), and Oman-Wheeler (1938) as a character for the separation of species of *Empoasca*. Paoli (1930) mentions that two great muscle bundles are attached to these apodemes and guesses that these muscles have something to do with the male sexual function, as they are lacking in the females.

In a paper entitled "A Suspected Sound-Producing Organ in Empoasca devastans" (1933), George has bestowed four pages including four figures on this organ. He describes the plates and the corresponding muscles — not quite correctly, however, as he states that the largest of these muscles is anteriorly attached to "the junction of the metathoracic and the first abdominal sterna". He believes that "the contraction of the oblique muscle, attached to the concave side of the plate, will turn the plate convex inside and concave outside" and that "if the plate is thus turned suddenly from concave to convex, and convex to concave, from the nature of the chitin a smart clicking sound ought to result". As we may learn from this account, George regards the apodemes of *Empoasca* as functionally analogous to the "tymbal" of cicadas. Of course, as the latter is a tergal organ, no homology with the apodemes of *Empoasca* is possible; nevertheless, George in his explanations of figures designates these apodemes as "timbal plates".

RIBAUT (1936) includes the possession of an "appareil stridulatoire" in the male among the five characters separating typhlocybids from jassids. He describes (p. 30) briefly the apodemes of the second abdominal stermum in Typhlocybids and the muscles attached to them. He states correctly that the anterior insertion of the largest of these muscles is found on the first abdominal sternum, which he believes serves as the vibratory membrane.

EVANS (1946) found a pair of "ridged bosses" on the first abdominal tergum of *Darthula* and *Actolion*. He compares these with the tymbals of cicadas and writes: "Whether these structures are sound-producing organs, and whether functional or not, cannot be determined from the dried specimens which have been available for study."

I have not been able to find any additional first-hand information on the sound-producing organ and its functions in the leaf-hoppers in the literature available to me. However, this subject has seemed to me well worth the trouble of a closer investigation. I have summarized the results of my studies very briefly in three earlier papers (1946, 1946/1947, 1948 b). A full account of these results is now presented below.

Chapter I comprises descriptions of the sound-producing organ in a series of Swedish species. The purpose of this paper is mainly to determine whether the sound-organ of cicadas is in reality peculiar to them. Descriptions of the integument and the muscles in the corresponding part of the body of representatives of as many different groups as possible are an indispensable part of such an analysis, of course. With the intention of arriving at an understanding of the structural variation of the sound-producing organ in the groups represented, as many species as possible have been examined and described. In fact, I have examined all the species of which I was able to get a sufficient material. In cicadids, as we know, the males only are in possession of a functional sound-organ of the kind here intended. If it is

assumed that this is the case in the remaining groups of Auchenorphyncha too, an investigation of the corresponding parts of the body of the females may be expected to throw light on the question of what parts of the male are essential as constituents of the organ in question. Therefore, the females of several forms have also been studied. However, the sound-organ of the cicadas has not been created from nothing; it is the result of a reconstruction and specialization of parts originally present in all insects. Thus, the big sound-producing tymbal-muscle is only a common segmental dorsoventral muscle (cf. Weber 1933). Therefore, it is only to be expected that the corresponding muscles and other parts will be found in other Auchenorrhyncha too, and, if this is the case, it does not prove that they have the capacity of working as a sound-producing organ. Hence the morphological investigation alone is not sufficient. It must be completed by a study on the sound-production. My observations on the latter in a number of species are presented in Chapter 2. The descriptions of the different calls I have tried to reconstruct in this chapter may be of some interest even in relation to other questions, but the principal aim of these studies has been to determine whether a power of sound-production is present at all, and whether differences in the sound produced may be connected with differences in the structure of the sound-organ. All the observations that would contribute to throw some light on the function of this organ are presented in this chapter. Further, several biological observations are related here. The biology of the sound-production is only a secondary subject of this paper, but I have found it best to publish in the present connection all the observations that I have hitherto made on the sound-production of our Auchenorrhyncha. When possible I have tried to discover whether the females are capable of any sound-production, in order to be able to combine the facts acquired in this way with the morphological conditions of the females.

The first two chapters together form the special part of this paper. In Chapter 3 the morphological results are summed up. The next chapter deals with the function of the sound-producing organ. The fact that the sound-organ exists even in *Auchenorrhyncha* other than the *Cicadidae* will modify our views on the taxonomy of the group. For the present, however, too much theorizing on the significance of the differences in the various genera would be premature until the studies have been extended even to families not represented in Sweden. Chapter 5, being an account of my speculations in this connection, contains but a few general conclusions and notes on certain points concerning native genera.

In Chapter 6 the results of a few experiments concerning the influence of external conditions on the sound-production are presented, and some biological aspects in this connection are considered. It is obvious, of course, that the question of the biological significance of the sound-production is too extensive and complex a problem to be discussed thoroughly on the basis of the observations hitherto made by me. I hope to be able to study the biology of the sound-production of the *Auchenorrhyncha* more closely in the future. The present observations are only a small contribution.

#### Material and Methods

The specimens examined have as a rule been collected by me in localities precised in the text in connection with the species. For my morphological studies I have used material fixed in 70 % alcohol and subsequently embedded in paraffin wax in the ordinary way. For this material I have mainly used the method of dissection of halved specimens in paraffin under xylol described by WEBER (1928). Further, thick longitudinal and transverse sections have been made with the aid of a razor or scalpel. For comparison, microtome sections have been made of material fixed in Carnov of a few species. These sections were stained with haematoxyline (Heidenhain) and eosin. For the study of the integument and the endoskeletal parts, longitudinally halved specimens were treated with KOH. The muscle preparations as well as the macerated animals were mounted in balsam. In some cases Berlese mixture replaced the balsam. Specimens fixed in alcohol were not available of a few important species: in these cases I had to be content with studying the sclerotic parts after treating dried specimens from my own collection with KOH. My drawings were made with the aid of an Abbe drawing camera. ·

For studying the sound-production, several methods have been used. The first time I heard a spontaneous sound-production from a leaf-hopper (Aphrodes bifasciatus o), I had enclosed the animal in a glass tube measuring  $1 \times 8$  centimetres with some parts of a plant, and put the open end of this tube in my ear. By this method I have heard most of the calls described in this paper, and several species caught during my travels I have been able to study in this way only. For certain purposes the simultaneous seeing and hearing of the animal has been desirable. Certain observations could be made with the tube with the insects in the ear and a mirror. Some calls are so strong that they can be heard very distinctly if the tube with the animal is placed on a suitable sound-board; in most cases I used for this purpose the belly of my violin. Another simple method employed in a few cases consists of a metal wire some decimetres in length, one end of which is rolled spirally round the tube with the animals, while the other end, also spirally wound. is stuck in another glass tube, the closed end of which is kept in the ear of the observer. In this way the insects in the first tube could be watched through the binocular magnifier. The metal wire conducted the sounds but produced in addition some disturbing noise. During the summer of 1947 I used a socalled American stethoscope. This instrument consists of a metal funnel, the wider opening of which is closed by a celluloid membrane, while the narrow end by means of a pair of rubber tubes is connected with two metal tubes inserted in the ears of the listener. The insects were kept in small cages made of celluloid and silk bolting-cloth a few millimetres in height and 2-4 centimetres in diameter. These cages were placed directly on the membrane of the stethoscope. By this arrangement 1 could watch the insects under the binocular magnifier.

To enable me to see the sound-producing apparatus or at least its membrane in function and simultaneously hear the sound produced I used the method of cutting off the wings of the living animal with a pointed pair of scissors and subsequently fixing it in a small pat of plastiline directly on the membrane of the stethoscope or microphone. This method was successful only with species having a "call of distress", which is used if they are kept in confinement. For a corresponding study of species not having this kind of sound-production, it is sometimes possible to benefit by the fact that many species during their death-struggle emit a shorter or longer call. For this purpose the wings are cut off and the animal is killed by a press on the thorax not too hard nor too light. Then the animal lying on the membrane of the stethoscope or microphone is studied under the binocular magnifier. Sometimes the emission of the "dying yell" will be delayed for a minute or two.

From the autumn of 1946 on I had at my disposal an apparatus consisting of microphones and an amplifier. I used two different microphones. One of them (Plate 1, figs. 1-2), made at the instrument makers laboratory of the University of Lund, consists of a crystal under a mica membrane walled in a lead box. When using this microphone the celluloid cage with the insects is put directly on the membrane (Pl. 1, fig. 2). Over the latter a semiglobular metal lid may be placed, if desired (Pl. 1, fig. 1). This lid is closed at the top by a metal stopper. If the lid with the stopper is placed on the microphone, light is completely excluded. The stopper may be exchanged for a cork with a thermometer. The weight of this microphone is about 3.6 kg, that of the lid 0.85 kg. The microphone may be connected up to a three-valve-amplifier for alternating current. This amplifier (Pl. 1, fig. 5) was made by Mr. G. CRONHAGE, engineer, of Riksby. Then the insect calls may be listened to with the aid of a pair of ordinary ear-phones connected to the amplifier, or the latter may be connected to an ordinary radio receiver by the gramophone input terminals, the calls then being audible from the loud speaker of the receiver. If the latter arrangement is adopted, so-called acoustical feed-back will readily set in, if the microphone without its lid is placed in the same room as the receiver. To prevent this I kept the microphone in a vibration isolating box of iron-plate 3 mm thick (Plate 1, fig. 3), lined on the inside with so-called stenite (A,-B, Arki, Stockholm). The lid of this box consists of three plates of glass of two different thicknesses separated by thin air layers, and a wooden frame. This box I kept on a substratum of cotton.

The microphone above described was used for making the gramophone records. These records were made with the assistance of the record department of Radiotjänst (the Swedish Broadcasting Corporation) and of the firm of Westin & Co. in Stockholm.

My second microphone was made by Mr. CRONHAGE and is of the electromagnetic kind. This microphone was at my disposal from the middle of the summer of 1947 and was used for certain temperature experiments in a thermostat. During these experiments the cages with the insects were placed directly on the membrane of the microphone, while the thermometer was resting on the margin of the latter. A cylinder of thick glass, above and below plugged with cotton (Plate 1, fig. 4), enclosed the microphone in order to avoid

too great losses of heat by the opening of the door of the thermostat at the reading off of the temperature, and to effect a certain vibration insulation.

For registering the rhythm of the calls I used a so-called radiograph (Bolinder, Pl. 1, fig. 6). This apparatus, by the courtesy of the Board of Management of the Royal Telegraph Service, was at my disposal during July, August and September 1947. The radiograph is made for the automatic registration of Morse marconigrams and writes with a special ink on a strip of paper set running at an adjustable speed by an electromotor, a so-called puller. The writing nib reacts by means of a vibrating movement with a frequency of 200 periods per second to impulses received. Higher frequencies therefore cannot be studied with the aid of this apparatus, but the drumming sounds emitted by many species of Auchenorrhyncha may be registered very satisfactorily, if they are not too weak. I used the radiograph connected to my amplifier mentioned above. At the same time the sounds may be heard if a pair of ear-phones is connected to the radiograph. A series of calls of a number of species registered in this way is reproduced on Plate 13.

For determining pitch I made use of comparison with the violin, when possible. During my travels I was compelled to be content with comparing with a tuning-fork. Of course these determinations of the pitch are but approximate, and when I used the tuning-fork only, a certain cause of uncertainty was present, viz. the difficulty of finding out the correct octave. As pointed out by Sotavalta (1947), male observers, for reasons analysed by this author, have a tendency to overestimate by one octave the pitch of sounds which they compare with their own singing-voice. The acoustic colour of the calls, too, is often very different from that of our ordinary musical instruments or our own voice. My estimations of pitch, therefore, must be taken with some reserve in many cases. One determination of frequency at least has been made with certainty by sound film recording (page 131; Pl. 12, figs. 1-4). This recording was made with a standard microphone by the Studio Hamberg in Stockholm, and by Mr. Waldersten of A.-B. Film-Teknik, Solna. Other sound film recordings were made from gramophone records. The system of sound film used was the so-called transversal one. From the sound film strips the pitch of the sound may be determined by counting the number of vertical marks per unit length of the "sound-track" and converting this length into seconds. Enlarged copies of parts of the sound-track of the Doratura film are reproduced on Plate 12. The speed of this film was 27.36 metres per minute. The height of the vertical bars of the sound-track illustrates the amplitude of the vibrations recorded.

## Nomenclature and Terminology

Following Evans (1946), I am here applying the division of the Auchenor-rhyncha into three groups: Fulgoromorpha, Cicadomorpha, and Jassidomorpha. No species representing the Cicadomorpha has been described in the present paper. The Jassidomorpha are subdivided into two superfamilies: Cercopoidea and Jassoidea. For the forms belonging to the Jassoidea I am applying, from reasons of convenience, the same system of families as I used in "Svensk insektfauna" (1946—47) and in "Catalogus insectorum Sueciae" (1948), not that proposed by Evans (1947).

For an understanding of the morphology I have used the works of SNODGRASS (1927, 1931, 1935) and Weber (1928, 1933). In the descriptions and drawings of the muscles I follow the system of denominations proposed by Weber. The numbering of the muscles, however, should not be understood as a homologizing with the muscles with the same numbers in the scheme of Weber (1933 pp. 33 ff.). For example, if several dorsal longitudinal muscles are present in the first abdominal segment, the notation I a dlm. will refer to the most medial of these, I a dlm2 being the most medial but one. and so on. Muscles are not necessarily homologous with those with the same numbers in different superfamilies or higher taxonomic units. On the other hand, I have tried to keep the same notations for homologous muscles within the same superfamily, as the Jassoidea. Thus, I a dvm2 is the same muscle in all representatives of the Jassoidea, and if this muscle is not present in a species of this group, as in Cicadella, the notation I a dvm2 is not used, even though several dorsoventral muscles are present in the first abdominal segment.

In recording the songs of some species, a modified system of musical notation has been used. The time value of the notes only approximately corresponds to the actual duration of the sounds. The rhythm of the calls could not easily be fitted into the musical bar system; barring has therefore been left out. As a substitute for barring, rhythm has been marked by the accent sign ('). A rapid drumming is indicated by "TREM". In many species the songs contain a gradually gliding falling or rising in pitch; this is indicated by the term "gliss" (glissando), a zigzag line connecting the notes marking the initial and the terminal pitch (see for instance the note examples on page 59).

The endeavours made to represent the sounds by letters must be taken for what they are: at best they will give an idea of my individual conception of sounds produced by an instrument totally different from the human organ of speech. However, this will be the case with similar endeavours made by numerous other authors to imitate sounds emitted by insects, frogs or birds.

The terms "tone", "note" and "phrase" are used approximately in ac-

cordance with the definitions of BAIER (1930), with the modifications necessary because this author, in formulating his definitions, had his attention directed to stridulation (in the sense of WEBER, cf. p. 4 supra). A "note", then, is a monosyllabic sound (not necessarily one produced by a single movement of the tymbal, which is termed a "beat"); the corresponding term for the drumming or rolling calls is "roll". By the term "song" is intended a fairly constant combination of notes (tones, rolls) and (or) phrases characteristic for the species and as a rule of a limited, not too variable length. A "song" may consist of one single phrase, tone, note or roll, or of a series of such of the same kind; if so, it is termed "simple". A "complicated" song consists of at least two "parts", one of which is a phrase, tone, note or roll or a series of phrases (tones etc.) of the same kind, the other a note (roll etc.) or a series of notes (rolls, phrases etc.) of another kind. Certain terms referring to the biological sense of the sounds emitted are derived from Faber (1932). "Dying yell" is the sound emitted by certain species during the deathstruggle.

The expressions "main tone" and "pitch" are used by me, in the present paper, for what my ear apprehended as a tone in the different calls. In some cases it is concluded that this tone represents the contraction frequency of the tymbal muscle. This terminology does not agree with that of Pierce (The Songs of Insects, Cambridge, Mass., 1948) according to which these expressions would always correspond to the specific vibration of the swinging membrane (tymbal) of the singing insect, while my "main tone", in the cases just referred to, corresponds to a "modulation frequency" of Pierce. I had no opportunity of studying Pierce's interesting work until my present paper was already in proof, but, even though his terminology, from a purely physical standpoint, is doubtless more correct than mine, I could not very well apply it without starting from my own conclusions on Page 112.

Special Part

#### CHAPTER 1

# Descriptions of the Structure of the Sound-Producing Organ in a Number of Species

#### FULGOROMORPHA

#### Family Araeopidae

#### Dicranotropis hamata (Boh.)

Male. In the aracopids, the sound-producing organ is composed of parts belonging to the metapostnotum, the first abdominal segment and the second abdominal segment. The metapostnotum of Dicranotropis of is a comparatively large, strongly sclerotized transverse bridge (Pl. 2, figs. 1, 2, Pl. 3, fig. 1, mpn), strengthened at the inside by a strong transverse phragma (phr). The latter carries on each side a narrow, strongly sclerotized process or arm directed obliquely downward, medially and orally (Pl. 2, fig. 2, Pl. 3, fig. 1, phra). Posteriorly, the metapostnotum touches in this region lateral parts of the first abdominal tergum. The metepimeron, on its hind border, carries the first abdominal spiracle (Pl. 2, figs. 1 and 2, sp<sub>3</sub>). As in the Cicadidae, this spiracle is displaced forward to the metathoracic region, while the second abdominal spiracle topographically belongs to the first abdominal segment (see below; cf. HANDLIRSCH 1899, VOGEL 1923). Ventrally the metepimeron passes into a narrow bridge, which fuses together with that of the other side to a longitudinal beam orally again divided into the shape of a Y (Pl. 3, fig. 1, f).

The first abdominal tergum is medially rather narrow, laterally a little broader (Pl. 2, figs. 1, 2, 4, I). The posterior segmental membrane is on the whole transversely vertical, as is also the case with the strongly deflexed anterior border of the second tergum. The lateral part of the first abdominal tergum is apparently in an articulating connection with the metapostnotum. Behind this connection on the inside of the lateral part of this tergum is a longitudinal fold or list (Pl. 2, figs. 1, 2 and 4, fo). The posterior lateral angle of the first abdominal tergum carries the second abdominal spiracle  $(sp_4)$ .

The first abdominal sternum (I ast) is a very narrow transverse strip carrying five stronger sclerotized parts: one median single hook-like lump (Pl. 2, figs. 2 and 4, h), and on each side 2 thickenings, one in the lateral end of the sternum, the other half-way between the latter and the median lump (matt). This is the most important muscle attachment in this region.

It is transversely longish, apparently hollow and very rough on its posterior surface.

The second abdominal tergum is a medially broad, convex, laterally narrowing plate (Pl. 2, figs. 1, 2, 4, II). Medially, as seen from above, it shows a pair of arched furrows divergent anteriorly and posteriorly (Pl. 2, fig. 1, s); a transverse curved furrow behind their middle connects them. The longitudinal furrows are represented on the inside by strong longitudinal semilunar lists (Pl. 2, fig. 2,  $Io_0$ ). More laterally there is a low transverse list  $(c_{ii})$ . The fore border of the second abdominal tergum is strongly deflexed, forming together with the intersegmental membrane a well marked transverse fold (pl). The deflexed fore border carries on each side in the region of the anterior ends of the longitudinal furrows a transverse row of 3—5 short hairs, probably sense hairs (br).

The second abdominal sternum is a comparatively broad and strong, in its major part darkly pigmented transverse plate (Pl. 2, fig. 4, *H ast*). The fore border is strongly thickened, forming a solid transverse beam (Pl. 2, fig. 2, *H ast*). Laterally this beam carries on each side an upright pole-like apodeme (Pl. 2, fig. 2, *apod*), the free end of which is about spatulate.

The most important muscles in the region of interest in this connection may be studied in figs. 3 and 4 on Plate 2. A strong cylindrical muscle I a  $dlm_1$  runs from the end of the arm of the metapostphragma of each side to the second abdominal tergum, attaching itself medially and laterally of the semilunar list  $fo_{11}$ . More laterally a weaker flat muscle I a  $dlm_2$  connects the hind border of the metaposinotum and the fore border of the second abdominal tergum. This muscle passes a little medially of the longitudinal list fo of the first abdominal tergum. In the second abdominal tergum a corresponding muscle II a dlm runs from the lateral transverse list of this tergum to the antecosta of the third abdominal segment.

In the ventral region the thickening matt of the first abdominal sternum is the attachment of no fewer than 5 muscles on each side. The largest of these I a plm<sub>2</sub> extends to the spatulate end of the apodeme of the second abdominal sternum. The muscle is nearly parallel to the apodeme. A smaller muscle I a vlm<sub>1</sub> extends in a posterior and somewhat lateral direction to the second abdominal sternum medially of the basis of the apodeme. A rather narrow muscle III vlm attaches itself on the metendosternum. A tolerably strong muscle I a dvm<sub>1</sub> has its dorsal attachment on a point on the first abdominal tergum situated medially and in front of the second abdominal spiracle, in the region of the hind end of the longitudinal list to. A fifth muscle a little weaker than the preceding, I a dvm2, is inserted immediately laterally of the second abdominal spiracle. Slightly in front of the dorsal insertion point of I a dvm2 is that of a shorter muscle I a dvm3, arising on the lateral end of the first abdominal sternum. An oblique muscle If a ism connects the lateral part of the second abdominal sternum with the lateral end of the third segment's antecosta. This muscle is parallel to a lateral longitudinal semilunar list  $fo_{\rm III}$  of the third abdominal tergum.

Female. The structure of the first two abdominal segments is much simplified if compared with that of the male. Muscle I a  $dlm_1$ , so strong in the male, is present in the female too, but is very much weaker. The arm of the metapostphragma is lost, and the second abdominal tergum is a simple transverse plate quite like the following terga; no furrows are present (Pl. 3, fig. 2).

Muscles I a  $dlm_2$ , II a dlm, and III vlm, being small even in the male, are present in the same dimensions, and so is II a ism. The apodeme of the second abdominal sternum is absent and is represented by a low transverse list on the inside of this sternum. To muscles I a  $vlm_1$  and I a  $vlm_2$  together corresponds a short, fan-like, backwards diverging muscle fascia between the median part of the first and the transverse list of the second abdominal sternum. A short and weak muscle arising on the lateral part of the first abdominal sternum and extending to the region just in front of the fourth spiracle probably represents I a  $dvm_3$  or perhaps all the muscles I a  $dvm_4$ , I a  $dvm_2$  and I a  $dvm_3$  of the male together, since I have not been able to find any independent equivalent of I a  $dvm_4$  or of I a  $dvm_2$ .

Material: about 50 males and 10 females (brachypterous and macropterous) from Upland, Solna.

#### Criomorphus moestus (Boh.)

Male. The sound-producing apparatus agrees in all essential parts so well with the same organ in *Dicranotropis* that I find a particular description unnecessary. All the muscles described in connection with this organ in *Dicranotropis* are present in *Cr. moestus*, too, in the same degree of perfection. Even the apodemes and other muscle attachments, strengthening lists, etc., mentioned in *Dicranotropis* are found in the corresponding places in *Criomorphus moestus*.

Female. As the female of Dicranotropis.

Material: 5  $\circlearrowleft \circlearrowleft$  and 2  $\circlearrowleft \circlearrowleft$  from Upland, Djursholm, all of them brachypterous.

#### Criomorphus albomarginatus Curt.

Male, I found no difference whatever in the structure of the sound-producing organ between this species and the preceding one.

Material: 5 brachypterous males from Upland, Experimentalfältet.

## Criomorphus bicarinatus (H.-S.)

Male, Exactly as in Dicranotropis hamata.

Material: 4 brachypterous males from Södermanland, Nacka.

## Achorotile albosignata (Dahlb.)

Male. In this species the sound-producing organ is constructed as in Dicranotropis hamata but with one important difference: the apodeme of the second abdominal sternum is absent. It is represented by an insignificant transverse elevation on the inside of each side of the second abdominal sternum. This elevation is the posterior attachment of a muscle homologous with I a  $vlm_2$  in Dicranotropis and arising from the inside of the first abdominal sternum half-way between its middle and lateral end. This muscle is here weak and difficult to distinguish from I a  $vlm_1$ . In other particulars, as far as I could find, the structure of the sound-producing apparatus agrees with that of Dicranotropis.

Material: 14 brachypterous males from Södermanland, Nacka.

#### Calligypona excisa (Mel.)

Male. The sound-producing organ is constructed of the same parts in the same arrangement as in Dicranotropis hamata. I found but one difference worth noting: muscle I a  $vlm_2$  in C, excisa is proportionately a good deal stronger. While this muscle in Dicranotropis is considerably weaker than I a  $dlm_1$  (see Pl. 2, fig. 3), that of the present species is certainly somewhat shorter but in return almost twice as thick as the latter. Even if the magnitude of the muscles is estimated in relation to that of the body, the difference depends without any doubt on the larger volume of I a  $vlm_2$  of C, excisa if compared with the same muscle in Dicranotropis.

Material: 7 brachypterous males from Halland, near Halmstad.

#### Calligypona elegantula (Boh.)

Male. As in Dicranotropis, Muscle I a  $vlm_2$  is about as thick as I a  $dlm_1$  but is as usual considerably shorter than this muscle.

Material: 9 macropterous males from Upland, Danderyd, Kevinge.

#### Calligypona dubia (Kbm.)

Male. I have been able to examine but one male that was in rather a bad state of preservation. However, it may be established that the sound-producing apparatus in its essential parts is similar to that of other species of this genus and of *Dicranotropis*.

Material: one brachypterous male from Upland, Danderyd.

## Calligypona angulosa Rib, in litt.

Male. As in Dicranotropis hamata, Muscle I a  $vlm_2$  is as thick as I a  $dlm_1$  or perhaps a trifle thicker.

Material: 7 brachypterous males from Ostrogothia, Rystad, Fröstad.

#### Calligypona pallens (Stål)

Male. I could examine only two specimens. The sound-producing organ is of the same type as in *Dicranotropis*. Muscle I a  $vlm_2$  is about as thick as I a  $dlm_1$ , and as the latter seems to be relatively shorter than usual, the two muscles are of approximately the same length.

Material: 2 brachypterous males from Ostrogothia, Rystad, Fröstad.

#### Calligypona aubei (Perr.)

Male. In all essential parts exactly as in C. pallens.

Material: two brachypterous males from Gotland, Visby.

## Calligypona albocarinata (Stål)

Male. As in C. pallens,

Material: 6 brachypterous males from Södermanland, Nacka.

#### Calligypona obscurella (Boh.)

Male. In all essential parts as in Dicranotropis. Muscle I a  $vlm_2$  is as thick as I a  $dlm_1$  but considerably shorter.

Material: 4 brachypterous and 4 macropterous males from Ostrogothia, Rystad, Bjursholmen.

#### Calligypona forcipata (Boh.)

Male and female. As in Dicranotropis hamata.

Material: 1  $\circlearrowleft$  and 2  $\circlearrowleft$  $\circlearrowleft$ , all brachypterous, from the south of Sweden.

#### Calligypona flaveola (F1.).

Male. In all essential particulars as in Dicranotropis.

Material: 1 brachypterous male from Upland, Spånga.

#### Calligypona denticauda (Boh.)

Male. Essentially as in Dicranotropis. Muscle I a  $vlm_2$  is about as thick as I a  $dlm_1$  but somewhat shorter, I a  $dvm_1$  is rather strong.

Material: 6 brachypterous males from Ostrogothia, Rystad, Fröstad.

#### Calligypona clypealis (J. Sahlb.)

Male. No appreciable difference from the Dicranotropis pattern. Muscle  $l \ a \ olm_2$  is at least as thick as  $l \ a \ dlm_1$  but much shorter.

Material: 2 brachypterous males from Upland, Djursholm, Ösbysjön Lake.

#### Calligypona exigua (Boh.)

Male. As in Dicranotropis.

Material: 8 brachypterous males from Ostrogothia, Rystad.

#### Calligypona brevipennis (Boh.)

Male. Muscle I a  $vlm_2$  is but half as long as and considerably thinner than I a  $dlm_1$ . In other respects nothing noteworthy.

Material: 3 brachypterous and 1 macropterous male.

#### Chloriona smaragdula (Stål)

Male. In all essential parts as in Dicranotropis hamata.

Material: 5 macropterous males from Upland, Solna, Råstasjön lake.

## Megamelus notula (Germ.)

Male. In this species muscle l a  $vlm_2$  is only one third of the length of l a  $dlm_1$  and considerably thinner. Here in its upper part it is uniform in thickness or thickest at its top, as the apodeme of the second abdominal

sternum is more dilated than in *Dicranotropis* and the species of *Calligypona* examined by me. In conjunction with the small dimensions of I a  $vlm_2$  the apodeme is much shorter than in *Dicranotropis* and *Calligypona*. In other details the apparatus is constructed as usual.

Material: 8 brachypterous males from Upland, Djursholm.

#### Megamelus venosus (Germ.)

Male. The structure of the sound-producing organ is in complete agreement with what is usual in Dicranotropis and Calliggpona. Muscle I a  $vlm_2$ , thus, is as thick as I a  $dlm_1$  and almost as long. In regard to this organ,  $Megamelus\ venosus$  is apparently not especially closely related to M, notula.

Material: 2 brachypterous males from Upland, Solna.

#### Stenocranus minutus (F.)

Male. The apodeme of the second abdominal sternum has quite a different form from that in Dicranotropis and Calligypona. It is short, relatively much shorter than in these genera, and broad (about three times as long as broad), approximately uniform in width, obliquely tongue-shaped, and directed more backwards than upwards. Muscle I a  $vlm_2$  is weak, shorter than I a  $dvm_1$  and I a  $dvm_2$  and about one fourth of the length of I a  $dlm_1$ . In other respects the organ agrees with that of Dicranotropis.

Material: 4 males from Upland, Danderyd.

#### Kelisia scotti (Fieb.) Scott

*Male.* The apodeme of the second abdominal sternum is shaped like a broad and short plate directed backwards, at which the short fan-like I a  $vlm_2$  attaches itself. I a  $vlm_2$  is considerably shorter than I a  $dvm_1$  and I a  $dvm_2$ , while I a  $dlm_1$  is two and a half times as long as any of these muscles.

Material: 2 males from Upland, Djursholm.

## Conometus limbatus (F.)

Male. The sound-producing apparatus recalls most closely that of Megamelus notula. Muscle I a  $vlm_2$  is considerably shorter than I a  $dvm_1$  and I a  $dvm_2$ ; its apodeme is short and narrow, distally strongly broadened.

Material: 8 brachypterous males from Upland, Djursholm.

#### Euidella speciosa (Boh.)

Male. The apodeme of the second abdominal sternum is a low transverse lobe directed upwards and backwards and is, then, much reduced if compared with the species of Calligypona. Muscle I a  $vlm_2$  is very short, fan-shaped. In other respects the apparatus has the usual structure.

Material: 10 males from Upland, Solna.

#### Family Cixiidae

#### Cixius nervosus (L.)

Male. Owing to lack of material I am not able to give any thorough description of the structure of the sound-producing organ in this species. This organ is more weakly developed than that of the aracopids, if the size of the animal is taken into consideration. Muscle I a  $dlm_1$  is very short, relatively much shorter than in the aracopids, and almost vertical. I have not been able to find any apodeme on the second abdominal sternum or muscle I a  $vlm_2$ .

Material: 3 males from Upland, Solna.

## Family Issidae

#### Ommatidiotus dissimilis (Fall.)

Male. Of this species I have studied dried material only, and in consequence I am not able to describe the musculature. It is apparent, however, that a sound-producing apparatus is present in *Ommutidiotus*. This apparatus seems to agree with that of the aracopids, at least in its principal features. The metapostphragma is laminate. The second abdominal sternum is furnished with a pair of upright apodemes.

Material: 2 brachypterous males from Småland, Annerstad.

#### JASSIDOMORPHA

#### CERCOPOIDEA

#### Family Cercopidae

#### Neophilaenus campestris (Fall.)

Male. (Plate 3, figs. 3—6). The metapostnotum (mpn) is a rather narrow transverse strip, laterally first somewhat broadened, then again narrowing towards the region of the first abdominal spiracle. Behind the metapostnotum, the dorsum of the first abdominal segment is medially membranous. The tergum of this segment, then, is divided into a pair of lateral plates (fig. 4, I), each subtrapezoidal in shape, the most acute angle being directed towards the middle line. Especially along its fore border this plate is strongly convex. Half-way towards its lateral end the tergal plate is strengthened on its inside by a longitudinal list (fig. 4, I0). More laterally there is an unpigmented convex surface I10, which is striated in a characteristic way by about twenty approximately parallel transverse lines with a different refraction from that of the spaces between them. Probably these lines are thickened sclerotic bars. I term this surface the striated tymbal by analogy with the tymbal in the Cicadidae. The lines of the tymbal are crossed by a longitudinal fold dividing them into a lateral and a medial part. Both parts of

the tymbal are convex. Laterally the first abdominal tergal plate carries the second abdominal spiracle  $(sp\ 4)$ .

The first abdominal sternum, in spite of a considerable reduction if compared with the more normal (3rd and following) sterna, is very distinctly developed as a transverse, normally sclerotized plate and very little specialized (figs. 3, 4, I ast). Along the hind border this plate carries a low transverse list, which on each side considerably laterally of the middle is furnished with an inconspicuous semi-circular lobe (matt). Between this lobe and the lateral end of the list is a smaller tubercular elevation.

The second abdominal tergum is little specialized. There is a distinct antecosta. The precosta is dilated in the middle.

The second abdominal sternum (fig. 3, *H ast*) is similar to the first but has a larger extension in the lateral direction. Along the hind border there is a transverse list carrying on each side laterally of the middle a muscle attachment in the form of a semilunar lobe. This lobe is placed a little more laterally than that of the first abdominal sternum.

Between the posterior border of the metapostnotum and the antecosta of the second abdominal tergum there stretch two longitudinal muscles (fig. 5  $I a dlm_1$  and  $I a dlm_2$ ). These muscles are situated rather close to each other and the median line. More laterally there runs a third longitudinal muscle La dlm, between the fore border of the first abdominal tergum and the antecosta of the second abdominal tergum; it is situated between the longitudinal fold of the first tergum and the tymbal. From the semilunar lobe on the list of the first abdominal sternum a relatively strong muscle extends to the caudal end of the longitudinal fold of the striated tymbal (fig. 5  $I \ a \ dv m_3$ ). Two weaker muscles,  $I \ a \ dv m_2$  and  $I \ a \ dv m_3$ , arise from the first abdominal sternum somewhat laterally of the origin of I a dvm<sub>1</sub>. I a dvm<sub>2</sub> goes to the hind border of the metapostnotum in front of the tymbal. In its ventral 2/s it is comparatively thick but suddenly becomes much thinner dorsally, I a doma is very thin and probably reduced. A short muscle I a doma attaches itself by both ends to membranous parts of the body wall near the fourth spiracle.

The ventral longitudinal musculature is weak but distinct. From the semilunar lobe of the second abdominal sternum there stretches a muscle H a dvm to the lateral end of the second abdominal tergum. Its dorsal attachment has a considerably more ventral (lateral) position than the tymbal, for which reason H a dvm is almost horizontal. Of the remaining muscles in this region the longitudinal muscle H a  $dlm_3$  may be mentioned. This muscle arises just behind the dorsal insertion point of H a dvm and dilates in its extension to the lateral parts of the antecosta of the third abdominal tergum. In this species this muscle is not especially strong and not stronger than the corresponding muscles in the following segments, but considering its robust development in Lepyronia (see below), I think I had better mention it here.

Female. In the female, the sound-producing organ consists of the same parts as in the male but is more weakly developed. This is especially true of muscles I a dom<sub>1</sub> and II a dom. The strengthening list on the inside of the first abdominal tergum is rudimentary and is represented by a more strongly pigmented longitudinal line, and the striation of the tymbal is indistinct.

Material: 18 males and 9 females from Scania.

#### Neophilaenus lineatus (L.)

Male. As in the preceding species. Muscles I a dom, and II a dom, however, are relatively stronger than in campestris.

Material: 6 males from Upland, Djursholm.

#### Philaenus spumarius (L.)

Male. On the whole as in Neophilaenus campestris,  $\circlearrowleft$ , but muscles I a  $dvm_1$ , H a dvm and H a  $dlm_3$  are somewhat stronger, especially H a dvm.

Material: 9 males from the south of Sweden.

## Aphrophora forneri Hpt.

Male. The sound-producing apparatus is constructed according to the same scheme as in Neophilaenus campestris. Muscles I a dlm<sub>2</sub> and I a dlm<sub>3</sub> are broad fasciac bordering immediately on each other. Muscle II a dvm I have not been able to find in Aphrophora forneri. Muscle I a dvm<sub>3</sub> is rather strong, much stronger than the other nuscles in this region. Dorsally it forks into two nuscles, the larger of these inserting itself immediately behind the striated tymbal, the other a little behind and laterally of this point but within the region of the first tergum. Muscles I a dvm<sub>2</sub> and I a dvm<sub>3</sub> are represented by one single weak muscle, as far as I could find; I a dvm<sub>4</sub> is small but distinct. Muscle II a dlm<sub>3</sub> is not stronger than the corresponding muscles in the following abdominal segments.

Female. Agrees with the corresponding parts in the male and is almost as well developed as in this sex.

Material: 8 males and 2 females from Upland,

## Aphrophora alni (Fall.)

Male and female. As in the preceding species. Muscle I a  $dvm_1$  is dorsally bifurcate. It is as strong in the female as in the male. The tymbal of the male of this species is represented in Plate 3, fig. 7 (tb).

Material: 4 males and 2 females from Upland, Solna.

## Lepyronia coleoptrata (L.)

Male. The sound-producing organ is more strongly developed than in the other cercopids I have examined. It is composed of the same parts as in Neophilaenus campestris. The tymbal has about 18 distinct arched furrows with a mainly transverse extension. At the lateral and caudal end of the tymbal muscle I a  $dvm_1$  is inserted. The muscle is very thick and strong, not forked. The dorsal longitudinal muscles in the region of the first abdominal segment are well developed, and so is II a  $dlm_1$ . Muscles I a  $dvm_2$ , I a  $dvm_3$  and II a dvm are weak. In return, the muscle corresponding to II a  $dlm_3$  in Neophilaenus is enormous. From its origin on the lateral part of the second abdominal tergum it dilates in the shape of a fan over the major part of the inside of the second abdominal tergum and attaches itself on the third abdominal tergum along an arched line stretching considerably behind the fore border of this tergum.

Female. In this sex the sound-producing organ is a good deal weaker than in the male, but it is nevertheless not relatively weaker than for example in the species of Aphrophora. Muscle I a  $dvm_1$  is fairly strong but considerably weaker than that of the male. II a  $dlm_3$  is not especially well developed.

Material: 11 males and 4 females from Upland, Danderyd and Djursholm.

#### JASSOIDEA

#### Family Membracidae

#### Centrotus cornutus (L.)

During my investigations on the sound-producing organ I unfortunately had no living or alcoholic material of this species, nor have I heard its soundproduction. There is no doubt, however, that this only representative of ours of the family Membracidae has a sound-producing organ homologous with that of other Auchenorrhyncha, In dried material it may be established that the first and second abdominal sterna in the males each have one pair of interior transverse dilatations analogous to the apodemes of many other iassoid forms. No doubt these dilatations (Plate 4, figs. 1 and 2, I a apod and II a apod) serve as attachments of muscles belonging to the sound-producing organ. These dilatations are lacking in the female, Further, the male has on the lateral part of the first abdominal tergum a convex surface finely transversely striated. There are at least twenty furrows crossed by a longitudinal fold, in the posterior end of which there is a thickening which is probably the insertion point of the sound-producing muscle. The major part of the first abdominal tergum with the tymbal above mentioned is concealed behind a laminate process from the metatergum, A striated tymbal similar to that of the male is present in the female too, but it is less convex and a little smaller.

#### Family Enacanthidae

## Euacanthus interruptus (L.)

Male. This male has a very strongly developed sound-producing apparatus (Pl. 4, figs. 3—7). In the region of the first abdominal dorsum there are several more strongly sclerotized and pigmented tergites (fig. 4). There is no striated tymbal as in the cercopids. The metapostnotum is a pair of transversally longish, convex plates (mpn), only laterally standing in a narrow connection with the metapimeron. Behind the metapostnotum in the middle is a single roundish plate I a  $tg_1$ , laterally the paired tergites I a  $tg_2$ , I a  $tg_3$  and pil. Of these tergites I a  $tg_3$  is convex and divided straight across by an oblique fold. Laterally I a  $tg_3$  stands in an articulate-like connection with the second abdominal tergum. Plate pil is armed with numerous short hairs, especially on its anterior border. The second abdominal tergum has a precosta rather broad in the middle but otherwise presents nothing noteworthy. In a distinct pleural plate laterally of pil there is the fourth spiracle (spir 4), while the third spiracle (spir 3) is situated in a weakly

sclerotized part of the integument just in front of the fourth a little behind the posterior border of the metepimeron.

The first abdominal sternum (fig. 5, I ast) is a transverse plate. Laterally it is forked into a parietal shorter branch passing into the membranous body wall, and an interior longer apophysis (fig. 3, apoph.). More medially the first abdominal sternum carries a pair of apodemes (I a apod), each consisting of one anterior and one posterior tongue-shaped sub-horizontal lobe. The posterior lobe reaches considerably behind the fore border of the second abdominal segment. A small backwards directed lobe is placed on the hind border of the first abdominal sternum just laterally of the apodeme.

The second abdominal sternum is a transverse plate (*H ast*) carrying on the inside laterally of the apodeme of the first abdominal sternum a short lobe or apodeme *H a apod*.

In the dorsum of the first abdominal segment several muscle bundles (1 a dlm) run from the fore or hind border of the metapostnotum to the antecosta of the second abdominal tergum. Arising on the metathoracal endosternum, two longitudinal muscles III vlm, and III vlm, extend to the anterior and lower surface of the anterior lobe of I a apod. Of these muscles III vlm<sub>1</sub> is strong, III vlm<sub>2</sub> insignificant. From the upper surface of I a apod there stretches a muscle I a dvm<sub>2</sub> to the metapostnotum. This muscle consists of two parts, one upper, shorter and thicker, and one lower, longer and narrower. The two parts are separated by a fibrous plate connected with the metendosternum by a thin figament. The narrower part of the muscle below the plate is more fibrous but still distinctly striated. The largest muscle of the first abdominal segment I a dvm, arises on the posterior lobe of the apodeme and is inserted on I a  $tq_3$  by a short funnel-shaped tendon. More laterally are the weaker dorsoventral muscles I a dvm3 and I a dvm4, the former arising on an insignificant sclerite a on the metepimeron (fig. 3), further the oblique muscle I a ism from the apex of the lateral apophysis of the first abdominal sternum to the region of the lateral end of the second abdominal antecosta, and a muscle I a vm from the under side of the distal part of the apophysis to the pleural region ventrally of the fourth spiracle. From the posterior surface of the first abdominal sternum extends on each side a longitudinal muscle I a vlm to II a apod. The next muscle in the same series runs from the second abdominal sternum skipping the third abdominal sternum to the fore border of the fourth abdominal sternum.

Female. In the female the apparatus of the male is much reduced. The first abdominal dorsum does not diverge so much from that of the male at a superficial examination, but the tergites are larger and coarser. The metapostnotum is laterally united with the metepimeron. The first abdominal sternum is stronger and broader than in the male, and the apophysis is present here too. Only weak rudiments, however, represent the apodemes of the first and second abdominal sterna in the male. The longitudinal musculature has about the same degree of development as in the male, and so has I a ism. Muscles I a dom<sub>1</sub> and I a dom<sub>2</sub> are much reduced and very thin, the latter of uniform thickness, the former still with a distinct tendon.

Material: 20 males and 6 females from different localities in the south of Sweden.

#### Family Proconiidae

#### Tettigella viridis (L.)

Male. The sound-producing organ recalls in certain respects that of Euacanthus, but presents several differences too (Pl. 5, figs. 1—5). The first abdominal tergum is much reduced (figs. 1, 3). Medially the dorsum is membranous. The metapostnotum (mpn) is laterally connected with the metepimeron and carries on the inside a phragma (phr). The latter is a roundish plate situated in a plane parallel with the integument in the vicinity. Laterally and a little behind the metapostnotum there is a striated tymbal consisting of a convex surface with 6 approximately concentric curved furrows (fig. 3, tb, fig. 5). Still more laterally there is a convex pilose surface (pil). Laterally of this surface we find spiracles 3 and 4, the former immediately behind the hind border of the metepimeron. On the latter below spiracle 3 there is a medially directed triangular lobe a. The second abdominal tergum is a rather narrow transverse plate (fig. 1, H). Its antecosta carries a phragma-like dilation (l) on each side about at the level of the tymbal.

The first abdominal sternum is a transverse plate (fig. 2 I ast) bearing on the inside an apodeme, consisting on each side of two horizontal lobes, one directed forwards and the other with a medial and somewhat caudal direction. This apodeme is considerably smaller than that of Euacanthus (I a apod). Laterally there is a finger-like apophysis (apoph) as in Euacanthus. The second abdominal sternum carries on each side a horizontal backwards directed tongue-shaped and black-pigmented apodeme (II a apod). This apodeme is comparatively very large and reaches far behind the hind border

of the third abdominal sternum.

From the metascutum an oblique longitudinal muscle (fig. 4 HI dlm) stretches to the suture between the metepimeron and the metapostnotum. From a ridge on the inside of the metapostnotum there extends a longitudinal muscle (I a dlm) to dilation I on the antecosta of the second tergum. From the hind surface of the same dilatation the corresponding muscle H a dlm runs to the antecosta of the third abdominal segment. Lobe t is very thin, for which reason the two muscles I a dlm and II a dlm on a longitudinal section through this lobe seem to be immediately united. The apodeme of the first abdominal sternum serves as an attachment of five muscles, in fig. 4 marked III vIm<sub>1</sub>, III vIm<sub>2</sub>, I a dvm<sub>1</sub>, I a dvm<sub>2</sub>, and I a vIm. The two first-mentioned muscles arise on the metendosternum, I a dvm<sub>1</sub>, arising from the medial lobe of the apodeme, is here fusiform and is inserted without a distinctly marked tendon immediately behind the tymbal. This muscle is well developed. I a dom<sub>2</sub>, arising from the anterior lobe of the apodeme, consists as in Euacanthus of one narrower ventral and one thicker dorsal part, the latter here being longer than the former, and attaches itself on the metapostphragma. The two parts of this muscle are separated by a transverse flat black-pigmented sclerite without a solid connection with the integument but united with the caudal and lateral part of the metendosternum by a ligament. This ligament is very difficult to see in most of my muscle preparations but stands boiling with KOII. In macerated preparations, therefore, only the black-pigmented sclerite and the ligament just mentioned are left of muscle I a dvm2. Muscle I a vlm runs from the hind surface of I a apod to

the upper surface of II a apod. From the lobiform sclerite a on the inner margin of the metepimeron there arises a weaker fusiform muscle I a  $dvm_s$  inserted by a distinct tendon on the first abdominal tergum in front of the tymbal. The apex of the apophysis of the first abdominal sternum is the attachment of a muscle (not drawn in the figures) corresponding to I a vm in Euacanthus. Muscles I a  $dvm_s$  and I a ism of the latter I have not found in Tettigella. From the hind border of the second abdominal sternum under the apodeme there arises a longitudinal muscle not differing from the corresponding muscles in the following segments except by the fact that the third sternum is skipped, the muscle being inserted on the fore border of the fourth abdominal sternum.

Female. The apparatus is rudimentary in the female. In the first abdominal dorsum there is a trace of a median tergite missing in the male. The metapostnotal phragma is reduced to an inconspicuous transverse ridge. The tymbal and the pilose surface are present. On the antecosta of the second abdominal tergum, the phragma-like dilatation I is lacking. The apodemes of the first and second abdominal sterna are reduced to insignificant elevations. Concerning the musculature, the longitudinal muscle III dlm is similar to that of the male, while I a dlm and II a dlm have more modest dimensions. III vlm, is small, III vlm, being about as large as in the male. The longitudinal muscles I a vlm and II a vlm are arranged on the whole as the corresponding muscles in the following segments, but I a vlm is only half as long as any of these, H a vlm runs, as in the male, directly to the fore border of the fourth sternum. Strikingly small if compared with the male are the dorsoventral muscles I a dvm<sub>1</sub>, I a dvm<sub>2</sub>, and I a dvm<sub>3</sub>, all of them being so thin that it is difficult to find them in the preparations. I a dvm2 is still divided into a lower thinner and an upper slightly thicker part, and from the point of division there stretches, as in the male, a thin ligament to the metendosternum; the dividing plate, however, is quite thin and unpigmented.

Material: 16 males and 9 females from Upland, Djursholm, and Småland, Annerstad.

## Family Eupelicidae

## Eupelix depressa (F.), f. cuspidata (F.)

Male. The sound-producing apparatus may be compared with that of Euacanthus interruptus. The metapostnotum is a narrow transverse tergite laterally united with the metapostnotum is a narrow transverse tergite laterally united with the metapostnotum carries a short stump-like process or phragma. Most of the dorsum of the first abdominal tergum is selerotized. There is a distinct striated tymbal. In front of this there is a transverse sickle-shaped interior strengthening. Immediately behind the striated tymbal there is the point of attachment of muscle I a  $dvm_1$  (the designations of Euacanthus being used here). More laterally there is the convex, pilose surface (pil) of Euacanthus and Tettigella. Still more laterally, at the hind border of the metapineron, is the third spiracle, and a little behind the latter, the fourth spiracle. The antecosta of the second abdominal tergum is on each side dilatated into a semilunar phragma-like lobe as in Tettigella. The first abdominal sternum (PI. 5, fig. 6,

I ast) carries on the inside on each side immediately laterally of the middle an apodeme consisting of a short forward directed lobe (al) and a much longer obliquely tongue-shaped one directed backwards (I a apod). The latter reaches behind the hind border of the second abdominal sternum. Laterally the first abdominal sternum carries on each side a vertical, pole-shaped, apically broadening apophysis (apoph) representing that of Tettigella and Euacanthus. The second abdominal sternum carries on the inside on each side more laterally than that of the first sternum a tongue-shaped, backwards directed apodeme (II a apod). This apodeme is considerably larger than that of the first abdominal sternum and reaches a little behind the fore border of the fourth abdominal sternum. The strong development of this apodeme is the most conspicuous difference between the sound-producing organs of Eupelix and Euacanthus.

I had only one male of this species preserved in alcohol at my disposal for dissection, unfortunately, and therefore I am unable to describe the musculature in detail. On the apodeme of the first abdominal sternum there arises a strong muscle that is inserted behind the tymbal. This muscle is homologous with I a dvm<sub>1</sub> in Euacanthus and is of the same type as in this form, ending dorsally in a funnel-shaped tendon. But in the male of Eupelix this muscle has attained an enormous size and is the largest muscle of the abdomen. Large and strong is also the muscle corresponding to I a vlm in Euacanthus, extending from the first abdominal sternum to the morphological anterior surface of the apodeme of the second abdominal sternum. The muscle homologous with I a dvm<sub>2</sub> in Euacanthus has about the same appearance as in this form, consisting of a dorsal thicker and a ventral thinner part, separated by a membranous transverse plate united with the metendosternum by a thin ligament. Between the metendosternum and the anterior lobe of the apodeme of the first abdominal sternum, there stretch a few bundles of muscles. In the first abdominal segment, further, are found a muscle corresponding to I a dvm3 in Euacanthus and Tettigella but stronger than in these species, and a cylindrical dorsal longitudinal muscle corresponding to I a dlm in Tettigella.

Female. The striated tymbal is present in the female too. In the ventral region, the apodemes of the first and second abdominal sterna in the male are represented by more modest substitutes (Pl. 5, fig. 7). The apodeme of the first abdominal sternum (I a apod) is a roundish lobe directed forward-medially; the lobe directed backwards is almost entirely absent. The lateral apophysis of the first abdominal sternum is represented by an insignificant knob-like elevation. The apodeme of the second abdominal sternum is represented by a very short but broad backwards directed lobe.

Of the female I have, unfortunately, but one rather bad muscle-preparation, for which reason 1 must here content myself with mentioning that the muscles corresponding to I a  $dvm_2$  and I a  $dvm_3$  in Euacanthus, have about the same degree of development in the female of Eupelix as in the male. I a  $dvm_2$  thus consists of the same two parts as in the male, and the fibrous plate separating the two parts is connected with the metendosternum by a thin ligament. The muscles running from the latter to the anterior lobe of the apodeme of the first abdominal sternum are normally developed.

Material: 5 males and 2 females from Ostrogothia, Askeby, Öland, Färjestaden, and Gotland, Tingstäde.

## Family Ledridae Ledra aurita (L.)

Male. From lack of a larger material I am not able to give an accurate account of the sound-producing organ of this very rare species. However, it does not differ in any important respect from that of euscelids, for example. There is no striated tymbal, instead the tergum of the first abdominal segment is furnished with list-shaped strengthenings on the inside. The first abdominal sternum possesses a medial pair of apodemes and on each side a lateral, vertical, apically disciform apophysis, both moderately developed. Muscle I a dvm1 is strong, voluminous, barrel-shaped, at the middle about as thick as half its length. Its tergal insertion is brought about by a funnelshaped tendon. The remaining dorsoventral muscles are weak. Special interest is afforded by muscle I a dom. It is very thin and but indistinctly striated. As usual it is inserted tergally on the metapostnotum. Near its lower end, however, the muscle is divided into two fibre-bundles, one of which, being much thinner than the other, stretches backwards and attaches itself to the first abdominal sternum, the other extending to the metendosternum. The entire muscle but especially the latter part is richly interfused with nonfibrous cells and is apparently degenerating. In the anterior branch near to the point of ramification there is a brownish accumulation of pigment perhaps a sclerite -- probably representing the transverse plate dividing in many other jassoid forms muscle I a dvm2 into a dorsal and a ventral part. The dorsal and ventral longitudinal musculature is not stronger than in normal abdominal segments.

Female. Muscle I a dvm, and the apodemes and the apophysis of the first abdominal sternum are poorly developed, the muscle yet being quite distinct and considerably stronger than the remaining dorsoventral muscles. Whether it is functional for sound-production I am unable to tell. Muscle I a  $dvm_2$  has the same degree of development as in the male.

Material: 2 males and 2 females from Ostrogothia, Törnevalla.

## Family Idioceridae Idiocerus lituratus (Fall.)

Male. The sound-producing organ has much in common with that of Euacanthus, Tettigella and Eupelix. In the first abdominal dorsum immediately behind the posterior border of the metascutellum there is a single small tergite (Pl. 5, fig. 9, I a  $tg_1$ ). Laterally of this on each side there is a somewhat larger transverse plate, the metapostnotum (mpn), laterally united with the metapimeron. Behind the metapostnotum there is a region in its major part weakly pigmented, thin-walled, in which, however, is found the obliquely transverse oblong tergite I a  $tg_2$  carrying a low transverse list on the inside. There is no striated tymbal. On the corresponding place we find instead a thickening in the integument (Pl. 5, fig. 10, I a  $tg_3$ ). Laterally of this is the convex tergite pil, well developed and strongly pigmented, provided anteriorly as usual with a number of short hairs. Laterally of pil is the third spiracle, caudally of the latter the fourth spiracle. The second abdominal dorsum consists medially of a transversely oblong plate with a well developed precosta. Behind the antecosta a short medial longitudinal

ridge is suspended (Pl. 5, fig. 10, c). Laterally the antecosta carries on each side a small-sized phragma-like process (H a phr). The second tergum is laterally more thin-walled and more weakly pigmented. Laterally it is defined by a longitudinal interior list (fo) or rather by two lists united at a very obtuse angle. The anterior of these lists runs immediately medially of the fourth spiracle. At the apex of the angle between the two lists there is a sclerotic lump (cl). The third abdominal tergum is a plate of about normal dimensions. Laterally it protrudes forwards in a broad lobe approaching tergite pil of the first abdominal dorsum. Medially the precosta of the third abdominal tergum is rather broad, attaining about one third of the width of this tergum along the middle line. The antecosta of the third abdominal tergum is developed on each side into a conspicuous. phragma-like, backwards directed plate (Pl. 5, fig. 10, III a phr), laterally reaching the vicinity of the lateral end of the tergum. This phragma is broadest just laterally of its medial end near the middle line of the tergum (see fig. 9, the dashed line), becomes laterally still narrower and then again broader, then narrower again. Thus this phragma has a B-like form. Where broadest it reaches about half-way from the antecosta to the hind border of the third tergum.

The first abdominal sternum carries on the inside a strongly sclerotized black-pigmented transverse bar and on each side just laterally of the middle an apodeme (Pl. 5, figs. 8 and 10, I a apod) consisting of a broad, on the anterior surface somewhat concave plate. Medially this plate is placed in an almost vertical plane perpendicular to the longitudinal axis of the body; laterally and anteriorly it turns into a more horizontal position and gives off a lateral, narrow, horizontal, forwards directed, strongly sclerotized process (figs. 8, 10, proc). More laterally the first sternum carries on the inside a short dentiform process. Laterally of the apodeme we find on each side two small sclerites without a solid connection with the first abdominal sternum but instead fixed to the metepimeron (fig. 10, a and b). This connection, I believe, is secondary, and the two sclerites will probably belong to the first abdominal segment.

The second abdominal sternum is rather narrow but has a normal length in the mediolateral direction. A little laterally of the middle it carries on each side a large, tongue-shaped, backwards directed, on the morphological anterior surface somewhat concave apodeme (figs. 8 and 10, *H a apod*). Caudally this apodeme reaches a little behind the fore border of the fourth abdominal sternum. Laterally the second abdominal sternum carries a lobiform, transversely upright apophysis (*H a apoph*).

Two thin muscles connect the metapostnotum with the metathorax. From the metapostnotum a rather strong longitudinal muscle I a dlm (Plate 6, fig. 1) stretches to the phragma of the second abdominal segment. From the posterior surface of this phragma a longitudinal muscle II a  $dlm_2$  runs to the phragma of the third abdominal tergum, while a still more voluminous muscle or bundle of muscles II a  $dlm_1$  medially of II a  $dlm_2$  extends from the medial longitudinal ridge of the second abdominal tergum and the antecosta of the latter to the phragma of the third abdominal tergum. In the ventral region a strong longitudinal muscle III vlm arising on the metendosternum runs to the anterior surface of the first abdominal apodeme. From the posterior surface of this apodeme a voluminous muscle I a  $vlm_1$ 

stretches to the morphological anterior surface of H a apod. On the anterior end of the lateral process (proc) of I a apod there arises a rather strong muscle I a  $dvm_2$ , attaching itself on the metapostnotum without a tendon. The ventral half of this muscle is much thinner than the dorsal and not distinctly striated. A somewhat pigmented transverse plate separates the two parts. The remaining dorsoventral muscles in the first abdominal segment are the much weaker I a dvm<sub>1</sub>, I a dvm<sub>3</sub> and I a dvm<sub>4</sub>, all attaching themselves at the dorsal integument by a distinct tendon. I a dom<sub>3</sub> arises on sclerite b and attaches itself on a point in the vicinity of I a  $tg_3$ . The fusiform I a dvm, extends from the lateral and basal part of I a apod to a point rather a long distance medially of the fourth spiracle, while the short and thick I a dvm<sub>4</sub> arising on the lateral end of the first abdominal sternum runs to a point between the fourth spiracle and the insertion of I a dvm<sub>1</sub>. From the lateral apophysis of the second abdominal sternum a muscle If a dom extends to its insertion at the longitudinal interior list laterally defining the second abdominal tergum, and from the lateral part of the second abdominal stermum a muscle bundle H a ism runs to the lateral lobe of III a phr. From the second abdominal sternum under II a apod there stretches a strong longitudinal muscle in a caudal and lateral direction to the fore border of the fourth abdominal sternum.

Female. In the female I a plir and H a phr are lacking (however, a small lobe of the most lateral part of the latter remains), and the corresponding longitudinal muscles have dimensions more normal for dorsal longitudinal abdominal muscles. Especially H a  $dlm_1$  is much smaller than in the male. I a apod and H a apod are absent but are represented by rather pronounced elevations. The longitudinal muscle HI  $vlm_1$  is still rather powerful, while I a vlm and H a vlm are much weaker, the former being far shorter than in the male. The dorsoventral muscles of the first two abdominal segments are very thin and difficult to see in the preparations.

Material: 8 males and 4 females from Upland, Solna and Bondkyrka, and from Ostrogothia and Småland.

#### Idiocerus albicans Kbm.

Male. From lack of material I am not able to give a detailed account of the sound-producing organ of this species. However, the organ is very well developed. The phragma of the third abdominal segment consists as in lituratus of a medial and a lateral lobe on each side. The medial lobe in albicans has attained a much stronger development than in lituratus, reaching where it is broadest far behind the hind border of the third abdominal segment. On the other hand, the lateral lobe is less developed than in lituratus and very insignificant if compared with the medial one. The precosta of the third abdominal tergum is medially rather broad, for which reason muscle H a  $dlm_1$  is very long; moreover, it is broad and powerful. Muscles I a  $dvm_1$  and I a  $dvm_2$  are considerably stronger than in lituratus. The apodeme of the second abdominal sternum does not reach the hind border of the third sternum.

Female. In the female, the apparatus of the male is not developed, all parts of it being represented by traces only.

Material: 2 males and 1 female from Blekinge, Lyckeby.

#### Idiocerus elegans Flor.

Male. I have only examined one single dried male of this species. The sound-producing apparatus seems to be well developed. The phragma of the second abdominal tergum is indistinct; that of the third tergum reaches 1/3 of the total width of this tergum, including the precosta. The lateral part of the phragma is insignificant. The apodemes of the first and second sterna are well developed. The anterior process of the former is indistinct, however; the latter reaches to about the middle of the fourth sternum. The lateral apophysis of the second abdominal sternum is small.

Material: 1 male from the south of Sweden.

#### Idiocerus stigmaticalis Lew.

Male. I have examined but one single dried male. The phragma of the second abdominal tergum is well developed; that of the third tergum has only  $^1/_3$  of the width of the latter, its lateral part being insignificant. The apodemes of the first and second sterna are well developed, the anterior process of the former being short and not pigmented; the apodeme of the second abdominal sternum reaches to about the middle of the fourth sternum.

Material: 1 male from Småland, Annerstad.

#### Family Macropsidae

#### Oncopsis flavicollis (L.)

Male, (Plate 6, figs. 2-4). The integument in the region of the first abdominal dorsum is partly concealed under a pair of short, broad, laminate processes from the metascutellum and is in its major part faintly pigmented and thin but apparently rather sclerotized. Foremost on each side is a tergite laterally connected with the metepimeron and representing a metapostnotum. From the inside of the metapostnotum issues a forwards directed auriform phragma (I a phr). The part of the first abdominal tergum situated behind the metapostnotum is very umbonated and partly thickened, and equipped on the inside with several strengthening folds and lists extending in different directions. Laterally of the metapostnotum there is a pilose convex sclerite corresponding to that described in the preceding genera (pil), and of similar appearance. In front and a little laterally of pil is the third spiracle, behind and laterally of this the fourth spiracle in a peritreme. Behind and somewhat medially of pil there is a lump-shaped thickening of the integument (scl). Immediately in front of this thickening there is an S-shaped strengthening in the integument. The upper (medial) half of this S enframes a strongly convex, elastic bladder (bt). Behind the thickening scl a small number of concentric curved furrows suggestive of the tymbal of Tettigella, Eupelix and the cercopids may be perceived with some difficulty. Immediately behind this "pseudo-tymbal" the second abdominal tergum begins and is without a distinct delimitation towards the first tergum in this region. Laterally of the "pseudo-tymbal" lies a more strongly pigmented plate belonging to the second tergum. For the rest, the second abdominal tergum is rather uniform and little reduced. On the inside along the fore border it

carries on each side a backwards directed auricular phragma II a phr, which is on the whole a mirror-image of the metapostphragma. More laterally the delimitation between the first two abdominal terga is indistinct, as mentioned above. There is no phragma on the third tergum, and the precosta of the latter is very narrow.

The first abdominal sternum is much reduced and consists essentially of a strongly sclerotized transverse bar that is situated in the preparations dorsally of the somewhat broader and less strongly specialized second sternum. The first sternum carries one pair of apodemes (figs. 2 and 3, I a apod), each consisting of an obliquely tongue-shaped, horizontal lobe directed medially and backwards. Laterally there is an apophysis (apoph), an upright, slender column with its distal end reaching the lump-shaped thickening of the first abdominal tergum. Behind the apodeme of the first abdominal sternum, the second sternum possesses on each side a considerably smaller, obliquely transverse triangular apodeme (H a apod).

From the metascutum a not very conspicuous longitudinal muscle extends on each side to the anterior surface of the metapostphragma. From the posterior surface of this phragma a very powerful muscle (Pl. 6, fig. 4, I a dlm) extends to the phragma of the second abdominal segment. The dorsal longitudinal musculature in the second and third abdominal segments is normally developed. On I a apod there arises a powerful cylindrical muscle I a dom, inserted by a distinct funnel-shaped tendon on a point immediately in front of the superior part of the S-shaped strengthening of the first abdominal tergum. A short and not very conspicuous muscle (not visible in fig. 4) runs from the apex of the apophysis of the first abdominal sternum to a point just medially of the tergal insertion of H a dvm; this is apparently an oblique intersegmental muscle. A rather strong muscle H a dvm (a little weaker than  $I = dvm_1$ ) arises on the apodeme of the second abdominal sternum and is inserted without a distinct tendon on the above-mentioned pigmented plate of the second abdominal tergum. Muscle HI vlm extends from the metathoracic endosternum to a lateral membranous part of the first abdominal sternum; it is not large. The latter is also the case with muscle I a vlm extending from the first abdominal sternum behind I a apod to the anterior surface of H a apod.

Female. The apparatus is much less developed than in the male; however, it may still be supposed to be capable of function. I a phr is represented by a low transverse list on the inside of the metapostnotum. The phragma of the second abdominal tergum exists as a thin sickle-shaped rim. The first abdominal tergum is less umbonated than in the male and lacks the system of interior strengthening lists present in that sex; on the contrary, the striated tymbal is far more distinct than in the male and possesses about 16 concentric curved lines concave backwards. The apodemes of the first and second abdominal sterna and the lateral apophysis of the former are lacking. Muscles I a dtm, I a dtm, and II a dtm are much weaker than in the male. I a dtm is inserted without a distinct tendon immediately behind the tymbal. The "pseudotymbal" of the male is apparently not equivalent to the tymbal of the female, as muscle I a dtm in the male is inserted in front of the pseudotymbal; in this respect the female agrees with conditions in Tettigetla and the cercopids.

Material: 13 males and 7 females from Upland, Solna.

#### Oncopsis tristis (Zett.)

Male. The apparatus has the same structure as in flavicollis. However, the lateral apophysis of the first abdominal sternum is considerably stouter and broader, and the apodeme of the second sternum is much larger than in flavicollis. The same is the case with muscle H a dvm.

Material: 14 males from Upland, Djursholm.

#### Oncopsis alni (Schrnk.)

Male. The sound-producing apparatus agrees with that of Oncopsis tristis. Muscle II a dvm is comparatively less strong, however.

Material: 4 males from Upland, Solna.

#### Macropsis tiliae (Germ.)

Male. The sound-producing organ agrees with that of the species of Oncopsis. As in these, the most powerful muscle in the region in question is  $I \ a \ dvm_1$ . In the next place  $I \ a \ dlm$  and  $II \ a \ dvm$  should be mentioned.  $II \ a \ apod$  is about as well developed as in Oncopsis alni.

Material: 6 males from Upland, Solna.

#### Macropsis planicollis (Thoms.)

Male. As in the preceding species. Muscle I a dlm is comparatively weakly developed.

Material: 3 males from the south of Sweden.

#### Macropsis fuscinervis (Boh.)

Male. Agrees in all essential parts with the conditions in M. planicollis, but muscle I a dlm is considerably longer and more powerful.

Material: 1 male from Ostrogothia, Rystad.

## Family Agalliidae

#### Agallia brachyptera (Boh.)

Male. (Plate 6, figs. 5—7). The metapostnotum is a narrow, transversely oblong plate (fig. 6, mpn) medially concealed under the metascutellum and laterally connected with the metapimeron. The metapostphragma is small and semilunar (I a phr). Behind the metapostnotum there is on each side a triangular tergite, in which the integument is medially thickened but laterally consists of a striated tymbal (tb), viz. a convex surface with seven arched, concentric furrows. Each of these arched lines forms about a quarter of an ellipse, the centre of which is situated caudally-medially; in other words, one end of each line is directed backwards, the other towards the middle line. A little in front of and laterally of the tymbal we find as usual a convex surface (pil) anteriorly fringed with short hairs. Just laterally (ventrally) of pil is the third spiracle, placed in close connection with the hind border

of the metepimeron. On this border still more ventrally there is an inconspicuous lobiform sclerite, the origin of muscle I a  $dvm_8$ . (Neither the sclerite nor the muscle are visible in the figures.) The second abdominal tergum is weakly pigmented but apparently rather well sclerotized. Its precosta carries on the inside a thickening suggestive of the back of a bird with the wings outstretched. The antecosta of the second tergum is developed on each side into a rather large, vertically dependent, transverse phragma  $(II \ a \ phr)$ . More laterally on the second abdominal tergum there is a sclerotic thickening irregular in form  $(II \ a \ cl)$ . The fourth spiracle is in the usual position (fig. 6,  $spir_4$ ). The third tergum carries on each side an obliquely tongue-shaped, apically somewhat broader phragma directed backwards and a little medially  $(III \ a \ phr)$ , posteriorly reaching just to the hind border of the third tergum or somewhat behind it. The first and second abdominal sterna each possess one pair of short semilunar apodemes directed backwards, and one pair of lateral, narrow, erect apophyses (figs. 5 and 6).

The muscles in the region in question are much the same as in Idiocerus. A small muscle from the metascutum attaches itself on the metapostphragma. Several thin muscles (Fig. 7, I a dlm) extend from the metapostnotum to the antecosta of the second abdominal tergum. From the phragma of the second tergum two muscles extend on each side to III a phr, viz. one medial H a dlm, to the apex of the third phragma, and one lateral H a dlm, to its basis. A third longitudinal muscle II a dlm2 extends from the base of the hind surface of H a phr to the fore border of the third abdominal tergum. Of these muscles II a dlm; is thick and powerful. The ventral longitudinal muscles III vlm, I a vlm and II a vlm are rather weak. Two strong dorsoventral muscles arise on I a apod: I a dvm1 extending to a point on the first abdominal tergum approximately representing the centre of the concentric arched lines of the tymbal and attaching itself by a funnel-shaped tendon, and I a dvm2 to the metaposinotum. The latter muscle consists of two parts separated by a transverse tendinous plate: one ventral, thinner and a little shorter, and one dorsal, thicker. Both of these parts are distinctly striated; in the ventral part, however, the striation is considerably coarser and sparser. Muscle I a dvm2 is not cylindrical in its dorsal part, its thickness in the mediolateral direction being much greater than in the craniocaudal direction, greatest at its attachment on the metapostnotum. This attachment is direct, there being no tendon. On the lobiform sclerite of the metepimeron above mentioned arises the rather thin muscle I a dvms inserted by a tendon on a point immediately in front of the tymbal. From the base of the apophysis of the first abdominal sternum there extends a short and comparatively thick muscle I a dvm<sub>4</sub> to a point just laterally of the tergal point of insertion of I a dvm<sub>1</sub>. Muscles I a dvm<sub>3</sub> and I a dvm<sub>4</sub> are not visible in fig. 7 but are equivalent to the muscles with the same numbers in Plate 4, fig. 7 (Euacanthus), for example. From the apodeme of the second abdominal sternum a dorsoventral muscle II a dvm extends on each side to II a cl, at whose lateral corner it is attached by a long, thin tendon. From the lateral apophysis of the second abdominal sternum a short muscle II a ism extends to the anterior lateral angle of the third abdominal tergum.

Female. In the female all the phragmata and apodemes of the male are represented by insignificant lists or tuberculiform elevations. In spite of this, the sound-producing organ is probably capable of function even in the

female, as the dorsoventral musculature in the first abdominal segment is tolerably well developed. Thus, muscle I a  $dvm_1$  is as strong as in the male; I a  $dvm_2$  is thinner than in the male but is still composed of two distinct parts. The tymbal is distinctly striated as in the male. The dorsal longitudinal musculature, on the other hand, is much reduced.

Material: 16 males and 8 females from Upland, Danderyd.

#### Agallia venosa (Fall.)

Male. The sound-producing organ agrees essentially with that of brachyptera, but the details are rather different. The tymbal has about 20 concentric curved lines. The second and especially the third abdominal phragmata are considerably smaller than those of brachyptera. The length of the third phragma is little more than one sixth of that of the third abdominal tergum. On the contrary, the apodeme and the lateral apophysis of the first abdominal sternum are larger than in brachuptera, while the apodeme of the second abdominal sternum is very large, tongue-shaped and directed backwards. and reaches to the middle of the fifth abdominal sternum. Muscle I a vlm, extending from the posterior surface of I a apod to the upper (morphologically anterior) surface of H a apod, is the most powerful muscle of the abdomen. Very strong, too, is muscle  $Ia\ dvm_4$ .  $Ia\ dvm_3$  is also stronger than in brachuptera, while I a dvm2, on the contrary, is somewhat weaker than in that species. The second tergum is pigmented and apparently less specialized than in brachyptera. The thickening H a cl of the latter is represented in nenosa by a folded structure of a totally different aspect. Muscle H a dvm seems to be weaker than in brachyptera. The dorsal longitudinal musculature is far weaker than in that species and but little stronger than normal.

Material: 4 males from Ostrogothia and Upland,

#### Family Megophthalmidae

## Paropia scánica (Fall.)

Male. (Plate 7, figs. 1—2). The metapostnotum is a relatively large, paired sclerite, the medial part of which is free along its fore border, while the lateral part is connected with the metepimeron. On the inside the metapostnotum carries a rather strong transverse phragma (Pl. 7, fig. 1, I a phr). For the rest, the first abdominal tergum is weakly pigmented and lacks conspicuous structures. There is no striated tymbal apart from some indistinct traces. Behind the lateral part of the metapostnotum runs an oblique interior list (I). The pilose surface (pil) is small and carries only about 9 hairs. The third and fourth spiracles are in the usual position. The precosta of the second abdominal tergum is medially rather broad. This tergum carries on each side a transverse phragma (II a phr). At the lateral end of the second abdominal tergum there is an irregular thickening (cl). The third abdominal tergum has a strong antecosta that is not parallel with the fore border of the tergum but is curved in and out, by which the width of the precosta is varied; on each side of the middle there is a trace of a phragma.

The metepimeron carries below on each side a triangular lobe (a); it is

firmly attached to the metepimeron but is, I believe, of abdominal origin, and represents sclerites a and b of Idiocerus (p. 30). The first abdominal sternum carries on each side a medial apodeme and a lateral apophysis. The apodeme (I a apod) has its largest extension in the medial and oral direction and is laminate and horizontal. The lateral apophysis (I a apoph) is narrow and erect. The second abdominal sternum has a pair of medial, vertically transverse apodemes (II a apoph) and on each side a lateral, bluntly lobiform apophysis (II a apoph).

From the inside of the metascutum there extends on each side a small muscle III dlm to I a phr. In the first abdominal tergum three pairs of longitudinal muscles  $Ia\ dlm_1$ ,  $Ia\ dlm_2$  and  $Ia\ dlm_3$  may be observed.  $Ia\ dlm_2$ running from I a phr to II a phr is rather strong (Fig. 2). A fairly broad muscle bundle II a dlm, extends from the hind surface of II a phr to the medial dilated part of the antecosta of the third abdominal tergum. The ventral longitudinal muscles are rather weak. The largest muscle of the abdomen is I a dvm2, consisting as in Idiocerus, Agallia, Euacanthus and Tettigella of two parts, one dorsal and one ventral, of which the dorsal and somewhat longer part here is not thicker than the ventral. The latter arises on the apodeme of the first abdominal sternum, the former being attached on the metapostnotum and metapostphragma. A fusiform muscle I a dvm<sub>3</sub> extends from sclerite a to a point in front of the middle of the oblique list l of the first abdominal tergum. The muscle is much weaker than I a  $dvm_2$ . Its tergal insertion is effected by a tendon. From lack of material I have not been able to follow and to identify with any certainty the weaker muscles of the first and second abdominal segments. Thus I have failed to find the muscle representing I a dvm1 of the female and of species described above. A muscle H a dom running from the apophysis of the second abdominal sternum or from this sternum laterally of the apophysis is also very thin and has not been reproduced in figure 2. A weak muscle II a ism extends from the lateral part of the second abdominal sternum to a lateral part of the antecosta of the third abdominal tergum.

Female. The female of this species differs in several respects in a remarkable way from the male. I a phr and H a phr are little developed but remain as well-marked transverse lists. There is a distinct striated tymbal (Pl. 7, fig. 4). It is ornamented with 7 distinct concentric curved lines. The pilose surface (pil) is larger than in the male and is armed with a much larger number of hairs. Sclerite a on the hind border of the metepimeron is smaller than in the male; the apodeme and apophysis of the first abdominal sternum, however, are as well developed as in that sex, and I a apod has a free border posteriorly as well as anteriorly. If a apod is weaker than in the male. The tergal longitudinal musculature is also considerably weaker than in the male, and the same is the case with muscle I a dvm<sub>2</sub>. The latter still consists of two parts, the ventral of which is yet thinner than the dorsal. Muscle I a dom3 is very thin and might easily be overlooked. On the contrary, muscle  $I \ a \ dvm_1$  is thick and powerful though less powerful than  $I \ a \ dvm_2$  in the male. It arises on the apodeme of the first abdominal sternum and occupies almost the whole of the upper surface of this apodeme; it is inserted by a funnel-shaped tendon on a point representing the centre of the concentric curved lines of the tymbal.

Material: 8 males and 5 females from Ostrogothia and Upland.

#### Family Euscelidae

#### Doratura stylata (Boh.)

Male, (Pl. 7, figs. 5-6). The metapostnotum is only laterally united with the metepimeron; it is a narrow, medially interrupted, laterally somewhat broader transverse bridge without a phragma. Behind the metapostnotum there lies in the middle a small single sclerite I a tg1. For the rest, the first tergum is in its major part brown-pigmented and rather thick-walled. Laterally there is a distinct striated tymbal (tb) with a dozen fine, parallel furrows. These are almost straight and directed obliquely forwards-upwards. The furrows are crossed by a shallow fold. Laterally of the metapostnotum there is a convex field armed with short hairs (pit). Spiracles 3 and 4 are placed as usual. Ventrally of the third spiracle, adjacent to the metepimeron, there is a narrow black-pigmented sclerite (a) apparently attached to the metepimeron by a ligament only. The antecosta of the second abdominal tergum is on each side in two places dilated into a phragma-like but rather small semilunar lobe (Pl. 7, fig. 5, II a phr). The third tergum lacks a phragma. The first abdominal sternum carries on each side rather laterally a fairly small, in front vertical and transverse, posteriorly horizontal apodeme (La apod). Behind this and somewhat more laterally the second sternum carries at the hind border a small, semilunar apodeme (II a apod).

A long, thin muscle III dlm extends on each side from the metascutum to the fore border of the metapostnotum, Between the posterior border of the metapostnotum and the phragma-like dilatations of the antecosta of the second abdominal tergum there stretch 3 bundles of longitudinal muscles (La dlm), all relatively strong. Muscle La dvm<sub>1</sub> arises as usual from La apod and extends to a point immediately behind the tymbal in the transverse fold. This muscle is powerful and is inserted by a funnel-shaped tendon. On the other hand, muscles I a dvm2 and I a dvm2 are very thin and difficult to see distinctly in the preparations. As usual, the former consists of two parts, the ventral of which is somewhat thinner than the dorsal. It is inserted on the metapostnotum laterally of the anterior attachment of the lateral I a dlm. I a dvm3 is fusiform, arises on the narrow sclerite a and is inserted by a long and thin tendon at the anterior border of the tymbal. Muscle H a dvm, arising from H a apod and inserted by a long and narrow tendon on the second abdominal tergum near the lateral end of the antecosta, is weak. The ventral longitudinal muscles III vlm and I a vlm are moderately well developed.

Female. The sound-producing apparatus is in all essentials practically identical with that of the male. The phragma-like dilatations of the second tergum and the apodemes of the first and second sterna are as well developed as in the other sex. This is true of the muscles too. Perhaps I a  $dvm_1$  is a trifle weaker than in the male, but the difference is insignificant.

Material: 30 males and 5 females from Upland, Solna.

## Doratura homophyla F1.

Male and female. The sound-producing apparatus agrees in all essential details with that of stylata.

Material: 1 male and 2 females from Scania.

## Graphocraerus ventralis (Fall.)

Male. The sound-producing organ may be compared most closely to that of Doratura, especially regarding the development of the musculature. However, there are certain differences, particularly in the sclerotized parts. The metapostnotum is interrupted in the middle. On the inside it carries a low phragma shaped like a semilunar list. There is no striated tymbal. On the corresponding place there is a pair of strengthening lists forming an angle with each other. One of these lists is semilunar. The second abdominal tergum possesses a small semilunar phragma. The first abdominal sternum has a pair of apodemes larger than in Doratura. They are horizontal, tongueshaped, directed backwards and reaching a little behind the hind border of the second abdominal sternum; their medial borders are secondarily coalescent from the base to near the apex. The first abdominal sternum has laterally an erect, apically somewhat dilated apophysis. The second abdominal sternum carries a pair of apodemes corresponding to those of the first sternum; they are separated by a broad interspace and are much shorter than the apodemes of the first abdominal sternum but are relatively somewhat larger than the corresponding parts in Doratura. As I mentioned above, the musculature on the whole agrees with that of Doratura. Thus, muscle I a dvm, is the most powerful and is tergally inserted by a funnelshaped tendon, while I a dvm2 and I a dvm3 are very weak, the latter being furnished at both ends with distinct tendons. The longitudinal musculature approximately as in Doratura.

Female. The apparatus resembles that of the male but is less developed. Its tergal sclerolized parts are as in the male, but the apodemes and apophyses of the first sternum are poorly developed, the former being represented only by a pair of small, triangular lobes separated by a broad interspace. Muscle  $I \ a \ dom_1$  is about half as thick as in the male, while the remaining muscles are about as much reduced. Muscle  $I \ a \ dvm_1$  is inserted tergally by a funnel-shaped tendon.

Material: 9 males and 7 females from Upland, Solna.

## Aphrodes bicinctus Schrnk.

Male (Plate 7, figs. 7—8, Pl. 8, figs. 1—2). The metapostnotum is a pair of sclerites laterally firmly united with the metapostnotum and medially meeting that of the other side (mpn). Behind the metapostnotum in the median line there is a single longish sclerite (fig. 8, I a  $tg_1$ ). For the rest, the first abdominal tergum is thin-walled but strongly sclerotized and furnished with several folds or lists running in various directions. Behind I a  $tg_1$  there is a transverse strengthening bar (tr). There is no striated tymbal, but the integument is strongly convex in the corresponding place (conv). Laterally of the metapostnotum lies the strongly convex surface anteriorly armed with short hairs corresponding to pil of Euacanthus and others. Spiracles 3 and 4 are in the usual positions. There is no distinct phragma on the metapostnotum, only a strong, low transverse list on the inside. The second abdominal tergum is shorter in the middle than laterally. On the inside this tergum carries two broadly tongue-shaped phragmata directed obliquely caudally and ventrally, laterally reaching just over the hind border

of the second tergum. Anterolaterally the second tergum ends in an anteriorly concave semilunar thickening.

The metepimeron carries on its posterior border below the middle a small triangular backwards directed tobe (Pl. 8, fig. 1, a). The first abdominal sternum (Pl. 7, fig. 7) is medially considerably narrower than laterally but is strengthened by a strong transverse bridge and carries one pair of apodemes and one pair of lateral apophyses. The apodemes are 2 broad, horizontal plates projecting beyond the fore and the hind margin respectively of the medial part of the first sternum anteriorly as well as posteriorly. At the back, these apodemes reach somewhat behind the hind border of the second abdominal sternum. The medial margin of each of these anodemes is free in front but is posteriorly secondarily coalescent with that of the other side. The lateral margin of the posterior apodemal lobe is laterally prolonged in a ridge-shaped strengthening on the inside of the first sternum. Laterally the first abdominal sternum carries a large, distally broadly dilated apophysis (anonh). The second abdominal sternum has one pair of apodemes, which is placed laterally of the apodemes of the first abdominal sternum and is erect, transverse and laminate (fig. 7 H a apod).

A pair of long, thin muscles III dlm stretch from the metascutum to a medial part of the metapostnotum. From the hind surface of the metapostnotal antecosta a little more laterally on each side two thin longitudinal muscles I a dlm<sub>1</sub> and I a dlm<sub>2</sub> extend to the fore side of II a pln. Muscle II a dlm is fairly thick and has, in consequence of the oblique position of the phragma, an almost vertical direction. The largest muscle of the abdomen is  $I a dvm_1$ , arising on the posterior lobe of I a apod and inserted dorsally on a point at the hind margin of the convex surface conv of the first abdominal tergum. Its insertion is effected by a funnel-shaped tendon. From the anterior part of I a apod muscle I a dvm<sub>2</sub> extends to the metapostnotum laterally of the point of insertion of I a dvm<sub>1</sub>, I a dvm<sub>2</sub> is much narrower than La dvm<sub>1</sub>, but, like that of several forms described above, it is divided into a dorsal thicker and a ventral thinner part. From the boundary between the two parts a ligament runs to the metendosternum. On process a on the meterimeron arises the still thinner I a dvm<sub>3</sub>, which is inserted by a long tendon on a point at the fore border of the convex surface conv of the first tergum at the level of the point of insertion of I a  $dvm_1$ . From the first abdominal tergum laterally of the place of origin of I a dvm, the small, thin  $I_{ij} dp_{III_{ij}}$  extends to a point laterally of the point of insertion of that muscle, and between the dilated part of the apophysis of the first abdominal sternum and the inside of the second tergum at the same level runs the short but thick I a ism with a broad attachment in both directions but especially on the apophysal side. From H a apod the fairly powerful H a dvm extends to a lateral part of the second abdominal tergum laterally of and near the tergal surface of attachment of I a ism. The ventral longitudinal musculature in this region is rather weakly developed.

Female. There is no phragma on the second abdominal tergum. The apodemes of the first and second abdominal sterna are poorly developed. In the first abdominal tergum there is a distinct striated tymbal on the usual place with 9 medio-lateral furrows. The dorsal longitudinal musculature is weak. Muscle I a  $dvm_1$  is much weaker than in the male but is still somewhat stronger than I a  $dvm_2$ . The latter, on the other hand, has the

same dimensions as in the male. Muscles I a ism and II a dom are considerably weaker than in the other sex.

Material: 17 males and 4 females from Solna.

#### Aphrodes bifasciatus (L.)

Male and female. In all essential details as in the corresponding sexes of bicinctus.

Material: 10 males and 6 females from Upland, Solna.

Aphrodes trifasciatus Fourer.

Male and female. As in bicinctus, Material: 4 males and 1 female from Upland, Ekerö.

#### Aphrodes flavostriatus (Don.)

Male. The sound-producing apparatus consists of the same parts as in bicinctus, but the details are remarkably different. The metapostnotum carries on each side a rather large, suspended and somewhat forwards directed, posteriorly concave phragma. Between the hind surface of this phragma and the fore surface of the phragma of the second abdominal tergum, which is well developed like that of bicinctus, and is of about the length of the second tergum at the corresponding place but, unlike that of bicinctus, is almost horizontal, extends a long and powerful longitudinal muscle. More laterally, from the hind border of the metapostnotum, a pair of muscle bundles relatively considerably stronger than I a dlm<sub>1</sub> and I a dlm<sub>2</sub> in bicinctus extends to the antecosta of the second tergum. On the contrary, muscle H a dlm is here much less important than in bicinctus. The apodemes of the first and second abdominal sterna are rather large, and transversely vertical. However, the apodemes of the first abdominal sternum are essentially smaller than in bicinctus with an interspace about as broad as one apodeme. The lateral apophysis of the first abdominal sternum is stumplike, vertical and small if compared with that of bicinctus. The apodemes of the second abdominal sternum are also separated by a broad interspace but are broader and larger than those of the first sternum and relatively much larger than in bicinctus. The lateral apophysis of the second abdominat sternum is insignificant. Among the dorsoventral muscles, I a dom2 is largest, relatively considerably stronger than in bicinctus. It is inserted on the metapostnotum laterally of its phragma and consists of the same two parts as in the above-mentioned species. Muscle I a dvm3 has relatively the same development as in bicinctus and arises as usual on a backwards directed triangular lobe on the hind border of the metepimeron. On the other hand, I have not been able to find any trace of I a dvm<sub>1</sub>. This muscle, so strongly developed in bicinctus, must at least be much reduced in flavostriatus. Il a dvm is about as strong (relatively) as in bicinctus. I a ism is insignificant. Much larger than any of the muscles above mentioned is III vim, extending from the anterior part of the metendosternum to the fore surface of the apodeme of the first abdominal sternum. This muscle is about as long as I a dvm2 but several times thicker. From the first abdominal sternum behind and laterally of the apodeme several short muscles extend to the fore surface of the apodeme of the second sternum.

Material: 11 males from Upland, Danderyd.

#### Opsius stactogalus Fieb.

Male. (Plate 8, figs. 3-6). The metapostnotum (mpn) is a narrow, transverse, sclerotized strip on each side, medially not reaching that of the other side. Behind the medial ends of the metapostnotal tergites in the region of the first abdominal dorsum there is an anteriorly three-lobed, posteriorly rounded, thick, lump-shaped sclerite I a tg, behind which is a transverse clamp-like strengthening tr. Laterally in the first abdominal tergum comes an umbonated area strengthened on the inside by narrow lists and folds running in different directions and together forming an irregular figure (conv). Laterally of this area there is as usual a pilose surface (pil). The precosta of the second abdominal tergum is broad, its antecosta strong. However, there are no distinct phragmata in the dorsal region of Opsius, Laterally of antecosta II a list-shaped, obtusely angular strengthening runs in the mediolateral direction as a prolongation of the antecosta  $(II \ a \ ac_2)$ . Just behind its lateral end is the second abdominal spiracle  $(spir_4)$ . but between this end and the spiracle the tergal integument is thinner along a short mediolateral distance. The first abdominal sternum consists of a thickened transverse plate (I ast). A little laterally of the middle this sternum carries on each side a broad, backwards directed apodeme (I a apod), near its lateral end a pole-like, nearly vertical, terminally laminate apophysis (I a apoph). The second abdominal sternum also carries one pair of apodemes longer than those of the first sternum, and one pair of lateral, pole-like, vertical apophyses smaller than those of the first abdominal sternum.

The strongest muscle is  $I \ a \ dvm_1$ , which is quite half as thick as its length and inserted by a conical tendon near the hind margin of the umbonated area conv. Powerful, too, is  $II \ a \ dvm$  extending from the upper, lateral surface of  $II \ a \ apod$  to a point on the lateral part of the second abdominal tergum in front of the spiracle. In this region the short but thick  $I \ a \ ism$  arising on the exterior surface of  $I \ a \ apoph$  is also inserted. Muscle  $I \ a \ dvm_2$  is thin and rather difficult to find in the preparations; it is not distinctly divided into two parts and is inserted on the lateral end of the metapostnotum. The dorsal longitudinal musculature is rather weak, the ventral not especially well developed, except  $I \ a \ vlm$  extending from the underside of  $I \ a \ apod$  to the upper surface of  $II \ a \ apod$ .

Female. The apparatus is much reduced or not developed. The dorsal region is less specialized than in the male, the sternal apodemes are represented by faint traces, and all muscles well developed in the male are very thin and insignificant in the female. Muscle I a  $dvm_2$  has about the same dimensions as in the male.

Material: 12 males and 4 females from Scania, Lund.

#### Macrosteles cristatus (Rib.)

Male. (Plate 8, fig. 7, Pl. 9, figs. 1—3). The development of the first abdominal tergum may be compared to that of Opsius. Thus, the metapost-

notum (mpn) is represented by a pair of narrow, transverse strips laterally united to the metepimeron and medially not reaching each other. Behind the metapostnotum there is in the middle a single anteriorly trilobed, posteriorly rounded, lump-shaped scierite I a tg, behind which comes the transverse, five-radiated strengthening tr. The latter is connected with the second abdominal antecosta by a longitudinal inner list. Laterally of these sclerites the integument is more thin-walled but strengthened by irregularly running folds and lists. At the lateral end of this tergum there is a semilunar list (1). As usual we find at the lateral end of the metapostnotum the pilose area pil. The second abdominal tergum carries on the inside a strong antecosta, and, in front of this, on each side a semilunar transverse list (sem). This list does not serve as an attachment for muscles but as a strengthening. The precosta has a strong longitudinal median list on the inside. The first abdominal sternum is a strongly sclerotized transverse bridge. It carries a pair of apodemes and a pair of lateral apophyses. The apodemes (I a apod) are obliquely tongue-shaped, horizontal and backwards directed; the apophyses diverge in the mediolateral direction. The second abdominal sternum is posteriorly strengthened on the inside by a transverse list, dilated laterally of the apodemes of the first sternum into an auricular apodeme H a apod. More laterally the transverse list is elevated into a thin, sharp, vertically transverse lobe.

The strongest muscle is I a  $dvm_1$ , extending as usual from I a  $apod_1$  to a point on the lateral part of the first abdominal dorsum, on which it is inserted by a funnel-shaped tendon. The remaining muscles are the usual ones and may be studied on Plate 9, fig. 3. It may be pointed out that muscle I a  $dvm_2$ , here divided into two parts, is angularly bent in consequence of the ligament connecting this muscle with the metendosternum being uncommonly short (Pl. 9, fig. 3, lig). The ventral part of I a  $dvm_2$  is also much shorter than the dorsal part.

Female. There is only an insignificant brown-pigmented sclerite representing the I a  $tg_1$  of the male. The strengthening tr is lacking. The differentiations in the shape of folds and lists characterizing the lateral region of the first abdominal tergum in the male are lacking in the female, and in the corresponding region there is instead on each side a large, brown pigmented plate of about the same structure as in the normal terga. On the precosta of the second abdominal tergum near the middle we find two insignificant forwards directed points presumably representing the two anterior radii of strengthening tr of the male. The antecosta of the second tergum is much weaker than in the male, the semilunar lists are absent. There is a rudimentary trace of I a apod more laterally than that of the male. Il a apod, being of small size already in the male, has about the same dimensions in the female too, while the transverse lobiform elevation of the second abdominal sternum in the male is lacking in the female. Muscles I a dvm1 and I a dvm2, especially the former, are strongly reduced to very thin strings. The longitudinal musculature, not being very well developed in the male, has about the same dimensions or is a trifle weaker in the female.

Material: 22 males and 11 females from the south of Sweden.

#### Platymetopius guttatus Fieb.

Male. The development of the tergal parts may be compared with the conditions in Macrosteles. The metapostnotum is medially open. Sclerite I a tan is small, trapezoidal, while the transverse strengthening tr is fused with the anterior border of the precosta of the second abdominal tergum, which is broad and furnished with a medial longitudinal list on the inside. Strengthening tr and the antecosta of the second abdominal tergum have each a strong transverse list on the inside. Laterally on the inside of the first abdominal dorsum there is on each side a pair of semilunar, transverse strengthening lists, the one on the lateral prolongation of the other. Muscle I a dvm, is inserted in the area behind these lists. The sternal endoskeleton agrees on the whole with the conditions in Macrosteles with the difference that the apodemes of the first abdominal sternum are fused by their medial borders. The lateral apophyses of the first sternum are rather large. The musculature exhibits nothing extraordinary. The dorsal longitudinal musculature of the first segment is tolerably powerful. The largest muscle is I a dvm, ending dorsally by a funnel-shaped tendon, I a dvm2 is thin and difficult to prepare. There is also a small, thin I a dvm<sub>3</sub> arising on a small, dark-pigmented sclerite attached to the metepimeron.

Female. In the tergal region all the parts above described in the male are present but are slightly less developed. Thus, I a  $tg_1$  here is but a thin, brown-pigmented plate. In the ventral area the apodemes of the first abdominal sternum and the lateral apophyses are reduced, the apodeme being more laterally placed than in the male. Muscle I a  $dom_1$  is considerably weaker than in the male, but its tergal insertion is still effected by a funnel-shaped tendon. This apparatus may very well be functional.

Material: 8 males and 4 females from Södermanland, Botkyrka.

#### Macustus grisescens (Zett.)

*Male.* (Plate 9, figs. 4-7). The metapostnotum (mpn) consists of a pair of transverse bridges narrowly separated in the middle. Laterally they are connected with the metepimeron. On the inside there is a low list but no distinct phragma. Behind the metapostnotum medially we find a small but i thick simple sclerite I a tg. Behind this tergite there is a broadly T-shaped strengthening in the integument (tr), the short, simple stem of which is posteriorly connected with the antecosta of the second abdominal tergum. Laterally of these parts the integument of the dorsum of the first segment consists anteriorly of the usual convex, short-haired surface pil, posteriorly of a large, partly strongly sclerotized area. Medially this area carries on the inside a T-shaped strengthening list (fig. 6, T). There is no distinct striated tymbal. The antecosta of the second abdominal tergum is strongly thickened and is continued laterally in two semilunar phragma-like lists, one medial and one lateral  $(l_1, l_2)$ . The first abdominal sternum carries medially a pair of rounded, on the whole horizontal apodemes (fig. 4, I a apod). These are fixed on the sternum at their lateral margins, their free border being directed forwards-medially-backwards. The posterior part, being longest, is laterally continued in a thin but rather broad list along the hind border of the first sternum; this list reaches the lateral apophysis of the first abdominal sternum

(apoph), a thin plate parallel with the integument in the corresponding region. The second abdominal sternum, too, is furnished with a pair of apodemes more lateral than I a apod; they are broadly tongue-shaped, directed backwards and laterally armed with a free, upwards directed point (figs. 4, 5, II a apod).

The musculature presents nothing remarkable (fig. 7). I a dvm<sub>1</sub> is powerful. It is inserted tergally at the posterior end of the T-shaped list on the inside of the first abdominal dorsum. I a dvm<sub>2</sub> is very thin but is still composed of two parts, the dorsal being slightly thicker. A ligament (lig) stretches from the boundary between both parts to the metathoracic endosternum. From the lateral end of the first abdominal sternum and its apophysis arise several short muscles (not all reproduced in fig. 7) extending to the region round the fourth spiracle.

Female. The apparatus is considerably weaker than in the male. As in that sex, a distinct striated tymbal is lacking, but the T-shaped list on the corresponding place is present. The apodeme and the apophysis of the first abdominal sternum are poorly developed. Muscle I a dom<sub>1</sub> is considerably thinner than in the male but is still no doubt functional. It is tergally inserted by a funnel-shaped tendon. In the remaining details the musculature agrees with that of the male.

Material: 18 males and 9 females from Upland.

#### Euscelis plebeius (Fall.)

Male. On the whole, the apparatus is composed as in Macustus, but the metapostnotum carries on each side a small suspended phragma. The second abdominal tergum, too, has a phragma, which is here backwards directed, horizontal and about as long as the second tergum. In correspondence with this, the dorsal longitudinal musculature is better developed than in Macustus. The apodemes of the first and second abdominal sterna and the lateral apophysis of the former (I a apod, II a apod and I a apoph) are relatively larger than in Macustus. Muscle I a  $dvm_1$  has about the same development as in that species, but I a  $dvm_2$  is slightly thicker than in Macustus.

Female. Phragmata, apodemes and muscles are more weakly developed than in the male, but no doubt the apparatus is functional. Muscle I a  $dom_i$  is tergally inserted by a funnel-shaped tendon.

Material: 6 males and 2 females from the south of Sweden.

## Streptanus marginatus (Kbm.)

Male. Distinct phragmata on the metapostnotum and the second abdominal tergum are absent, but the antecosta of the latter is very strong. The first and second abdominal apodemes are larger than those of Macustus. The dorsal longitudinal musculature is no stronger than in that species. I a dvm<sub>1</sub> has about the same development as in Macustus grisescens, I a dvm<sub>2</sub> being thin but relatively somewhat thicker than in grisescens. The ventral longitudinal musculature is stronger than in that species; this is true especially of the muscle running from the hind surface of the first abdominal sternum to II a apod. This muscle is rather short but thick.

Female. The organ is relatively weaker than in the female of Euscelis

plebeius. This is especially true of the rather thin muscle I a  $dvm_1$ ; however, this muscle is still inserted dorsally by a funnel-shaped tendon.

Material: 15 males and 7 females from Ostrogothia and Upland.

#### Streptanus aemulans (Kbm.)

Male. The organ is on the whole similar to that of Macustus grisescens. The metapostnotum has a strong interior list on each side. The second abdominal tergum carries a rather considerable phragma on each side. The first and second abdominal sterna each with a pair of apodemes, those of the second sternum being longest, sub-rectangular, tongue-shaped and reaching to the fore border of the fourth sternum. Musculature about as in arisescens, but the dorsal muscles are stronger.

Female. The apparatus is considerably weaker than in the male with shorter apodemes and thinner muscles, but is possibly still functional.

Material: 7 males and 1 female from Upland, Solna.

#### Diplocolenus abdominalis (F.)

Male. The apparatus is of the same type as in Macustus but is weaker. The simple sclerite I a  $ty_1$  is indistinct. There are no phragmata on the metapost-notum and the second abdominal tergum; the latter, however, has a relatively strong antecosta. There is no striated tymbal; on the corresponding place we find a T-shaped strengthening consisting of a transverse anterior and a shorter longitudinal posterior list, the latter starting near the middle of the former. A transverse interior list occupies the fore border of the second abdominal tergum, being connected with the latter by a short longitudinal list. The convex area pil on the dorsum of the first abdominal segment medially of the third spiracle is small but distinct. The number of hairs is small. The apodemes of the first abdominal sternum are small, backwards directed, and separated by a broad interspace. A small, narrow, erect lateral apophysis is present. The apodemes of the second abdominal sternum are situated behind those of the first sternum; they are small but considerably larger than the latter.

The musculature is of quite the same structure as in *Macustus* but weaker, even relatively. As usual, I a  $dvm_1$  is largest; this muscle, however, does not reach the relative size of that of Macustus. It is inserted tergally by an indistinctly funnel-shaped tendon. I a  $dvm_2$  is weak; its division into two parts is indistinct, the dorsal part being considerably longer than the ventral. The longitudinal musculature is moderately developed.

Female. The apparatus has about the same degree of development as in the male; the largest muscle I a  $dvm_1$ , however, is still somewhat weaker.

Material: 18 males and 5 females from Upland, Solna.

#### Psammotettix cephalotes (H.-S)

Male and female. In all essential parts as in Diplocolenus abdominalis. The apparatus of the female is only slightly weaker than that of the male.

Material: 9 males and 6 females from Gotland.

#### Speudotettix subfusculus (Fall.)

Male. The apparatus is of the same type as in Macustus. Distinct phragmata on the metapostnotum and the second abdominal tergum are lacking, but the antecosta of the latter is strong. There is no striated tymbal; the pilose area pil is moderately developed. The apodeme of the first abdominal sternum is about half as long as the second abdominal sternum, the lateral apophysis about as in Macustus; the apodeme of the second abdominal sternum is relatively large and broad but does not nearly reach the hind border of the third abdominal sternum. As in Macustus, muscle I a dominal is powerful and is tergally inserted by a funnel-shaped tendon. I a dominal is weak but somewhat thicker than in Macustus. It consists of a dorsal thicker and longer and a ventral thinner and shorter part: the former is here not of uniform thickness, being thickest in its lower part. The dorsal longitudinal musculature shows nothing extraordinary and is weak, the ventral being slightly stronger.

Female. As in the male, but the apodemes of the first and second abdominal sterna are much less developed. Muscle I a  $dvm_1$  is less than half as thick as in the male but is inserted tergally by a funnel-shaped tendon. I a  $dvm_2$  and the remaining muscles are also somewhat weaker than in the male.

Material: 5 males and 2 females from Upland, Solna.

#### Athysanus argentatus (F.)

Male. The organ has the same structure as in Macustus grisescens. In relation to the size of the animal, however, the musculature is considerably less powerful than in that species.

Female. Although the same muscles are present as in the male, they are much weaker. Whether they have any sound-producing function is doubtful.

Material: 1 male and 3 females from Solna.

#### Limotettix striatulus (Fall.)

Male. The organ is similar to that of Euscelis plebeius. Thus, there is a distinct suspended phragma on the second abdominal tergum, and the dorsal longitudinal musculature is well developed. The ventral musculature and the apodemes reflect the conditions in Euscelis and others.

Female. Phragmata, apodemes and muscles as usual much less developed than in the male.

Material: 4 males and 2 females from Upland.

#### Thamnotettix confinis (Zett.)

Male. I found no difference from the conditions in Speudotettix sub-fusculus.

Material: 3 males from Upland. I have not examined the female of this species.

#### Solenopyx sulphurellus (Zett.)

Male. The structure of the dorsal region agrees in all essential details with the conditions in Macustus grisescens and Streptanus marginatus. The trans-

verse strengthening tr is fused with the fore border of the second abdominal precosta. In the ventral region we find the usual apodemes and apophyses, of which I a apod is thin, unpigmented, moderately large and connected medially with that of the other side. If a apod is somewhat larger and thicker, rounded. The musculature is the same as in the forms above mentioned and others.

Female. The tergites are smaller and less differentiated but have the same appearance as in the male if viewed from above. The ventral apodemes are poorly developed; I a apod has a more lateral position and does not touch that of the other side. The musculature is considerably weaker than in the male, but I a dvm<sub>1</sub> has still its funnel-shaped tendon.

Material: 7 males and 7 females from Upland, Solna.

#### Family Typhlocybidae

#### Empoasca virgator Rib.

Male. (Plate 10, figs. 1-4). The dorsum of the first abdominal segment is medially thin, membranous. An insignificant sclerite I a tg<sub>1</sub> is visible in the middle. More laterally there is a larger, weakly pigmented, elastic tergal plate including a metapostnotum (mpn) visible from the surface as an oblique list anteriorly and laterally united with the metepimeron, on the inside of which it is prolonged as a list-shaped muscle-attachment. Behind the lateral part of this metapostnotum there is a convex, thin-walled area armed anteriorly on the outside with some small spines (pil). The second abdominal tergum consists of a broadly T-shaped sclerotized surface merging laterally and in front into the sclerotized part of the first abdominal dorsum. It has a strong antecosta and a relatively broad precosta. Laterally this tergum is defined by two thicker sclerites, one anterior sickle-shaped in front of the fourth spiracle, and one posterior hook-like (fig. 3 cl). Laterally of these parts the integument is membranous, in the living animal usually convex. Behind the second abdominal tergum there is a broad intersegmental membrane. The third abdominal tergum has a strong antecosta; the precosta is medially produced in a lobe nearly touching the posterior medial lobe of the second tergum.

In the intersegmental membrane between the metasternum and the first abdominal sternum there is a transverse, narrow sclerite (fig. 2, trscl). The first abdominal sternum is a transverse, narrow, strongly sclerotized beam curved if seen from the front. On the upper side this sternum carries a transverse ridge laterally terminated by a tubercular muscle attachment (matt). Laterally the first sternum is bifurcate with somewhat curved ends apparently forming a sort of articulation with the lateral part of the second abdominal sternum. The latter is a strongly sclerotized transverse plate. Laterally there is on this plate a cavity and a hook-like process for the articulation (art) with the first abdominal sternum. Still more laterally the second sternum carries a pair of lobes (II a apoph) for the attachment of muscles. Posteriorly this sternum gives off a pair of large, parallel, tongue-shaped, backwards directed apodemes (II a apod), each being about twice as long as its width and reaching to the middle of the fifth abdominal sternum.

The longitudinal musculature of the dorsal region is rather well developed (fig. 4). Of the dorsoventral muscles in the first abdominal segment, I a dvm<sub>2</sub> is the strongest without being especially powerful. Its dorsal part is several times longer but a little thinner than the ventral, somewhat bulbiform part. This muscle is inserted in the lateral region of the metapostnotum, just medially and in front of the pilose area pil. The two muscles I a dvm2 diverge uncommonly strongly upwards and form together a rather broad V-shaped figure. Arising from the first abdominal sternum, muscle I a dvm1 runs to a point near the lateral part of the second abdominal precosta; this muscle has small dimensions but is not rudimentary. It is fusiform without a distinct tendon. Some weaker muscles extend from the first abdominal sternum to the region of the second abdominal spiracle (spir4), and one muscle from this sternum (I a ism) is inserted on the posterior sclerite (cl) of the lateral part of the second abdominal sternum. The longitudinal musculature from the metasternum to the first abdominal sternum is normally developed. From the transverse ridge of the first abdominal sternum a long, thick muscle I a vlm extends to the posterior part of the apodeme of the second abdominal sternum. This is the largest muscle of the abdomen. From the lateral muscle attachments of the second abdominal sternum, broad muscle bundles spread out to the lateral part of the antecosta of the third abdominal tergum and over the region behind that part.

Female. The dorsal region is similar to that of the male, but the antecostae of the first and second segments are weaker. In the ventral region, there is no articulation between the first and second sterna, both being less sclerotized than in the male. The transverse ridge of the first sternum is weak. On the second sternum, the tongue-shaped apodemes so conspicuous in the male are absent, insignificant transverse ridges alone offering attachments for muscles. The dorsal longitudinal musculature has about the same development as in the succeeding non-specialized segments and is, thus, considerably weaker than in the male. This is especially true of muscle Il a dlm. Muscle I a dvm<sub>2</sub> is very weak and difficult to find in the preparations. Like that of the male it consists of a dorsal longer and a ventral shorter part; here these parts are of about the same thickness and are connected by a still narrower, fibrous ligament. On the contrary, muscle  $I \ a \ dvm_1$  is quite perceptibly stronger than in the male. In addition, it is longer than in the male, its origin being more medially placed on the first abdominal sternum than in that sex. It is inserted just behind the convex area pil, medially and in front of the fourth spiracle. Muscle III vlm has the same degree of development as in the male; the ventral musculature in the region of the first abdominal segment does not differ from that in the succeeding segments except by the shorter length of the muscles. The oblique muscles II a ism are weak.

Material: 18 males and 15 females from Upland, Uppsala, Ultuna.

## Empoasca smaragdula (Fall.)

Male. As the male of virgator; the metapostnotum, however, has a small but distinct phragma on each side. Even the antecosta of the third abdominal tergum is strongly developed and medially dilated into a small phragma on each side. The dorsal longitudinal musculature is stronger than in virgator.

Muscle I a  $dvm_2$  is more powerful than that of the latter, its ventral part being short but thicker than the dorsal and with a finer striation. The apodeme of the second abdominal sternum is shorter than in *virgator* and does not reach to the middle of the fourth abdominal sternum. In conjunction with this, muscle I a vlm is weaker.

I have not examined the female of this species.

Material: 4 males from Upland, Solna.

#### Empoasca strigilifera Oss.

Male. On the whole as in smaragdula  $\bigcirc$ . Metapostnotum and the third abdominal tergum have each a small but distinct pair of phragmata. The dorsal longitudinal musculature is well developed, and so is I a  $dvm_2$ , this being thickest in the ventral, shorter part. The apodeme of the second abdominal sternum reaches a trifle behind the middle of the fourth abdominal sternum.

Female. As the female of virgator. Muscle I a  $dvm_2$  is very thin but distinctly striated. A ligament from the boundary between the dorsal and the ventral part of this muscle connects it with the metendosternum. The two parts of the muscle are equally thick. Muscle I a  $dvm_1$  is somewhat weaker than in virgator  $\diamondsuit$ .

Material: 1 male and 2 females from Småland.

#### Empoasca sordidula Oss.

Male. The metapostnotum carries a small but distinct phragma. The antecosta of the second tergum, too, is dilated into a small phragma on each side. In front of the latter, the precosta carries on the inside near its fore border a transverse antecosta-like ridge. Laterally this ridge is fused with the true antecosta. The phragmata of the metapostnotum and the second abdominal tergum are directed forwards. Laterally there is but one thick sclerite, which instead is much larger than either of the two in virgator; it has its largest extension in the longitudinal direction of the body. The phragmata of the third abdominal tergum are very large and strong as in certain species of Idiocerus. They are broadly tongue-shaped, broader than their length, directed backwards, and reach just past the middle of the fourth abdominal tergum. Muscle II a dlm has attained a corresponding stout development. I a dvm2 is about as strong as in smaragdula: its ventral part is somewhat thicker than the dorsal. The transverse ridge of the first abdominal sternum is here represented by a pair of distinct apodemes. The apodemes of the second sternum reach about to the hind border of the fourth sternum. Muscle I a vlm has a corresponding development.

Female. As in the same sex of virgator.

Material: 8 males and 4 females from Jämtland, Frösön.

#### Empoasca rufescens Mel.

Male. Comes nearest to sordidula. The metapostnotum and the second abdominal tergum, however, are devoid of distinct phragmata. The phragmata of the third abdominal tergum are obliquely tongue-shaped, somewhat

diverging backwards, almost as long as broad, and reach nearly to the hind border of the fourth tergum. The second abdominal tergum is weakly developed. Posteriorly it merges gradually into the equally thin-walled precosta of the third abdominal tergum. Laterally in the region of the fourth spiracle there is but one thick sclerite, which is smaller than in sordidula and apparently represents the anterior sclerite in virgator. The apodemes of the second abdominal sternum are rather narrowly tongue-shaped and reach about to the middle of the fifth sternum. Of the dorsal muscles, I a dlm is perhaps a trifle weaker than in the above described species of Empoasca. If a dlm is powerful as in sordidula, I a dvm<sub>2</sub> is well developed. Its ventral part is here thinner than the dorsal and nearly as long as the latter. Muscle I a vlm is powerful.

Female. As the female of virgator. As in the male, however, there is but one lateral thick sclerite in the region of the fourth spiracle. Moreover, this sclerite is smaller than in the male.

Material: 10 males and 5 females from Upland, Solna.

#### Cicadella atropunctata (Goeze)

Male, (Plate 11, figs. 1-4). The metapostnotum (mpn) is reduced to a rough muscle attachment on each side of the metepimeron near its upper end. The first abdominal dorsum is membranous in its major part. Medially there is a small tergite I a tg1, laterally of that a convex membranous area (fig. 1, ma). Still more laterally there is a sclerotized, elastic surface (conv) containing an oblique interior list extending from the metapostnotum to a lateral part of the precosta of the second abdominal tergum (fig. 1, 1). Laterally of this surface is the usual convex, anteriorly pilose surface pil. The second abdominal tergum (H a tq) has a moderately developed antecosta and a narrow precosta. The precosta carries laterally on each side an antecosta-like interior strengthening (str) reaching laterally to the posterior end of the oblique list I. From the lateral end of the antecosta runs a second narrow, obliquely transverse list  $l_2$ . This represents the anterior boundary of a convex, elastic area of the integument. In the same region there is a thick, club-shaped sclerite (ct) stretching forwards to the vicinity of the hind border of the pilose surface pil. The area behind the antecosta of the second abdominal tergum is convex, thin-walled and elastic except in the middle, where there is a narrow membranous zone (mz). Laterally and anteriorly this elastic area descends sharply towards the elastic area just mentioned; its lateral boundary is a semilunar, somewhat thicker surface carrying medially a short interior longitudinal list (l<sub>3</sub>). Laterally of this area the integument is membranous.

On the metepimeron there is below on each side a narrow triangular sclerite (figs. 2, 3, a) pointing towards the middle. The first abdominal sternum consists of a transverse, broadly U-shaped, strongly sclerotized plate (I ast). In the intersegmental membrane in front of this plate there is a longish, posteriorly broader sclerite (scl) articulating against the under side of the first abdominal sternum. In front of this sclerite the integument is rather thick along a median line and constitutes a firm longitudinal bridge. If seen in a lateral view on a longitudinal section (figs. 3, 4), this bridge forms a salient angle with sclerite scl. Probably this part of the ventral

integument offers an elastic resistance to the movements of the first abdominal sternum. Laterally the first sternum consists on each side of a wing-like process (apoph) reaching rather far upwards on the sides of the body. The posterior border of this process is strongly sclerotized; the proximal transition of the process into the body of the first sternum is more thin and flexible. In the posterior part of this region the first abdominal sternum forms a sort of articulation with a short, strong, horn-like process from the lateral part of the second abdominal sternum. This process (fig. 2, h) lies on the underside of the first sternum and has a ligamentous connection with the latter. The second abdominal sternum is posteriorly in the middle fused with the third abdominal sternum. From its upper side there arises a pair of tongue-shaped, backwards directed apodemes with somewhat elevated borders (figs. 2, 3, II a apod). These apodemes reach a little behind the hind border of the fifth abdominal sternum. Each apodeme is about half as broad as long. At the basis each of them carries on the medial side a vertical triangular process (proc). Laterally the second sternum carries an almost vertical apophysis (II a apoph) reaching about to the level of the apex of the apophysis of the first abdominal sternum. At the basis of this apophysis the second sternum gives off the horn-like process h above mentioned.

The longitudinal musculature of the dorsal region is moderately strong. In the first abdominal segment it is divided into two muscle bundles on each side (1 a  $dlm_1$ , 1 a  $dlm_2$ ). On the process a on the metepimeron there arises a fusiform muscle I a  $dvm_3$  — which is probably homologous with the I a dpm, of Aphrodes bicinctus and others — inserted by a rather long tendon on a point behind the pilose surface pil near the fore end of the thick sclerite cl. More laterally and caudally a thin cylindrical muscle La dvm extends from the first sternum to a point behind the insertion point of  $I = a dvm_3$ . On the first sternum at the basis of the wing-like process there arises a relatively powerful fusiform muscle I a ism inserted near the lateral end of the second abdominal antecosta. Behind and somewhat laterally of this muscle there is a long but thin cylindrical muscle II a dvm running from a lateral point on the basal part of the second abdominal sternum to the middle of the descending surface on the lateral part of the second abdominal tergum. A similar long and very thin muscle H a ism, extends to a point on the antecosta of the third abdominal tergum. From the metendosternum two muscles extend on each side to the fore surface of the first abdominal sternum. These longitudinal muscles are normally developed. From the hind surface of the first abdominal sternum three pairs of muscles extend to the apodemes of the second abdominal sternum. Of these, on each side two medial muscles, one lower and one upper, are inserted on the medial process proc on the basis of the apodeme; the third, much stronger muscle (fig. 4, I a vlm<sub>s</sub>) runs from lateral surfaces on the hind side of the first sternum to the posterior end of the apodeme. From the extreme end of the lateral apophysis of the second abdominal sternum a broad, fan-like muscle bundle II a ism<sub>2</sub> dilates to the lateral part of the antecosta of the third abdominal tergum.

Female. The dorsal region is similar to that of the male but is less specialized. The dorsum of the first segment has about the same appearance as in the male, the convex membranous areas ma being present here also.

Laterally of these there is on each side an elastic, weakly pigmented area with an oblique interior list as in the male, more laterally the usual pilose surface pil is present. The antecosta and precosta of the second tergum are reduced in comparison to those of the male and are more strongly pigmented. The medial membranous part of the integument behind the antecosta is broader than in the male, the lateral sclerotized area is more strongly pigmented than in the opposite sex and shows only traces of the lists described above. Sclerite cl is also reduced and is represented merely by a longitudinal asperity on the inside of the integument. The metepimeral muscle attachment a is rudimentary. The intersegmental membrane between the metasternum and the first abdominal sternum is membranous even in the middle. The first and second abdominal sterna are transverse, narrow plates with tracks for the attachment of muscles but without apodemes. The wing-like processes on the first sternum are absent. The second and third abdominal sterna are separated.

The dorsal and ventral longitudinal musculature is normally developed, corresponding to that of the remaining abdominal segments. Muscles I a  $dvm_3$  and I a ism are very weak, thin as threads. The strongest dorsoventral muscle is I a  $dvm_1$ , which is lacking in the male. This muscle arises on the first abdominal sternum somewhat laterally of the middle and is inserted on the first abdominal tergum just in front of the lateral end of the antecosta of the second tergum. It is almost cylindrical, rather long and not quite as thick as I a  $dvm_3$  in the male. The remaining dorsoventral muscles as in the male.

Material: 48 males and 12 females from Upland, Solna.

## Other typhlocybids

In Typhlocyba ulmi (L.), the apparatus is composed, broadly speaking, as in Cicadella. There are certain differences, but as my material is defective, I shall not enter upon these. In Erythroneura hyperici (H.-S.), on the other hand, the apparatus is of the same type as in Empoasca with a powerful I a  $dvm_2$  and powerful dorsal longitudinal muscles. Muscle I a vlm, on the contrary, has much more modest dimensions than in the typhlocybids described above, and the apodeme of the second abdominal sternum does not reach to the middle of the third sternum.

#### CHAPTER 2

Descriptions of the Sound-Production in a Number of Species, with Biological Remarks

#### FULGOROMORPHA

## Family Aracopidae

Dicranotropis hamata (Boh.)

Male. I listened to the sound-production of this species on 22 June, 1945, at 5.35 p.m. Cluckings pitched in about c¹, emitted singly or in an irregular rapid succession, are often heard. These calls sound like a plucking on rubber strings, or a rapping on hollow wood. Sometimes a dull "boooch" or "biiiiir" pitched in g¹ are heard. The latter sound lasts for two or three seconds. I heard these calls even in the dark on 23 June, 1945, at five minutes past midnight.

Dying-yell of the male: a short buzz pitched in f1,

Material from Upland, Solna.

## Criomorphus albomarginatus Curt.

Male. A sound-production from this male was studied on 10 July, 1945, at 3 p.m. outdoors in good weather. Females were present. The song consisted of a series of alternating rolls of two different kinds, one of which sounded like the winding up of an alarum or a toy motor car, the other recalling the hammering of a woodpecker. The last-mentioned roll may be changed to a still more rapid buzzing. This song may be vocalized thus:

"rrra — rrrrr — rrra — rrrrr — rrra — rrrrr", and so on. On one occasion the song consisted of seven rolls of each of these two kinds together lasting during a period of 10 seconds, after which followed 10 more seconds of an irregular, sometimes interrupted buzzing slowly decreasing in intensity of sound. Sometimes single clackings or knockings or longer or shorter series of such may be heard.

Material from Upland, Experimentalfältet.

## Criomorphus moestus (Boh.)

Male. A sound-production was heard from a few newly caught males on 3 June, 1945, at 2 p.m. outdoors. Females were not present. The calls con-

sisted of short gruntings like those of a pig. Each of the gruntings lasted not quite a second. I heard the same sort of calls from the same males in the presence of two females indoors at 10.10 p.m. on the same day, the males having then been in confinement for several hours. On this occasion the electric light was on. Later in the night in darkness no sound-production was heard. The animals were sitting motionless on their grass straws in the tube. Even in the cases where a sound-production was heard it was sparse.

Sometimes a more lengthy, irregular creaking sound (intervals between the single beats varying in length) may be heard. I heard it for example on 11 June, 1947, at about 10 p.m. indoors.

Material from Upland, Djursholm.

## Criomorphus bicarinatus (H.-S.)

Male, I studied the sound-production of this male on 23 June, 1945, from 7 to 8 o'clock in the evening and on 24 June, 1945, at about seven o'clock in the morning. The species is very willing to give its calls, and these are loud enough to be heard if the tube with the animal is placed on a soundboard like the belly of a violin. The sound most often heard consists of a low-pitched humming or a rapid drumming. The pitch was in some cases estimated as D. In other specimens the pitch was somewhat higher. Often very short calls repeated at rather regular intervals are heard. But still oftener the animal emits a humming prolonged for several minutes. During this humming the intensity of sound decreases and increases and the frequency of the drum-beats is varied in a way sometimes tolerably regular in one case with one rise and one fall of intensity per second -, but as often or oftener quite irregular. A male who was busy emitting this kind of song seemed to be very combative. Now and then he went hunting for his male fellow-prisoners in the tube apparently intending to drive them away, trying to push them with his fore legs. The abdomen of this humming male was distinctly vibrating vertically. In another case I observed two males apparently trying to sing each other down. They were sitting motionless opposite each other, with an interspace of about a millimetre only between their faces, rapidly vibrating with their abdomens. This competition lasted for several minutes without interruption. Now and then some other male approached from behind. The singing male with his hind end directed towards the new-comer apparently noticed the approach of the latter at a distance of a few millimetres and to parry him stretched out his hind legs backwards without interrupting his singing. This gesture of the hind legs seemed, in fact, to have the effect intended, as it stopped the potential aggressor or even made him retire.

Besides this monotonous humming, the male has the power of emitting a somewhat more complicated call (the common song), in which a similar but quite short drumming is one part alternating with a series of hammering notes in a higher pitch:

#### Achorotile albosignata (Dahlb.)

Male. Specimens of this species were captured on 23 June, 1945, at about 3 p.m. I heard the calls of the species immediately after collection and studied them more closely on the same day at 5.50 p.m., from 7 to 8 on the same evening and at 7 o'clock on the following morning. The males were often perceived vibrating with their abdomens in the vertical direction. Several kinds of calls were heard:

- 1) An often repeated clacking sound pitched in a<sup>1</sup>, e<sup>1</sup> or g<sup>1</sup>.
- 2) A short raucous vibrating "chaigh" in e<sup>1</sup>, sometimes prolonged for several seconds: "chaigh-aigh - aigh". Apparently this call was emitted mainly in connection with the rows common among the males of this species as well as those of *Criomorphus bicarinatus*. This is, then, a call of rivalry.
- 3) A low buzzing in e<sup>1</sup> with regular interruptions: "zzzzzzzaigh! zzzzzzzzaigh!" each of these notes lasting a couple of seconds.
- 4) The sound just described is often combined with a woody hammering sound as a rule consisting of six beats pitched in  $d^1$ :

5) This song may be still more perfected by the buzzing being prolonged for several minutes, during which the hammerings are repeated in regular turns:

6) A woody drumming in d<sup>1</sup> may be prolonged for several minutes with insignificant interruptions or with a lower frequency now and then. This kind of sound-production I heard on 24 June, 1945, at seven a.m.

The dying-yell of the male is a short drumming pitched in f<sup>1</sup>.

## Calligypona dubia (Kbm.)

Male. I listened to the song of this species from a single brachypterous male indoors in good weather on 9 June, 1945, at 5.25 p.m. and for a while after this time. The song consists of a rolling sound, as from some sort of machine, regularly rising and falling in intensity:

This song may be prolonged for a longer or shorter time, a few seconds as a rule.

This song was registered on the radiograph on 18 July, 1947, at 8.40 p.m. (Plate 13, fig. 7).

Material from Upland, Danderyd, Kevinge.

#### Calligypona pellucida (F.)

Male. I listened to the sound-production of a few macropterous males of this species together with some females on 9 June, 1945, from 5.25 p.m.

indoors in good weather. The song consists as a rule of a rolling sound falling in pitch, immediately followed by a series of clackings: "rrrrroooch - t - t - t - t". Sometimes the sequence of the two parts of this song is reversed: "t - t - t - t - rrrrrrrr" (radiograph record on 17 July, 1947, at 1.47 p.m.: Plate 13, fig. 9). This song lasts about three seconds.

Material from Upland, Danderyd, Kevinge.

#### Calligypona obscurella (Boh.)

Male. The sound-production of this male was studied in good weather on 21 May, 1945, at about 2 p.m., and on 8 June, 1948, from 10 a.m. to 2 p.m. The song consisted usually of a series of the same raucous note rather low in pitch: "vovovovovovovovovovo" (3 seconds) or "rorororororo" (2 seconds). Sometimes this series of notes was succeeded by a few clacking sounds, sometimes by a buzzing tone lasting one or two seconds. This tone was lower in intensity but considerably higher in pitch than the first part of this call.

On 8 June, 1948, two singing males were studied through the binocular magnifier, their wings having been cut off. The sounds were simultaneously heard with the aid of microphone and ear-phones. During the first part of the song, the abdomen of the male was vigorously jerked up and down and vibrated simultaneously with a much smaller amplitude, each of the notes of this part of the song corresponding to one sinking and one raising of the abdomen. During the second, buzzing part of the call, the abdomen was not perceptibly moved, but the lateral part of the first abdominal tergum vibrated distinctly. The vibration and the sound ceased simultaneously.

Material from Ostrogothia, Rystad, and Upland, Solna.

## Calligypona elegantula (Boh.)

Male. The first time I listened to the sound-production of this species was on 20 May, 1945, at about ten a.m. The weather was nice and warm. The song was rather faint. It began with a couple of short croaking notes "cha-cha-" followed by a rhythmical buzzing as from a sewing-machine. This song lasts for about ten seconds.

In the night (about 11.30), the light in the room having been switched off, I heard more irregular chirping sounds from this species.

From a macropterous male kept in a celluloid cage in the company of a male of *Achorotile albosignata* 1 heard on 24 June, 1947, from 9.30 to 9.44 p.m. a continuous concert of the following character:

first a series of about seven "fffffo":s lasting about 4 seconds. Then immediately 19—20 "trrr":s or drummings irregular in length, then a fresh series of "ffffo":s, etc. During the first, hissing part of the "ffffo", the ab-

domen of the animal was sunk rather slowly while vibrating distinctly. Then it was rapidly raised and the "o" was heard. During the rolls "trrr" the abdomen vibrated with a smaller amplitude. At the same time the wings were kept somewhat obliquely elevated over the abdomen and vibrated with the same rate. Each "drum-beat" corresponded to one movement up and down of the abdomen. As soon as the *Calligypona* male had finished its song, the *Achorotile* male immediately gave a concert of one minute. After that both kept silent.

Material from Ostrogothia, Rystad, Fröstad (1945), and Upland, Solna (1947).

#### Calligypona angulosa Rib. (in litt.)

Radiograph recordings of this call were made on 19 July, 1947, from 7.29—7.35 p.m. The radiograph reacted only to the first part of the song (Plate 13, fig. 11). 5 notes of this part take a time of 0.53 second. A gramophone record of this song has been made, and this record has been transferred to sound-film. According to this film, the croakings of the first part of the song have a main tone frequency of about 490 cycles per second. This tone is richly accompanied by high overtones. The tone of the latter part falls in frequency from about 180 to about 160 cycles per second. It is also richly intermingled with overtones.

Sometimes single clackings are heard. The pitch is varied individually.

This species I heard singing even at night (about 11 o'clock), the light in the room having been put out.

Material from Ostrogothia, Rystad, Fröstad (1945), and from Upland, Stockholm, Skuggan (1947).

## Calligypona albocarinata (Stål)

Male. I heard a sound-production from the male of this species on 24 June, 1945, at 4.50 and 8.50 p.m. The common song consists of two parts. The first part is a rapid woody hammering, the second being a voiced sound in a falling pitch. The latter may be vocalized as "biiiiiir". This song takes a time of four seconds:



Sometimes only the tremolo is heard, which is then as a rule prolonged up to half a minute and decreases in rate towards the end.

Material from Södermanland, Nacka, Erstavik.

#### Calligypona cxcisa (Mel.)

Male. The sound-production of this male was studied on 3 August, 1945, at 3 p.m. outdoors and on the following day at 7.15 a.m. and 10 p.m. A simple song consisting of a tone falling in pitch is often emitted, for example:



This sound is often heard as the second part of a song consisting of two parts, the first being a longer or shorter series of a more or less irregular croaking sound in some cases pitched at e<sup>4</sup>: "ca-ca-ca-ca..." or "corr-corr-corr-corr-..", etc. I usually counted 4—5 of these croakings per second, but towards the end of the series the rate generally increased.

Another call is a hoarse croaking sound of about one second: "craaah", An unrhythmically repeated smacking in a¹ is often heard.

Material from the seashore in the vicinity of Halmstad.

#### Calligypona aubei (Perr.)

Male. The song of the male of this species was heard on 22 July, 1945, at 8.30 and 8.50 p.m. I have tried to reproduce it in the following way:



This song lasts for about 3 seconds. It consists, then, of two parts: first a series of usually 3—7 more voiceless drum-beats or rattlings, then a lengthy tone falling in pitch. Sometimes the first part is prolonged, occasionally it is produced singly as a simple call.

Material from Gotland, Visby.

## Calligypona exigua (Boh.)

Male. This small species has an unrhythmical smacking call, louder than in elegantula, alternating with a rancous buzzing or wailing "aaaigh-aaaigh". This call takes a time of a few seconds. Another call reminds one of denticauda: "t-t-t-t-tr-trrrrr" (3 seconds). I heard these calls in nice warm weather at about ten o'clock on 20 May, 1945.

Material from Ostrogothia, Rystad.

#### Calligypona denticauda (Boh.)

Male. My observations on the sound-production of this male were made on 20 May, 1945, at about 1 p.m. It is rather variable. Sometimes single short creakings or tappings are emitted. On other occasions you hear several

such creakings in rapid succession: "tr-tr-tr-tr-tr-tr" or "t-t-t-t-t" or "trrrrrrr". Each of these series can last for a couple of seconds. Another call may be vocalized thus: "trrrrra trrrr, trrrrra trrrr, and so on. Each "trrrrra trrr" lasts a couple of seconds. A longer song of up to half a minute or so may be composed in the following way: "t - t - t - t - trrrr - rrrrrr mmmmmm - trrrrrrr - mmmmmm - trrrrr - mmmmmm . . .", and so on. One "trrrrr-mmmmm" lasts for about 2 seconds. By "mmmm" I have tried to vocalize a low-pitched nasal tone suggestive of the voiced "humming" which may be produced by a person with his mouth closed.

Material from Ostrogothia, Rystad.

## Calligypona straminea (Stål)

Male. I heard the sound-production of this species and made radiograph records of it on 19 July, 1947, from 7.43-7.46 p.m. I only heard one kind of song:

Thus, a series of (as a rule 13-14) rolls is immediately followed by a short, more accentuated rolling (Plate 13, fig. 10). Usually the male emits several such series in succession, one series of 13 + 1 rolls taking a time of about 2.5 seconds, six consecutive series 18.3 seconds. During these observations, several males were kept in a cage without the company of females.

Material from Upland, Stockholm, Skuggan.

## Calligupona clupealis (J. Sahlb.)

Male. On 3 June, 1945, at about four o'clock in the afternoon I collected in good weather two brachypterous males and a few females of C. clypealis. Immediately after collecting them I tried to hear the calls of the animals, but in vain. The insects were kept in a glass tube with some straws of Calamagrostis lanceolata, At 8.35 the same evening I resumed my study of the animals indoors. The two males were then engaged in a lively singing competition. Practically without interruption they sang poecilochronously till 9.35, when I stopped listening. Five minutes later, when I wanted to start again, the song had ceased. Later during the evening I only heard single short buzzes.

One of the males carried an acarid larva which had attached itself on the left side of the dorsum of its host in the region of the first and second abdominal segments. This apparently did not prevent the Calligypona male from singing. The song consisted of a purring buzz interrupted once in 2-5 seconds or sometimes considerably more often by a short, low-pitched tone: "rrrrrrr-zzu-rrrrrrrrrrrrzzu-rrrrrrrzzu...". The pitch was different in the two specimens.

Material from Upland, Djursholm.

## Chloriona smaragdula (Stål)

Male. The male of this species has a low, clacking call, repeated with single clackings now and then. Further, I have often heard an unvoiced

creaking or drumming call lasting about a second. This was also included as a part in a longer complicated song I heard on 25 June, 1945, at 9 a.m. (indoors): "crrrrrr - k - k - crrrrr - cheigh - crrrrr - che-igh - crrrrrr che--igh - crrrrr - k - k - k". The sound here vocalized as "cheigh" is pitched at f1 or sometimes d1. The drumming, on the other hand, is rather slow with a rate of about six beats per second, while the cheighing appears to consist of much more rapid rolls.

Material from Upland, Solna.

#### Chloriona vasconica Rib.

Male. I have heard the following sounds from this male:

- 1) Low, single clackings as in smaragdula.
- 2) A dull "brrrrr" or "booooooh" pitched very low.
- 3) On 24 June, 1945, at about 10 p.m. in a dark room I heard a song mainly in f<sup>1</sup> lasting a couple of minutes:



4) On 24 June, 1945, at 2 p.m. I heard a call that may be compared to the purring of a cat or to a discrete snore. In other words, this call consisted of a rolling sound lasting a few seconds and repeated several times with pauses of the same length.

Material from Upland, Solna.

## Megamelus notula (Germ.)

Male. A sound-production from a few males without the company of females on Carex sp. in a cage was heard on 26 July, 1947, from 7-7.30 p.m. The calls consisted of short (0.14-0.17 seconds) voiced notes: "brrrr" or "borrr" in a low bass. For a while two males sang alternately, but the intervals between the individual notes were very unequal. This alternating song was registered on the radiograph (Plate 13, fig. 3).

Material from Upland, Laduviken.

## Megamelus venosus (Germ.)

Male. The sound-production of this species was studied on a dozen males without the company of females in a celluloid cage containing some grass blades on 21 September, 1947, from 11 a.m. to 1.30 p.m. Temperature on the occasion: 23°-24° C. There are several different calls.

1. The common song consists of two or three parts. The first part, which is often lacking, may be compared to a nasal tone with the pitch somewhere in the small octave. As a rule this tone lasts  $\frac{1}{2}-\frac{2}{3}$  second. Then begins

2. The second part (the bleating) of the song above described is sometimes produced isolatedly. It is somewhat more uncommon to hear the

bellowing (third part) separately.

3. I often heard a call consisting of a series of more or less regularly repeated tapping sounds which might have been produced by striking on a board with a piece of wood. In other specimens, the individual notes may be compared to short croakings: "cr - cr - cr - cr - cr - cr". In some cases, such series of croakings may be short; in one case they consisted of 13 croakings in a period of a little more than three seconds (radiograph record, see Plate 13, fig. 6). In other cases they may be considerably longer, lasting one or several minutes. I sometimes heard this call from a male while other males in the cage were singing the common song (1, above) simultaneously.

4. The species has at least one additional characteristic call, but as I have heard it once only, I am not able to describe it.

Material from Upland, Djursholm.

## Stenocranus minutus (F.)

Male. I have heard a sound-production only twice: indoors on 27 May, 1945, at 3.22 p.m., the weather being good, and on 30 March, 1946, at 1.55 p.m. The animals were kept in glass tubes, in the latter case on a small twig of spruce (*Picca excelsa*). The call consisted of a short, quick chattering like that of a magpie.

Material from Upland, Djursholm and Solna.

## Euidella speciosa (Boh.)

Male. The sound-production of this male was studied indoors on 3 June. 1945, at 8.25 p.m. and at 11 a.m. the following day. The sound consisted of a repeated irregular (non-rhythmical) clucking or clacking. In 5 seconds I counted 10 clackings. I first heard 10—15 consecutive clackings, then a pause of varying length, then a new series of clackings, and so on. Females were not present.

On 22 June, 1945, at 6.05 p.m. I heard from a single male a song consisting of a not very rapid drumming as on wood, succeeded by a short croaking: "trrrrrrr - craah".

Material from Upland, Solna and Djursholm.

#### Family Cixiidae

#### Cixius nervosus (L.)

Male. I have had an opportunity of hearing the sound-production of this species only twice, the first time from one single male captured with three females on Tilia on 11 July, 1945. The male emitted his call only sparsely. I heard it for example at the following times of the day: 2.30, 6.00, 8.22 and 9.20 p.m., and at about 2.30 a.m. during the following night. The call consisted of a roll lasting for one second or somewhat longer. The tonal quality was rather dully voiced. In some case I estimated the pitch at II, in another at f. As may be expected from a species of this size, the intensity of sound is relatively considerable. When the tube with the animal had been placed on my violin, the roll could be heard at a distance of 70 cm from the edge of the violin nearest to the observer. These observations were made on the isolated male. If females were present, he seemed troubled and tried to escape, frequently by making a vigorous leap.

Radiograph records were made on 21 July, 1947, between 8.21 and 8.33 p.m. by electric light. A single male on a small twig of birch (*Betula*) in a cage was used. According to the version of the radiograph (Plate 13, figs. 1 and 2), the first half of the call has a greater intensity of sound or a higher frequency than the latter. This was not appreciable during the listening.

Material from Upland, Solna,

#### Cixius similis (Kbm.)

Male. Sound-production heard on 8 June, 1947, at about 1 p.m. from a single male just captured. The call consisted of a short, low-pitched roll or creaking tone of about one second.

Material from Södermanland, Nacka, Erstavik.

#### **JASSIDOMORPHA**

CERCOPOIDEA

## Family Cercopidae

## Neophilaenus lineatus (L.)

Male. The sound-production of this species was studied on 14 July, 1945, during the afternoon. Now and then the male emitted an irregular laughing

call pitched in d¹: "ho - ho - hoho - ho - hoho - ho - ho". Such a series takes a time of 3—4 seconds.

From a couple in copula I heard a somewhat diverging variant of this call. After collection the animals were brought home in a glass tube, and at 4.35 o'clock I found that one male and one female were occupied in copulation. As soon as I started to listen I heard a laughing call in a<sup>1</sup> from

per second. Each call continued for 2—3 seconds. The external genitalia of the members of the pair remained united till about 9 o'clock in the evening, and during this time the laughing call was heard now and then. I have since heard this call even from males without female company.

At 7.37 p.m. the same day I heard from my males a tone falling in pitch

lasting about a second:

Material from Upland, Djursholm.

#### Philaenus spumarius (L.)

-wa-wa...". Each song lasts a few seconds (Radiograph record, Plate 13, fig. 14). If several males are kept together in the same tube, they readily strike up a chorus or an alternating song (poecilochronous singing), sometimes one male singing singly, sometimes several singing simultaneously. In this way they will croak for several minutes. It is quite clear that these males do apprehend each other's calls: if several males are together, the calls of one of them is a signal for the others to join in. Between the choruses there are long pauses in which no one sings. If only one male is in the tube, however, he does not allow his solitude to prevent him from emitting his call now and then.

One of the males I had under observation on this occasion accompanied his croakings by a lower creaking sound sometimes beginning a few seconds before the croaking started and ceasing a few seconds after it had ended. The quality of sound of the croaking is somewhat raucous but not unmusical.

From a copulating couple I heard the same day at 6 o'clock and for a while afterwards a similar croaking sound repeated in rapid succession but without

any rhythm and pitched at e<sup>t</sup> or d<sup>1</sup>: "ya - ya - ya-ya-ya - - ya - yaya - ya -

- ya - yaya . . .". The diverging pitch was no peculiarity of this male (if the male and not the female was responsible for these calls): as soon as copulation had ceased he emitted the same call in c<sup>1</sup> above described.

Material from Upland, Solna.

## Aphrophora alni (Fall.)

Male. As a sign of apprehension or dissatisfaction this male emits a smacking sound usually repeated in rapid succession and at intervals of

irregular length. The same sound is emitted if the animal is held fast by a wing or a leg. The pitch is difficult to make out.

The common song of the male is a raucous "corr, corr, corr". A series of eight such croakings may take a time of 5 seconds. I heard this call for example on 12 July, 1945, at 8.35 p.m. I made radiograph records of this call on 21 July, 1947, from 8.48 to 9.00 p.m. A single male on a birch twig in a celluloid cage was used; the cage was illuminated by an electric lamp. This male was rather liberal with his croakings. He emitted them in a series of 7—72 in succession. Each of these croakings seemed to consist of 4—6 vibrations, each croaking lasting for about  $\frac{1}{6}$  of a second, the intervals being of 0.5—1.3 seconds (see Plate 13, fig. 12).

Female. Even the female has the capacity of emitting the call of distress or dissatisfaction described above for the male.

Material from Upland, Solna.

## Aphrophora forneri (Hpt.)

Material from Upland, Bondkyrka.

## Lepyronia coleoptrata (L.)

Male. 1) This species has a smacking call like Aphrophora alni. Here it is less hard, however, and consists essentially of high overtones. Sometimes it might be compared to the "chip-chip" of the common house-sparrow (Passer domesticus). At all events, however, the sound expresses distress and is emitted if the animal is held firmly or if it has, for example, stuck fast by its wings in condensed moisture on the inside of the glass tube. In such cases of obvious distress, the rate of this sound-production is very high with several smackings a second. If the cause of the discontent is more vague, the intervals between the single smackings are longer.

Thanks to the proneness of the animal to emit this call if held fast, I have been able to study the method of its production. I cut off the wings of a specimen on the right side with the aid of a fine pair of scissors and fixed the animal on a small plastiline pad, after which I studied it through a binocular magnifier. This examination showed that the lateral parts of the dorsum in the region of the first abdominal segment vibrated vigorously; these parts, being convex in a position of repose, were turned from concave to convex in rapid succession. The movements were at about the same rate as the smackings just heard from the same specimen. The whole abdomen, too, assumed a vibrating movement, which seemed to be secondary, however.

2) Further, the male has a drumming or laughing call "hahahaha" (7—8 notes per second). The rhythm is most regular, so that this call reminds one of the fire of a distant machine-gun. Each call consists of only 4—6 "shots", as a rule. I have heard this kind of sound-production for example on 13 July, 1945, at 5.00, 7.15 and 10.40 p.m., in the last-mentioned case by electric light. For these observations two males were kept together in a

tube, no females being present. They performed this call as an amoebochronous song. The "fire" of the "gun" of one male was immediately returned by the other without any perceptible pause and without overlapping. However, each of the males performed only three or four calls of this kind, then both of them were silent. I was able to separate the "voices" of the two individuals thanks to the fact that one of them was scated a longer distance from my ear than the other, which made the calls of the former sound weaker. In intensity of sound this call agrees approximately with that of the call described below. Perhaps this is a "call of rivalry".

3) During the same evening at 8.58 o'clock I heard a loud buzzing or drumming sound pitched at A (or perhaps  $A_1$ ) lasting for eleven minutes without interruptions longer than about a second. The followed an amoebochronous singing of the kind above described lasting for about one minute, and after that the drumming continued for a few minutes but with somewhat longer pauses now and then. The tube with the insects having been placed on the belty of my violin, the sound could be heard at a distance of one yard. Through a magnifier I could easily see that the abdomen of one of the males vibrated vertically, though with a much smaller amplitude than might have been expected with regard to the intensity of sound.

On 19 July, 1947, I tried to determine the frequency of these drummings with the aid of the radiograph. This, however, did not succeed entirely. On some occasions a rate of 30—40 periods a second could be established (Plate 13, fig. 13), but as a rule it was considerably higher, the radiograph giving a record consisting of an almost even band without distinct peaks even at the maximum speed of the puller.

I have heard no "dying-yell" from this male. If the animals are put in alcohol, they soon emit the call of distress as in (1) above, but the sound becomes rapidly weaker and ceases totally after a few seconds.

Female. The female, too, is able to emit the smacking "sound of distress" above described and makes use of this power as assiduously as the male. The method of producing this call is also quite the same as in the male.

Material from Upland, Djursholm and Danderyd, Kevinge.

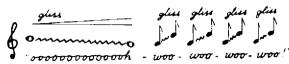
#### JASSOIDEA

#### Family Euacanthidae

#### Euacanthus interruptus (L.)

Male. When in captivity, this male is rather parsimonious with his sound-production. In spite of many endeavours I had not heard it until 2 August, 1947, when I kept two males in a cage without the company of females. The sound-production was heard a few times between 6 p.m. and 8 p.m. The song consists of two parts: first comes a lengthy tone beginning rather high in the treble and continuously falling in pitch towards the end; then a series of usually 2—4 short cooing notes, each rising in pitch towards the end. Sometimes the second part is omitted. Plate 13, fig. 17, gives but an incomplete rendering of this call, as the radiograph did not react to the beginning of the first part. I have not been able to determine the pitch. An

attempt at reproducing this call by musical notation and letters looks like this:



The first part lasts 3—4 seconds, the second part taking for a series of 3—4 notes one second or somewhat longer.

Material from Upland, Solna.

# Family Proconiidae

# Tettigella viridis (L.)

Male. A sound-production from this male was heard in 1944 and on 14 July, 1945, at 5.05 o'clock and several times on the same evening, partly by electric light, and also just after 11 p.m., the light having been put out. The species has a deep bellowing, very low-pitched voiced call. The pitch varies round D. Often the call begins pitched at D sharp or still somewhat higher only to glide down to D or somewhat lower. At times the sound is more raucous. Each of these bellowing notes continues about one second.

Material from Upland, Djursholm.

# Family Eupelicidae

Eupelix depressa (F.), f. cuspidata (F.)

Male. On 22 May, 1945, I found one male and one female of this species and put them together in a glass tube with a few stalks of grass. Very soon I was able to listen to the sound-production of the male. The calls consisted of two alternating parts: a rather strong raucous voiced note, that could

be vocalized as "eea", and a series of a few low smackings "t". This song seemed to be a call of courtship and was emitted only when the male was near the female. It was composed of the two parts above described in the following way: "eca - eca - eca - eca - t - t - eca - t - t - t - eca - t - t --t-t-eea-t-t-eea...". Thus, the song consisted of repeated "eea":s exactly one note of this kind per second — each followed by as a rule three smackings; at the beginning of the song this smacking was absent and did not begin until the singing had got well started. In 45 seconds I counted 45 such series of one "cea" and at most three "t":s. During the singing the abdomen vibrated vertically. Soon this vibration became rather strong and set the whole body in such agitated motion that the male was forced (?) to shift his foothold once a second in pace with the music. In this way a sort of dance or marking time was executed, interrupted, however, now and then by short, rapid movements in the direction of the female. The latter often tried to escape by running or by a leap. Sometimes the male made a short pause in his music but recommenced it if he found himself near the female.

Having mounted the female and being busy trying to connect his genitalia to hers, the male continued his singing. During copulation he kept silent. The act of copulation took in the case observed a time of 15 minutes. When it was over, the male again performed a short song of the same kind as that above described. These observations were made by the light of an electric bulb at about 10 p.m. Next day the music could be listened to in daylight but only in the presence of the female.

The same male emitted a similar but more irregular call when he found himself in distress. Observations on these matters were made on the morning of the 24 May. If the animal was seized by a leg or one of the fore wings with the aid of fine tweezers, I was able to see through the binocular magnifier that it made vigorous vibrating movements with its abdomen. By pressing the handle of the tweezers to the tragus of my ear so that the auditory duct was closed, the insect's call of distress was heard. (This method for hearing the calls of very small insects was indicated by Santschi in 1909.)

I then cut off the wings of the male near their base with a pair of scissors and stuck the animal by some of its legs on a pad of plastiline, after which I studied it through the binocular magnifier. My specimen, however, now seemed very exhausted. Nevertheless on a couple of occasions I observed vibrating movements in the lateral parts of the first abdominal dorsum. At the same time the entire abdomen vibrated in the vertical direction. I conclude that the lateral parts of the first abdominal tergum are the vibrating membrane of the sound-producing apparatus of  $Eupelix \circlearrowleft$ . The vibrations of the abdomen will be secondary or have a modifying effect on the sound.

Material from Ostrogothia, Askeby.

# Family Ledridae

#### Ledra aurita (L.)

Male. I have heard the call of this male twice, namely on 7 July, 1946, at 10.55 a.m. just after capturing the animals, and at 7.13 on the following morning (single male). The call consisted of a tone falling in pitch and repeated once per second:



On the first occasion I heard 18 "tunings" in succession taking, then, a time of 18 seconds. On the second occasion only 5 notes were apprehended. Two males were at my disposal for listening, but they did not seem very talkative, the above mentioned being the total result of repeated listening during one day and the following morning. The presence of females apparently did not have any stimulating effect on the males in this respect. Nothing was heard from the males during the night.

Material: two males and two females from Ostrogothia, Törnevalla, Elvestad.

#### Family Idloceridae

#### Idiocerus laminatus Fl.

Male. The sound-production of this male was studied on 13 July, 1947, from 2.28 to 7.45 p.m. The call consists of a buzzing of somewhat more than half a second, succeeded by a series of, as a rule, three clackings: "brrrr - t - t - t". Radiograph record, see Plate 13, fig. 23. As the figure shows, the first, buzzing part consists of 10—15 beats, emitted at a rate of twenty per second. The clackings of the second part sound like pluckings on the teeth of a comb. I have made a gramophone record of this call, and this record has been transmitted to sound-film. By this method the pitch of the beats of both parts of the song has been determined as 1120 cycles per second.

As a rule, these calls are emitted in regular succession: 4 calls in 6 seconds. If two males are together, they almost always perform a regular alternating song. Then each of the males extends the pauses between his calls a little, so that room is made for those of the other male. By this arrangement five calls are emitted in six seconds, two from one male and three from the other. (See Pl. 13, fig. 23. In this figure six calls from each male are recorded, the records of one of the specimens being much more distinctly marked than those of the other, because the former was seated closer to the membrane of the microphone than the latter.) The alternating singing usually ends with a row, one of the males trying to push the other away. This alternating singing may, then, be interpreted as a call of rivalry, even though females were not present during these observations.

During the first, drumming part of this call, the abdomen of the male vibrates vigorously. I did not perceive any movement of the abdomen corresponding to the clackings of the second part.

Material from Upland, Solna.

#### Idiocerus populi (L.)

Male. I studied the call of this male on the evening of 14 July, 1947, from 9 to 10 o'clock. It is very similar to that of laminatus. It consists, then, of two parts: first a drumming for somewhat more than half a second, then a series of clackings of the same kind as in laminatus. The drumming, however, is considerably slower with, as a rule, only six distinct beats, at a rate, then, of about 11 beats per second (see Plate 13, figs. 24 and 25). The gramophone-sound-film record, however, reveals that each of these beats consists of two consecutive groups of vibrations separated by a distinct pause, the vibrations of the first group having a much smaller amplitude than those of the second group. It seems to me that this suggests that the sound-producing membrane is here first made concave, which, by the resistance of the contracted muscle, will result in a swinging with a smaller amplitude, and then by the relaxing of the muscle regains its convexity and is able to vibrate more freely. This is mere guesswork, of course. The phenomenon in question might perhaps also be explained as the result of an alternating action of two different muscles. The main tone of these beats has a frequency of about 312 c.p.s. (= cycles per second): it is accompanied by a high overtone. This overtone has a greater amplitude in the clackings of the second part of the call, where it has a frequency of about 3750 c.p.s.

If two males were kept together, they performed an alternating song less distinctly amoebochronous, however, than in laminatus. More often than in the latter species (in cases observed by me), one of the males had to repeat his call without receiving an answer from the other, and in the heat of the competition a certain tendency of passing on to poecilochronous singing was noticeable.

Material from Upland, Solna.

#### Idiocerus fulgidus (F.)

Male. The sound-production of this species was studied on 16 July, 1947, from 7.30 to 9 p.m. The call is very similar to those of populi and laminatus described above. Thus, it consists of two parts: a drumming apparently rather low-pitched, and a subsequent series of clackings with a considerably higher pitch. If compared with that of populi, the rate of the call is much more rapid, and the call takes a shorter time (Plate 13, figs. 20—22). The initial part is very similar to that of laminatus, having a rate of about 30 beats per second, but the latter part consists of a greater number of clackings and takes a longer time than in that species. According to a gramophone record subsequently transferred to sound-film, the main tone frequency of the single beats of the drumming is about 378 c.p.s. There is a high overtone with a small amplitude. The tone frequency of the clackings of the second part of the call is 1300—1400 c.p.s.

In the six males studied by me, which were kept together in pairs, no tendency of alternating or poecilochronous singing was noticed.

Material from Upland, Stockholm, Hortus Bergianus.

#### Idiocerus confusus Fl.

Male. I studied and made a radiograph record of the common call of this species on 24 July, 1947, from about 8 to 9 in the evening. I kept two males in a cage with twigs of Salix sp. This male has a call reminding one of those of I. populi, laminatus and fulgidus, consisting, then, of a series of clackings and a drumming, but with the difference that the clacking part, which is suggestive of the fire from a machine-gun, here precedes the drumming (Plate 13, fig. 27). The first part consists of 10-15, the second of 6-7 beats, the call taking a time of about 1.8 seconds. The call of this species, however, varies much more than those of the relatives mentioned. Now and then a call consisting of three parts instead of two is heard: first the two described above, the "machine-gun" and the roll of drum, then immediately afterwards a slower series of weaker clackings - about ten clackings during a second or so - more high-pitched. A song of this kind with three parts in one case took a time of 2.2 seconds. Radiograph record, see Plate 13, fig. 26. On the other hand, a male of this species in the presence of another, in the heat of competition, often emits a prolonged "machine-gun fire" of several seconds omitting the other two parts of the common song. This male is inclined to sing amoebochronously but oftener poecilochronously.

Material from Upland, Solna.

#### Idiocerus elegans Fl.

Male. Heard and recorded on the radiograph on 26 July, 1947, from 8—8.30 p.m. Two males were kept on Salix sp. in a cage, no females present. The male has 1) a cackling call apparently expressing distress or dissatisfaction, 2) a barking or sharp croaking, very short, distinctly vibrating call. Each of these croakings takes a time of about 0.1 second. Often a series of a few such croakings with tolerably regular intervals is emitted (Plate 13, fig. 28). As the figure shows, a series of six croakings takes a time of two seconds.

Material from Upland, Lake Laduviken.

#### Family Macropsidae

#### Oncopsis flavicollis (L.)

Male. It was a long time before I succeeded in hearing the sound-production of this species. If a few specimens are put together in a tube or cage, one or two of the lively animals always run about disturbing the others. They often jump or try to fly. Both the jumping and the flying manoeuvres produce sounds considerably stronger than those emitted with the aid of the tymbal apparatus. Agitated animals running about often get involved in what reminds one of involuntary wrestling and then often emit short whining sounds.

On 21 June, 1945, at 8.45 in the morning I heard a call lasting for about three seconds resembling the sound made by letting a finger-nail glide rather slowly over the teeth of a comb (the teeth being of uniform length). After a little while the same call was again heard but prolonged to about 20 seconds with short interruptions. At these observations, both sexes were kept together in the same tube.

At 8.40 p.m. on 20 June a call consisting of two alternating, rather prolonged tones was heard: "aaaah-ooooh-aaaah-ooooh-aaaah-ooooh...". Each pair of notes ("aaaah-ooooh") continues for about one second. This song lasted for about half a minute. The later notes were longer than the earlier ones.

The pitch of the two tones was difficult to determine. The lower tone could scarcely be apprehended as a tone: I distinctly heard the single vibrations but was not able to count them. I had the impression that the main tone was a low-pitched G, perhaps in the great octave or still lower. The higher tone recalled the raucous, flat sound produced on a violin by pressing the hair of the bow rather hard against the string and moving the bow very slowly. A sound of indeterminable pitch appearing to be rather high-pitched will be obtained, as the main tone is drowned among the raucous overtones. I estimated the main tone at d¹ or perhaps d².

In the afternoon and evening of 21 June, both sexes were studied separately. Thus I had a few males in one tube and some females in another and devoted my attention to the two tubes in turn. From the males I heard at 5.15 p.m. a song of about half a minute, beginning by two alternating, buzzing tones, one low, the other much higher in pitch:



(5 seconds), after which the call passed into a more irregular drumming of varying pitch and decreasing intensity. In another similar song both tones were considerably lower in pitch. On another occasion this song continued for 70 seconds.

At about 11.30 p.m. in darkness I heard from the males a sound consisting of a regular rapping. I have heard this sound from the females too, but I am uncertain if it is produced by the tymbal apparatus.

Female. From the females the song described above has not been heard. However, the female often emits a raucous call sounding as though produced on the violin by pressing the hair of the bow hard against the string and bowing slowly (cf. the male above). Often this call rather gives the impression of a voiceless hissing. As mentioned above, the male also emits this call now and then, but it is heard much more often from the female. Each of these sounds lasts about a second. Sometimes it is frequently repeated. The pitch is variable—if this expression can be used in this connection. On one occasion it seemed to be d¹, on another a, and in a third it was considerably lower. The female often produces this sound while running about in the tube. Apparently it is a sign of distress or animation.

In one case I have heard from the female a series of regular rappings (about 6 per second) during a period of about 10 seconds. This observation was made at 10.55 p.m. by electric light. Whether this sound was produced by the tymbal apparatus or by the moving of the extremities or in some third way I could not tell.

The call of distress of this female is not emitted if she is kept fettered by a wing or a leg. In this case only the sounds which result from the floundering and fluttering of the animal are heard. The dying insect, however, emits at times a sound quite similar to that compared above to the sound produced by stroking the teeth of a comb. This "dying-yell" I have heard from both sexes. Of 22 males and 15 females put in alcohol, one male and three females emitted this yell within one or two minutes. Each "dying-yell" lasted about two seconds. The animals had then sunk to the bottom of the tube and had ceased struggling with their legs. Further, four specimens of each sex were killed in a tube containing a few small pieces of potassium cyanide. Then one male and one female emitted the "dying-yell".

Material from Upland, Solna.

#### Oncopsis alni (Schruk.)

Male and female. Both sexes of this species are able to emit a call usually consisting of a raucous hissing sound; sometimes it is harder and recalls the sound produced if a finger-nail is moved over the teeth of a comb. This call is heard oftener from the female than from the male and seems to be a sign of distress or dissatisfaction. Each note has a length of  $^{-1}/_2$ —1 second and is usually repeated at short intervals. Sometimes the notes and the intervals are still shorter, this sound-production then resembling Morse signalling. On one occasion the "pitch" was estimated at  $h^1$ . The same call from the male, heard on 5 July, 1945, I estimated at  $g^1$ .

A still harder, short, vibrating note from the male, heard on 5 July, 1945, at 10.45 p.m., was pitched at A, a moment later at G.

At 11.03 on the same night I heard from a single male a short call also resembling the "comb-sound" alluded to above:



The above observations were made on males or females isolated from the opposite sex. Once when a female and a male were kept together, the male made several attempts to start copulation. When he had mounted the dorsum of the female, I heard some calls consisting of a rather dull droning sound and of varying length. Whether this call was emitted by the male or by the female I could not tell.

Material from Upland, Solna.

#### Oncopsis tristis (Zett.)

Male. A sound-production of this male was heard on 14 July, 1945, at 6.04 p.m. It consisted of a voiceless rolling sound of about 4 seconds: "trrrrrrrr". Material from Upland, Djursholm.

#### Macropsis tiliae (Germ.)

Male. This male has several different calls.

- 1) A brief whining or chirping sound pitched at c¹, d¹ or d¹ sharp. Sometimes the high overtones dominate and the sound becomes much more high-pitched. These notes are frequently repeated at irregular intervals. Sometimes the notes are produced in such rapid succession that in its rhythm this sound-production resembles Morse telegraphy (Plate 13, fig. 19). This impression is strengthened by the individual notes being of varying length. This kind of sound-production is apparently emitted when the male is agitated often while in lively movement or when he has got into trouble of some sort. If he is seized with a pair of tweezers by a leg or a wing, he emits this call. It is quite similar to the call of distress described above for Oncopsis flavicollis and alni, especially the females. But I have not heard it from the females of tiliae. If the tube with the tiliae male is placed on the belly of the violin, the sound is heard at a distance of one decimetre.
  - 2) On a few occasions I have heard a short "zzee" pitched at c2 sharp.
- 3) Sometimes single, short, cooing or croaking, low-pitched sounds are heard.
- 4) On some occasions for example on 11 July, 1945, at 8.30 p.m. and at 9.58 in electric light a prolonged, more voiceless, woody drumming of two or three seconds or longer was heard. The pitch seemed to be d¹, sometimes a little higher or lower.
- 5) Sometimes I heard a cutting but simultaneously vibrating, prolonged, high-pitched sound. It might be compared to the sound produced by cutting glass with a diamond, but it is distinctly vibrating as when a fine file is rubbed with the point of a knife at a uniform speed. The duration of this sound is about one second each time.

- 6) The sounds described as 4) and 5) are often combined, the former suddenly changing into the latter.
- 7) From a single male in a celluloid cage I heard on 10 July, 1947, from 8.51—9.06 a call consisting of a continuous, prolonged drumming varying in rate. Often the rate was only one or two beats per second, sometimes, however, the frequency was much increased; moreover short strong rolls were delivered at tolerably regular intervals. Once or twice these rolls were prolonged to a length of several seconds. (Plate 13, fig. 18). When the listening and the record-making were discontinued at 9.06, the male had not yet finished his drumming.
- 8) The common song of this male consists of two parts. The first of these is a low buzzing and simultaneously a series of clacking sounds emitted at intervals of more or less regular length. These clackings are much louder than the buzzing. The second part immediately succeeding the first usually consists of the cutting and vibrating sound described above under 5). In a very imperfect way the whole of this song may be vocalized thus (the

clackings represented by the letter g):

# 

In a variant of this song the second part consisted of a prolonged, low-pitched, rapid drumming. This song lasts 3—7 seconds. The variation in length is dependent on the number of clackings and on the length of the second part, which may be varied. — I have heard this song even in the night at about one a.m., the light in the room having been put out 1 ½ hour before.

Female. From the female Macropsis tiliae I have heard the "dying yell" only. It consisted of a short rattling buzz.

Material from Upland, Solna.

#### Macropsis planicollis (Thoms.)

- Male. 1) From this male I often heard "morse telegraphy" varying in pitch, the latter being for example f¹ or g¹. The rate is very rapid and the individual notes are short. Sometimes I have heard a more continuous call consisting of such notes emitted in extremely rapid succession. The tonal quality is often brittle and thin. On other occasions, however, it may be considerably deeper and more voiced. On the other hand, the main tone is often drowned among high-pitched overtones. Sounds of this kind were also heard after 11 p.m. in darkness.
- 2) On 12 July, 1945, at 6.40 p.m. I heard from two males without female company a sharp "zeep" pitched at a¹; at 9.54 on the same evening I heard several such notes in succession.
- 3) At 6.36 p.m. of the same day I heard from the same males a tone falling in pitch (from f¹ to e¹) in a glissando: "cheeew".
- 4) At 9.27 and at 9.54 p.m. on the same evening I heard from the two males in the tube a somewhat more complicated sound that in a very imperfect way might be vocalized thus: "crrrrvaaaeeee". The call begins,

then, with a rather noisy buzzing, continuously passing into a brittle, needle-sharp tone (estimated as a richly accompanied by high overtones).

5) As a call of distress I have heard a continuous regular drumming from the male.

Material from Upland, Solna, Råsunda.

#### Macropsis virescens (F.)

Male. I heard a sound-production from the male of this species on 20 July, 1945, for example at 7.40 and 8.19 p.m. It consisted of a prolonged voiced drumming in a pitch estimated as g¹, sometimes irregular and relatively slow, sometimes with a high rate as from a speedy Morse telegraphist or typist. The length of the single notes was varying. The sound quality is suggestive of a plucking on tautly stretched rubber strings or on the teeth of a comb. Further, a more swishing buzz (high overtones) is often heard. These calls may be emitted during several minutes at a stretch. The male often emits these sounds while briskly running about in the cage.

Material from Upland, Solna, Råsunda.

#### Macropsis fuscinervis (Boh.)

Male. The sound-production of this male was studied on 29 July, 1945, at 2.20 and at 3.20 p.m. Sometimes a short croaking with irregular intervals was heard: "crah, crah" or "chah, chah", sometimes a chirping: "cheerrr - chee-chee" or "cheerrr-cheer-cher-chee-cheerrr . . .". The latter call has the estimated pitch of c² or f² with a rich admixture of high overtones, and seems to express distress or displeasure. These observations were made on a single male.

Material from Ostrogothia, Rystad.

# Family Agalliidae Agallia brachyptera (Boh.)

Male. This small species has a comparatively mighty "voice" and uses it willingly. I have heard several different calls irrespective of whether females were present or not.

- 1) A prolonged drumming as by a pencil on a sheet of paper is often heard. These rolls may last a few seconds or considerably longer. The intervals between the single beats vary in length. Radiograph record (made on 7 July, 1947) on Plate 13, fig. 30.
- 2) Another call very often emitted is a vibrating tone falling in pitch, for example:



This call varies very much in length — it is a question of about one second — as well as in pitch and in interval of pitch. Usually it is combined with call 1), the latter either immediately preceding or concluding call 2) or both.

3) Another more characteristic call I have heard many times, for example on 10 July, 1945, immediately after collecting the specimens at 4.30 p.m., and later on the same day from the same specimens at 5.15 and from 7.15 to 10.15 partly in electric light, and finally at about 11 o'clock after the light had been put out in the room. On the following morning I heard it at 6.22 and 9.12. This call consists of two parts, the first being a short roll of undecided pitch, the second immediately following being a still shorter, usually relatively pure musical tone varying very much in pitch. The call may be vocalized thus: "trrrrrr-aigh". The tone of the second part might be compared to one produced on a violin played with the mute on, or to tones produced by singing or humming with the mouth pressed against a comb, on the back of which a strip of paper is stretched. (An "instrument" of this kind is often "played" by children.) In other words, the tone is very thin and rather shrill. By the gramophone-sound-film method the pitch has been determined in one case. It was 1100-1136 c.p.s. in both parts of the call, corresponding to a pitch at co sharp — do. But as the rate of the drumming in the first part is not less than 45 beats per second (determined in the same way), which would in itself give the impression of a tone to the human car, this first part appears to be much more low-pitched to the listener. — This call, consisting of a roll followed by a tone, may be emitted singly, but just as often a longer or shorter series of several consecutive calls of this kind is heard. (Radiograph record: Pl. 13. fig. 29.)

Now and then I have also heard characteristic variants of this call. One such variant was heard on 10 July, 1945, at 9.50 p.m. in electric light: "rrrr-cluck-rrrr-cluck-rrrr-cluck-rrrr-cluck-rrrr-cluck-rrrr-cluck-rrrr-cluck-rrrr-cluck-rrrr-cluck-rrrr-cluck". Such a series of 8 phrases ("rrrr-cluck":s) took a time of about 10 seconds. The clucking sound was estimated at the pitch of e<sup>t</sup>.

Another variant heard on the same evening consisted of a similar series, but each of the calls comprised three parts instead of two: first a short roll as above, then two short differently pitched tones. Unfortunately the whole of it passed too fast to allow me to make a closer study.

A third variant was heard once during the same evening. It was throughout more unvoiced and may be vocalized thus: "rrrr-tetede-rrrr-tetede-rrrr-tetede-rrrr-tetede-rrrr-tetede . . .". The sound vocalized as "tetede" resembles three short sharp beats of a pencil on a sheet of paper.

Material from Upland, Solna and Danderyd.

#### Agallia venosa (Fall.)

Male. From two males kept together in a tube without the company of females I heard on 10 July, 1945, at 8.30 p.m. a call consisting of a series of two or more clackings followed by a prolonged high-pitched sound reminding one of that produced if a metal point is rasped against a

A buzzing of two or several seconds is sometimes heard (Pl. 13, fig. 31). Material from Upland, Solna.

#### Family Jassidae

#### Jassus lanio (L.)

Male. This large species might reasonably be expected to have a loud, distinct call. However, this is not the case. The sound certainly appears to be emitted by a voluminous apparatus, but it is so muffled and diffuse that it becomes but poorly audible. I have distinguished three somewhat different forms of the sound-production of this male.

1) The sound most often heard from this male consists of an unrhythmical drumming or "puffing" of a character very difficult to describe. It might be compared to the sound produced by rubbing or drumming with the fingers on an ordinary rubber toy balloon. This will result in a toneless sound which might be vocalized as "pff". This sound is often emitted in such rapid succession that one could speak of a drumming, but it is quite unrhythmical. Sometimes a lower but more rapid and more distinct unrhythmical clacking sound is simultaneously emitted. Biologically this call is related to or identical with those described above from both sexes of Oncopsis alni and under 1) from the male of Macropsis tiliae. Thus, it is apparently produced as a sign of distress or dissatisfaction. Two males kept in the same tube apparently did not like each other's company, and one of them continually repeated this call. The abdomen of the male jerks vertically synchronously with this sound-production, as I have observed by the aid of a mirror. The single male trying to escape from the narrow tube also emits this call. I studied it during the afternoon and evening of 19 July, 1945. The presence of females did not affect this sound-production of the males.

If in more obvious distress, the male emits a somewhat harder drumming. If the wings of the male are cut off and if he is stuck fast by the legs in a pad of plastiline, it is easy to see through the binocular magnifier that the lateral, convex parts of the first abdominal tergum occasionally vibrate rather vigorously.

- 2) On the same afternoon at 5.08 and 7.38 I heard from the male a somewhat harder and more regular drumming beginning unrhythmically, however. Each time it lasted  $^{1}/_{2}$ —1 minute with interruptions now and then. During this sound-production the insect was sitting quietly with the point of its rostrum pressed against an oak-twig which had been placed in the tube. Apparently the animal was absorbed in sucking. The abdomen was vibrating vertically.
- 3) At 8.53 on the same evening I heard a similar drumming lasting about a minute. This time, however, the drumming was concluded by five or six more rapid rolls, each of about three seconds, in a more hissing quality of sound. Each of these rolls increased in strength towards the end.

I have not heard any "dying-yell" from this male, but as the female has been heard emitting such a yell, this is probably only accidental.

Female. From the female of Jassus lanio I have heard a spontaneous sound-production once only, namely on 19 July, 1945, at 7.45 p.m. The call consisted of a short drumming "korrrrr" of about one second. Several females were together in the tube. From females just put in alcohol I have two or three times heard a "dying-yell" consisting of a short buzz.

Material from Upland, Solna.

# Family Megophthalmidae

#### Paropia scanica (Fall.)

Male. I heard the call of this male the first time in the summer of 1944.1 studied it more closely on 13 July, 1945, at 9.00 and 9.25 p.m., and at 6.30 on the following morning. The call consists of a low but very distinct and regular drumming accompanied by a stronger, much sparser but equally distinct and regular hammering sound like that made by beating on wood with a pencil. This call may last a varying length of time, a few seconds. In 3 seconds I counted 10—15 beats of the "hammer". The call may be reproduced thus:

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the rate of the drumming, however, being slower than that of the tip of the human tongue while pronouncing the rolling r. Females were not present on these occasions.

A gramophone record has been made of this call, and this record has been transferred to sound-film. According to this record, the weaker drumming consists of beats emitted at a rate of 40—50 per second and with a tone frequency of about 1000 c.p.s. The hammerings, on the other hand, seem each to consist of two parts separated by a very short pause: the first with a tone frequency of about 1000 and a smaller amplitude (greater, however, than that of the beats of the weaker drumming), the second 1/70th of a second later with a much greater amplitude and a tone frequency of about 3700 c.p.s. I believe that the first part of the hammering beat corresponds to the tymbal membrane being made concave, the second to its returning to the convex state.

On 17 July, 1947, two females were kept in a cage on a twig of Galium boreale. At about 9.30 p.m. one male was introduced into this cage. By listening with microphone and ear-phones I found that a lively concert was in progress. The calls were of exactly the same kind as those emitted by single males or by several males without the company of females, but they were now produced much more frequently. The radiograph was kept connected to the amplifier during six minutes, and in this time 75 reiterations of the little tune of the male were registered, each lasting 2—3 seconds (Plate 13, figs. 15 and 16). The pauses were about as long as the calls or sometimes slightly longer. During the pauses a weaker, unrhythmical noise was heard in the car-phones, originating from the "dance" of the male, as I found later. By the aid of the stethoscope and the binocular magnifier I established, after finishing the radiograph recording, that the male performed between the calls a sort of dance consisting of rapid

jerks of the foot-hold of the extremities and spasmodic movements with the body. Regarding the vivacity of these movements, the animal moved very short distances now forwards, now backwards, now sideways, sometimes practically not altering its position at all. During these movements the male, as it seemed, happened to mount the body of one of the females, and for a fraction of a second he apparently made an attempt to start copulation. This did not succeed, however, and the male continued his singing and dancing on the body of the female for about a minute, after which he, still singing and dancing, left her behind him only to continue the same kind of activity in other parts of the little cage (the diameter of which did not exceed two centimetres). At 10 p.m. the observations were interrupted, unfortunately, for which reason the end of the performance was not seen. Next morning the song and dance had ceased, the male was seated on one spot in the cage, while the females now and then moved to and fro.

On 18 July at 10.52 a.m. I put one additional male and one female in the little cage. Its inhabitants were now observed during an hour. The performance of the preceding day was now repeated, but the entertainment was performed by the male newcomer alone, the other male emitting his call only occasionally and doing no dancing. The new male made several attempts to start copulation with one or other of the females present, but none of these attempts were successful. He preceded each attempt by singing and dancing for a while in the manner above described. The females now and then went about in the cage and seemed, in fact, to seek the company of the singing male. Often, however, they passed him by. When the male had mounted the dorsum of a female, the latter did nothing to facilitate his undertaking even though he seemed to intensify his dancing very much on these occasions and in spite of his vigorous endeavours to start the act of copulation. If the male had reached the venter of the female, he deflected the tip of his abdomen under hers and tried to unite his genitalia with hers; to facilitate this he raised his fore wings obliquely upwards-backwards. But in all the cases observed, his efforts failed owing to the female at this phase beginning to move and walking away. Then the male usually continued his singing and dancing for a minute or so, after which he made a pause to suck at the parts of plants placed in the cage. The singing often continued during the sucking, but the dancing was suspended. Sometimes he apparently lost all interest in the females and stopped hunting for them and ceased singing and dancing. Then he sometimes kept still, sometimes ran about, now and then getting into touch with some of the females also running about. At such meetings the interrupted courting was often recommenced.

During singing the abdomen of the male vibrated distinctly in the vertical direction. The "hammerings" seemed to correspond to pronounced, rapid movements of the abdomen.

Female. I listened to the sound-production of the female on 25 August, 1946, immediately after capturing her at about 3 p.m. and later in the afternoon. This sound-production consists of an unrhythmical, rapid series of clackings. The number of clackings per second may be 15 or more or less. The length of these series is also very variable. This call apparently expresses discontent or distress and is produced, for example, when the animal is held fast, but also while it is walking about. As the sound was seldom emitted except when the female was walking, I was uncertain whether it

was really produced by the tymbal apparatus. This problem was solved in the following way. One female was fixed by plastiline on the membrane of the microphone, the wings being deflected, so that the entire dorsum of the abdomen was visible. The animal was observed through the binocular magnifier. It was established that the clackings heard in the ear-phones were exactly synchronous with rapid movements of the lateral parts of the first abdominal tergum.

Material from Upland, Solna, Danderyd, and Värmdö.

#### Family Ulopidae

#### Ulopa reticulata (F.)

Male and female. Both sexes have the power of emitting a weak clacking sound in unrhythmical, often rapid succession. This sound reminds one of the call of distress of Aphrophora and Oncopsis spp. I heard it on 23 June, 1945, at about 2 o'clock and at 9 p.m., and on 30 September, 1946, from 1.30 to 2.00 p.m. After removing one fore wing and fixing the animal with plastiline on the microphone membrane I established through the binocular magnifier that each of these clackings corresponds to a rapid movement in the lateral part of the first abdominal tergum.

Further, the species has another call consisting of short but rather strong rolls. Each of these begins with single clackings and lasts two or three seconds. I heard a few such rolls in succession from a male and a female seated close to each other on a twig of heather (Calluna vulgaris) on 30 September, 1946, at about 1.30 p.m. Both were quite motionless, and it was impossible to see if the sound was produced by the male or by the female. Soon, however, the male moved a short distance away, and this kind of sound-production was heard no more.

Material from Södermanland, Nacka (1945), and Upland, Ekerö (1946).

#### Family Euscelidae

#### Doratura stylata (Boh.)

Male and female. Both sexes have the power of emitting calls of two totally different types. 1) A rather hard, woody drumming buzz of varying length. Once this call (from the male) lasted about three seconds, in another case half a minute, in both cases with irregular short interruptions now and then. I have heard this call many times at different hours of the day and night. At the production of these sounds, the whole abdomen vibrates vigorously in a vertical direction synchronously with the beats of the call. This call seems to express agitation. The insects are often running about very briskly while producing these sounds. It is difficult to tell whether the tymbal apparatus alone is the origin of the sounds or if they are produced by a sort of rattling with the whole abdomen.

2) Both sexes, further, are able to produce calls consisting of a raucous tone pitched at A—g, depending on the temperature (see below page 130). The male now and then emits a call consisting of a longer and a shorter

tone of that kind: "tooooor-to" or "tiiiiir-ter". Usually the male emits this call a few times in succession with short pauses. As Plate 13, fig. 40, shows, this call takes a time of about 0.8 second. If several males are kept together, this call is heard now and then whether females are present or not. Sunshine stimulates this kind of sound-production. I have not established whether light or heat is most important in this connection. Further, the call is stimulated by the presence of other singing males, a call from one male often being answered by his neighbours of the same sex. But I have not heard any more continuous alternating singing with this call from males without female company.

From single males or from males in the company of other males a song resembling the invitation call of the female (see below) is sometimes heard. But white the latter consists of notes of a fairly constant length, this song of the male is more irregular, consisting of a mixture of long and short notes, even though the longer notes may very often be produced in an unbroken succession. The longer notes are shorter than the longer tone of the "toooooor-to" call but longer than the second tone of the latter. The pitch of this call is about a semitone lower than that of the "toooooor-to" call emitted by the same individual at the same temperature. This kind of singing may last several minutes at a stretch. It might be vocalized thus:

The female has the power of emitting a call of the same quality of sound but consisting of notes of a tolerably constant length longer than the second but somewhat shorter than the first part of the "toooooor-to" call of the male (see Plate 13, fig. 41). On one occasion I counted 100 notes of this kind per minute. The female often continues this sound-production for several minutes. This call is sometimes emitted even by females without the company of males. However, this call is of sexual signification. Having emitted this call, the female does not offer any resistance to eventual attempts at copulation made by a male. I studied this call during several successive days in August 1947. The following observations made on 25 August may serve as an example.

At 6.50 p.m., six females and two males of *Doratura stylata* were put into a celluloid cage. This cage was approximately circular, having a diameter of 3 centimetres and a height of 5 millimetres. A long leaf of grass was coiled along the walls of the cage on its inside. After about two minutes one of the males emitted his "toooooor-to". Immediately one of the females took up her above described song. Then the male began his similar song, so that the two songs, the regular one of the female and the more irregular one of the male, proceeded simultaneously. The pitch of the female's song was a semitone lower than that of the male, a singular musical effect thus being produced. A fragment of this duet may be vocalized thus:

 $\begin{array}{l} \mathbb{Q}\colon \ tooor\text{-}tooop\text{-}tooor\text{-}toooo$ 

(In another similar duet heard a few days earlier, the male showed a tend-

ency towards prolonging his longer notes to a length of several seconds, so that the structure of the duet became about as follows:

At the beginning of the song both singers were sitting on the grass leaf but in opposite parts of the cage. After a few minutes the female moved down on to the floor of the cage, which brought her a trifle nearer to the male. She remained on this spot during the rest of her singing. At about 7 p.m. the male ceased singing, but the female continued. During the subsequent minutes both males moved in very short marches along the grass leaf to a spot just behind the female. They seemed to be in no hurry, sitting still for long periods. Now and then one of them emitted a short note of the usual kind. The fact that the female was sitting on the floor seemed to confuse their searching for her. In the meanwhile the remaining five females were restlessly running about in the cage. One of them happened to land on the back of one of the males. A vigorous leap removed the latter to the floor. Then he went at a slow pace towards the singing female. Having reached her, he made an attempt to connect his genitalia with her head, then he made a right-about turn and now succeeded in starting copulation. The female then ceased singing (at 7.12 p.m.), having sung continuously for twenty minutes. During copulation both parties kept silent. They were lying on their sides, their ventral surfaces turned towards each other and with their legs partly drawn together. After 5 minutes one of the other females in the cage happened to tread on the copulating pair, at which a vigorous leap of one of the parties broke off the copulation. During the following minutes no sound-production was heard from the cage, for which reason I ceased listening for this time.

I have had the opportunity of making similar observations several times. The procedure may be complicated by a number of specimens greater than two taking part in the singing, in which case either males or females may be over-represented. Sometimes two females may be singing a duet, and then the song may be perfectly synchronous for long periods; however, this is not always the case. Normally the prelude of the pairing, then, consists of the following four phases:

- 1) The male emits his "toooooor-to", which is a sort of enticing call directed to females in the vicinity.
- 2) The female answers with her call of invitation, accompanied by the courting song of the male.
- 3) The male ceases singing and begins to search for the female, guided, no doubt, by her singing.
  - 4) Copulation starts and the female ceases singing.

Females not emitting and not having just emitted this invitation call are unwilling to copulate. At least all attempts I have seen made by males to begin pairing with females not having answered their calls were rejected by these females.

At this kind of sound-production, the abdomen does not vibrate visibly at a low magnification. By intent watching I have found that the abdomen

is raised a little during the notes of the calls only to sink back immediately at the beginning of the pauses.

Material from Upland, Solna.

#### Doratura homophyla (FL)

Male. From the male of this species I have only heard (on 1 August, 1945, at 5.05 p.m.) a call in a pitch estimated at a: "caw-caw".

Material from Scania.

# Graphocraerus ventralis (Fall.)

Male. This male is very willing to emit his calls. I heard its sound-production for example on 7 July, 1945, at 2.00, 3.30 and 11.30 p.m., on the morning of the following day, and on 9 July at five minutes past midnight, the light in the room having been put out about one hour before.

The call consists of a series of about 30 raucous hammering sounds. The pitch was in one case estimated at H, in another at d, in a third case at d¹. These sounds might have been produced on a violin by bowing at a very rapid staccato rate. The last 5—8 beats are more rattling and appear to be pitched higher. This call takes a time of about 4 seconds. The sound is rather strong and gives an audible resonance if the tube with the animals is placed on the belly of the violin. These observations were made on males without the company of females. I have not heard any call of distress from this species, nor any "dying-yell".

Material from Upland, Solna.

# Aphrodes bifasciatus (L.)

Male. This species was the first from which I ever heard any spontaneous sound-production. If a few males are kept together in a tube, their calls will be heard now and then. I have distinguished four different calls from the male.

- 1) Single, short, raucous, whining sounds, the pitch estimated at  $g^1$ ,  $h^1$  or  $c^2$ .
- 2) On several occasions I have heard a call in a pitch estimated at a¹ or h¹, sounding as if it had been produced by plucking on a taut rubber string. The single clackings vary somewhat in length and are usually produced in series in rapid succession, so that in some respects this sound-production reminds one of Morse telegraphy. Apparently this is a call of distress. If a male is held fast by a leg with the aid of a pair of tweezers, he emits this call. Thanks to this fact I have been able to study its origin through the binocular magnifier, the wings having been removed and the animal stuck fast on a pad of plastiline on the membrane of the microphone. Vigorous vibrations were occasionally observed in the lateral parts of the first abdominal tergum. These vibrations were exactly synchronous with the clackings simultaneously heard in the ear-phones. If the abdomen of the animal is free, it joins in the vibration: if not, the vibrations of the lateral parts of the first abdominal tergum will nevertheless take place. This

seems to show that the latter vibrations are the primary phenomenon, the movement of the abdomen the secondary one.

3) I have heard the "common song" of the male on several occasions, for example on 7 July, 1945, at 5.50 p.m., the next day at 9.50 a.m., several times between 6.30 and 10.45 p.m. (partly by electric light), and on 9 July at twelve minutes past midnight, the light in the room having been put out over an hour before. This song consists of three parts in unbroken succession. The first part I am not able to vocalize. It resembles the sound of a heavy, somewhat badly oiled rotatory machine of some kind, for example the engine of an old motor car, which someone is trying to start with the aid of a crank. This first part consists of 3-6 "revolutions" (phrases), each consisting in its turn of 4-6 whizzing or rattling beats, one of which is always more strongly accentuated than the others. This part takes a time of 4.-6 seconds. It is immediately succeeded by the second part. a strong drumming sound. The engine has begun running! This part lasts 3-4 seconds. The third part, too, consists of a regular drumming at the same rate as the second part but much weaker and apparently pitched lower. It may continue somewhat longer than the second part, 5 -7 seconds. Radiograph record, see Plate 13, figs. 33 - 34. In musical notation this song may be reproduced thus:



As Figure 34 shows, the force and tempo of the first part are often considerably increased towards its end. The pitch varies individually very much; the above is only estimated. The accentuated notes of the first part and the whole of the second part give an audible resonance if the tube with the insects is placed on the belly of a violin. In view of this fact I have been able to study the animals through a magnifier while listening to their singing. During the singing, the abdomen vibrates in the vertical direction, distinctly more strongly in the second part of the song. The accentuated notes of the first part correspond to a more distinct jerk of the whole abdomen towards the substratum. The abdomen, however, is kept well elevated over the latter; it is not a question of a knocking of the abdomen on the substratum. As a rule the males sit still while singing. I have never heard more than one male singing simultaneously, nor have I heard any alternating singing, even if so many as ten males are kept together in the same tube. After the conclusion of a song of this kind, the same male may immediately start a new one, or he may make a shorter or longer pause. This song is heard independently of the presence or absence of females. If females are present, they do not seem noticeably interested in the song. The males, on the other hand, often get agitated and start running about, apparently intending to find and disturb the singing male. However, I have not seen any such distinct rows in this species as in certain aracopids (Criomorphus

bicarinatus, Achorotile), nor does the singing Aphrodes bifasciatus appear to take any notice of the activity of his comrades.

4) On 7 July, 1945, at 5.25 p.m. I heard a song lasting for several minutes consisting of a rather voiceless rattling in a pitch estimated at c<sup>2</sup>: "t-trr-trrr-trrr-trrr-t-t-t-trr...". I have heard this call only once.

Female. The female has the power of emitting a weak, clacking "call of distress". Each of these clackings corresponds to a rapid jerk in the region of the striated tymbal. The amplitude of these jerks is very small.

Material from Upland, Solna.

#### Aphrodes trifasciatus (Fourer.)

Male. I heard the call of this male on 15 July, 1945, on a few occasions, for example at 5.43, 8.28, 9.17, 9.30 and 9.50 p.m. I made a gramophone record of it on 31 July, 1947, at about midday, radiograph records having been made one evening earlier. The song resembles that of Aphrodes bifasciatus described above as No. 3, but is nevertheless very distinct. It consists of two or three parts, the part described below as the second being sometimes missing. The first part may be compared to the corresponding part of the common song of A. bifasciatus but varies much more in length and in structure. It consists of a longer or shorter -- in one case lasting for 30 seconds, in another for only 5 seconds - series of clacking sounds. The single clackings are rather toneless but contain a distinct rolling sound. Some of these clackings are much more accentuated than others in an often tolerably regular rhythm. This part, then, begins with a few relatively strong but sparse clackings. Soon comes a phase in which every second clacking is accentuated, then the accent is laid on every third or every fourth note, the tempo of the whole increasing. Thus this part may resemble the sound produced by a person trying to start a heavy, rotatory machine of some kind with a crank. Often, however, it is so far from regular that this association is obscured. In one case I counted 12 accentuated clackings in 10 seconds. The second part is a rapid drumming of a few seconds. The third part consists of a series of trilling notes higher in pitch. In one case the third part took a time of 10 seconds and consisted of 25 notes, in another case I counted 26 notes. The last trilling note is more prolonged than the others and falls towards the end in intensity of sound, finally fading away altogether. A very imperfect endcayour to vocalize this song is the following:

-greeo-greeo-greeo-greeo-greeceeeeeeeeeeeeeeeeeeeeee. Radiograph record, see Plate 13, fig. 35. By the gramophone-sound-film method, the tone frequency of the beats of the first two parts was determined at 274—293 c.p.s., that of the trillings in the third part at about 1170 c.p.s.

If the first part of this song is a more irregular version of the correspond-

ing one of A. bifasciatus, the rest of it is different in a very characteristic

way in both species.

During this song the abdomen of the male vibrates at the rate of the single beats. During the third part, the abdomen moves besides independently of the vibrations at a slower rate: upwards at each "gree" and then downwards at the sound reproduced as "o".

From the male of trifasciatus are sometimes heard shorter, less well-defined calls, as once a "tirr" (estimated pitch d2), in another case a "kr-krrr".

Material from Upland, Ekerö.

# Aphrodes bicinctus (Schrnk.)

Male. From this male I have often heard short raucous tones or bleatings rather high in pitch lasting for one second or less.

On 18 July, 1945, at 8 p.m. I heard from a tube with a few males but without females a dull voiced drumming of a few seconds with the estimated pitch of F.

A more characteristic call was heard from this male in 1944 and on 18 July, 1945, at 7.45, 8.20, and 9.58 p.m. In my notes from 1944 I described this call as consisting of a raucous tone regularly alternating with

a duller sound, and tried to vocalize it thus: "chah-um-chah-um-chah-um-

-chah-um". A call like this takes about two seconds, but the calls may also be longer. The rancous note sounded as if produced by scratching with a finger-nail over the teeth of a comb. While singing the male kept still on

The male I heard in 1945 sounded somewhat different. His call consisted, like that of the 1944 male, of a longer or shorter series of raucous notes sounding as if produced by rasping over the teeth of a comb. The pitch was estimated at c<sup>2</sup>. The sound alternating with these raucous notes consisted, however, in this case of a low — somehow remote — clacking. Once the song was commenced by a short drumming "trrrr", in the remaining cases observed by a vague scraping sound like that made by a chair being dragged across the floor. The song may be vocalized very imperfectly thus:

"trrr - cha - ck - cha - ck - cha - ck - cha - ek . . . .". The duration of this song varies. Once this music first lasted 25 seconds at a stretch. After a pause of a few seconds it was continued during about one minute with short interruptions now and then. The rate of the notes varies. In one case three

"cha-ck":s were emitted in a second, but the rate may be slower or more

On 20 July, 1947, another call was heard from two males kept together in a cage. The time was somewhere between 2.45 and 3.30 p.m. The cage having been placed in the sunshine entering through the window, one of the males now and then emitted a call that cannot be vocalized. It consisted of two parts, the first being a rolling sound as from some machine; the first "revolution" of this machine was powerful, the subsequent ones weaker but increasing in intensity towards the end of this part. The second part consisted of a short, squeaking, high-pitched note rising in pitch towards its end and followed by a short, weaker roll lower in pitch. The whole of it took a time of 1.25-1.5 seconds. Plate 13, fig. 37, gives the radiograph record of this call; as appears from it, the squeaking mentioned above is represented by a particularly strongly marked band, the following weaker sound by a series of closer transverse lines. The animals stopped emitting sounds of this kind when the sunshine had left the cage but recommenced as soon as the microphone with the cage was again placed in the sun. In the evening I started listening again; now the other male gave the concert: at least the call had changed somewhat, the initial roll not being especially strong (Plate 13, fig. 36).

Material from Upland, Solna.

# Aphrodes flavostriatus (Don.)

Male, 1) This male often emits a short whining call: "chew" or "chewchew" or "chacha".

2) I heard a more characteristic call on 13 July, 1945, at 7.49 p.m. and several times later during the evening, further at about 6.30 on the following morning. It consists of two parts, the first often being a series of a few weak, sighing sounds, the second 2-5 croaking rolls: "hu-hu-hu-krrair--krrair-krrair". Instead of the sighings, the first part may consist of a rolling buzz: "krrrer-krrair-krrair-krrair". This call lasted 2-4 seconds. Females were not present.

A radiograph record of the latter call was made on 21 July, 1947, at about 9.30 p.m. in electric light, using three males in a cage with twigs of Galium boreale (see Plate 13, fig. 38). As the first part of the call (the sighing) is very weak, the radiograph reacted to this part only by a small number of transverse lines. — By the gramophone-sound-film method, the tone frequency of the single beats has been determined at about 1150 cycles per second. There are, however, still higher overtones in addition. Each of the "sighings" in the first part of the call consists of a beat with this frequency. Each of the croakings of the latter part consists of 5-6 beats, which are closer in the latter part of the croaking, corresponding, then, to a rise in frequency. The frequency of the main tone rises from 18 to 40 c.p.s. But this low "main tone" is quite drowned by the overtone being the specific tone of the swinging membrane (1150 c.p.s. as mentioned above), owing to which the pitch of the tone heard will be estimated much higher.

No "call of distress" has been heard from this male, nor any "dying yell". Material from Upland, Danderyd, Kevinge.

# Aphrodes fuscofasciatus (Goeze)

Male. The call of this species was studied on 17 July, 1947, from four males kept together with one female in a cage with Galium boreale by electric light. The call was emitted sparsely; from 8.45 to 9.30 p.m. I heard it 4 or 5 times. It consisted of a sound like that emitted by a rotatory, somewhat rattling machine such as a wooden toy cart, for example. Each call lasted

7—8 seconds with a frequency of 7.7—7.8 beats per second (radiograph record, see Plate 13, fig. 39).

Material from Upland, Solna.

#### Opsius stactogalus Fieb.

Male. I heard the call of this male on 30 July, 1945, at 8 p.m. It consisted of a few short, raucous, consecutive notes (three notes in 2 seconds): "chirr-chirr". The pitch was estimated at a<sup>1</sup>.

Material from Scania, Lund.

#### Macrosteles cristatus (Rib.)

Male. The sound-production of this male was heard on 24 August, 1946, a few times between 5 and 7 p.m. The weather was warm and sunny, but the call was yet heard only a few times. It consisted of a grating or clucking sound sometimes recalling the crowing of a young cock though lower in pitch, usually however considerably shorter.

Material from Upland, Solna, Råsunda.

#### Balclutha punctata (Thunb.)

Material from Upland, Uppsala, Ultuna, and from Upland, Solna.

#### Platymetopius guttatus Fieb.

Male. A sound-production was heard from this male immediately after collection on 21 July, 1946, at 4.43 p.m. outdoors (warm, sunny weather), and indoors on the evening of the same day at about 8.30, and further on 16 August, 1947, at 6.30—7 p.m. The call is emitted rather frequently and consists of a raucous chattering like that of a magpie. Each call consists of 3—6 notes emitted at an estimated rate of 10—15 per second. Pitch is difficult to estimate, as the sound quality is so very raucous.

Female. I heard the call of the female on 21 July, 1946, at 9.20 and 9.50 p.m. in the light of an electric lamp, and on 16 August, 1947, from 6.30 to 7 p.m. It is similar to that of the male but appears lower in pitch.

Material from Södermanland, Botkyrka, Ahlby (1946), and from Upland, Ekerö (1947).

#### Psammotettix cephalotes (H.-S.)

Male. Heard on 23 July, 1945, at 6 p.m. The call consisted of a repeated croaking, each note lasting  $^{4}/_{3}$  second or so and with short pauses: "cuh-cuh-cuh-cuh-ruh". The pitch was estimated at  $^{4}$ , a or still lower.

Material from Gotland.

#### Psammotettix confinis (Dahlb.)

Male. Sound-production heard on 22 August, 1947, at 7.20 p.m. from two males indoors in electric light. The call consisted, like that of cephalotes, of a repeated croaking or clucking: "cuh - cuh - cuh - cuh". About two such croakings are heard in a second, the intervals being irregular. I have not had the opportunity of making a closer comparison with the call of cephalotes.

Material from Upland, Solna.

#### Diplocolenus abdominalis (F.)

Male. I heard a sound-production of this species on 17 June, 1945, at 3 p.m. outdoors and at 7.25 indoors from two males without the company of females. The call consisted of a low woody buzzing or creaking with irregular interruptions now and then. No "call of distress".

Material from Upland, Solna.

#### Mocuellus collinus (Boh.)

Male. A call of this male was heard a few times on 17 August, 1947, between 8.30 and 9 p.m. from two males in a cage in electric light. It consisted of a tone of a fraction of a second falling in pitch in a glissando from f<sup>1</sup> to d<sup>1</sup> (pitch estimated).

Material from Upland, Solna, Bergshamra.

#### Streptanus acmulans (Kbm.)

Male. After several unsuccessful endeavours, I heard the sound-production of this male for the first time on 4 October, 1945. From 1.40 p.m. and during the following two hours I heard the call a few times, first once from a single male, then several times after a female had been put into the tube. The call consisted of a rather strong dull rolling alternating with another similar yet stronger, more raucous and toneless one: "RRRRrrrrRRRRrrrr RRRRrrrr RRRRrrrr RRRRrrrr had been put into the tube." Usually the alternating parts are produced very regularly so that both are held for an equal time, one part of each taking together about a second; sometimes, however, the song may be more irregular. In one case the duration of the song was 12 seconds with seven rolls of each kind, in another more representative one about 20 seconds with 20 pairs of rolls. In most cases the song is concluded by a somewhat more prolonged roll of the more voiced kind.

During this singing the abdomen of the male vibrated vertically, periods of stronger and weaker vibrations alternating at the same rate as the alternating parts of the song. In fact, the periods of vibrations with the greater amplitude correspond to the stronger and more toneless parts of the call.

This male always kept still while singing. Often he emitted his call while sucking on the blade of grass in his tube. During his endeavours to approach the female — who was always demurring — he was quite silent, as well as during his walking in the tube. But having stopped he often very soon emitted his call. Sometimes the latter was repeated with very short intervals (a few — some twenty or thirty seconds), but as a rule the pauses lasted a few minutes.

Later in the evening I again listened to the sound-production of this male. I heard it at 8, 9.10, 9.40, 9.50 and 11.03 p.m. in electric light. If the tube with the animal was placed on the belly of my violin, the sound became audible at a distance of two decimetres. Now I again studied the correlation between the alternating parts of the sound and the variation in the vibrations of the abdomen. As mentioned above, the amplitude of the vibrations is smaller during the more voiced part of the call. During this phase the abdomen is kept more raised over the substratum. As the less voiced part succeeds the other, the abdomen sinks towards the substratum, while the amplitude of the vibrations increases.

Finally I heard this song on 5 October at 1.05 a.m., the light in the room

having been put out an hour and ten minutes.

In the morning the observations were continued. To begin with, the male kept quite silent. The tube was then placed in the light of a strong electric bulb, with the result that the animal already after a minute struck up its song. During half an hour (9.30—10 a.m.) the male was kept now in the light of the bulb, now in the sunlight, and continued its singing in the same way as on the preceding day -- with pauses of one or a few minutes. He was even not restrained by my cutting off his wings on the left side with a small pair of scissors. Thanks to this I was able to establish that the first and second abdominal terga, especially the lateral part of the first tergum, vibrated vigorously during the sound-production. These vibrations were synchronous with those of the whole abdomen but were as strong during the phases of the latter vibrating with the smaller amplitude. Apparently the vibrations of the first abdominal tergum were the primary cause of the vibrations of the abdomen, the amplitude of the latter vibrations being influenced by the alternating raising and lowering of the abdomen doubtless brought about by the action of special muscles. By these raisings and lowerings the conditions of tension in the region of the dorsum of the abdominal basis are varied, the quality of the sound produced being thereby modified.

Radiograph record (made on 6 July, 1947), see Plate 13, fig. 43. By the gramophone-sound-film method, the tone frequency of the beats in the voiced parts of the song was determined at 1092 c.p.s.

See further Chapter 6.

Material from Upland, Solna.

#### Streptanus marginatus (Kbm.)

Male. I listened to the sound-production of this species for example on 20 May, 1945, at 8.18 a.m., and on 22 May, 1945, at 10.30 p.m., and further on 17 June, 1945, at 9.47 p.m., in the latter two cases by electric light. The common song consists of two parts: first a prolonged low-pitched raucous tone, then a series of short notes higher in pitch and recalling the croaking of a frog. This song may be vocalized thus: "koooooooooooo (or korrrrrrrrrr)

- kwa ' (about 4 seconds). Often the song is concluded by a weaker rattling noise. Radiograph record, see Plate 13, figs. 44, 45. The pitch of the individual notes was determined by the gramophone-sound-film method at 732—805 c.p.s.

The sound producing male was studied on 12 June, 1947, with the aid of a

stethoscope. During the first part of the call, the abdomen is stretched a little and lowered towards the substratum while vibrating vertically in a small amplitude. The croakings of the latter part of the song correspond to movements of the abdomen with a much greater amplitude. During the singing, the male was often observed sucking on the grass blades in the cage. However, I have also heard it singing while sitting on the wall of the celluloid cage.

Material from Ostrogothia, Rystad, and Upland, Solna.

#### Streptanus sordidus (Zett.)

Male. The sound-production of one male of this species in a celluloid cage was studied on 7 September, 1947, from 3.22 to 4.30 p.m., and from 9-10 on the following morning. The sound-production is stimulated by sunshine or the rays from an electric lamp. The common song usually consists of three parts, the first being a uniform buzzing or drumming, during which the abdomen vibrates vertically. This part may last for 1—5 seconds. Sometimes it is accompanied by a sparser smacking sound produced by movements with the wings. These are then raised in a direction obliquely backwards-upwards-laterally and are immediately rapidly clapped down again into the position of repose. These smackings may occur in a number of 1-4 during the first part. Then begins immediately the second part. consisting of the same drumming as before but stronger and not uniform although with rhythmically alternating variation in strength. The frequency of the beats in this part was in one case 35 per second, the rate of the accentuation 10 per 13 seconds. This part varied in length from 5.5 to 14 seconds. The accents in this part correspond to a more marked rapid lowering of the abdomen towards the substratum. Then follows the third part, which is similar to the second but uniform and decreasing in frequency and strength towards the end. This part may last a second or two or may be

Material from Upland, Djursholm.

#### Macustus grisescens (Zett.)

Male. The sound-production was studied on 10 June, 1945, at 6.30 p.m. indoors in the presence of females. The call consisted of longer or shorter series

of a barking sound: "wa - wa - wa - wa - wa". In one case I counted 12 notes in three seconds. The pitch was estimated at c¹. The sound was strong enough to be audible if the tube with the animals was placed on the belly of my violin.

Material from Upland, Experimentalfältet.

#### Athysanus argentatus (F.)

Male. On 23 July, 1945, at 11.47 p.m. I heard indoors from this male a clacking or woody knocking sound: "ko ko". The sound recalled the clack-

ing produced by the base of the tongue and the soft palate with the mouth closed and the teeth clenched. The pitch was estimated at c¹. On 24 July at 6.40 a.m. I heard a call consisting of three croaking notes like those of a crow: "kaah-kaah-kaah". This call lasted about four seconds. The pitch was estimated at c¹, falling, however, by about half a semitone towards the end of each note.

Further, this male has a call resembling a somewhat hoarse and anything but sonorous trumpet-blast or a series of such. I heard this call and made a radiograph record of it on 29 July, 1947, at about 9 p.m. from three males in a cage with some grass by electric light. The sound recalls the "toooooor-to" of *Doratura stylata* of (see above page 81). In *Athysanus* it is stronger, however. Sometimes only a single note lasting ½ of a second or so is heard. Often, however, I heard first a longer tone falling in pitch towards the end, then a small number (1—5) of much shorter notes together lasting about one second, the whole song thereby somewhat recalling the cackling of a hen: "koooor-ko-ko-ko-ko" (radiograph record, see Plate 13, fig. 47).

Material from Upland, lake Laduviken.

#### Athysanus quadrum (Boh.)

Male. I listened to and made a radiograph record of the call of this male on 18 July, 1947, from 8.55 p.m. on indoors. The call consisted of a series of hammering sounds. The rate was 8 beats per second (Plate 13, fig. 48). The length of these series varied from 2 to 3 seconds.

Material from Upland, Stockholm, Fiskartorpsbacken.

#### Doliotettix pallens (Zett.)

Short, vowel-like sounds are often emitted.

Material from Upland, Djursholm.

#### Laburrus impictifrons (Boh.)

Male. On 1 August, 1945, at 1.30 p.m. I heard from this male a croaking call in the estimated pitch of d<sup>1</sup>: "korr-korr' or "quarr-quarr'. A call consisting of three such croakings lasts about two seconds. The call is often commenced by a short creaking sound. Another call I heard on the same day ten minutes later consisted of an unvoiced low-frequent drumming.

Material from Scania.

#### Limotettix striatulus (Fall.)

Male. I heard a call of this male on 15 July, 1945, at 6.22 p.m. and several times during the same evening, for example at 9.04 and 9.22. It consisted usually of a jarring or buzzing bleating of about one second: "vaaaaair" or "buuuuur", and pitched (estimated) at G, H or c. Sometimes the pitch appeared to be much higher, the main tone being drowned in the mass of overtones. The pitch usually falls somewhat towards the end. As a rule this call is heard singly now and then. Sometimes however several calls of this kind may be emitted in rather close succession.

At 9.25 on the same evening I heard from the same males a spitting sound in combination with the bleating above described: "sput - vaair - sput - vaair". This spitting sound is more unvoiced and appears more highly pitched. It is stronger than the bleating.

Material from Upland, Ekerö.

#### Rhopalopyx preyssleri (H.-S.)

Male. This male often emits single short clacking or croaking sounds in a pitch estimated at a<sup>1</sup> or a<sup>1</sup> sharp. Sometimes such clackings are emitted in rapid succession.

From a male without the company of females I heard on 7 September, 1945, a more regular call. It consisted of three or four series of a rattling noise like that made by a toy engine with wooden trucks. Each of these series consisted of 4 or 5 beats and then one more in a much higher pitch as if the engine needed oiling. Each series lasted about one second, the series following immediately upon each other.

Material from Upland, Solna.

#### Rhopalopyx flavcolus (Boh.)

Male. The sound-production of this species was studied on 14 July, 1945. At 2.30 and at 5.22 p.m. I heard from my males a prolonged screaming call in the estimated pitch of d<sup>2</sup>: "krrrrreeeee" or "krrrrraaaai". This scream lasted each time about one and a half seconds.

At 5.19 and later on the same evening I heard from the males a short clacking call much varying in pitch: "tick, tick" or "teck, teck" or "ko, ko". These clackings are emitted in unrhythmical, sometimes rapid succession.

Material from Upland, Djursholm.

#### Allygus mixtus (F.)

Male. The call of this male was heard twice on 11 July, 1947, between 10 and 10.30 p.m. The male was on this occasion sitting alone in a cage in the light of an electric lamp hanging from the ceiling of the room. The call began with a weaker, undecided drumming and then continued with three strong croaking rolls: "korrr-korrr-korrr". (See Plate 13, fig. 49.) Then followed a pause of a few seconds succeeded by a weak buzzing of about two seconds. This last buzzing was heard in the ear-phones but was too weak to be registered by the radiograph.

Material from Upland, Solna,

#### Allygus commutatus Scott.

Material from Upland, Solna.

#### Hesium biguttatum (Fall.)

The male emitted this call with rather long intervals. Having put a female into his tube, I imagined that the call was emitted somewhat more readily, often twice in almost immediate succession.

Material from Upland, Solna.

#### Thamnotettix confinis (Zett.)

Male. Sound-production studied on 17 June, 1945, from 5 to 6.15 p.m. indoors, and after 10 during the same night. The call is rather weak for a species of this size and consists of a cooing sound: "koooooh-koooooh". A call like this consisting of two notes lasted about one second. Pitch varied much. In one case it was estimated at a sharp, in another at d¹. Females were present. I was not able to establish any "call of distress".

Material from Upland, Solna.

#### Speudotettix subfusculus (Fall.)

Male. I studied the sound-production of this species on 26 May, 1945, between 12 and 1 p.m. The call resembles the croaking of a crow. Thus it begins with a rolling sound and ends with a short vowel-like sound. This note is repeated after a pause of about one second. 3—10 such croakings are heard in succession. During the time of ten seconds I counted six or

seven notes with their intervals: "krroh - krroh - krr

krroh". Females were not present. I have heard this call even at night, on 27 May, 1945, at five minutes past twelve, the light in the room having been put out at twelve, and at 1.40 during the same night, the room having been in darkness for one hour and forty minutes.

Material from Upland, Solna.

#### Solenopyx sulphurellus (Zett.)

Male. A call from this species was heard on 6 August, 1945, between 10.40 a.m., and 12.25 p.m. It consisted of a rather unvoiced croaking of about one and a half seconds: "krrrr" or "krrooh", repeated now and then. In addition I heard from time to time a clacking sound.

Material from Vestrogothia, vicinity of Borås.

#### Solenopyx kozhevnikovi (Zachv.)

Male. Sound-production heard from two males on 7 September, 1947, from 2.50 to 3 p.m. It resembles that of S. sulphurellus, consisting sometimes of single clackings, sometimes of a short croaking repeated in irregular succession. Sometimes the latter is emitted in rapid succession with 4—5 croakings per second, usually however only one or two notes per second and in all only 3—5 each time are heard.

Material from Upland, Djursholm.

#### Cicadula quinquenotata (Boh.)

Male. From the male of this species I heard on 26 August, 1945, at 7.20 p. m. indoors a short croaking estimated at h<sup>1</sup> repeated in unrhythmical suc-

cession: "yeh - yeh - yeh - yeh . . .", and so on. An instant later I heard from the same males a more prolonged violin tone of about one second in a pitch once estimated at  $c^2$ , in another case at  $d^2$ : "aaaair". Females were not present.

Material from Upland, Djursholm,

#### Family Typhlocybidae

#### Dikraneura aurcola (Fall.)

Male. This male seems to be little inclined to sing in captivity. In spite of my assiduous listening I have heard a sound-production from this male only once, on 15 July, 1945, at 10.19 p.m., namely a single raucous tone in an estimated pitch of d¹ lasting not quite a second. Whether the species normally has only this call and what the biological significance of it may be I could not tell.

Material from Upland, Ekerö.

#### Dikraneura citrinella (Zett.)

Male. I heard a call of the male of this species on 23 July, 1945, at 11 p.m., and on the following morning at 4.30. It consisted of a fine, flexible violin tone falling in pitch, for example:



The interval between the highest and lowest tone varies in individual cases. Sometimes the tone is prolonged and may rest for some time on some intermediate tone. Sometimes the pitch rises somewhat towards the end.

Immediately before this call a regular series of clacking sounds is often heard.

Material from Gotland.

#### Notus flavipennis (Zett.)

Male. The call of this species was heard on 5 August, 1944, in the middle of the day outdoors, and on 24 June, 1945, between 9 and 10 p.m. indoors. The call is very weak but is not destitute of a certain clang. As a rule only

short single sounds that could be vocalized as "kolo" or "klo" are heard. The pitch I usually estimated at g1. Only once have I heard a more continuous little tune (on 24 June, 1945, at 9.50 p.m.):



Material from Daisland, Åmål (1944) and Södermanland, Nacka (1945).

# Empoasca viridula (Fall.)

Male. This small species is very vivacious and unwilling to keep quiet in captivity. The sound produced by its attempts at flight in the tube or cage is much louder than those due to its sound-producing organ. I heard its common song for the first time on 20 June, 1945, at about 3 p.m. from specimens just captured. The weather was fine. On this occasion I had not time to study the call more closely. Later I heard it at 11.45 on the same day in we-we". The rate, then, was three notes per second. The sound was very weak and appeared as if it were whispered. Thus I have heard this call only twice in spite of repeated listenings on several occasions. The pitch I have not been able to determine. Females were present on both occasions.

This species often emits another call consisting of a short laughing sound: "hahahaha". This call is heard immediately after the moving (by flight, etc.) of a male. I have not heard any call of distress from this species. Material from Upland, Solna.

# Empoasca virgator Rib.

Male, On 12 July, 1945, I heard two different calls from this male: 1) A short, fine, thin tone in the estimated pitch of a or h lasting a fraction of a second: "cheigh". This call is heard now and then, sometimes with intervals of several minutes, sometimes however much more often. I heard it for example at 9.27 p.m. and in darkness just after 11 p.m.

2) At 9.42 I heard a call consisting of an unvoiced drumming immediately followed by a hard, sharp, prolonged high-pitched tone. This call lasted about 4 seconds. As I have heard this call only once I have not been able to determine the pitch.

The above observations were made on one single male. Material from Upland, Solna, Råsunda.

# Empoasca smaragdula (Fall.)

Male. On 8 July, 1947, a sound-production was heard from 4 males a few times between 8 and 9 p.m. The call consisted of a drumming lasting 1-2 seconds. (See Plate 13, fig. 32.) The rate increases strongly towards the end, then the roll ceases abruptly.

Material from Upland, Solna.

#### Cicadella notata (Curt.)

Male. I studied the sound-production of this species indoors first on 9 June, 1945, at 11.32 p.m., then on 11 June, 1945, from 5 to 10.40 p.m., and on the following morning from 8.45 to 9.30. This male sings, then, during the darkest part of the night as well as during the day, his inclination for singing being perhaps somewhat greater in the morning. The call of the species consists of a rolling sound immediately continued by a tone rapidly rising in pitch. The call, then, begins as a tremolo and ends with a glissando:



This call lasts about one second. It is often emitted singly but is equally often preceded or concluded or both by a short, more accentuated sound:



This call lasts at most 2 seconds.

Late in the evening of the 11 June I heard several times repeated short tones: "aih", lasting a fraction of a second. The pitch was estimated at g<sup>1</sup> or a<sup>1</sup>. The common song above described was then performed very sparsely.

As would be expected of this small species, the sound is rather weak.

The observations were made on one or two males without female company. Material from Upland, Solna.

#### Typhlocyba tersa Edw.

Male. The sound-production of this male was studied on 12 September, 1946, at 3.45 p.m. and at 9.49 on the following morning. It consisted of a short, raucous note: "charr", lasting a fraction of a second. Pitch not determined but apparently rather high, with a mixture of overtones.

Material from Upland, Stockholm, Hortus Bergianus.

#### Typhlocyba rosae (L.)

Male. I heard a call from one male kept in a cage together with two others on a rose leaf on 25 October, 1947, at 11.50 a.m. It consisted of a series of seven voiced notes: "tor - tor - tor - tor - tor - tor - trrr". The pitch seemed to be somewhere in the great octave, the last two notes being two tones lower than the others.

Material from Upland, Solna, Bergshamra.

#### Erythroneura hyperici (H.-S.)

Male. The call of this male consists of a short weak note sounding as if produced by a strong lash in the air with a hard flexible switch. Each note was abruptly finished as if the switch had been arrested in its movement. Sometimes, however, the sound recalls sooner a plucking on the teeth of a comb. The pitch was in some cases estimated at a<sup>1</sup>, in others at h<sup>1</sup> or c<sup>2</sup>. The calls were emitted rather often without any rhythm, with three notes per second or so: "chuchut - chut - chut - chut - chut - chut - chut . . .". This concert could last many minutes at a stretch. Sometimes the music is composed of two tones, for example:



Not infrequently an alternating singing is heard from two males. On one occasion I observed two singing males sitting close to each other on a leaf of Hypericum perforatum. They made rapid movements with their abdomens in the tempo of the music. For one "chuchut" the abdomen moves twice up and down. Little by little three additional males gathered near to the two singers on the same leaf but without taking part in the singing. The females present in the tube appeared indifferent. The song of one of the males was estimated at a<sup>1</sup>, that of the other at c<sup>2</sup>.



These observations were made on 11 June, 1945, at 2.30 indoors. I have also heard the call of this species in darkness, for example on 23 June, 1945, at 12.15 a.m.

Material from Upland, Danderyd, Kevinge.

#### CHAPTER 3

# The Morphology of the Sound-Producing Organ

In all male forms examined by me the integument in the region of the first abdominal dorsum is partly strongly sclerotized in such a manner that a thin but elastic membrane is present. In certain genera, such as Idiocerus, Agallia, Cicadella and Empoasca, the second abdominal tergum is partly of this nature, too. In the cercopids, Centrotus, Tettigella, Agallia, Eupelix, Paropia Q. Oncopsis Q. Doratura and Aphrodes Q. the first abdominal dorsum contains laterally a convex, hyaline and thin but well sclerotized, elastic surface adorned by a number of parallel or concentric lines of deviating refraction (Plate 3, figs. 4 and 7, Plate 5, figs. 1 and 3, Plate 6, fig. 6, Plate 7, fig. 5, tb; Plate 7, figs. 3 and 4). I suppose that the integument in these lines is thinner than in the interspaces, the latter corresponding to the ridges of the tymbal of the Cicadidae. In the present paper I am therefore terming this striated surface the "striated tymbal". This striated tymbal is present, though less developed, also in the females of the genera mentioned, while, on the other hand, in Paropia, Oncopsis and Aphrodes it is well developed only in the female sex. Evans (1946, p. 42) mentions in Darthula and Actalion (family Aetalionidae) "a ridged boss on each side of the first abdominal tergite". Evans himself conjectures that this boss may be a part of a sound-producing organ. In Ledra, Eucanthus, Idiocerus, the cuscelids (except Aphrodes Q and Doratura), the typhlocybids and aracopids, Cixius and Ommatidiotus, a striated tymbal is absent. In these forms there is instead a system of strengthening inner lists and often clump-shaped sclerites in the same region and sometimes in the adjacent part of the second abdominal tergum, too. More laterally there is in the first abdominal dorsum a convex, thin-walled and often membranous surface anteriorly armed with a varying number of short hairs. This surface is small in the cercopids and is absent in all representatives of Fulgoromorpha examined by me. I assume that this is a sense organ. In the figures it is indicated by the abbreviation "pil" (pilose surface). In the araeopids there are instead a few short hairs on each side of the fore border of the second abdominal tergum (Plate 2, figs. 1 and 4, br). In the Fulgoromorpha, the metapostnotum is rather large and has a well developed phragma. The metapostnotum is considerably smaller in the cercopids and much reduced in the remaining forms. Phragma-like processes are however present on the metapostnotum even in the males of Paropia, Oncopsis, Tettigella, Eupelix, Agallia, Aphrodes flavostriatus, Graphocraerus, Euscelis and several species of Empoasca. The second and third abdominal terga, too. possess in some forms phragma-like dilations owing to the strong development of the dorsal longitudinal musculature. Thus the antecosta of the second abdominal tergum has phragma-like processes in the males of Tettigella, Eupelix, Idiocerus, Oncopsis, Macropsis, Agallia, Aphrodes, Doratura, Macustus, Euscelis, Streptanus, Limotettix, and Empoasca sordidula. The third abdominal tergum has phragma-like dilations in the males of Idiocerus, Agallia and several species of Empoasca. These phragmata are lacking in the females except in Doratura and the Fulgoromorpha, the latter possessing a less developed metapostphragma even in the female sex. In the araeopids and cixiids there are, indeed, in the metathorax well developed lateral dorsal longitudinal muscles serving the flight, these being lacking in brachypterous araeopids. In araeopids and cixiids the second abdominal tergum is devoid of phragmata in spite of the dorsal longitudinal musculature of the first abdominal segment being strongly developed. In these the second tergum is instead strongly vaulted into a convex, shield-like surface with inner strengthening lists. This shield is the posterior attachment of the longitudinal muscles from the metapostnotum.

The first abdominal sternum in all forms examined by me has a small extension in the longitudinal direction of the body but stretches often rather widely in the lateral direction. In the males and in the females possessing a functional sound-producing organ, this sternum is strongly sclerotized. In many forms there are paired apodemes for the attachment of muscles. The development of these apodemes is dependent on that of the muscles; in females without a functional sound-producing organ the apodemes are lacking. If seen from the front the first abdominal sternum is usually more or less broadly U-shaped. Laterally there are often pole-like or laminate inner processes (apophyses). Sometimes these seem to be lateral prolongations of the medial apodemes, often however they are - as MyERS (1928) points out for the cicadids - not endoskeletal parts but differentiations of the lateral part of the first sternum. These apophyses are attachments of certain muscles. The second abdominal sternum also in many male forms carries apodemes of a varying length in relation to the development of the ventral longitudinal muscles of the first abdominal segment. In Tettigella, Idiocerus, Opsius and most typhlocybids, these apodemes are more or less concave, tongue-shaped and directed horizontally backwards. Here they distinctly consist of two lamellae, one anterior (upper) and one posterior (lower). In the araeopids they are in most cases pole-like and almost vertical. In the females of all these forms (except Doratura) they are lacking or rudimentary.

Among the dorsoventral muscles in the region of the first abdominal segment, the muscle described and reproduced as I a  $dvm_1$  will first and foremost attract our attention. This muscle arises on the first abdominal sternum more medially the better it is developed, and is inserted at the hind border of the striated tymbal if such is present or, if there is no striated tymbal, on the corresponding spot somewhat anteriorly of the antecosta of the second abdominal tergum. I believe that this muscle is homologous in all forms examined by me where it is present and homologous with the tymbal muscle of the cicadas, too. This might be uncertain only for the Fulgoromorpha, as the conditions in this group are so deviating, but I am inclined to assume that it is a question of the same muscle even here. This muscle is generally much weaker in the females. In the female of Doratura stylata it is as well developed as in the male. In the female of Paropia, the male of which lacks this muscle, it is also well developed. It is of small size in the males of Empoasca but is

somewhat stronger in the females of this genus. In the male of *Cicadella atropunctata* I have not been able to find it, while it is relatively well developed in the female of the same species. When I a  $dvm_t$  is well developed it often ends dorsally in a tendinous plate and its tergal insertion is brought about by a short tendon.

Among the remaining dorsoventral muscles, the peculiar composite muscle present in Ledra, Euacanthus, Tettigella, Eupelix, Idiocerus, Agallia, Paropia and the euscelids and in Empoasca and Erythroneura hyperici indicated as I a dvm<sub>2</sub> in these forms must be noted. It is lacking in the cixiids and araeopids; whether the muscle in the cercopids also designated as I a dvm<sub>2</sub> may be homologous with the former is dubious, even though it is inserted on the metapostnotum in the cercopids, too. Further it is lacking in Oncopsis and Macropsis and in Cicadella atropunctata. The muscle arises on the first abdominal sternum or on its apodeme usually somewhat in front of I a dom, and is attached dorsally on the metapostnotum or its phragma without a tendon. Its tergal attachment usually has a more medial position than the insertion point of I a dvm<sub>1</sub>. In most cases the tergal attachment is more lateral than the sternal, muscles I a dvm<sub>2</sub> of the two sides diverging upwards into the shape of a V. In Erythroneura hyperici, in which these muscles are very powerful, they converge somewhat upwards on the contrary, as the distance between their dorsal attachments is smaller than that between the ventral. This muscle consists of two parts, one dorsal and one ventral, separated by a transverse tendinous plate that is thin in most forms, rather thick and blackpigmented in Tettigella. This plate is connected with the metendosternum by a more or less long figament. As a rule this ligament is very thin and difficult to follow in the preparations. In Ledra and Macrosteles it is relatively short, thick and richly interfused with cells. In most cases the dorsal part of the muscle is thicker than the ventral. In Paropia of both parts are about equally long, but in Ledra, Macrosteles and Empoasca the ventral part is much shorter than the dorsal. When this muscle is well developed in the male, as is the case in Paropia, Tettigella, Euacanthus, Agallia, Idiocerus, Empoasca and Erythroneura hyperici, it is always much weaker in the female. Therefore I do not hesitate about regarding this muscle as belonging to the soundproducing organ.

Evans (1941, p. 47) has found muscle I a  $dvm_2$  in Eurymela (family Eurymelidae). He states that "they are attached dorsally to the hind margin of the metanotum". He conjectures that these muscles in the Cicadidae have "migrated for a short distance posteriorly" and apparently believes that they are homologous with the tymbal muscles of cicadas. According to my opinion this cannot be the case, as my muscle I a  $dvm_1$  is doubtless homologous with the tymbal muscle of cicadas, and as I a  $dvm_1$  and I a  $dvm_2$  are coexistent in many forms. In all forms examined by me that possess the muscle in question (I a  $dvm_2$  of the Jassoidea), it is dorsally attached on the metapostnotum, which is primarily — at least in its major part — a constituent of the first abdominal segment.

Regarding its origin this muscle is enigmatic. It appears to be composed of two muscles, one ventral and one dorsal. We might conjecture that the ventral part was primarily a ventral longitudinal muscle between the metasternum and the first abdominal sternum, the dorsal an intersegmental dorsoventral one extending between the metasternum and the metapostnotum, or, if the

statement of Evans on the attachment of this muscle on the metanotum in Eurymela is correct, a metathoracic dorsoventral muscle. The transverse plate separating the two parts of I a  $dvm_2$  might be a detached part of the metasternum, which is, as we have seen, still connected with its origin by the ligament above mentioned. Of course this is only guesswork, there are other possible explanations. By a study of the conditions in groups not represented in the present paper this question will no doubt be answered in the future.

Among the remaining dorsoventral muscles in the region of the first abdominal segment, that denominated I a dvm3 in the Jassoidea should finally be mentioned. This muscle arises from a sclerite usually not very firmly attached to the posterior border of the ventral part of the metepimeron, and is inserted by an usually long, thin tendon on the first abdominal tergum somewhat in front of the insertion point of I a  $dvm_1$ . The denomination of this muscle is based on the assumption that the sclerite mentioned is primarily a part of the first abdominal sternum that has secondarily been attached to the metepimeron. If this is not the ease, the muscle is an intersegmental dorsoventral one. It is present in Euacanthus, Tettigella, Eupelix, Idiocerus, Agallia, Paropia, Doratura and the remaining euscelids, and in Cicadella. In most cases it is small and not or little stronger in the male than in the female. In Paropia and Cicadella, this muscle is much stronger in the male than in the female, and as I a  $dvm_1$  is absent in these males, it is possible that I a  $dvm_2$ in these forms serves the sound-production as a substitute for I a  $dvm_1$ . An oblique muscle I a ism, extending from the first abdominal sternum to a lateral part of the second abdominal tergum, is more or less well developed in many jassoid forms. In Cicadella atropunctata of this muscle is the strongest dorsoventral muscle in the region of the first and second abdominal segments. Neither this oblique muscle nor the dorsoventral muscle of the second abdominal segment, H a dvm, present in cercopids and the Jassoidea and especially well developed in the males of Oncopsis, Agallia and Opsius, raise any difficulties in respect of their morphological interpretation.

The longitudinal musculature in the dorsal and ventral areas offers no morphological problems. It is apparent from the descriptions in Chapter 1 that the dorsal and ventral longitudinal muscles in the males may be very strongly developed, those of the females having more normal proportions. The size of these muscles may be very different even in species belonging to the same genus. These matters are of importance especially for an understanding of the function of the sound-producing apparatus in these cases, for which reason these muscles will not be discussed in greater detail until the next chapter.

#### CHAPTER 4

# Discussion of the Function of the Sound-Producing Apparatus

Before proceeding to discuss the function of the different types of sound-producing organs in our small Auchenorrhyncha I think it appropriate to touch briefly upon what we know about the corresponding organ of the Cicadidae.

This is not the proper place for presenting any complete list of the workers who have occupied themselves with this apparatus. The reader who is especially interested in the comprehensive literature on this subject is referred to the voluminous bibliography in MYERS (1929). The honour of being the originator of the prevalent opinion on the origin of the calls of cicadas and on the structure and function of the sound-producing organ is generally ascribed to RÉAUMUR (1740). According to Myers, however, Casserio, Pontedera, Felici and Laurenti has each independently, earlier than Réaumur, described the tymbal apparatus of the cicadas and explained its function. The interpretation of Reaumur was purely theoretical, as this naturalist had never seen a living cicada, but it has been confirmed by several authors, who by experiments and morphological studies have shown that the sound is produced by a pair of powerful dorsoventral muscles in the first abdominal segment by their contractions setting a pair of so-called tymbals ("Schallplatten" Weber) in vibration. These tymbals consist of specialized lateral parts of the first abdominal tergum. They are traversed by a number of mainly parallel ribs giving them steadiness and elasticity. A short but clear account of the structure of this organ in Melampsalta muta and scricea and of its function is to be found in Myers (1929, pp. 74-78), from which I take the liberty to cite the following:

"We are reduced then to the tymbals and their muscles. The former are convex, and if they be pulled inwards and released by manipulation of the muscles in a moist specimen, they will regain their former convexity by the elasticity residing especially in the strongly bowed ribs. This is accompanied by a sharp click like that emitted by a tin can similarly indented — and these clicks, rapidly repeated, constitute the song of the cicada."

The above account is representative of the current interpretation of the manner of function of the tymbal apparatus of the cicada. Below I designate this interpretation "the tin can theory". Only for the sake of completeness I think I had better mention a couple of variants deviating to a certain extent from this interpretation. Graber (1876) suggested that the sound was pro-

<sup>&</sup>lt;sup>1</sup> There is no reason for discussing here the theory of Landons (1867) on the third

duced by the rubbing of the ribs of the tymbal against each other. The same hypothesis was adopted by Lucas (1887). According to Hingston (1920), one of the ribs on the tymbal of Platylomia brevis is on one side armed with a tooth fitting into a cavity on the nearest side of one of the neighbouring ribs. By the contraction of the tymbal muscle this tooth is set in vibration and strikes against the rib with the cavity, the sound being thus generated (according to this author). As MYERS (1928) points out, this interpretation, even if valid for the species examined by HINGSTON, cannot be generalized, as these specializations certainly do not exist in most other cicadas. Solier (1837) believed that the fibre bundles of which the tymbal muscle is composed contract alternately, the chitinous plate with the tendon thus making a tilting movement. Haswell (1886) launches a similar conception:

"Under ordinary circumstances the sounds follow one another with sufficient quickness to produce a continuous note, and this is effected, not by the contraction of the muscle as a whole, but by the successive contractions of the individual fasciculi, all of which act on the horny plate, and thus the movements of the muscle on the tendon during the production of the note resemble those of the hammer-board of a piano when a number of the keys are being struck in quick succession."

Most authors, however, explain the origin of the sound in conformity with the above-cited account of MYERS: the tymbal muscle by its contraction makes the tymbal concave; when this muscle is relaxed, the tymbal by means of its elasticity regains its convex shape, and a "click" is heard. "By a rapid succession of such clicks" (Morgan 1886) the song of the cicada is produced. Although the popular comparison with "a tin can" would suggest that there is one click when the tymbal is made concave and a fresh click when it springs back to the convex state, it seems as though the authors do not count more than one click for each contraction with the following relaxation,

The "tin can theory", however, does not reign supreme. PROCHNOW (1907) expresses himself in the following manner (p. 529):

"Wenn die Verbiegung der Membran nach Kontraktion des Muskels eingetreten ist, so bewirkt die Elastizität der Membran, die durch die Verdickungslisten wie durch die Krümmung vergrössert wird, einen schnellen Ausgleich der Verbiegung in entgegengesetzter Richtung und ein Pendeln um die Gleichgewichtslage der Membran, solange, bis die ursprüngliche Stellung wieder eingetreten ist oder von neuem eine Verbiegung einsetzt. Jeder stärkeren Verbiegung der Membran entspricht offenbar ein Anschwellen des Tones, dem allmählichen Nachlassen ein Abflauen des Tones."

This author mentions nothing about the tymbal being made concave or about any "clicking". This interpretation does not suggest a comparison with a tin can but rather with the plucking on the strings of a mandoline with a plectrum or a finger. This "mandoline string theory", however, has at least one essential constituent in common with the tin can theory: the pitch of the sounds produced is independent of the frequency of the muscle contractions. Apparently it is assumed that this frequency is too low to correspond to what is apprehended as a tone by the human ear. If a tone is heard at all,

therefore, it will be identical with the so-called specific tone of the vibrating membrane.

CARLET (1877) stated that the tymbal of the cicada was not made concave during normal singing, both the tymbal and the muscle vibrating with a very small amplitude. "... mais la membrane elle-même conserve toujours sa forme convexe et ne se renverse jamais, pendant le chant, chez les Cigales adultes." This observation could be interpreted in favour of the mandoline. string theory; however, there is a third theoretical possibility. If the muscle vibrated rapidly enough, a tone corresponding to the frequency of its contractions would be produced. At the same time the membrane would produce, by vibrations of a smaller amplitude, its specific tone, which would decide the character of the sound.

Several authors, by experiments and other observations, have confirmed that the tymbal of cicadas may be made concave and then convex and that a "click" is heard as a result of this. Others express themselves so vaguely that it is not clear how they do conceive the origin of the sound in detail, There is no doubt that in many cases the calls are produced either according to the tin can theory or to the mandoline string theory. But it is indubitable that the whole truth of the sound-production of cicadas is not covered solely by this explanation.

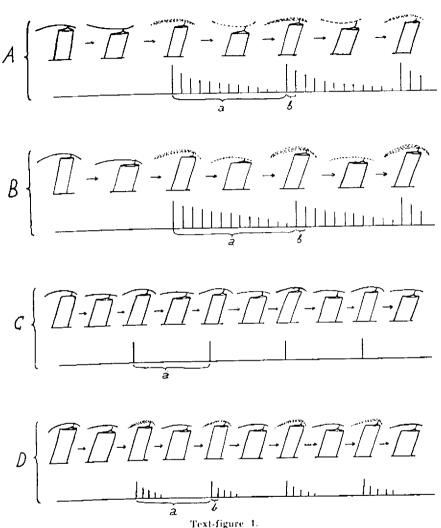
Text-figure 1 is an endeavour to make the most important explanations of the sound-production of cicadas clear by a schematized reproduction. The simple figures of the sound-organ will be understood without long-winded explanations. When the curved figure reproducing the membrane (tymbal) is dotted, this indicates that the membrane is thought to be vibrating. The horizontal line under each series of figures represents time, the vertical marks each representing one vibration of the tymbal (and of the air). The frequency of the vibrations, then, may be established by dividing the horizontal length of a second (not marked in the figure) by the horizontal length of the interspace between the marks. Thus, if the length of a second is abbreviated to s, the frequency of muscle contractions will be  $\frac{s}{a}$ , the frequency of the specific

tone of the membrane  $\frac{s}{k}$ . The vertical length of the marks represents the

amplitude of the vibrations. Further, the figures are drawn on the assumption that the interval between one contraction and the following relaxation (r) is the same as the interval between one relaxation and the subsequent contraction (c), though I am aware that this is not necessarily — perhaps seldom — the case, r probably often being much smaller than c. The figures are given, as the indulgent reader will realize, in order to facilitate a comparison between four theoretical possibilities (A-D) in certain respects, not to produce exhaustive explanations, which the present writer is not capable of doing.

Fig. 1 A reproduces the "tin can" explanation. It is assumed that the contraction of the muscle does not prevent the membrane from continuing its swinging. If  $\frac{s}{a}$  is too small a value to correspond to a tone perceptible to the human ear, the pitch will correspond to the frequency  $\frac{s}{b}$ . The calls produced

spiracle as the generator of the sound. This theory has been exhaustively refuted by GRABER (1876), LEPORI (1869), LUCAS (1887), MAYER (1876, 1877), MORGAN (1886), VAN HASSELT (1882), and others.



will consist of trilling or drumming sounds. -- The figure does not pay regard to the possibility that one "click" is produced at each contraction, another at each relaxation, giving a "click" frequency of  $\frac{2s}{a}$ . Even if this be sometimes the case, it is not probable that the vibrations in the contraction click have the same amplitude as those in the relaxation click, as the membrane in the latter phase must be able to vibrate more freely than in the former.

Fig. 1 B gives the "mandoline string" explanation with the same assumption as that made for the above case. If  $\frac{s}{a}$  is not high enough to give a tone audible to the human ear, the pitch is determined by the frequency  $\frac{s}{k}$ . In this case the sound will be a trilling or drumming sound or a quavering tone.

Fig. 1 C reproduces the possibility that the frequency of the vibration of the membrane (and the tone frequency) is identical with the frequency of the muscle contractions, the latter being great enough to give an audible tone. This version is doubtless exclusively theoretical, as every elastic membrane set in motion will always get into vibration with its specific frequency. The corresponding reality is represented by fig. 1 D. This alternative is apparently nearly related to the "mandoline string" explanation, the crucial difference being that, in alternative D, the frequency of muscle contractions is high enough to decide the pitch of the main tone, the frequency  $\frac{s}{b}$  giving

the sound its specific character (acoustic colour). Returning to our small Auchenorrhyncha I ask myself: Which of these explanations is (or are) valid for the sound-production of our species?

In Lepyronia, Eupelix and Streptanus aemulans I have observed vigorous vibrations in the lateral parts of the first abdominal tergum, these being made concave and convex in alternation. In these species I have not simultaneously heard the sounds produced, but the rate of the movements agreed with that of the calls just heard from the animals. In Aphrodes bifasciatus, Ulopa reticulata and the female of Paropia scanica I have simultaneously seen the movements and heard the sounds and established an exact synchronism. In these cases the movements were low-frequent (with a small number of vibrations per second or less). In Aphrodes the amplitude of the vibration was small, the membrane apparently not being made concave. I think it is quite certain that the clacking and drumming noises made by these species and many others are produced in accordance either with the "tin can theory" or with the "mandoline string theory". And how would this be effected if not by the contractions of muscle I a dvm1, which is well developed in these forms and is inserted in the region in question? Probably I a dvm<sub>1</sub> in all cases where it is well developed has the function of the most important sound-producing muscle. But on the other hand I believe that in many species this muscle is capable of a higher frequency of contractions producing a tone corresponding to the alternative reproduced in fig. 1 D.

In studying Chapter 2 the reader has doubtless observed that the calls of our Auchenorrhyncha may be divided into three groups: 1) single clackings or beats are emitted by most species; 2) more prolonged drumming or trilling calls are the most important constituents of the common songs of Cixius, Lepyronia, Paropia, Idiocerus, Aphrodes, Graphocraerus, Streptanus and Hesium, only to mention some characteristic examples; 3) more even tones as from a flute or violin or the human voice are produced for example by Doratura, Athysanus argentatus, Dikraneura citrinella and Cicadella notata. In Agallia and many araeopids we find calls that form a combination of the type of sound last mentioned and the others. The single clackings and the calls of type 2) will be produced in accordance with the tin can theory and the mandoline string theory, and the sounds of type 3) I conjecture correspond to the fig. 1 D alternative.

As to the fin can theory I wish to draw the reader's attention to what has been said on pages 78 (Paropia of) and 69 (Idiocerus populi of) with regard to certain observations on the sound-film records. It seems as if the contraction of the muscle in these cases produced a sound distinct from that of the relaxation but with a much smaller amplitude of the vibrations. Of course it cannot be proved that this explanation is correct, but it is not improbable, I believe.

I am now going to discuss alternative D as an explanation of the origin of the sounds of type 3. In *Doratura* the pitch of the common tooting call has appeared to rise with the temperature (within the temperature interval represented in my experiments, cf. Chapter 5, pp. 130—131). This is easy to understand if it is assumed that the tone frequency is identical with the frequency of the muscle contractions, making the phenomenon a fresh example among several earlier established of the frequency of contraction of insect muscles rising with the temperature. Thus, Sotavalta (1947) found a correlation between the temperature within certain intervals and the "wing-stroke frequency" of Hemaris Juciformis and certain Diptera. According to Kraemer (1932), "die Zuckungszeit" of certain muscles in Dytiscus marginalis and Lucanus cervus falls with a rising temperature within a certain interval. If the tone frequency in the case of Doratura were not identical with the frequency of the muscle contractions, a periodical variation in the amplitude of the single vibrations would be expected, visible for example on the soundfilm record (Plate 12, figs. 1—3), which is not the case. On Plate 12, fig. 4, a piece of sound-film of the call of Doratura stylata of is reproduced; this strip, by a different technical arrangement when the record was made, renders possible a finer analysis of the sound than that which could be effected by figures 1-3, though made on the same occasion using the same individual insect. Each of the high marks of the records in figs. 1—3 is represented in fig. 4 by a group of finer marks. Apparently these correspond to the specific vibration of the sound-producing membrane, each group representing one contraction with the subsequent relaxation of the muscle. The resemblance of this sound film record to the theoretical fig. 1 D is striking, at least. If this interpretation is assumed to be correct, the frequency of the contractions of the muscle would rise from about 115 to about 200 per second at a temperature rising from  $\pm 25^{\circ}$  to  $\pm 41^{\circ}$  C.

The "dying yell" of Typhlocyba ulmi consists of an even tone with a pitch, according to my observations, of about d² (at room temperature), corresponding to a frequency of about 580 c.p.s. For the frequency of contraction of an insect muscle this is certainly a very high value, but it is by far exceeded by the wing-stroke frequency of certain Diptera (SOTAVALTA 1947). In Forcipomyia sp., SOTAVALTA found a wing stroke frequency of up to 1046 per second. Then there is nothing improbable in the assumption that the sound-producing muscle of Typhlocyba would be capable of producing contractions with the frequency of 580 per second.

In certain forms, such as the males of Aphrodes flavostriatus, Paropia, Cicadella, Empoasca and other typhlocybids, muscle I a  $dvm_1$  is weak or even absent. In these, other dorsoventral muscles (I a  $dvm_3$  and I a ism (in Cicadella)) are better developed. Probably these muscles have undertaken the functions of I a  $dvm_1$  in the other forms. However, whether muscle I a  $dvm_3$  is present or not, the structure of the sound-producing organ is complicated

by the presence of several other muscles. As these are as a rule much weaker in mute females, they must play some part in the sound-production. Even in cicadas there are in the same region several other muscles in addition to the tymbal muscles, though most authors have not mentioned them. SNOD-GRASS (1925) gives a reproduction of the musculature in the first and second abdominal segments in *Magicicada septendecim* (l.c. p. 446, fig. 31. I have also examined this species). It appears from this figure that there are dorsal as well as ventral longitudinal muscles. In many of our small *Auchenor-rhyncha*, as we have seen from Chapter 1, these longitudinal muscles — dorsal or ventral or both — are very well developed.

According to my opinion, these muscles deviate only by their stronger development from the corresponding longitudinal muscles in the "normal" abdominal segments. This stronger development meets increased demands on the force and amplitude of the movements executed by these muscles. The purpose of the dorsal longitudinal muscles is the concertina-like compression of the dorsum in the region in question. The ventral longitudinal muscles will shorten the venter in the same way. By this shortening of the venter the abdomen is lowered and the dorsum is stretched. Thus the ventral longitudinal muscles are the antagonists of the dorsal. In many species a stretching of the tergum is perhaps a condition precedent for the action of the dorsoventral muscles resulting in a sound-production. In others, an alternating contraction of the dorsal and ventral longitudinal muscles will effect a varying extent of tension in the dorsum of the abdominal basis with its clastic sound-producing membranes. By this varying tension a differentiation of the quality of sound is arrived at. In the species the calls of which consist of drumming rolls, this is easy to understand. Take the common song of Streptanus aemulans, for example. This song consists of a prolonged roll that, however, is not uniform but is composed of a regular alternation of stronger and weaker series of beats with the same frequency. During the singing the abdomen is alternately raised and lowered synchronously with the alternation of the strength and quality of the sound. Probably muscle I a dvm, in this case as well as in most others is the primary generator of the sound, the longitudinal muscles by the raising and lowering of the abdomen modifying the character of the sound. Similar raisings and lowerings of the abdomen have been observed also in cicadas (cf. CARLET 1877, MORGAN 1886 et al.) and it has been stated that these movements even here correspond to variations in the quality of the sound. It has been supposed that these variations were due to the altering of the space between the abdomen and the ventral opercula by the lifting and sinking of the abdomen. Even if this may be true for the cicadas, this explanation cannot be valid for the remaining Auchenorrhyncha, as the opercula are absent in these. It is conceivable, however, that the varying of the space between the abdomen and the wings effected by the movements of the former may play a similar part in this connection.

I do not a priori deny the possibility that the longitudinal muscles in certain cases may have a more direct sound-producing function. The membranes in the first and second abdominal terga might be buckled not only by the direct pulling of a dorsoventral muscle inserted on them as I a  $dvm_i$ : a buckling of that kind might be effected also by a rapid contraction of the dorsal longitudinal muscles. In certain cases when the abdomen is perceived

<sup>1</sup> Frequency: 3650 c.p.s.

vibrating at the rate of the single beats of the sound in a very great amplitude, this explanation is perhaps conceivable. This might for example be the case with the call of agitation of *Doratura*. Further, this manner of function might be possible for the mightly dorsal longitudinal muscles of the first abdominal segment in the aracopids. However, in the first-mentioned case the phenomenon is as easily explained as the result of vigorous, low-frequent contractions of muscle I a  $dvm_1$ , a rapid pull in the first abdominal tergum effecting a jerk upwards of the whole abdomen. And the powerful longitudinal muscles of the aracopids as well as those of other Auchenorrhyncha may very well have the sole task of changing the state of buckling and tension of the tymbal membranes, by which the action of muscle I a  $dvm_1$  will result in sounds of varying quality. At all events I do not believe that these muscles act by high-frequent contractions.

Of course I am not able to offer a complete explanation of the function of the sound-producing organ for all cases. I will suggest the possibilities imaginable in broad outline only. I shall dwell briefly upon three special problems apparently offering difficulties of interpretation. These are: 1) the strongly developed ventral longitudinal muscles in the first abdominal segment of the typhlocybids; 2) muscle I a  $dvm_2$  in the Jassoidea; and 3) the aracopids with the almost vertical muscle I a  $vlm_2$ .

1. The most striking feature in the typhlocybids, for example the species of Empoasca, Cicadella atropunctata and Typhlocyba ulmi, is the relatively colossal development of one of the ventral longitudinal muscles in the first abdominal segment (I a vlm in Empoasca, I a vlm3 in Cicadella). Upon cursory deliberation it seems self-evident that this muscle is the primary producer of sound. After examination of the conditions in Empoasca devastans, GEORGE (1933) concluded that the apodeme of the second abdominal sternum served as the tymbal of a sound-producing apparatus analogous to that of the cicadas. This theory is properly speaking scarcely worth discussing. Nothing in the structure of this apodeme points to its function being that supposed by George. This apodeme agrees exactly in all essential parts with many other endoskeletal structures in the insect body, whose purpose is to allow a strong development in length and thickness of a segmental muscle. It is on all sides embedded in soft parts, by which its supposed function as a sound-producing membrane must be much impeded. When George states that the great muscle is inserted anteriorly on "the junction of the hind margin of the metathoracic and the first abdominal sterna", this statement at all events does not agree with the conditions present in our Swedish species of Empoasca and other typhlocybids examined by me, in which the muscle without exception is attached anteriorly on the hind border of the first abdominal sternum or on the apodeme of the latter. A more reasonable assumption would be that the first abdominal sternum is set in sound-producing vibration by the muscle in question. In my opinion this assumption would mean an unnecessary theoretical deviation from the explanation valid for other Jassoidea. Without strong support in direct observations I am not willing to accept this hypothesis. If we are to cling to the supposition that the large ventral longitudinal muscle is one of the primary sound-producers, a third theory is conceivable, namely that the whole abdomen would be set in vibrations transformed into sound waves in the elastic tergal parts of the first and second abdominal segments. Possibly this theory is valid for certain rattling sounds produced by these insects. We must remember, however, that the difference between the sound-producing organ of the typhlocybids and that of the remaining Jassoidea is of a quantitative nature only. In certain typhlocybids, such as Erythroneura hyperici, the ventral longitudinal muscles of the first abdominal segment and the apodeme of the second abdominal sternum are relatively insignificant, muscle I a dvm2 being the largest muscle in this region in the species mentioned. Until more experience has been acquired I find it most probable that the dorsoventral muscles in the first and second abdominal segments even in the typhlocybids are the direct producers of sound, while the longitudinal muscles in question have the main task of contracting the ventral region and, by this action, of extending the dorsum with its elastic, sound-producing membranes. At the first moment it certainly seems very singular that a muscle that is assumed to have only an accessory function should have much larger dimensions than the primarily soundproducing muscle, but after all this is not at all unreasonable. The force necessary to set a thin, elastic membrane in vibration by a muscle inserted directly on the former or on its margin is doubtless insignificant if compared with that required to keep this membrane stretched, especially if the stretching must be effected indirectly. The dorsoventral muscles I a dom<sub>3</sub> and I a ism and II a dom in the typhlocybids are certainly much weaker than I a dvm, in most jassoid forms, but they are relatively not weaker than I a dvm, in Neophilaenus, in which species this muscle beyond any doubt is the most important sound-producing muscle. The calls of the typhlocybids are, further, even relatively very faint.

As the typhlocybids apparently have no "calls of distress", it is unfortunately very difficult to see the sound-producing parts in function. In order to do so, I have tried to take advantage of the "dying yell" (see above p. 9) emitted by these males. In the species I studied in this connection, Typhlocyba ulmi and Cicadella atropunctata, the dying-yell consists of a prolonged monotonous high-pitched tone recalling that of a distant violin. No movement whatever could be perceived in the animal emitting this yell through the binocular magnifier. But when I touched the dorsum of the first and second abdominal segments very lightly with a fine needle, a rattling noise was heard like that produced if a vibrating tuning-fork is touched with a point of some kind. Then it was apparent that these tergal parts were engaged in high-frequent vibrations of small amplitude. How these vibrations were produced could not be discerned, and for the present, therefore, I must content myself with mere guesswork, leading me, as I have said above, to the conclusion that the sound is probably produced in the same way as in other Auchenorrhuncha.

2. Another rather difficult problem is presented by muscle I a  $dvm_2$  of most jassoid forms (see Chapters 1 and 3). This muscle arises on a rather medial part of the first abdominal sternum anteriorly of the sternal attachment of I a  $dvm_1$  (when present), and is inserted dorsally on the metapostnotum or metapostphragma. As this muscle may be well developed whether I a  $dvm_1$  is strong or weak or even absent, it is certainly no substitute for the latter. The metapostnotum is probably not immovably attached to the metepimeron but is able to turn hinge-like round the line of this attachment. On the other hand, the first sternum is probably not so firmly anchored that it might not be lifted upwards by the contraction of a powerful muscle.

Such a lifting, however, might be counteracted by the contraction of the ventral longitudinal muscles of the third thoracic and first abdominal segments. Especially singular is the ventral attachment of I a  $dvm_2$  in Idioceru§ at the apex of a rather thin, long process from the apodeme of the first abdominal sternum. It seems as if this process would act as a lever and by the contraction of I a dvm<sub>2</sub> turn the first abdominal sternum round a transverse axis. Such a turning of this sternum, if practicable, seems to be counteracted by a contraction of the powerful ventral musculature, as muscle III vlm is attached higher up than I a vlm. Dorsally I a dvm2 is generally attached more medially than the remaining dorsoventral muscles. Possibly this muscle by deflecting the metapostnotum is able to produce clicking sounds by dintings in the first abdominal tergum. It is conceivable that the muscle has this function in the male of Paropia, for example. Another explanation, however, is that this muscle by its contraction will draw the dorsum and sternum in the region in question closer to each other, making the transverse section of the first abdominal segment broader and lower. This will result in changed conditions of tension in the tergal membrane and then in modifications in the quality of sound. Another possible result of this change of the transverse section of the first abdominal segment is the following. Muscle I a dom, will be shortened or relaxed. The stiffness of this muscle will be changed, and that will react upon the tension of the tergal membrane and the sound. At more high-frequent contractions of muscle I a dvm, it is not impossible that the frequency of the contractions would be changed by such a shortening of the muscle. It seems as if the amplitude of the contractions would be dependent on the length of the muscle in its position of repose, and if so, why not the frequency, too? Perhaps there is no parallel to this assumption in muscle physiology, but it is not unreasonable. This assumption would provide an explanation of the mechanism of the changes of frequency so characteristic for the songs of many of our Auchenorrhyncha.

3. The third problem is the organ of aracopids, especially muscle I a vlm<sub>2</sub>. In most species of this family (Dicranotropis, Calligypona, Chloriona but not Stenocranus, Kelisia, Achorotile), this muscle is almost vertical. It is, however, approximately parallel with muscle I a  $dlm_1$  (see Plate 2), the latter having the task of compressing the first abdominal tergum, which causes the abdomen to be somewhat raised. I a  $vlm_2$  will then work as the antagonist of  $I = a \, dlm_1$ . By alternating action these muscles will perhaps cause a rattling motion of the whole abdomen resulting in drumming noises. Probably, however, muscle I a vlm<sub>2</sub> in the cases when it is nearly vertical will somewhat lift the first abdominal sternum, the latter being here on all sides surrounded by membranous parts of the integument. By this, muscle I a  $dom_1$  would be shortened with the same results as those outlined above for the action of muscle I a  $dvm_2$  in the jassoid groups. The same argumentation on the possible consequences of this shortening as adduced above for the jassoid families will be valid also for the aracopids, in whose calls changes of frequency in glissando are very common.

The reader will find this discussion very hypothetical. The interesting problems in question may be solved only by further studies partly by methods not hitherto at the disposal of the present writer.

#### CHAPTER 5

# Is the Tymbal Apparatus of any Taxonomic Importance?

Of course it is tempting to try and revise the system of the Auchenor-rhyncha on the basis of my comparative studies on the sound-producing organ. Indeed, it has almost been a rule in the history of zoology for the investigator who has more thoroughly described an organ in a series of forms to attempt to construct a new "phylogenetic" classification of the group in question. In the present case, however, representatives of more families should be examined before the drawing of too extensive conclusions. I am only going to permit myself a few reflections that suggest themselves.

The presence or absence of muscle I a  $dvm_2$  in jassoid forms will no doubt in the future allow conclusions of taxonomic value. This muscle with its very characteristic structure is certainly homologous in all forms possessing it. Among the jassoid groups studied by me it is lacking only in the Macropsidae and in Cicadella and Typhlocyba in the typhlocybids. Is this absence primary or secondary? For the macropsids this cannot be decided with any certainty for the present. In the typhlocybids lacking I a  $dvm_2$  this absence is doubtless secondary.

The similarity of the sound-producing organs of *Empoasca* and *Idiocerus* is very striking (I am thinking of the tendency to form phragmata on the third abdominal tergum, for example). Of course this similarity may be a case of convergence.

Further, an alluring subject for speculations is provided by the conditions in the females. In the cicadas, according to the unanimous statements of all authors who have occupied themselves with the sound-production of these insects, the females are mute, lacking a functional tymbal apparatus. (Here I leave the stridulating organ of Tettigadinae Jacobi out of consideration.) It may be mentioned, however, that Weir (1877) stated that he had heard a "stridulation" from the female of Cicada montana (Cicadetta m.). In the cercopids and certain jassoid genera the females possess a functional sound-producing organ of the same type as that of the male, though weaker. The simplest and apparently most primitive tymbal apparatus is that of the cercopids such as Aphrophora, Philaenus and Neophilaenus, though already the male of Lepyronia has a better developed organ. In Paropia the female possesses a rather well developed sound-producing organ, the most important muscle of which is I a dvm<sub>1</sub>, not found in the male. This muscle is present not only in most Jassoidea but also in the Cercopidae, Araeopidae, Cixiidae

<sup>&</sup>lt;sup>1</sup> Jacobi 1907; cf. also Varley 1939.

and Cicadidae, while I a dvm2 has been found only in the Jassoidea. From these facts I feel justified in concluding that the female of Paropia represents a more primitive stage than the male of the same species. This female has a distinct striated tymbal which is, in the male, only represented by traces. In Doratura both sexes possess practically identical tymbal organs in the same state of development. The most important parts of these organs are the same as in  $Paropia \ \mathcal{P}$ . Probably this is the original condition. Nevertheless the modest proportions of muscle I a dvm<sub>2</sub> and other muscles in Doratura and other jassoid forms may very well be a case of reduction, of course. Where the females are without a sound-producing organ, this lack is probably due to reduction. Evans (1940) draws similar conclusions from his study of the morphology of the singular mute cicada Tettigarcta. As a striated tymbal is present among the Jassoidea as well as in the Cercopidae (and Cicadidae), it must be an early acquisition. The complications present in the different groups, such as the strong development of the longitudinal musculature in many forms, are later specializations.

The longitudinal musculature especially shows great variation even in the same genus (for example in *Idiocerus*, *Aphrodes*, *Empoasca*). This is easily explicable for reasons of expediency: if it were assumed that the specimens of the same species do apprehend the calls of each other and that these have some biological significance, it is of course important that they are able to distinguish the calls of the same species from those of nearly related species. From this point of view the specific variation of the sound-producing organ is analogous to that of the genitalia of the males. For this reason caution must be recommended in exploiting the differences in the sound-producing organ for taxonomic purposes. I therefore refrain from such exploitation for the present. Only in one case do I wish to make an observation.

The genus *Doratura* has by me (1947, 1948 a, and in the present paper) been reckoned to the family *Euscelidae*. Evans (1947) places it in the tribus *Aphrodini* in the subfamily *Aphrodinae* of the family *Jassidoe*, and LINDBERG (1947) classifies it as belonging to his family *Deltocephalidae*. However, this genus occupies an isolated status among Swedish euscelids by the possession in both sexes of a well developed sound-producing organ with a distinct striated tymbal.

#### CHAPTER 6

# Contributions to the Knowledge of the Sound-Production from Biological Aspects

The complex of biological problems in connection with the sound-production is partly of special nature. The influence of external conditions may modify the sound-production quantitatively or qualitatively in a way that may be specific for the individual forms or groups or common to the Auchenorrhyncha as distinct from other insects. On the other hand, it may be a question of problems of a more general character affecting other insects and other animals as well as the Auchenorrhyncha. The results of experiments and other observations presented below are only of preliminary nature. Only a small number of species have been studied, for which reason the results reached must not be generalized too much. The unravelling of general biological problems connected with the sound-production is not the purpose of the present paper, but as the observations made may nevertheless be of a certain interest even in such relations, an account of them is given below. Thanks to their great contentment, several of our small Auchenorrhyncha are very suitable objects for experimentation, and I recommend their study to everyone who is interested in the biological problems of the sound-production of insects.

#### A. The influence of external conditions

The experiments described below are impaired by certain apparent defects. If the influence of an isolated external factor on the biological manifestations of a living thing is to be established, the remaining variable conditions should be made constant. This has not been possible as regards the humidity of the air, as the inclination for singing of the *Auchenorrhyncha* depends on their feeling comfortable, the latter implying that parts of their host plants are present in the cages. A measuring of the humidity in the immediate proximity of these plant parts has not been possible. For the same reason the importance of the humidity of the air has not been studied at all. This importance is doubtless great. If the air is not damp enough, the animals will die very rapidly; on the other hand, I have found that they cease singing entirely if the humidity is so great that moisture condenses on the inside walls of the tube or cage.

It is often very evident that sunlight has a strongly stimulating effect on the singing, but the making out if this is dependent on the rise in temperature only or if the light in itself is of any importance has met with difficulties, as the temperature in comparing sunlight with shade could not be kept con-

<sup>&</sup>lt;sup>1</sup> P. 47: "Tettigarcta has no trace of auditory organs in either sex, but has tymbals in both sexes, and only slightly less development of tymbal muscles in the female than in the male. Therefore one can reasonably conjecture that it is descended from an early cicadan stock that possessed in both sexes well-developed sound-producing organs and also sound-detecting organs."

stant. By experiments with indirect daylight or artificial light it has appeared as though temperature at all events were more important than light, but I have the impression that direct sunlight often has a more stimulating effect than that which could be explained solely by a reference to the rise in temperature.

According to many authors (Carlet 1877, Davis 1894, Gibb 1860, Krumbach 1917, Myers and Myers 1924, and others), the cicadas sing mainly during the day, only exceptionally in the night. According to Distant (1897), Platypleura haglundi Stål sings at nightfall just before sunset. Myers (1929) reports from the literature some statements on the occasional singing of cicadas during the night. According to Annandale (1900), several Malay cicadas sing at night. Experimental investigations on the influence of temperature, light or daily rhythm have apparently not been made.

#### 1. The influence of light

On 25—26 August, 1946, I made the following experiment. Six males and two females of *Erythroneura hyperici* (material from Upland, Värmdö) were introduced into a celluloid cage with some leaves of *Hypericum*. The cage was placed directly on the membrane of the microphone reproduced in Plate 1, fig. 2. During 10 periods of 15 minutes each alternatively in darkness (by the lid of the microphone being on, see Plate 1, fig. 1) and in natural or electric light, the number of calls emitted was counted. It is to be noted that one of the males died during the night of the 25/26 August, for which reason the figures from the two days are not directly comparable. The result of this experiment is shown in Table 1.

Table 1. (Erythroneura hyperici)

|      |                 | Light conditions                     | Sounc<br>nun | t-production<br>iber of calls)  |
|------|-----------------|--------------------------------------|--------------|---|
| Date | Time            | Light conditions                     | total        | -production<br>ber of calls)<br>per individual<br>132<br>114<br>96<br>114<br>86<br>54<br>23<br>29 |
| 25/A | 6.44— 6.59 p.m. | Darkness                             | 791          | 132   |
| "    | 7.00— 7.15 "    | Daylight indoors near the window     | 681          | 114   |
| ••   | 7.16 7.31 "     | Darkness                             | 575          | 96  |
| **   | 7.32 7.47 "     | Electric light (25 W at a distance   |              |   |
|      |                 | of 2 dm)                             | 685          | 114   |
| 11   | 9.37 9.52 "     | Darkness (that had prevailed since   |              |   |
|      |                 | 7.47 p.m.)                           | 517          | 86  |
| **   | 9.5::10.08 "    | Electric light as above              | 323          | 5 <b>4</b>  |
| 26/8 | 6.37— 6.52 a.m. | Darkness (prevailing since 10.08 the |              |   |
|      |                 | preceding night)                     | 116          | 23  |
| ••   | 6.56 7.11 "     | Daylight at the window (cloudy       |              |   |
|      |                 | weather)                             | 146          | 29  |
| **   | 8.59 9.14 "     | Daylight at the window (since        |              |   |
|      |                 | 6.56 a.m.)                           | 139          | 28  |
| 19   | 9.15 9.30 "     | Darkness                             | 266          | 53  |

Temperature:  $\pm$  18°— $\pm$  19° C. — The great difference in the size of the figures from the two days will be explained by the death of one specimen and by the deteriorated ecological conditions in the cage (nourishment and humidity) owing to the withering of the *Hypericum* leaves.

A corresponding experiment was made on 26 August, 1946, with five males

of Empoasca viridula (from Upland, Solna). The calls counted were of the laughing kind (cf. 96). The number of calls during periods of 15 minutes in varying conditions of light was counted. Temperature:  $+18^{\circ} - +19^{\circ}$  C. The result may be seen from Table 2.

Table 2. (Empoasca viridula)

|                  |                      | , ,                                 | Sound-production  |
|------------------|----------------------|-------------------------------------|-------------------|
| Date             | Time                 | Light conditions                    | (number of calls) |
| 26/ <sub>8</sub> | 4.17— 4.32 p.m.      | Daylight at the window (cloudy)     | 46                |
| **               | 4.32— 4.47 "         | Darkness (lid on the microphone)    | 25                |
| "                | 4.47 5.02 "          | Daylight as above                   | 20                |
| **               | 5.02 5.17 "          | Darkness                            | 30                |
| **               | 5.28 5.43 "          | Daylight                            | 30                |
| **               | 5.43 5.58 "          | Darkness                            | 24                |
| **               | 5.58— 8.18 "         | First daylight, then electric light | Not counted       |
| **               | 8.18— 8.33 "         | Electric light (a 25 W lamp at a    |                   |
|                  |                      | distance of 2 decimetres)           | 38                |
| "                | 8.33 8.48 "          | Darkness                            | 15                |
| **               | 8.49 9.04 "          | Electric light                      | 26                |
| **               | 9.04 9.19 "          | Darkness                            | 20                |
| **               | 9.19—10.58 "         | Darkness                            | Not counted       |
| **               | 10.5811.13 "         | Darkness                            | 4                 |
| 26- ·27/8        | 11.13 p.m.—6.12 a.m. | Darkness                            | Not counted       |
| <sup>27</sup> /a | 6.12— 6.27 a.m.      | Darkness                            | 16                |
| ,,               | 6.27— 6.42 "         | Daylight at the window              | 25                |
| . **             | 6.42 a.m.—4.07 p.m.  | Daylight                            | Not counted       |
| **               | 4.07 4.22 p.m.       | Daylight                            | 15                |
|                  |                      |                                     |                   |

Several experiments have been made with Streptanus aemulans (material from Upland, Solna). One of these was made on 3—4 October, 1946. The animals were as usual placed in a cage with a leaf of Agropyrum repens kept fresh by its basal end being stuck into a small glass tube containing water. Two males captured on 3 October at about 3 p.m. were used. The cage was placed on the membrane of the microphone alternatively in daylight immediately inside a window and in darkness (the same place, the lid of the microphone on), or alternatively in sunlight through the window, in the shade of a flower pot in the same window, and in darkness. During the night the lid of the microphone was kept on. The result may be studied in Table 3.

Table 3. (Streptanus aemulans)

| Date | Time            | Light conditions         | Temperature<br>(cenligrade) | Sound-production (number of calls) |
|------|-----------------|--------------------------|-----------------------------|------------------------------------|
| 3/10 | 3.30 3.40 p.m.  | Daylight, cloudy weather | + 24                        | 7                                  |
| 1)   | 3.40 3.50 "     | Darkness                 | + 24                        | 3                                  |
| **   | 3.50 4.00 "     | Daylight                 | + 24                        | 1                                  |
| ,,   | 4.00 4.10 "     | Darkness                 | +24                         | 5                                  |
| **   | 4.10 4.20 "     | Daylight                 | + 24                        | 1                                  |
| **   | 4.20-4.30 "     | Darkness                 | + 24                        | 3                                  |
| 4/10 | 8.50— 9.00 a.m. | Darkness                 | + 19.5                      | 2                                  |
| **   | 9.00 9.15 "     | Daylight, shade          | + 19.5 - + 23               | 5                                  |
| **   | 9.15 9.30 "     | Sunlight                 | +23-+26.5                   | 16                                 |
| **   | 9.30 9.45 "     | Darkness                 | +26.5                       | 6                                  |
| 17   | 9.45-10.00 "    | Daylight, shade          | +26.5-+25.5                 | 5 11                               |

Here the experiment was interrupted in consequence of a misadventure. Instead of the two males hitherto used four new males were captured and the experiment was continued with these. Result in the following Table.

Table 4. (Streptanus aemulans)

| Date | Time             | Light conditions | Temperature<br>(centigrade) | Sound-production (number of calls) |
|------|------------------|------------------|-----------------------------|------------------------------------|
| 4/10 | 10.45—11.00 a.m. | Sunlight         | +28-+26                     | 29                                 |
| 710  | 11.00-11.15      | Darkness         | $+\ 26 -+\ 31.5$            | 13                                 |
| ,,   | 11.15—11.30 "    | Daylight, shade  | +31.5-+27.5                 | 13                                 |
| 11   | 11.3011.45 "     | Sunlight         | +27.5-+28                   | 14                                 |
| 41   | 11.45—12.00      | Darkness         | $+\ 28+\ 31.5$              | 11                                 |
| **   | 12.00—12.15 p.m. | Daylight, shade  | +31.5 - + 25                | 10                                 |
| 11   | 12.1512.30       | Sunlight         | $+\ 25-+\ 28.5$             | 13                                 |
| **   | 12.3012.45       | Darkness         | +28.5-+29                   | 11                                 |
| +1   | 12.45— 1.00 "    | Daylight, shade  | +29-+26.5                   | 9                                  |
| ,,   | 1.00 1.15 "      | Sunlight         | + 26.5 - + 27.5             | 5 10                               |
| **   | 1.15— 1.30 "     | Darkness         | + 27.5                      | 3                                  |
| **   | 1.30— 1.45 "     | Daylight, shade  | $+\ 27.5 - +\ 26$           | 5                                  |
| ••   | 1.45 2.00 "      | Sunlight         | +26                         | 1                                  |
|      |                  |                  |                             |                                    |

It must be mentioned that the weather was cold and damp when the animals were captured. The sudden rise in temperature when they were transferred to the indoor conditions will provide an explanation of the high figure for the first 15 minutes of Table 4.

From these experiments it seems as if the light conditions do not affect the disposition towards sound-production appreciably. In the experiment just described I have not been able to keep the temperature constant, on the contrary it has varied within rather wide limits. Therefore it cannot be made out from these figures whether darkness does favour or restrain the soundproduction. To be able to make the temperature more constant I have carried out the following experiment with Streptanus acmulans in a thermostat (the thermostat of Plate 1, fig. 4, but with the microphone of figs. 1 and 2). The microphone without its lid was placed at a distance of 1 decimetre from the electric lamp which was the source of heat in the thermostat (a 40 Watt glow-lamp). The door of the thermostat was closed and the lamp was kept burning for 15 minutes, causing the temperature to rise about 2 degrees centigrade. Then the electric current was switched off, so that darkness prevailed in the thermostat. After 15 minutes the temperature had again fallen to about the original value, and the current was switched on, and so on. The number of calls was counted during the single periods. The experiment was begun on 5 October, 1946, with the same four males as in the preceding experiment plus one more male. The experiment was interrupted at 2.30 p.m. and the cage with the males was kept in a closed pot with damp sand till 7 Oct. at 9 a.m., when the experiment was continued. In the meantime, however, three of the original five males had died. Though the results of the experiments of the two days have been summarized below in the same table (Table 5), the figures should not be judged without consideration being paid to the different number of specimens experimented on.

Table 5. (Streptanus aemulans)

|      |                 |                              | •                           | •                   |          |                            |
|------|-----------------|------------------------------|-----------------------------|---------------------|----------|----------------------------|
| Date | Time            | Light conditions             | Temperature<br>(centigrade) | Number of specimens | (numbe   | production<br>or of calls) |
|      |                 | •                            | •                           | •                   | in light | in darkness                |
| 5/10 | 11.00—11.15 a.m |                              | +29-+26.5                   | 5                   | _        | 2                          |
| "    | 11.1511.30 "    | Light                        | $+\ 26.5 - +\ 30$           |                     | i        | -                          |
| 17   | 11,3011.45      | Darkness                     | + 30 -+ 28                  | **                  |          | 2                          |
| **   | 11.45-12.00 "   | Light                        | +28-+30                     | ••                  | 2        |                            |
| **   | 12.00—12.15 p.m | . Darkness                   | +30-+28                     | ••                  |          | 3                          |
| ,,   | 12.1512.30 "    | Light                        | +28-+30                     |                     | 4        | _                          |
| ,•   | 12.30-12.45 "   | Darkness                     | +30-+28                     |                     | _        | 4                          |
| **   | 12.45 1.00 "    | Light                        | $\pm 28 - + 30$             | **                  | 1        | _                          |
| 17   | 1.00— 1.15 "    | Darkness                     | +30-+28                     | **                  |          | 2                          |
| **   | 1.15 1.30 "     | Light                        | + 28 - + 30                 | **                  | 4        |                            |
| "    | 1.30 1.45       | Darkness                     | +30-+28                     | **                  | ~        | 3                          |
| 11   | 1.45 2.00 "     | Light                        | +28-+30                     | **                  | 5        |                            |
| **   | 2.00 2.15 "     | Darkness                     | +30-+29                     | 51                  |          | 2                          |
| **   | 2.15 2.30 "     | Light                        | +29-+31                     | **                  | 1        |                            |
| 7/10 | 9,00 9,15 a.m.  | . Darkness                   | $+\ 28-+\ 26$               | 2                   | -        | 0                          |
| 11   | 9.15 9.30 "     | Light                        | +26-+30                     | **                  | 0        | <u>—</u>                   |
| **   | 9.30— 9.45 "    | Darkness                     | + 30 - + 28                 | **                  |          | ĺ                          |
| 11   | 9.45-10.00 "    | Light                        | +28-+31                     | **                  | 0        | _                          |
| 11   | 10.00-10.15 "   | <ul> <li>Darkness</li> </ul> | +31-+28                     | ,,                  | _        | 1                          |
| **   | 10.1510.30 "    | Light                        | +28-+30                     | 17                  | 9        |                            |
| 11   | 10.30-10.45 "   | Darkness                     | +30-+28                     | "                   |          | 11                         |
| **   | 10.4511.00 "    | Light                        | + 28+ 31.5                  | ••                  | 3        |                            |
| 17   | 11.00-11.15     | Darkness                     | + 31.5+ 30                  | **                  | •        | 4                          |
| **   | 11.15—11.30     | Light                        | +30-+31.5                   | 11                  | 2        | _                          |
| "    | 11.30—11.45     | Darkness                     | <b>-</b>                    | *1                  |          | 1                          |
| **   | 11.45- 12.00 "  | Light                        | +30-+31.5                   | ,,                  | 1        | _                          |
| 11   | 12.00—12.15 p.m | .,                           | + 31.5+ 30                  | **                  |          | 0                          |
| ,,   | 12.15—12.30     | Light                        | + 30-+ 31.5                 | **                  | 1        |                            |
|      |                 |                              |                             | Total               | 34       | 36                         |

The figures of the above Table dating from the 7 October show a distinct maximum between 10.15 and 10.45 a.m. I believe that this maximum corresponds to an optimum of humidity. As I mentioned, the cage had been kept in a pot with moist sand, i.e. in an atmosphere with a relative humidity of 100 %. The moisture had condensed on the inside of the cage in great drops. A humidity of this magnitude checks the sound-production. The heat in the thermostat had caused the water to evaporate, and during this process the relative humidity must have remained at about 100 %. When all the liquid had evaporated, the humidity would apparently decrease. After the passing of the optimum, too low a humidity has prevailed, and in consequence the sound-production again decreased. Regarding the effect of light, this experiment had apparently the same result as the preceding: no appreciable difference in the sound-production in darkness and in light.

However, an objection might be raised against these experiments, namely that the frequent changes from light to darkness and vice versa imply unnatural conditions. It might be supposed that in natural conditions the ani-

mals are silent during the dark part of the night, for example, either directly in connection with the changes of light, or in relation to the daily rhythm. A condition of silence might be that the animals are undisturbed, so that a state of rest would ensue. The experiments described in Tables 6 and 7 are supposed to preclude this objection. Table 6 represents an experiment with six males of *Erythroneura hyperici* in a cage with *Hypericum perforatum*, the plant being kept fresh by inserting the basal end of the stem in a small tube containing water. The cage was put on the microphone and both were placed in the window.

Table 6. (Erythroneura hyperici)

| Date                | Time                 | Light conditions                      | Temperature<br>(centigrade) | Sound-production (number of calls) |
|---------------------|----------------------|---------------------------------------|-----------------------------|------------------------------------|
| 30/8                | 4.10 4.25 p.m.       | Daylight, cloudy                      |                             |                                    |
|                     | -                    | weather                               | +20                         | 1160                               |
| ,.                  | 7.45 8.00 "          | Almost dark                           | + 19                        | 635                                |
| 17                  | 8.00 8.15 "          | Darkness (lid of the                  |                             |                                    |
|                     |                      | microphone ou)                        | + 19                        | 485                                |
| **                  | 9.00 9.15 "          | Darkness as above                     | + 19                        | 860                                |
| ,,                  | 10.00—10.15          | 11 25 21                              | + 19                        | 1025                               |
| **                  | 11.0011.15           | 11 17                                 | + 19                        | 347                                |
| 30-31/ <sub>8</sub> | 11.15 p.m.—8.42 a.m. | Lid off: first natural darkness, then |                             |                                    |
|                     |                      | daylight                              | + 19                        | Not counted                        |
| \$1/8               | 8.42— 8.57 a.m.      | Daylight, cloudy                      |                             |                                    |
| 7.6                 |                      | weather                               | - - 19                      | 550                                |
| ,,                  | 12.1512.30 "         | Daylight, cloudy                      |                             |                                    |
|                     |                      | weather                               | + 19                        | 605                                |

It seems from this experiment also as if this species does sing during the night as well as during the day.

Table 7 gives the result of a similar experiment with 11 males of Streptanus marginatus captured in Upland, Solna, on 14 June, 1947, at about 12.30 p.m. The animals were kept in a celluloid cage with some leaves of a Festuca sp. The cage was placed on the membrane of the microphone in a south window about one decimetre from the pane. The experiment commenced at 4 p.m., the animals having been left half an hour to accustom themselves to the conditions in the cage. The number of calls during each hour was counted. The thermometer stood on the microphone. In the Table the columns for temperature and light give the conditions prevailing at the beginning of the hour. The lid of the microphone was off during the whole experiment; no artificial light was used.

Apparently this species at this season of the year sings at all times of the day irrespective of the light conditions. It is true that the nights in the middle of June are very light in the latitude of Stockholm, the sun being below the horizon for  $5^{-1}/_2$  hours only. In order to ascertain if absolute darkness made any difference, the lid of the microphone was laid on at 1 p.m. The number of calls was then counted during the hour between 4 and 5 p.m., the animals still being in absolute darkness. The temperature was  $+23.5^{\circ}$  C. During this hour only 15 calls were heard. But the animals in the cage were heard

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Table 7. (Streptanus marginatus)

| Date | Time       | Light conditions                     | Temperature<br>(centigrade) | Sound-production (number of calls) |
|------|------------|--------------------------------------|-----------------------------|------------------------------------|
| 14/6 | 4— 5 p.m.  | Daylight, cloudy weather             | 20                          | 66                                 |
| 1)   | 5— 6 "     | Daylight, sunny weather              | 20.5                        | 63                                 |
| **   | 6— 7 "     | 11 11 11                             | 20.3                        | 74                                 |
| **   | 78"        | 31 25                                | 20                          | 89                                 |
| 11   | 8— 9 "     | Light                                | 20                          | 80                                 |
| **   | 9—10 "     | Dusk beginning                       | 19.8                        | 141                                |
| *1   | 1011       | Nightfall                            | 19                          | 106                                |
| **   | 11-12 "    | Rather dark (partially overcast)     | 19                          | 76                                 |
| 15/6 | 12 1 a.m.  | Rather dark outdoors                 | 19                          | 91                                 |
| **   | 1 2 "      | Dawn                                 | 19                          | 162                                |
| ,,   | 2— 3 "     | Rather light                         | 19                          | 157                                |
| 11   | 3- · 4 "   | Light, sunshine outdoors             | 19                          | 165                                |
| **   | 4 5 "      | 13 99 91                             | 19                          | 178                                |
| **   | 5— 6 "     | 33                                   | 19.5                        | 158                                |
| **   | 6— 7 "     | 11 22 21                             | 19.5                        | 111                                |
| **   | 7— 8 "     | Sunshine but partially overcast      | !                           |                                    |
|      |            | outdoors                             | 19.5                        | 94                                 |
| **   | 8 9 "      | Sunshine outdoors                    | 20                          | 128                                |
| **   | 9-12 "     | _                                    | _                           | Not counted                        |
| **   | 12— 1 p.m. | Weather partially overcast, sunshing | :                           |                                    |
|      |            | now and then                         | 22.5                        | 129                                |

running and leaping very vivaciously. No doubt this has a disturbing effect on the singing. On other occasions I have also found that absolute darkness seems to have a disquieting effect on *Str. marginatus*.

In summing up the above experiments I have to state, then, that I have not been able to establish any appreciable effect of light on the disposition for singing in the species used for experimentation.

#### 2. The influence of temperature

#### a) The effect of temperature on the inclination for singing

In order to ascertain the effect of temperature on the rate of the singing I first made a couple of experiments with Erythroneura hyperici (from Upland, Danderyd). Five males of this species were captured on 1 September, 1946, and put into a cage with a twig of Hypericum. The cage was placed on the membrane of the microphone reproduced in Plate 1, fig. 2, and the lid of the microphone was laid on. Then the microphone was kept in a thermostat at a temperature of  $\pm 3^{\circ}$  C until the following day at 10.30 a.m., when the microphone was taken out of the thermostat and placed in my workroom. The stopper of the lid was replaced by a cork with a thermometer, and the microphone was connected to the amplifier. The microphone was allowed gradually to attain room temperature. When this temperature had been reached (at 12.35 p.m.), the warming up was continued in a thermostat. At 3.03 p.m. the temperature had risen to  $\pm 37^{\circ}$  C, and then the current to the

thermostat was switched off. At 3.28 the door of the thermostat was opened to expedite the cooling down of the microphone. During all this the sound-production was listened to for certain periods (see Table 8). As the lid was kept on during the whole experiment, darkness was complete around the specimens.

Table 8. (Erythroneura hyperici)

| Time             | Temperature<br>(centigrade) | Sound-production (number of calls) |
|------------------|-----------------------------|------------------------------------|
| 10.3010.45 a.m.  | + 9-+ 13                    | 0                                  |
| 10.45-10.50      | + 13-+ 14                   | 70                                 |
| 11,20—11.25      | + 16 -+ 16.5                | 161                                |
| 11.50—11.55      | +17-+17.5                   | 125                                |
| 12.25—12.30 p.m. | + 19 - + 19.5               | 197                                |
| 12.55 1.00 "     | +23-+25                     | 218                                |
| 1.55 2.00 "      | +31+32                      | 328                                |
| 2.50— 2.55 "     | +34-+35                     | 0                                  |
| 3.03— 3.08 "     | + 37                        | 0                                  |
| 3.28— 3.33 "     | + 36                        | Ð                                  |
| 3.33— 3.38 "     | $+\ 36-+\ 35$               | 0                                  |
| 3.38 3.43 "      | $+\ 35-+\ 33.5$             | 0                                  |
| 3.43→ 3.48 "     | +33.5 -+33                  | 0                                  |
| 3.48 - 3.53 "    | + 33-+ 32                   | 3                                  |
| 3.53 3.58 "      | +32-+31                     | 35                                 |
| 3.58— 4.03       | +31-+30.5                   | 0                                  |
| 4.03— 4.08 "     | +30.5 -+30                  | 49                                 |
| 4.08— 4.13 "     | +30+29                      | 35                                 |
| • • • • •        |                             |                                    |

From this experiment it seems as if a temperature optimum would be present at about 30° C.

The above experiment was repeated on 15 Sept., 1946, in exactly the same way. Five males of Erythroncura hyperici were used for the experiment. Since 5 p.m. on the preceding day these had been kept in their cage on the microphone, with the lid on, in a thermostat at a temperature of  $\pm 3^{\circ}$  C. At the beginning of the listening on 15 Sept. at 11.55 a.m. the temperature in the microphone, the lid of which was still on, was  $\pm 8^{\circ}$  C. The microphone was then allowed to be warmed up by the air in the room. From 1 p.m., a temperature of  $\pm 14.5$  degrees C. having been attained, the warming up was continued in a thermostat till 3.15 p.m., when the temperature had risen to  $\pm 38^{\circ}$  C. Then the current to the thermostat was switched off and the door of the latter opened, to allow the microphone to cool down gradually. At 4 p.m., when the temperature had fallen to  $\pm 27^{\circ}$ , the experiment was terminated. In this experiment the sound-production was counted without intermission. The result appears from Table 9.

By comparing Tables 8 and 9 we find that the upper limit of temperature is about the same in both experiments, the lower limit and the optimum being different. However, it should be noted that in these experiments the humidity has not been made constant. The humidity is probably of considerable importance in this connection. It is possible that the humidity has not been the same in the two experiments. Further, the relative humidity is probably different in the rising and the falling part of the temperature curve.

Table 9. (Erythroneura hyperici)

| Time                  | Temperature<br>(centigrade) | Sound-production (number of calls) |
|-----------------------|-----------------------------|------------------------------------|
| 11.55 a.m.—12.15 p.m. | + 8 - + 10.5                | 0                                  |
| 12.15—12.30 p.m.      | + 10.5 - + 12               | 0                                  |
| 12.30-12.45 "         | $+\ 12-+\ 13.5$             | 0                                  |
| 12.45 1.00 "          | + 13.5 - + 14.5             | 0                                  |
| 1.00— 1.15 "          | $+\ 14.5 - +\ 16$           | 1                                  |
| 1.15 1.30 "           | + 16 - + 18                 | 249                                |
| 1.30→ 1.45 "          | + 18 - + 20                 | 12                                 |
| 1.45 - 2.00           | +20-+22                     | 0                                  |
| 2.00— 2.15 "          | +22-+26                     | 502                                |
| 2.15— 2.30 "          | +26-+29                     | 110                                |
| 2.30 2.45 "           | + 29 - + 32                 | 45                                 |
| 2.45 - 3.00 "         | +32-+35                     | 52                                 |
| 3.00 3.15 "           | + 35 - + 38                 | 0                                  |
| 3.15 3.30 "           | +38-+34                     | 0                                  |
| 3.30→ 3.45 "          | +34-+30                     | 77                                 |
| 3.45 4.00 "           | + 30-+ 27                   | 331                                |

Regarding Erythroneura hyperici, we must further remember that this species has a strong inclination for anaphonous singing. If one individual begins to sing, one or several of the others present as a rule strike up, too. Long periods of incessant singing alternate with pauses in which no one sings. The greater the number of males together, the rarer are these pauses. If they nevertheless occur, the numerical contrast between them and the singing periods will of course be greater if many specimens are together. Therefore, for instance, the pause in the sound-production present between  $18^{\circ}$  and  $22^{\circ}$  in Table 9 has probably nothing to do with the effect of the temperature. The singing stopped by mere chance, and then a while passed before any male felt inclined to take it up again.

As a result of these two experiments we may conclude that the sound-production is rather dependent on the temperature. The interval of temperature within which singing is performed is, however, rather long and stretches, in so far as conclusions may be drawn from these experiments, for E, hyperici from  $\pm 13^{\circ}$  to  $\pm 35^{\circ}$  C in darkness and in the presence of fresh parts of the host plant. These limits of temperature are not identical with the limits of the general zone of effective temperature of the species, as the animals could be heard running about in the cage at temperatures outside both these limits.

In the following two experiments males of Streptanus aemulans (from Solna) were used. The first experiment was made on 6 Sept., 1946, with three males who had been imprisoned since 1 p.m. of the preceding day on the membrane of the microphone under its lid, in darkness, then, and at room temperature. As the experiment was commenced at 12.25 p.m. the temperature was  $\pm$  19° C: it was allowed to rise gradually in a thermostat. At 3.30, the temperature having risen to  $\pm$  39°, the current to the thermostat was switched off and the door was opened. At 4.15 p.m. the temperature had fallen to  $\pm$  29° and the experiment was terminated. The result may be seen in Table 10.

Table 10. (Streptanus aemulans)

| Table 101 (Strepters        |                             |                                       |  |  |  |  |
|-----------------------------|-----------------------------|---------------------------------------|--|--|--|--|
| Time                        | Temperature<br>(centigrade) | Sound-production<br>(number of calls) |  |  |  |  |
| 12.45—1.00 p.m.             | + 19                        | 0                                     |  |  |  |  |
|                             | + 19                        | 0                                     |  |  |  |  |
| 1.00— 1.15—"<br>1.15—1.30—" | + 19+ 22                    | 3                                     |  |  |  |  |
| 1.39 1.45                   | + 22 - + 26                 | 12                                    |  |  |  |  |
| 1.452.00                    | +26-+29                     | 13                                    |  |  |  |  |
| 2.00—2.15                   | +29-+32.5                   | 10                                    |  |  |  |  |
| 2.15-2.30 "                 | +32.5-+35                   | 6                                     |  |  |  |  |
|                             | + 35+ 36.5                  | 6                                     |  |  |  |  |
| 2.302.45 "                  | +36.5-+37.5                 | 2                                     |  |  |  |  |
| 2.45—3.00 "<br>3.00—3.15 "  | +37.5-+38.5                 | 3                                     |  |  |  |  |
| 3.15—3.30                   | +38.5-+39                   | 1                                     |  |  |  |  |
|                             | + 39—+ 36                   | 0                                     |  |  |  |  |
| 3.30— 3.45 "                | + 36—+ 32.5                 | 0                                     |  |  |  |  |
| 3.45—4.00 "<br>4.00—4.15 "  | + 32.5—+ 29                 | 1                                     |  |  |  |  |
|                             |                             |                                       |  |  |  |  |

Another experiment with Str. aemulans was made in the same way as those described in Tables 8 and 9 with Erythroneura hyperici. The experiment was performed on 13 Sept., 1946, with two males who had been kept in darkness under the lid of the microphone in a thermostat at a temperature of  $\pm 3^{\circ}$ . When the listening commenced at 9.45 a.m., the temperature in the microphone, the lid of which was kept on during the experiment, was  $\pm 8^{\circ}$  C. The current was switched on to the other thermostat and the door of the latter was closed at 10.45 a.m. The current was switched off at 12.30 p.m., and the door of the thermostat was opened a quarter of an hour later. The experiment was terminated when the temperature had fallen to  $\pm 26^{\circ}$  C. Result in the following Table.

Table 11. (Streptanus aemulans)

| I III/IC I X     | (Local Province             |                                       |
|------------------|-----------------------------|---------------------------------------|
| Time             | Temperature<br>(centigrade) | Sound-production<br>(number of calls) |
| 9.45—10.00 a.m.  | + 8-+ 11                    | 0                                     |
| 10.00—10.15      | + 11— $+$ 13.5              | 0                                     |
| 10.15—10.30      | + 13.5 + 15                 | 1                                     |
| 10.30-10.45      | + 15                        | 0                                     |
| 10.45—11.00      | + 15.5 -+ 19                | 0                                     |
| 11.00-11.15      | + 19 - + 23                 | 1                                     |
| 11.15—11.30      | + 23+-27                    | 2                                     |
| - 11.30—11.45    | +27-+30                     | 6                                     |
| 11.45-12.00      | + 30 -+ 34                  | 10                                    |
| 12.00-12.15 p.m. | +34+36                      | 5                                     |
| 12.15—12.30      | +36-+38.5                   | 0                                     |
| 12.30—12.45      | + 38.5                      | 0                                     |
| 12.45 1.00 "     | +38.5-+35.5                 | 0                                     |
| 1.00 1.15        | +35.5 -+33                  | 2                                     |
| 1.15=- 1.30 "    | + 33 -+ 31                  | 2                                     |
| 1.30 1.45        | +31-+29                     | 0                                     |
| 1.45 2.00 "      | +29-+27.5                   | 1                                     |
| 2.00 2.15        | +27.5-+27                   | 1                                     |
| 2.15 2.30 "      | + 27 - + 26                 | 0                                     |
|                  |                             |                                       |

In a third experiment made on 10 Sept. with two males of the same species in exactly the same way as that in Table 11 only 7 calls were emitted. The experiment lasted from 9 a.m. to 1.45 p.m., the temperature rising from  $+8^{\circ}$  C to  $+39^{\circ}$  and then falling to  $+27^{\circ}$ . The first call came between  $+19^{\circ}$  and  $+23^{\circ}$ , the second between  $+31.5^{\circ}$  and  $+33.5^{\circ}$ , no fewer than four between  $+33.5^{\circ}$  and  $+35^{\circ}$ , and the last between  $+36.5^{\circ}$  and  $+38^{\circ}$ . In the falling part of the temperature curve no calls were emitted. In a fourth similar experiment on 6 Sept. with two males of Str. aemulans, in all 5 calls were heard, all between  $+31^{\circ}$  and  $+38.5^{\circ}$  in the rising part of the temperature curve, a small maximum with two calls lying between  $+35^{\circ}$  and  $+36.5^{\circ}$ .

Anaphonous singing is not appreciable in this species. It seems as if the limits of the temperature zone of sound-production as well as the temperature optimum are somewhat higher than in *Erythroneura hyperici*.

Apparently the above experiments show that the temperature conditions are very important for the quantity of singing. The common song is emitted only within a certain temperature interval that is probably different in the various species, and there is a certain temperature optimum, when the inclination for singing is strongest. To what extent this optimum may be displaced by the influence of other factors, such as humidity, light, etc., has not yet been established.

# b) The effect of temperature on the tone frequency

According to Fulton (1932), the pitch of the calls of certain Orthoptera varies with the temperature. The same is the case with the wing-stroke frequency of Diptera and possibly Lepidoptera but not with that of Hymenoptera and Colcoptera (Sotavalta 1947). I have studied the influence of temperature on the pitch of the song of Doratura stylata of. This species was selected because it has a monotonous voiced call, the pitch of which is relatively easy to determine by listening and comparison with a tuning-fork (a1), and because material is easily acquired. The experiments have been made partly by listening and comparison with the tuning-fork, partly by sound-film recording.

1. Experiments with acoustic determination of pitch. These have been performed in the following way. A microphone (the magnetic microphone mentioned in the introduction, page 9) was kept in a cylinder of thick glass plugged at both ends with cotton-wool inside a thermostat (Plate 1, fig. 4). On the membrane of the microphone was the cage with the Doratura male (only one specimen was used in each experiment), and on the edge of the microphone the thermometer was placed. At the beginning of each experiment room temperature prevailed. After the door of the thermostat had been closed, the current was switched on. The source of heat in this thermostat was two electric bulbs, one of 60 and the other of 38 watts. When a more gradual rise in temperature was desired, only one of these lamps was kept burning. The microphone was connected to the amplifier, which was placed outside the thermostat, and the amplifier was connected to the gramophone input terminals of a radio receiver with a loud speaker. By this arrangement the calls emitted were heard with about the same loudness as the voice of a person in the same room, if not too loud-voiced, and were therefore easily studied. At each call emitted the pitch was determined, the time noted and the temperature in the glass cylinder read off. For this purpose it was necessary to open the door of the thermostat, but owing to the glass cylinder too great losses of heat were avoided. In each experiment a fresh specimen of the leaf-hopper was used. It must be noted that the *Doratura* male (as mentioned before) has two different tooting calls: one consisting of a long and a short note: "toooooor-to", and one recalling the song of invitation of the female (see page 81). The pitch of the latter is usually somewhat lower than that of the former. For this reason only the "toooooor-to" call has been studied. Four different experiments are described in Table 12.

Table 12. (Doratura stylata)

| I     | experimen            |       |      | 2        |       |      | 3<br>25., |             |      | 4                  |       |
|-------|----------------------|-------|------|----------|-------|------|-----------|-------------|------|--------------------|-------|
| Time  | Date "/s 1!<br>Temp. | Pitch | Time | Тешр.    | Pitch | Time | Temp.     | Pitch       | Time | Temp.              | Pitch |
|       | •                    |       | 2.06 | +23.5    | A     |      |           |             |      |                    |       |
| 9.51  | + 25                 | Λ #   | 2.10 | + 25     | Λ #   | 1.23 | +25       | $\Lambda =$ |      |                    |       |
| 9.56  | + 26.5               | В     | 2.14 | + 26.5   | В     | 1.30 | + 26      | В           |      |                    |       |
| 10.06 | + 28.5               | c     | 2.19 | +27.5    | В     | 1.40 | 4- 28     | c           |      |                    |       |
| 10.00 | + 31                 | đ     | 2.24 | $\pm 28$ | C.    | 2.03 | + 31      | d           |      |                    |       |
| 10.24 | 1 77.2               |       | 2.35 | + 30     | d     | 2.20 | + 33      | e           | 1.35 | - <del> -</del> 33 | e     |
|       |                      |       | 2.48 | $\pm 32$ | d #   | 2.40 | + 35.5    | f           | 1.45 | +34.5              | e +-  |
|       |                      |       | 3.02 | + 34     | f.    |      |           |             | 2.03 | + 37               | f     |
|       |                      |       | 3.14 | + 35     | e +   |      |           |             | 2.27 | + 39               | í#    |
|       |                      |       | 3.32 | +37      | ſ     |      |           |             | 2.35 | +40                | g     |
|       |                      |       | 3.58 | +40      | g     |      |           |             |      |                    |       |

Of course these determinations of pitch are only approximate. For this reason I have refrained from giving the tone frequency in figures. However, it is very evident from these experiments that the pitch rises with the temperature within a certain interval.

2. Experiments with sound-film recording. A sound-film recording of the tooting calls of Doratura stylata of at a rising temperature was made on 28 Sept., 1947, in collaboration with Mr. L. Hamberg, engineer, in Stockholm. Unfortunately the projected experimental arrangements proved useless and had to be replaced by improvised devices. One consequence of this was that the temperature in the cage with the leaf-hopper could not be read off exactly. The arrangements used were the following. In the vibration isolating box reproduced on Plate 1, fig. 3, we kept a Western-Electric microphone, the upper grating of which had been unscrewed, so that the cage with the animal could be placed closer to the membrane. The microphone and the cage were well embedded in cotton on all sides except that directed towards the glass lid of the box. Between the cage and the glass lid a short thermometer was placed. The warming up of the interior of the box was effected by the sun being allowed to shine through the lid. As the sun then shone directly on the bulb of the thermometer it cannot be asserted that the latter showed the temperature prevailing in the cage. Probably the microphone and the cage were warmed up much more slowly than the thermometer. Sound-filming was then performed for about 6 minutes with short pauses now and then. During this time the temperature of the thermometer rose from  $\pm 25^{\circ}$  C to + 41° C. When the film had been developed it was established that the tone

frequency of the "toooooor-to" call had risen from 121.3 c.p.s. at the beginning of the experiment to 153.4 c.p.s. at its end (see Plate 12, figs. 1—3).

The lowest frequency registered in this experiment, 121.3 c.p.s., corresponding to the initial temperature, represents approximately the pitch of B ( $a^4=435$  c.p.s.). In Table 12 this corresponds to a temperature of about 26.5° C. This is in tolerable agreement with the facts. At the end of the experiment the frequency of the calls was 153.4 (d#), in Table 12 corresponding to a temperature of about 32° C. The thermometer in the box showed at this point of time 41° C but, as I mentioned above, the temperature in the cage was probably lower. Owing to the technical defects in this experiment it cannot be made the basis of too far-reaching conclusions, but it will at least support the results of the experiments described in Table 12.

As the experiment described above was not quite satisfactory, I did it over again, in July, 1948, in collaboration with Mr. WALDERSTEN. The arrangements were about the same as those in the above experiment, but a larger vibration isolating box was used. The cage with the *Doratura* male and the bulb of the thermometer were placed close to each other and the membrane of the microphone. This time the microphone etc. were not kept embedded in cotton. The warming up of the interior of the box was effected as in the 1947 experiment, but the cage and the bulb of the thermometer were kept in the shade. The recording took about an hour with occasional short pauses. From time to time the temperature was spoken into the film by an extra microphone. The figures below give the frequencies of the calls (the longer notes of the "toooooor-to" calls) in chronological order, the temperatures (in degrees C) read off being given in italics:

29°, 147, 148, 148, 147, 152, 147, 148, 146, 148, 147, 29.5°, 151, 150, 152, 152, 150, 30°, 151, 150, 151, 153, 153, 153, 154, 154, (Pause.) 32°, 153, 156, 155, 156, 153, 153, 156, 154, 155, 157, 161. (Pause.) 33°, 165, 166, 166, 167, 167, 164, 165, 33.5°, 166, 168, 167, 166, 171, 171, 168, near 34°, 170. (Pause.) 36.5, 179, 180, 173, 179, 178, 178, 180, 180, 178, 178, 175, 178, 179, 179, 177, 178, 176, 177, 174, 177, 179, 179, 179, 180, 181, 181, 176, 180, 178, 180, 176, 36.5°, 182, 180, 180, 183, 37°, 176, 176, 177, 175. (Pause.) 38.5°, 186, 186, 184, 185, 184, 186, 39°, (Pause.) 39.5, 192, 197, 198, 196, 197, 39.7°, 193, 194, 195, 39.9°, 197, 198, 40°, 192, 199, 197, 199, 198, 199, 194, 197, 40.5°, 199, 201, 200, 194, 40.6°, 202, 203, 203, 203, 41°, 198, 195, 200, 41.3°, 198, 200, 199.

The pitch of the call rose, then, from  $d+at+29^{\circ}$  C to not quite gis at  $+40.6^{\circ}$  C. The differences, if compared with Table 12, are no doubt due to individual variation.

I believe, then, that I have shown that the pitch of the call of *Doratura sty-lata*  $\circlearrowleft$  rises with the temperature within the temperature interval of these experiments. In Chapter 4, page 112, certain consequences of this for an understanding of the function of the sound-producing organ have been discussed.

#### 3. The significance of the season

Many of our *Auchenorrhyncha* hibernate in this country in the adult stage. I have tried to ascertain whether these species are inclined to emit their calls even during the cold season of the year, if the temperature is made suitable.

<sup>&</sup>lt;sup>1</sup> Microphone: Super-cardioid Unidyne (Shure Brothers, Chicago).

On 22 March, 1946, I collected from spruces in Solna (Upland) a few specimens  $(\bigcirc \bigcirc \bigcirc)$  of *Empoasca flavescens, Erythroneura tiliae* and *Balclutha punctata*, but my endeavours to hear any sound-production from these specimens during that and the following day were resultless. (It should be observed that I have not heard any sound-production from the two first-mentioned species in summer either.) The experiment was repeated on 30 March with fresh specimens of *Empoasca* and *Balclutha*. On this day nothing was heard from them, but on the following one between 3 and 4 p.m. I heard single rolls now and then from the *Balclutha* specimens (1  $\bigcirc$  and 3  $\bigcirc$  in the same tube).

On 30 March I found one male of Stenocranus minutus. About half an hour after catching the animal, it having been kept in room temperature on a twig of spruce, it emitted a low-frequent chattering call lasting for a few seconds. The time was 1.55 p.m. The male died on the following day.

In the middle of March, 1946, the covering of snow was still thick in this part of Sweden, but at the end of the month it had almost entirely melted away.

#### B. The effect of attacks of parasites

It is self-evident that specimens attacked by parasites (pipunculids, dryinids or strepsipters) are more or less affected by this attack. It has often been pointed out that the attack causes more or less distinct reductions in the genital parts of the host. In this connection I will content myself by referring to the papers of LINDBERG (1939, 1946) on these matters in Finnish Chloriona species.

The sound-producing organ is also affected by an attack of parasites. Such an attack often causes very strong reductions of this organ. Lindberg (II. cc.) has observed that the shield-shaped medial plate on the second abdominal tergum ("Tergitschild") characteristic for Chloriona and other araeopids is strongly reduced or entirely absent in specimens attacked by Elenchinus and Pipunculus. Above I have described this plate (in Dicranotropis and others) as the posterior attachment of muscle I a dlm<sub>1</sub>, which, as we have seen, belongs to the sound-producing organ. GIARD (1889) stated that the apodemes of the second abdominal sternum (first abdominal sternum according to this author) were reduced in males of Typhlocyba parasitized by Ateleneura and Aphelopus.

I have not made any investigations on the reduction of the tymbal apparatus by the attack of parasites. But I have often been able to observe incidentally the results of such attacks, especially those of pipunculids. Many of my listening endeavours have been resultless because I did not in time discover that my observation material was parasitized. In certain species the percentage of parasitization is sometimes so high that fixed material for dissection at first thought satisfactory proved upon closer study to be quite inadequate. In 1946, I found a very high percentage of parasitization in my fixed material of *Idiocerus populi*. The unknown parasites had, however, apparently left their hosts in an earlier stage without killing them. The inner organs of the abdomen had apparently been consumed for the most part, the abdomen being shrunk and slack. The black pigment was more weakly developed than in normal individuals, and the normally

bright orange surfaces on the face were pale. The phragma of the third tergum was rather constantly reduced to half its width, the muscles and other parts in a corresponding degree. These reductions were so constant in the different individuals that I at first believed that these specimens represented a distinct species. Apparently owing to the high percentage of this kind of parasitization in this species I did not succeed in hearing any sound-production from it until 1947. Jassus lanio is also very often parasitized in exactly the same way, and from such specimens I have not heard any sound-production.

However, the influence of the parasite is not always sufficient to prevent sound-production. This is apparent from the following observation. From a male of Streptanus aemulans I heard on 21 Sept., 1947, a quite normal song of the kind described on page 89. As the abdomen of the specimen was suspiciously swollen, the animal was killed and dissected, it then being revealed that the major part of the abdomen was occupied by a large pipunculid. Nevertheless the sound-producing organ was not appreciably reduced. Other males parasitized in this way have always proved mute. A reduction of the sound-producing organ such as that described above in Idiocerus is probably due to an attack of parasites in an early stage of the host's development. At later attacks, the parasite larva not having grown too large when the host reaches the adult stage, the organs of the latter may possibly still be tolerably normal and are not devoured by the parasite until later.

# C. The biological significance of the sound-production

FABER (1929, 1933, 1936) has systematized the calls of German Orthoptera from biological aspects. With certain modifications his division may be applied to the calls of the Auchenorrhyncha, too. Thus I believe that I have been able to distinguish the following principal biological types of calls: 1) the "common song" ("Gewöhnlicher Gesang" FABER); "call of courtship" ("Werbegesang"); 3) "call of invitation" of the female; 4) "calls of pairing"; 5) "calls of rivalry" ("Rivalenlaute"); 6) "calls of distress". Not all calls could be fitted into these groups, and a number of calls I have not been able to study sufficiently to be able to classify them from a biological point of view.

#### 1. The "common song" (♂)

In most species I have heard calls that may be assigned to this group, but only from the males. In many species, for example Agallia brachyptera, several well developed calls belong to this group. Most complicated, characteristic songs must be placed in it. According to the definition of FABER, these calls are emitted independent of the presence of other individuals of either sex. Their biological significance is, therefore, obscure. The song of other males may, however, stimulate the inclination for singing and lead to an answering of the former (anaphony). In Erythroneura hyperici sometimes a tolerably regular alternation, sometimes a poecilochronous singing is performed. The latter is often the case if more than two males are together. In Idiocerus laminatus I have heard a quite regular alternation (see Plate 13, fig. 23). In other species of Idiocerus, poecilochronous singing is more common. Although the species of Idiocerus use their common song for anapho-

nous singing, the latter often leads to one of the singers losing his temper and trying to push the other away. On the other hand, Erythroneura hyperici may continue anaphonous singing for hours, but I have never observed any fuss. In Calligypona clypealis I once heard a poecilochronous singing. Synchronous (or perhaps sooner a prolonged poecilochronous) singing occurs in Criomorphus bicarinatus, but the call in question borders on the "call of rivalry". Lepyronia coleoptrata reacts anaphonously by a specific call in complete alternation.

Sometimes it may be difficult to make out whether a call should be assigned to this or some other group. Paropia of uses the same call as "common song" and as "call of courtship"; in the latter case the male emits his little time over and over again in unbroken succession and accompanies it with a sort of dance. It is also uncertain whether the "toooooor-to" call of Doratura stulata should be placed here. This call is emitted whether other individuals are present or not. But if a female inclined for pairing is present, she immediately answers the call of the male by her "call of invitation", the male accompanies her by his "call of courtship", and the performance leads in due time to pairing (see pages 81-82). The "toooooor-to" call apparently seryes as a call of sexual enticement. In Chapter 5 (p. 118) I have expressed the opinion that Doratura by having a sound-producing organ equally well developed in both sexes represents a primary condition. If this theory is applied to the calls too, an explanation of the origin of the "common song" would be conceivable. If the external conditions are good, a Doratura male now and then emits his "toooooor-to" call. Even if several females are present, the most common course is perhaps for no one to answer, as no female present is inclined for pairing. Then the human listener will find the call of the male meaningless. If, on the other hand, a female inclined for pairing is present she will answer, and the prelude to copulation is in full swing. In most other species, however, the female has lost the capacity of answering by a call. Perhaps the male has now other means of finding her, or the female has taken over the searching rôle. Nevertheless the call of the male may have kept its original purpose as an enticing call in general.

#### 2. "Call of courtship" (3)

This is a call apparently intended to prepare the female for attempts at copulation on the part of the male or to make her more inclined for pairing. In *Paropia* and *Eupelix* this call is accompanied by a characteristic "dance" and is emitted in immediate conjunction with the attempts at copulation. In *Doratura* it accompanies the "call of invitation" of the female but ceases (always?) a short time before the beginning of the sexual act. This kind of call I have heard from these three species only.

#### 3. "Call of invitation" (♀)

Only from *Doratura stylata*  $\mathcal{Q}$  have I heard this kind of call apparently emitted in order to lead the male to the female or to inform him that she is willing to copulate.

#### 4. "Call of pairing"

These calls are emitted during the act of copulation. I have heard them only from *Philaenus spumarius* and *Neophilaenus lineatus*, whether from the male or the female I could not tell.

#### 5. "Calls of rivalry" (o)

Only from Achorotile albosignata have I heard a call that I am able to assign to this group with any certainty. Compare further Criomorphus bicarinatus and the species of Idiocerus.

# 6. "Calls of distress"

Calls of distress or dissatisfaction ("complaint cry" BAIER) I have heard from Aphrophora alni  $(\circlearrowleft \circlearrowleft)$ , A. forneri  $(\circlearrowleft \circlearrowleft)$ , Lepyronia  $(\circlearrowleft \circlearrowleft)$ , Eupelix  $(\circlearrowleft)$ , Paropia  $(\circlearrowleft)$ , Ulopa  $(\circlearrowleft \circlearrowleft)$ , Oncopsis flavicollis  $(\circlearrowleft \circlearrowleft)$ , O. alni  $(\circlearrowleft \circlearrowleft)$ , Macropsis tiliae  $(\circlearrowleft)$ , M. haupti  $(\circlearrowleft)$ , M. fuscinervis  $(\circlearrowleft)$ , Idiocerus elegans  $(\circlearrowleft)$ , Jassus lanio  $(\circlearrowleft)$ , and Aphrodes bifasciatus  $(\circlearrowleft \circlearrowleft)$ . No representative of the Fulgoromorpha or of the Typhlocybidae has been heard to emit a sound-production of this sort. These calls are of a simple kind and are apparently emitted when the animals feel themselves in trouble of some kind, for example when they try to escape from their confinement. Not all the above species, however, will emit this call if they are held fast. Here belong the "cries of agony" heard by several authors from cicadas attacked by birds or wasps or seized by a human hand. In the male Eupelix this call is similar to the call of courtship, only more irregular. I refrain from theorizing about the significance of these calls. As they are so weak (in our species), they will hardly scare any enemy.

#### 7. Other calls

In Empoasca viridula of there occurs a laughing call emitted when the male has just finished a flying-trip. This call apparently corresponds to what Faber (1932, p. 54) described in Stauroderus morio.

Certain other calls I have not been able to study sufficiently to place them in any biological group. This is the case, for example, with the laughing call emitted by both sexes of *Platymetopius guttatus*, which is the only call I have heard from this species.

# D. Do the Auchenorrhyncha hear?

The problem of whether the cicadas can hear has long been the subject of discussion. The statement of Solier (1837) that a cicada may be induced to approach by a whistling imitation of its call is well-known. Myers (1929) cites from the literature a number of similar cases as well as examples of female cicadas seen seeking out the singing male. On the other hand, the famous experiment of Fabre (1897) with the salute cannons he had fired without this causing cicadas singing in the vicinity to interrupt their singing even for an instant, is much quoted. Like Lutz (1924) I do not find this experiment particularly conclusive. The sound-perceptive organ of the cicadas is probably adjusted to a limited tone interval corresponding to their own calls. Possibly the perception of these calls will even by reflex action result in a certain manner of reaction. On the other hand, the cicadas have a well developed faculty of vision usually sufficient to warn them against most possible dangers. Why then burden the organ of hearing with the task of

collecting a multitude of sound impressions which the insect at all events is not capable of interpreting? Since Vogel (1922, 1923) revealed that the long familiar so-called "mirror" thought to be part of the sound-producing organ is in reality a constituent of a well developed tympanal organ, most scientists will admit the probability that the cicadas at all events are capable of some kind of sound-perception.

I have examined microtome sections of Graphocraerus and some other species very thoroughly, but in spite of this I have not found any organ similar to the tympanal organ of the cicadas, nor any other organ I would interpret as a sound-perceptive organ. In Philaenus spumarius there is a Johnston's organ in the second antennal joint; it is very similar to that of Sigara (EGGERS 1928, p. 125, Fig. 63). EGGERS holds the view that this organ in most cases is an instrument for the registering of antennal movements.

The question of the hearing of insects has been much discussed. This discussion has been made more complicated by many workers having felt obliged to separate a perception of air-born vibrations by a specific auditory sense from a perception of the vibrations by the tactile sense. This presentation of the problem will, in my opinion, very easily turn into a battle of words. Even in insects with a well developed tympanal organ apparently specially constructed for the interception of vibrations of the air, we shall of course never be able to gain a real conception of how the animal subjectively apprehends these. It is necessary to avoid anthropomorphistic ideas in this connection!

If hearing is defined as a perception by an organ constructed for the interception of air vibrations, the problem has been simplified in some degree, but this definition is not theoretically satisfactory. We apprehend as sound also vibrations conducted by fluid and solid bodies. When we speak about our own hearing, the medium is apparently a secondary matter in comparison with our specific way of apprehending certain mechanical phenomena as "sounds". On the other hand, insects, with their rigid exoskeleton that might have been constructed for the sole purpose of resonance for vibrations of the air, might very likely be able to apprehend these without any specific organ at all.

After a study of the tympanal organ of the large cicadas, most entomophysiologists will probably admit that this organ must be adapted for the interception of sound-waves and will then classify it as an auditory organ. The calls of cicadas, as we know, are often very penetrating and audible to the human ear at a distance of many yards. The calls of our small Auchenorrhyncha, on the other hand, are very low-voiced. If the air-vibrations produced by these small insects are to be apprehended at a distance greater than a few centimetres, a very sensitive auditory organ will be necessary. I believe that the vibrations produced by the tymbal organ of one specimen are conducted to other individuals mainly by the solid substratum — as a rule some part of a plant — and only in a less degree by the air. If it could be established that the animals do in this way apprehend the calls of each other as such — is this to be termed hearing or not? A matter of taste!

Do the Auchenorrhyncha then apprehend and recognize the calls of their equals? In some cases this is so obvious that there is no reasonable cause for doubt. I refer to the above-described observations on anaphonous singing in

Idiocerus laminatus (p. 69) and Lepyronia (p. 66), and on the pairing preludes of Doratura (p. 81—82). Theoretically the objection may of course be made that I have not taken measures in my experiments to avoid the possibility of the animals seeing the vibrating movements of the abdomens of their singing comrades and reacting to that. Especially in Doratura, however, these movements are so small that I find this assumption very far-fetched.

#### Summary

- 1. I have examined material fixed in alcohol of 79 Swedish species of Auchenorrhyncha, in all over 900 specimens, and stained microtome sections of some species. All Swedish families except Achilidae, Issidae, Membracidae, Cicadidae, Jassidae (= Bythoscopidae) and Errhomenellidae are represented.
- 2. In all males thus examined I have found an organ apparently in its essential parts homologous with the tymbal apparatus of the *Cicadidae* even if it is certainly much modified in some groups.
- 3. In Centrotus (Membracidae) and Ommatidiotus (Issidae) I have examined dried material and found structures indicating that a sound-producing organ of the same kind is present also in these forms.
- 4. My endeavours to hear the calls of our small Auchenorrhyncha have in most cases been successful. Hitherto I have heard a sound-production of some kind from 96 species (among these Jassus lanio (L.) (family Jassidae)). From most of these I have heard several different kinds of calls. Only in a few cases have I failed to hear any sound-production from a species. I believe that these failures were due to unsuitable experimental conditions.
- 5. On the basis of these results I feel convinced that the possession of a functional tymbal apparatus is general among the Auchenorrhyncha.
- 6. In all forms where muscle I a  $dvn_{t_1}$  is well developed, the manner of function of the tymbal apparatus is essentially the same as in the Cicadidae: elastic parts of the lateral integument in the first (in some cases probably also the second) abdominal tergum are set in vibration by this muscle. In other cases other muscles seem to have taken over the function of I a  $dvn_1$ ; sometimes however the function is more obscure.
- 7. In some cases I have observed that the lateral parts of the first abdominal tergum are dinted in and out in connection with the sound-production. Single clacking sounds are often produced in this way. More prolonged drumming calls are produced by the rapid succession of such clackings, in some cases also by low-frequent muscle contractions with a smaller amplitude. Then the pitch of the calls will depend on the qualities of the vibrating membrane, the tone frequency being identical with the specific vibration frequency of the membrane. In other cases, however, the frequency of the muscle contractions is higher and identical with the tone frequency of the main tone of the call produced.
- 8. In cercopids and some jassoid forms the female possesses a functional sound-producing organ of the same kind as that of the male though more weakly developed. In *Paropia* the female has a functional tymbal apparatus more primitive in structure than that of the male. In *Doratura* both sexes

have a sound-producing organ of the same type and equally well developed. I believe that this is the primary condition.

- 9. Anaphonous singing occurs in many species. The female of *Doratura* stylata has a call with a sexual significance.
- 10. I have not been able to find any appreciable effect of different light conditions on the rate of the sound-production. The temperature is of greater importance in this respect. In *Doratura* the pitch of certain calls rises with the temperature within a certain temperature interval.

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# Explanation of the Plates

Plate 1. Some of the apparatus used. Fig. 1: the crystal microphone, lid on; Fig. 2: same without lid, a celluloid cage on the membrane; Fig. 3: same in the vibration isolating box; Fig. 4: magnetic microphone in glass cylinder inside thermostat; Fig. 5: amplifier with crystal microphone and ear-phones; Fig. 6: the radiograph.

Plate 2. Fig. 1: Dicranotropis hamata  $\sigma^2$ , metapostnotum and dorsum of first three abdominal segments from above (I, II, III = first, second, third abdominal terga; other denominations, see text); Fig. 2: same species, integument and endoskeleton in the region of the sound-producing organ, right half seen from the inside (II ast = second abdominal sternum); Fig. 3: same as in Fig. 2 but with musculature; Fig. 4: same, transverse section showing the first two abdominal segments from the front, musculature reproduced only in the left half of the drawing (right half of the animal). Scienotized surfaces dotted.

Plate 3. Fig. 1: Diemnotropis hamata  $\mathcal{O}$ , metapostnotum and metepimeron from behind and below; Fig. 2: Diemnotropis hamata  $\mathcal{O}$ , left half of dorsum of the first three abdominal segments and hind border of metanotum from above; Fig. 3: Neophilaenus campestris  $\mathcal{O}$ , first three abdominal sterna from above; Fig. 4: same species, right half of hind part of metathorax and abdominal basis from the inside; Fig. 5: same as in Fig. 4 with muscles; Fig. 6: same species, right half of first abdominal segment in transverse section, seen from the front, soft parts except muscles removed; Fig. 7: Aphrophora alni  $\mathcal{O}$ , left part of first abdominal tergum with the striated tymbal (tb), from above.

Plate 4. Fig. 1: Centrotus cornutus  $\mathcal{O}$ , transverse section in front of first abdominal segment seen from the front, soft parts removed, showing first abdominal sternum with apodemes (I a apod), tergal details not reproduced; Fig. 2: same as in the preceding figure, first abdominal sternum removed, showing second abdominal sternum with apodemes (II a apod); Fig. 3: Euacanthus interruptus  $\mathcal{O}$ , right half of integument of first three abdominal segments and hind part of metathorax from inside; Fig. 4: same species,  $\mathcal{O}$ , dorsum of first two abdominal segments and hind part of metathorax from above (settles metascutellum); Fig. 5: same species,  $\mathcal{O}$ , sterna of first three abdominal segments from above; Fig. 6: same as in Fig. 3 but with muscles; Fig. 7: right half of abdomen seen from the front with muscles of first abdominal segment, other soft parts removed.

Plate 5. Fig. 1: Tettigella viridis,  $\mathcal{O}$ , dorsum of first three abdominal segments and hind border of metanotum from above; Fig. 2: same species,  $\mathcal{O}$ , first three abdominal sterna from above; Fig. 3: same species,  $\mathcal{O}$ , integument and endoskeleton of right half of hind part of metathorux and first three abdominal segments, from inside; Fig. 4: same region with muscles; Fig. 5: same species,  $\mathcal{O}$ , striated tymbal more magnified, tend = tendon; Fig. 6: Eupelix depressa, f. cuspidata,  $\mathcal{O}$ , first two abdominal sterna from above; Fig. 7: same species,  $\mathcal{Q}$ , first two abdominal sterna from above; Fig. 8: Idiocerus lituratus,  $\mathcal{O}$ , first three abdominal sterna from above; Fig. 9: same species,  $\mathcal{O}$ , hind border of metatergum and dorsum of first three abdominal segments from above; Fig. 10: same species,  $\mathcal{O}$ , right half of integument and endoskeleton of hind part of metathorax and of first

three abdominal segments and fore border of the fourth seen from inside. (In this figure the tergum and sternum of the third abdominal segment are much displaced in relation to each other.)

Plate 6. Fig. 1: Idiocerus lituratus, o, same region as in Plate 5, Fig. 10, but with muscles; Fig. 2: Oncopsis flavicollis, o, right half of integument and endoskeleton of hind part of metathorax and of first three abdominal segments from inside; Fig. 3: same species, o, first two abdominal sterna from above; Fig. 4: same region as in Fig. 2 but with muscles; Fig. 5: Agallia brachyptera, o, first two abdominal sterna from above; Fig. 6: same species, o, right half of integument and endoskeleton of hind part of metathorax and first three abdominal segments from inside; Fig. 7: same species, o, same region with muscles.

Plate 7. Fig. 1: Paropia scanica,  $\mathcal{O}$ , right half of integument and endoskeleton of hind part of metanotum and first three abdominal segments from inside; Fig. 2: same species and sex, same region with muscles; Fig. 3: Agallia brachyptera,  $\mathcal{O}$ , right striated tymbal from inside (tend = tendon); Fig. 4: same of Paropia scanica,  $\mathcal{O}$ ; Fig. 5: Doratura stylata,  $\mathcal{O}$ , integument and endoskeleton of right half of hind part of metathorax and of first three abdominal sterna; Fig. 6: same species,  $\mathcal{O}$ , same region with muscles; Fig. 7: Aphrodes bicinctus,  $\mathcal{O}$ , first two abdominal sterna from above; Fig. 8: same species,  $\mathcal{O}$ , hind part of metanotum and dorsum of first two abdominal segments from above.

Plate 8. Fig. 1: Aphrodes bicinctus, O, right half of integument and endoskeleton of hind part of metathorax and first three abdominal segments from inside; Fig. 2: same with muscles; Fig. 3: Opsius stactogalus, O, hind part of metanotum and dorsum of the basis of abdomen from above; Fig. 4: same species, O, first two abdominal sterna from above; Fig. 5: same species, O, right half of integument and endoskeleton of hind part of metathorax and abdominal basis from inside; Fig. 6: same species, O, same region with muscles; Fig. 7: Macrosteles cristatus, O, hind part of metanotum and dorsum of abdominal basis from above.

Plate 9. Fig. 1: Macrosteles cristatus,  $\mathcal{O}$ , right half of integument and endoskeleton of hind part of metathorax and abdominal basis from inside; Fig. 2: same species,  $\mathcal{O}$ , first two abdominal sterna and hind border of metasternum from above; Fig. 3: same species,  $\mathcal{O}$ , same region as in Fig. 1 with muscles; Fig. 4: Macustus grisescens,  $\mathcal{O}$ , left part of first two abdominal sterna from behind; Fig. 5: same species,  $\mathcal{O}$ , left part of second abdominal sternum from above; Fig. 6: same species,  $\mathcal{O}$ , right half of integument and endoskeleton of hind part of metathorax and abdominal basis from inside; Fig. 7: same species,  $\mathcal{O}$ , same region as in Fig. 6 with muscles.

Plate 10. Fig. 1: Empoasca virgator, O, hind part of metanotum and dorsum of first three abdominal segments from above; Fig. 2: same species, O, hind part of metasternum and venter of abdominal basis from above; the apophysis of the second abd. sternum is cut off; Fig. 3: same species, O, right half of integument and endoskeleton of metathorax and abdominal basis from inside; Fig. 4: same species, O, same region as in the preceding figure with muscles.

Plate 11. Fig. 1: Cicadella atropunctata,  $\mathcal{O}$ , hind part of metanotum and dorsum of three basal abdominal segments from above; Fig. 2: same species,  $\mathcal{O}$ , corresponding ventral parts from above; Fig. 3: same species,  $\mathcal{O}$ , integument and endoskeleton of right half of metathorax and abdominal basis from inside; Fig. 4: same species,  $\mathcal{O}$ , same region as in Fig. 3 with muscles.

Plate 12. Enlarged positive copies of sound-track of four strips of sound-film of Doratura stylata, of, the first note of the "toooooor-to" call. Figs. 1-3 correspond to the

temperature experiment described on pages 130—131, Fig. 1 representing the lowest (initial) temperature, Fig. 3 the highest. Each of the high transverse marks represents one vibration of the main tone. The strip reproduced in Fig. 4 was made with the aid of another technical arrangement allowing a finer analysis, the fine transverse marks apparently representing the specific vibration of the membrane. The arrow indicates the moving direction of the film during exposure.

Plate 13. Radiograph records of calls of the species mentioned below. Unless otherwise stated, the calls represent the common song of the male. The horizontal lines under the records indicate the length of a second. The records should be read from left to right! - Fig. 1: Cixius nervosus; Fig. 2: same; Fig. 3: Megamelus notula (two specimens): Fig. 4: Megamelus venosus; Fig. 5: same; Fig. 6: Megamelus venosus, another call of the male; Fig. 7: Calligypona dubia; Fig. 8: Calligypona pellucida; Fig. 9: same species, common song (Fig. 8 representing another call); Fig. 10: Calligypona straminea; Fig. 11: Calligypona angulosa (first part only); Fig. 12: Aphrophora alni; Fig. 13: part of prolonged drumming of Lepyronia coleoptrata of; Fig. 14: Philaenus spumarius; Fig. 15: Paropia scanica; Fig. 16: same; Fig. 17: Euacanthus interruptus (beginning of first part not recorded); Fig. 18: Macropsis tiliae (see text p. 74, number 7); Fig. 19: same species. O, (see text, number 1); Fig. 20: Idiocerus Julgidus; Fig. 21: same; Fig. 22: same from another specimen; Fig. 23: alternating singing from two males of Idiocerus laminatus (six calls from each), one of them sitting farther away from the membrane of the microphone: Fig. 24: Idiocerus populi; Fig. 25: same (two calls); Fig. 26: Idiocerus confusus; Fig. 27: same (two calls); Fig. 28: Idiocerus elegans; Fig. 29: Agallia brachyptera (see text p. 76, number 3); Fig. 30; same species, another call (see text p. 75, Number 1); Fig. 31; Agallia venosa (not the common song, see p. 77); Fig. 32: Empoasca smaragdula (the only call I have heard); Fig. 33: Aphrodes bifasciatus; Fig. 34: same, another male; Fig. 35: Aphrodes trifasciatus; Fig. 36: Aphrodes bicinctus (see p. 87); Fig. 37; same species, another specimen. two calls; Fig. 38: Aphrodes flavostriatus; Fig. 39: Aphrodes fuscofasciatus; Fig. 40: Doratura stylata of, "toooooor-to" call (three calls); Doratura stylata Q, part of call of invitation; Fig. 42: Graphocracrus ventralis, three calls; Fig. 43: Streptanus aemulans; Fig. 44: Streptanus marginatus; Fig. 45: same; Fig. 46: Streptanus sordidus; Fig. 47: Athusanus argentatus, four calls; Fig. 48: Athysanus quadrum; Fig. 49: Allygus mixtus (first part); Fig. 50: Allygus commutatus.

# List of Abbreviations

- a  $\sim$  selectic on the metepimeron; ac  $\sim$  antecosta; ac $_2\sim$  lateral antecosta-like list; al  $\equiv$ anterior lobe; apod + apodeme; apoph - apophysis; ast + abdominal sternum.
  - b= sclerite on the metepimeron; bl  $\mathbb{R}$  bladder; br  $\cong$  bristles.
  - $\frac{\pi}{c}$  —inner list; el ==clump-like selerite; conv == convex area; c.p.s. == cycles per second. dlm = dorsal longitudinal muscle; ds = dorsal shield; dvm = dorsoventral muscle.
  - f = furca; fo = fold.

h = hook.

ism := oblique intersegmental muscle.

 $1 \equiv \text{list, lobe; lig} \equiv \text{ligament.}$ 

ma = membranous area; matter muscle attachment; mpn = metapostnotum; mz = matter metapostnotummembranous zone.

phr - phragma; phra - phragma arm; pil - pilose area: pl ... fold (plica); proc == process.

- s furrow (sulcus); scl sclerite; sclt melascutellum; sem semilunar list; sp =spiracle; spir spiracle; stg spiracle; str strengthening.
- T T-shaped strengthening; the striated tymbal; temp temperature; tend = tendon; tg | tergite; tpl | tendinous plate (tendon of muscle); tr | transverse sclerite or strengthenmg; trsel - transverse sclerite.
  - vlm ventral longitudinal muscle; vm ventral intrasegmental muscle.
- I, H. III (etc.) , first, second, third (etc.) abdominal tergum; I a, II a, III a -: belonging to the first, second, third abdominal segment; III vlm (dlm) .\_ ventral (dorsal) longitudinal intersegmental muscle extending from metathorax to first abdominal segment; III st = metasternum.

The system of muscle denominations is that proposed by WEBER.

