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Morphology of the Vibration-Producing Organ in Adult Rice  
Brown Planthopper, *Nilaparvata lugens* (STÅL)  
(Homoptera: Delphacidae)<sup>1</sup>

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A vibration-producing organ in adult *Nilaparvata lugens* (STÅL) was located in the posterior region of the metathorax and the basal two abdominal segments. The largest muscle at the region was a paired dorsal longitudinal one running from the metaphragma to the 2nd tergite. In the male, this muscle is anteriorly attached to the arm of the metaphragma and posteriorly to the tymbal composed of the basal two tergites, and is considered to have the most important function in vibrating the male tymbal. In the female, which has no tymbal, the muscle is attached to the metaphragma without an arm and is thought to produce the vibration of the whole abdomen. In the male 1st abdominal segment, two pairs of large dorsoventral muscles which probably have subsidiary roles in producing the vibration signals were observed. The female has only one pair of smaller corresponding muscles which seem to have no substantial function in producing her vibration signal. Ventral longitudinal muscles running almost vertically from the 1st sternite to the apodemes of the 2nd sternite were observed only in the male and were believed to control unnecessary abdominal movements during his vibration signals.

INTRODUCTION

DUMORTIER (1963) classified the mechanisms of sound-production in Arthropoda into the following six categories: 1) friction of different regions, 2) vibration of membranes, 3) expulsion of a fluid (gas or liquid), 4) shocks to the substrate, 5) vibration of appendages, and 6) friction of non-differentiated regions. Among these the vibration of membranes seems almost completely limited to Homoptera Auchenorrhyncha (OSSIANNILSSON, 1949; LESTON and PRINGLE, 1963; SMITH, Jr. and GEORGHIOU, 1972). In other groups of insects, only a few species of Lepidoptera (BLEST et al., 1963; KAY, 1969) and probably some Heteroptera (LESTON and PRINGLE, 1963) use this mechanism.

The male cicada is the best known insect producing sounds by membranal vibration, i.e., the tymbal mechanism (e.g., PRINGLE, 1953, 1954; HAGIWARA, 1956; AIDLEY, 1969; REID, 1971; YOUNG, 1972). OSSIANNILSSON (1949) found a pair of elastic and striated regions, called striated tymbals, on the 1st tergite or the basal two tergites in

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many Homoptera Auchenorrhyncha other than Cicadidae. Although he found no striated tymbal in delphacid males, from their morphological characteristics it was concluded that their sound-producing organs were located in the metaphragma and the basal two abdominal segments. In addition, he considered that delphacid females could not produce sounds since their organs are much more simplified than those of the males. However, delphacid females were later described as producing faint sounds in their mating behavior (STRÜBING, 1958; STRÜBING and HASSE, 1975). It was further clarified that both sexes of the three species of delphacid adults including *N. lugens* communicate through vibration signals transmitted to their host plants (ICHIKAWA, 1976).

Our present knowledge of the tymbal organ of *N. lugens* indicates that the basal two tergites of the male function as a tymbal and that there are longitudinal and dorsoventral muscles possibly having the function of vibrating this tymbal (ISHII and ICHIKAWA, 1975; ICHIKAWA, 1976). However, the detailed structure of the male tymbal organ and the mechanism of the production of the vibration signal by the female remain to be studied. This paper deals with the integumental structure and musculature of the vibration-producing organ in both sexes of adult *N. lugens* and the probable mechanisms of the signal production.

#### MATERIALS AND METHODS

*Insects used.* Macropterous adults of *Nilaparvata lugens* were collected from a hopper-burned paddy field in Kagawa Prefecture in October, 1981. Some were killed immediately after collection as samples for microscopic observation. The others were reared in our laboratory under the same conditions as ICHIKAWA (1982) as a stock culture. Insects used in anatomical investigations were obtained from the stock culture.

*Observation of the integumental structure.* Integumental structure of the outer surface of the posterior region of the metathorax and the basal region of the abdomen were observed from a dorsal direction under a binocular microscope using specimens which had been kept in 70 % ethanol. To observe the inner integumental structure, specimens kept in 90 % ethanol were used. The body was sagittally halved or transversely cut with a razor at the metathorax, the 1st or the 2nd tergite was treated with 10 % KOH aqueous solution to save the scleroid structures and then kept in ethanol until observation.

*Observation of the musculature.* Macropterous adults whose legs and wings had been amputated were fixed in 3 % glutaraldehyde in 0.1 M phosphate buffer, pH 7.2, for 2 hr at 4°C and embedded in SPURR's resin after dehydration with ethanol series (50–100 %). Serial cross and sagittal sections (each 10 μm thick) were made with a Sorvall MT-2 ultramicrotome using glass knives. Sections on water were stretched by an alcohol lamp and mounted in glycerol. Microscopic observation was made with a Zeiss photomicroscope equipped with an epifluorescence condenser III RS and a mercury high-pressure lamp. The filter set used for incident-light fluorescence microscopy was a BP 400–440 excitation filter with peak transmittance of 400 to 440 nm, chromatic beam splitter FT 460 and barrier filter 470. Microphotographs for fluorescent images were taken with Kodak Tri-X pan film. To directly observe musculatures and muscle attachments, sagittally halved specimens were stained with hematoxyline and

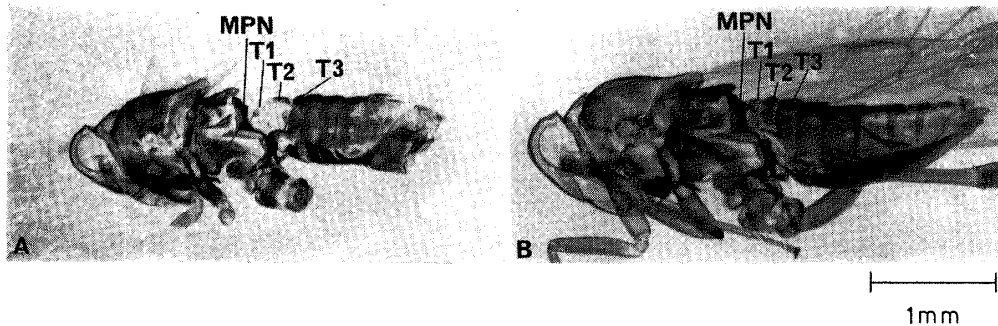


Fig. 1. Integumental structure of the right half of the whole body seen from inside. A: male, B: female. Specimens were treated with 10% KOH aqueous solution. MPN: metapostnotum, T1: the 1st tergite, T2: the 2nd tergite, T3: the 3rd tergite.

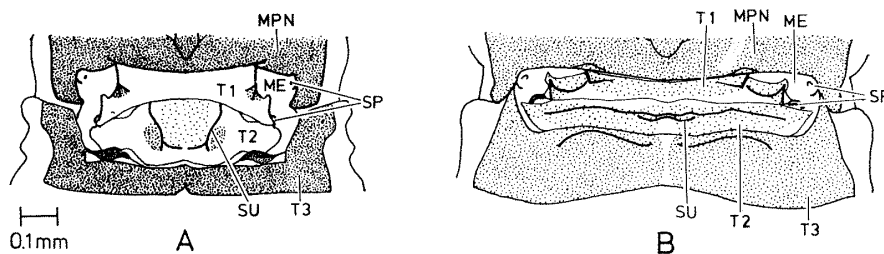


Fig. 2. The basal part of abdomen and its adjacent segments in dorsal view. A: male, B: female. ME: membrane, SP: spiracle, SU: suture. See Fig. 1 for other abbreviations.

eosin, dehydrated with ethanol and dissected in xylen under a binocular microscope.

Muscles were classified into dorsal longitudinal muscle (DLM), ventral longitudinal muscle (VLM), dorsoventral muscle (DVM) and intersegmental muscle (ISM). The number given each muscle in the text and the figures is for convenience only and is homologous in the two sexes.

## RESULTS

### *Integumental structure of the vibration-producing organ*

#### *Male*

The basal two tergites are quite different in shape and color from other tergites having a dark cuticle (Fig. 1 A). The whole of the basal two tergites except the central pigmented area of the 2nd tergite is yellowish white (Fig. 2 A). As the basal two sternites are remarkably compressed in a longitudinal direction, the basal two tergites and their lateral membranous parts seem completely surrounded by the metapostnotum and the 3rd tergite (Fig. 2 A).

The posterior margin of the metapostnotum is interiorly strengthened by a transverse metaphragma which has a pair of strongly sclerotized processes, phragma arms protruding centrally in a caudal aspect and anteriorly in a lateral aspect (Figs. 3 A and 4 A). The 1st tergite connects tightly with the metapostnotum at two points just behind the base of the phragma arms. Posterior margin of the 1st tergite is broadly excavated in a dorsal view, and the 2nd tergite has a posterior margin slightly bilobed

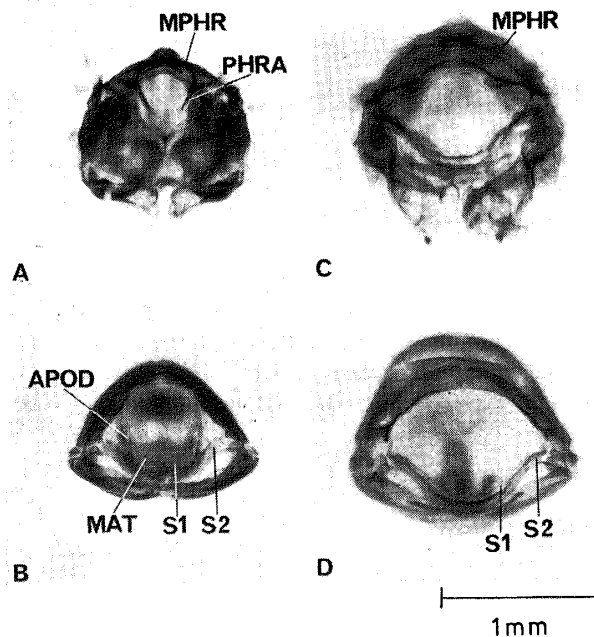


Fig. 3. Integumental structure of the posterior region of the metathorax (A and C, from behind) and the basal region of the abdomen (B and D, from the front). A and B: male, C and D: female. Specimens were treated with 10% KOH aqueous solution. APOD: apodeme, MAT: muscle attachment, MPHR: metaphragma, PHRA: phragma arm, S1: the 1st sternite, S2: the 2nd sternite.

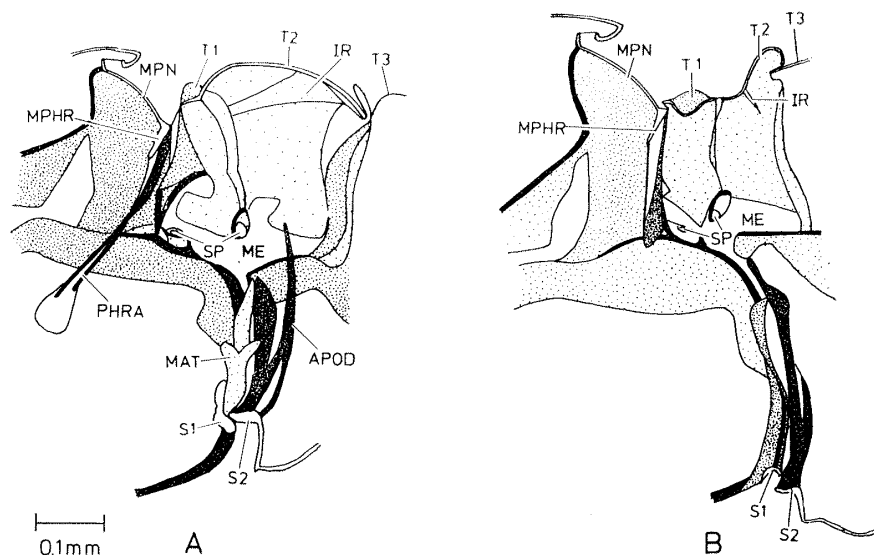


Fig. 4. Integumental structure of the right half of the posterior region of the metathorax, the basal part of the abdomen seen from inside. A: male, B: female. IR: internal ridge. See Figs. 1, 2 and 3 for other abbreviations.

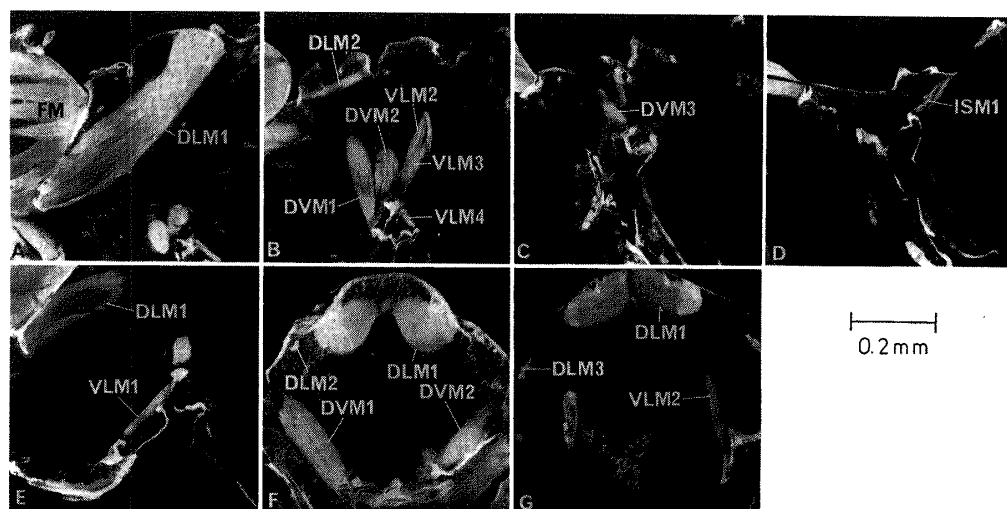


Fig. 5. Male muscles of the posterior region of the metathorax and the basal part of the abdomen. A, B, C, D and E: sagittal section, F and G: transverse section, F: the 1st abdominal segment, G: the 2nd abdominal segment. F and G were cut slightly oblique to the midline. DLM: dorsal longitudinal muscle, DVM: dorsoventral muscle, FM: flight muscle, ISM: intersegmental muscle, VLM: ventral longitudinal muscle.

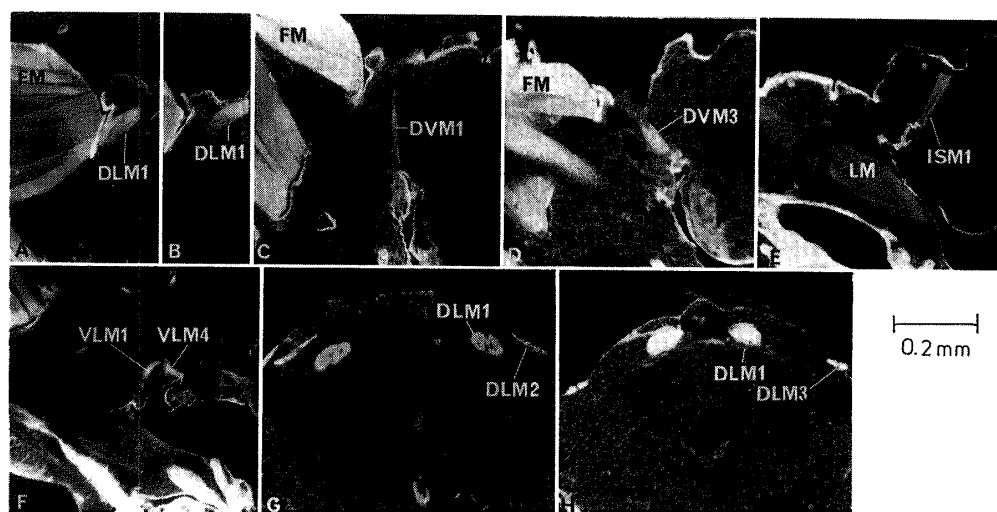


Fig. 6. Female muscles of the metathorax and the basal part of the abdomen. A, B, C, D, E and F: sagittal section, G and H: transverse section, G: the 1st abdominal segment, H: the 2nd abdominal segment. LM: leg muscle. See Fig. 5 for other abbreviations.

medially (Fig. 2 A). A pair of longitudinal sutures each having a transverse branch at the posterior part can be seen at the central pigmented area of the 2nd tergite (Fig. 2 A); these are lines marking internal ridges (Fig. 4 A). The membrane between the 2nd and the 3rd tergites is folded (Fig. 4 A).

The 1st and the 2nd sternites are not merely short transverse plates but have the following characteristic structures. The 1st sternite has a pair of muscle attachments (Figs. 3 B and 4 A). Pigments do not accumulate except on the attachments. The

2nd sternite has a pair of almost vertical pole-like apodemes (Figs. 3 B and 4 A).

#### *Female*

The basal two tergites are colored and sclerotized as other posterior tergites, and the 2nd is much shorter than that of the male (Figs. 1 B and 2 B). The basal two sternites are remarkably compressed in a longitudinal direction like those of the male. Accordingly, the basal two tergites and their lateral membranous parts seem to be completely surrounded by the metapostnotum and the 3rd tergite as in the male (Fig. 2 B).

The posterior margin of the metapostnotum is interiorly strengthened by a transverse metaphragma like the male; the metaphragma, however, has no phragma arm (Figs. 3 C and 4 B). The 1st tergite tightly connects with the metapostnotum at two points which correspond to those of the male mentioned above. A transverse suture observed in the center of the 2nd tergite (Fig. 2 B) is a line marking an internal ridge (Fig. 4 B).

Unlike the male, the basal two sternites have no distinct muscle attachment (Figs. 3 D and 4 B).

#### *Musculature of the vibration-producing organ*

Excepting flight muscles and leg muscles in the metathorax, the following muscles were observed in pairs in the posterior region of the metathorax and the basal two abdominal segments of each sex.

#### *Male*

Three dorsal longitudinal muscles labelled DLM1, DLM2 and DLM3 were observed (Figs. 5 A, B, E, F, G and 7 A). DLM1, the thickest and longest muscle in the region, is exceptionally large and cylindrical and runs from the distal part of the metaphragma arm to the 2nd tergite at which the muscle is firmly attached to the inner surface and the internal ridge. It is apparent from Fig. 5 G that the ridge is not merely a sheet of a plate but a cuticular fold. DLM2 runs from the hind border of the metapostnotum to the front border of the 2nd tergite, and DLM3 from the front border of the 2nd tergite to the antecosta of the 3rd tergite (Fig. 7 A).

Three dorsoventral muscles labelled DVM1, DVM2 and DVM3 were observed in the 1st abdominal segment (Figs. 5 B, C, F and 7 A). DVM1 and DVM2 are very thick and cylindrical, the former running from the muscle attachment of the 1st sternite to the anterior point of the 1st tergite. DVM2 runs from the same muscle attachment to the immediate front of the spiracle on the 1st tergite. DVM3 is much smaller and flat, and is most laterally inserted from the sternite to the tergite.

Four ventral longitudinal muscles labelled VLM1, VLM2, VLM3 and VLM4 were observed in the posterior region of the metathorax and the basal two abdominal segments (Figs. 5 B, E, G and 7 A). VLM2 is cylindrical and the largest of the four. This muscle runs from the muscle attachment of the 1st sternite to the tip of the pole-like apodeme of the 2nd sternite; stretching almost vertically, this seems to be a dorsoventral muscle. VLM3 also runs from the muscle attachment to the pole-like apodeme, but is much thinner than VLM2. VLM1 and VLM4 run from the muscle attachment to the metathorax and the 2nd sternite, respectively.

One small and lateral intersegmental muscle called ISM1 runs from the 2nd sternite to the antecosta of the 3rd tergite (Figs. 5 D and 7 A).

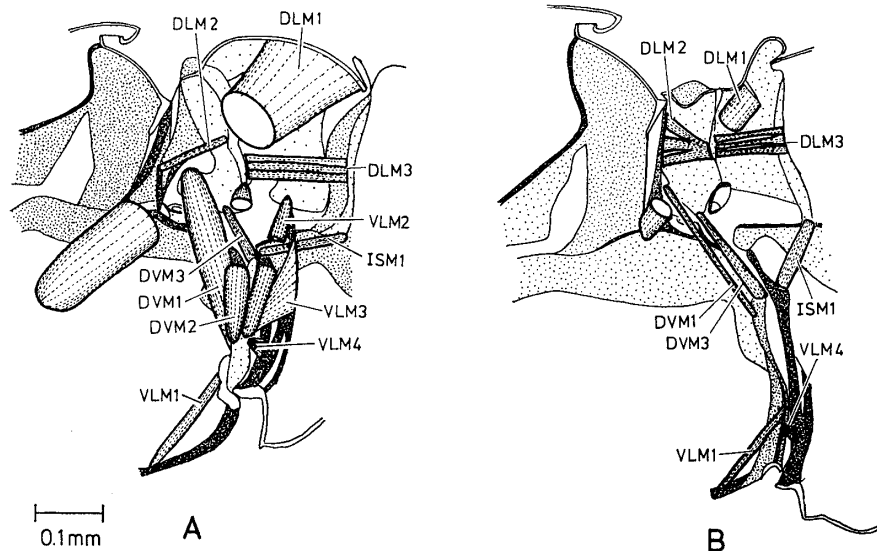


Fig. 7. Semi-diagrammatic view of the musculature of the right half of the posterior region of the metathorax and the basal part of abdomen seen from inside. A: male, B: female. DLM1, DVM2 and VLM2 were partly removed to show other muscles. Flight muscles and leg muscles of the thorax are omitted. See Fig. 5 for abbreviations.

#### Female

On the whole, the muscles of the female in the posterior region of the metathorax and the basal two abdominal segments are much smaller than those of the male and somewhat reduced in number.

Three dorsal longitudinal muscles, DLM1, DLM2 and DLM3, were observed in the same regions as corresponding muscles of the male (Figs. 6 A, B, G, H and 7 B). DLM1 runs from the metaphragma to the transverse internal ridge of the 2nd tergite, and the region of the metaphragma where the muscle is inserted corresponds to the base of the phragma arm of the male. Although female DLM1 is much smaller and shorter than male DLM1, this cylindrical muscle is the largest one in the region.

Two dorsoventral muscles, DVM1 and DVM3, were observed in the 1st abdominal segment (Figs. 6 C, D and 7 B). Though the female has a far smaller DVM than the male, the female DVM3 is not greatly different in size. No muscle corresponding to the male DVM2 was observed.

Two small ventral longitudinal muscles, VLM1 and VLM4, were observed in the corresponding regions of the male (Figs. 6 F and 7 B). The muscle corresponding to male VLM2 or VLM3 was not observed.

One small intersegmental muscle, ISM1, was observed in the same region as male ISM1 (Fig. 6 E).

#### DISCUSSION

The sense of vibrations of solid structures (vibration sense) has been discriminated from that of airborne sounds (auditory sense) (AUTRUM, 1941; AUTRUM and SCHNEIDER, 1948; DETHIER, 1963; SCHWARTZKOPFF, 1964; MARKL, 1969). Therefore, a vibration-

producing organ is thought more likely than a sound-producing organ in a special apparatus adapted to produce vibrations by which animals communicate. In Homoptera Auchenorrhyncha, intraspecific communication in several species of Delphacidae including *N. lugens* and Deltocephalidae is known to be mediated by vibration signals transmitted to their host plants (ICHIKAWA, 1976, 1979; ARAI, 1977; INOUE, 1982); thus, the organs emitting these vibration signals can properly be called "vibration-producing" organs. Auditory organs have not been identified in Homoptera Auchenorrhyncha other than Cicadidae, though they have been known to emit faint species-specific sounds (OSSIANNILSSON, 1949; LESTON and PRINGLE, 1963; SMITH, Jr. and GEORGHIOU, 1972). Therefore, it is probable that the organs referred to as sound-producing organs are included in the vibration-producing organs.

The structure of the vibration-producing organs in *N. lugens* described in the present paper is very similar to those of Swedish delphacid species (OSSIANNILSSON, 1949) in both sexes. These studies showed that the vibration-producing organs of delphacid males are far more complex than those of the females. In *N. lugens* for example, a pair of phragma arms on the metaphragma, a pair of pole-like apodemes on the 2nd sternite and a pair of ridges on the 1st sternite which function as muscle attachments, are present only in the male. In addition, the muscles attached to these structures such as DLM1 and DVM1 are much more powerful than the homologous muscles of the female. The development of large muscle attachments and large muscles in the female abdomen might be inconsistent with the production of a large number of eggs.

In *N. lugens*, the female invitation signal (ICHIKAWA, 1982) is produced by the vibration of the whole abdomen in a dorso-ventral direction (ICHIKAWA and ISHII, 1974; ICHIKAWA et al., 1975). DLM1 is the probable muscle causing this abdominal vibration in the light of its peculiar position; it is also the largest in the female abdomen except for the muscles which move the ovipositor. The contraction of DLM1 must lower the whole abdomen, because this muscle runs obliquely downward and anteriorly from the plate-like 2nd tergite to the strongly sclerotized metaphragma. The abdomen must return to its previous position immediately after the following relaxation of this muscle. As it was observed that one pulse of the invitation signal was produced with each return movement of the abdomen (ICHIKAWA et al., 1975), the damped oscillation composing each pulse is probably produced by unnoticed free decreased vibrations of the abdomen after the return movement.

OSSIANNILSSON (1949) supposed that his *I a dlm*<sub>1</sub> in delphacid males (our DLM1) had only the function of changing the state of buckling and the tension of the tergal plates. However, we believe that this muscle is the most important in the production of vibration signals for the following reasons. Male DLM1 is a homologous muscle with female DLM1, which is thought to be the muscle producing the invitation signal. A pair of DLM1 which come in close proximity with each other firmly attach to the sclerotized area located in the center of the 2nd tergite. This is no doubt the best position to add effective force to vibrate the large tymbal composed of the basal two tergites. As DLM1 stretches obliquely downward and anteriorly and there is a folded membrane at the posterior margin of the tymbal, the tymbal, especially its posterior part, must move downward in a large amplitude when DLM1 contracts.

In the male cicada, *Graptopsaltria nigrofuscata*, each damped tone produced by tymbal vibrations caused by a contraction of the tymbal muscle is modified by the tetanic contraction of the tensor muscle (HAGIWARA, 1956). In *N. lugens*, each pulse of



the main long part of the calling signal of the male is not composed of a simple damped oscillation like the female invitation signal, but of a complex waveform (ICHIKAWA, 1976). Male *N. lugens* has two pairs of large dorsoventral muscles, DVM1 and DVM2, in the 1st abdominal segment. These muscles must function to modify the basic pattern of tymbal vibrations probably caused by the action of DLM1. The following two manners of modification are possible: one is that DVM1 and DVM2 function as tensor muscles; the other is that these muscles function as accessory tymbal muscles independently producing a part of the calling signal because of their direct insertion in the anterior and lateral parts of the tymbal. On the other hand, DVM1 and DVM2 of female *N. lugens* must not function to modify her signal, because these muscles are far smaller than those of conspecific male.

OSSIANNILSSON (1949) inferred that his *I a vlm<sub>2</sub>* in delphacid males (our VLM2) has one of the following two functions: 1) it causes a rattling motion of the whole abdomen in cooperation with his *I a dlm<sub>1</sub>* (our DLM1), and drumming noises are produced by this motion; 2) when this muscle is nearly vertical, it somewhat lifts the 1st sternite resulting in changes in the frequency of the call by the shortening of his *I a dvm<sub>1</sub>* (our DVM1). However, we believe that VLM2 and VLM3 in male *N. lugens* function to control unnecessary vibration of the entire abdomen during signal emission. The probable mechanism of the control is as follows. A part of the force exerted by the contraction of DLM1 functions to pull down the abdomen, though most of the force is used for the downward movement of the tymbal as previously discussed. When the force directed to pull down the whole abdomen is exerted, the ventral side of the abdomen is bent downward at the basal margin. Thus, the pole-like apodemes on the 2nd sternite tend to lean backward. As VLM2 and VLM3 stretch from the 1st sternite to the apodemes, the backward movement of the apodemes is restrained when the force directed to the 1st sternite is exerted by the contraction of these muscles, especially large VLM2 which is attached to the tip of the apodemes. The above-mentioned mechanism to retain the position of the apodemes must check the downward movement of the 2nd and following abdominal segments and large ensuing vibrations of the entire abdomen. On the other hand, the vibration of the abdomen during signal emission in female *N. lugens* must be due to the lack of VLM2, VLM3 and pole-like apodemes.

Our foregoing discussion on *N. lugens* must apply to other delphacid insects because of the structural similarity in their vibration-producing organs as described in this section. Receptive females of several delphacid species such as *Calligypona lugbrina* (STRÜBING, 1958), *Sogata orizicola* (McMILLIAN, 1963), *N. lugens*, *Laodelphax striatellus* and *Sogatella furcifera* (ICHIKAWA and ISHII, 1974; ICHIKAWA et al., 1975) perform abdominal vibration during their mating behavior. Such a behavioral similarity in delphacid females of different genera also supports the validity of this generalization. In male delphacid insects, our DLM1 must be the major tymbal muscle, and our DVM2 and DVM3 are probably tensor muscles or accessory tymbal muscles. In female delphacid insects, our DLM1 cannot be called the tymbal muscle, because they have no specialized tymbal like the males, and the action of this muscle is apparently to vibrate whole abdomen.

Homoptera Auchenorrhyncha is classified into the following four superfamilies: Fulgoroidea including Delphacidae, Cercopoidea, Cicadelloidea and Cicadoidea (EVANS, 1963). In most males of Cicadoidea, there are a pair of tymbals on the 1st tergite, and a powerful dorsoventral muscle, a tymbal muscle, which projects from the

ventral sclerite of the 1st sternite to the apodeme stretching from each of the two tymbals. In many species belonging to Cercopoidea and Cicadelloidea, OSSIANNILSSON (1949) found a pair of dorsoventral muscles labelled *I a dum*<sub>1</sub> with several other muscles in the 1st abdominal segment. As he pointed out, this must be a homologous muscle with the tymbal muscle of Cicadoidea because, projecting from the 1st sternite, it is always inserted in each of the two striated tymbals if they are present, or in corresponding spots in insects having no such tymbals. On the other hand, the vibration-producing organ in Delphacidae does not seem to be a strictly homologous organ with the sound-producing organ in Cicadoidea, because the vibration-producing organ in Delphacidae apparently functions mainly through the action of a pair of dorsal longitudinal muscles, our DLMI, as discussed in former paragraphs. None of the other families of Fulgoroidea seems to have been studied in as great detail as Delphacidae for the mechanism producing their vibration signals. Therefore, it is necessary to obtain more information on other Fulgoroidea species than Delphacidae to clarify the evolutionary process of this mechanism in this group.

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