

ASPECTS OF THE MORPHOLOGY OF THE OVIPOSITOR OF
Hylotrupes bajulus (L.)
(COLEOPTERA: CERAMBYCIDAE)

by

Joseph Thomas Mares

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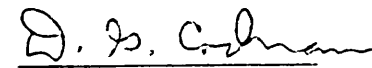
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Entomology

APPROVED:


Dr. W. H. Robinson


Dr. J. L. Eaton


Dr. D. G. Cochran

July, 1984
Blacksburg, Virginia

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This thesis is dedicated,
with love, to my wife Melanie,
and to my parents, Tom and Pat Mares

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INTRODUCTION

Hylotrupes bajulus is a serious pest of seasoned softwoods (pine, spruce, fir). The larval stage of this cerambycid feeds in wood and can take 2-10 years to develop into an adult. During this long life cycle the larva can cause both cosmetic and structural damage to infested wood. H. bajulus is known to occur world-wide, and in the areas where it is established, it is of significant economic importance (Howick 1966). In the United States, H. bajulus distribution is primarily restricted to areas east of the Mississippi River. In the eastern and southern U.S., H. bajulus is second to termites as an insect pest of structural wood (St. George 1957, McIntyre 1961).

H. bajulus was first reported in North America over 200 years ago (Moore 1978). Robinson and Cannon (1979) believe that H. bajulus was first introduced into the U. S. through the port city of Philadelphia, Pennsylvania. Further spread may have come about as a result of western expansion. In Virginia, H. bajulus is equally distributed throughout the three geographic regions. H. bajulus occurrence has been reported in 86 of the 99 counties in Virginia (Cannon and Robinson 1982a).

The female H. bajulus oviposits in cracks and crevices of seasoned softwoods. The eggs are deposited in 2-5

batches over a period of several days (Cannon and Robinson 1983). Each batch contains approximately 35 eggs, and they are arranged in a fan-shaped pattern. Becker (1943) reported that α - and β -pinenes act as attractants to ovipositing females. Higgs and Evans (1977) determined that H. bajulus larvae have present in their frass pheromones which affect the oviposition behavior of the adult female. Doppelreiter (1979) found the presence of a female sex pheromone.

H. bajulus larvae feed in the sapwood portion of seasoned softwoods. As early instar larvae, they feed close to the surface of the wood without breaking through; older larvae penetrate deeper into the wood (Schuch 1937). Becker (1949) indicated that the growth of the larvae was highly dependent on the protein content of the wood. Rasmussen (1967) and Cannon and Robinson (1981b) reported on the influence of temperature, wood moisture, and relative humidity on larval growth and development. Cannon (1979) observed that in the U. S. the larval developmental period ranged from 2-11 years. Environmental conditions most suitable for H. bajulus development in the U. S. are 20-30° C and 60-80% relative humidity (Cannon and Robinson 1981a).

The majority of research on H. bajulus has centered on the influence of environmental factors on the larval stages.

There has been little research on the biology, behavior, and morphology of the adult beetles. Durr (1954) and Cannon and Robinson (1981a) studied adult mating behavior. Morphological studies of the H. bajulus female were conducted by Wandellock (1906), Weidner (1936), and Durr (1956). Their studies emphasized only the general structure of the ovipositor. There has been no research conducted on the fine structure of the female H. bajulus ovipositor, especially with reference to the types of sensory receptors it contains.

The objectives of the research presented here are 1) to describe and illustrate the fine structure of the female H. bajulus ovipositor; 2) to elucidate the type and number of various sensory receptors present on the ovipositor; and 3) to interpret the probable function of these sensilla based on morphological characteristics.

LITERATURE REVIEW

Taxonomy

The genus Hylotrupes contains a single species, H. bajulus. Linnaeus described H. bajulus as Cerambyx bajulus in 1758, and Fabricius in 1775 transferred this species to the genus Callidium. In 1834, Serville placed C. bajulus into the genus Hylotrupes. Hylotrupes bajulus is of the tribe Callidiini, subfamily Cerambycinae.

Geographical Distribution

A comprehensive review of the world distribution of H. bajulus was prepared by Becker (1968, 1979). According to his review, H. bajulus can be found on every major continent. In the areas of H. bajulus populations, severe damage to wooden structures can occur. Durr (1954) studied the distribution of H. bajulus in South Africa and found the populations to be concentrated along the coastlines, especially in the Western Province. He speculated that optimal conditions in these areas were responsible for this occurrence. Howick and Carr (1971) stated that H. bajulus was not yet established in Australia, though climatic conditions are suitable to allow for its establishment. Several authors (Parkin 1934, Kaufman 1947, White 1954,

1959, Lea 1976, Lea and Bravery 1978) have published on the presence of H. bajulus in England. Their studies indicated that most H. bajulus infestations are confined to southern England, with isolated cases of infestations reported throughout England. Knudsen (1966) observed H. bajulus populations to be concentrated in certain areas in southern Norway. He attributed this limited distribution to the harsher environmental conditions found further north.

In the United States, H. bajulus is known to occur in most states east of the Mississippi River, and along the gulf coast from Florida west to Texas (St. George 1957, McIntyre 1961). H. bajulus has been present in the U. S. for over 150 years (St. George 1957, Robinson and Cannon 1979). Moore (1978) believed H. bajulus was not yet established in the wild in the U. S. Cannon and Robinson (1982a) collected H. bajulus larvae and adults in buildings and lumber at two lumber yards and a sawmill. Cannon (1979) studied the survivability of H. bajulus larvae in the wild, and discovered first-instar larvae could survive six months exposure to natural conditions. These results indicate that H. bajulus may be able to become established in areas outside of man-made structures.

Biology

The biology of H. bajulus has been studied in Europe, South Africa and the U. S. Becker (1943) found H. bajulus larvae to develop best at 82.4-84.2° F and 40-50% relative humidity. Becker (1949) determined that the growth rate of the larvae is linear in response to increasing protein content of the wood. Rasmussen (1956a,b, 1957, 1958) in a series of experiments, demonstrated that larval growth is greatly accelerated by adding peptone, yeast extracts, and small amounts of cholesterol to wood and filter paper feeding blocks. Korting (1960) found a correlation between a decrease in wood weight and the amount of larval feeding.

Durr (1954, 1956) compiled a comprehensive study on H. bajulus biology in South Africa. Durr (1956) observed that H. bajulus females in South Africa were more fecund than H. bajulus females in Europe. Durr also noticed differences in the lengths of the egg and pupal period. Durr (1954) believed these differences to be a result of the more favorable environmental conditions in South Africa.

Cymorek (1968) reported that placing full-grown larvae into a cold room for a long period of time (8 weeks at 5° C) resulted in a higher percentage of pupation and a shorter pupal period when compared to those results from larvae held at room temperature, outdoor winter conditions, in a cellar,

and in moderately cool rooms. Cymorek (1968) also observed that adults are strong fliers and showed the optimum temperature for flight to be about 30° C. Rasmussen (1961) discovered that, in Denmark, H. bajulus larvae develop better under slated roofs, which have a hotter microclimate, than under tiled roofs, which have a cooler microclimate. This is in direct contrast to what Durr (1954) observed in South Africa. Rasmussen (1961) believed the contrast is due to the differences in macroclimate between Denmark and South Africa.

H. bajulus biology in the U. S. had not been well studied until recently. McIntyre observed that contrary to its common name, Old House Borer, the beetle more often attacks new buildings in the U.S. Vongkaluang (1978) researched the survival and development of first-instar larvae as affected by temperature and relative humidity. Vongkaluang reported that wood with a moisture content of 10% or less was detrimental to first-instar larval growth and development, regardless of the temperature. Recent studies on H. bajulus biology in the U. S. have been conducted by Cannon (1979, 1982) and Cannon and Robinson (1981a, 1983). Cannon and Robinson (1983) described the North American biotype of H. bajulus. They noticed that the N. A. biotype of H. bajulus females oviposits more eggs

(\bar{x} =165.1) than the South African biotype (\bar{x} =119.4) and the European biotype (\bar{x} =105.2). Cannon and Robinson (1983) also noted that N. A. females deposit more egg batches (\bar{x} =4.3) over a longer period of time (\bar{x} =5.2 days) than the South African biotype (\bar{x} egg batches=2.5; \bar{x} days=3.9). Differences in egg size, incubation period, larval weight, and larval developmental time were observed. From these results the authors suggested that the environmental conditions in North America were less suitable for H. bajulus larval development than in South Africa, but more suitable than the environmental conditions found in Europe. Cannon and Robinson (1981b) studied the growth and development of larvae as it occurs in house basements, attics, and in the laboratory. Their results indicated that wood consumption and growth was greatest in the laboratory. Results from the basement and attic showed the basement to be a more suitable environment for larval development. Apparently the extreme fluctuations in temperature and relative humidity in the attic affected larval feeding and growth. Cannon (1979, 1982) provided a detailed literature review on H. bajulus biology and habits in the U.S. and around the world.

Laboratory Rearing

White (1962) found that by impregnating wood with a 0.50% aqueous solution of bacto-peptone, a significant increase in larval development could be achieved. Berry (1972) described a technique for enriching the laboratory rearing blocks with proteins and vitamins to accelerate H. bajulus larval growth. Cannon and Robinson (1982b) developed an artificial diet for H. bajulus. This diet contained yeast extract, bacto-peptone, and cholesterol in addition to yellow pine sawdust and other nutrients, which made the diet nutritionally acceptable for the larvae. The diet reduced larval developmental time by 25-30% and mortality by 10-30% over conventional rearing methods.

Control

Various types of chemical control of H. bajulus have been tested. Fumigation is the only recommended control of H. bajulus in Australia (Hadlington and Campbell 1956, Howick 1966, Howick and Carr 1971). Different insecticides applied to the surface of infested wood have been studied to determine their toxicity to all H. bajulus life stages. Durr (1954) tested various applications of pentachlorophenol, DDT, other insecticides and some wood preservatives. Results indicated all compounds tested were

toxic to the various life stages of H. bajulus, but it was noted that young larvae can survive up to 11 months in treated wood. McIntyre (1961) prescribed the use of 2% chlordane or 0.5% lindane applied to wood surfaces. Marovic (1976) experimented with Xyloline (2% lindane in oil) and Balsamal (2% lindane/2% malathion in oil) to determine their effectiveness in protecting a house built of spruce and pine from attack by H. bajulus. Results showed the two insecticides to be 100% effective after 5 years. Twelve different organic tin compounds were tested on newly hatched H. bajulus larvae; several of the compounds proved to be quite toxic to the larvae (Becker 1978). Knudsen (1969) reported that storing timber in sea water or fresh water for a few weeks before use did not fully protect the wood against attack by H. bajulus. Doppelreiter (1980) tested the toxicity of the insect growth regulator diflubenzuron on newly hatched H. bajulus larvae. Results indicated complete or almost complete control at 8 and 12 weeks, with toxic values ranging from 0.25-0.12 kg/m³ wood at 8 weeks to 0.06-0.03 kg/m³ wood at 12 weeks.

Several biological control agents have been reported for H. bajulus (Linsley 1964, Kuehne and Becker 1974, Nagy 1975, Serment 1976, Torossian 1974). These agents included several families of parasitic Hymenoptera (Bethyridae, Braconidae, Scolythyridae), several species of the family

Cleridae (Coleoptera), and an ectoparasitic mite. These agents apparently have no significant role in reducing H. bajulus populations (Linsley 1964).

Ovipositor Morphology

There are two main theories concerning the origin of insect ovipositors. One theory proposes that the ovipositor of Insecta is comprised of secondary integumental outgrowths from the sternum (Matsuda 1976); the other proposes that the ovipositor is appendicular in nature, formed from the gonapophyses of the primary segmental appendages of genital segments 8 and 9 (Matsuda 1976). Matsuda, in his review of the literature concerning the evolution of external genitalia, concluded that while a wide range of insects possess external genitalia of an appendicular nature, there exists evidence to indicate that at least in some species, the genitalia are sternal in origin.

The morphology of cerambycid genitalia has been studied by several authors (Wandellock 1906, Tanner 1927, Iuga and Rosca 1962, Crowson 1981). There are differences of opinion in the number of abdominal segments described in the family Cerambycidae. Wandellock (1906) believed the H. bajulus ovipositor to be comprised of segments 7-10. Iuga and Rosca (1962) in their description of the family Cerambycidae

stated that only 9 abdominal segments are present in the subfamily to which H. bajulus belongs. Jeannel (1949) also believed there were only 9 abdominal segments in Cerambycidae. However, Bitsch (1979) described the cerambycid ovipositor as being formed by abdominal segments 8, 9, and the remnants of 10. Crowson (1981) reported that the proctiger, which is commonly associated with the 10th tergite, might at least be partially homologous to the 9th tergite.

Scudder (1971) classified ovipositors as one of two types. Type I ovipositors are those formed by the extension or modification of the posterior abdominal segments. Smith (1969) used the term antovipositor to describe this type of ovipositor; the term oviscapt has also been used (Crampton 1942). Type II ovipositors are formed from ventral processes of the 8th and 9th abdominal segments. The ovipositor of H. bajulus is a Type I ovipositor. In this paper, the term ovipositor is used to describe the functional egg-laying tube of the female H. bajulus, based on the definition of an ovipositor by Torre-Bueno (1937) and Tuxen (1970).

Wandellock (1906), Weidner (1936), and Durr (1956) described the general gross structure of the H. bajulus ovipositor. Durr (1956) provided basic information on egg,

larval, pupal, and adult morphology. Durr's description of the female abdomen and genitalia was brief and largely based upon the work of Weidner (1936). Weidner's (1936) paper presented a sketch of the female H. bajulus ovipositor, but dealt more with internal structures than with external morphology. Wandellock (1906) gave a more detailed account of the ovipositor, and noted the presence of four whiplike bristles and numerous blunt projections on the tip of the styli. However, Wandellock ascribed no function for these bristles and projections.

Sensory Receptors

The presence of sensory receptors on the insect body has been known for over 150 years (Slifer 1961). Nagel (1892, 1894) in a series of experiments with some predaceous diving beetles of the genus Dytiscus, determined the presence of chemoreceptors on the mouthparts of the larvae and adults. Nagel was the first to suggest that receptor cuticle does not need pores in order to be stimulated. Snodgrass (1935) and Wigglesworth (1939) detailed the types and functions of sensory organs. Snodgrass (1935) and Chapman (1982) stated that cuticular sensory organs are comprised of several cells: the sensory celi (or cells), the trichogen cell which secretes the receptor cuticle, and

the tormogen cell which secretes the socket cuticle. Zacharuk (1980) reported that sensilla may have up to five cells associated with the sensory neurons, but usually average four cells. These cells include the trichogen cell, tormogen cell, accessory cell, and neurilemma.

Mechanoreceptors

Horridge (1965) listed four main types of cuticular mechanoreceptors based on external morphology of the receptor; trichoid sensilla, coeloconic sensilla, ampullacea sensilla, and campaniform sensilla. Horridge generalized that those receptors innervated by a single dendrite function solely as mechanoreceptors. Dethier (1963) stated that mechanoreceptors are more numerous on parts of the insect body which come in contact with a substrate, on extended parts of the body, or on areas between joints, segments, or other areas close to one another. Thurm (1964) used electrophysiological and morphological techniques to study the hair plate and campaniform sensilla on the honey bee and determined that compression of the tubular body in the dendrite of the sensory receptor is the mechanism by which the receptors are stimulated.

Dethier (1963) divided mechanoreceptors into two classes, velocity sensitive and pressure sensitive, based on their physiological responses to stimuli. Velocity sensitive receptors are stimulated by the interaction of the insect and its surrounding environment; the receptor firing only during a change in stimulus. Pressure sensitive receptors provide information to the insect concerning the position of the various body segments and appendages in relation to each other; the receptor responding continually to stress or deformation. Slifer (1961) and McIver (1975) reviewed the fine structure of cuticular mechanoreceptors, including external morphology, nerve innervation, and possible functions of the receptors.

Chemoreceptors

Altner and Prillinger (1980) presented a detailed review on the ultrastructure of olfactory, gustatory, thermo- and hygrometers in invertebrates, concentrating on those receptor types found in the insects. They assailed the use of external morphological features alone as a means of categorizing sensilla types. Instead, a classification scheme based on several types of morphological characteristics including presence or absence of pore(s) and the number of associated sensory cells was outlined.

Zacharuk (1980) also prepared an extensive literature review on insect chemosensilla studies which have taken place the past ten years.

Dethier (1953) divided the chemical sensing ability of insects into three groups; olfactory, gustatory, and a common chemical sense. Olfactory receptors respond to low concentrations of chemicals volatile at room temperature; gustatory receptors respond to higher concentrations of chemicals which might not be volatile at room temperature (Dethier 1953). Common chemical sense is a type of chemoreception separate from gustation or olfaction. This sense is stimulated by high concentrations of irritating substances such as ammonia or chlorine. Even when olfactory receptors are removed, insects still react to high concentrations of these substances. The sites of stimulation were not located (Dethier 1953).

Slifer (1960) reported on a dye technique for rapidly identifying chemoreceptors in the insect cuticle. She found that by placing prepared whole specimens into a 0.5% solution of crystal violet, and then clearing the specimens in xylol, permeable areas on the cuticle, and pores at the tips of chemoreceptors would be stained.

Ovipositor Sensilla

Salt (1937) provided some of the first evidence of chemoreceptors being on ovipositors when he observed that the female Trichogramma evanescens (Westwood), a parasitic hymenopteran, determines whether or not its host has been parasitized only after the ovipositor has been inserted. Lloyd (1940) and Varley (1941) in separate experiments, also observed that the ovipositors of parasitic hymenopterans might be sensitive to stimuli while the ovipositor is inserted in the host. Wolbarsht and Dethier (1958) used electrophysiological techniques to demonstrate the presence of single and multiple innervated chemoreceptors on the ovipositor and other areas on the blow fly, Phormia regina, (Meigen). They observed that singly innervated sensilla respond to chemical but not mechanical stimulation, and that multiple innervated sensilla respond to both chemical and mechanical stimulation. Wallis (1962) in follow-up research, found through behavioral and electrophysiological studies the presence of olfactory pegs on the anal leaflets of Phormia regina. Wallis demonstrated the sensitivity of these pegs to solutions of NaCl, Na₂CO₃, and (NH₄)₂CO₃; he surmised that the pegs mediated oviposition in the blowfly.

Ovipositor sensilla have been observed to occur in other insects as well. Hawke (1973) described the presence

of multicellular sensilla and single cell campaniform sensilla on the ovipositor of the Orgilus lepidus (Musebeck), a parasitic hymenopteran. Based on behavioral studies, it was suggested that the campaniform sensilla detected stress in the ovipositor cuticle and the multiple innervated sensilla respond to ovipositional stimuli or deterrents. Hooper (1972) used scanning and transmission electron microscopy to examine the ovipositor of the face fly, Musca autumnalis (De Geer). Long tactile hairs, campaniform sensilla, multiple innervated dendrites, and anal leaflet pegs were found on the ovipositor. Based on morphological evidence such as number of dendrites and, for the anal leaflet pegs, size of the pore, it was deduced that both gustatory and olfactory receptors were present. This was also the first report of a fly ovipositor possessing campaniform sensilla. Behan and Ryan (1977), working with the carrot rust fly, Psila rosa (F.) and the cabbage root fly, Delia brassicae (Weidemann), observed numerous sensory receptors on both ovipositors. P. rosa was found to possess only trichoid sensilla on its ovipositor. Behan and Ryan assumed that most of these sensilla were mechanoreceptors, although they did point out that previous research had determined trichoid sensilla to be olfactory receptors on certain insect antennae. D. brassicae possesses trichoid

sensilla, basiconic sensilla, and styloconic sensilla. It was noted that each trichoid sensilla was innervated by a single neuron, and therefore believed to serve as mechanoreceptors. While the number of dendrites that innervated the other two types of sensilla was not reported, Behan and Ryan proposed that the styloconic sensilla were contact chemoreceptors, and that the basiconic sensilla were possibly olfactory receptors, based solely on the two receptor types location on the ovipositor. Greany (1977), working with Biosteres (Opius) longicaudatus (Ashmead), a braconid wasp, also utilized scanning and transmission electron microscopy to detail types of receptors present on the ovipositor, and suggested possible functions of the receptors based on morphological characteristics. Results demonstrated the presence of two receptor types; only one of which was visible externally. This receptor was observed to possess a pore at the tip of the dome-shaped peg, and innervated by two neurons. One neuron terminates at the base of the receptor and the other terminates at the pore opening. These receptors were presumed to function as a contact chemoreceptor, with a possible mechanoreceptor function. The second receptor type is beneath the cuticle of the ovipositor and is innervated by a single dendrite. It was proposed that this receptor type functions only as a

mechanoreceptor, due to its location in the cuticle and single neuron innervation.

Yamaoka (1971) showed that by destroying the sensory hairs on the anal papillae in female silkworm moth, Bombyx mori (L.), the egg-laying behavior could be disrupted. Yamaoka observed that the female, through the use of the ovipositor, could detect 3-dimensional relationships of the oviposition site. Chadha and Roome (1980) reported that sensory hairs on the ovipositor, antennae, and tarsi of two noctuid moths were involved in oviposition site selection. The authors proposed the hairs on ovipositor prevented the moths from ovipositing on surfaces which may be chemically harmful to the eggs.

MATERIALS AND METHODS

Adult females of H. bajulus were selected from the VPI & SU old house borer colony; additional females were obtained from Dr. S. Cymorek in West Germany. Whole mounts of ovipositors were examined by light microscopy. A total of ten ovipositors were used to obtain the mean lengths of the ovipositor and the individual sections.

Measurements of the 8th abdominal segment were taken from the base of the 8th sternite to the distal edge of the 8th sternum. Measurements of the intersegmental membrane 8/9 were taken from the distal edge of the 8th sternum to the proximal edge of the 9th segment. Measurements of the 9th abdominal segment were taken from the base of the 9th segment to the tip of the vulva. Total ovipositor length was calculated by adding the lengths of the three sections. The gonostyli were not included in the total ovipositor length due to the variations in angle of the individual styli.

Counts of sensory receptor types and numbers were taken from scanning electron microscope (SEM) photographs and from mounted specimens observed under the light microscope (LM). Measurements of the various sensory receptors were obtained from the SEM photographs and from the mounted specimens. Individual receptors were measured from the base of the receptor to its tip.

Material for SEM was prepared by fixing in a solution of 5% glutaraldehyde/3% formaldehyde/picric acid in 0.1 M Na cacodylate for 48 hours. The specimens were washed in 0.1 M Na cacodylate buffer and post-fixed in 1% osmium tetroxide in 0.1 M Na cacodylate buffer for 2 hours. After fixation, the specimens were dehydrated in an ethanol series (20, 40, 60, 80, 100, 100, 100). Following dehydration, specimens were critical point dried in a Ladd critical point dryer, using CO₂. The specimens were then mounted on stubs with double-sided sticky tape and coated with approximately 200Å^o of gold in an SPI sputter coater. Silver paint was applied to a portion of the specimens to reduce charging. The specimens were viewed and photographed using a JEOL JSM-35 C SEM at an accelerating voltage of 15 kV.

Specimens for transmission electron microscopy (TEM) were fixed, post-fixed and dehydrated in the same manner as the SEM samples. Following dehydration, the specimens were embedded in Poly/Bed 812 (Polysciences Inc., Warrington, PA). Sections were cut at 800 to 1000Å^o with a diamond knife on an LKB Ultratome IV and picked up on Formvar coated, carbon stabilized copper grids. The specimens were stained with uranyl acetate and Reynold's lead citrate for five minutes in each. The specimens were viewed and photographed using a Zeiss EM10-CA transmission electron microscope at an accelerating voltage of 80 kV.

Specimens for light microscopy photography were prepared in the same manner as the TEM specimens. Thick sections were taken at 1 μ with a glass knife on an LKB Ultratome IV ultramicrotome. The sections were stained for 20-30 seconds on a hot plate at a low setting using 1% toluidine blue in 1% borax. The specimens were observed and photographed using a Zeiss photomicroscope I.

RESULTS

General Morphology of the Ovipositor

The ovipositor of the female H. bajulus is a long, tubular structure formed by the modified 8th and 9th abdominal segments (Fig. 1). These two segments are retracted, one within the other, into the 7th abdominal segment when not in use. When fully extended the ovipositor is, on the average, 18.55 mm long from the proximal edge of the 8th segment to the distal edge of the 9th segment, and 0.86 mm at its widest point (segment 8)(Table 1). The 9th abdominal segment forms the genitalia of the female (Lindroth 1957). A pair of styli are located at the distal edge of the 9th segment.

Segment 7 and 8. The 7th abdominal segment is modified to form a protective covering for the retracted ovipositor. The last visible spiracle is located proximally on the pleural region of this segment. The tergite and sternite of segment 7 are densely covered with setae, particularly along their borders.

The 8th abdominal segment is modified to form the basal part of the ovipositor (Fig. 2). This segment has a mean length of 2.67 mm and is 0.86 mm at its widest point. The tergum is membranous medially, but sclerotized laterally,

Figure 1. Partially extended ovipositor of *H. bajulus*, ventral view, showing intersegmental membrane (IM); baculum (BA); hemisternite (HS); coxite (CO); stylus (ST); vulva (VU).

Figure 2. Basal segment of ovipositor, lateral view, showing modified abdominal segments 7 and 8.

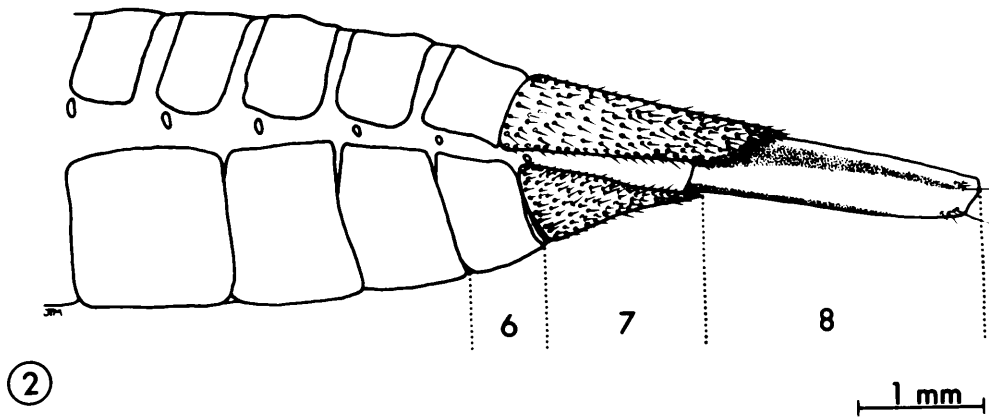
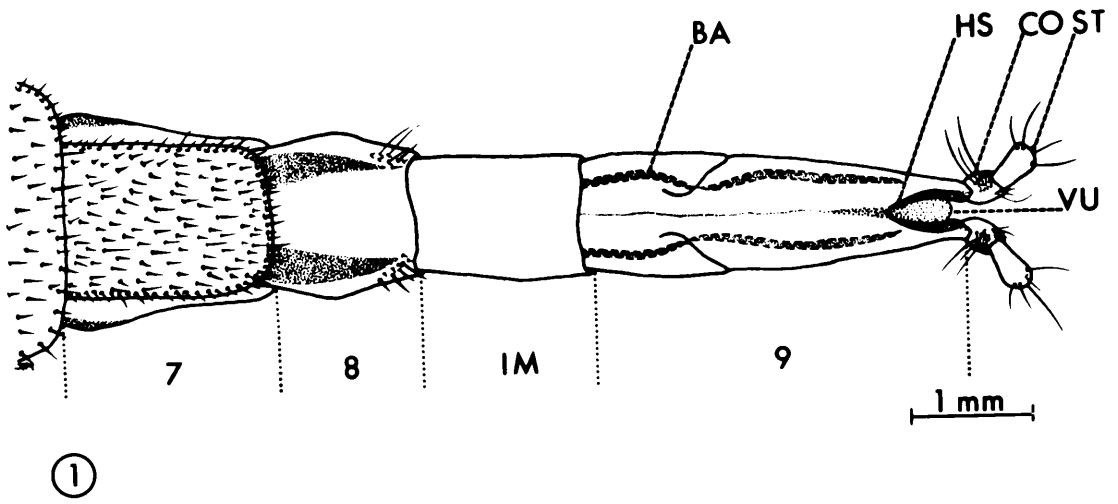


Table 1. Measurements of ovipositor¹ and its segments

Ovipositor Segments	x	S.D.	Range
<u>OVIPOSITOR</u>			
Length (mm)	18.85	1.24	15.95 - 20.27
Width (mm)	0.86	0.08	0.68 - 0.99
<u>SEGMENT 8</u>			
Length (mm)	2.67	0.05	2.57 - 2.70
Width (mm)	0.86	0.08	0.68 - 0.99
<u>INTERSEGMENTAL MEMBRANE 8/9</u>			
Length (mm)	10.01	0.96	7.57 - 11.00
<u>SEGMENT 9</u>			
Length (mm)	6.16	0.34	5.72 - 6.66
Width (mm)	0.54	0.56	0.45 - 0.63
<u>STYLUS</u>			
<u>Coxite</u> Length (μ)	199.86	11.41	175.00 - 216.22
<u>Stylus</u> Length (μ)	187.88	19.49	152.37 - 214.39

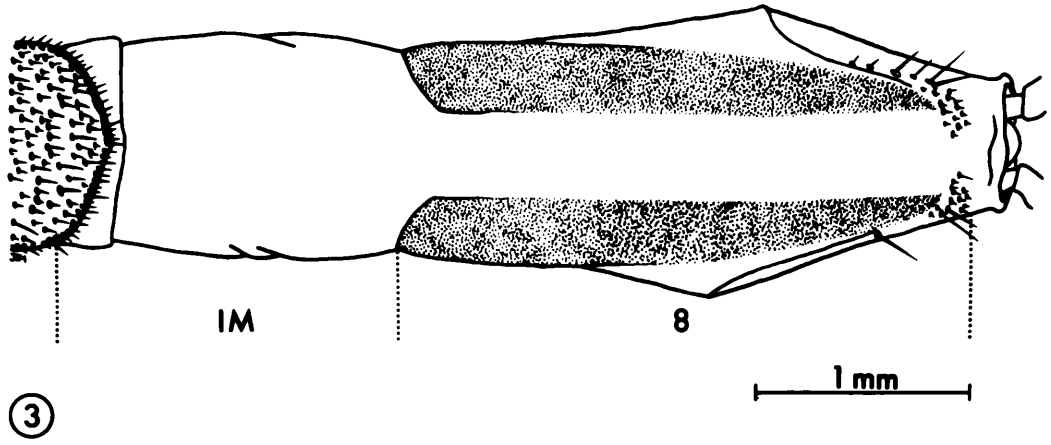
¹N=10 ovipositors

the proximal edges of which extend lateroventrally (Fig. 3). The tergum has a smooth, unsculptured cuticle. Two types of sensory receptors are located on the distal edge of the tergum: tactile hairs, and trichoid sensilla. Approximately 6 long tactile hairs (\bar{x} length = 0.39 mm) are found along the laterodorsal edge. Approximately 25 trichoid sensilla (\bar{x} length = 0.05 mm) are interspersed among the tactile hairs and along the distal medial edge (Table 2).

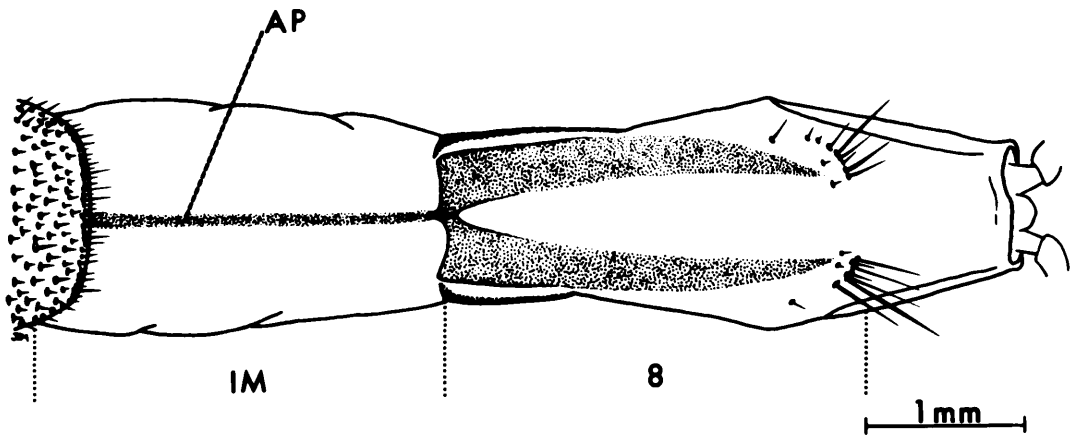
The 8th sternal sclerite is split along the midline to form a bifurcated sternite joined together only at the proximal, mediastinal area (Fig. 4). Arising from the proximal tip of this sternite is an internal median apodeme which extends free into the abdominal cavity. Muscles arise from the proximal tip of this apodeme and insert into the proximal lateroventral edges of the 8th abdominal tergite. The cuticle on the sternum of this segment has a leaflike pattern (Fig. 9). Two types of setae located on the distal ventral edge correspond to those types found dorsally. An average of 12 long tactile hairs (\bar{x} length = 0.47 mm) are distributed along the lateral and medial edge; approximately 8 trichoid sensilla (\bar{x} length = 0.05 mm) are interspersed among the tactile hairs.

Figure 3. Modified abdominal segment 8, dorsal view.

Figure 4. Modified abdominal segment 8, ventral view. Note internal apodeme (AP).



③



④

Table 2. Type, number and length of sensilla on ovipositor¹ segments

Ovipositor Segment	\bar{x}	S.D.	Range
<u>SEGMENT 8</u>			
<u>Tergum:</u>			
Tactile hairs			
number	6.0	1.34	4.0 - 9.0
length (mm)	0.39	0.13	0.16 - 0.68
Trichoid receptors			
number	25.0	4.58	17.0 - 33.0
length (mm)	0.05	0.13	0.02 - 0.16
<u>Sternum:</u>			
Tactile hairs			
number	12.1	2.98	8.0 - 18.0
length (mm)	0.46	0.02	0.18 - 0.75
Trichoid receptors			
number	8.0	2.37	3.0 - 11.0
length (mm)	0.05	0.03	0.02 - 0.13
<u>SEGMENT 9</u>			
<u>Tergum:</u>			
Campaniform receptors			
number	120.70	12.03	108.0 - 147.0
Basiconic receptors			
number	62.0	12.99	45.0 - 88.0
<u>Sternum:</u>			
Campaniform receptors			
number	124.6	11.74	105.0 - 141.0
Basiconic receptors			
number	65.7	5.62	56.0 - 74.0
<u>STYLUS</u>			
<u>Coxite:</u>			
Tactile hairs			
number	11.4	2.33	9.0 - 14.0
length (μ)	102.42	44.42	42.50 - 195.92
Long Trichoid receptors			
number	24.4	2.16	21.0 - 29.0
length (μ)	22.85	6.10	10.91 - 37.70
Short Trichoid receptors			
number	12.8	2.15	10.0 - 16.0
length (μ)	3.32	0.60	2.20 - 4.60
Basiconic receptors			
number	32.7	2.39	27.0 - 38.0
length (μ)	1.05	0.08	0.92 - 1.20
<u>Stylus:</u>			
Tactile hairs			
number	5.4	0.49	5.0 - 7.0
length (μ)	107.06	43.33	37.70 - 186.67
Basiconic receptors (tip)			
number	30.1	4.18	24.0 - 38.0
length (μ)	2.90	1.92	1.30 - 11.30
Basiconic receptors (sides)			
number	14.4	2.11	11.0 - 18.0
length (μ)	1.52	0.16	1.33 - 1.80

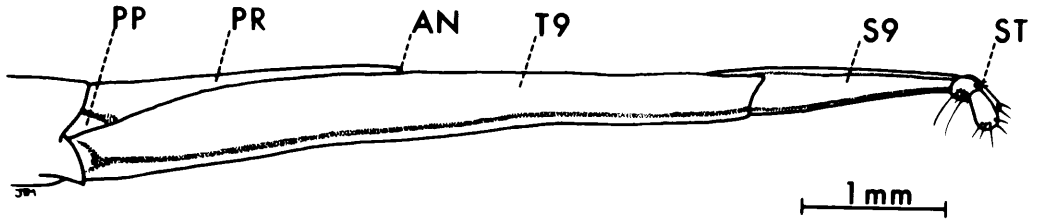
¹N=10 ovipositors

Figure 5. Modified abdominal segment 9, lateral view, showing paraproct (PP); proctiger (PR); anus (AN); tergum (T9); sternum (S9); stylus (ST).

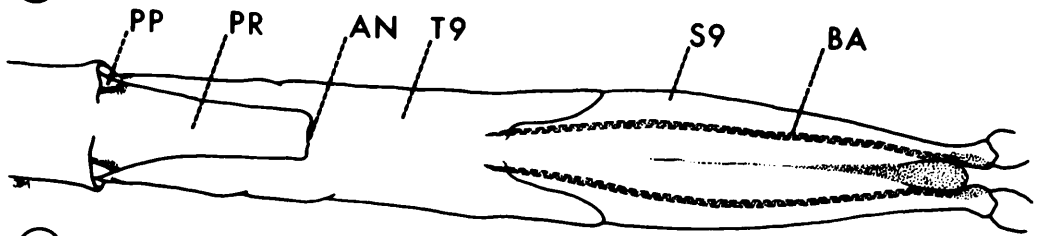
Figure 6. Modified abdominal segment 9, dorsal view.

Figure 7. Modified abdominal segment 9, ventral view.

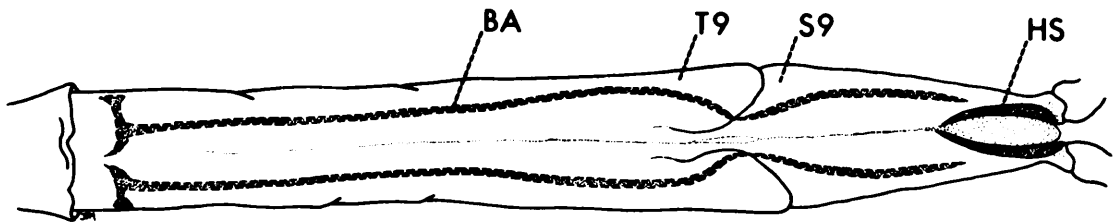
Figure 8. Distal tip of abdominal segment 9, ventral view, showing attachment of styli.



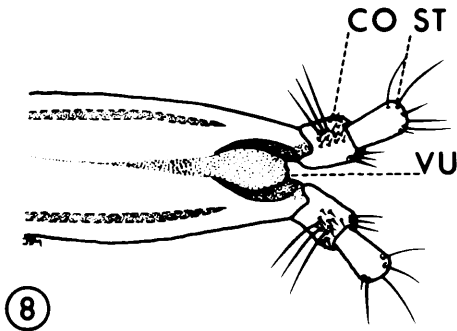
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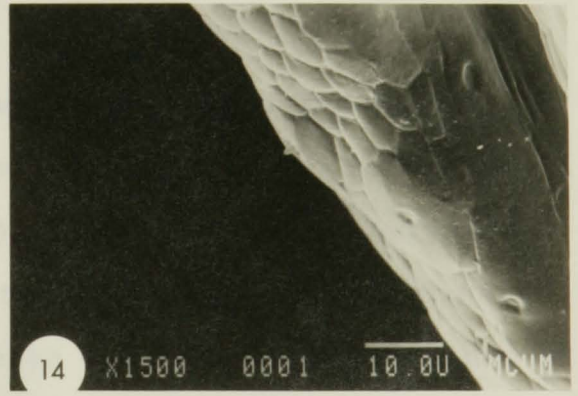
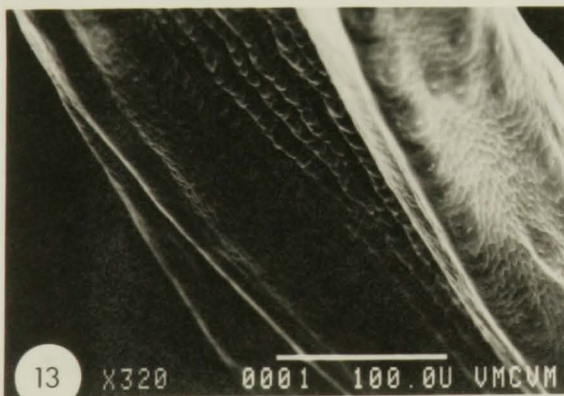
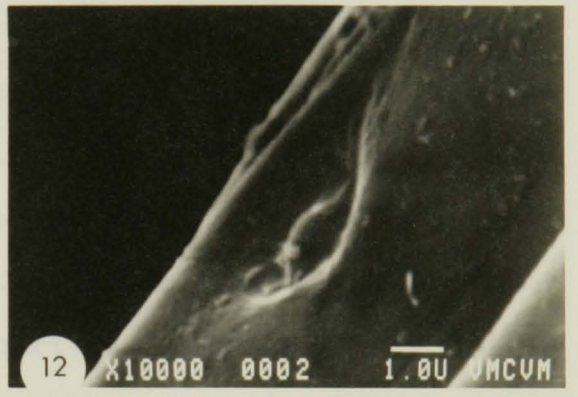
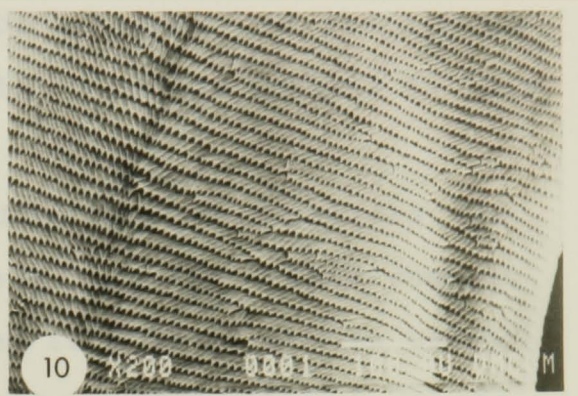
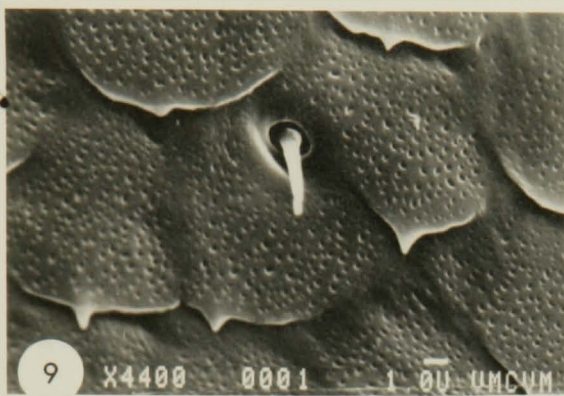


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- Figure 9. Cuticle pattern of 8th sternum.
- Figure 10. Cuticle of intersegmental membrane 8/9.
- Figure 11. Cuticle pattern of 9th tergum. Note basiconic sensillum.
- Figure 12. Campaniform receptor on 9th tergum.
- Figure 13. Cuticle pattern of 9th sternum. Note sensilla.
- Figure 14. Basiconic sensillum and campaniform receptors on 9th sternum.



8/9 Intersegmental Membrane. The 8/9 intersegmental membrane makes up half the length of the ovipositor. This membrane is approximately 10.01 mm long and the cuticle is arranged in rows of closely packed sagittate projections (Fig. 10). There are no visible sensilla located on this membrane.

Segment 9 The 9th abdominal segment comprises the genital segment in the female H. bajulus. This segment averages 6.16 mm in length and is 0.54 mm at its widest point (Fig. 5). Located dorsal to this segment at the proximal end is the proctiger, a short flattened tubular structure which bears the anus. Situated on either side of the basal portion of the proctiger are a pair of small lobes known as the paraprocts. The proctiger, possibly the remnants of the 10th abdominal tergite, is separated from the paraprocts by a pair of short, sclerified internal rods (Fig. 6). A pair of styli are situated at the distal end of the 9th segment.

The 9th tergum is relatively unmodified and membranous for most of its length. The cuticle of the 9th tergum has a reticulate pattern (Fig. 11). The 9th tergum extends lateroventrally to form a protective sheath around most of the 9th sternum. Located beneath the lateroventral edges of the tergal cuticle are a pair of sclerotized support rods (=

baculi), which extend the length of the tergum. There are two types of sensory receptors located along the lateroventral edges of the tergum: campaniform receptors and basiconic sensilla (Table 2, Figs. 11 and 12). An average of 121 campaniform receptors and 62 basiconic sensilla are located along these edges.

The 9th sternum extends out from the protective sheath of the 9th tergum approximately a third of its length. The 9th sternite is divided along its midline to form a pair of hemisternites which surround the vulva (Fig. 7). Articulating with each hemisternite at its distal end is a stylus; the vulva opens distally between the stylus-bearing arms of the two hemisternites (Fig. 8). The dorsal side of the 9th sternum has two baculi just beneath the cuticle which extend the length of the visible dorsal part of the sternum (Fig. 6). Ventrally there are a pair of baculi which extend from the proximal tips of the hemisternites to the distal tip of the lateroventral edges of the 9th tergum. The cuticle of the 9th sternum is formed into folds medially, both on the dorsal and ventral sides; laterally the cuticle is reticulate-coriaceous in texture (Fig. 13).

The 9th sternum has two types of sensilla which correspond to those types found on the 9th tergum. Approximately 125 campaniform receptors and 66 basiconic

sensilla are located on the laterodorsal side of the 9th sternum (Fig. 14). Approximately a third more campaniform receptors and basiconic sensilla are located on the ventral side than on the dorsal side of the 9th sternum (Table 2, Figs. 15, 16, 17).

Styli. The styli of the ovipositor consist of a basal coxite and an apical stylus (Fig. 18). The coxites have an average length of 199.86 μ each. The styli have a mean length of 187.88 μ each.

The coxite bears four types of sensory receptors: long tactile hairs, medium trichoid sensilla, short trichoid sensilla, and basiconic sensilla. Approximately 11 long (\bar{x} length = 102.42 μ) tactile hairs are located along the distal dorsolateral border and mediad ventrally (Fig. 18). Interspersed among these long tactile hairs and in the medial ventrolateral portion of the coxite are, on the average, 24 medium (\bar{x} length = 22.85 μ) trichoid sensilla (Fig. 19). Situated around the peripheral area of the medium trichoid sensilla region are approximately 13 short (\bar{x} length = 3.32 μ) trichoid sensilla (Fig. 20). The cuticle in this region has a reticulate structure. Located around the areas of trichoid sensilla and long tactile hairs, in smooth cuticle, are an average of 33 short (\bar{x} length = 1.05 μ) basiconic sensilla (Fig. 21).

Figure 15. Basiconic sensilla and campaniform receptors on 9th sternum.

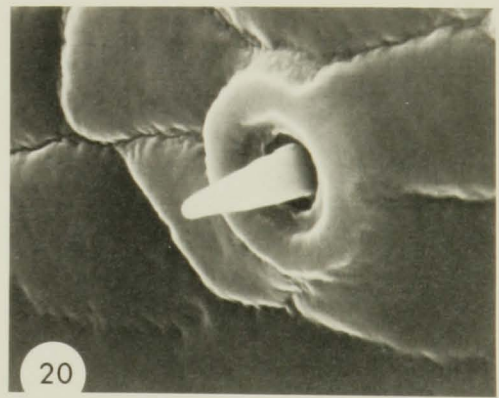
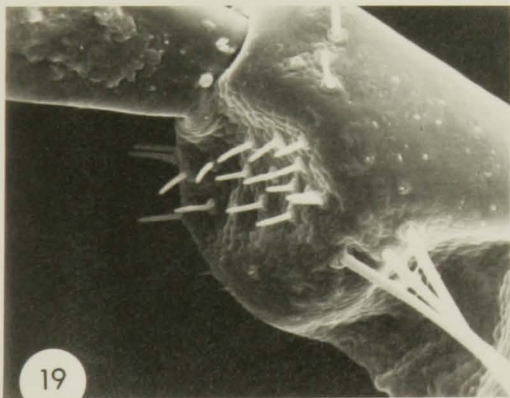
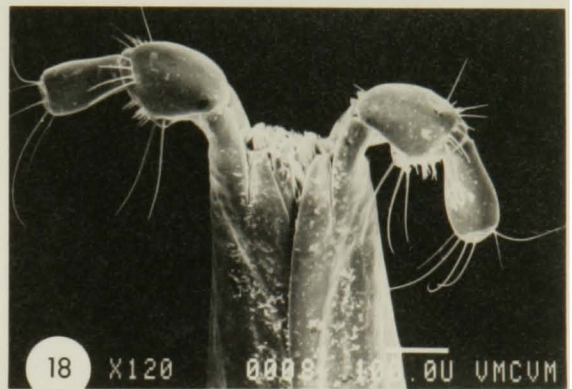
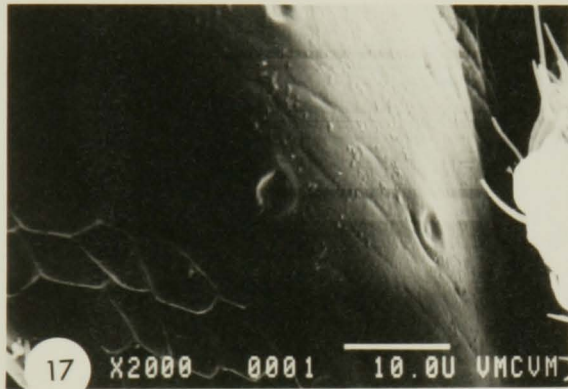
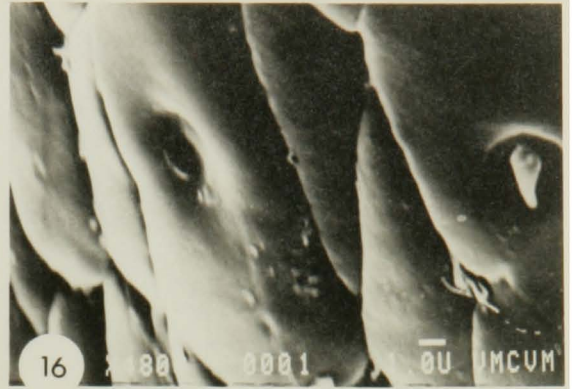
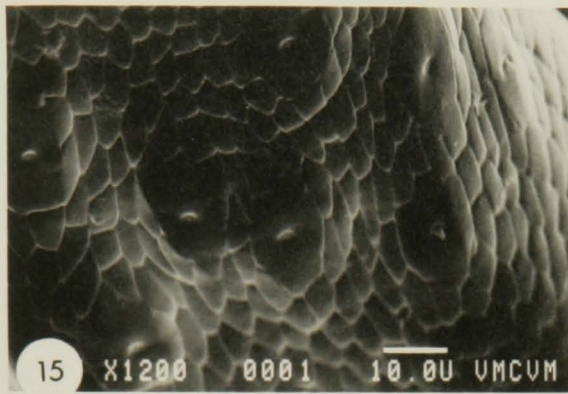
Figure 16. Close-up of campaniform receptor and basiconic sensillum on 9th sternum.

Figure 17. Campaniform receptors on 9th sternum.

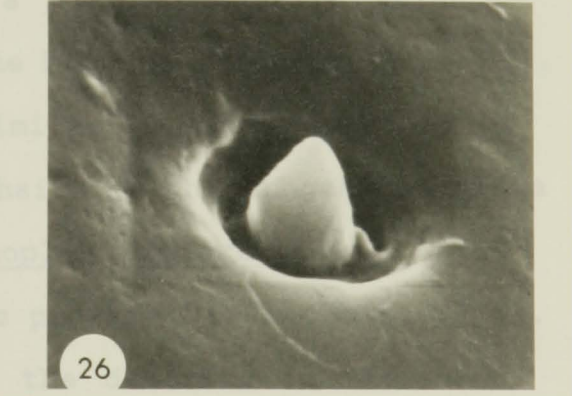
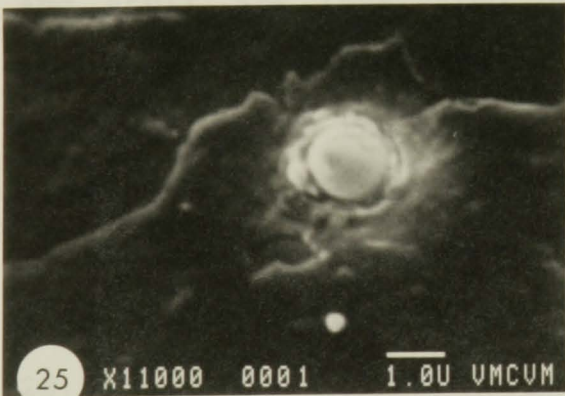
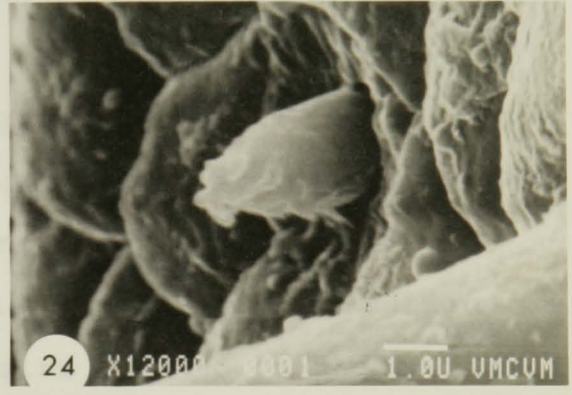
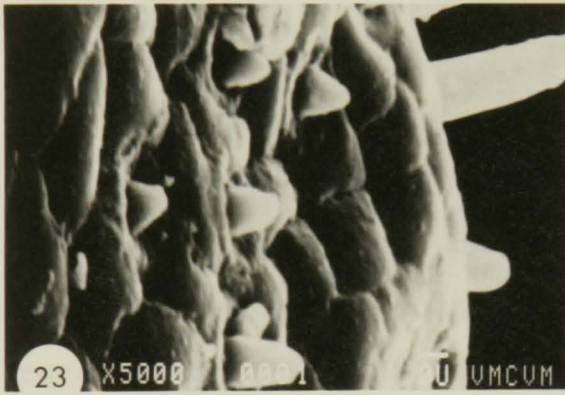
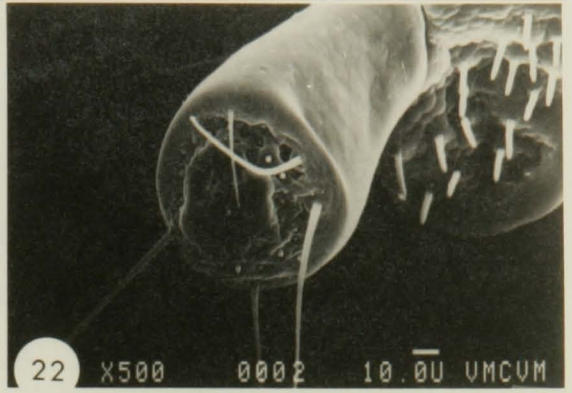
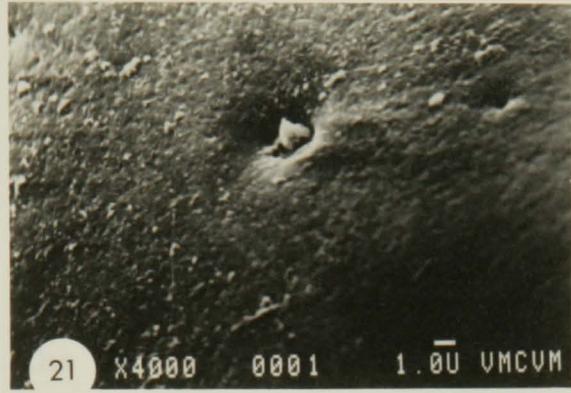
Figure 18. Distal tip of ovipositor, ventral view, showing attachment of coxites and styli. Note long tactile hairs and medium trichoid sensilla on coxites.

Figure 19. Medium trichoid sensilla on coxite (500x).

Figure 20. Short trichoid sensillum on coxite (5000x).



- Figure 21. Basiconic sensillum on coxite.
- Figure 22. Long tactile hairs and short basiconic sensilla on stylus.
- Figure 23. Arrangement of basiconic sensilla on stylus.
- Figure 24. Close-up of basiconic sensillum on stylus tip.
- Figure 25. Basiconic sensillum on lateral side of stylus.
- Figure 26. Basiconic sensillum on lateral side of stylus (12000x).



The stylus bears two types of sensilla: long tactile hairs and short basiconic sensilla (Fig. 22). Surrounding the periphery of the distal edge of the stylus are approximately 5 long (\bar{x} length = 107.06 μ) tactile hairs. Interspersed among and to the interior of this ring of hairs are located approximately 30 short (\bar{x} length = 2.90 μ) basiconic sensilla (Figs. 23, 24). Approximately 14 short (\bar{x} length = 1.52 μ) basiconic sensilla are distributed over the rest of the stylus (Figs. 25, 26). The stylus cuticle is smooth along its entire length, and reticulate at its distal tip.

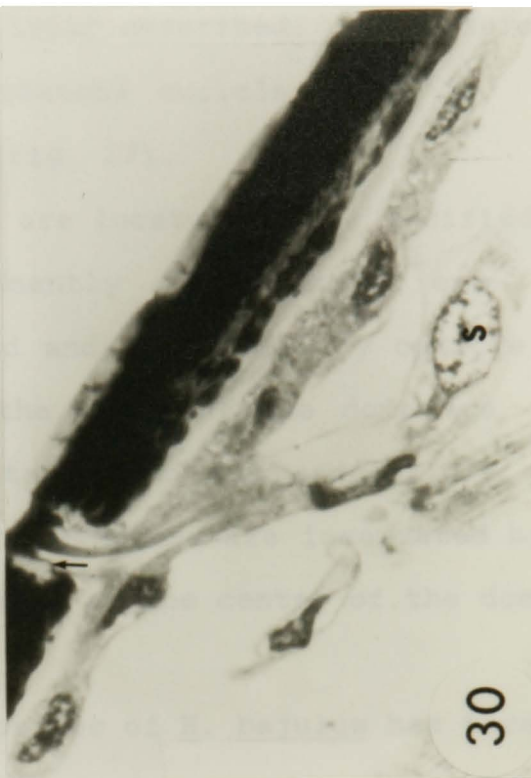
Fine Structure of Ovipositor Sensilla

Mechanoreceptors. The ovipositor of H. bajulus has two types of sensilla that function strictly as mechanoreceptors: long tactile hairs, and campaniform receptors. The long tactile hairs located on the coxites and styli are innervated by a single dendrite which terminates in the cuticle at the base of the hair (Fig. 27). The dendrite of the hair is similar to that described by Slifer (1961) for the tactile hairs on the subgenital plate of the male grasshopper Melanoplus differentialis. The dendrite has knobby projections proximal to its tip (Figs. 28, 29). Closely adhering to the dendrite is the dark scolopale cap. The dendrite is embedded in a granular

- Figure 27. Base of a long tactile hair on the coxite. Note dendrite innervation into hair (arrow). (IM)
- Figure 28. Dendrite of long tactile hair. Note granular substance surrounding dendrite tip. (TEM)
- Figure 29. Dendrite of long tactile hair. Note knobby projections at bottom portion of dendrite (d), and dark scolopale surrounding dendrite tip. (TEM)
- Figure 30. Campaniform receptor and associated dendrite. Note sensory cell (s) and cuticular hinge (arrow). (IM)



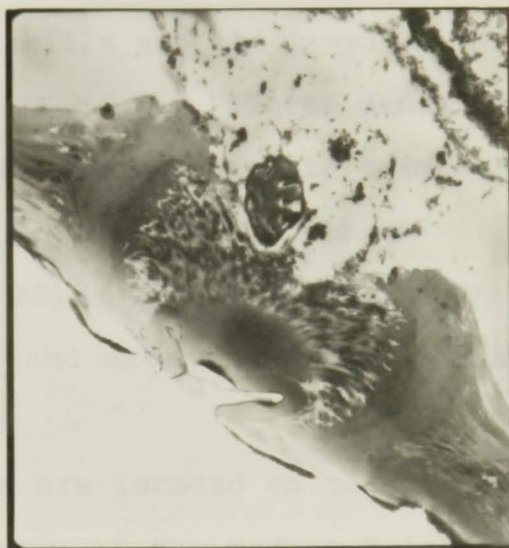
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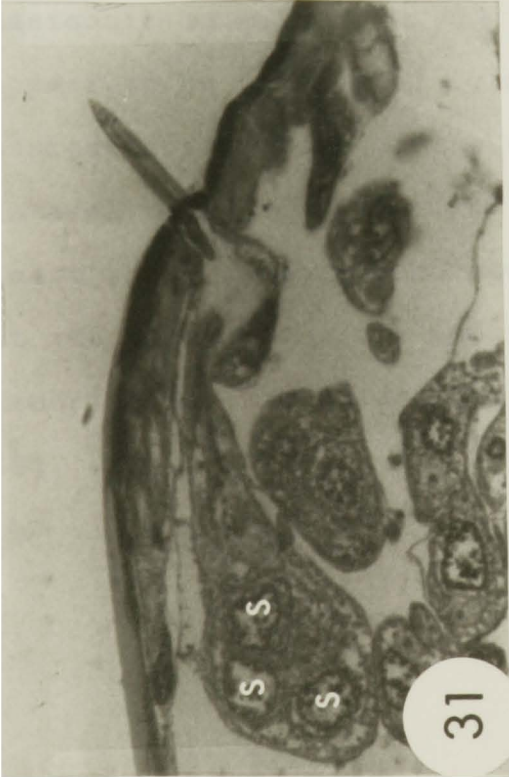
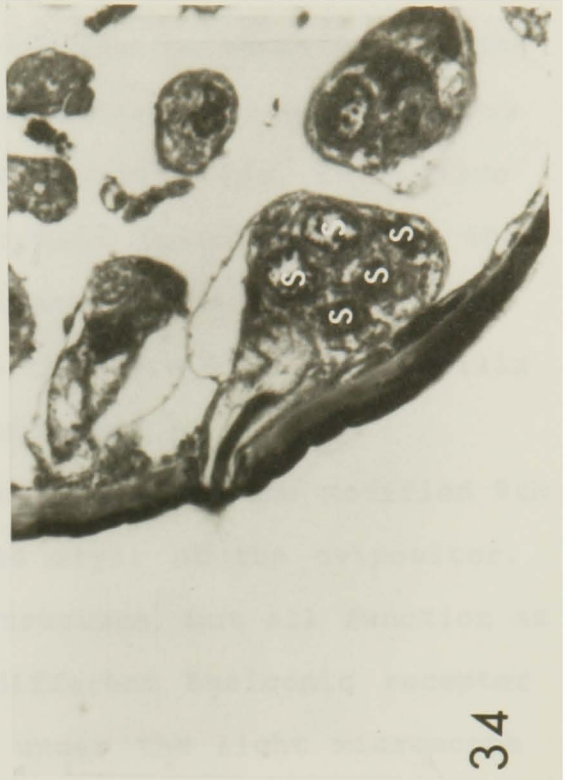
matrix similar to what Slifer (1961) described. The base of the hair is surrounded by thickened cuticle which is situated in a membranous ring (Fig. 27).

The campaniform receptors are located on the modified 9th abdominal segment, predominantly at the distal end. These receptors are dome-shaped and surrounded by cuticle (McIver 1975). Connected to the edges of the dome are cuticular hinges which are attached to the endocuticle (McIver 1975). The campaniform receptors are innervated by a single dendrite which terminates at the center of the dome (Fig. 30).

Chemoreceptors. The ovipositor of H. bajulus has three types of sensilla which function as chemoreceptors: medium trichoid sensilla, short trichoid sensilla, and basiconic sensilla. The medium trichoid sensilla are located on the coxites of the styli. These sensilla are thick-walled and situated in a membranous socket (Fig. 31). Three dendrites innervate these sensilla, one of which appears to terminate at the base of the receptor, thus indicating a mechanoreceptor function (Fig. 32). The other dendrites enter the lumen of the receptor and extend upwards towards the tip (Fig. 33).

The short trichoid sensilla are located on the coxites of the styli, around the periphery of the medium trichoid

- Figure 31. Medium trichoid sensillum of coxite. Note sensory cells (s) and dendrites (d). (LM)
- Figure 32. Innervation of dendrite into base of receptor (arrow). (LM)
- Figure 33. Medium trichoid sensillum. Note dendrite extending into receptor lumen (arrow). (LM)
- Figure 34. Short trichoid sensillum. Note sensory cells (s) and associated dendrites extending into receptor lumen. (LM)



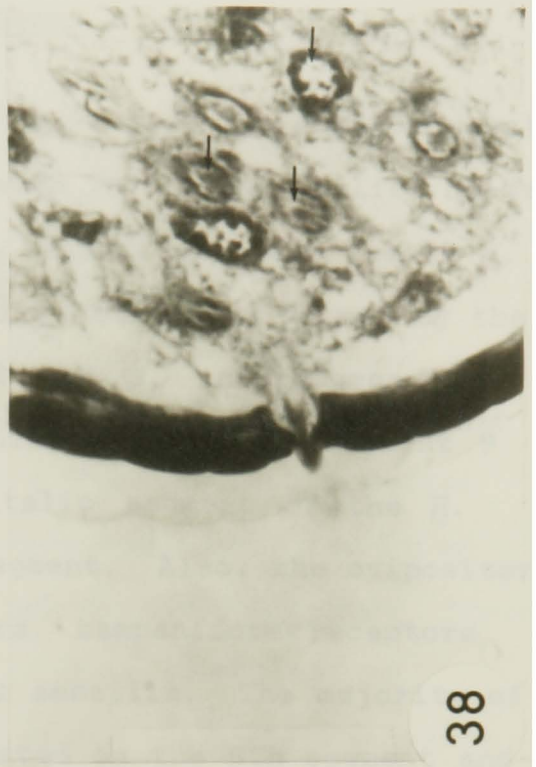
sensilla. These sensilla are similar in structure to the medium trichoid sensilla, being situated in a membranous socket surrounded by a ring of cuticle (Fig. 20). Five sensory neurons appear to innervate these receptors; the dendrites extending into the lumen of the receptor (Fig. 34). One dendrite attaches to the base of these sensilla and serves a mechanoreceptor function.

The basiconic sensilla are located on the modified 9th abdominal segment, coxites, and styli of the ovipositor. These sensilla vary in their structure, but all function as contact chemoreceptors. The different basiconic receptor types viewed and photographed under the light microscope appear to have varying numbers of sensory neurons. The basiconic receptors on the modified 9th abdominal segment appear to be innervated by a single dendrite (Fig. 35). The basiconic receptors of the coxites and the receptors on the lateral sides of the styli appear to be innervated by at least three sensory dendrites (Fig. 36). The basiconic pegs at the stylus tip are innervated by at least one sensory dendrite and may be innervated by several others (Figs. 37, 38).

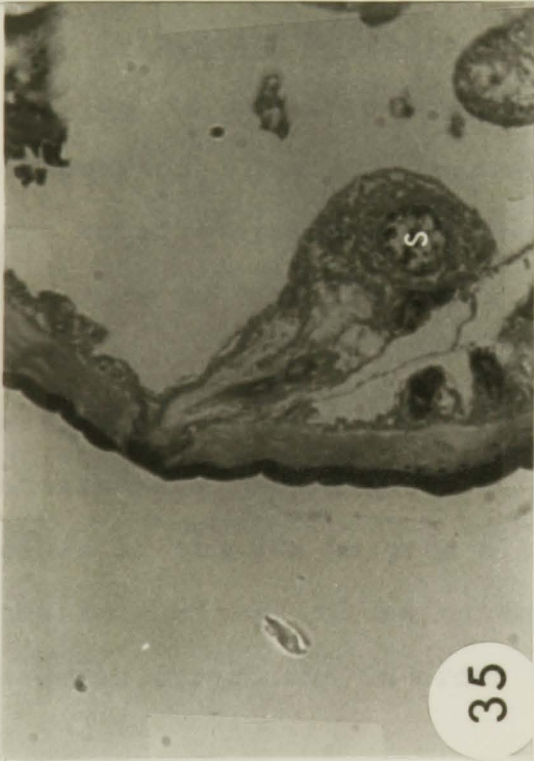
- Figure 35. Basiconic receptor of segment 9. Note single sensory cell (s) and dendrite. (LM)
- Figure 36. Basiconic receptor on coxite. Note three sensory cell (s) and dendrites (d). (LM)
- Figure 37. Basiconic receptor at tip of stylus. Note single sensory cell (s); also note nearby sensory cells (arrows). (LM)
- Figure 38. Basiconic receptor at tip of stylus. Note the number of sensory cells (arrows point to three). (LM)



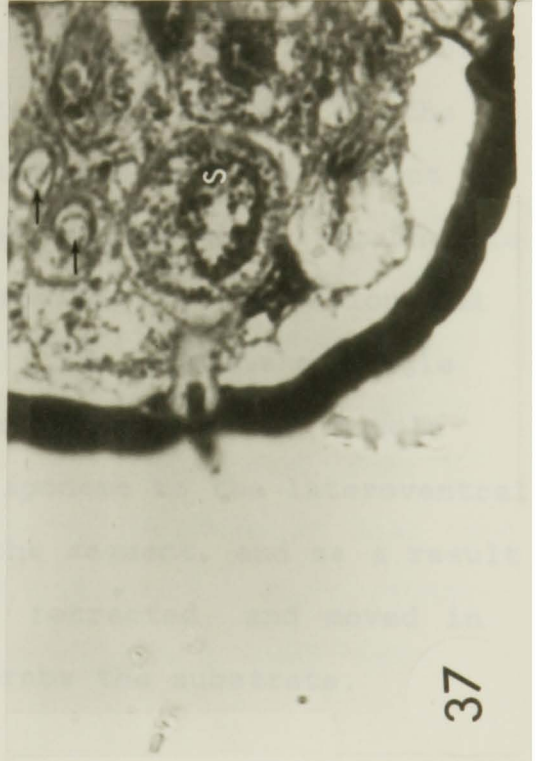
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DISCUSSION

Cerambycids are believed to have lost the gonapophyseal ovipositor (Gustafson 1950, Matsuda 1976); this belief holds true with the female H. bajulus ovipositor. The female H. bajulus ovipositor is a retractable structure formed by the elongated abdominal segments 8 and 9, intersegmental membrane 8/9, and the appendicular remnants of segment 9 (coxites and styli). The genitalic segment of the H. bajulus ovipositor is the 9th segment. Also, the ovipositor possesses numerous tactile hairs, campaniform receptors, trichoid sensilla, and basiconic sensilla. The majority of these sensory receptors are located on the 9th segment and on the styli.

Ovipositor Morphology. The 8th abdominal segment of H. bajulus is modified to form the basal segment of the ovipositor. The 8th segment comprises only 14 percent of the total ovipositor length. The apodeme which attaches to the base of the 8th sternite provides for extension and retraction of the 8th segment. The apodeme's single articulation with the 8th sternite, plus the muscle attachments from the tip of the apodeme to the lateroventral edges of the 8th tergite allow the segment, and as a result the ovipositor, to be extended, retracted, and moved in several directions in order to probe the substrate.

There is a significantly greater ($p < 0.05$) number of long tactile hairs on the ventral side than on the dorsal side of the 8th segment. Also, there is a significantly greater ($p < 0.05$) number of trichoid sensilla located on the dorsal side than on the ventral side of the 8th segment. The long hairs on the 8th segment probably function as mechanoreceptors, providing initial information as to the height of the crack or crevice. The trichoid sensilla probably also function as mechanoreceptors, providing information on the physical texture of the substrate. These trichoid sensilla may serve a dual function as chemoreceptors as Boeckh (1965) found they did on insect antennae. I think that the trichoid sensilla on the 8th segment are primarily mechanoreceptors.

The intersegmental membrane 8/9 is elongated and is approximately 3.75 times longer than segment 8. Wandellock (1906) reported a membrane length of only 3 times greater than segment 8, and did not give the measurements for either. The intersegmental membrane 8/9 comprises approximately 53 percent of the total ovipositor length. This length is important to the egg-laying habits of H. bajulus. It allows the ovipositor to be extended deep into cracks and crevices of seasoned softwoods. Durr (1956) suggested the female H. bajulus deposits eggs into

appropriate cracks and crevices in wood to give the first-instars a foothold in their attempts to enter the wood. The elongation of the intersegmental membrane 8/9 greatly increases the length of the ovipositor and allows for placement of eggs into cracks of a suitable size to enhance first-instar larval penetration into the wood. Also, the placement of eggs into narrow cracks and crevices may limit their accessibility to predators or parasites. By ovipositing deep into the substrate, the female may be placing the eggs into a more constant environment and allow for a greater percentage of egg hatch.

The 9th abdominal or genitalic segment comprises 33 percent of the total ovipositor length. Located dorsal to the 9th tergum at the proximal end are the proctiger and paraprocts. The anus is located at the tip of the proctiger. The proctiger represents the remnants of the 10th tergite (Torre-Bueno 1937). Most authors (Wandellock 1906, Tanner 1927, Jeannel 1949, Crowson 1981) agree that the proctiger represents the remnants of the 10th tergite, although there is little supporting evidence to show the anterior movement of segment 10 in Coleoptera. Crowson (1981) suggested the sclerotized rods on each side of the proctiger might be partially homologous to the 9th tergite. The paraprocts are small lobes situated on either side of

the proctiger. Crowson (1981) inappropriately labeled the 9th tergum as the paraprocts.

The 9th tergum forms almost a completely enclosed sheath around the proximal two-thirds of sternum 9. There are no apparent sensory receptors on the dorsal side of tergum 9. The anus is situated dorsal to the 9th tergum, and perhaps the dorsal side of the 9th tergum is devoid of sensory receptors to prevent stimulation or injury by excretory products.

The lateroventral edges of the 9th tergum cover approximately two-thirds of the ventral portion of the 9th sternum. Located beneath the cuticle at the edges of the tergum and extending anteriorly to the basal portion of the segment are a pair of support rods, also referred to as baculi (singular=baculum). Tuxen (1970) defined baculi as the rod-like apophyses of tergum or sternum 9 in Coleoptera. The baculi provide support for the mostly membranous 9th segment.

The 9th sternum extends approximately one-third its length out beneath the 9th tergum. This finding agrees with Bitsch's (1979) opinion that the 9th tergite and sternite have been shifted one in back of the other in Cerambycidae. This theory contradicts Iuga and Rosca (1962) who reported that this segment represents the 9th gonopod. It also

contradicts Crowson (1981) who reported that the 9th sternite in female cerambycids is always divided to form a pair of valvifers. The 9th sternite is split medially to form a pair of hemisternites. This agrees with Bitsch's (1979) findings and Lindroth's (1957) definition of hemisternites. The hemisternites surround the vulva and provide support for and articulation with the styli. Approximately half of the total number of sensory receptors of segment 9 are located on sternum 9.

The gonostyli of segment 9 are subdivided into basal coxites and apical styli. This interpretation agrees with other authors (Wandellock 1906, Tanner 1927, Iuga and Rosca 1962, Matsuda 1976, Bitsch 1979, Crowson 1981), although Tanner (1927) incorrectly labeled the 9th sternum as part of the coxite. The gonostyli bear an array of long tactile hairs, trichoid sensilla, and basiconic receptors.

The gonostyli may be involved in the final determination of an oviposition site. During oviposition the styli are the most distal structures to probe the cracks and crevices of the wood. The long tactile hairs may have a mechanoreceptive function in determining whether or not the crack is of the correct size to allow the first-instar larva to penetrate the wood. The trichoid sensilla may also be mechanoreceptors, serving to detect the topography of the

crack; or they may be involved in positioning the eggs in the typical fan-shaped pattern. Some trichoid sensilla and the basiconic sensilla bear a morphological appearance to chemoreceptors. These sensilla may play an important role in determining whether or not the wood is of an appropriate type to allow for larval growth and development.

Ovipositor Sensilla. This study demonstrates the presence of both mechanoreceptors and chemoreceptors on the ovipositor of the female H. bajulus, based on external morphological features and internal cellular characteristics.

Mechanoreceptors. The female H. bajulus ovipositor possesses tactile hairs and campaniform receptors which function as mechanoreceptors. The long tactile hairs of the ovipositor are located on the coxites and styli. The hairs have grooved cuticle and a single dendrite innervation. These hairs are similar to the tactile hairs described by McIver (1975). The hairs may serve several functions. The female H. bajulus may prefer to oviposit eggs in cracks and crevices of a size suitable to allow for first-instar larval penetration. Cannon (1979) reported that H. bajulus eggs have a mean width of 0.45 mm. The long tactile hairs on the coxites and styli have a mean length of 102.42 μ and 107.06 μ respectively. However, the tactile hair lengths range

from 42.50 μ - 195.92 μ on the coxites and from 37.70 μ - 186.67 μ on the styli. Considering the fact that the tactile hairs are located both dorsally and ventrally, their combined lengths can be equal to or greater than the width of the eggs. The longer tactile hairs may be utilized in finding a crack or crevice which closely corresponds to the size of the egg. This size crack might provide protection from predators, parasites, and adverse environmental conditions, plus provide for first-instar penetration. The shorter tactile hairs may provide additional information on the topography of the substrate. Yamaoka (1971) found that sensory hairs on the anal papillae of the female Bombyx mori regulate egg laying behavior. The female H. bajulus oviposits eggs in a fan-shaped arrangement. The tactile hairs may be involved in determining the egg deposition pattern.

The campaniform sensilla on the ovipositor are located on the modified 9th abdominal segment. These sensilla are innervated by a single dendrite. McIver (1975) described similar receptors and stated they provide information on cuticle stress. As the female H. bajulus probes the wood, the campaniform sensilla may provide information on the position of the ovipositor in relation to the rest of the body, the degree of bend in the ovipositor, and the angle at

which it is bent or twisted. These sensory receptors may also provide information on the location of the eggs as they pass down the oviduct. The campaniform receptors located at the distal end of the 9th segment, near the attachment of the styli may provide information on the movement and position of the styli; especially when the eggs are passing out from the vulva.

Chemoreceptors. Based in part on Altner and Prillinger's (1980) morphological classification scheme for insect sensilla, it was determined that the ovipositor of the female H. bajulus possesses three types of chemoreceptors. The medium trichoid sensilla, located on the coxites of the styli, are innervated by three dendrites. Two of the dendrites extend into the lumen of the receptor, signifying a contact chemoreceptor function; the third dendrite inserts at the base of the sensillum, apparently serving a mechanoreceptor function. The short trichoid sensilla are innervated by five sensory dendrites. These sensilla are similar to thick-walled pegs described by Slifer (1961); a common chemical sensory function was ascribed to these types of sensilla. The number of dendrites innervating the basiconic sensilla appears to vary within and among the different types and locations. Zacharuk (1980) stated that the number of sensory neurons

can vary from 1 to as many as 10; 3-6 are the usual number of dendrites present. Whatever the dendrite number, these basiconic sensilla apparently function as contact chemoreceptors.

All three types of chemoreceptors are located on the ovipositor in areas which come in close contact with the oviposition substrate. Several factors appear to influence oviposition site selection for the female H. bajulus. Becker (1943) reported that α - and β -pinenes have a stimulatory effect on oviposition. Higgs and Evans (1977) observed that females prefer to oviposit in infested wood; they demonstrated that a pheromone was present in the larval frass which at low concentrations stimulated oviposition. The female H. bajulus has been observed dragging her ovipositor over the wood, preferring to oviposit in seasoned softwoods. The various chemoreceptors on the ovipositor may be providing information on the type of wood being probed, the amount of moisture in the wood, determining whether or not the wood is actively infested, and the level of infestation. Chadha and Roome (1980) found that chemoreceptors on the ovipositor of some noctuid moths prevent oviposition on surfaces which may be chemically harmful to the eggs. Further studies involving the physiological responses of the different sensilla types to

various chemicals are needed to ascertain the chemicals which influence and regulate the oviposition behavior of the female H. bajulus.

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VITA

Joseph T. Mares was born August 18, 1960, in Salt Lake City, Utah. He is the seventh child of Thomas P. Mares and M. Patricia Mares. In June 1978, he graduated from James W. Robinson Secondary School in Fairfax, Virginia. He began undergraduate studies at James Madison University in the same year. In 1982, he received his Bachelor of Science degree in Biology. He began graduate studies at Virginia Polytechnic Institute and State University, Blacksburg, Virginia, in 1982, working towards a Master of Science degree in Entomology. On July 2, 1983 he was happily married to Melanie Jean Pickens of Baltimore, Maryland. He is a member of Gamma Sigma Delta, Beta Beta Beta National Biological Honor Society, and the Entomological Society of America. Presently, he is a July candidate for a Masters of Science degree in Entomology.

Joseph T. Mares

ASPECTS OF THE MORPHOLOGY OF THE OVIPOSITOR OF
Hylotrupes bajulus (L.)
(COLEOPTERA: CERAMBYCIDAE)

by

Joseph Thomas Mares

(ABSTRACT)

Hylotrupes bajulus (L.) is a serious pest of seasoned softwoods. The female oviposits in the cracks and crevices of the wood, and the larvae can survive and feed in the wood for 2-10 years. The female H. bajulus has an elongated ovipositor comprised of the modified abdominal segments 8 and 9, intersegmental membrane 8/9, and pair of distal gonostyli. When not in use, the ovipositor is retracted within abdominal segment 7.

The 8th abdominal segment forms the proximal end of the ovipositor. An internal apodeme attached to the base of the 8th sternite allows for extension and retraction of the ovipositor. The intersegmental membrane 8/9 makes up half the length of the ovipositor. The 9th abdominal segment, along with the gonostyli, comprise the distal part of the ovipositor. The 9th sternum is split along the midline to form a pair of hemisternites. The gonostyli are comprised of basal coxites and apical styli. The gonostyli are the only remnants of the appendicular ovipositor.

Several types of sensory receptors are found on the ovipositor. Segment 8 has both long tactile hairs and short trichoid sensilla. Intersegmental membrane 8/9 has no visible sensory receptors. Segment 9 has campaniform receptors and short trichoid sensilla. The gonostyli have several types of sensory receptors including long tactile hairs, medium trichoid sensilla, short trichoid sensilla, and basiconic receptors.

The long tactile hairs and campaniform receptors are innervated by a single dendrite, thus functioning as mechanoreceptors. The medium trichoid are innervated by three dendrites, two of which extend into the lumen of the receptor. The short trichoid sensilla are innervated by five sensory neurons. The basiconic receptors are innervated by 1-3 dendrites, depending on the type and location of the receptor. All three types of sensilla function as contact chemoreceptors, and may provide information on the suitability of the oviposition substrate.