# THE LIFE HISTORY, HABITS AND PHYLOGENETIC RELATIONSHIPS OF *Ithycerus noveboracensis* (FORSTER), (NEW YORK WEEVIL) (COLEOPTERA: CURCULIONOIDEA)

by

Paul Michael Sanborne

A thesis
presented in partial fulfillment of the requirements
for the degree of Master of Science

Department of Biology
Lakehead University
Thunder Bay, Ontario
July, 1979

# TABLE OF CONTENTS

DISCUSSION ------------------------------------------------------

# LIST OF TABLES

# LIST OF FIGURES

FIGURE(S)

FIGURE(S)

# ABSTRACT

Larvae of *Ithycerus* are described for the first time. Ten instars are identified with the possibility of more to be found. The pupa remains unknown. Spiracular air tubes and orifices show allometric growth and this, combined with body and head capsule measurements, is used to separate instars. Female and male reproductive systems are described. Females have two ovarioles per ovary. Adult and larval stages have four cryptonephric Malphigian tubules in the digestive tract. Adult and larval nervous systems appear to be primitive in possessing long connectives between ganglia. The first instar larva of *Arrhenodes minutus* (Drury) is described for the first time. The first illustrations of *Antliarrhinus* larvae are included. *Ithycerus noveboracensis* (Forster) has a two year life cycle at least and possibly three. Adults do not overwinter.

Three families of woody plants are associated with *Ithycerus*, the Betulaceae, Juglandaceae and Fagaceae, with a preference for species of Fagaceae. Adults are also occasionally found on introduced fruit trees (Rosaceae). There is no obvious courtship in *Ithycerus*. Oviposition takes place in soil; eggs are laid singly and covered with fecal matter. The larvae feed on the vascular cambium of the roots of host plants.

Several grooming movements and modes new for Coleoptera were discovered in *Ithycerus* and include bilateral fore-midleg rub, mid-hindleg rub (third mode), bilateral hindleg rub (third mode), simultaneous fore-midleg rub (one side), mid-hindleg rub (other side) and flagellum extend. Female *A. minutus* rapidly flutter the tips of their antennae against the tip of the rostrum to dislodge wood particles trapped there while drilling egg holes.

Evidence is presented for the possibility of evolution of three forms of *Ithycerus* in pleistocene refugia. The family Ithyceridae is maintained on the basis of new characters, primarily larval. The family is viewed as the most primitive of the four apionid-like families recognized in this study, the others being Brenthidae, Antliarrhinidae status nov. and Apionidae. The family Antliarrhinidae is placed near Apionidae. Adult and larval ventral nervous systems are discussed in light of their possible value as phylogenetic indicators. An evolutionary sequence is postulated for the numbers and positions of sensilla on the labra of larvae.

# INTRODUCTION

The higher classification and phylogenetic relationships of *Ithycerus noveboracensis* (Forster) ~~has~~ have been a matter of curiosity and concern for many years. Adult morphology provided few clues with the result that there are many conflicting views. A list of priorities was developed in a meeting of weevil workers in Washington, D.C., August, 1976, and *Ithycerus* was placed at the top. It was felt that a suitable solution to the 'mystery of the New York Weevil' would be found only if the larva was discovered. It was my good fortune to be the first to find it. This was accomplished through rearing experiments in 1977 and 1978 and later I found wild larvae on the roots of *Fagus grandifolia* Ehrh. (American Beech).

The first account of the habits of *Ithycerus* was by Riley (1871). He reported damage to buds of Bur Oak (*Quercus macrocarpa* Michx.) and described how females cut slits in twigs for the purpose of laying eggs. He also included a drawing of a legless larva and identified it as *Ithycerus*. He was mistaken in the site of oviposition and in the identification of the larva as my results will show.

The first description of *I. noveboracensis* was by Forster (1771) under the name *Curculio noveboracensis*. In 1823, Schoenherr included *Rhynchites curculionoides* in *Ithycerus* and included a description of the genus. This type was later found to be a synonym of *C. noveboracensis* Forster (Schoenherr, 1826). The uncertainty of the systematic placement of *Ithycerus* is shown in Table 1.

Table 1. History of the higher classification of *Ithycerus*.

| AUTHOR | SYSTEMATIC PLACEMENT |
|---|---|
| Schoenherr (1823, 1826, 1833) | Curculionidae: Ithycerinae |
| Horn (1873) | Curculionidae: Ithycerinae |
| Leconte (1876, 1883) | Curculionidae: Ithycerinae |
| Leng (1920, 1933) | Belidae |
| Ting (1936) | Belidae |
| Bruhn (1947) | Belidae |
| Crowson (1955) | Apionidae: Ithycerinae |
| Morimoto (1962) | Brenthidae: Ithycerinae |
| Kissinger (1968) | Apionidae: Ithycerinae |
| Morimoto (1976) | Ithyceridae, near Belidae |
| Vanin (1976) | Not Belidae |
| Sanborne ~~(1979)~~ | Ithyceridae, near Brenthidae |

The following objectives were achieved in this study: in addition to egg and larval descriptions of *Ithycerus*, for the first time, the first instar larva of *Arrhenodes minutus* (Drury) ~~is~~ (Brenthidae) is described and the larva of *Antliarrhinus* is illustrated; detailed descriptions of the internal systems of *Ithycerus* larvae and adults are presented and include reproductive systems and genitalia of males and females, digestive tracts and ventral nervous systems; the life history and behaviour of *Ithycerus* is discussed, including larval development times, adult longevity, feeding habits, courtship

and mating, oviposition, grooming, predators and parasites. Host plant associations, distribution, geographic variation and biogeography are also treated and a phylogenetic system for Ithyceridae, Brenthidae, Antliarrhinidae stat. nov. and Apionidae postulated. Discussions are also included on the value of ventral nervous systems as phylogenetic indicators in the Curculionoidea and the evolution of the numbers and positions of larval labral sensilla.

# LITERATURE REVIEW

The publications cited below were primarily used to determine character distributions in larvae and adults which aided the construction of the phylogeny presented at the end of this paper. Other publications used are cited in the appropriate sections in the body of the text.

Burke and Anderson (1976) produced a bibliography of all taxonomically important references dealing with the study of Curculionoidea larvae. Böving and Craighead (1930) produced a classification of larval Coleoptera and included a number of species of Curculionoidea. Van Emden (1938, 1946, 1950, 1952) looked at weevils having two dorsal folds on each abdominal segment, egg bursters and examined large numbers of broad-nosed weevils. His works on weevil larvae were an important contribution and stand as the basis of most studies being done today. Gardner (1932a, 1932b, 1934a, 1934b, 1935, 1936, 1938) examined many species of Indian Curculionoidea, including Anthribidae, Brenthidae, Platypodidae, Scolytidae and Curculionidae. Anderson (1941, 1947a, 1947b, 1948a, 1948b, 1952) was the first to devote full-time studies on the larvae of North American Curculionoidea with important works on Anthribidae and Curculionidae (Rhynchophorinae, Cossoninae). He also produced a paper on Hawaiian *Proterhinus* (Aglycyderidae) and devised a system of labelling larval characters which is still widely used today. Peterson (1951) illustrated quite a few species of Curculionoidea but did not provide descriptions. Crowson's classification of Coleoptera (1955, 1967) based on larval and adult characters is an important work, and was a valuable aid in this study. Thomas (1957, 1967) discussed larval anatomy, looked at gastric caeca in larvae and adults of Scolytidae, and devised a system of terminology to suit this group. May (1966, 1967, 1978) published on Curculionidae and devised a system of terminology based on Anderson (1947b) and Thomas (~~1947b~~, 1957) to suit new interpretations and new characters. Muniz and Barrera (1969) gave the first account of the larva of a species of *Rhopalotria* (Oxycorynidae). Browne (1972) looked at larvae of old world Platypodidae. Ahmad and Burke (1972) studied the larvae of the tribe Anthonomini (Curculionidae). Clarke, Burke, Anderson (1978) looked at larvae and pupae of some species of *Tychius* (Curculionidae), and attempted a phylogenetic analysis of the characters.

## MATERIALS AND METHODS

About 900 adults and 600 larvae of *Ithycerus noveboracensis* (Forster) were examined. I collected 42 adults in two study areas, Parkhill Conservation Area, Parkhill, Ontario, and Pinery Provincial Park, Grand Bend, Ontario, and 2 adults from King Mountain, Old Chelsea, Quebec, Canada. All but 4 larvae were reared from these specimens. The other 4 larvae were collected on the roots of *Fagus grandifolia* Ehrh. (American Beech) in Parkhill. Other material examined is shown in Table 2. In addition to the species of Curculionoidea listed in the Table, larvae from two species of Chrysomelidae, *Chrysomela sp.*, *Calligrapha sp.*, were also examined.

The following institutions and private collections, with abbreviations used in the text, kindly loaned specimens to me.

| | |
|---|---|
| UK | University of Kansas, Lawrence, Kansas, 66045, U.S.A., Peter D. Ashlock |
| INHS | Illinois Natural History Survey, Urbana, Illinois, 61801, U.S.A., Donald W. Webb |
| HAH | Henry and Anne Howden, 23 Trillium, Ottawa, Ontario, Canada |
| MSU | Michigan State University, East Lansing, Michigan, 48824, U.S.A., Roland L. Fischer |
| VPSU | Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 24061, U.S.A., Michael Kosztarab |

Table 2. Adults and larvae of species of Curculionoidea (excluding *Ithycerus*) examined.

| SPECIES | FAMILY | N |  | LOCALITY | COLLECTOR |
|---|---|---|---|---|---|
|  |  | ADULTS | LARVAE |  |  |
| *Cimberis elongatus* | Nemonychidae | 4 |  | Constance Bay, Ont. | W. Brown |
| *Euparius marmoreus* (Olivier) | Anthribidae | 15 |  | Parkhill, Ont. | M. Sanborne |
| *Euparius marmoreus* (Olivier) | Anthribidae |  | 3 |  | A. Howden |
| *Allandrus sp.* | Anthribidae | 1 |  | Ottawa, Ont. | M. Sanborne |
| *Dicordylus marmoratus* (Philippi) | Belidae | 2 |  | Chile | H.&A. Howden |
| Unidentified | Belidae |  | 1 | Australia | A. Howden |
| *Proterhinus sp.* | Aglycyderidae | 1 |  | Hawaii |  |
| *Aglycyderes sp.* | Aglycyderidae | 8 |  | Canary Islands | R.A. Crowson |
| *Rhynchites bicolor* Fabricius | Attelabidae | 2 |  | British Columbia, Can. |  |
| *Attelabus bipustulatus* Fabricius | Attelabidae | 8 |  | Constance Bay, Ont. | M. Sanborne |
| *Euscelus coccolobae* Wolcott | Attelabidae |  | 1 | Puerto Rico |  |
| *Arrhenodes minutus* (Drury) | Brenthidae | 58 | 25 | Constance Bay, Ont. | M. Sanborne |
| *Antliarrhinus sp.* | Antliarrhinidae | 4 | 9 | South Africa |  |
| *Apion longirostra* | Apionidae | 2 |  |  |  |
| *Dendroctonus sp.* | Scolytidae |  | 6 | Constance Bay, Ont. | M. Sanborne |
| *Gnathotrichus sp.* | Scolytidae | 4 |  | Parkhill, Ont. | M. Sanborne |
| Unidentified | Scolytidae |  | 4 | Constance Bay, Ont. | M. Sanborne |
| *Listronotus sp.* | Curculionidae | 50 | 120 | Thunder Bay, Ont. | M. Sanborne |
| *Pissodes strobi sp.* (Peck) | Curculionidae | 8 |  | Constance Bay, Ont. | M. Sanborne |
| *Liparus sp.* | Curculionidae | 10 |  | Thunder Bay, Ont. | M. Sanborne |

Table 2 continued

| SPECIES | FAMILY | N<br>ADULTS | <br>LARVAE | LOCALITY | COLLECTOR |
|---|---|---|---|---|---|
| *Magdalis barbita* (Say) | Curculionidae | 38 | 1 | Parkhill, Ont. | M. Sanborne |
| *Curculio sp.* | Curculionidae | | 42 | Stanley, Ont. | M. Sanborne |
| *Gymnaetron sp.* | Curculionidae | 22 | 133 | Constance Bay, Ont. | M. Sanborne |
| *Acanthoscelidius acephalus* (Say) | Curculionidae | 36 | 111 | Stanley, Ont. | M. Sanborne |
| *Cossonus platalea* Say | Curculionidae | 60 | 1 | Parkhill, Ont. | M. Sanborne |

| | |
|---|---|
| PSU | Pennsylvania State University, Frost Entomological Museum, University ~~of~~ at Park, Pennsylvania, 16802, U.S.A., S. W. Frost |
| CU | Clemson University, Clemson, South Carolina, 29631, U.S.A., John C. Morse |
| UM | University of Michigan, Ann Arbor, Michigan, 48104, U.S.A., Joan Miller |
| HU | Harvard University, Cambridge, Massachusetts, 02138, U.S.A., Alfred F. Newton |
| UNH | University of New Hampshire, Durham, New Hampshire, 03824, U.S.A., Wallace J. Morse |
| UMSP | University of Minnesota, St. Paul, Minnesota, 550101, U.S.A., Philip J. Clausen |
| ISU | Iowa State University, Ames, Iowa, 50010, U.S.A., Thomas A. Chandler |
| COU | Cornell University, Ithaca, New York, 14853, U.S.A., L. L. Pechuman |
| KSU | Kansas State University, Manhatten, Kansas, 66506, U.S.A., H. D. Blocker |
| UMC | University of Missouri, Columbia, Missouri, 65201, U.S.A., Wilbur R. Enns |
| PU | Purdue University, Lafayette, Indiana, 47907, U.S.A., A. Provonsha |
| AMNH | American Museum of Natural History, New York, New York, 10024, U.S.A., L. Herman |

| | |
|---|---|
| USNM | United States National Museum, Washington, D.C., 20560, U.S.A., D. R. Whitehead |
| CAES | Connecticut Agricultural Experiment Station, New Haven, Connecticut, 06504, U.S.A., Kenneth A. Welch |
| UMW | University of Madison-Wisconsin, Madison, Wisconsin, 53706, U.S.A., Steven Krauth |
| NCSU | North Carolina State University, Raleigh, North Carolina, 27607, U.S.A., D. L. Stephan |
| IISC | Iowa Insect Survey Collection, Iowa Wesleyan College, Mount Pleasant, Iowa, 52641, U.S.A., D. D. Millspaugh |
| CNC | Canadian National Collection, Biosystematics Research Institute, Ottawa, Ontario, K1A 0C6, Canada, Don Bright |
| RAC | R. A. Crowson, University of Glasgow, Glasgow, Scotland. |

## Collecting Sites

Two different sites were chosen in Southwestern Ontario for studies on *Ithycerus*. The first was the Parkhill Conservation Area on the outskirts of Parkhill, Ontario. The wooded portion of the site comprised mixed hardwoods, mainly Bitternut Hickory (*Carya cordiformis* [Wang] K. Koch Koch) and Red Maple (*Acer rubrum* L.). In association with these species were scattered elements of Black Oak (*Quercus* velutina ~~*velcutina*~~ Lam.), Red Oak (*Quercus rubra* L.), White Oak (*Quercus alba* L.), Bur Oak (*Quercus macrocarpa* Michx.), American Beech (*Fagus grandifolia* Ehrh.), Shagbark Hickory (*Carya ovata* [Mill.] K Koch), Ironwood (*Ostrya virginiana* [Mill.] K. Koch Koch), and Blue Beech

(*Carpinus caroliniana* Walt.). The soil was rich with a deep humus layer on a sand base and the understorey ~~understory~~ comprised many herbaceous species. The woods were humid and the soil moist throughout the study and apparently remained so during the growing season. The canopy, though open in some spots, tended to be closed.

The second study area was Pinery Provincial Park, on the shore of Lake Huron, just south of Grand Bend, Ontario, and about 25 km. from Parkhill. The park, approximately 15 km. long and 1.5 km. wide, was bounded on the east by a paved highway and on the west by Lake Huron. The entire area was vegetation covered sand dunes comprising an oak-pine complex with open canopy. The site was very dry and the Understorey ~~understory~~ comprised mainly drought resistant species, primarily grasses.

Eight species of oaks were present and included White Oak, the dominant species, Bur Oak, Swamp White Oak (*Q. bicolor* Willd.), Black Oak, Red Oak, Chinquapin Oak (*Q. muehlenbergii* Engelm.), Dwarf Chinquapin Oak (*Q. prinoides* Willd.), and Pin Oak (*Q. palustris* Muenchh.). Two species of pine were common, Red Pine (*Pinus resinosa* Ait.) and White Pine (*P. strobus* L.). Red Pine was the dominant species, as White Pine was almost completely logged out at the turn of the century. Mixed hardwoods grew along the banks of the Ausable River which divided the park in two. The extreme southern end of the park near the mouth of the river is classified as true Carolinian forest, characterized by species such as sassafras (*Sassafras albidum* [Nutt.] Nees) and tulip trees (*Lirodendron tulipifera* L.). The area chosen for intensive study was centrally located in the eastern half of the park and consisted mainly of White Oak in association with Black Oak and a few White Pine.

## Collecting Adults and Larvae of *Ithycerus*

Success in collecting large numbers of adults required a knowledge of their active periods during the day and host preferences. At the Parkhill site, the preferred host was American Beech; White Oak was virtually absent. At the Pinery, the preferred host was White Oak, and American Beech was entirely absent. The best collecting times at both sites were between 12:00 noon and 4:00 p.m. when adults were found on the trunks of the host trees. At other times, the adults were in the canopy and out of reach. As collections were made during late May and June, it is not known if there were significant changes in activity patterns after this time.

On a scaly barked host such as White Oak, adults were located in cracks in the bark, or they were exposed by lifting the scales with a heavy bladed hunting knife, and captured by hand. Adults were found mainly on the shaded sides of trees and moved to new hiding places in response to the shifting position of the sun.

On smooth barked hosts such as American Beech, adults were located on dark patches such as scars and knots or in spaces between closely growing branches, limbs and trunks. The occupation of these ~~These sites were probably~~ sites probably provided some protection against predation due to the cryptic colouration ~~selected to take advantage of the cryptic colouration the adults~~ in this species. ~~possess~~.

Tree size was also a probable factor in adult distribution. Measurements of diameter breast high (d.b.h.) were ~~carried out on~~ taken at the Pinery on White Oaks ~~White Oaks at the Pinery~~ which carried adults. Trees with a d.b.h. in the range of 22 — 40 cm. appeared to carry greater numbers of adults than smaller or larger trees. The reason is probably not selection by the adults, but rather it is related to successful larval development. That is, small trees do not have large enough roots to support larvae and large trees have roots with thick scaly bark which probably prevent most first instar larvae from reaching the vascular cambium and phloem, their food source.

The site of larval development and ~~their~~ larval food requirements were determined from rearing experiments done in 1977 on larvae reared from adults captured on King Mountain, Old Chelsea, Quebec. The search for wild larvae was directed at the root systems of the tree species associated with the adults. This information was initially taken from label data on museum specimens. However, trees ~~initially~~ ~~randomly~~ selected in April and May, 1978, produced no larvae. I then began excavating trees on which newly emerged adults were found. ~~and located 4~~ Four *Ithycerus* larvae and 2 teneral adults were located at a depth of about 25 cm. on the roots of American Beech at the Parkhill site. Excavations were carried out with a garden trowel, beginning at the base of the tree and working outward to expose the lateral roots; a hunting knife was used near the roots. No larvae were found on White Oak roots at the Pinery site. ~~as~~ However, their deep root systems took four to five times longer to expose ~~them~~ than the shallow systems of

American Beech. Thus, a far greater number of Beech trees were sampled. This does not imply *Ithycerus* larvae do not develop on White Oak roots. With the exception of the larvae collected on Beech roots, all the larvae in my possession were reared on roots of White and Bur Oak.

### Rearing Techniques

Captured adults of *Ithycerus* were placed in rearing cages (Fig. 31) with no more than three pairs in each. Four to six twigs of White Oak, Bur Oak or Beech were collected for adult food for each cage. Twigs with large numbers of leaves were selected. Initial rearing experiments done in 1977 indicated that only leaf buds, acorn buds, twig bark and leaf petioles were eaten as food. The leaves were cut off, leaving only the petioles, to slow the rate of water loss. Prior to placing the twigs in the cages, the ends were cut at an angle, wrapped in dampened folded paper towelling and wedged halfway into water-filled plastic tubes. Water levels were checked daily and distilled water added when necessary. Twigs could be kept fresh for up to a week using this method. The tubes were put in the cages at an angle to prevent dripping and to allow the twig branches to touch the floors of the cages; this made it easier for the weevils to reach the food supply.

Rumpled tissue paper was placed on the floors of the cages to enable upturned beetles to right themselves. The need for this became evident after three individuals died of apparent exhaustion. They do not have an efficient method of righting themselves, being hampered by their large bulk. No other deaths of this kind occurred after the paper was added.

Initial rearing experiments indicated that *Ithycerus* females lay their eggs in soil. I prepared a plastic bucket with an inside diameter of 26 cm. by filling it halfway with soil collected from the Pinery site and added two White Oak saplings and a clump of grass. This provided an adequate stimulus for the females who readily oviposited in the container. Each day, during the late afternoon, I removed females from the cages and placed them in the bucket. I found that I could only handle four at one time without losing track of where the eggs were laid. Each time an egg was deposited, it was removed from the bucket and placed in a small greenhouse bedding box (Fig. 32). By noting the behaviour of the females, it became clear when they had deposited their daily production of eggs. Ovipositing females kept their heads lowered to the soil, probed small depressions with their rostrums, and tapped the substrate with their antennae. No attempts to escape the bucket were made during this activity. Females which had finished ovipositing ran around with heads and antennae raised and attempted to escape by climbing the sides of the bucket or attempted to fly from the tops of the saplings. At this point, the females were returned to the cages and another group of four placed inside the bucket.

The eggs from all females over a four to five day period were placed in a single bedding box labelled with the dates of oviposition and the number of eggs collected. The eggs were covered with a Centimetre ~~centimeter~~ of soil, and the containers were dampened with distilled water and incubated at 22 degrees C. The soil layer covering the eggs was always kept damp with distilled water.

Three weeks from the last day recorded on the labels, the boxes were checked for larvae. The contents were carefully spread over paper towelling. I found it was not necessary to separate the eggs and place them near the soil surface as before. The boxes were then checked at three day intervals until the first larvae appeared, an average of six weeks after egg deposition. Larvae were collected, killed and preserved daily until at least a week had passed without the appearance of more larvae.

After several hundred first instar larvae had been preserved, an attempt was made to rear additional instars. I prepared a flower pot, 20 cm. in height with an inside diameter of 23 cm., in the following manner. Bur Oak roots from a relict stand in Stanley, Northwestern Ontario, were collected as food for the larvae. Roots with a diameter of 2 — 3 cm. were cut into lengths small enough to fit easily into the flower pot. A layer of about 6 cm. of dampened soil was placed in the bottom of the pot, and three or four root sections were pressed in firmly. The roots were removed and the blunt end of a pencil was used to make small depressions in the impressions left by the roots, usually four for each root. A single first instar larva was placed in each depression. The roots were replaced without pressing and covered to a depth of 4 cm. with soil.

This procedure was repeated until four layers of roots were laid down and covered. It was necessary to first press the roots into the soil each time to prevent the larvae from being crushed by the weight of the soil and roots added above. This method placed the larvae near the food source, and only one larva was believed to have been accidently crushed out of the total reared in this manner. There was no evidence of cannibalism.

The pot was checked once a week for new larval instars. The soil was carefully loosened with a teaspoon and removed one layer at a time. Larvae were usually found on the root surface in cells with a roof of frass, exuvia and soil. Occasionally, larvae were found free in the soil. Moulting took place in the cells and the cast off skins were collected and preserved in 75% ethanol. If the soil check indicated that larval moulting was just beginning, another check was made three or four days later to ensure that the new larval instars were sufficiently hardened for collecting and preserving. Newly moulted larvae were preferred because of less wear and tear on them as a result of feeding and soil abrasion. Regular soil checks for new instar larvae seemed to reduce~~d~~ fungal growth, probably due to light exposure and drying during the search process. Fungal growth was also reduced by washing the roots in distilled water each time they were removed from the pot and allowing their surfaces to dry before replacing them. When the third instar larvae matured, fresh roots having a diameter of 4 — 5 cm. were added. After the first snowfall, roots were collected and frozen for later use. These roots decayed rapidly in the pot, but their food value did not seem to diminish as a result of freezing; the larvae remained vigorous and healthy with no observed mortality.

Larvae were killed in hot water after body size and colouration were noted and preserved in 75% ethanol. The method produced nicely straightened larvae.

### Illustrations

Photographs were taken with an Olympus OM-2 35 mm. camera equipped with a 50 mm. lens and a single flash. Kodak 35 mm. black and white film, ASA 125, was used and processed in Kodak Microdol-X, a fine grain developer. Scanning electron microscope photomicrographs were taken on a Cambridge Stereoscan 6000 equipped with a 35 mm camera. All films were printed on Kodak Rapid Polycontrast II resin coated F paper using tray processing methods.

Drawings were made using Wild M5 dissecting and Wild M12 compound microscopes equipped with drawing tubes ~~camera lucidas~~, and ~~then~~ applied with pencil on good bond paper. The drawings were then transferred to tracing paper. Usually the most representative half of bilaterally symmetrical structures was transferred. This paper was ~~then~~ folded over and the second half of the drawing was completed. These drawings were ~~then~~ traced onto a medium weight opaque drafting film using erasable black ink. This facilitated corrections which are often difficult when paper is used for final drawings. After stipling was added, the drawings were cut out and placed on mounting boards.

The system of labelling larval structures and chaetotaxy follows that of Anderson (~~1947~~ 1947a) and Amhad and Burke (1972); and that of male and female reproductive systems and genitalia, Burke (1959), Clark (1977), and Hamilton (~~1978~~ 1979). The ~~identify~~ identification of certain features of digestive tracts was determined from Snodgrass (1935).

Three seta bearing areas found in both *I. noveboracensis* and *A. minutus* larvae could not be adequately identified by these systems. The anterolateral corners of the pronotum are distinctly separate from the main pronotal plate in both these species. This structure has been named the *lateral pronotal lobe*. A second seta bearing lobe anterior to the pedal area of the prothorax is obscured in whole larvae by the lower mouthparts. Its close association with the cervical membrane gives the structure its name, the *lateral cervical lobe*, and may be analogous to the lateral cervical sclerite of adults. Setae found on the dorsal region of the cervical membrane near the pronotal plate are called *dorsal cervical setae.*

## Specimen Preparations and Dissections

A method described by Goulet (1977) was used for the examination of whole larvae. The larvae are cleared in hot 10% KOH and impregnated with 100% glycerine, then mounted in glycerine on ringed slides. The method allows detailed and rapid examination of larvae.

For detailed examination of head capsules, they were removed from the body, cleared in KOH, rinsed in distilled water, temporarily mounted in glycerine on well slides under coverslips, and stored in ethanol in small vials.

Mouthparts were removed from the head capsule after clearing. All structures were mounted on slides in euparol and each mount replicated at least once to ensure that all details were accurately observed. Maxillae were separated from the labium and mounted dorsally and ventrally. The labium was mounted with ventral side up.

Dissections of the digestive tracts and nervous sytems of larvae were done by making an incision along the body wall between the pleural and epipleural areas, dorsally around the anus and back along the body wall to the head capsule. The dorsal body wall was separated from the larva, leaving the internal organs intact. A cut was made through the oesophagus where it leaves the head capsule and another through the rectum, as close to the anus as possible. The entire digestive tract was removed and stored in 75% ethanol for later examination. When done properly, the ventral nervous system could be seen along the inside of the ventral body wall.

The nervous system was removed with #0 insect pins by teasing the abdominal ganglia free from the body wall and working toward the head. When the abdominal ganglia and the three thoracic ganglia were free, the ventral body wall was cut away from the head capsule, just behind the labium. The brain and suboesophageal ganglion were exposed by splitting the head capsule along the epicranial suture. A cut was made through the pharynx and the entire nervous system and remnants of the gut were lifted away from the head capsule. The oesophagus was removed from between the brain and suboesophageal ganglion by gentle teasing with insect pins. The nervous system was stained in acid~~-fuschin~~ fuchsin, rinsed in 95% ethanol, and mounted on a glass slide in euparol.

Dissections of adult weevils preserved in 75% ethanol were begun by removing the legs, to help stabilize the specimen in an upright position. The elytra and hind wings were removed, then the pronotum, mesonotum metanotum and abdominal tergum were cut away, exposing the internal organs. The fifth visible sternite was removed in order to free the hind most internal organs and a cut was made through the oesophagus, just behind the head, and the entire digestive tract and reproductive system were teased free with an inspect pin. The two systems were carefully separated and stored in 75% ethanol. The head capsule was chipped away, using fine forceps, to expose the brain and ocular lobes. The occipital foramen had to be split dorsally to allow the removal of the brain and suboesophageal ganglion. It was then possible to remove the brain and ventral nervous system intact. The nervous system was stained in acid ~~fuschin~~ fuchsin and mounted on a glass slide in euparol.

Dissections of the genitalia of dried specimens were done by softening the specimens in boiling water, separating the abdomen, removing the genitalic structures from the abdomen, and clearing them in hot 10% KOH. The structures were rinsed in distilled water and stored in 75% ethanol.

Larval specimens examined with the scanning electron microscope

(SEM) were prepared using the critical drying point method (Anderson, 1969). The larvae were cleaned and dehydrated through a series of ethanol baths of increasing concentration up to 100%. The final liquid medium in this procedure was $CO_2$ which does not mix with ethanol, so that the larvae were run through a similar series of amyl acetate which is miscible with $CO_2$. The larvae, still wet with amyl acetate, were placed in small, perforated plastic vials and soaked in liquid $CO_2$ for at least 30 minutes in the pressurized chamber of the critical point drying unit. When the $CO_2$ was released, the result was perfectly dried, turgid specimens. The specimens were given a ground coating of carbon, gold coated and mounted on stubs with silver mounting paint, inserted in the SEM, and photographed.

## Measurements

Body measurements provided morphological criteria for the separation of *Ithycerus* larval instars.

Larval body lengths were done by making three separate measurements along the division between the pleural and epipleural areas. The first measurement was taken from the anterior margin of the head capsule to the posterior margin of the metathorax. The second measurement was taken from the anterior margin of the first abdominal segment to the posterior margin of the fourth abdominal segment. The third measurement was taken from the anterior margin of the fifth abdominal segment to the tip of the anus. The three measurements were added together to calculate a total body length.

Head capsule widths were measured between the widest points.

Ratios of the length of the anterior airtube *versus* width of the spiracular orifice were calculated for thoracic and abdominal spiracles. The anterior airtubes were measured because they are longer than the posterior airtubes. The widths of the spiracular orifices were made along their transverse axes between the inner margins of the peritreme. Both thoracic spiracles and abdominal spiracles 1, 2 and 3 (both sides) of each specimen were measured and a mean ratio of airtube length *versus* spiracular orifice width for each larval instar was calculated.

Ratios for the widths of abdominal spiracular orifices *versus* their length were calculated for each *Ithycerus* larval instar and are called orifice ratios. Widths were measured along the transverse axes of the orifices between the outer margins of the peritreme and lengths were measured from the midpoint of the airtube bases to the outside margin of the peritreme.

Measurements on *Ithycerus* adults included head length, elytra length, pronotum length and width, ocular width and numbers of yellow scales. Head length was measured from the median notch of the fused labrum to the transverse groove located medially between the compound eyes. Elytra length was measured from the anterior margin of the scutellum along the line formed by the meeting of the two elytra to the tips of the elytra. No attempt was made to account for the natural curvature of the elytra; the insects were positioned so that both the scutellum and the tips of the elytra were in focus. The width of the pronotum was measured between the midpoints and the length along the midline. Ocular width was the transverse distance between the midpoints of the compound eyes. The light patches of pubescence in *Ithycerus* are white and yellow scales. The patches chosen for counting were located posteriorly on the seventh interval where the elytra curve toward the apices. Patches of equal size were counted, usually the fourth or fifth from the base of the elytron.

# RESULTS

## Egg and Larval Characters of *Ithycerus noveboracensis*

Description of Eggs — Length 1.2-2.2 mm. (Fig. 56), (10 specimens); $\bar{x}$ = 1.7 mm., subspherical, about 1.5 X longer than wide but variable; external surface of chorion formed of hexagonal facets with impressed borders (Figs. 57, 58); enlarged view of facets show surface to be strongly punctate with numerous aeropyles (Fig. 59). Eggs laid singly in soil, covered carefully with fecal matter, pale yellow when first deposited but begin to darken in a few minutes; turn dark brown to black in one to two days.

### First Instar Larvae (15 Specimens)

COLOUR — Body, light yellow soon after eclosion, acquiring a green to brown tint as a result of food material in the digestive tract. Head, medium yellow, anterior 1/4 of frons light brown, increasing to dark brown along anterior margin; anterolateral corners of frons light brown; mandibular fossae dark brown, grading posteriorly to light brown in genal region. Basal 2/3 of basal article of maxillary palpus dark brown, apical 1/3 unpigmented; apical article of maxillary palpus dark brown except at apex. Colour and degree of pigmentation same for articles of labial palpus. Lateral extensions of premental sclerite dark brown; median portion of premental sclerite light yellow. Mandibles dark brown to black.

BODY — Length 2.4-3.3 mm., $\overline{x}$ = 2.8 mm; robust, strongly curved, cylindrical, dorsum strongly convex, sternum less strongly convex (Figs. 33, 61). Tuberclelike to spinelike asperities generally and rather densely distributed over entire body; spinelike asperities increase in length near setal bases (Fig. 85), and are more prevalent on exposed surfaces, particularly pleural and dorsal areas; tuberclelike asperities prevalent in recesses of body folds, very abundant on sternal region of thorax (Fig. 77).

HEAD — Free (Figs. 33, 61); width .60-.72 mm., $\overline{x}$ = .68 mm., tapering posteriorly, margins only weakly converging toward mandibles from midpoint of head capsule (Fig. 34). Entire surface of epicranium without microsculpture. Anterior, lateral and posterior ocelli present (Fig. 36), pigmented; lateral and posterior ocelli in some specimens not pigmented. Hypopharyngeal bracon (Fig. 35) present, well developed. Frontal sutures complete, meeting articulating membrane of mandibles, distinct throughout their entire length. Epicranial suture about 3/4 long as head capsule. Endocarinal suture about 1/2 as long as anterior portion of frons; endocarina distinct, extending from posterior margin of head capsule to approximately the midpoint of the anterior portion of frons, broadest at posterior margin of head capsule. Setae of head capsule all rounded, never longitudinally ridged.

*Antenna* — Completely enclosed by frontal area, supported by conspicuous frontal ridge; directed downwards toward mandible

(Figs. 62, 64, 70, 74, 75); consists of membranous basal article, 1 large, subconical accessory appendage, about as wide as long, 1 large, elongate, bifurcate (rarely not) accessory appendage, about as long as subconical appendage, 1 elongate, more or less sharply pointed seta, about 1/2 as long as bifurcate appendage, 3 shorter, blunt setae, and at least 2 coeloconic sensilla (Fig. 64).

*Frons* — Bears 5 pair of setae and 2 pair of sensilla (Fig. 34); setae 1, 2, 3 long, 4 short, 5 long; upper sensilla of frons mesad between setae 1 and 3; lower sensilla between setae 3 and 4; diameter of lower sensilla approximately 2X the diameter of upper sensilla; anterior portion of frons strongly constricted and elongated above setae 1 to approximately the midpoint of the head capsule.

*Dorsal Epicranium* — Bears 5 pair of setae and 3 pair of sensilla (Fig. 34), setae 1, 2 moderately long, 4, 5 long, setae 3 very short; dorsal epicranial sensilla 1 on vertex, posterior to sensilla 2 which are posterior to dorsal epicranial setae 1; sensilla 3 between and mesad to dorsal epicranial setae 4, 5.

*Lateral Epicranium* — Bears 2 pair of long setae and 8 pair of sensilla (Fig. 35); lateral epicranial sensilla 1 high on vertex, opposite posterior epicranial setae 1; lateral sensilla 8 between and somewhat distad of lateral epicranial setae 1, 2; sensilla 2, 3, 4, 5, 6, 7 distributed as in Fig. 36.

*Ventral Epicranium* — With 2 pair of setae and 3 pair of sensilla (Fig. 35); setae 1 short, setae 2 moderately long; ventral epicranial sensilla 1 posterior to ventral epicranial setae 1, near midpoint of head capsule; sensilla 2 opposite of ventral epicranial setae 2, on margin of oral cavity; sensilla 3 anterior to and between ventral epicranial setae 2 and ventral epicranial sensilla 2.

*Posterior Epicranium* — Bears 4 pair of minute setae and 2 pair of sensilla (Fig. 35); posterior epicranial sensilla 1 posterior to posterior epicranial setae 1; posterior epicranial sensilla 2 anterior to posterior epicranial setae 4. Posterior epicranial setae and sensilla, dorsal epicranial setae 2, 3, 4 and 5 and dorsal epicranial sensilla 3 positioned on distinct suturelike line running from apex of epicranial suture to point opposite and distad of lateral margin of anterior portion of frons.

*Clypeus* — Approximately 4X wider than long, bears 3 pair of setae and 1 pair of sensilla (Figs. 34, 68); setae ~~1~~ 3 short, 1/2 as long as setae ~~2~~ 1 and ~~3~~ 2; clypeal sensilla slightly anterior to clypeal setae 2. Tuberclelike asperities present on anterolateral corners.

*Labrum* — With 4 pair of setae and a single basal sensillum (Fig. 68) setae 1, 2, 3 approx. equal in length ~~1, 2 and approximate equal length~~, moderately long; setae ~~for~~ 4 shorter. Epipharyngeal lining (Fig. 38) bears 7 anterolateral setae, 1 pair of submarginal lateral setae and 4 anteromedian setae; anterolateral setae 1 short; anterolateral setae 2, 3, 4, 5, 6 and 7 moderately long, approximately equal length; submarginal lateral setae long, robust; anteromedian setae 1 longer than anterolateral setae 2; labral rods long, extending beyond posterior margin of clypeus, subparallel; epipharyngeal sensory pores positioned medially as pair of clusters, each consisting of 3 sensilla; pair of epipharyngeal sensilla posterior to sensory pores at position corresponding to posterior margin of labrum. Tuberclelike asperities present on posterolateral corners.

*Mandibles* — Very large, somewhat elongated, triangular (Fig. 37), weakly bidentate at apices with 3 teeth-like processes at base of incisor area; basal 1/2 of external surface of mandibles coarsely sculptured; 1 pair setae, equal length, and 3 sensilla present.

*Maxilla* — Maxillary palpus (Figs. 40, 65, 66, 67) with 2 articles; apical article approximately 3/4 as long as basal article; bears 1 sensillum and 8 or 9 apical basiconic sensory papillae of equal length (Fig. 66) arranged in a circle around a shorter, wider central basiconic sensory papilla; free rodlike accessory process (Fig. 66) present; basal article bears 2 sensilla, 1 short lateral seta. Stipes bears 4 setae and 3 sensilla on ventral surface; setae 1, 3, 4 long, 2 short; mala with 17 or 18 setae arranged in an evident row (Fig. 39) dorsally, 4 setae ventrally; dorsals 1, 2, 3, 4 moderately long, 5, 6, 7, 8, 9, 10 short, 11, 12 moderately long, 13, 14, 15, 16, 17 (17 sometimes absent), 18 long; anterior ventral setae blunt, peglike, of equal length; posterior ventral setae sharply pointed, subequal in length.

*Labium* — Labial palpus (Figs. 41, 65) with 2 articles; apical article 3/4 as long as basal article; bears 1 sensillum and 8 basiconic sensory papillae arranged in a circle around a central, shorter broader basiconic sensory papilla. Premental sclerite (Fig. 41) with posterior median projection; anterior median projection indistinct; lateral projections distinct, bear 1 pair of minute setae and 1 pair of sensilla; prementum bears 1 pair of long setae and 1 pair of sensilla; postmentum with 3 pair of setae; setae 2 much longer than setae 1 and 3; setae 1 and 3 approximately equal in length; spinelike asperities present on posterolateral corners of postmentum.

THORAX — Narrows slightly towards head (Fig. 45); mesonotum and metanotum as wide as dorsum of abdominal segments I, II, wider than remaining abdominal segments. Dorsum of prothorax entirely covered by lightly pigmented, sclerotized pronotal plate bearing 9 pair of setae and 2 pair of sensilla (Fig. 45); sensilla 1 mesad between pronotal setae 1 and 2; sensilla 2 laterad a short distance from pronotal setae 2, toward mid-dorsal line. Lateral pronotal lobe with 3 setae (Fig. 42). Thoracic spiracle intersegmental, between prothorax and mesothroax (Figs. 42, 50, 52, 54) bicameral, with 11-13 annuli on each airtube; anterior airtube slightly longer than posterior airtube; anterior airtube averages 1.4 X longer than the diameter of of the spiracular orifice; spiracular orifice circular, continues internally as short sclerotized tube to where it joins tracheal system;

inner surfaces of tube with rings with rings of dense, short, flattened pointed setae (asperities?) which are directed internally (Figs. 52, 54). Predorsum of meso and metathorax (Figs. 42, 45) bears 3 setae (only setae on one side of body described, after Amhad and Burke, 1972); seta 1 long, setae 2, 3 minute; postdorsum of meso and metathorax bears 4 setae; setae 1, 3, 4 long, seta 2 short, and a small fold along their posterior margins, traversing the mid-dorsal line, the folds without setae. Alar areas of meso and metathorax each have 2 moderately long setae. Spiracular areas of meso and metathorax each with 4 setae. Epipleural lobes of meso and meta thorax each bear 2 long setae. Pleural lobe of prothorax bears 2 long setae; pleural lobes of meso and metathorax each bear 1 long seta. Dorsal cervical membrane anterior to lateral pronotal lobe with 2 minute setae; lateral cervical lobe (Fig. 42) bears 3 short setae; pro, meso and metathorax bear well developed 2-segmented legs (Figs. 44, 78, 79); coxal areas (= pedal areas of legless curculionoids) bearing meso and metathoracic legs each have 9 setae; seta 1 long, 2, 3 minute, 4,5 long, 6 minute, 7 long, 8, 9 minute; coxal area of prothoracic leg with 8 setae, seta 9 absent; positions and relative lengths same as meso and metacoxal areas (seta 1 of pleural lobe of prothorax may be homologous with seta 8 of meso and metacoxal areas). Basal segments of thoracic legs each with 6 apical setae (Fig. 44) arranged more or less in a circle and 4-6 randomly positioned sensilla; apical segments of thoracic legs bear 5 apical setae arranged in a circle and 6-8 randomly distributed sensilla; apical seta 1 very short, 2, 3, 4 and 5 moderately long; apical segments of thoracic legs with conical, membranous projections at their apices which are bare of setae and lack sensilla. Sternal areas of thorax each bear 2 pair of setae; setae 1 long, on each side of mid-ventral line (Fig. 77); setae 2 minute, near anterolateral margins of sterna.

ABDOMEN — With 8 pair of lateral, bicameral spiracles, each with 7-9 annuli on each airtube (Figs. 51, 53, 55); anterior airtubes of spiracles 2.8-3.5 X longer than the widths of the spiracular orifices, $\bar{x}$ = 3.2; spiracular orifices circular (Fig. 51); spiracles with orifice ratio .80 — 1.10, $\bar{x}$ = .90. Abdominal segments I-VIII each with 2 dorsal folds (Figs. 33, 43, 46); abdominal segments I-IV each with an additional small fold, without setae, along the posterior margin of the postdorsum, traversing the mid-dorsal line; segments I-VIII with 1 long, 1 minute predorsal setae and 4 postdorsal setae; postdorsal seta 1, 3 long, 2, 4 short. Spiracular areas of segments I-VIII each bear 4 setae; seta 1 long, seta 2 short, setae 3, 4 minute. Epipleura of segments I-VIII each bear 3 setae; seta 1 short, setae 2, 3 long. Pleural lobes of segments I-VIII each have 2 setae, seta 1 moderately long, 2 long. Pedal areas of segments I-VIII each bear 1 moderately long seta. Eusterna (Fig. 47) of segments I-VIII bear 1 minute, anterior seta and 1 moderately long seta on each side of mid-ventral line. Dorsal folds of abdominal segment IX indistinct (Fig. 33); segment IX bears 1 predorsal and 4 postdorsal setae; spiracular setae absent; epipleurum with 2 short setae; pleural lobe bears 1 moderately long seta; pedal area, eusternum and sternum with 1, 2, 1 setae respectively. Anus terminal; dorsal lobe of anus prominent (Figs. 81, 82, 83), without setae; lateral anal lobes each bear 3 setae; seta 1 minute, 2, 3 short; ventral anal lobe without setae; inner surfaces of anal lobes bear numerous divided asperities having 2 or more, usually more, spinelike projections (Figs. 82, 84) which grade into undivided asperities on the more exposed surfaces; anal slit transversely X-shaped; upper arms approximately 2X longer than lower arms.

## Descriptions of Larval Stages Beyond First Instar

For the most part, the above description characterizes the larvae of *Ithycerus*. However, certain larval features were observed to vary through progressive larval moults, but could not be adequately characterized. The lengths of all setae increase through all instars but their lengths, relative to the structures from which they arise, decrease. The dimensions of membranous structures vary considerably due to inconsistencies in killing, straightening and preserving methods. The setae borne on the sclerotized pronotal plate do not occupy exactly the same positions from individual to individual, so that setal lengths relative to the distance between the setae could not be accurately measured. The lengths of setae themselves were subject to substantial variation, and the difficulty in measuring them was further compounded by variation in the degree of curl as a result of killing, preservation and growth anomalies. Pigmentation tends to intensify in each new larval instar, but there is apparently no measurable change in the extent to which specific structures are pigmented. The following larval features could be characterized and provided morphological criteria for separating instars with a high degree of accuracy. Nine larval instars are separated based on these features. A tenth instar was found but was allowed to develop undisturbed in hopes of obtaining the pupal stage.

### Second Instar Larvae (20 Specimens)

BODY — Length 4.2-6.0 mm., $\bar{x}$ = 5.2 mm.

HEAD — Width at widest point 1.0-1.1 mm., $\bar{x}$ = 1.1 mm.

THORAX — Anterior airtube of spiracle 1.28-1.39 X longer than the width of the spiracular orifice, $\bar{x}$ = 1.36; margins of peritreme strongly invaginated along three sides, producing starlike configuration with 3 elongate, round tipped arms; corresponding sides of short sclerotized spiracular tube also strongly invaginated forming tricuspid valve, resulting in almost complete closure of tube; tricuspid valve retained through all proceeding instars, becoming more conspicuous.

ABDOMEN — Anterior airtubes of spiracles 1.9-2.5 X longer than the widths of the spiracular orifices, $\bar{x}$ = 2.2; orifices of spiracles subcircular; orifice ratio .67-.78; $\bar{x}$ = .70.

### Third Instar Larvae (10 Specimens)

BODY — Length 6.8-7.2 mm., $\bar{x}$ = 7.1 mm.

HEAD — Width at widest point 1.3-1.6 mm., $\bar{x}$ = 1.4 mm.

THORAX — Anterior airtube of spiracle .44-.58 X as long as the width of the spiracular orifice, $\bar{x}$ = .51; peritreme now assumes a triangular shape which is maintained through the remaining larval instars (Figs. 52, 54).

ABDOMEN — Anterior airtubes of spiracles .61-.82 X as long as the width of the spiracular orifices, $\bar{x}$ = .72; spiracular orifices broadly elliptical; orifice ratio .58-.63, $\bar{x}$ = .60.

Fourth Instar Larvae (6 Specimens)

BODY — Length 11.3-13.4 mm., $\bar{x}$ = 12.5 mm.

HEAD — Width at widest point 2.3-2.6 mm., $\bar{x}$ = 2.5 mm.

THORAX — Anterior airtube of spiracle .33-.45 X as long as the width of the spiracular orifice, $\bar{x}$ = .40.

ABDOMEN — Anterior airtubes of spiracles .52-.50 X as long as the widths of the spiracular orifices, $\bar{x}$ = .47; spiracular orifices elliptical; orifice ratio .50-.57, $\bar{x}$ = .56.

Fifth Instar Larvae (5 Specimens)

BODY — Length 12.0-17.6 mm., $\bar{x}$ = 14.8 mm.

HEAD — Width at widest point 2.7-3.0 mm., $\bar{x}$ = 2.9.

THORAX — Anterior airtube of thoracic spiracle .25-.34 X as long as width of the spiracular orifice, $\bar{x}$ = .31.

ABDOMEN — Anterior airtubes of spiracles .27-.35 X as long as widths of spiracular orifices, $\bar{x}$ = .33; orifices of abdominal spiracles elongate-elliptical; orifice ratio .46-.52, $\bar{x}$ = 50.

### Sixth Instar Larvae (6 Specimens)

BODY — Length 16.8-22.5 mm., $\bar{x}$ = 19.3 mm. (Fig. 61).

HEAD — Width at widest point 3.3-3.8 mm., $\bar{x}$ = 3.5 mm.

THORAX — Anterior airtube of spiracle .24-.26 X as long as the width of the spiracular orifice, $\bar{x}$ = .25.

ABDOMEN — Anterior airtubes of spiracles .25-.32 X as long as the widths of the spiracular orifices, $\bar{x}$ = .30; orifices of spiracles elongate; orifice ratio .40-.43, $\bar{x}$ = .41.

### Seventh Instar Larvae (6 Specimens)

BODY — Length 21.8-24.8 mm., $\bar{x}$ = 23.0 mm.

HEAD — Width at widest point 4.2-4.5 mm., $\bar{x}$ = 4.3 mm.

THORAX — Anterior airtube of spiracular .17-.23 X as long as the width of the spiracular orifice, $\bar{x}$ = .21 (Fig. 54)

ABDOMEN — Anterior airtubes of spiracles .24-.29 X as long as the widths of the spiracular orifices; $\bar{x}$ = .27; spiracular orifices strongly elongate; orifice ratio .27-.35, $\bar{x}$ = .31 (Fig. 55).

### Eighth Instar Larvae (2 Specimens)

BODY — Length 20.3 - 21 mm. In *Ithycerus*, maximum growth is apparently achieved before ~~final~~ last instar. Thus, length cannot be used as a character for separating seventh instars from proceeding instars. Sexual dimorphism in size is another probable factor at this stage of development.

HEAD — Width at widest point 4.4-4.8 mm.

THORAX — Due to very few specimens of eighth and ninth instar larvae, significant differences in the ratios of air/tube length to orifice width were not detectable between seventh, eighth and ninth instars.

ABDOMEN — As in thorax, no detectable differences found in ratios of air/tube length to width of orifice in seventh, eighth and ninth instars. Orifice ratios .24 and .26.

Ninth Instar Larvae (2 Specimens)

BODY — 20.5 mm. and 21.0 mm.

HEAD — Width at widest point 4.7 mm and 5.1 mm.

Ninth instar larvae were placed back in a rearing pot without further measurements for further development.

A single tenth instar was identified but left undisturbed. Rearing experiments were initiated for the third time and larger numbers of later instars are expected.

*Diagnosis* — The following combination of characters separate *Ithycerus* larvae from all other larvae known for the Curculionoidea and is construed to be evidence in support of maintaining separate family status for the genus as proposed by Morimoto (1976). The diagnostic characters of larval Ithyceridae are: (1) frontal sutures complete, distinguishable throughout their length, meeting articulating membrane of mandibles; (2) endocarina distinct; (3) antenna supported by conspicuous frontal ridge, bearing an elongate, bifurcate (usually) accessory appendage, 1 elongate, short seta, 3 very short, blunt setae, at least 2 coeloconic sensilla; (4) 3 ocelli; (5) labrum with 4 pairs of setae and single basal sensillum; (6) epipharynx with 7 pair of anterolateral setae, 1 pair submarginal lateral setae, 4 anteromedian setae; (7) mala with 17-18 dorsal setae arranged in evident row; (8) mandibles very large, elongate, triangular, weakly bidentate at apices with 3 teeth-like processes at base of incisor area; (9) thoracic spiracle intersegmental; peritreme becoming triangular and greatly enlarged beyond first instar; spiracular tube strongly invaginated along 3 sides forming tricuspid valve; spiracular tube ringed with flattened setae which are directed internally; (10) thorax bears conspicuous, 2-segmented legs which bear membranous, conical apical projections; (11) abdominal segments with 2 dorsal folds; (12) epipleura of abdominal segments 1-VIII with 3 setae; (13) anus terminal; anal slit transversely X-shaped; (14) nine or more instars.

## Descriptions of Reproductive Systems and Genitalia of *Ithycerus*

*Male Reproductive System* — A pair of small, bilobed testes (Fig. 86); each lobe scalloped around edges and divided by septa into approximately 16 testicular follicles; when freshly removed, lobes are completely enclosed by tangled mat of trachea; vas deferens divided apically on each side forming two small ducts which insert in the centre of each lobe from below; vas deferens expanded below to form large disc-shaped seminal vesicles which are divided by septa into 8-10 lobes; edges of lobes scalloped; a pair of long coiled accessory glands merge with bases of vas deferens; together these insert in the centres of the seminal vesicles from above; ducts from testes unite below seminal vesicles forming a single, long ejaculatory duct; diameter of duct decreases throughout length to where it passes through muscular sheath of endophallus and opens as gonopore at endophallus.

*Male Genitalia* — Anterior portion of aedeagus consists of pair of broad median struts (Figs. 86, 87, 89) which fuse broadly posteriorly; a heavily sclerotized median apodemelike extension runs posteriorly from bases of median struts to but not joining median lobe (Figs. 87, 89); two smaller, heavily sclerotized extensions project posteriorly from basolateral corners of median struts to and join median lobe; spaces between the three extensions consist of thinly sclerotized, unpigmented zones so that entire anterior portion of aedeagus forms into a tubular structure; median lobe spatulate. Tegmen consists of broad, heavily sclerotized ring; cap-piece of ring bears a pair of lateral lobes which extend posteriorly; margins of lateral lobes bear long setae (Fig. 87); basal piece of ring bears tegmenal strut which projects anteriorly below apices of median struts of aedeagus. Ninth sternite consists of long, cylindrical apodeme which diverges posteriorly into two short rodlike extensions (Fig. 88); tips of extensions with thinly sclerotized projections for the attachment of membrane connecting ninth sternite to ninth tergite; ninth tergite (Figs. 95, 96) with moderately long, anteriorly directed apodeme, bears lateral arms, each arm with thin, sclerotized flange along anterior margin of apical 1/2 for attachment of muscle, posterior margin of tergite with median bilobed extension, intersegmental membrane broadly attached to posterior margin and bears two small setae in trough formed by lobes. Internal sac with transfer apparatus (Figs. 90, 92, 93, 94) consisting of two C-shaped, slotted sclerites; forms very long flagellum (Fig. 92); everted internal sac bears two sclerites, one dorsally and one ventrally, which may represent tenth tergite and sternite (Figs. 90, 91, 92); ventral sclerite small, with short posterior apodeme and two lateral lobes; dorsal sclerite large, with short posterior apodeme and two long, lateral lobes which recurve inward posteriorly.

*Female Reproductive System* — Ovaries paired, each with two ovarioles (Figs. 97, 98); terminal filaments from each ovariole unite to form suspensory ligaments which unite anteriorly above alimentary canal; ovariole pairs open into lateral oviducts; lateral oviducts converge posteriorly to form common oviduct. Spermathecal duct and spermathecal gland each have separate insertion on globular 'head' of sclerotized spermatheca (Fig. 102); spermatheca C-shaped with 'tail' of spermatheca strongly curved. Accessory glands absent.

*Female Genitalia* — Spiculum gastrale (Fig. 99) spatulate with truncated posterior margin; bears anterior apodeme which is approximately equal in length to posterior portion; with numerous minute ventral setae on posterolateral corners; two larger setae arise medially just below posterior margin; median field circular, thinly sclerotized, transparent. A sclerotized coxite on each side of ovipositor, each with articulated stylus; posterior half of coxites inflated, anterior half laterally compressed; numerous minute setae borne externally and internally on posterior halves; styli bare.

## Descriptions of the Digestive Tracts of *Ithycerus* Larvae and Adults

### LARVAE (Fig. 48)

*Anterior Gut* — Pharynx lightly sclerotized anteriorly, narrow, opens into tubular oesophagus; crop absent; proventriculus consists of eight membranous invaginations which lack setae.

*Mid Gut* — Anterior portion greatly enlarged, posterior portion tubular; anterior end of posterior portion looped so that it lies beneath enlarged anterior portion; posterior end of posterior portion looped so that it passes under anterior end of posterior portion; bears numerous, elongate caeca which arise all around circumference.

*Hind Gut* — Four cryptonephric Malphigian tubules arise posterior to caeca; distal ends imbedded in fat tissue surrounding anterior portion of mid gut but do not insert on it; colon long, tubular, with marked constriction at rectum; rectum tubular, slightly expanded, without annular constrictions.

ADULT (Fig. 49)

*Anterior Gut* — Pharynx narrow, lightly sclerotized anteriorly; opens to tubular oesophagus; crop absent; proventriculus consists of eight membranous invaginations, each bearing Y-shaped row of loosely aggregated flattened setae; tips of setae often divided.

*Mid Gut* — Anterior portion tubular, only slightly expanded when empty, greatly expanded after feeding; posterior portion tubular, with numerous, short, elongated caeca emerging all around circumference for 1/2 its length.

*Hind Gut* — Forms a loop; rectum with annular constrictions throughout its length; four cryptonephric Malphigian tubules arise on 1/2 the circumference of intestine posterior to caeca and insert on 1/2 the circumference of intestine anterior to constriction between colon and rectum; portion of intestine between insertion of Malphigian tubules and constriction between colon and rectum with numerous internal rectal papillae.

## Descriptions of Ventral Nervous System and Cerebrum of *Ithycerus* Larvae and Adults

*Larvae* — Ventral nervous system consists of suboesophageal ganglion, three thoracic ganglia and eight abdominal ganglia; seventh and eighth abdominal ganglia solidly fused (Fig. 166); abdominal ganglia lie along internal surface of ventral body wall and extend posteriorly to anterior margin of eighth sternum; four thin nerve branches from fused seventh and eighth abd. ganglia extend posteriorly to innervate ninth, tenth abd. segments and posterior end of gut; abd. ganglia I-VI each have two thin nerve branches arising laterally which branch into many small nerve endings; abd. ganglia separated by short, thick connectives, ganglia somewhat elongated; seventh and eighth fused ganglia form body which is approximately 2X larger than abd. ganglia I-VI which are of equal size; thoracic ganglion I very large, elongated, separated from thoracic ganglion II by thick connectives a distance approximately equal to length of thoracic ganglion II; thoracic ganglion II approximately 1.5X larger than thoracic ganglion III; separated from thoracic ganglion III by short, thick connectives; thoracic ganglion III approximately same size as abd. ganglion I; suboesophageal ganglion approximately same size as thoracic ganglion II; separated from thoracic ganglion I by short, thick connectives; cerebrum consists of two pear-shaped lobes which are fused posteriorly; lobes somewhat dorsoventrally flattened; suboesophageal ganglion separated from cerebrum by long, thick connectives which are folded posteriorly, suboesophageal ganglion located below and slightly posterior to cerebrum.

*Adults* — Ventral nervous system (Fig. 176) consists of suboesophageal ganglion, three thoracic ganglia and three abdominal ganglia; second and third abd. ganglia weakly fused; third abd. ganglia compound, consists of four fused abd. ganglia (fifth, sixth, seventh and eighth); second and third abd. ganglia lie above third visible sternite; first abd. ganglion (= abd. ganglion III) equidistant from thoracic ganglion III (= thoracic ganglion III and abd. ganglia I and II) and second and third fused abd. ganglia; separated from these by very long connectives; thoracic ganglion III fused with thoracic ganglion II; lateral margins of thoracic ganglion III with three thick nerve branches on each side; two anterior branches extend laterally into thoracic cavity, third extends posteriorly towards abdomen; thoracic ganglion II somewhat 4-sided, also with three thick nerve branches arising from lateral margins on each side; first and second branches extend anterolaterally into thoracic cavity, third branch directed posterolaterlly; thoracic ganglion I separated from thoracic ganglion II by very thick connectives a distance approximately equal to length of thoracic ganglion II; two large nerve branches extend anterolaterally from each side; suboesophageal ganglion separated from thoracic ganglion I by fairly long, thick connectives; suboesophageal ganglion separated from cerebrum by connectives which are approximately 2X as long as connectives between suboesophageal ganglion and thoracic ganglion I; these connectives folded posteriorly so that suboesophageal ganglion occurs below and somewhat posterior to cerebrum; cerebrum transverse, i.e. lobes form straight line, not folded anteriorly.

## Larval Characters of First Instar *Arrhenodes minutus* (Drury)

COLOUR — Body white; head, pronotal plate, 'shoulder patch' asperities sternal plate, testaceous; anterior margin of frons, mandibular fossae, brown to dark brown; mandibles black; lower mouthparts, except premental sclerite, testaceous; premental sclerite, medium brown.

BODY — Length 1.8-2.3 mm., $\overline{x}$ = 2.1 mm. (10 specimens), slender, elongate, moderately curved, cylindrical (Fig. 127). Abdominal segments VIII, IX swollen laterally (Fig. 127). Spinelike asperities conspicuous on epipleural, spiracular and dorsal areas of body; absent dorsally on abd. seg. VII, VIII, IX, absent on pleural, pedal areas of abd. seg. I - VIII, present on these areas on segment IX and on anal folds, present on sternum of mesothorax and segment IX, absent on all other segments. Tuberclelike asperities and divided spinelike asperities generally distributed in recesses of thoracic (Fig. 119) and abdominal folds except sternum of abd. seg. I-VIII.

HEAD — Free (Figs. 108, 127), width .39-.46 mm., $\overline{x}$ = .41 mm., about as wide as long, broadly rounded posteriorly, tapering strongly toward mandibles from midpoint of head capsule. Frons and dorsal epicranium with beaded microsculpture, ending on posterior epicranium, lateral and ventral epicranium smooth. Ocelli absent. Hypopharyngeal bracon (Fig. 131) distinct, very strongly developed. Frontal sutures complete, meeting articulating membrane of mandibles, somewhat indistinct anteriorly.

Epicranial suture less than 1/2 as long as head capsule. Posterior endocarina approximately 1/3 as long as head capsule. Setae of head capsule usually ridged longitudinally (Fig. 109).

*Antenna* — Inset into frontal area (Figs. 108, 109), consists of 1 elongate, subconical accessory appendage, 1 elongate, sharply pointed accessory appendage, 1 elongate, blunt seta, 1/2 as long as pointed accessory appendage, 3 smaller blunt setae and at least 2 coeloconic sensilla.

*Frons* — Very large, approximately .7X as long as wide (Figs. 107, 128), broadly triangular with ~~anterior~~ anterolateral margins bent toward mandibles. Five pair of frontal setae present; setae 1, 3, 4, 5 very long, setae 2 long; 2 pair of sensilla present, sensilla 1 anterior to setae 1, sensilla 2 posterior to setae 3.

*Dorsal Epicranium* — Bears 5 pair of setae (Fig. 128); setae 1 moderately long, 2, 3 long, 4, 5 very long; 3 pair of sensilla present, sensilla 1 high on vertex, posterior to sensilla 2, sensilla 2 posterior to setae 1, sensilla 3 between setae 4, 5.

*Lateral Epicranium* — Two pair of setae present (Fig. 128); setae 1 short, setae 2 long; 2 pair of sensilla present; sensilla 1 laterad of dorsal epicranial setae 1 and posterior to lateral epicranial setae 1, sensilla 2 located between setae 1 and 2.

*Posterior Epicranium* — Four pair of minute setae and 1 pair of sensilla present (Fig. 128), posterior to setae 1.

*Ventral Epicranium* — Two pair of setae present (Fig. 131); setae 1 very short, laterad of anterior corners of tentorial bar, setae 2 short, posterior to mandibular fossae; 3 pair of sensilla present; sensilla 1 laterad of posterior corners of tentorial bar, sensilla 2 laterad of midpoint of tentorial bar, sensilla 3 anterior to setae 1.

*Clypeus* — Approximately 3X wider than long (Figs. 110, 111), anterior margin convex, evenly arcuate, posterior margin fused to frons, frontoclypeal suture absent; bears 3 pair of setae; setae 1 longer than setae 2 which is longer than setae 3; 1 pair of sensilla occur anterior to and mesad between setae 1, 2.

*Labrum* — As wide as long (Figs. 110, 111) with 3 pair of setae and 1 pair of setal pits (setae 4 absent); setae 1, 2 of equal length and longer than setae 3; single basal sensillum present.

*Epipharynx* — Bears 3 pair of anterolateral setae, 4 anteromedian setae (Fig. 135); anterolateral setae 1, 2 short, of equal length, setae 3 minute; anteromedian setae 1 minute, pointed, anteromedian setae 2 minute, blunt; labral rods short, converging slightly posteriorly; sensory pores arranged in two clusters, each consisting of 3 sensilla, a median pair of sensilla occurs posterior to clusters, third pair of sensilla posterior to posterior setae; posterior setae positioned one above the other between posterior and median sensilla.

*Mandibles* — Short, robust, triangular, 2 teeth at apices and 1 subapical tooth (Figs. 111, 136); bear 1 pair of equal length setae and 3 sensilla.

*Maxilla* — Maxillary palpus (Figs. 132, 134) consists of 2 articles; basal article with 2 sensilla and 1 short, peglike lateral seta; articulating membrane of palpus with several rows of spinelike asperities; apical article about as long as basal, bears 1 sensillum and 12 or 13 minute sensory papillae; apex of apical article strongly oblique externally; stipes bears 4 setae and 3 sensilla; setae 1, 4 long, 2 very short, 3 short; mala with 18 dorsal setae arranged in an evident row and 3 ventral setae; dorsal setae 1-13 become progressively shorter anteriorly, 14 minute, 15, 16, 17, 18 short, peglike; 1 ventral sensillum present.

*Labium* — Labial palpus (Fig. 133) consists of 2 articles; apical article bears 1 sensillum and at least 9 minute sensory papillae; basal article about as long as apical, bears 1 sensillum; premental sclerite complete, with lateral, anteromedian and posteromedian projections, lateral projections with 1 pair of minute setae and 1 pair of sensilla; glassa bears 2 pair of setae and 2 pair of sensilla; anterior setae short, slender, posterior setae stouter, longer; prementum bears 1 pair of moderately long setae and 1 pair of sensilla; postmentum with 3 pair of setae, setae 1 short, 2 long, 3 moderately long.

THORAX — Slightly wider than abdomen (Fig. 127). Pronotum bears sclerotized plate with 6 pair of setae and 2 pair of sensilla, lateral pronotal lobe bears 1 pair of setae. Thoracic spiracle (Figs. 116, 129) bicameral, with 8-9 annuli on each airtube, located on intersegmental membrane between prothorax and mesothorax. Mesothorax and metathorax each bear 2 short predorsal setae, 4 short postdorsal setae, 2 short alar setae, approximately equal in length, 3 spiracular setae, 1 short epipleural seta, and 1 moderately long pleural seta; mesothorax bears triangular patches of interleafed, transversely flattened asperities on posterior margins of postdorsum (Figs. 113, 114). Lateral cervical lobe bears 2 short setae, dorsal cervical region with 2 short setae. Prothorax with 2 moderately long spiracular setae and 2 pleural setae, 1 moderately long and 2 short. Prothorax, mesothorax and metathorax each bear short, 2-segmented legs (Fig. 118); articulating membrane of basal segments usually with 4 sensilla; basal segment with 5 apical setae, 4 of which are moderately long and the fifth short, apical segment bears 7 setae, 2 of which are moderately long, 2 short and 3 minute setae; coxal area of prothoracic leg bears 4 setae, setae 1, 2 minute, setae 3, 4 located between leg and sternum, moderately long; coxal areas of meso and metathoracic legs with 5 setae, setae 1, 2, 3 minute, 4, 5 moderately long. Sternal area of prothorax sclerotized, bears 1 pair of long setae; sternal areas of meso and metathorax membranous, bear 1 pair of long setae.

ABDOMEN — With 8 pair of lateral, bicameral spiracles (Fig. 130), 4-5 annuli present on each airtube, anterior airtube longer than posterior. Segments I-VIII with 3 dorsal folds. Egg bursters present on spiracular areas of segments I-VIII, above spiracles.

*Predorsum* — Segments I-VII with 3 predorsal setae, segments VIII and IX bear 2 predorsal setae; seta 1 of segments I-VI short, 2, 3 minute; predorsal seta 1 of segment VII moderately long, 2 short, 3 minute; seta 1 of segment VIII long, seta 2 short; setae 1, 2 of segment IX very long (Fig. 127).

*Postdorsum* — Segments I-IX with 4 postdorsal setae; setae 1, 2, 3, 4 of segments I-VI all short; setae 1,3 of segments VII, VIII long, 2, 4 short; setae 1, 2, 3, 4 of segment IX very long, not in a line, 2, 4 posterior to 1, 3.

*Spiracular Area* — Segments I-VI with 5 spiracular setae; segments VII, VIII each bear 4 setae, spiracular setae absent on segment IX; setae 2, 3 of segment I borne on egg burster (Fig. 122); seta 2 of segments II-VIII borne on egg burster (Fig. 121), seta 3 on spiracular area. Setae 1, 2, 3 of segments I-VI short, 4, 5 minute; setae 1, 2 of segment VII moderately long, 3, 4 minute; setae 1, 2 of segment VIII long, 3, 4 minute.

*Ventral Area* — Epipleura of segments I-VIII with 2 setae, seta 1 short, 2 moderately long; epipleurum of segment IX bears 1 moderately long seta. Pleural areas of segments I-VII with 2 setae, seta 1 moderately long, 2 short; pleural area of segment VIII with 1 moderately long seta. Pedal areas of segments I-VIII with 1 moderately long seta. Eusternum of segments I-IX with 1 minute anterior seta and 1 moderately long posterior seta. Sternal areas of segments I-VIII each with 1 pair of long setae; sternum of segment IX with 1 pair of moderately long setae.

*Anus* — Terminal (Figs. 123, 124), with 1 pair of short setae on each side of dorsal lobe (may be pleural and pedal setae of segment IX); anal slit U-shaped dorsally with a longitudinal slit ventrally; internal surfaces of anal folds bear divided asperities (Fig. 126) which grade to undivided, spinelike asperities (Fig. 125) on more exposed areas.

## Life History of *Ithycerus*

### Egg and Larval Development

Table 3. Number of eggs and larvae collected from rearing experiments, 1978

| DATES OF OVIPOSITION | EGGS COLLECTED | TIME (DAYS) TO ECLOSION | TIME TO PEAK ECLOSION | NUMBER HATCHED | % HATCHED |
|---|---|---|---|---|---|
| VI-3-7 | 58 | 35-53 | 46 | 45 | 77.6 |
| VI-8-11 | 53 | 37-57 | 48 | 36 | 67.9 |
| VI-12-15 | 103 | 41-54 | 43 | 61 | 59.0 |
| VI-16-21 | 174 | 37-55 | 48 | 80 | 46.0 |
| VI-22-26 | 164 | 33-50 | 43 | 28 | 17.0[†] |
| VI-27-30 | 208 | 39-51 | 42 | 96 | 46.0 |
| VII-1-4 | 122 | 41-55 | 47 | 62 | 50.8 |
| VII-5-9 | 153 | 39-55 | 45 | 64 | 41.8 |
| VII-10-12 | 162 | 38-52 | 42 | 43 | 26.5 |
| VII-13-18 | 140 | 40-48 | 42 | 24 | 17.0 |
| VII-19-23 | 134 | 39-45 | 41 | 10 | 7.5 |
| VII-24-27 | 134 | 43 | 43 | 1 | .7 |
| VII-28-VIII-2 | 145 | 38-44 | 40 | 5 | 3.4 |
| VIII ~~VII~~-3-22 | 247 | - | - | 0 | 0.0 |
|  | Total = 1997 |  | Avg. = ~~44~~ 45 | Total = 555 | Avg. = 27.8 |

[†] The soil used in the bedding box to incubate these eggs was contaminated with eggs of a species of Tipulidae which hatched and presumably destroyed a large number of *Ithycerus* eggs before being discovered.

The information given in Table 4 was collected from 61 larvae reared between August 10, 1978, and June 22, 1979. The ranges given indicate when the first of the remaining larvae (specimens representing the various instars were killed and preserved) had moulted to when the last larva had moulted. The range given for eggs to first instar represents the average times for all the first instars collected (approximately 400).

Table 4. Development times for larval ~~instars~~ Stages of *Ithycerus*.

| ~~INSTAR~~ STAGE | NO. OF DAYS ~~TO MOULT~~ IN STAGE |
|---|---|
| EGG - FIRST | 39-42 |
| FIRST - SECOND | 11-14 |
| SECOND - THIRD | 13-19 |
| THIRD - FOURTH | 15-23 |
| FOURTH - FIFTH | 11-19 |
| FIFTH - SIXTH | 23-29 |
| SIXTH - SEVENTH | 25-33 |
| SEVENTH - EIGHTH | 40 |
| EIGHTH - NINTH | 39 |
| NINTH - TENTH | 45 |

## Adult Longevity

Careful note was made of the number of days each *Ithycerus* adult survived in captivity. The starting time was date of capture which is assumed in all cases to have been the day, or very near it, of emergence from the ground, because collections were begun several weeks before any adult was found to about eight days after the first adult was captured. It is not known how long teneral adults remain in the ground, so that the lifespans recorded refer only to the time above ground.

One female died after 58 days (May 25 - July 17). The longest surviving female lived for 92 days. The average lifespan for 12 females was calculated to be 84 days.

The first male to die also lived for 58 days. The longest surviving male lived for 81 days, and the average lifespan for 10 males was 70 days.

### Flight Period

Table 5. Months during which *Ithycerus* adults have been captured.

| MONTH | NUMBER OF SPECIMENS |
|---|---|
| APRIL | 4 |
| MAY | 205 |
| JUNE | 380 |
| JULY | 132 |
| AUGUST | 9 |
| SEPTEMBER | 3 |

## Plant Species Associated with *Ithycerus*

Table 6 indicates plant species on which *Ithycerus* adults have been collected. The information was taken from labels accompanying museum specimens and from my own collecting experiences.

Table 6. Plant species and families* associated with *Ithycerus* adults.

| SPECIES OR GENUS | COMMON NAME | FAMILY | DATE COLLECTED | LOCALITY | NUMBER OF SPECIMENS | |
|---|---|---|---|---|---|---|
| *Fagus grandifolia* | American Beech | Fagaceae | VII-16 | Riverton, New Jersey | 1M | 1F |
| *Fagus grandifolia* | American Beech | Fagaceae | VI-13 | Oyster Bay, Long Island | 1 | 0 |
| *Fagus grandifolia* | American Beech | Fagaceae | VI-1 | Parkhill, Ontario | 8 | 10 |
| *Fagus grandifolia* | American Beech | Fagaceae | VII-10 | Beech Grove, Quebec | 1 | 0 |
| *Castanea dentata* | Chestnut | Fagaceae | | Tryon, North Carolina | 0 | 1 |
| *Quercus alba* | White Oak | Fagaceae | VI-6 | Bronxville, New York | 0 | 1 |
| *Quercus alba* | White Oak | Fagaceae | VII-3 | Litchfield, Connecticut | 1 | 0 |
| *Quercus alba* | White Oak | Fagaceae | V-28 | Oakwood, Illinois | 0 | 1 |
| *Quercus alba* | White Oak | Fagaceae | VI-1-8 | Grand Bend, Ontario | 11 | 8 |
| *Q. bicolor* | Swamp White | Fagaceae | VI-9 | Bronxville, New York | 0 | 1 |
| *Q. coccinea* | Scarlett Oak | Fagaceae | VI-23 | Lichfield, Connecticut | 1M | 1F |
| *Q. macrocarpa* | Bur Oak | Fagaceae | | Wingra Lake, Wisconsin | 1 | 0 |

Table 6 continued

| SPECIES OR GENUS | COMMON NAME | FAMILY | DATE COLLECTED | LOCALITY | NUMBER OF SPECIMENS | |
|---|---|---|---|---|---|---|
| *Q. Prinus* | Chestnut Oak | Fagaceae | IV-10 | Bethlehem, Pennsylvania | 1 | 1 |
| *Q. ellipsoides* | Jack Oak | Fagaceae | | Wood County, Wisconsin | 0 | 1 |
| *Q. borealis* | —— Oak | Fagaceae | VI-26 | Dane County, Wisconsin | 1 | 0 |
| *Quercus sp.* | —— Oak | Fagaceae | V-19 | Carbondale, Illinois | 1 | 0 |
| *Quercus sp.* | —— Oak | Fagaceae | IV-26 | Muncie, Illinois | 1 | 0 |
| *Quercus sp.* | —— Oak | Fagaceae | V-13 | Oregon, Illinois | 2 | 0 |
| *Quercus sp.* | —— Oak | Fagaceae | V-14-VII-3 | Livingston Co., Michigan | 11 | 5 |
| *Quercus sp.* | —— Oak | Fagaceae | VI-27 | Sherbourne, Massachusetts | 1 | 0 |
| *Quercus sp.* | —— Oak | Fagaceae | VI-27 | Clark County, Indiana | 0 | 1 |
| *Quercus sp.* | —— Oak | Fagaceae | VI-1 | Fort Coulonge, Quebec | 0 | 1 |
| *Quercus sp.* | —— Oak | Fagaceae | VI-4 | Ojibway, Ontario | 4 | 2 |
| *Juglans cinerea* | Walnut | Juglandaceae | V-27 | Lynne, Connecticut | 0 | 1 |

Table 6 continued

| SPECIES OR GENUS | COMMON NAME | FAMILY | DATE COLLECTED | LOCALITY | NUMBER OF SPECIMENS | |
|---|---|---|---|---|---|---|
| *Carya cordiformis* | Bitternut Hickory | Juglandaceae | VI-4 | Parkhill, Ontario | 1M | 2F |
| *Carya sp.* | Hickory | Juglandaceae | VI-26 | Prince George Co., Ontario | 0 | 1 |
| *Carya sp.* | Hickory | Juglandaceae | V-18 | Marshall, Illinois | 1 | 0 |
| *Carpinus caroliniana* | Blue Beech | Betulaceae | VI-3-6 | Parkhill, Ontario | 0 | 2 |
| *Carpinus caroliniana* | Blue Beech | Betulaceae | | | 0 | 1 |
| *Betula populifolia* | Birch | Betulaceae | VI-20 | Springfield, Massachusetts | 0 | 1 |
| *Alnus sp.* | Alder | Betulaceae | VII-16 | West Paris, Maine | 0 | 1 |
| *Pyrus Malus* | Apple | Rosaceae | V-3 | Long Creek, South Carolina | 4 | 5 |
| *Pyrus Malus* | Apple | Rosaceae | VI-12 | Byron, Minnesota | 15 | 23 |
| *Pyrus Malus* | Apple | Rosaceae | V-24 | Polk County, Iowa | 1 | 0 |
| *Pyrus Malus* | Apple | Rosaceae | V-19 | Rogersville, Missouri | 1 | 1 |
| *Pyrus Malus* | Apple | Rosaceae | VI-21 | Harvard, Illinois | 0 | 1 |

Table 6 continued

| SPECIES OR GENUS | COMMON NAME | FAMILY | DATE COLLECTED | LOCALITY | NUMBER OF SPECIMENS | |
|---|---|---|---|---|---|---|
| *Pyrus Malus* | Apple | Rosaceae | V-7 | Okonoka, West Virginia | 1 | 0 |
| *Pyrus Malus* | Apple | Rosaceae | V-2 | Newton County, Missouri | 0 | 1 |
| *Pyrus Malus* | Apple | Rosaceae | VI-22 | Sidna, Virginia | 2 | 4 |
| *Prunus Persica* | Peach | Rosaceae | VI-1 | Mystic, Connecticut | 1 | 0 |
| | Fruit Trees | Rosaceae | V-31 | Southern Illinois | 0 | 1 |

*Nomenclature follows that of Gleason and Cronquist (1963).

## Grooming in *Ithycerus*

Terminology proposed by Valentine (1973) is used in the following descriptions of grooming behaviour observed in *Ithycerus* adults. *Cleaning movements*, as defined by Valentine (1973), occur when appendages are passed through the mouthparts. Valentine defines *rubbing* as "a variety of actions involving moving or progressive contact of a leg with another appendage or the general body surface". A third aspect of grooming is termed *positioning* by Valentine (1973) and includes specific movements of the elytra, hindwings and vesicles (Melyridae).

### CLEANING

*(1) Palpus Clean:* The palps appear to be chewed by the maxillae as described by Valentine (1973) and assisted by movements of the mandibles. It was commonly observed in males and females after feeding and during rest periods. It was also performed by females during mating and oviposition.

*(2) Foreleg Clean:* This was observed only once. The right foreleg of a female was drawn through the mouthparts while being chewed by the maxillae and mandibles.

### RUBBING

*(1) Antenna Rub:* The ventral margins of the foretibia are rubbed along the dorsal surfaces of both antennae simultaneously. This was

done by lowering the head and standing on or near the bases of the antennae; then, the head was lifted, causing the antennae to be pulled through and rubbed for their entire length. The rubbing occurred while being positioned across twigs (Fig. 23), along twigs (Fig. 24), or on flat surfaces such as cage floors (Fig. 30). It occurred during times of activity and rest, though more often during the latter.

*(2) Body-Hindleg Rub:* This was rarely observed. The tibia and tarsi of a hindleg are rubbed along the sides of the abdomen. Bilateral movements (both sides at the same time) were not observed.

*(3) Bilateral Foreleg Rub:* Two modes were recorded for this movement. The first and most common involved the rubbing of the tibia and tarsi of the forelegs below the head while the individual rested on a twig (Fig. 26). In the second mode, the tarsi and tibia of the forelegs were rubbed anterior to the head while the individual was on a flat surface such as the cage floor or perched lengthwise on a twig. In all situations, the ventral surfaces of the tibia and tarsi of one leg were rubbed on the dorsal surfaces of the other, then the positions were reversed so that the other surfaces were rubbed.

*(4) Fore-Midleg Rub:* Two modes were recorded for this movement. In the first, the tibia and tarsi of the fore and midlegs of either side were rubbed below the body while the individual rested on a twig (Fig. 16). On flat surfaces, the legs being rubbed were raised and extended to the side of the body. This latter mode was commonly seen when the insects were active, particularly in females which were

were placed in the egg-laying container. Presumably, the sand in this container became trapped in the tarsal pads and stimulated the rubbing.

*(5) Bilateral Fore-Midleg Rub:* This was observed on twigs and flat surfaces. On twigs, all four legs were allowed to dangle below the body. On flat surfaces (Fig. 28), the legs were extended away from the body with the midlegs usually touching the surface.

*(6) Mid-Hindleg Rub:* Three modes have been recorded for this. The most common mode occurred when the individuals rested on twigs with the mid and hindlegs dangling below the body. The second occurred on flat surfaces with the two legs involved being raised and extended away from the body (Fig. 25). The third, rarely seen, was observed when individuals rested on twigs; the hind leg was bent and firmly planted on the twig (Fig. 15), while the tiba and tarsi of the midleg was rubbed against it.

*(7) Bilateral Mid-Hindleg Rub:* Two modes were recorded for this movement. The first and most common occurred while individuals rested lengthwise along twigs. The mid and hindlegs of both sides were allowed to dangle below the body with the front legs gripping the twig. On flat surfaces, the hindlegs rested on the substrate and were extended away from the body as they were being rubbed by the midlegs (Fig. 29).

*(8) Bilateral Hindleg Rub:* Three modes were recorded for this movement. The first occurred on twigs and flat surfaces. In an

upright position, the fore and midlegs were extended so that the body was raised and tilted forward and the hindlegs were rubbed beneath the abdomen. In the second mode, the body was positioned across a twig so that the hindlegs dangled below the abdomen (Figs. 17-22). The tibia and tarsi of one leg were passed down the dorsal surfaces of the other and were then drawn back up against the ventral surfaces. When this was completed, the positions of the legs were often reversed. The third very rare mode was observed when individuals hung upside down from the roofs of the cages or from twigs. The abdomen was allowed to drop down slightly and the hindlegs were rubbed above the abdomen.

*(9) Fore-Midleg, Mid-Hindleg Rub:* In this unusual movement (not to be confused with Valentine's fore-mid-hindleg rub which involves the three legs from one side), the foretibia and tarsi were rubbed against the midtibia and tarsi on one side of the body while, at the same time, the tibia and tarsi of the mid and hindlegs were rubbed on the other side. This rubbing movement was observed on twigs and flat surfaces (Fig. 27). In both situations, the body weight was supported by the sternum with the remaining two legs acting as stabilizers.

## POSITIONING

*(1) Elytra Raise:* This was not the rapid rising and falling of the elytra described by Valentine (1973). The elytra were raised with some separation and lowered slowly. This was assisted by the abdomen which was slightly extended while being raised and lowered.

*(2) Wing Extend:* The wing apices were straightened so that they were visible beyond the tips of the elytra and then refolded. The unfolding and folding were assisted by the abdomen and occurred rapidly when individuals were walking or more slowly when resting. Separation of the elytra was usually noticeable.

*(3) Wing Unfold:* To paraphrase Valentine (1973), the elytra were raised and the wings completely unfolded as if readying for flight, then quickly refolded. It was not possible to separate this positioning movement from aborted flight attempts unless those attempts were accompanied by the rapid flutter of the wings.

*(4) Flagellum Extend:* Males at rest were often observed to evert the internal sac so that the flagellum was completely extended (Fig. 8). The flagellum was usually curled and uncurled several times before being retracted. On one occasion, it appeared as if the male was deliberately rubbing the flagellum against the twig it was perched on.

## Distribution, Geographic Variation and Biogeography of *Ithycerus*

There are two distinct adult colour forms in three separate geographical areas (Fig. 194). A northern grey form exists in which there is low contrast between light and dark patches of pubescence and two southern melanic forms which have highly contrasting light and dark patches. The high contrast is produced by fewer yellow and more dark brown scales than are present on individuals of the northern grey form

Table 7. Comparison of adult characters of three populations of *Ithycerus*. Measurements (in mm.) express ranges.

| POPULATION | CHARACTERS | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | HEAD LENGTH | | ELYTRA LENGTH | | PRONOTUM LENGTH | | PRONOTUM WIDTH | | OCULAR WIDTH | | YELLOW SCALES | |
| | *M* | *F* | *M* | *F* | *M* | *F* | *M* | *F* | *M* | *F* | *M* | *F* |
| NORTHERN | 1.98 | 2.10 | 7.67 | 9.36 | 2.28 | 2.58 | 2.40 | 2.76 | .78 | .84 | 20 | 25 |
| | | | | | | | | | | | (34) | (50) |
| GREY FORM | 2.28 | 2.46 | 9.49 | 11.50 | 2.82 | 3.36 | 2.88 | 3.48 | .96 | 1.08 | 65 | 70 |
| SOUTHERN | 2.16 | 2.16 | 8.58 | 10.14 | 2.58 | 2.82 | 2.58 | 3.00 | .84 | .90 | 5 | 6 |
| | | | | | | | | | | | (15) | (31) |
| MELANIC | 2.15 | 2.58 | 9.60 | 11.60 | 3.00 | 3.24 | 3.00 | 3.36 | 1.02 | 1.08 | 27 | 58 |
| (APPALACH.) | | | | | | | | | | | | |
| SOUTHERN | 2.04 | 2.16 | 7.67 | 10.92 | 2.40 | 3.00 | 2.52 | 3.06 | .78 | .96 | 0 | 18 |
| MELANIC | | | | | | | | | | | | |
| (OZARKS) | | | | | | | | | | | | |

Based on 50 males and 50 females of northern form; 12 males and 12 females of southern appalachian form; 1 male and 1 female of southern ozark form. Numbers in brackets are averages.

and the pubescence is generally less dense, allowing more of the dark exoskeleton to show through.

Table 7 shows structural differences between the three colour forms. Statistical analysis was not done because the southern population samples were too small and the regions around the areas they were found were not collected well enough to indicate whether or not intermediate forms exist which link the three forms.

## Phylogenetic Relationships of *Ithycerus*

Four families are recognized in the apionid evolutionary line: Ithyceridae, Brenthidae, Antliarrhinidae and Apionidae. Table 8 is a compilation of 36 characters with their ancestral and derived states expressed. The emphasis is on larval characters with important adult characters included. The dendrogram (Fig. 195) proposed to illustrate the relationships between the four families was constructed according to the guidelines provided by Hennig (1966), Ross (1974), Mayr (1969), and Crowson (1967, 1970). The dendrogram presented in Fig. 195 was proposed by Crowson (personal communication).

Table 8. Comparison of selected larval and adult characters in the families Ithyceridae, Brenthidae, Antliarrhinidae and Apionidae.

| CHARACTER | CHARACTER STATES | |
|---|---|---|
| | ANCESTRAL | DERIVED |
| LARVAE | | |
| Food Habits | Associated with woody plants mainly (1) | Associated with herbaceous plants mainly (1') |
| No. of Dorsal Folds on Abdominal Segments | 2(2) | 3(2') or 4(2'') |
| No. of Setae on abd. Epipleura | 3(3) | Less than 3(3') |
| Thoracic Legs | Present (4) | Absent (4') |
| Antenna | Supported by frontal ridge (5) | Frontal ridge absent (5') |
| No. of Ocelli | 3(6) | 2(6'), 1(6'') or 0(6''') |
| No. of Articles, Maxillary Palps | 2(7) | 1(7') |
| No. of Articles, Labial Palps | 2(8) | 1(8') |
| Pairs of Setae on Labrum | 4(9) | 3, setal pits of 4th pair present (9')<br>3, setal pits of 4th pair absent (9'')<br>2 (9''') or 1(9'''') |

Table 8 continued

| CHARACTER | CHARACTER STATES<br>ANCESTRAL | DERIVED |
|---|---|---|
| Single Basal Sensillum of Labrum | Present (10) | Absent (10') |
| No. of Sensillum on Clypeus | 2(11) | 0(11') |
| No. of Setae on Clypeus | 3 pair (12) | 2 pair (12')<br>1 pair (12'')<br>0 pair (12''') |
| Anterior Margin of Clypeus | Not divided (13) | Weakly to strongly divided (13') |
| Labral Rods | Present (14) | Absent (14') |
| Labral Rods | Long (15) | Short (15') |
| Pronotal Plate | Present (16) | Absent (16') |
| Frontal Sutures | Complete (17) | Incomplete (17') |
| Head Capsule | Large, heavily sclerotized (18) | Small, weakly sclerotized (18') |
| Head Capsule | Epicranial setae distinct (19) | Epicranial setae mostly indistinct (reduced) (19') |
| Head Capsule | Occipital foramen small (20) | Occipital foramen large (20') |
| Ventral Nervous System | Abd. ganglia separated by distinct connectives, ganglia elongated (21) | Abd. ganglia not separated, connectives greatly reduced, ganglia round, beadlike (21') |

Table 8 continued

| CHARACTER | CHARACTER STATES | |
|---|---|---|
| | ANCESTRAL | DERIVED |
| Egg bursters | Present (22) | Absent (22') |
| **ADULT** | | |
| Antenna | Straight (23) | Geniculate (23') |
| Ovarioles | 3 per ovary (24) | 2 per ovary (24') |
| Accessory gland(s) of female reprod. system | Present (25) | Absent (25') |
| Gular Sutures | Single (26) | Double (26') |
| Cerebrum | Paired lobes transverse (27) | Paired lobes folded anteriorly, narrowly fused (27')<br>Lobes anteriorly folded, broadly fused (27'') |
| Ventral Nervous System | All ganglia separated by long connectives except 2nd and 3rd thoracic and with 3 abd. ganglia (28) | 2 isolated abd. ganglia, long connectives (28')<br>Extensive fusion of all ganglia (28'')<br>Ganglia separated by long connectives as result of secondary elongation of abdomen (28''') |
| Hind Wings | 4 anal veins (29) | 3 anal veins (29')<br>2 anal veins (29'')<br>1 anal vein (29''') |
| Hind Wings | Median vein present (30) | Median vein absent (30') |

Table 8 continued

| CHARACTER | CHARACTER STATES |  |
|---|---|---|
|  | ANCESTRAL | DERIVED |
| Hind Wings | R-s vein present (31) | R-s vein absent (31') |
| Hind Wings | Radial cell large, triangular (Figs. 180-188) (32) | Radial cell small or absent (32') |
| Hind Wings | Jugal lobe present (33) | Jugal lobe absent (33') |
| Labial Palps | 3 segmented (34) | 2 segmented (34')<br>1 segmented (34'') |
| Maxillary Palps | 3 segmented (35) | 2 segmented (35) |
| Maxillary Palps | Move horizontally (36) | Move vertically (36') |

# DISCUSSION

## Eggs of *Ithycerus*

The eggs are very large in comparison to those laid by most Curculionoidea. In addition, they are laid singly rather than in batches. The habit of laying eggs singly has been observed in some species of broadnosed (broad-nosed) weevils such as *Otiorrhyncus*, *Sitona* and *Alophus* (van Emden, 1950), and the eggs of at least two species of *Otiorrhyncus* darken with exposure to air as in *Ithycerus*. The eggs of species *Barynotus* darken as well, but their eggs are laid in batches (van Emden, 1950). The pigmentation ~~probably aids~~ may aid in concealing the eggs from predators and parasites. The habit of *Ithycerus* females covering eggs with fecal matter has not been reported in any other species of Curculionoidea, although it has been observed in some Chrysomelidae (A. Howden, personal communication). This probably helps to further conceal the eggs, as well as provide protection against dessication.

I have not been able to locate photomicrographs of the external surface of the chorion of other weevil eggs in the literature. However, honeycombed surfaces are apparently fairly common in other insect orders, e.g. Hymenoptera.

## Larval Characters

A few selected larval characters are discussed here in terms of their structure as related to function. Perhaps two of the most striking features of *Ithycerus* larvae are the very large, heavily sclerotized head capsule and mandibles. These features can be readily correlated to feeding habits. The head capsule houses a massive set of muscles which operate the mandibles. The mandibles must be powerful in order to penetrate the tough outer layers of root bark so that the larvae can feed on the nutrient high vascular cambium and ~~phloem~~ phloem layers. *Ithycerus* larvae feed voraciously and attain a very large size.

Support for the head capsule is provided by a heavily sclerotized tentorial bar and well developed hypopharyngeal bracon and the occipital foramen is quite small.

Similar adaptations are found in the head capsules of *A. minutus*. These larvae must be able to bore through the extremely dense wood of hardwoods such as oak. The tentorial bar of this species is larger than in *Ithycerus*, as is the broad, heavily sclerotized hypopharyngeal bracon.

In contrast, the head capsules of *Antliarrhinus* larvae (Fig. 139) are much smaller in relation to body size and are weakly sclerotized, the mandibles are small, the tentorial bar is reduced, the hypopharyngeal bracon is thin and the occipital foramen is very large. These larvae feed on the soft tissues inside cycad seeds. Similar reductions are seen in many larvae of Curculionidae which feed on soft tissues such as those found in fruits, seeds and stems of many herbaceous plants.

Another conspicuous feature of *Ithycerus* is the presence of thoracic legs. These apparently serve no ambulatory function. They are, however, well endowed with a stiff setae and numerous sensilla so that the legs probably have a sensory function. The legs of *A. minutus* are similarly developed though they are less conspicuous. Legs are absent in *Antliarrhinus* as they are in most species of Curculionoidea.

The prothorax of *Ithycerus* larvae bears a large, heavily sclerotized pronotal plate. It functions in packing soil and exuvia as the larvae tunnel along root surfaces on their backs. Touching an exposed larva causes it to pull its head in as far as possible and elevates the pronotal plate in a kind of defense posture. The plate bears numerous stiff setae and two pair of sensilla and, therefore, probably has a sensory function as well.

A similar but smaller plate is found on *A. minutus* larvae and probably has similar functions. It is probably used to better advantage as a defense mechanism. The head and pronotal plate, together with the sclerotized prosternum, can plug a larva tunnel completely and may present an armoured shield against the attacks of predators in the tunnels such as mites.

The inner surfaces of the anal folds of *Ithycerus* and *A. minutus* bear many divided spinelike asperities which are directed internally from their bases, then curve upward like curled fingers on a human hand. These apparently act like miniature pitch forks in pushing fecal matter out of the anus during muscle contractions. Similar asperities are found in the digestive tracts of adults of *Aglycyderes*, posterior to the proventriculus (not illustrated). These asperities may be common in the digestive tracts of larvae and adults of many Curculionoidea.

Egg bursters, sharply pointed, posteriorly directed asperities, have been found on abdominal segments I-VIII on first instar larvae of *A. minutus*. They occur above the spiracles among the spiracular setae. It has not been proven that they are actually used to break through the chorion during eclosion, but they are shed in later instars. I have not been able to examine second instar larvae and, therefore, am not sure at what stage these structures are shed.

Larvae of *A. minutus* and some other brenthids possess a pair of triangular patches of asperities on the posterolateral margins of the mesonotum (Figs. 113, 114). It is not known if these are used for traction or for stridulation or both (perhaps neither).

## Life History

### Life Cycle

Field studies and rearing experiments indicate that *Ithycerus* has a two year life cycle at least and possibly three. Four ninth instar larvae have been identified from larvae reared between July, 1978, and March, 1979. A tenth instar has been identified from larvae which were reared between August, 1978, and June, 1979. At no time did feeding cease during these periods.

Captive females continued to lay eggs throughout the time they were alive, an average of 12 weeks. However, eggs laid during June hatched in greater numbers than those laid in July (Table 3). In other words, it seems that the viability of eggs decreases as the age of the female increases. The average time to eclosion for all eggs was six weeks and there was no significant differences between those laid in June and those in July. In contrast, eggs collected from the King Mountain specimens hatched after three to four weeks. This is probably an adaptation ~~attributed~~ to the shorter warm season as compared to Southwestern Ontario.

The time required for all larvae to reach fourth instar was 98 days and 117 to reach fifth. The growing season in Southwestern Ontario is approximately 120 days. Therefore, *Ithycerus* larvae probably spend the first winter in the ground at least as fifth instars. The four wild larvae I collected were subsequently identified as a fifth, sixth and 2 seventh instars and this was in late May — early June. The development times shown in Table 4 indicate that the second winter is probably spent as ninth instars. The two teneral adults I collected in late May still had very soft exoskeletons which indicates that pupation takes place in the spring rather than the fall.

Although *Ithycerus* adults are rather long lived in captivity, there is no evidence that they are capable of overwintering. In captivity, they experienced no climatic stress and expended very little energy in locating food. Thus, their lives are very likely extended in captivity.

## Flight Period

Adult *Ithycerus* are most abundant May through July with peak abundance in June (see Table 5). Emergence dates vary from south to north,as might be expected,with earlier times usually recorded farther south. The earliest reported dates of capture are April 10, Bethlehem, Pennyslvania; April 18, Arkansas; and April 26, Muncie, Indiana. The latest reported dates of capture are September 4-6, Saugus, Massachusetts; and September 31, in Indiana.

## Predators and Parasites

There are no recorded observations of any predator eating an *Ithycerus* adult. However, it seems unlikely that they would be free from predation. The most likely suspects would be woodpeckers. In Pinery Provincial Park, seven species have been recorded. I observed several species searching for insects on White Oak trunks. They did so by knocking off the loose scales and thus would expose any *Ithycerus* adult hiding beneath one.

The only recorded parasite of adults is a small tachinid fly, *Hyalomyodes weedii.* This species has also been recorded as a parasite of adults of Alleculidae, Chrysomelidae, Coccinelidae, Curculionidae and Pterophoridae (Arnaud, 1978). A single specimen was reared by A. Howden from an adult collected on King Mountain, Old Chelsea, Quebec, August, 1971.

No egg parasites or larval parasites are known as yet. By accident, I discovered that humus dwelling larvae of Tipulidae (Diptera) are probably occasional egg predators.

## Plant Species Associated With *Ithycerus*

Table 6 indicates that *Ithycerus* has a relatively restricted host range. Adults are regularly associated with species of three closely related families of woody plants: the Betulaceae, Juglandaceae and Fagaceae. Label data and my own collecting experience show that species of Fagaceae are the preferred hosts, particularly White Oak and American Beech. In the Pinery study area, the latter species is absent and adults were captured on White Oak only. In the Parkhill study area, very few White Oaks were present and approximately equal numbers of adults were collected on Beech and Bitternut Hickory. A few were also collected on Blue Beech. This indicates that host preferences are affected by host plant species composition and that White Oaks are not required to sustain populations of *Ithycerus*.

It is interesting to compare the distribution of *I. noveboracensis* with the distribution of some of its hosts. Fig. 194 shows its distribution with respect to White Oak. With the exception of Fort Coulonge, Quebec, and Chippewa County, Minnesota, all localities for *Ithycerus* lie within the boundaries of the White Oak distribution in spite of the fact that several host species occur beyond these boundaries, e.g., Bur Oak and Beech. This is difficult to interpret since the distribution of *Ithycerus* could be limited by the same climatic conditions which limit White Oak or it is gradually evolving a specificity to White Oak.

In addition to the three families listed above, large numbers of adults are occasionally taken on introduced species of cultivated fruit trees, i.e., apple, plum and peach (Rosaceae). In fact, *Ithycerus* was regarded as a serious pest of orchards and nurseries at the turn of the century (Lugger, 1899, ~~1902~~). This problem has been eliminated as a result of modern insecticides. The most recent record of this was in 1956 in Minnesota where large numbers of adults were collected on apple trees (in UMSP collection).

This feeding habit is not a local phenomenon, as it has been recorded in South Carolina, north to Virginia and New York, west to Missouri, and northwest to Minnesota. At present, this is viewed as a secondary adaptation in feeding habits and may be the result of similar chemical compounds present in natural hosts and some species of Rosaceae. This is only speculation as no tests have been carried out in an attempt to verify this.

## Feeding Behaviour

Adults feed mainly on new season's growth and include in their diet the bark of shoots, leaf petioles, leaf buds and acorn buds (Figs. 10, 11, 12, 13, 14). ~~Lugger~~ Washburn (1902) reports that leaves of plums are also eaten and includes a photograph of adults clinging to partially skeletonized leaves. I have attempted to verify this habit by placing twigs with leaves intact into rearing cages on several occasions and have never seen evidence of leaves being eaten.

Adult *Ithycerus* do not have a crop (Fig. 49) and the proventriculus consists only of eight rows of loosely aggregated setae. Consequently,

~~all~~ most food material ingested is passed directly to the large stomach (Fig. 49).

Observations in the field and laboratory indicate that feeding is temperature regulated. Feeding does not occur when it is too hot or cold, and they become inactive during these periods. Extremes of heat and cold usually occur during the day and late evening, respectively, and feeding was usually observed in the morning and began again in early evening. During late morning and throughout the afternoon, most adults seemed to leave the canopy and were found on tree trunks.

Larvae develop on the roots of host plants by feeding on the vascular cambium. The external bark ~~and~~ vascular cambium and phloem layers are completely removed, exposing the inner ~~phloem~~ xylem layer. Feeding is done primarily on the lower surfaces of lateral roots and larvae travel on their backs in the tunnels formed. The roofs of the tunnels comprise frass and exuvia mixed with soil. The change to new instars occurs at the end of tunnels which are expanded. Occasionally, cells for this purpose were found away from the roots, the walls of the cells comprising packed soil and exuvia. The larva of *Ithycerus* also lacks a crop (Fig. 48) and the proventriculus (Fig. 48) consists of eight membranous invaginations which lack setae. As in adults, all ingested food material is passed directly into the midgut.

## Courtship and Mating

Newly emerged adults were found to begin sexual activity about 10 days after being placed in the rearing cages and, after two weeks, peak activity appeared to have been reached.

There is no obvious courtship in *Ithycerus*, at least under laboratory conditions. Males, upon recognizing females, climbed on their backs and attempted to copulate. Males became noticeably excited when females were returned to the cages after having been removed for egg collecting purposes. This seems to indicate that females produce pheromones for attracting males.

Mating occurred most often during the times described for feeding. As a result, males sacrifice a large portion of feeding times in order to locate and mate with females. However, their smaller size means they would eat less than females. Females spend a great deal of time feeding. They probably need a great deal of food to supply their large bulk and to produce eggs.

During copulation, all six legs of the male were used to grasp the female (Fig. 7). Mounted females often wandered about the cages, fed or groomed themselves (Fig. 7). Males reacted to movement by rapidly tapping the female's elytra and pronotum with their forelegs, as if trying to calm them. On a number of occasions, I watched females trying to dislodge males by violently rocking from side to side with little success. This was not surprising considering the development of the male genital apparatus (Figs. 86-94). Once the long flagellum and transfer apparatus were in place, successful mating seemed assured.

The only time aggressive behaviour was observed occurred when males attempted copulation or during copulation. During attempted copulation, a pair would often be dislodged from their perch and end up firmly entangled in one another's legs. Females usually resorted to chewing off parts of the males' legs and antennae in order to escape. When another male approached a mating pair, it would sometimes begin chewing the legs of the copulating male. In both situations, the aggression which took place appeared so casual that it gave the impression that the victims were unaware that they were being slowly dismembered.

## Oviposition

Oviposition sites chosen by females were usually small depressions in the soil, around the bases of the saplings provided, or around the edges of the clump of grass which was also placed in the bucket. When a site was chosen, the female turned around and backed the tip of her abdomen into the soil and, with a rotating motion, forced the ovipositor into the depression. This was aided by the eighth tergite which was used as a small shovel. When the preparations were completed, the female raised her body by extending the forelegs (Fig. 9), then proceeded to deposit a single egg (Fig. 56). After the egg was in place, the female lowered her body and then carefully covered the egg with fecal matter. Drawing the tip of the abdomen back and forth across the egg, the fecal matter was carefully spread using the eighth tergite and coxites. The time required to prepare the site, deposit the egg, and cover it varied greatly but usually lasted two or three minutes. Age was an important factor in the amount of time required, and very old females took as long as 10-15 minutes. The number of eggs deposited in a day varied with age as well. Young, healthy females deposited as many as eight, while very old ones produced one or two each day. Rearing experiments showed that females continued to lay eggs for their entire adult life. The average number of eggs laid per female was 157, based on 12 individuals.

## Grooming

Cleaning movements in *Ithycerus* appear to be absent for the most part. This might be attributed to the structure of the head and rostrum. For example, the antennae do not seem to be able to reach far enough forward to be passed through the mouthparts. Valentine (1973) postulates that cleaning movements are primitive behaviours and further speculates that reductions in mouthparts and other specializations in the Curculionoidea have resulted in the loss of oral grooming functions in most species. Excellent examples can be found among the Brenthidae and the closely related *Antliarrhinus* where, in the females at least, the rostrum has become so elongated and the mouthparts so reduced that it is absolutely impossible for oral grooming to occur.

*Palpus clean* has been partially compensated for in at least one species of Brenthidae. Female *Arrhenodes minutus* were observed removing wood particles, trapped in their mouthparts while drilling egg holes, using the tips of their antennae against the mouthparts. Thus, apparently, a rubbing movement has been substituted for a cleaning movement which was lost.

The following grooming movements and modes recorded for *Ithycerus* are apparently new for Coleoptera and specifically the Curculionoidea. All other rubbing movements described for *Ithycerus* have been observed in other species of Curculionoidea by Valentine (1973). The new movements or modes are as follows: (1) Bilateral Fore-Midleg Rub; (2) Mid-Hindleg Rub, third mode; (3) Bilateral Hindleg Rub, third mode; (4) Fore-Midleg, one side, Mid-Hindleg, other side Rub.

Of the four positioning movements described for *Ithycerus*, only *flagellum extend* is new for the Curculionoidea and Coleoptera as well.

The grooming movements described as new in *Ithycerus* may well appear in other species of Coleoptera when these are studied more closely. Valentine (1973) points out that in no way can we be sure an individual will perform its entire repertoire, no matter how long it is observed. Specific stimuli are apparently required to initiate grooming movements. Valentine (1973) lists the following as probable sources of stimuli: state of activity, substrate, availability of food and water, temperature, light intensity, humidity, exposure to insecticides and nutritional history. I would broaden 'insecticides' to include any chemical substance which would act as an irritant.

Valentine also discusses the possibility of grooming movements used as displacement activity. Several instances of grooming while *Ithycerus* adults were upturned on flat surfaces may represent such activity. In this situation, it was very difficult for individuals to right themselves. I have observed fore-midleg rub, mid-hindleg rub and bilateral hindleg rub while individuals were upturned. It could be that these were attempts to improve traction, but I felt that these were not normal responses. I also observed individuals biting their own limbs in conjunction with grooming which intensified the feeling that, to be somewhat anthropomorphic, the individuals were venting their 'frustration' at not being able to right themselves.

## Distribution, Geographic Variation and Biogeography of *Ithycerus*

The results in Table 7 and the distribution of the three colour forms (Fig. 194) indicate that there may be three distinct subspecies of *Ithycerus noveboracensis*. The geographic areas occupied by the two southern melanic forms are thought to have been refugia for organisms which survived the glacial periods, some speciating there as a result of geographical isolation. It is a very similar situation to the one described by Ross and Ricker (1971) in their ~~(1971) in his~~ study of the winter stonefly genus *Allocapnia*.

The two southern forms are distinguishable from the northern form on the basis of colour and larger size of the males. The females show no differences other than colour. The difficulty lies in separating the two southern forms from each other. The two specimens examined from the Ozarks in Missouri have fewer yellow scales than the southern Appalachian specimens, but this is too small a sample from which to draw strong conclusions. In view of this and insufficient collecting in nearby regions, I decided to refrain from calling the three forms subspecies until further information is gathered.

## Phylogenetic Relationships of *Ithycerus* With Additional Notes on Phylogeny of the Curculionoidea

Ithyceridae, Brenthidae, Antliarrhinidae and Apionidae are believed to constitute a monophyletic unit among the Curculionoidea. The principles and method of construction of the phylogenetic system have been dealt with in detail by Hennig (1966), Mayr (1969) and Ross (1974). The system is based upon the determination of sister groups. Sister groups are recognized by the presence of shared derived characters, not ancestral characters, as outlined by Ross (1974).

Ancestral (commonly shared characters) and derived states have been postulated for characters of adult and larval stages. This was done by comparisons with other families of the Curculionoidea (ex-group comparison) and group trends. I relied on the latter as apparently large numbers of extinctions occurred in the more primitive families of Curculionoidea with the result that few groups can be related on the basis of shared derived features.

A summary of the ancestral and derived states of selected characters is given in Table 8. Ancestral states have been numbered from 1-37. Derived states of the same character are identified by one or more superscript marks ('); thus 2'' indicates the second derived state of the second character listed in the Table. Ancestral states were ~~derived~~ postulated as follows:

### LARVAE

*Food Habits* — This was indirectly assessed. ~~Groups~~ ~~Weevils~~ Weevil families which are viewed as primitive on the basis of morphological features are, for the most part, associated with woody plants while more derived families are usually associated with ~~highly derived~~ ~~herbacious~~ herbaceous plant species.

*Dorsal Folds of the Abdomen* — Two dorsal folds occur most frequently and are deemed ancestral.

*Setae of Abdominal Epipleura* — Determined by ex-group comparison. The trend is in the reduction of the numbers of setae present. Thus, three setae are believed to be ancestral; less than three, derived.

*Thoracic Legs* — Though not commonly shared among the Curculionoidea, they are deemed ancestral on the basis of ex-group comparisons with other families of Coleoptera and on the ~~basis~~ belief that characters are lost more often than they are gained.

*Antennal Frontal Ridge* — Not commonly shared among Curculionoidea, but believed to be ancestral on the basis of ex-group comparison with other families of Coleoptera and on ~~that~~ the ~~basis~~ belief that characters are lost more often than they are gained.

*Number of Ocelli* — Determined by ex-group comparison among Curculionoidea, other Coleoptera and other insect orders, e.g., Mecoptera. The trend is toward loss of ocelli; thus, in *Ithycerus*, 3 ocelli are deemed to be ancestral.

*Number of Articles of Maxillary Palpus* — The ancestral state is 3 in Curculionoidea with a trend toward reduction. Therefore, 2 articles are deemed ancestral in the apionid line of evolution though derived with respect to more primitive families.

*Number of Articles of Labial Palpus* — Two articles occur most frequently and are deemed ancestral.

*Pairs of Setae on Labium* — Ex-group comparison with other families of Curculionoidea indicates a trend toward loss of pairs. Four pairs are deemed ancestral.

*Single Basal Sensillum of Labrum* — The presence of this sensillum is a commonly shared feature and is considered ancestral.

*Number of Sensilla on Clypeus* — Two pairs most commonly seen and are considered ancestral.

*Number of Setae on* Clypeus *~~Setae~~* — Three pairs commonly shared and are deemed ancestral.

*Anterior Margin of Clypeus* Ex-group comparisons indicate that undivided clypeus is ancestral state.

Labral *~~Labial~~ Rods* — Present in most Curculionoidea. Their presence is ancestral.

*Pronotal Plate* — Ex-group comparisons indicate that presence of sclerotized pronotal plate is ancestral. It has been lost many times in unrelated species.

*Frontal Sutures* — Frontal sutures meeting articulating membrane of mandibles shared by all species and is thus ancestral.

*Head Capsule* — Ex-group comparisons indicate that large, heavily sclerotized head capsules are ancestral. Correlated with feeding habits.

*Head Capsule* — Ex-group comparisons indicate that conspicuous epicranial setae are ancestral, with trend to reduction.

*Head Capsule* — Ex-group comparisons show that small occipital foramen correlated with large, heavily sclerotized head capsule and is therefore ancestral.

*Ventral Nervous System* — Distinct connectives between ganglia with ganglia longer than wide are ancestral. Determined by ex-group comparison. This may be complicated in a few instances by secondary elongation of the abdomen. These are considered rare.

*Egg Bursters* — Determined to be ancestral, if present, by ex-group comparisons.

ADULTS

*Antenna* — Straight antennae in majority of species are considered ancestral.

*Ovarioles* — Ex-group comparisons indicate trend in loss of ovarioles. Three ovarioles are considered ancestral.

*Accessory Glands* — Most species lack accessory glands in the reproductive systems of females, yet it is believed that their presence may be ancestral. This decision is based on the view that structures are lost more often than they are gained.

*Gular Sutures* — The presence of a single gular suture in all species is considered ancestral.

*Cerebrum* — Paired lobes of cerebrum transverse are ancestral. Determined by ex-group comparison.

*Ventral Nervous System* — All ganglia except second and third thoracic ganglia isolated by distinct connectives are ancestral. Determined by ex-group comparison. Trend is toward extensive fusion of ganglia. Secondary elongation of connectives as a result of secondary elongation of abdomen complicates matters.

*Hind Wings* — Four anal veins are ancestral as determined by ex-group comparison.

*Hind Wings* — Median vein present is ancestral as determined by ex-group comparison.

*Hind Wings* — The presence of R-s vein is ancestral. Determined by ex-group comparison.

*Hind Wings* — Presence of large, triangular radial cell is ancestral. Determined by ex-group comparison.

*Hind Wings* — Presence of well-developed jugal lobe is ancestral. Determined by ex-group comparison.

*Labial Palps* — Ex-group comparison indicates trend toward loss. Presence of 3 articles is believed to be ancestral.

*Maxillary Palps* — Palps which move in horizontal plane are considered to be ancestral. Determined by ex-group comparison.

From the character states deemed to be derived and on the basis of group trends, the relationships of the four families recognized are characterized as follows:

ITHYCERIDAE — This family appears to resemble most closely hypothetical ancestor A (Fig. ~~194~~ 195) in possessing many ancestral characteristics and few derived ones. It is a relict group, occurring only in eastern North America. It seems to be rather static, in an evolutionary sense.

Crowson (1955) and Morimoto (1962) showed affinities between *Ithycerus* and Brenthidae based on adult features. However, Morimoto (1976) separated the genus from Brenthidae, gave it family status, Ithyceridae, and placed it near Belidae. This was based on the structure of the abdominal sternum and the presence of eight abdominal spiracles. He described the abdomen as 'anthribid type' in which all the visible sternites are similarly inflected, except the sixth and seventh which are deeply inflected. He defined a 'curculionid type' abdomen as one in which the third and fourth sternites (first and second visible sternites) are solidly fused together, while the others remain free. Clearly, this is the situation in *Ithycerus*. Therefore, while I support the view that the genus should be maintained in its own family, I do so on new evidence.

I do not think it is necessary to analyze character by character the differences between the larva of *Ithycerus* and those of Belidae (Figs. 147-159). The illustrations make ~~made~~ this self-evident. My observations and those of Vanin (1976) should be sufficient proof that no close relationship exists between these two families as postulated by several authors in the past (Leng, 1920, 1933; Ting, 1936; Bruhn, 1947).

BRENTHIDAE — The chaeotaxy and arrangement of sensilla of the epicranium, antenna, clypeus, labrum, mandibles, mala of the maxilla, stipes and labium of the larva of *Arrhenodes minutus* are completely homologous in *Ithycerus*. In addition, the structure of the mandibles and thoracic legs is very similar. These comparisons indicate to me a fairly close relationship between Brenthidae and Ithyceridae.

The wing veination (Fig. 189), particularly the shape of the radius, is the same type as in Antliarrhinidae (Fig. 190) and Apionidae (Fig. 191). The shape of the larval labral rods and chaeotaxy of the epipharynx is also of the type seen in Antliarrhinidae (Fig. 135) and Apionidae (van Emden, 1938; Parnell, 1964; Williams, 1968). There are also similarities in the number and arrangement of the basiconic sensory papillae of the maxillary palpi (not illustrated) of the larvae. For these reasons, Brenthidae has been placed between Ithyceridae and the families Antliarrhinidae and Apionidae and shares a common ancestor with those two families.

**ANTLIARRHINIDAE** — This is a relict group, occurring only in South Africa on cycads.

In my opinion, many of the larval features of this family (Figs. 137-146) are identical to some species of Apionidae; for example, *Apion* (van Emden, 1938; Parnell, 1964; Williams, 1968). Features which are particularly apionid-like are the chaetotaxy of the frons, clypeus, labrum and antenna, the structure of the mandibles and strongly divided clypeus found in a large number of species.

The possession of an accessory gland in the female reproductive system, three ovarioles per ovary, association with cycads, and relict distribution are probable evidence for the primitive nature of Antliarrhinidae. The strong sexual dimorphism, found also in many brenthids, and the similarities in the larva to Apionidae are my reasons for placing the family between Brenthidae and Apionidae, as an apparent sister group of the Apionidae.

An alternative arrangement (Fig. 196) can be argued if the number of ovarioles is used as a point of division (Crowson, personal communication). By so doing, it would link Ithyceridae, Brenthidae and Apionidae to a common ancestor having only two ovarioles per ovary. ~~However, it would mean that many of the characteristics shared by Apionidae and to a common ancestor having only two ovarioles per ovary~~. However, it would mean that many of the characteristics shared by Apionidae and Antliarrhinidae ~~are the result of~~ would have to be viewed as convergent evolution. I believe that the losses which resulted in two ovarioles per ovary occurred independently in Ithyceridae, Brenthidae, Apionidae and Curculionidae.

It could be argued that wing veination (hind wings) in *Ithycerus* is not ancestral (see Table 8), but is the result of a secondary increase in body size, producing an unstable fourth anal vein (Figs. 185-188), (Crowson, personal communication). It could also mean that the instability is a result of the initial stages of a secondary decrease in body size. In other words, it may mean that the fourth anal vein is being lost rather than being acquired.

APIONIDAE — This family is perhaps the most highly derived of the families discussed. Its placement is by reason of its apparent close relationship with Antliarrhinidae.

It is very possible that neither of the phylogenetic schemes (Fig. 195-196) presented are correct. However, I believe that any subsequent phylogeny should maintain a relatively close relationship between the families Ithyceridae and Brenthidae as expressed in Figs. 195 and 196. Alternative phylogenies which show this relationship are illustrated in Figs. 197-199. They are variations of Figs. 195 and 196, which reflect a difference of opinion as to the placement of the families Antliarrhinidae and Curculionidae.

During the course of this study, it was found that certain generalizations could be made concerning the morphology and evolution of the cerebrum and ventral nervous systems of larval and adult Curculionoidea. In addition, an evolutionary sequence has been postulated for the numbers and positions of larval labral sensilla (Fig. 200).

The ancestral state of larval ventral nervous systems may have resembled that of *Listronotus* (Fig. 169). There are eight distinct abdominal ganglia, three distinct thoracic ganglia, suboesophageal ganglia and the cerebrum, all of which are separated by conspicuous connectives. Figs. 160 and 161 illustrate the nervous systems of species of *Chrysomela* and *Calligrapha* (Chrysomelidae) and serve as a limited 'ex-group' comparison. The similarity between *Chrysomela* and *Listronotus* is obvious, even down to the close positions of the seventh and eighth abdominal ganglia. A virtually identical nervous system has been described for a sixth instar *Choristoneura occidentalis* (Lepidoptera: Tortricidae), (Schroen *et al.*, 1978).

The ventral nervous system of *Ithycerus* is believed to be a somewhat intermediate stage of evolution (Fig. 166), while that of a species of *Brachyrhinus* is probably a highly derived state (Fig. 168).

The value of these systems as a phylogenetic indicator has yet to be determined, but the postulated evolutionary stage of the examples shown correlate well with the systematic positions occupied by the species.

Adult nervous systems show similar trends in fusion but the morphology of the cerebrum shows much more variation than its counterpart in larvae. The ancestral state of the cerebrum is postulated to be transverse paired lobes (Figs. 170, 172, 173). Vanin (1976) reports the same condition in *Homalocerus* (Belidae). An intermediate stage is postulated for *Aglycyderes* (Aglycyderidae), (not illustrated), in which the paired lobes are ~~directly~~ directed anteriorly yet remain essentially separate. A highly derived state is postulated for *Attelabus* (Fig. 171) and *Magdalis* (Fig. 179) in which there is extensive fusion of the anteriorly directed lobes.

Long connectives between the ganglia (Figs. 170, 172, 173) appear to be correlated with a transverse cerebrum. As yet, I have not seen a transverse cerebrum with a ventral nervous system showing extensive fusion of ganglia as in Apionidae (Aslam, 1961) or as in Figs. 171 and 179. However, long connectives are observed in nervous systems having anteriorly directed cerebral lobes. Such a condition is found in *Aglycyderes* and *Antliarrhinus*. The long connectives in *Antliarrhinus* may be the result of secondary elongation of the abdomen. In general, it seems that fusion begins with the abdominal ganglia and proceeds anteriorly to the brain. In the extreme state, all ganglia are fused, as in Apionidae. The suboesophageal ganglion in *Antliarrhinus* is very closely associated with the cerebrum. It is conceivable that the nervous system of this genus and that of Apionidae were similar, but secondary elongation of the abdomen and thorax may have produced secondary elongation of the connectives. The head, with the associated suboesophageal ganglion, would not necessarily have been affected. Crowson (personal communication) postulates secondary elongation of the abdomen in Brenthidae and Belidae. That may be correct, but I feel it may have lengthened connectives which were already distinct, resembling perhaps the condition in *Pissodes*. I say this because of my belief that transverse cerebral lobes (present in Brenthidae and Belidae) are correlated with long connectives.

As with larvae, the value of adult nervous systems as phylogenetic indicators has yet to be proven. However, there is a good correlation between the postulated evolutionary state of the systems examined and the systematic positions occupied by the species possessing them.

A scheme has been devised for the evolution of the numbers and positions of larval labral sensilla (Fig. 197). It is based on my own observations of Belidae and its relatives, Curculionidae, Scolytidae, and Anderson's work on Rhynchophorinae (1948a).

I have invoked fusion reduction and migration to account for the various patterns observed. A hypothetical ancestor is postulated, having four basal sensilla moreorless equally distributed across the labrum. Belidae possesses a state most closely resembling the postulated ancestral state. Lateral migration of the two inner sensilla and fusion with the outer two could account for the two basal sensilla occurring in Nemonychidae, Anthribidae, Oxycorynidae, Aglycyderidae and Attelabidae.

The anterior migration of the outer two sensilla would account for the state observed in *Sphenophorus* (Rhynchophorinae). Migration and fusion of the two inner sensilla could then result in the pattern observed in *Rhodobaenus* (Rhynchophorinae). The anterior migration of the central basal sensillum would produce the pattern observed for some Scolytidae and Curculionidae (e.g., Cossoninae). Loss of the basal sensillum observed in *Rhodobaenus* would result in two anterior sensilla as possessed by *Metamasius* (Rhychophorinae) and some Curculionidae. There is no obvious intermediate step between the *Rhodobaenus* state and the possession of a single basal sensillum in *Dryophthorus*, as this involves the sudden loss of the anterior pair of sensilla. However, this would seem to be the most obvious path. A similar evolutionary sequence may have occurred in the apionid line of evolution, producing a single basal sensillum in Ithyceridae, Brenthidae and some Apionidae. The next logical step would be the loss of this sensillum as observed in *Antliarrhinus* and some Apionidae.

A method to test the validity of these sequences would be to trace and count nerve endings to the sensilla. For example, two nerve endings might indicate the fusion of two sensilla ~~ganglia~~.

## SUMMARY

(1) Methods are described for the successful rearing of larvae and adults of *Ithycerus noveboracensis*.

(2) Ten larval instars were identified by direct observation, body and head capsule measurements and allometric growth patterns in spiracular airtubes and orifices. It is possible more will be found. The pupa is still unknown.

(3) Descriptions of adult and larval internal systems are presented, including male and female reproductive systems and genitalia, digestive tracts and ventral nervous systems. There are two ovarioles per ovary in females. All stages have four cryptonephric Malphigian tubules in the digestive tract. The nervous systems of larvae and adults seem to be quite primitive.

(4) The first instar larva of *Arrhenodes minutus* is described for the first time. Egg bursters are present on the first eight abdominal segments.

(5) Life history studies on *Ithycerus* indicate at least a two year life cycle and possibly three. Adults do not overwinter.

(6) Three families of woody plants are associated with *Ithycerus*, the Betulaceae, Juglandaceae and Fagaceae. There is a preference for species of Fagaceae. Adults are occasionally reported on introduced species of fruit trees (Rosaceae) and this is viewed as a secondary adaptation in feeding habits.

(7) Apparently, there is no courtship in *Ithycerus*.

(8) Oviposition took place in small depressions in the soil, near the bases of host trees. Eggs were laid singly (maximum of eight per day recorded) and took an average of six weeks to hatch. Each egg was carefully covered with fecal matter.

(9) Various grooming methods and modes are described for *Ithycerus* adults, several of which are new for Coleoptera.

(10) Separate family status is maintained for *Ithycerus*, primarily on the basis of larval characters, and it is placed near Brenthidae.

(11) The genus *Antliarrhinus* is elevated to family rank and placed near Apionidae on the basis of larval characters.

(12) Ventral nervous systems are discussed in regard to their possible use as phylogenetic indicators. Systems with the paired lobes of the cerebrum transverse and ganglia separated by long connectives are considered primitive.

(13) An evolutionary sequence is proposed for the numbers and positions of larval labral sensilla. Four basal sensilla in Belidae is considered primitive.

# ACKNOWLEDGEMENTS

I extend my most sincere appreciation to my supervisor, Dr. Richard Freitag, Lakehead University, for his efforts in obtaining the funds necessary to complete this study, for giving me the benefit of his knowledge and experience in helping me make decisions on the myriad of problems which arose and for allowing me the freedom to develop the project as I saw fit. I thank Mrs. Anne Howden, Ottawa, Ontario, for convincing me to do this study, for her help in obtaining specimens and in locating certain important publications. I express my gratitude to my external examiner, R. A. Crowson, University of Glasgow, who took the time to answer my many letters and in so doing overlooked errors and my inexperience in certain matters. I am very grateful to Dr. Alistair MacDonald, Lakehead University, for teaching me some of the fundamentals of photography and microphotography. I thank Mr. Allen MacKenzie, Lakehead University, for showing me how to prepare specimens for the SEM and for the many hours he spent photographing them.

I am particularly indebted to Mr. Donald Pearson, former Resources Manager of the Ausable-Bayfield Conservation Authority for permission to conduct field studies at the Parkhill Conservation area in 1978, and his successor, Mr. W. A. Mungall, for permission to continue these studies in 1979; and to Mr. D. R. Fortner, District Manager, Ontario Ministry of

Natural Resources, Chatham, Ontario, for allowing me to conduct similar studies in Pinery Provincial Park, Grand Bend, Ontario, in 1978 and 1979. In conclusion, I would like to thank Fiona Karlstedt for her unstinting help in preparing the typescript.

# BIBLIOGRAPHY

Ahmad, M. and H. R. Burke. 1972. Larvae of the weevil tribe Anthonomini (Coleoptera: Curculionidae). Misc. Publ., Entomol. Soc. Amer. 8(2): 31-81, 121 figs.

Anderson, T. F. 1969. Electron microscopy of micro-organisms, in Physical Techniques in Biological Research. A. W. Pollister. Vol. 2, part A.

Anderson, W. H. 1941. On some larvae of the genus *Proterhinus* (Coleoptera: Aglycyderidae). Proc. Haw. Entomol. Soc. XI(1):25-35.

______________. 1947a. A terminology for the anatomical characters useful in the taxonomy of weevil larvae. Proc. Entomol. Soc. Wash. 49(5): 123-32.

______________. 1947b. Larvae of some genera of Anthribidae (Coleoptera), Ann. Entomol. Soc. Amer. 40(3):489-517, 52 figs.

______________. 1948a. Larvae of some genera of Calendrinae (= Rhynchophorinae) and Stromboscerinae (Coleoptera: Curculionidae). Ann. Entomol. Soc. Amer. 41(4):413-37, 19 figs.

______________. 1948b. A key to the larvae of some species of *Hypera* Germar, 1817 (= *Phytonomus* Schoenherr, 1823). Proc. Entomol. Soc. Wash. 50(2):25-34, 30 figs.

______________. 1952. Larvae of some genera of Cossoninae (Coleoptera: Curculionidae). Ann Entomol. Soc. Amer. 45(2):281-309, 22 figs.

Arnaud, P. H. Jr. 1978. A host-parasite catalogue of north american Tachinidae (Diptera). Misc. Publ. No. 1319, Sci. Educ. Admin., U.S.D.A., Washington D. C. 860 pp.

Aslam, N. A. 1961. An assessement of some internal characters in the higher classification of the Curculionidae s. l. (Coleoptera). Trans. Roy. Entomol. Soc. London. 113:417-89, 186 figs.

Böving, A. G. and F. C. Craighead. 1930. An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomol. Amer. 11(1): 1-351, 125 pls.

Browne, F. G. 1972. Larvae of the principal old world genera of the Platypodinae (Coleoptera:Platypodidae). Trans. Roy. Entomol. Soc. London 124(2):167-90, 54 figs.

Bruhn, A. F. 1947. The external genitalia of some Rhynchophora. Great Basin Nat. 8:1-35.

Burke, H. R. 1959. Morphology of the reproductive systems of the cotton boll weevil (Coleoptera: Curculionidae). Ann. Entomol. Soc. Amer. 52:287-94, 7 figs.

Burke, H. R. and D. M. Anderson. 1976. Systematics of larvae and pupae of american Curculionoidea: status report, historical review and bibliography. Southwest Entomologist. 1:56-73.

Clarke, W. E. 1977. Male genitalia of some Curculionoidea (Coleoptera): musculature and discussion of function. Coleopt. Bull. 31(2):101-115, 15 figs.

Clarke, W. E., H. R. Burke and D. M. Anderson. 1978. The genus *Tychius* Germar (Coleoptera : Curculionidae). Larvae and pupae of some species with evaluation of their characters in phylogenetic analysis.

Crowson, R. A. 1955. The natural classification of the families of Coleoptera. Nathaniel Lloyd, London. 187 pp.

____________. 1967. The natural classification of the families of

Coleoptera. (Reprint), with appendix to 1955 ed. E. W. Classey Ltd. Middlesex, England. 214 pp.

__________. 1970. The systematic value of characters of immature stages Ch. 14, in Classification and Biology, p. 186-95. Heinmann Educational Books , Ltd., London.

Emden, F. I. van. 1938. On the taxonomy of Rhynchophora larvae (Coleoptera) Trans. Roy. Entomol. Soc. London. 87:1-37, 108 figs.

__________. 1946. Egg bursters in some more families of polyphagous beetles and some general remarks on egg bursters. Proc. Roy. Entomol. Soc. London. Series A, 21:81-97, 11 figs.

__________. 1950. Eggs egg laying habits and larvae of short-nosed weevils. Proc. 8th Int. Congr. Entomol., Stockholm, pp. 365-72, 15 figs.

__________. 1952. On the taxonomy of Rhynchophora larvae: Adelognatha and Alophinae (Insecta: Coleoptera). Proc. Zool. Soc. London. 122:651-795, 153 figs.

Forster, J. R. 1771. Novae species insectorum. Centuria I, London. 100 pp.

Gardner, J. C. M. 1932a. Immature stages of Indian Coleoptera (10) (Anthribidae). Indian Forest Records. 16(11):327-35, 20 figs.

__________. 1932b. Immature stages of Indian Coleoptera (11) (Platypodidae). Indian Forest Records. 17(3):1-10, 25 figs.

__________. 1934a. Immature stages of Indian Coleoptera (14) (Curculionidae). Indian Forest Records. 20(2):1-42, 6 pls.

__________. 1934b. Immature stages of Indian Coleoptera (15) (Scolytidae). Indian Forest Records. 20(8):1-17.

__________. 1935. Immature stages of Indian Coleoptera (18)

(Brenthidae). Indian Forest Records. 1(7):139-50, 31 figs.

________________. 1936. Immature stages of Indian Coleoptera (19) (Anthribidae). Indian Forest Records. 2(2):99-113, 31 figs.

Goulet, H. 1977. Technique for the study of immature Coleoptera in glycerine. Coleopt. Bull. 31(4):381-382.

Hamilton, R. W. 1979. Taxonomic use of endophallic structures in Rhynchitidae of America, north of Mexico (Coleoptera: Curculionoidea), with notes on nomenclature. Ann. Entomol. Soc. Amer. 72(1):29-34, 16 figs.

Hennig, W. 1966. Phylogenetic Systematics. Translated by D. D. Davis and R. Zangerl. Univ. Ill. Press. 263 pp.

Kissinger, D. G. 1968. Curculionidae subfamily Apionidae of North and Central America. Taxonomic Publications, South Lancaster, Mass. 559 figs.

LeConte, J. L. and G. H. Horn. 1876. The Rhynchophora of America, north of Mexico. Proc. Amer. Phil. Soc. 15(96):1-455.

LeConte, J. L. 1883. Coleoptera of North America. Smithsonian Collections. 26:459-98.

Leng C. W. 1920. Catalogue of the Coleoptera of America, north of Mexico. Mount Vernon, New York.

Leng, C. W. and A. J. Mutchler. 1933. Catalogue of the Coleoptera of America, north of Mexico, second and third supplements, 1925-32. Mount Vernon, New York. 112 pp.

Lugger, Otto. 1899 ~~1889~~. Genuine snout-beetles. Minn. Agric. Exp. Stat. Bull. 66:271-73.

May, B. 1966. Identification of the immature forms of some common soil inhabiting weevils, with notes on their biology. N. Z. J. Agric. Res. 9:286-316.

______. 1967. Immature stages of Curculionidae 1. Some genera in the tribe Araucariini (Cossoninae). N. Z. J. Sci. 10(3):644-60, 50 figs.

______. 1978. Immature stages of Curculionidae (Coleoptera): Some species in the genus *Pantorhytes* Faust (Pachyrhynchini) from the Papuan region and phylogenetic implications of certain characters. J. Aust. Entomol. Soc. 17:351-60, 18 figs.

Mayr, E. 1969. Principles of Systematic Zoology. McGraw-Hill Book Co. New York, St. Louis, San Francisco, Toronto, London, Sydney. 428 pp.

Morimoto, K. 1962. Comparative morphology and phylogeny of the superfamily Curculionoidea of Japan. J. Fac. Agric., Kyushu Univ. 11(4):331-73, 408 figs.

__________. 1976. Notes on the family characters of Apionidae and Brentidae (Coleoptera), with key to the related families. Kontyu, Tokyo. 44(4):469-76, 5 figs.

Muniz, R. and A. Barrera. 1969. *Rhopalotria dimidiata* Chevrolat, 1878: Estudio morfologico del adulto y descripcion de la larva (Curculionidae: Oxycoryninae). Rev. de la Soc. Mex. His. Nat. 30:205-22, 32 figs.

Parnell, J. R. 1964. The external morphology of the larvae and notes on the pupae of *Bruchidus ater* (Marsh.), (Coleoptera: Bruchidae) and *Apion fuscirostra* F. (Coleoptera: Curculionidae). Entomol. Mon. Mag. 100(1198-9):83-7, 15 figs.

Peterson, A. 1951. Larvae of Insects. Part II Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. 1st ed., Edward Bros., Inc., Ann Arbor. 146 pp.

Riley, C. V. 1871. Third annual report on the noxious, beneficial and other insects of the state of Missouri. Jefferson City, Missouri. 175 pp., 75 woodcuts.

Ross, H. H. and W. E. Ricker. 1971. The classification, evolution and dispersal of the winter stonefly genus *Allocapnia*. Ill. Biol. Monog. 45:1-166.

Ross, H. H. 1974. Biological Systematics. Addison-Wesley Publishing Co., Inc. 345 pp.

Schoenherr, C. J. 1823. Curculionides. Tabula synoptica Familiae Curculionidum. Isis von Oken, heft X (Oct.), columns 1132-1146.

______________. 1826. Curculionidum dispositio methodica cum genera characteribus..., Lipsiae. 338 pp.

______________. 1833. Genera et species Curculionidum, I, Paris. 681 pp.

Schroen, C. K., R. B. Roberts and J. F. Gustafson. 1978. Nervous system of 6th stage western spruce budworm larvae, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae). J. Ins. Morpho. and Embryo. 7(5/6):427-33, 4 figs.

Snodgrass, R. E. 1935. Principles of Insect Morphology. Mcgraw-Hill Book Co., New York, London. 667 pp.

Thomas, J. B. 1957. The use of larval anatomy in the study of bark beetles (Coleoptera: Scolytidae). Can Entomol., Supplement 5:1-43. 105 figs.

__________. 1967. A comparative study of gastric caeca in adult and larval stages of bark beetles (Coleoptera: Scolytidae). Proc. Entomol.

Soc. Ontario. 97:71-90, 52 figs.

Ting, P. C. 1936. The mouthparts of the coleopterous group Rhynchophora. Microentomology. 1(3):93-114, 8 figs.

Valentine, B. D. 1973. Grooming Behaviour in Coleoptera. Coleopt. Bull. 27(2):63-73.

Vanin, S. A. 1976. Taxonomic revision of the South American Belidae (Coleoptera). Arq. de Zool. Mus. de Zool. da Univ. Sao Paulo, Sao Paulo. 28(1):1-75, 136 figs.

Williams, P. 1968. The larvae of *Apion immune* Kirby and *Apion malvae* (F.) (Coleoptera: Curculionidae). Proc. Roy. Entomol. Soc. London. Series A, 43(1-3):21-26, 11 figs.

Gardner, J.C.M. 1938. Immature stages of Indian Coleoptera (24) (Curculionidae) Indian Forest Records. 3(12):227-61, 6 pls.

Horn, G.H. 1873. Contributions to a knowledge of the Curculionidae of the United States. Proc. Amer. Phil. Soc. 13: 407-469.

Gleason, H.A and A. Cronquist. 1963. Manual of Vascular plants of northeastern United States and adjacent Canada. D. Van Nostrand Company. New York, Cincinnati; Toronto, London, Melbourne. 810 pp.

Washburn, F.L. 1902. Insects injurious in 1902. Minn. Agric. Exp. Sta. Bull. 77:65

## Figures 1 - 8

Fig. 1:- *Ithycerus* male, eighth tergite indicated as identification aid.

Fig. 2:- Female, apical genital slit indicated as identification aid.

Fig. 3:- Male, arrow indicates rounded apices of elytra.

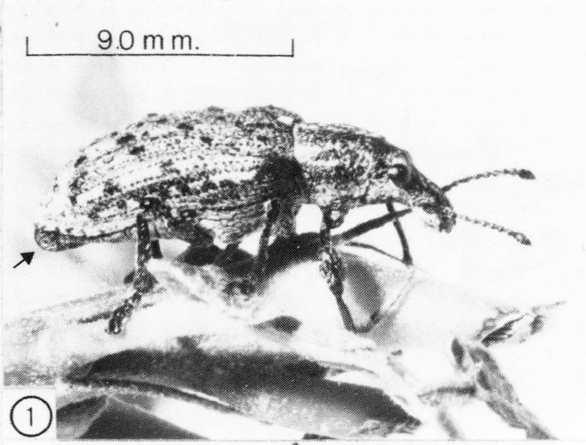
Fig. 4:- Female, arrow indicates tapered apices of elytra.

Fig. 5:- Male feeding on shoot bark and showing feeding stance.

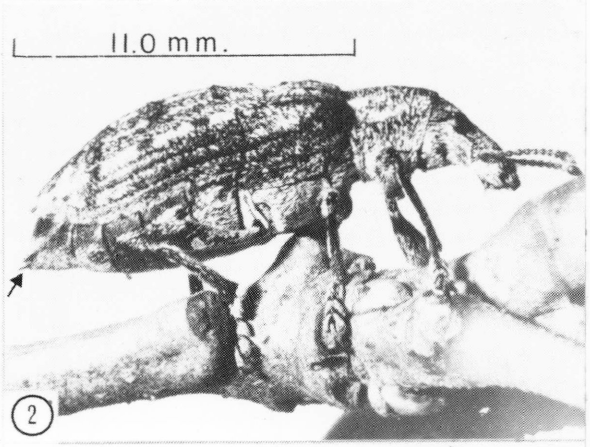
Fig. 6:- Male feeding, disturbed by observer.

Fig. 7:- Female feeding while mounted by male, arrow indicates position of male's hind legs.

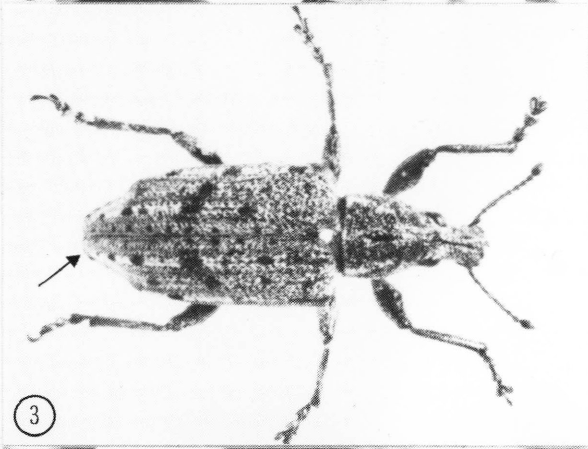
Fig. 8:- Male, arrows indicate folded over eighth tergite and everted internal sac. Eversion initiated by placing male in refrigerator.



①



②

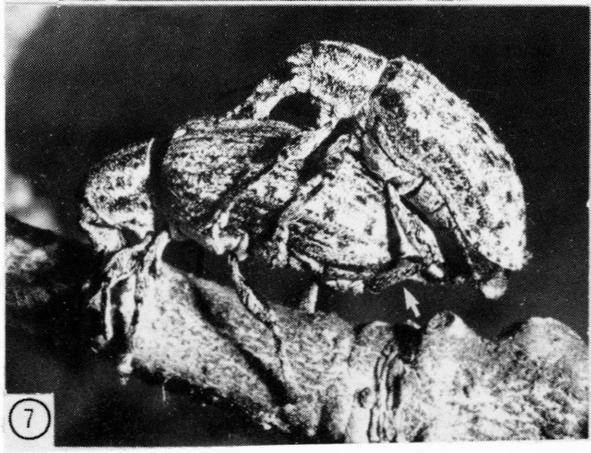


③

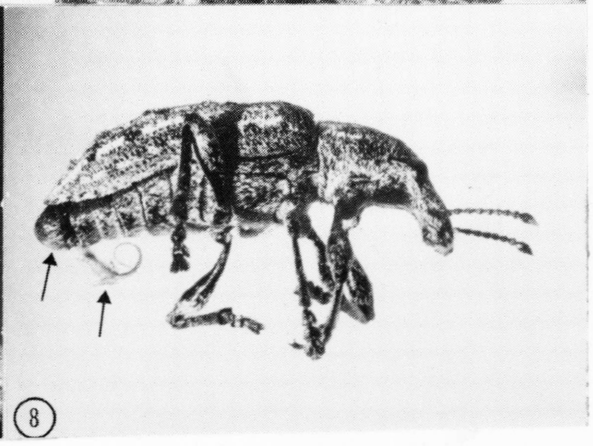
④

⑤

⑥



⑦



⑧

## Figures 9 - 16

Fig. 9:- Ovipositing female, *Ithycerus*.

Fig. 10:- Feeding damage to shoot bark, caused by adult.

Fig. 11:- Feeding damage to acorn buds and petioles.

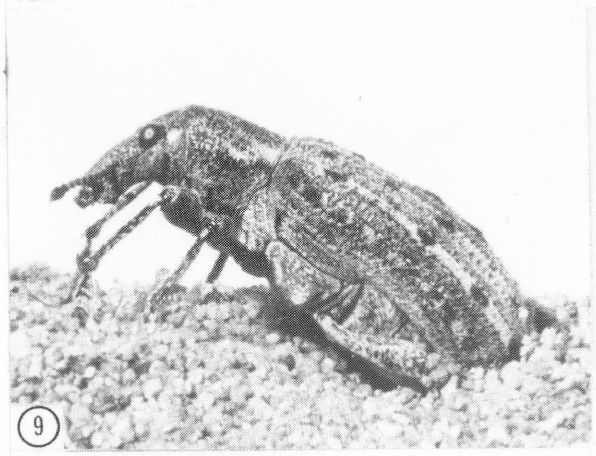
Fig. 12:- Feeding damage to leaf buds.

Fig. 13:- Feeding damage to two year old growth.

Fig. 14:- Feeding damage to leaf petioles.

Fig. 15:- Mid-hindleg rub, third mode.

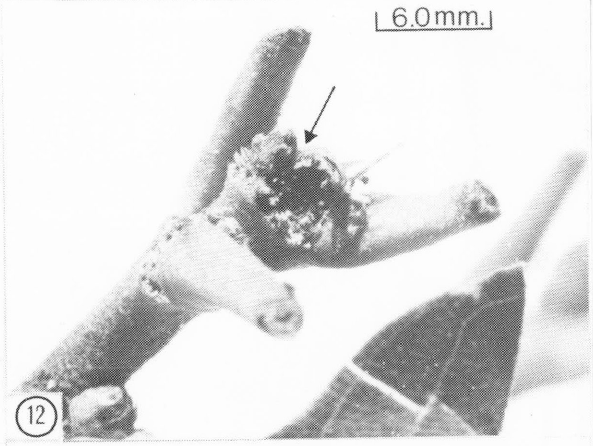
Fig. 16:- Fore-midleg rub, first mode.



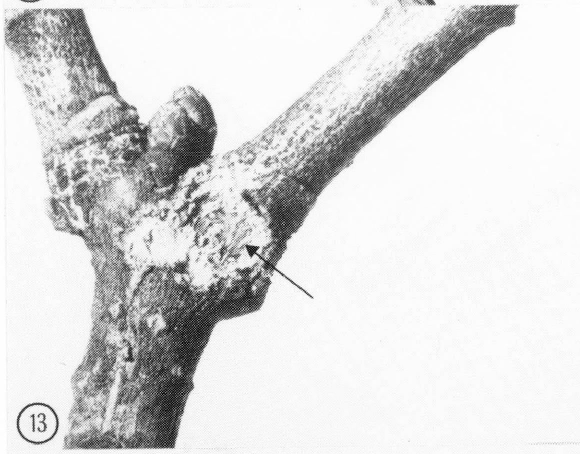
⑨

⑩

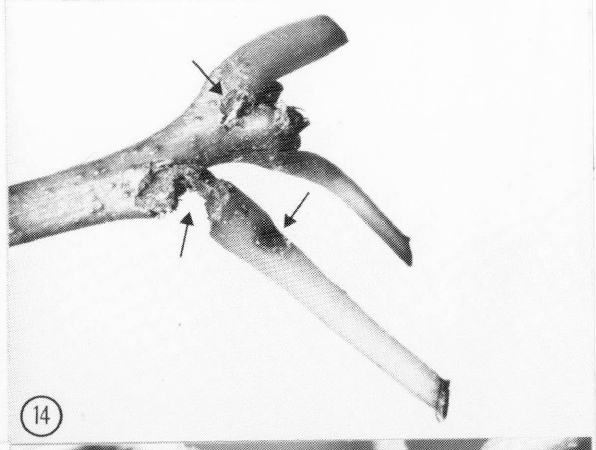
⑪



⑫



⑬



⑭

⑮

⑯

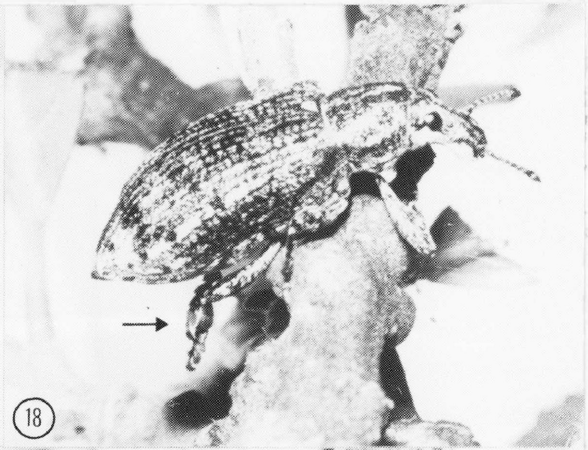
## Figures 17 - 24

Fig. 17 - 22:- Bilateral hindleg rub, below abdomen, complete sequence.

Fig. 23:- Bilateral antenna rub, positioned across twig.

Fig. 24:- Bilateral antenna rub, positioned along twig.

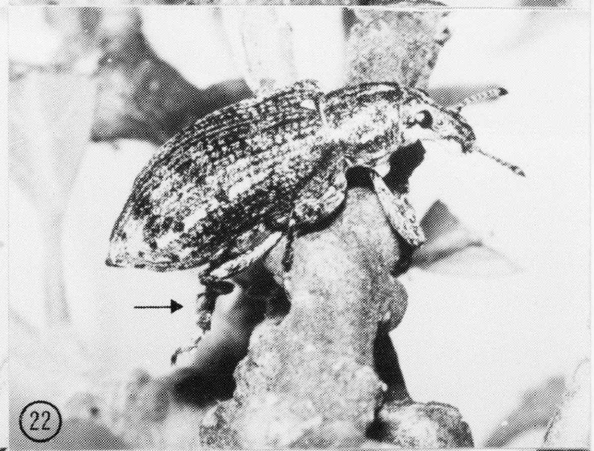

⑰


⑱


⑲


⑳


㉑


㉒


㉓


㉔

## Figures 25 - 32

Fig. 25:- Mid-hindleg rub, second mode.

Fig. 26:- Bilateral foreleg rub, first mode.

Fig. 27:- Fore-midleg, mid-hindleg rub.

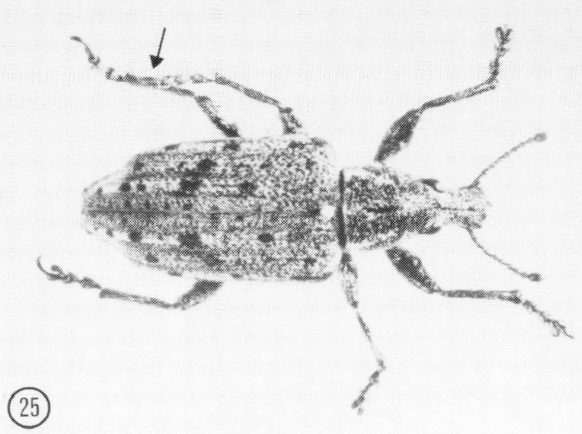
Fig. 28:- Bilateral fore-midleg rub.

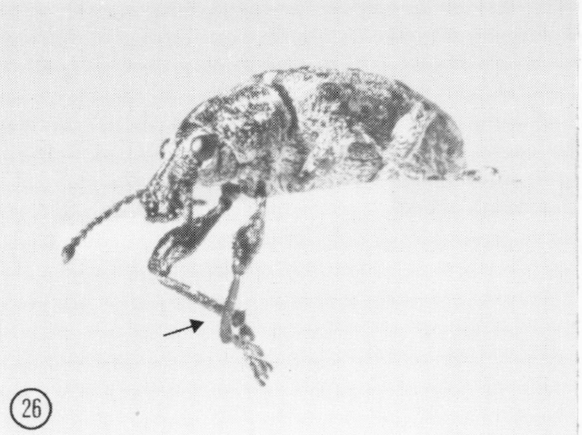
Fig. 29:- Bilateral mid-hindleg rub, second mode.

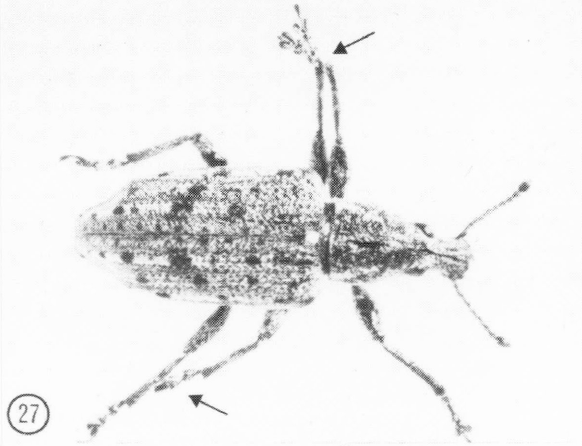
Fig. 30:- Bilateral antenna rub.

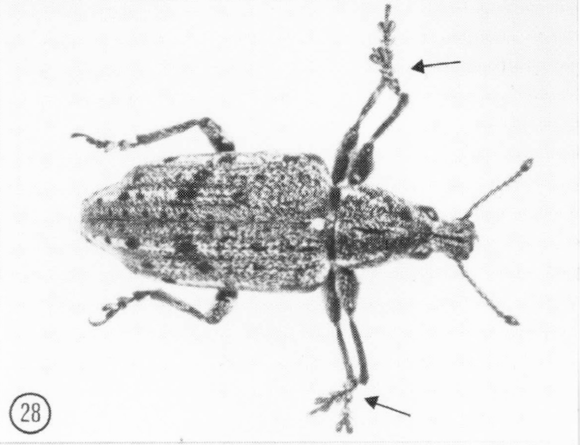
Fig. 31:- Cage used for rearing *Ithycerus* adults.

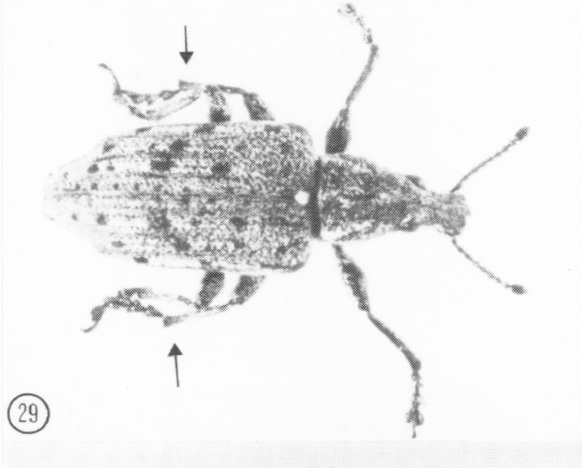
Fig. 32:- Bedding boxes used for incubating *Ithycerus* eggs.

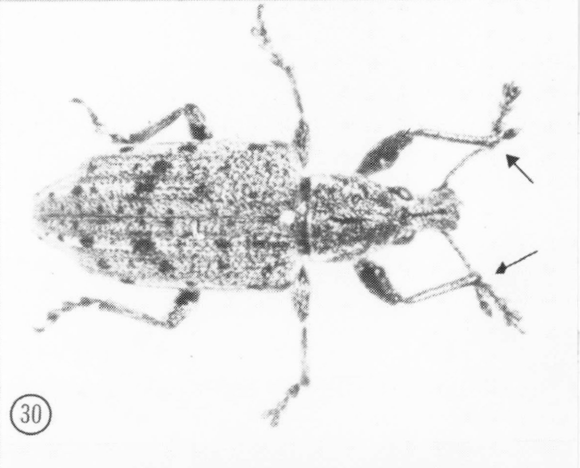
㉕


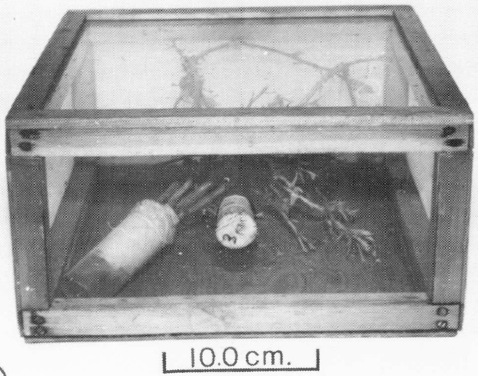
㉖


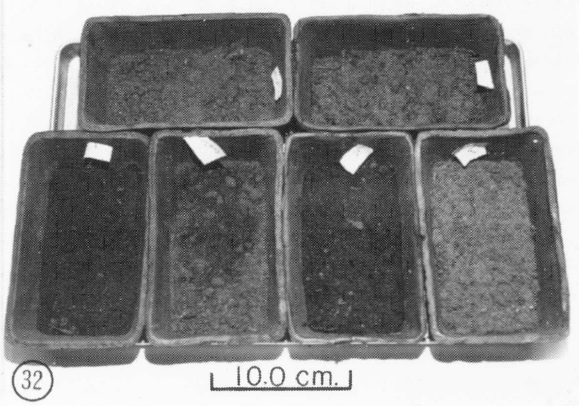
㉗


㉘


㉙


㉚


㉛


㉜


Figures 33 - 37

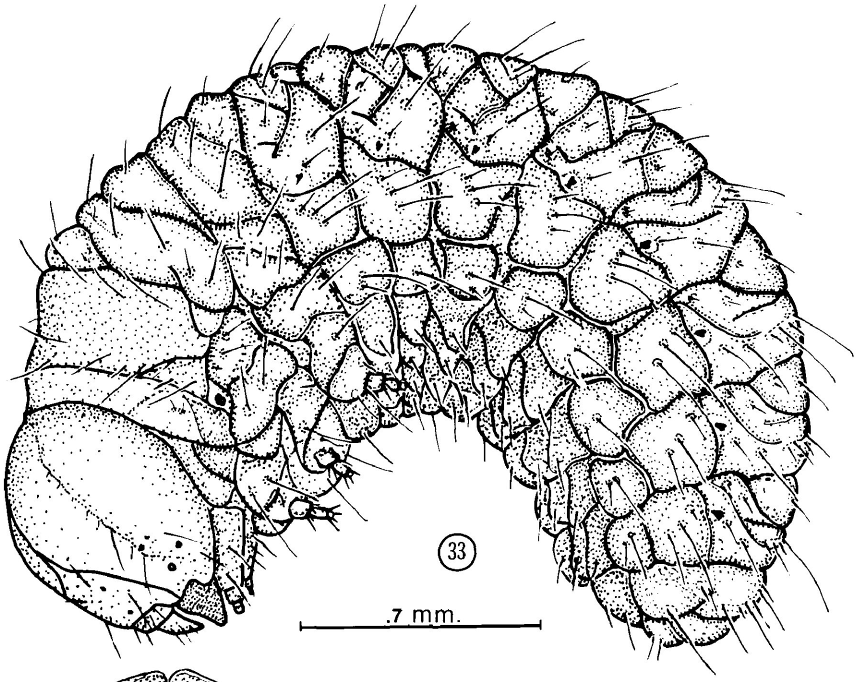
Fig. 33:- First instar larva, *Ithycerus*, lateral view.

Fig. 34:- Dorsal view of head capsule, first instar larva, ES - epicranial suture, pesl - posterior epicranial sensilla, pes - posterior epicranial setae, des - dorsal epicranial setae, desl - dorsal epicranial sensilla, Enc - endocarinal suture, FS - frontal suture, Fsl - frontal sensilla, Fs - frontal setae, Fr - frons, Cl - clypeus, Cls - clypeal setae, Clsl - clypeal sensilla.

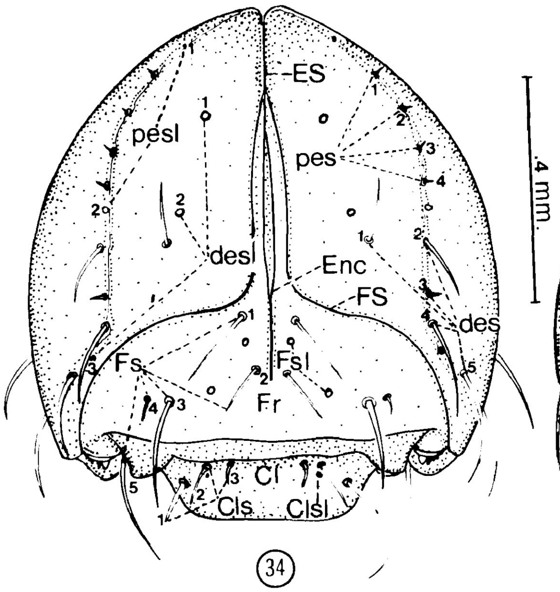
Fig. 35:- Ventral view of head capsule, first instar larva, les - lateral epicranial setae, lesl - lateral epicranial sensilla, ves - ventral epicranial setae, vesl - ventral epicranial sensilla, OcF - occipital foramen, TB - tentorial bar, Hb- hypopharyngeal bracon.

Fig. 36:- Lateral view of head capsule, sixth instar larva, Oc - ocelli.

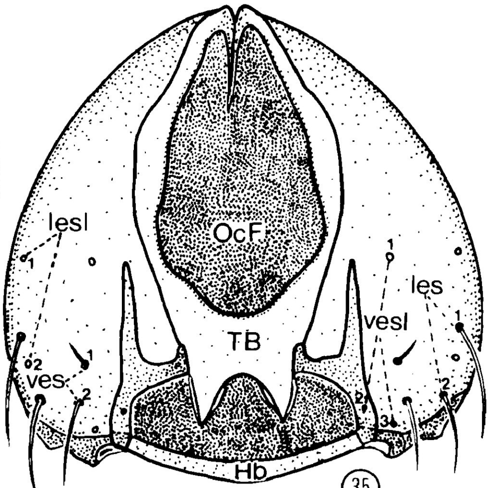
Fig. 37:- Mandible, first instar larva, Ms - mandibular setae, Msl - mandibular sensilla.


.7 mm.

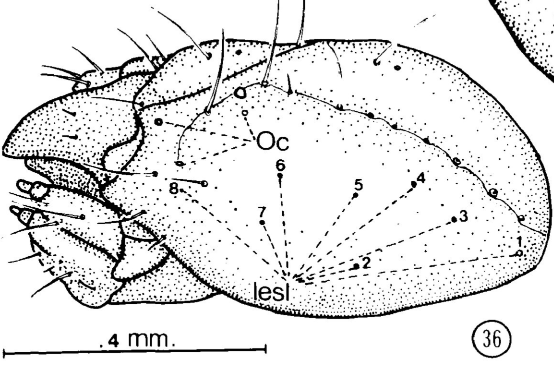
33


ES
pesl
pes
1
2
3
4
2
desl
Enc
FS
des
1
2
3
4
5
Fs
Fsl
Fr
Cl
Cls
Clsl
1
2
3
4
5
.4 mm.

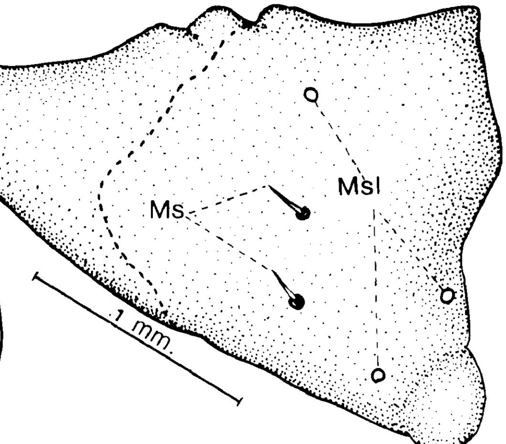
34


OcF
lesl
les
TB
vesl
ves
Hb
1
2
3

35


Oc
1
2
3
4
5
6
7
8
lesl
.4 mm.

36


Ms
Msl
1 mm.

37

Figures 38 - 41

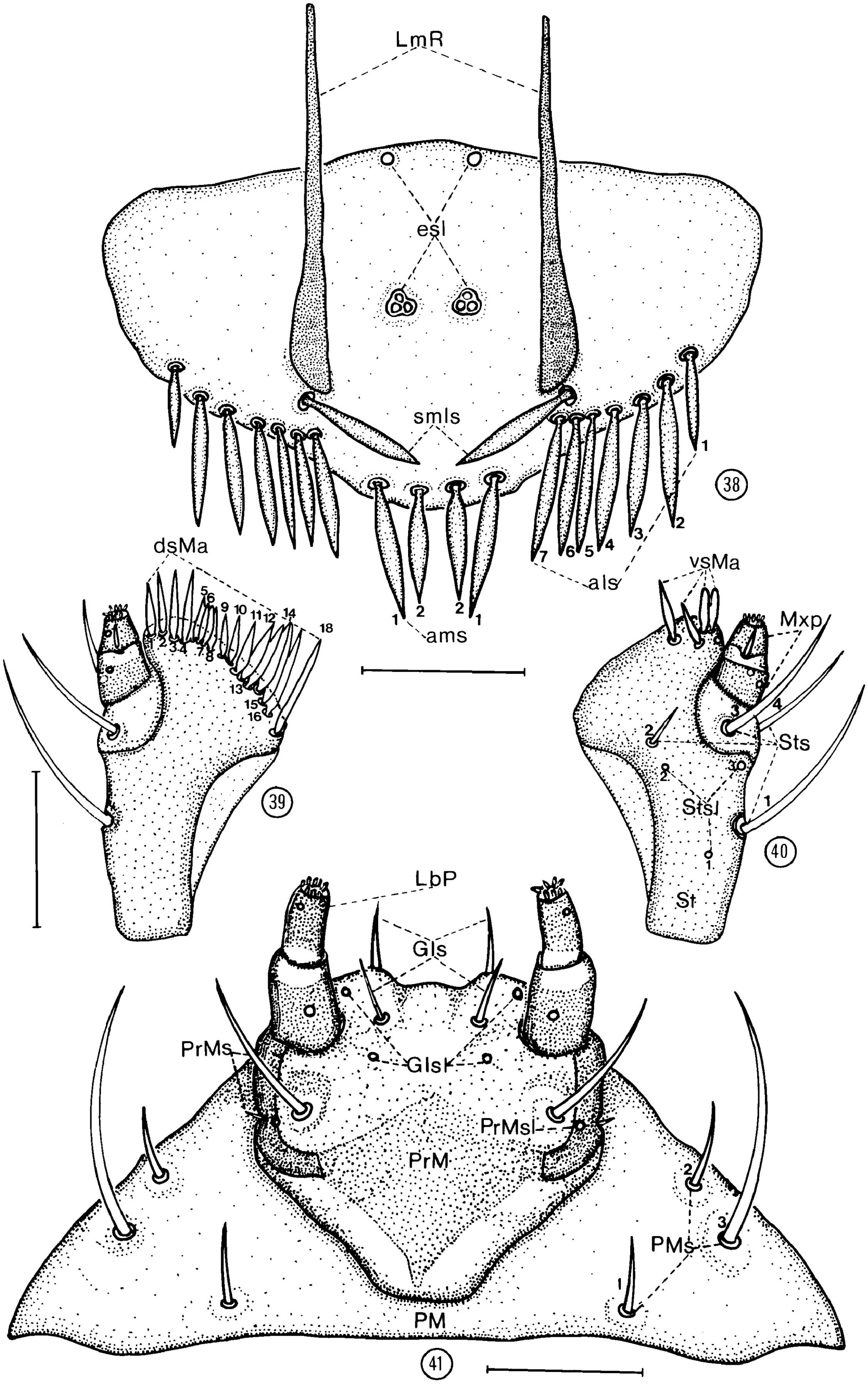
Fig. 38:- Epipharynx, first instar larva, *Ithycerus*, LmR - labral rods, esl - epipharyngeal sensilla, smls - submarginal lateral setae, als - anterolateral setae, ams - anteromedian setae.

Fig. 39:- Dorsal view of maxilla, first instar larva, dsMa - dorsal setae of maxilla.

Fig. 40:- Ventral view of maxilla, vsMa - ventral setae of maxilla, Mxp - maxillary palpus, Sts - stipal setae, Stsl - stipal sensilla.

Fig. 41:- Labrum, sixth instar larva, Lbp - labial palpus, Gls - glossal setae, Glsl - glossal sensilla, PrM - prementum, PrMs - premental setae, PrMsl - premental sensilla, PM - postmentum, PMs - postmental setae.

scale = .1 mm.



㊳

㊴

㊵

㊶

LmR
esl
smls
1
2
3
4
5
6
7
als
1
2
2
1
ams
dsMa
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 18
vsMa
Mxp
3
4
2
Sts
2
3
Stsl
1
1
St
LbP
Gls
Glsl
PrMs
PrMsl
PrM
2
3
PMs
1
PM

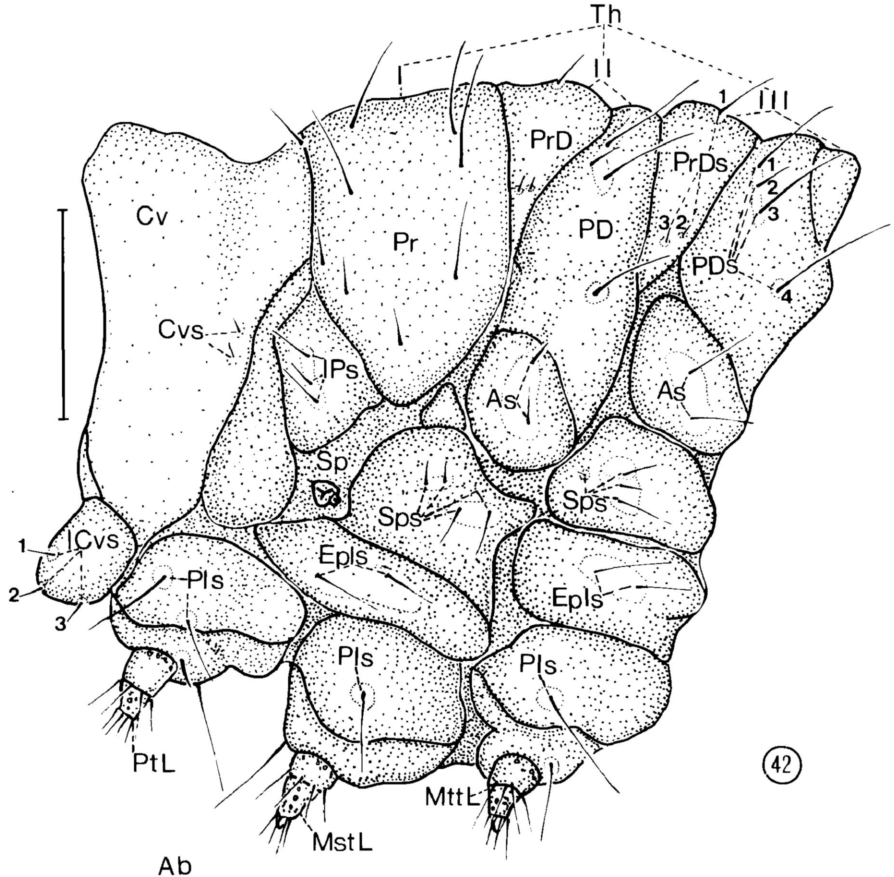
Figures 42 - 44

Fig. 42:- Lateral view of thorax, sixth instar larva, *Ithycerus* Cv - cervical membrane, Cvs - cervical setae, lCvs - lateral cervical setae, Pr - pronotum, lPrs - lateral pronotal setae, Sp - spiracle, Sps - spiracular setae, Pls - pleural setae, Epls - epipleural setae, Th - thorax, PrD - predorsum, PrDs - predorsal setae, PD - postdorsum, PDs - postdorsal setae, As - alar setae, Ptl - prothoracic leg, Mstl - mesothoracic leg, Mttl - metathoracic leg.

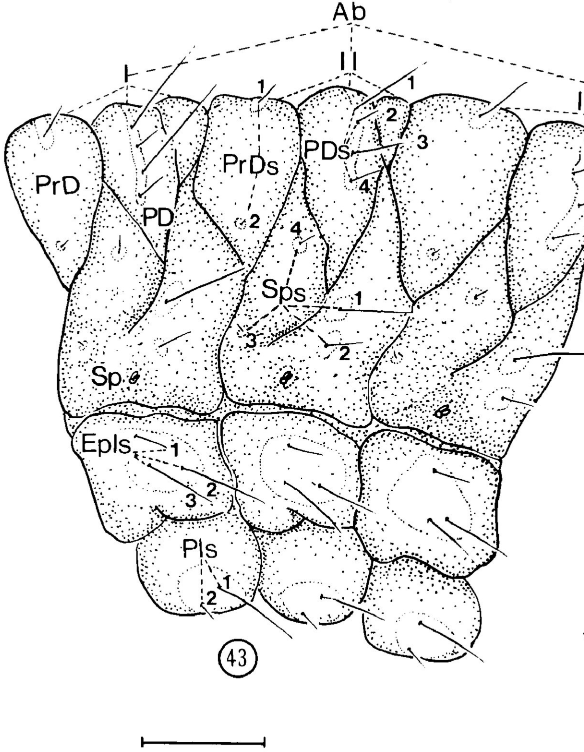
Fig. 43:- Abdominal segments I, II, III, sixth instar larva, lateral view.

Fig. 44:- Mesothoracic leg, sixth instar larva, Cxs - coxal setae (bold numbers with broken line indicators), bold numbers without line indicators - apical setae of basal segment of leg, small numbers - apical setae of apical setae of leg, ST - sternum.

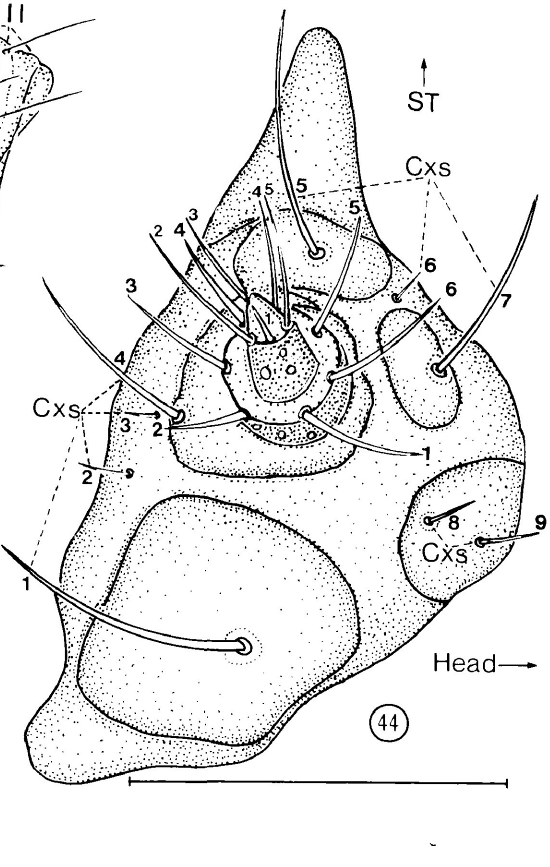
scale = 1.0 mm.


Th
I
II
III
PrD
PrDs
1
2
3
PD
PDs
4
Cv
Pr
Cvs
Ps
As
As
Sp
Sps
Sps
Cvs
1
2
3
Pls
Epls
Epls
Pls
Pls
PtL
MstL
MttL

㊷


Ab
I
II
III
1
1
2
3
4
PrD
PD
PrDs
PDs
2
4
Sps
1
3
2
Sp
Epls
1
2
3
Pls
1
2

㊸


ST
Cxs
4 5
5
5
2
3
4
3
6
6
7
4
Cxs
3
2
2
1
8
9
Cxs
1
Head

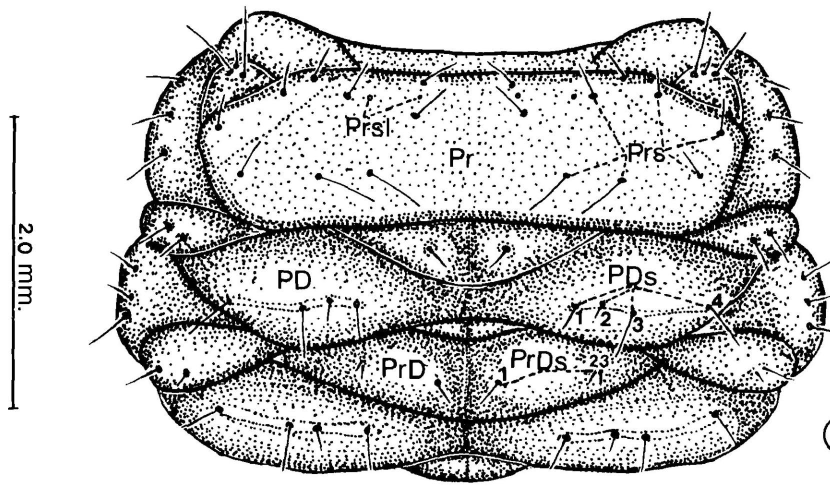
㊹

Figures 45 - 47

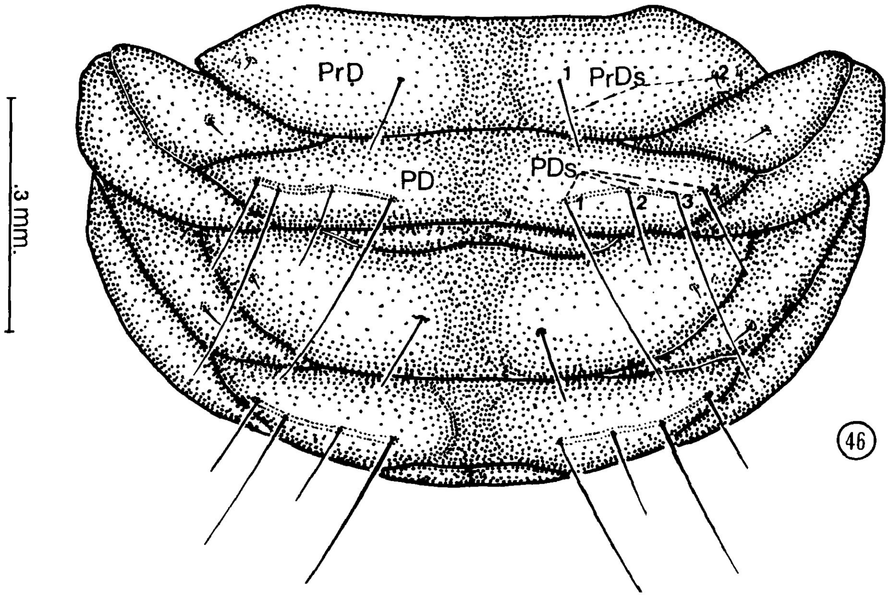
Fig. 45:- Dorsal view of thoracic segments I, II, III, seventh instar larva, Prs - pronotal setae, Prsl - pronotal sensilla.

Fig. 46:- Abdominal segments III, IV, first instar larva.

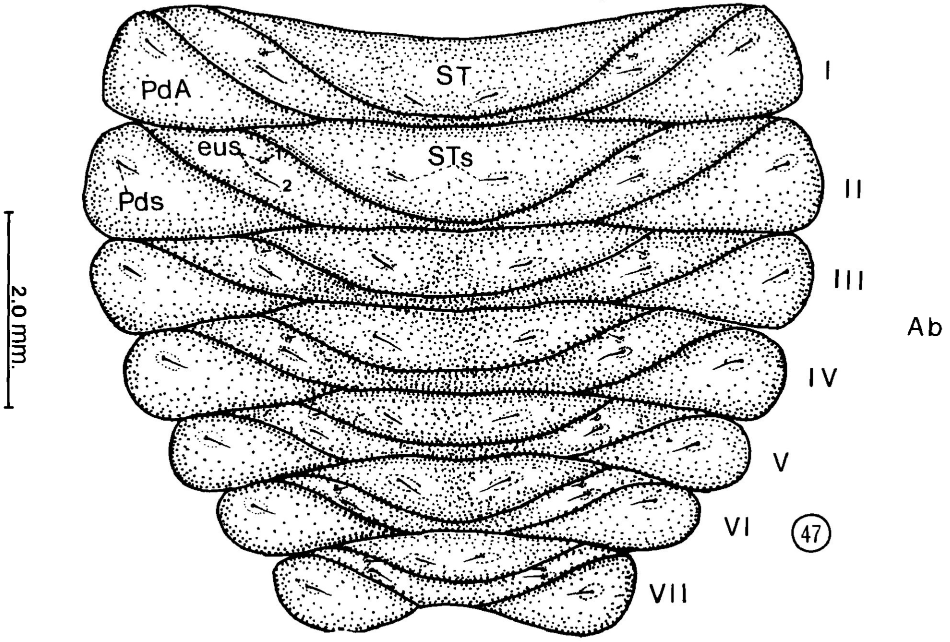
Fig. 47:- Sternum of abdominal segments I - VII, seventh instar larva, PdA - pedal area, Pds - pedal setae, ST - sternum, STs - sternal setae.


2.0 mm.
Prsl
Pr
Prs
PD
PDs
1
2
3
4
PrD
PrDs
1
2
3

㊺


.3 mm.
PrD
PrDs
1
2
PD
PDs
1
2
3

㊻


2.0 mm.
PdA
ST
I
eus
1
2
STs
II
Pds
III
Ab
IV
V
VI
VII

㊼

## Figures 48 - 55

Fig. 48:- Digestive tract, seventh instar larva, *Ithycerus,* Prov - proventriculus.

Fig. 49:- Digestive tract, adult *Ithycerus,* GC - gastric caeca, RP - rectal papillae, An - anus.

Fig. 50:- Thoracic spiracle, first instar larva, AT - airtube, Anu - annulation, Or - orifice, Prt - peritreme.

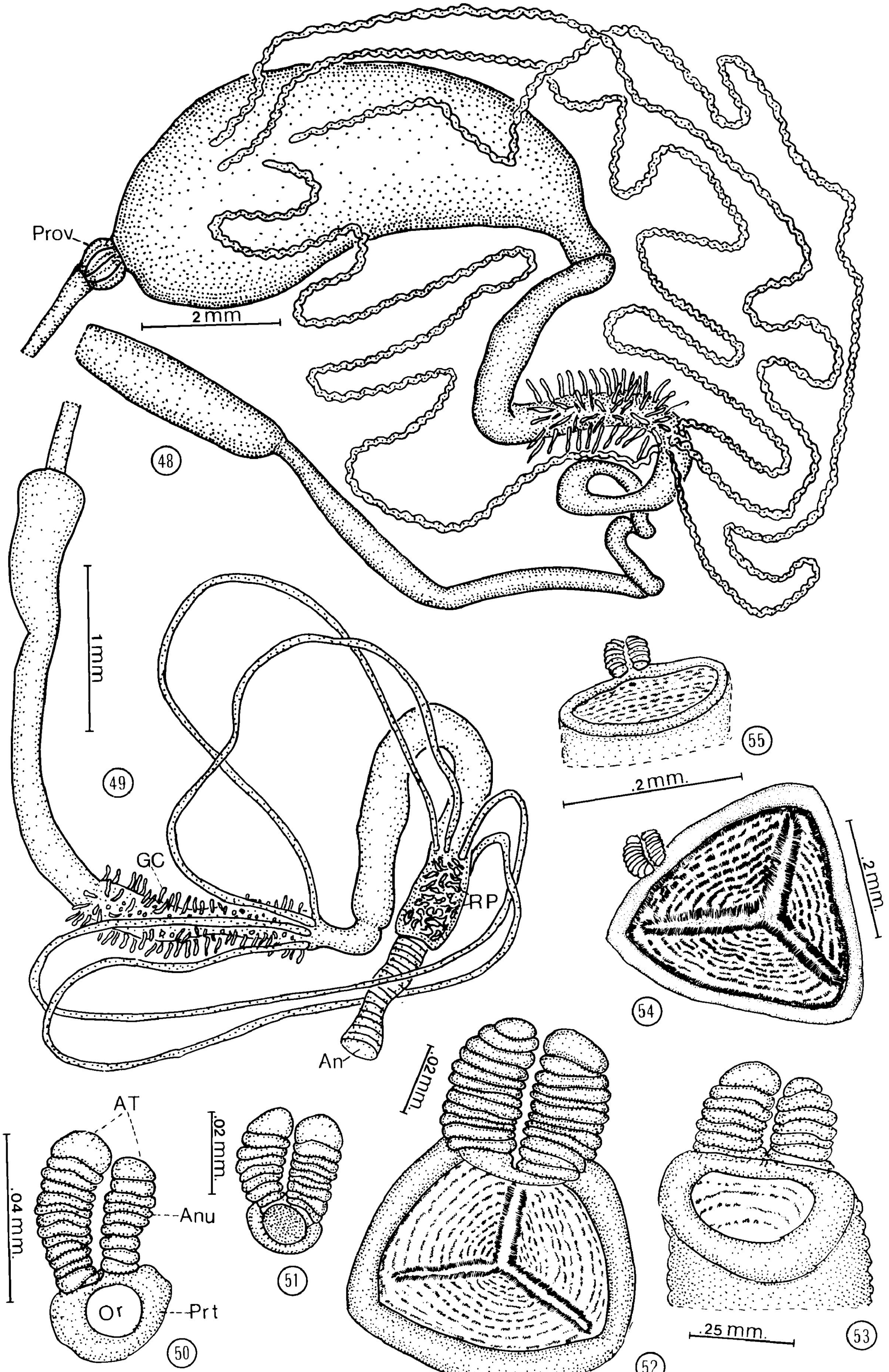
Fig. 51:- Abdominal spiracle, first instar larva.

Fig. 52:- Thoracic spiracle, third instar larva.

Fig. 53:- Abdominal spiracle, third instar larva.

Fig. 54:- Thoracic spiracle, seventh instar larva.

Fig. 55:- Abdominal spiracle, seventh instar larva.


Prov
2 mm
48
1 mm
49
GC
RP
An
55
2 mm.
54
.2 mm.
AT
.04 mm.
Anu
Or
Prt
50
.02 mm.
51
.02 mm.
52
.25 mm.
53

## Figures 56 - 61

Fig. 56:- *Ithycerus* eggs.

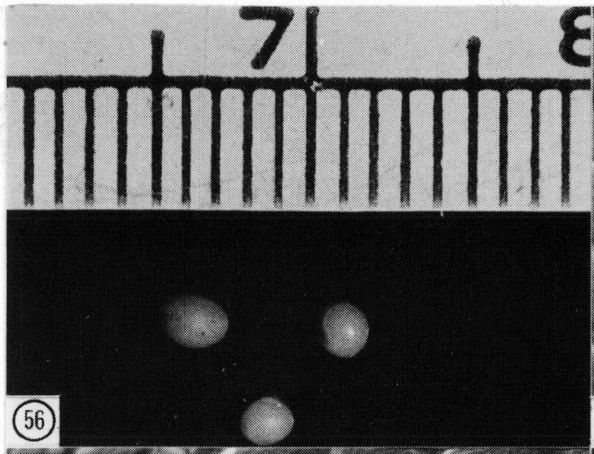
Fig. 57:- Enlarged portion of chorion, SEM photomicrigraph.

Fig. 58:- Chorion enlarged further.

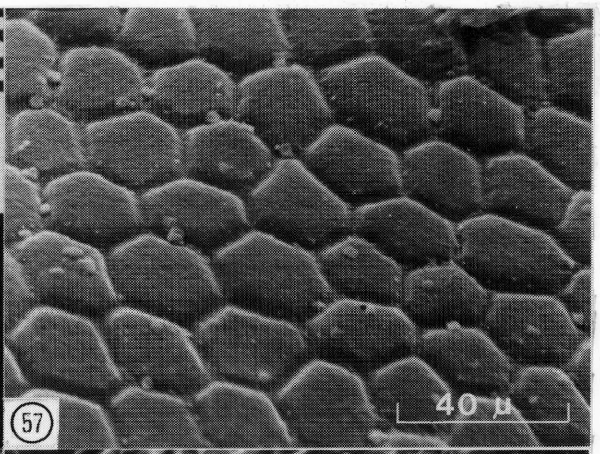
Fig. 59:- Microsculpture of single hexagonal facet of chorion showing aeropyles.

Fig. 60:- First instar larva moments before eclosion.

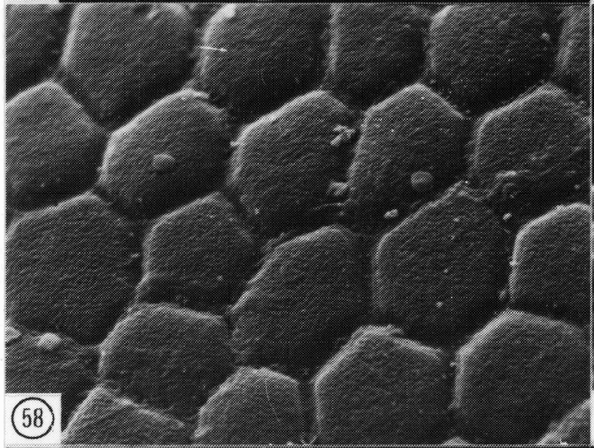
Fig. 61:- Lateral view of sixth instar larva.



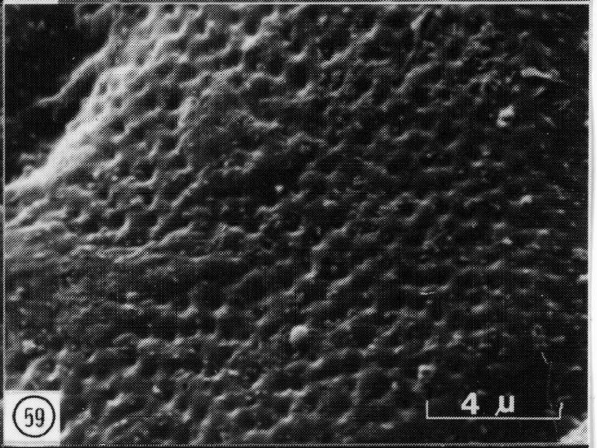
(56)



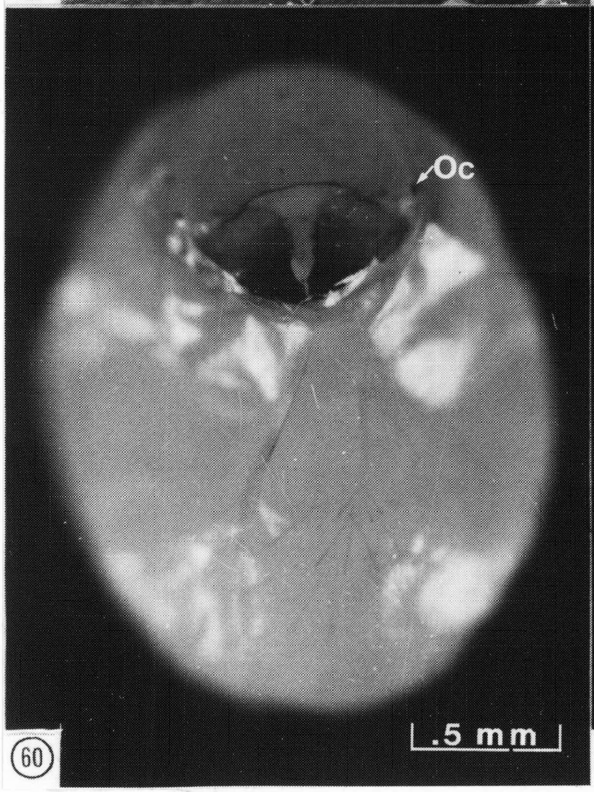
(57)



(58)



(59)



(60)

(61)

## Figures 62 - 69

## SEM Photomicrographs, First Instar Larva, *Ithycerus*

Fig. 62:- Head capsule, ant - antenna.

Fig. 63:- Lateral view of head capsule.

Fig. 64:- Antenna, ac ap - accessory appendage, ants - antennal setae, ccsl - coeloconic sensilla.

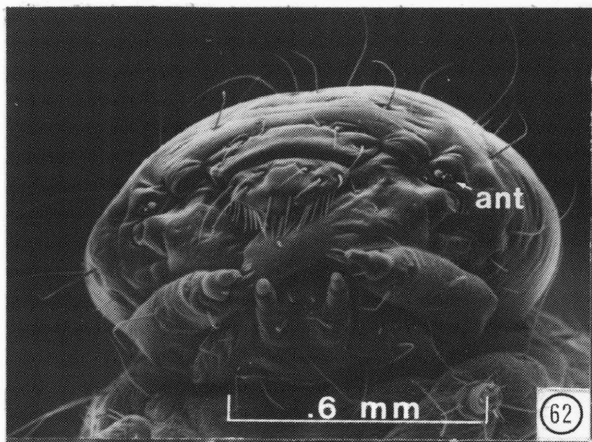
Fig. 65:- Ventral view of lower mouthparts.

Fig. 66:- Maxillary palpus, bsp - basiconic sensory papillae, msl - maxillary sensillum, fap - free rodlike accessory appendage

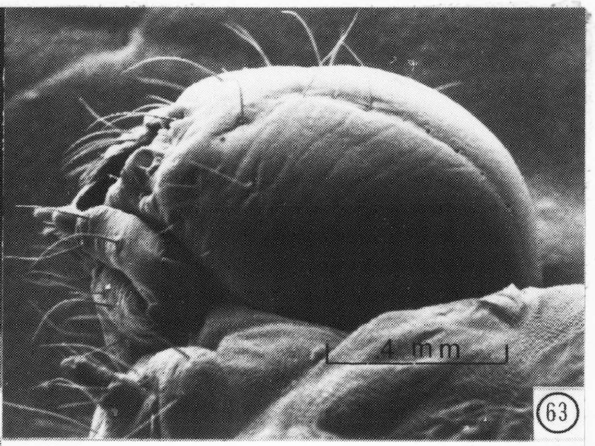
Fig. 67:- Labial and maxillary palpi.

Fig. 68:- Clypeus and labrum.

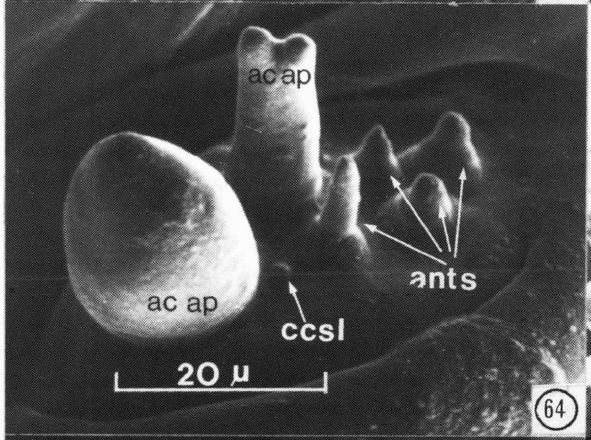
Fig. 69:- Basal sensillum of labrum.



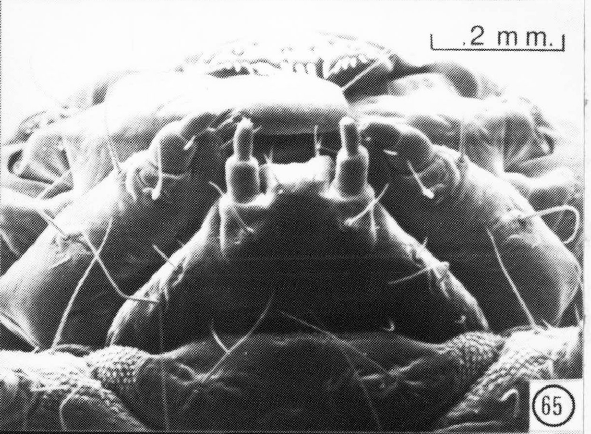
(62)



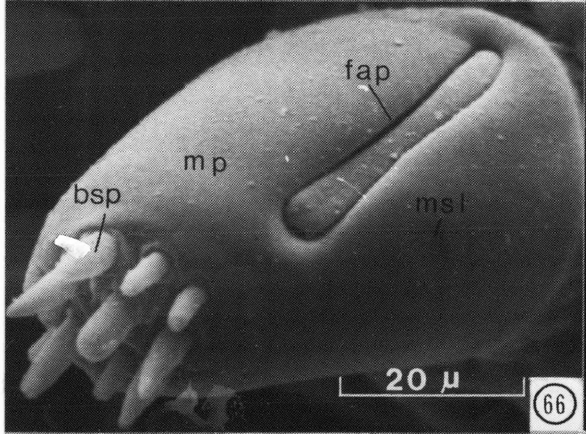
(63)



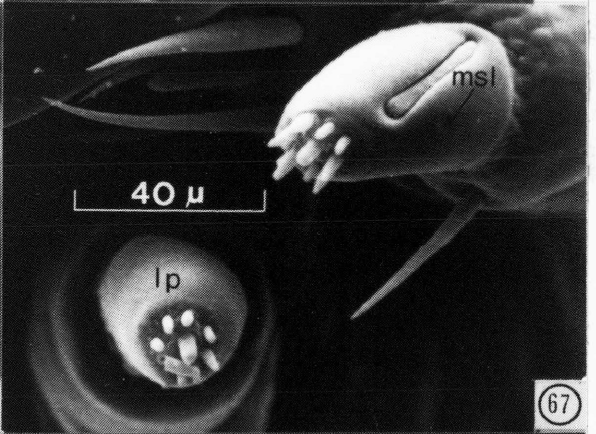
(64)



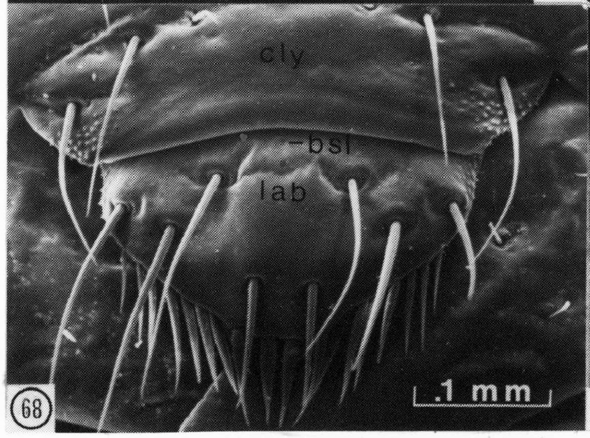
(65)



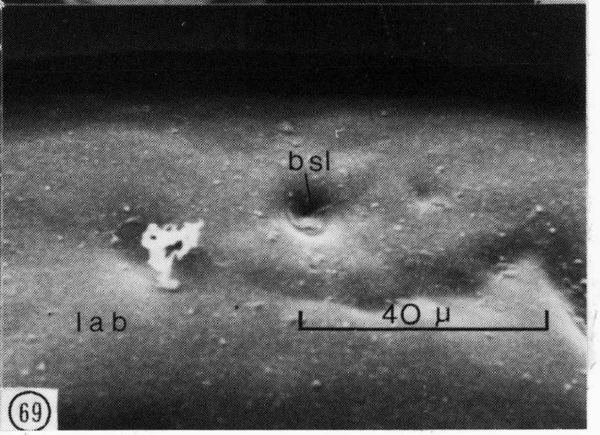
(66)



(67)



(68)



(69)

## Figures 70 - 77

## SEM Photomicrographs, First Instar Larva, *Ithycerus*

Fig. 70:- Lateral view of head capsule,
Ant R - antennal ridge.

Fig. 71:- Setal base.

Fig. 72:- Upper sensillum of frons.

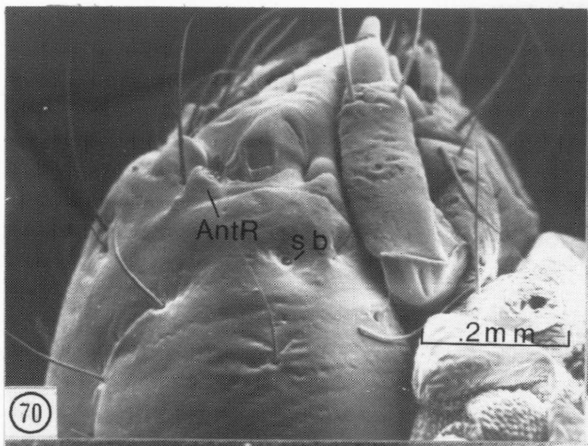
Fig. 73:- Lower sensillum of frons.

Fig. 74:- Frontal view of antennal ridge,
base of mandible.

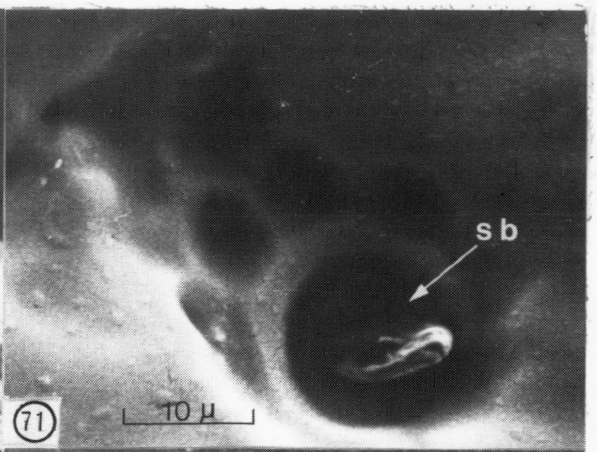
Fig. 75:- Antennal ridge, enlarged.

Fig. 76:- Posterior epicranial seta 3.

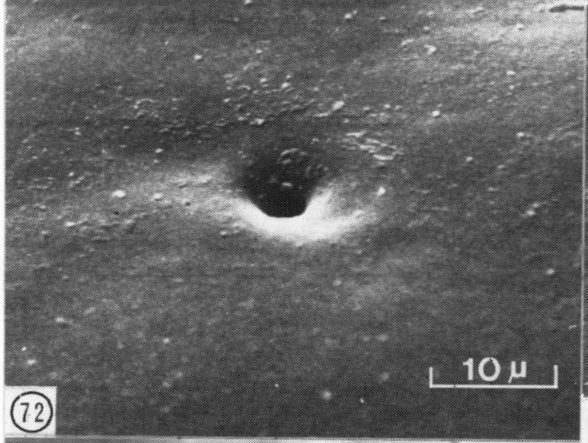
Fig. 77:- Prothoracic and mesothoracic
sterna.



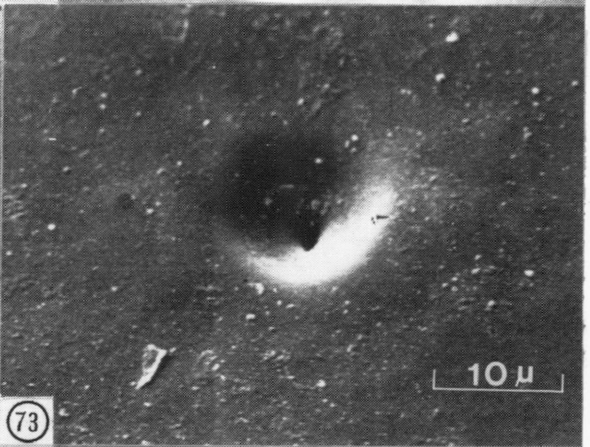
(70)



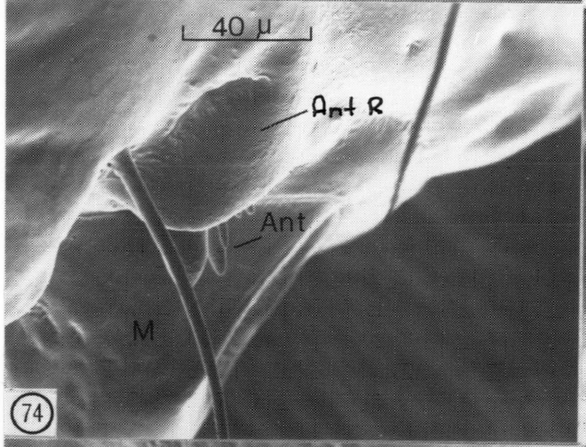
(71)



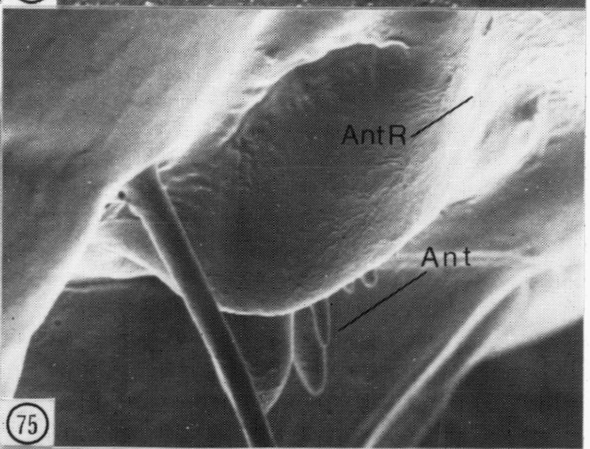
(72)



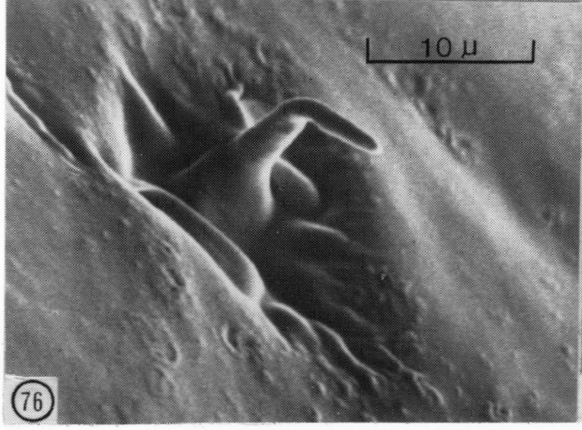
(73)



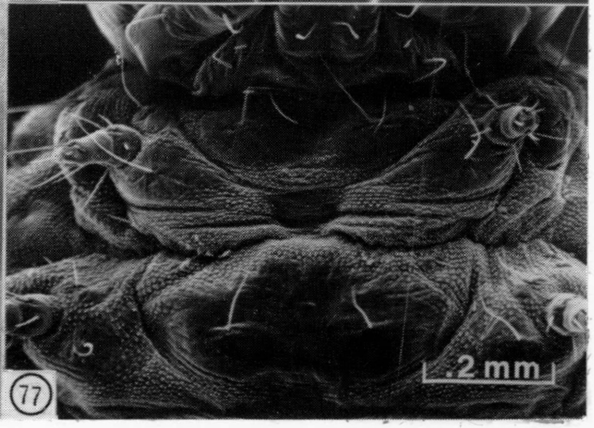
(74)



(75)



(76)



(77)

## Figures 78 -85

## SEM Photomicrographs, First Instar Larva, *Ithycerus*

Fig 78:- Mesothoracic and metathoracic legs.

Fig. 79:- Mesothoracic leg, lateral view.

Fig. 80:- Epipleurum (3 setae), pleurum (2 setae).

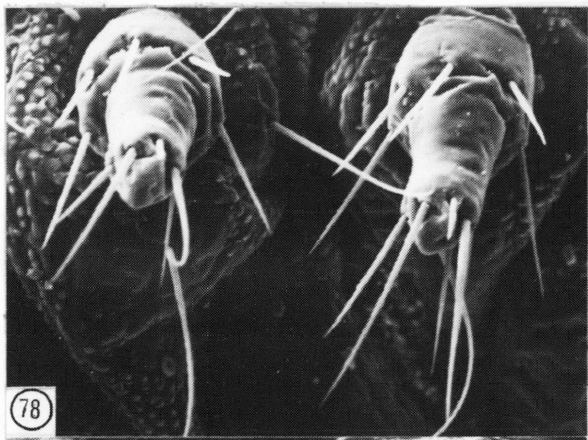
Fig. 81:- Ninth abdominal segment and anus.

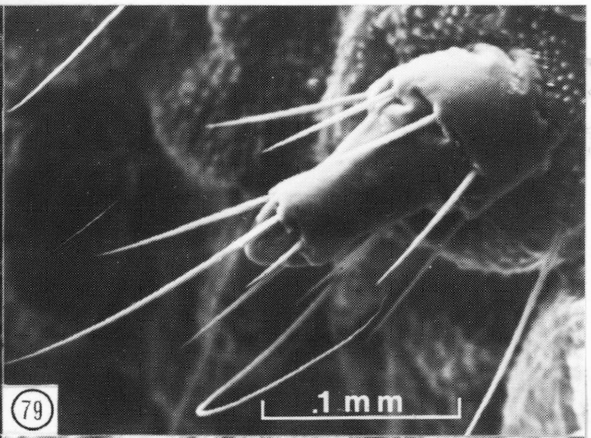
Fig. 82:- Anus, enlarged view.

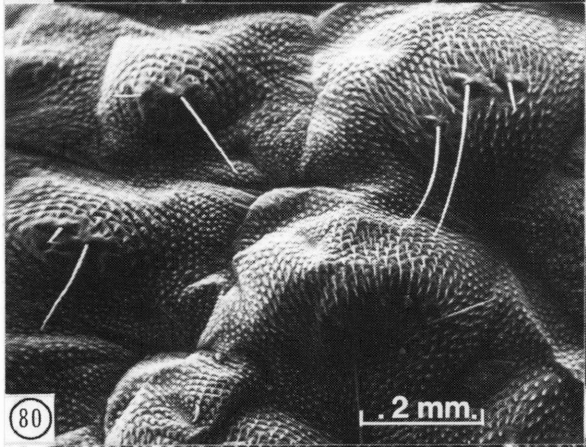
Fig. 83:- Anus, partially protruded.

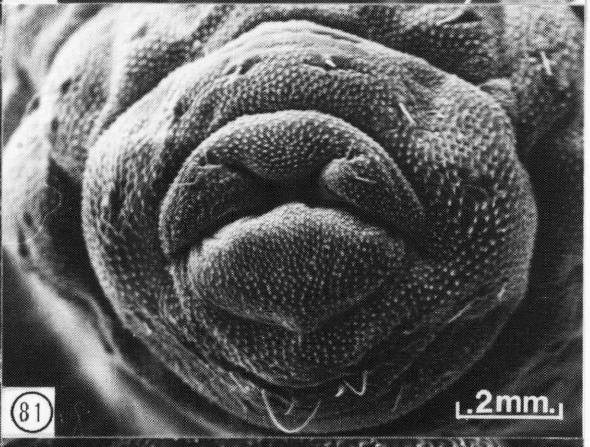
Fig. 84:- Divided asperities of anal lobes.

Fig. 85:- Spinelike asperities on epipleurum.

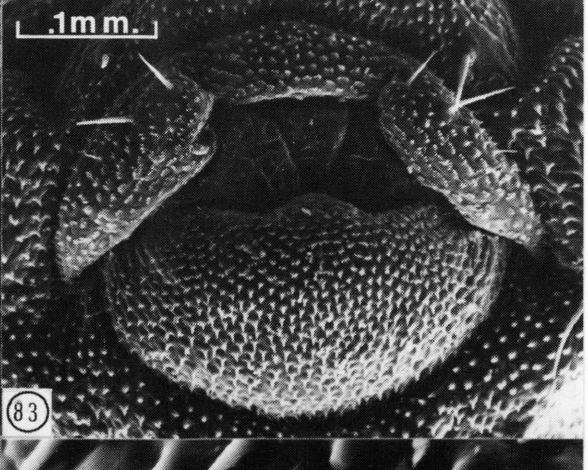

(78)

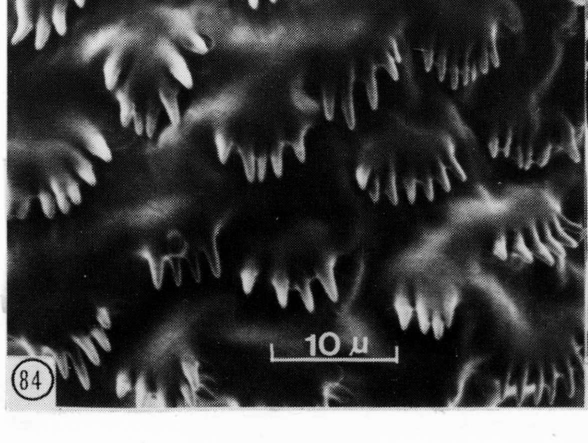

(79)

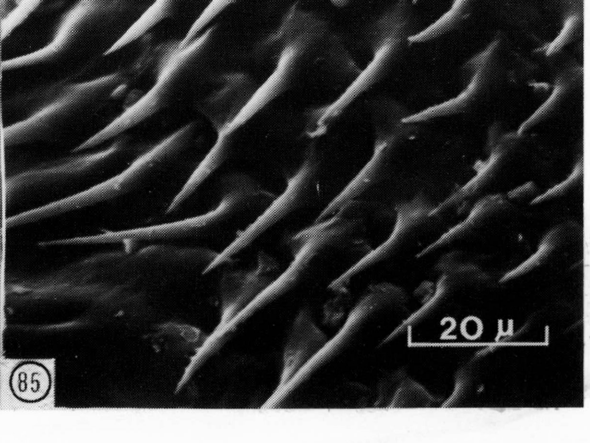

(80)


(81)


(82)


(83)


(84)


(85)

## Figures 86 - 96

## *Ithycerus* Male

## Reproductive System, Genitalia and Associated Structures

Fig. 86:- Male reproductive system, Enph - endophallus, EjD - ejaculatory duct, VD - vas deferens, Tes - testicles, SV - seminal vesicles, Ac Gl - accessory gland.

Fig. 87:- Aedeagus, MeS - median strut, bpt - basal piece of tegmen, ll - lateral lobe, Mel - median lobe.

Fig. 88:- Ninth sternite.

Fig. 89:- Genitalia, Teg - tegmen, tegs - tegmenal strut, Gpr - gonopore.

Fig. 90:- Ventral view of everted internal sac showing tenth (?) sternite and transfer apparatus.

Fig. 91:- Dorsal view of everted internal sac showing tenth (?) tergite

Fig. 92:- Everted internal sac, Flag - flagellum.

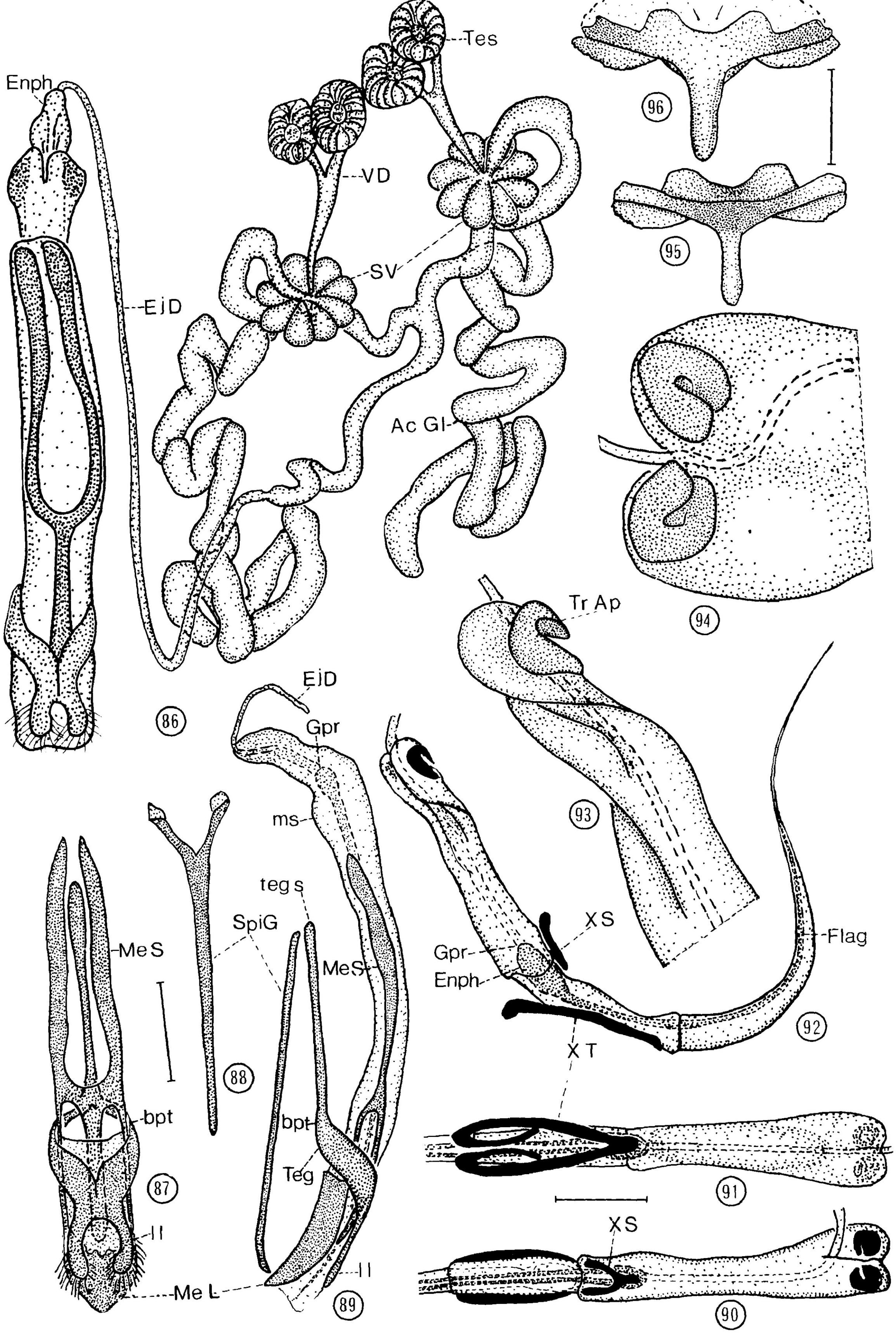
Fig. 93:- Tr Ap - transfer apparatus.

Fig. 94:- Enlarged view of transfer apparatus.

Fig. 95:- Dorsal view of ninth tergite with part of intersegmental membrane attached and bearing two small setae.

Fig. 96:- Ventral view of ninth tergite.

scale = 1.0 mm.


Enph
Tes
VD
SV
EjD
Ac Gl
96
95
94
Tr Ap
86
EjD
Gpr
ms
teg s
SpiG
MeS
MeS
88
93
XS
Gpr
Enph
Flag
92
XT
bpt
bpt
Teg
87
91
ll
ll
Me L
89
XS
90

## Figures 97 - 102

## *Ithycerus* Female

## Reproductive System and Genitalia

Fig. 97:- Dorsal view of ovaries,
Spt - Spermatheca.

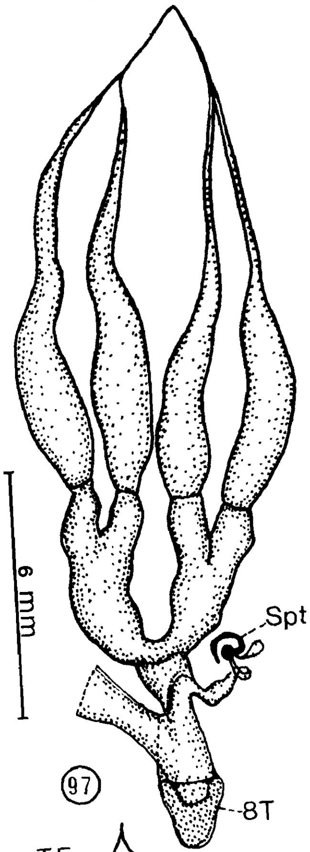
Fig. 98:- Ventral view of ovaries,
Ovl - ovariole, L Ovid - lateral oviduct,
C Ovid - Common oviduct, 8S - 8th sternite.

Fig. 99:- Eighth sternite = spiculum gastrale.

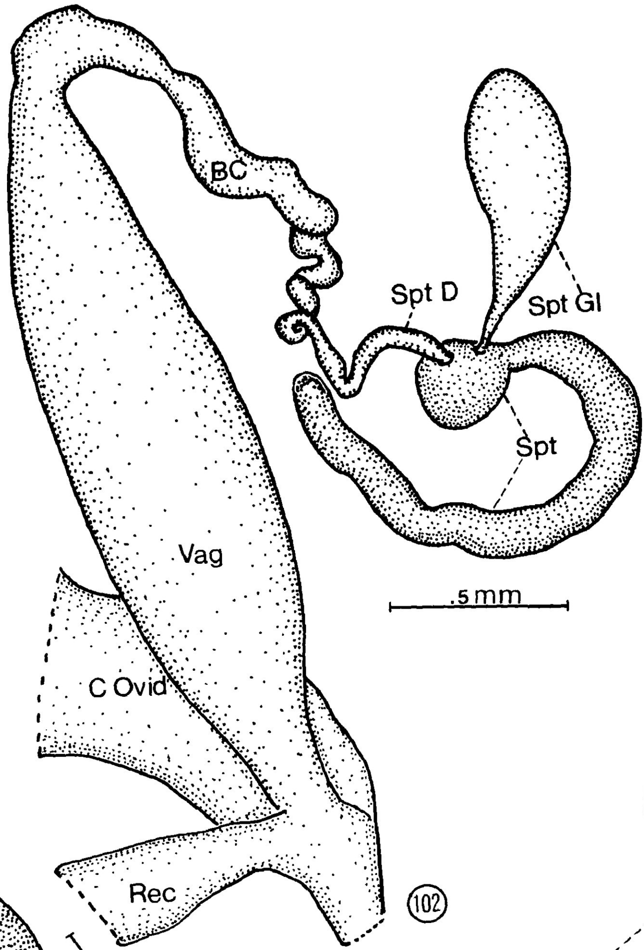
Fig. 100:- Internal view of coxite and stylus.

Fig. 101:- External view of coxite and stylus.

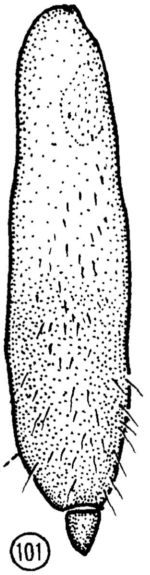
Fig. 102:- Spt G - spermathecal gland, Spt D - spermathecal duct, BC - bursa copulatrix,
Vag - vagina, Rec - rectum.



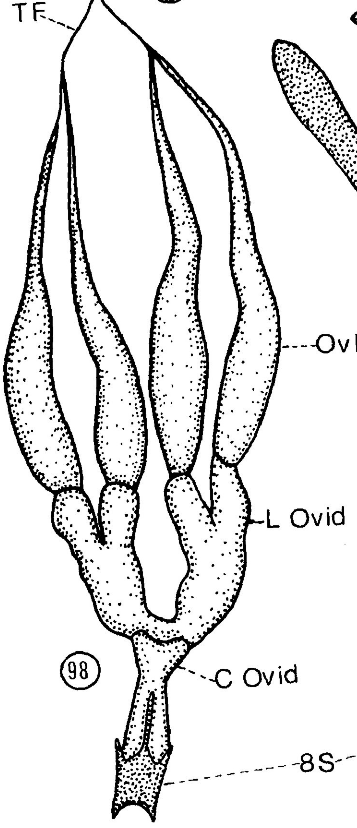
(97)



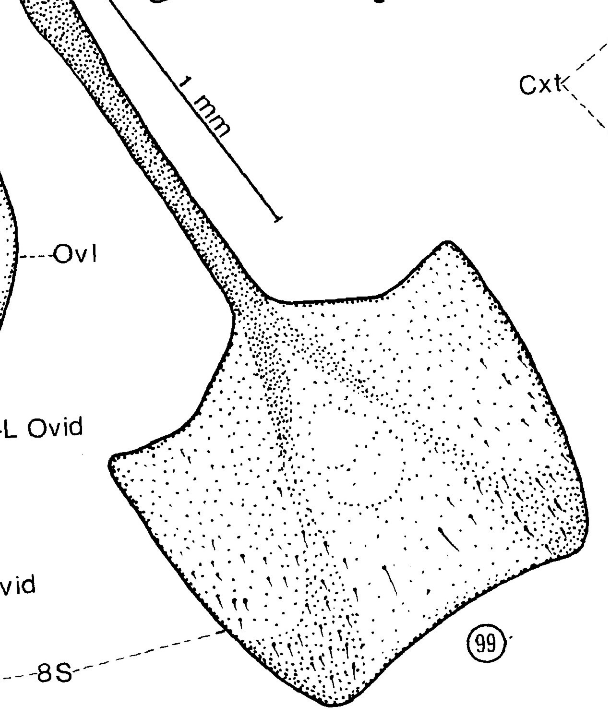
(102)



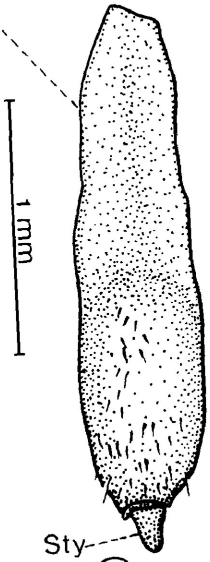
(101)



(98)



(99)



(100)

Figures 103 - 110

Fig. 103:- *Arrhenodes minutus* male.

Fig. 104:- *Arrhenodes minutus* female.

Fig. 105:- Lateral view of male.

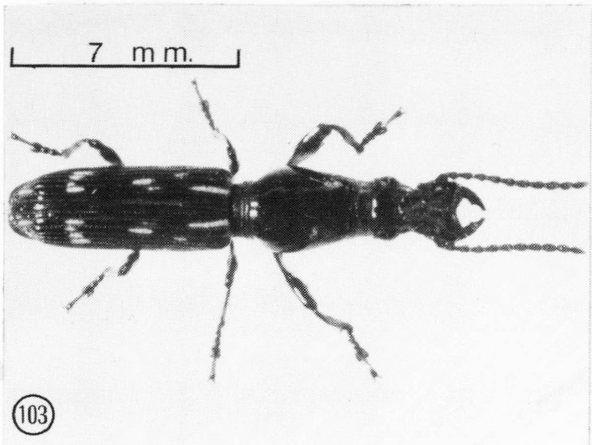
Fig. 106:- Lateral view of female.

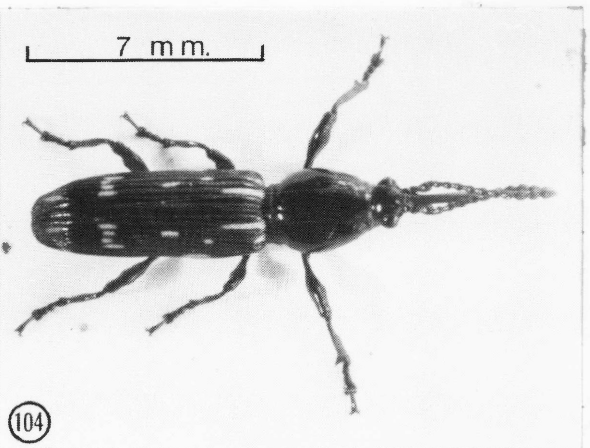
Fig. 107:- Dorsal view of head capsule, first instar, *A. minutus*, SEM photomicrograph.

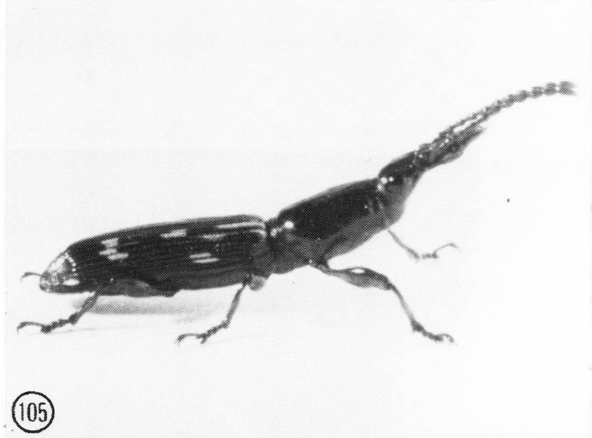
Fig. 108:- Lateral view of head capsule, SEM photomicrograph.

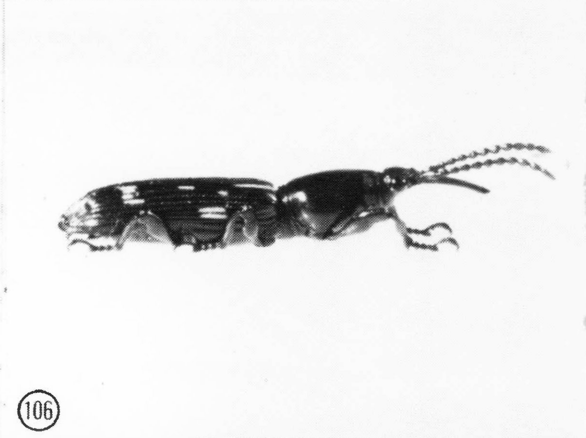
Fig. 109:- Antenna, SEM photomicrograph.

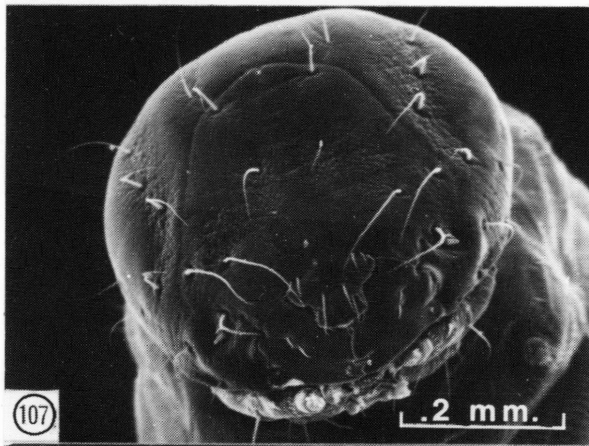
Fig. 110:- Clypeus, labrum, first instar larva, SEM photomicrograph.

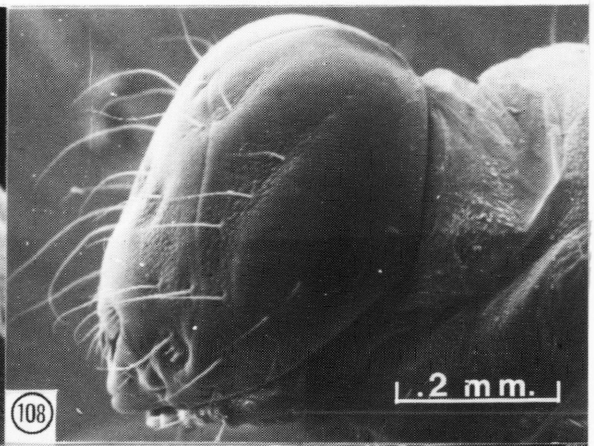

(103)

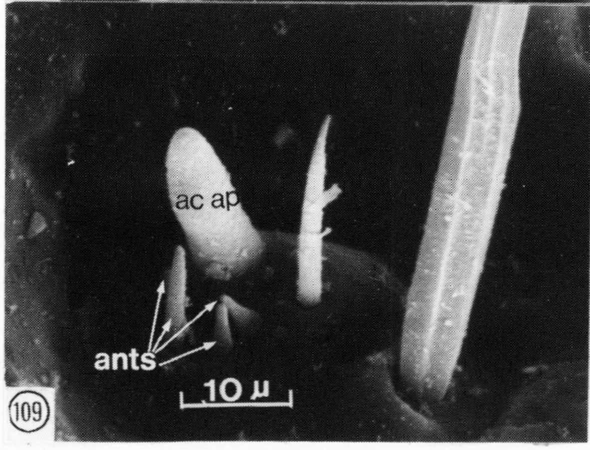

(104)

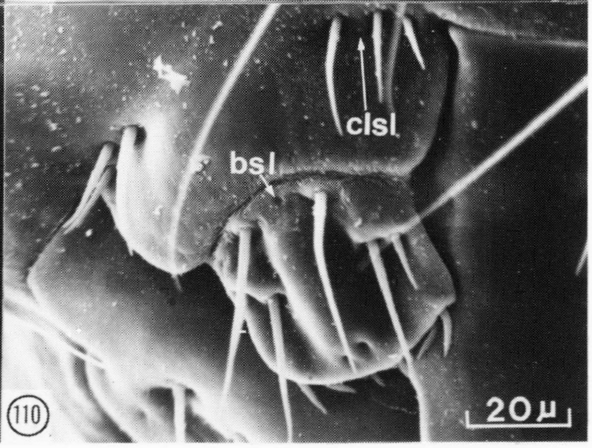

(105)


(106)


(107)


(108)


(109)


(110)

## Figures 111 - 118

*Arrhenodes minutus*

SEM Photomicrographs, First Instar Larva

Fig. 111:- Frons, clypeus, labrum and mandibles.

Fig. 112:- Basal sensillum of labrum.

Fig. 113:- Lateral view of thorax,

asp - asperities.

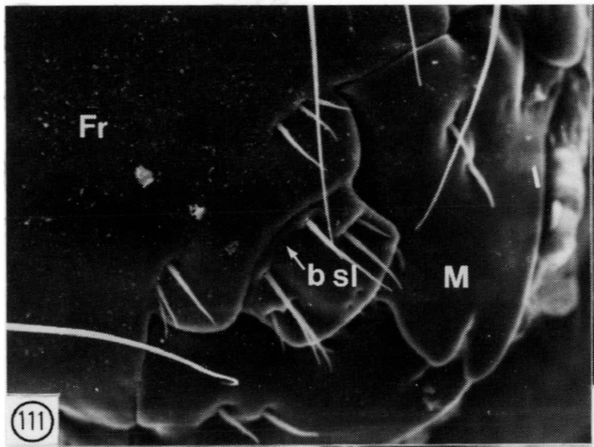
Fig. 114:- Asperities.

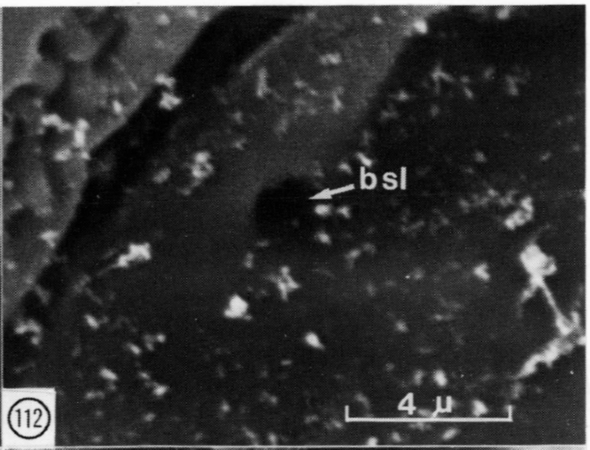
Fig. 115:- Thoracic spiracle.

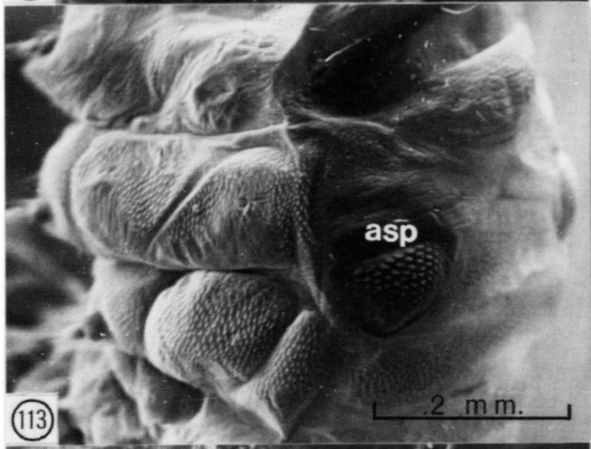
Fig. 116:- Thoracic spiracle.

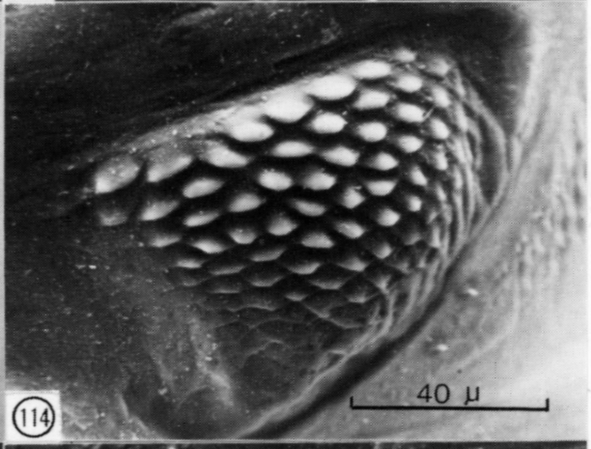
Fig. 117:- Thoracic pleura and legs.

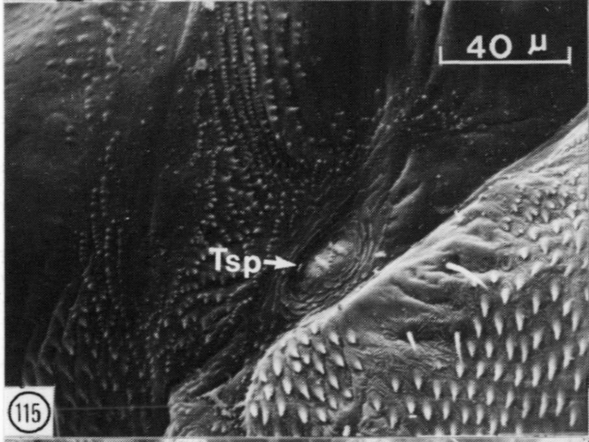
Fig. 118:- Lateral view of metathoracic leg.

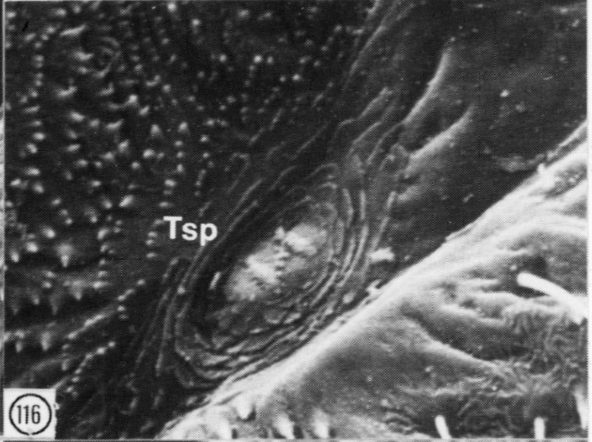

Fr
b sl
M
(111)

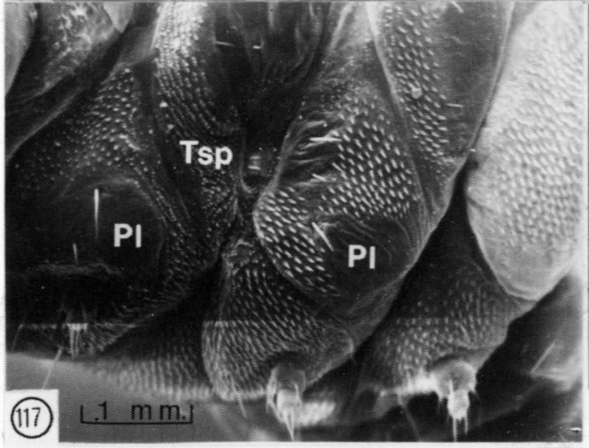

b sl
4 µ
(112)

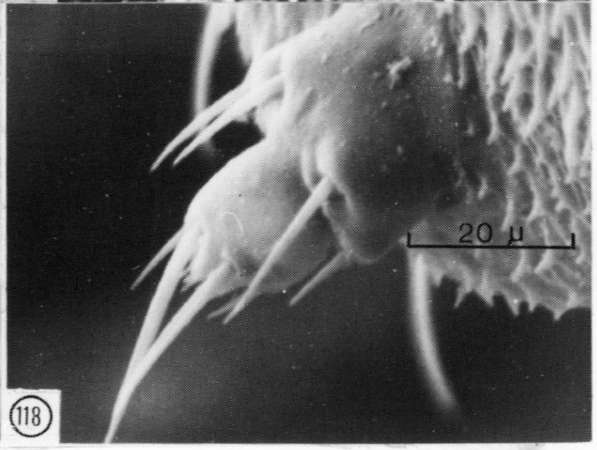

asp
.2 mm.
(113)


40 µ
(114)


40 µ
Tsp
(115)


Tsp
(116)


Tsp
Pl
Pl
(117)
.1 mm.


20 µ
(118)

Figures 119 - 126

*Arrhenodes minutus*

SEM Photo micrographs, First Instar Larva

Fig. 119:- Divided asperities in recesses of body folds.

Fig. 120:- Spinelike asperities on body folds.

Fig. 121:- Egg burster with one seta on abd. segment VII.

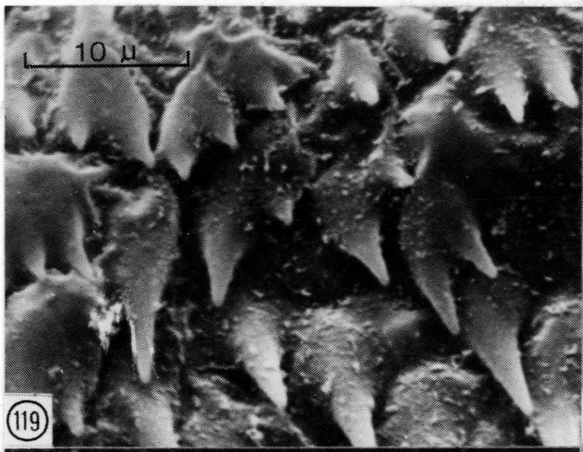
Fig. 122:- Egg burster with two setae on abd. segment I.

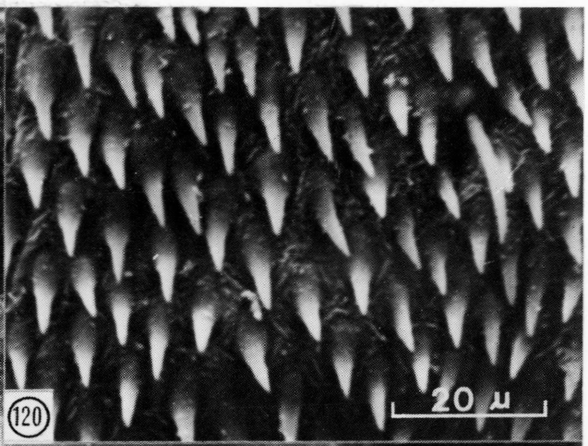
Fig. 123:- Ninth abdominal segment and anus.

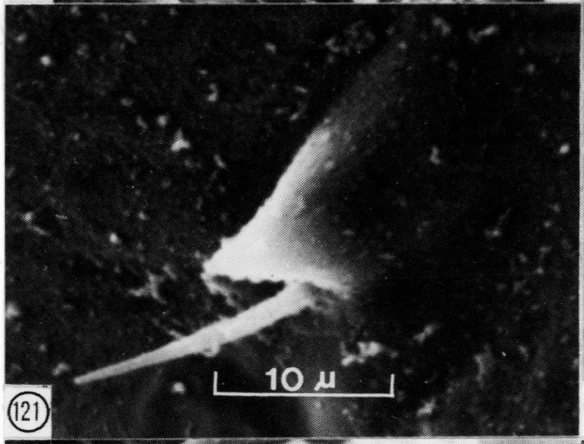
Fig. 124:- Anus.

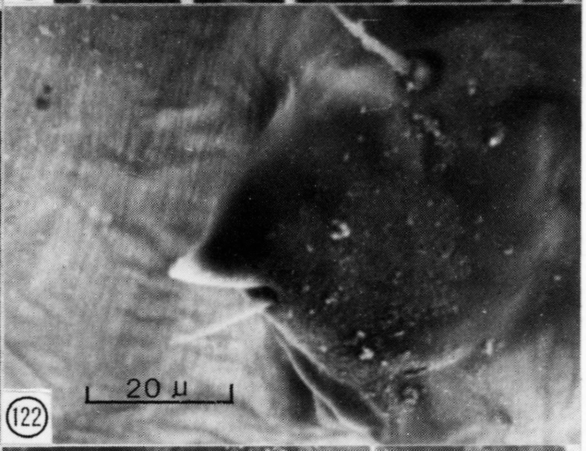
Fig. 125:- Spinelike asperities on anal folds.

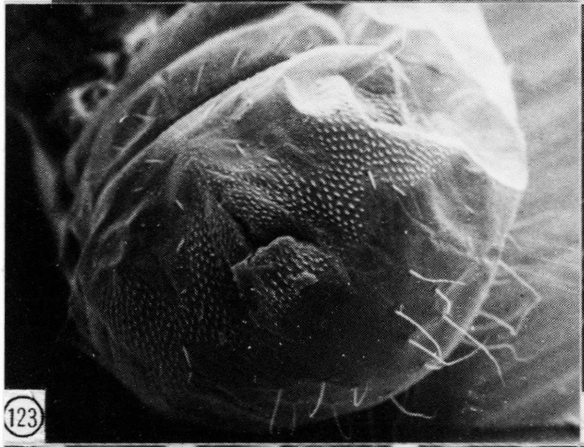
Fig. 126:- Divided asperities on surface of anal fold.

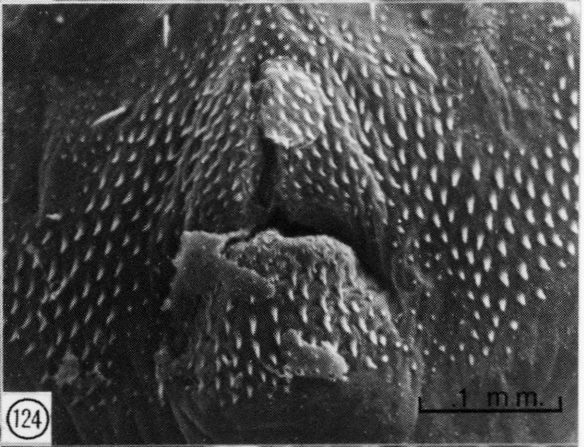

(119)

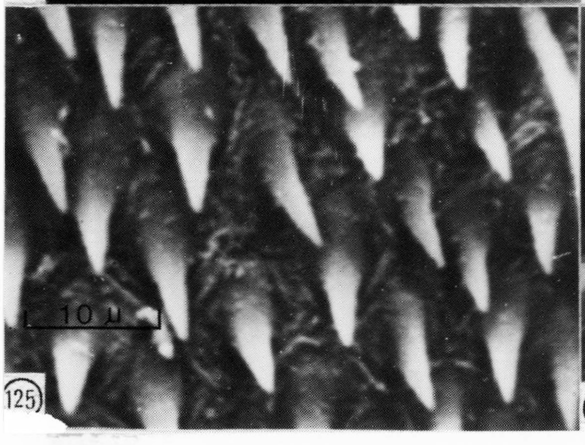

(120)

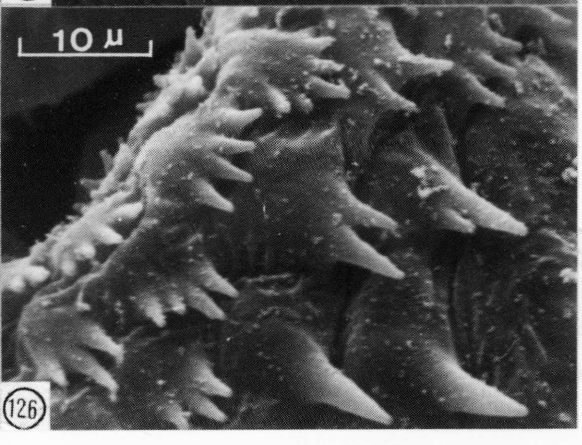

(121)


(122)


(123)


(124)


(125)


(126)

Figures 127 - 131

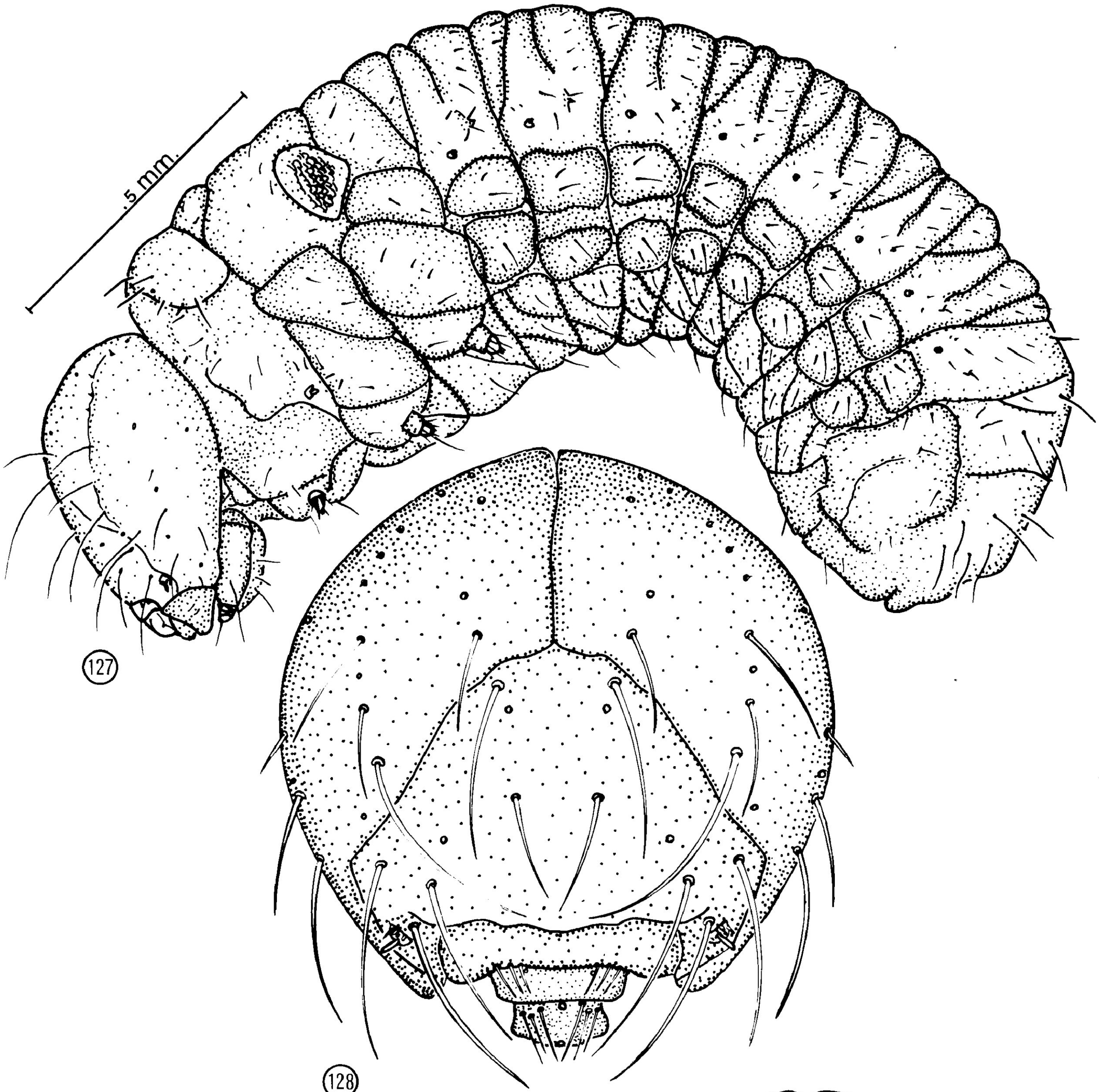
Fig. 127:- *A. minutus*, first instar larva.

Fig. 128:- Dorsal view of head capsule.

Fig. 129:- Thoracic spiracle.

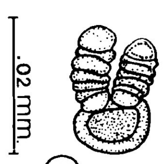
Fig. 130:- Abdominal spiracle.

Fig. 131:- Ventral view of head capsule.



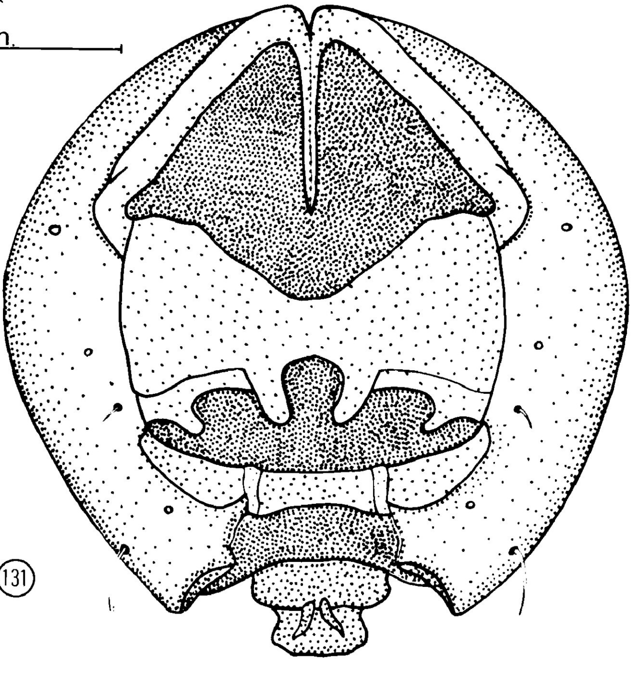
⑫⑦

⑫⑧



⑫⑨

⑬⓪



⑬①

Figures 132 - 138

Fig. 132:- *A. minutus*, first instar larva, ventral view of maxilla.

Fig. 133:- Labrum.

Fig. 134:- Dorsal view of maxilla.

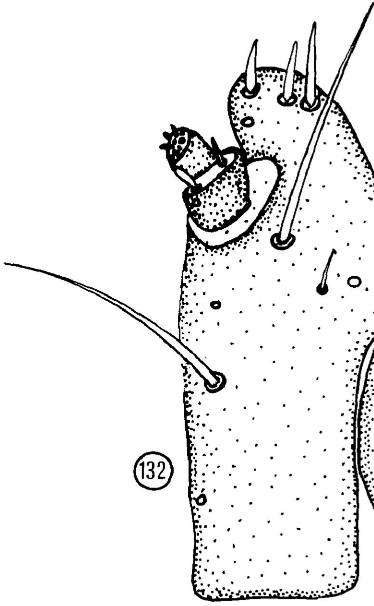
Fig. 135:- Epipharynx.

Fig. 136:- Mandible.

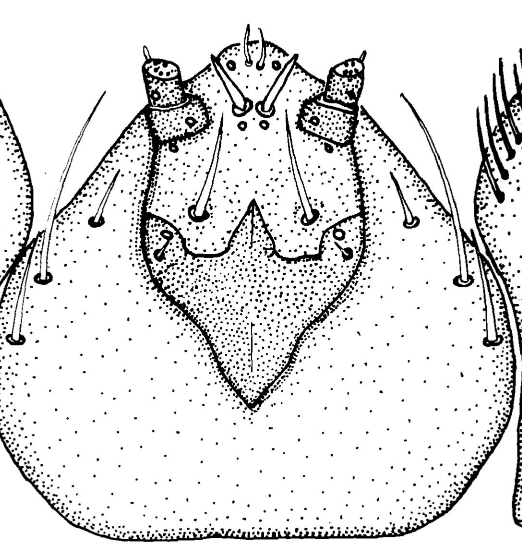
Fig. 137:- *Antliarrhinus sp.*, ventral view of head capsule.

Fig. 138:- Frons, clypeus, labrum, antenna.

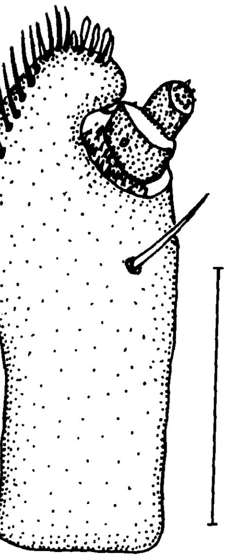
Scale = .1 mm.



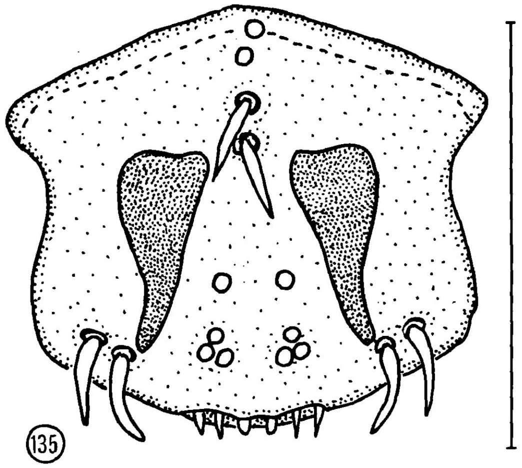
132



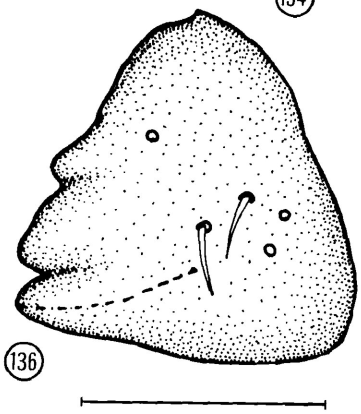
133



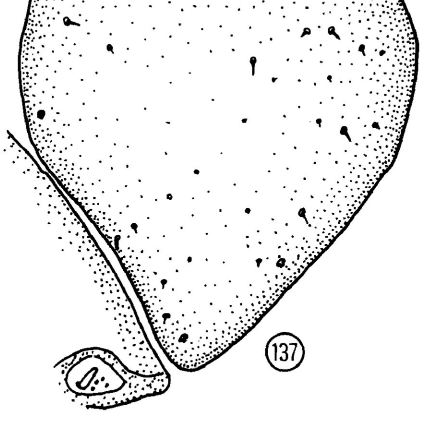
134



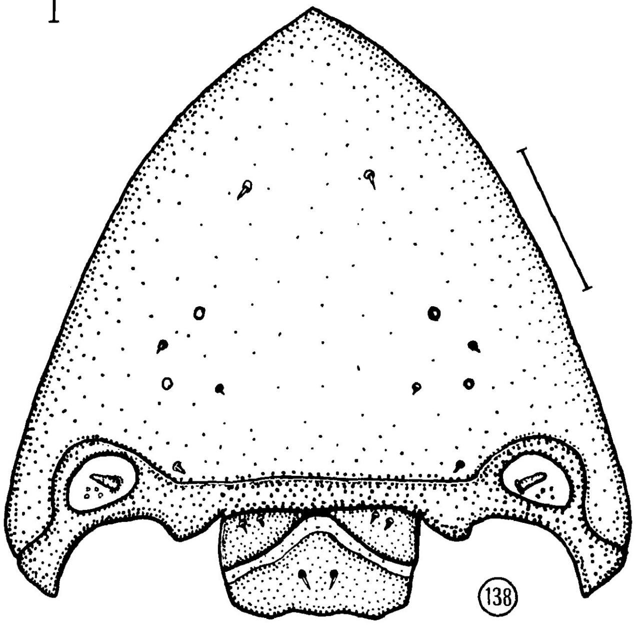
135



136



137



138

## Figures 139 - 146

Fig. 139:- *Antliarrhinus sp.*, ventral view of head capsule.

Fig. 140:- Abdominal spiracle.

Fig. 141:- Thoracic spiracle.

Fig. 142:- Dorsal view of maxilla.

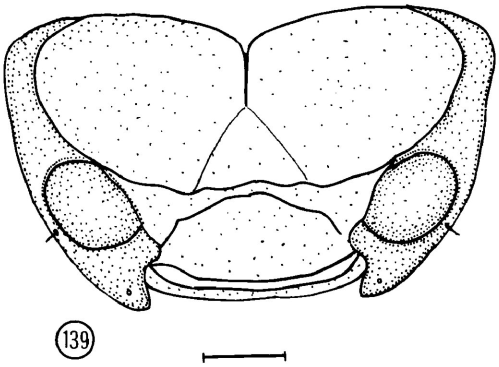
Fig. 143:- Labium.

Fig. 144:- Ventral view of maxilla.

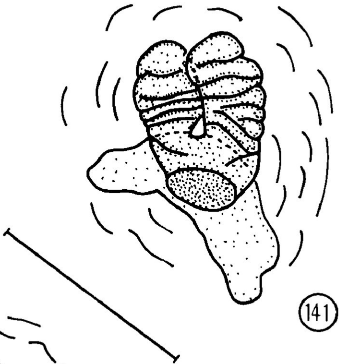
Fig. 145:- Epipharynx.

Fig. 146:- Mandible.

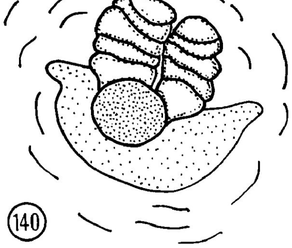
Scale = .1mm



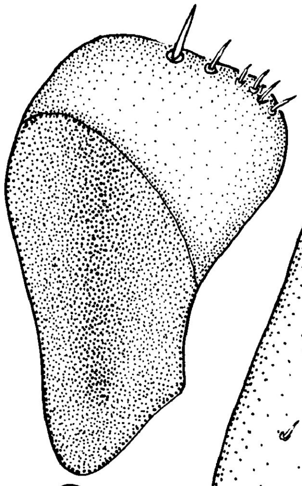
139



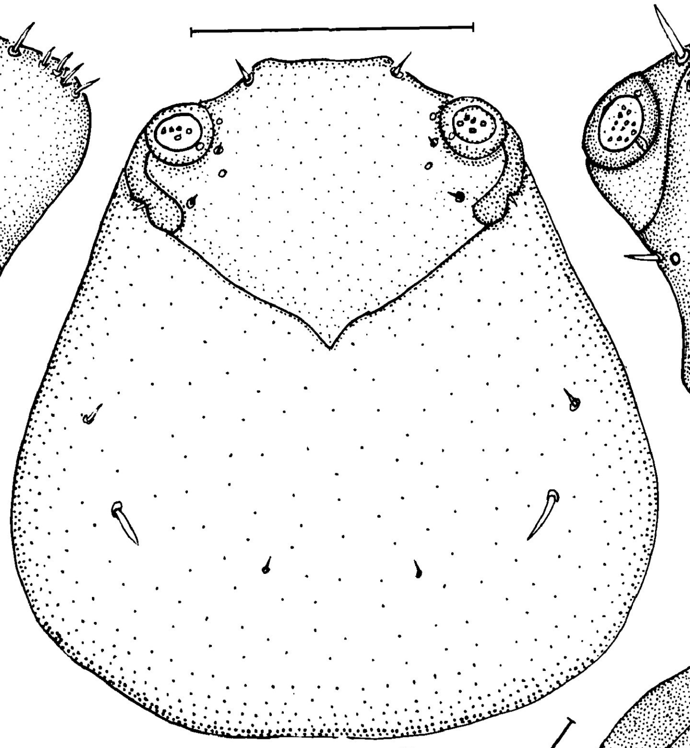
141



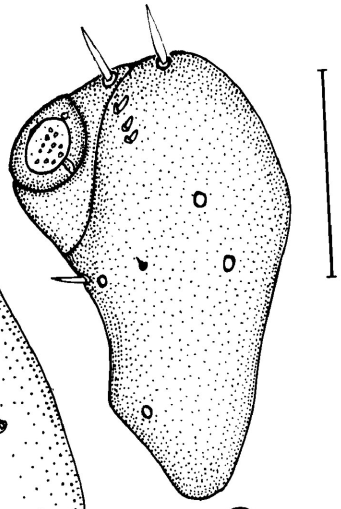
140



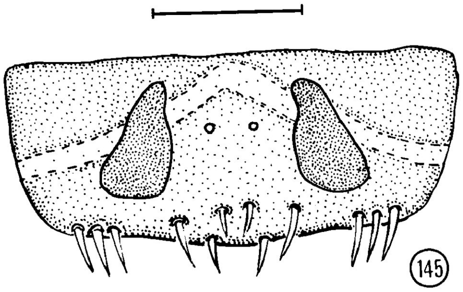
142



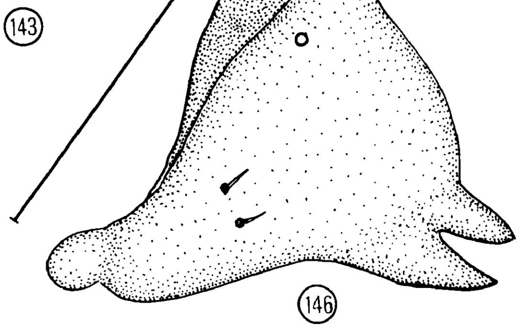
143



144



145



146

Figures 147 - 151

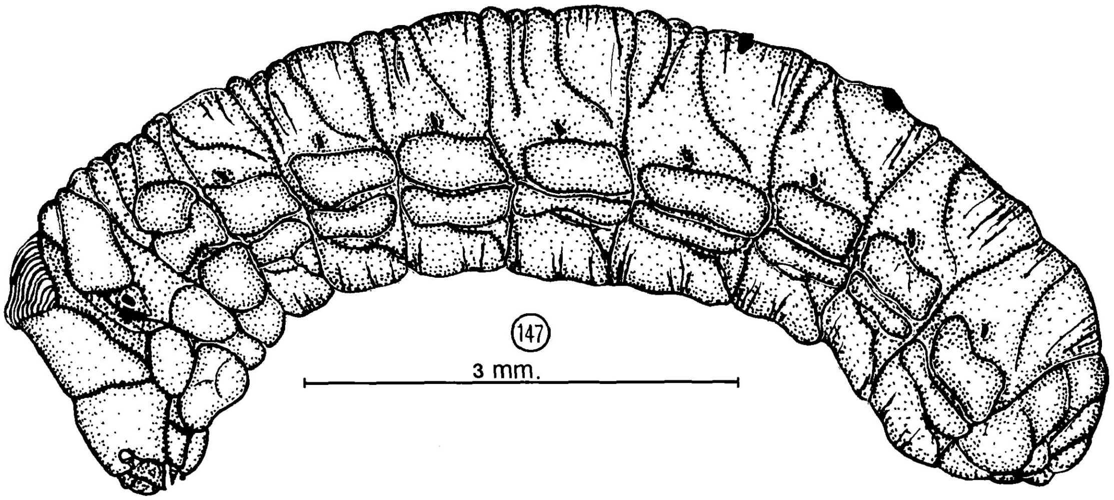
Fig. 147:- Unidentified larva of Belidae,
(Australia) lateral view.

Fig. 148:- Dorsal view of head capsule.

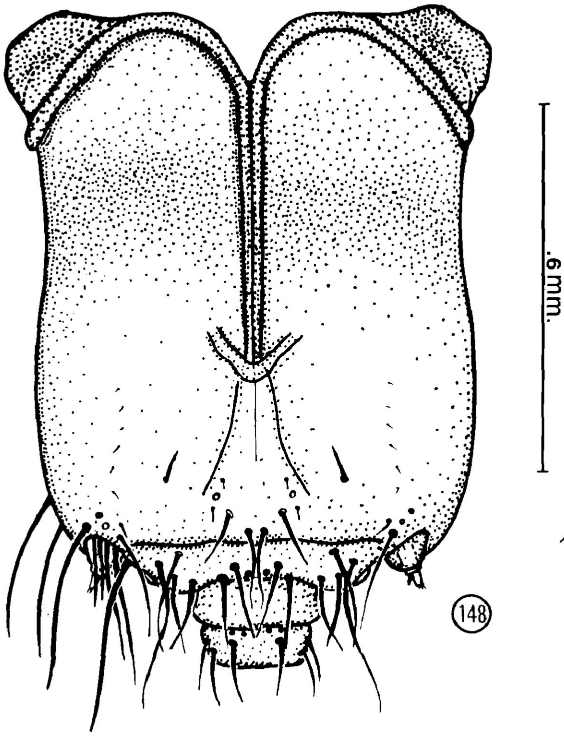
Fig. 149:- Ventral view of head capsule.

Fig. 150:- Labrum.

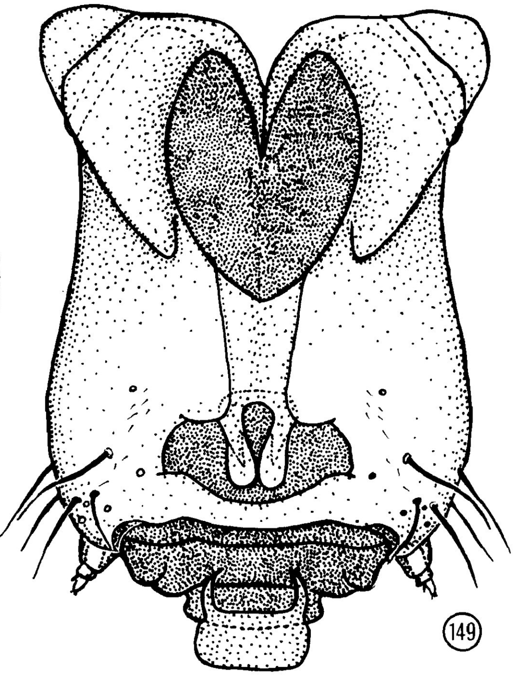
Fig. 151:- Epipharynx.



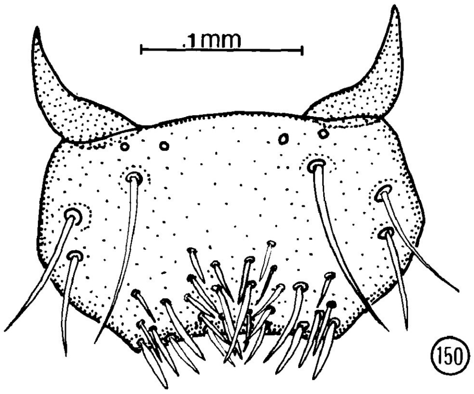
(147)



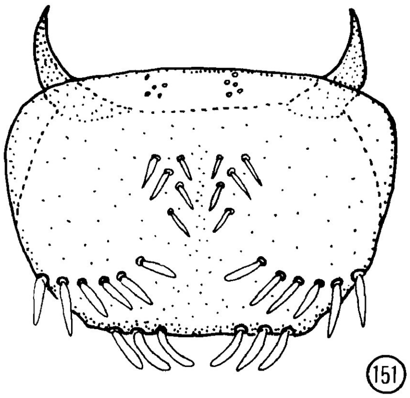
(148)



(149)



(150)



(151)

## Figures 152 - 159

Fig. 152:- Unidentified belid larva, ventral view of maxilla.

Fig. 153:- Labium.

Fig. 154:- Dorsal view of maxilla.

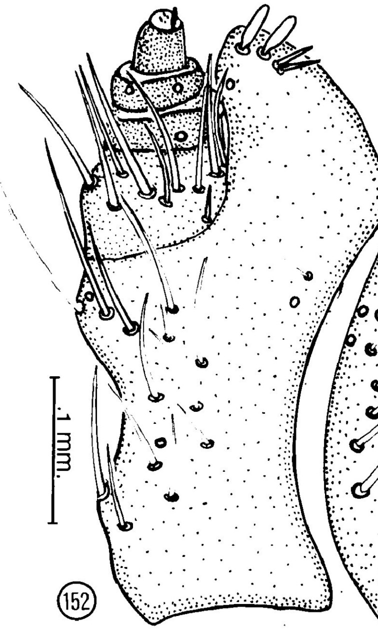
Fig. 155:- Thoracic segments I, II, III, lateral view.

Fig. 156:- Proventriculus, 3 of 12 folds, only one fold with all setae and asperities included.

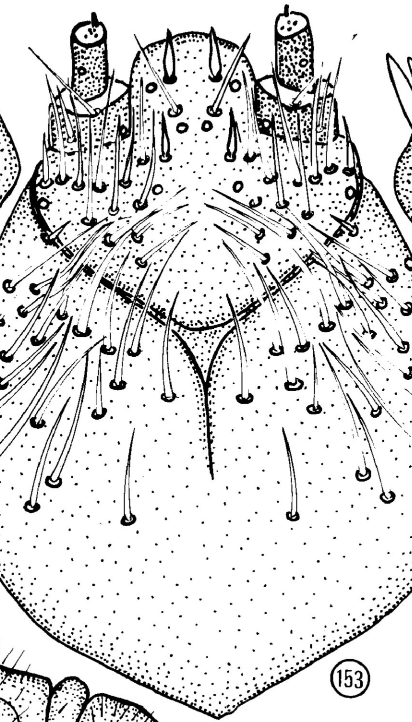
Fig. 157:- Lateral view of third abdominal segment.

Fig. 158:- Fourth and fifth abdominal sterna.

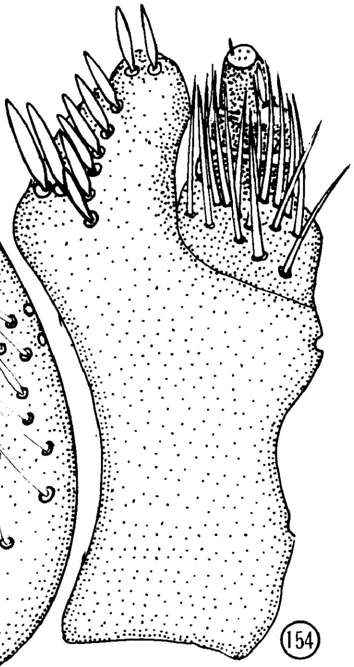
Fig. 159:- Anus.



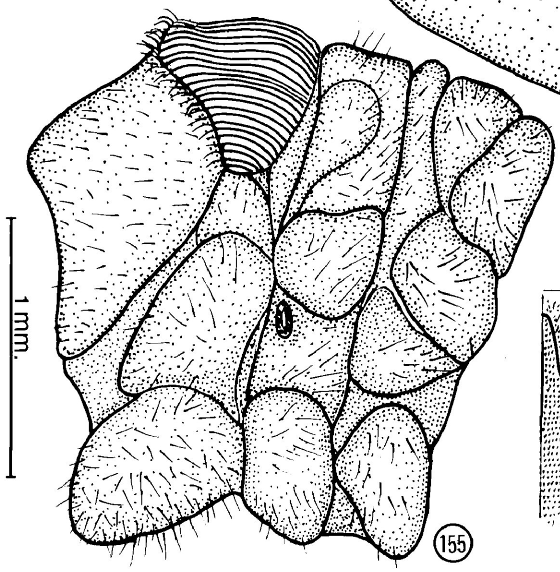
(152)



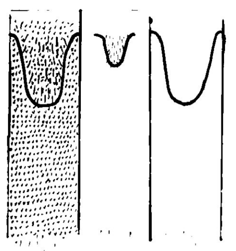
(153)



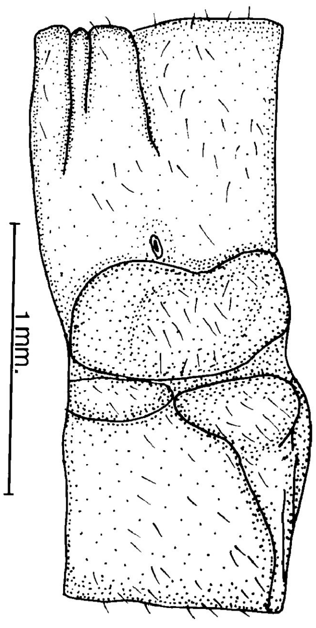
(154)



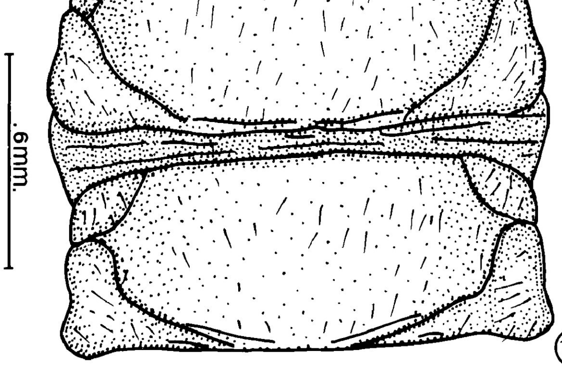
(155)



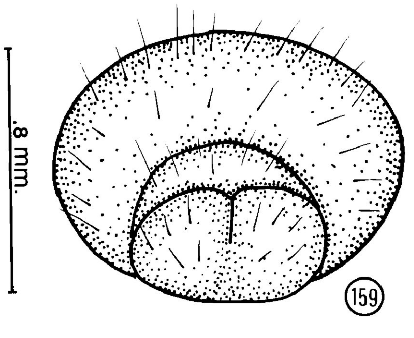
(156)



(157)



(158)



(159)

## Figures 160 - 169

## Larval Ventral Nervous Systems

## Chrysomelidae and Curculionidae

Fig. 160:- *Chrysomela sp.*, Cer - Cerebrum,
Se G - Suboesophageal ganglion,
Ab G - Abdominal ganglion.

Fig. 161:- *Calligrapha sp.*, final instar larva.

Fig. 162:- *Dendroctonus sp.* (Scolytidae).

Fig. 163:- Unidentified scolytid larva from red pine.

Fig. 164:- *Curculio sp.* (Curculionidae).

Fig. 165:- *Gymnaetron sp.* (Curculionidae).

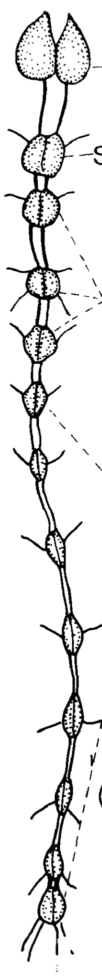
Fig. 166:- *Ithycerus noveboracensis* (Ithyceridae).

Fig. 167:- *Acanthoscelidius acephalus* (Curculionidae).

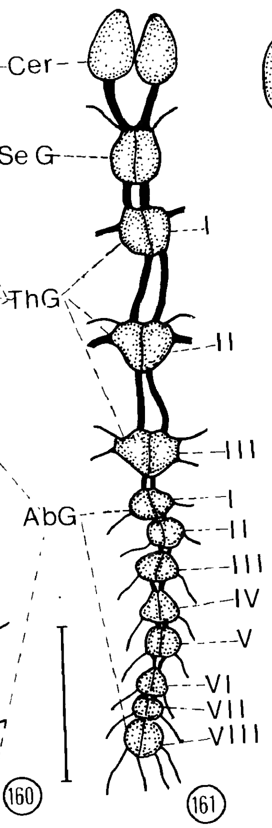
Fig. 168:- *Brachyrhinus sp.* (Curculionidae).

Fig. 169:- *Listronotus sp.* (Curculionidae).

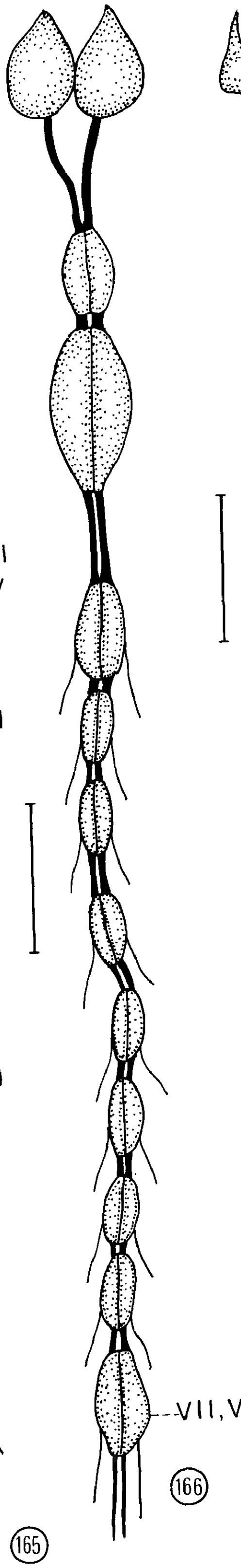
scale = .5 mm.



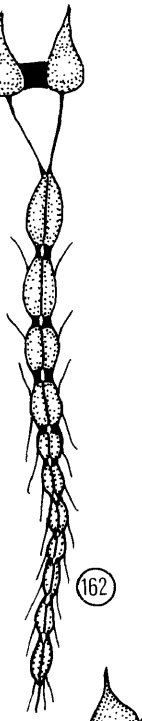
160



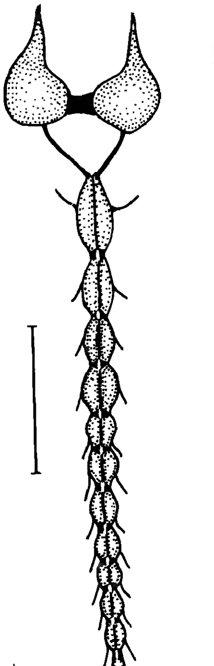
161



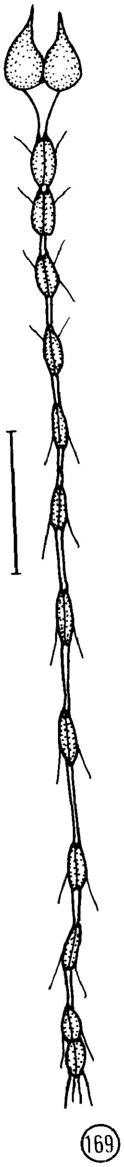
166



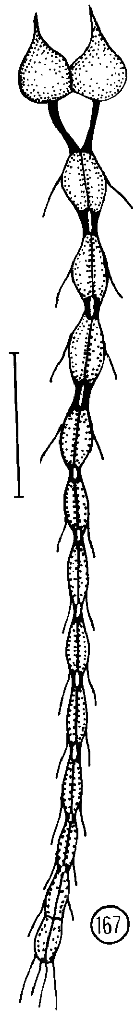
162



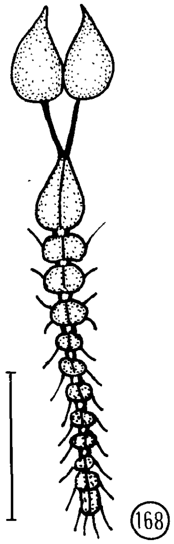
163



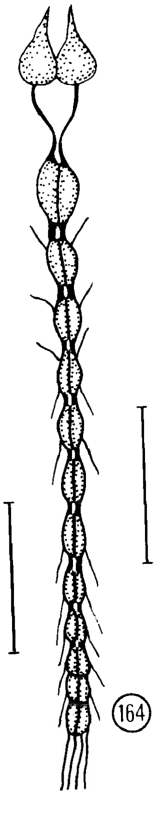
169



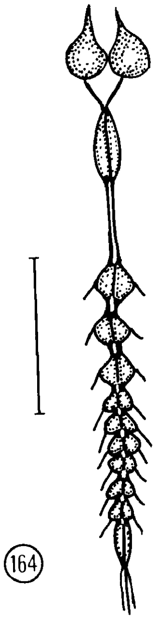
167



168



164



165

## Figures 170 - 179

## Adult Ventral Nervous Systems - Curculionoidea

Fig. 170:- *Euparius marmoreus* (Anthribidae).

Fig. 171:- *Attelabus bipustulatus* (Attelabidae).

Fig. 172:- *Ithycerus noveboracensis* (Ithyceridae)

Fig. 173:- *Arrhenodes minutus* (Brenthidae)

Fig. 174:- *Antliarrhinus sp.* (Antliarrhinidae).

Fig. 175:- *Gnathotrichus sp.* (Scolytidae).

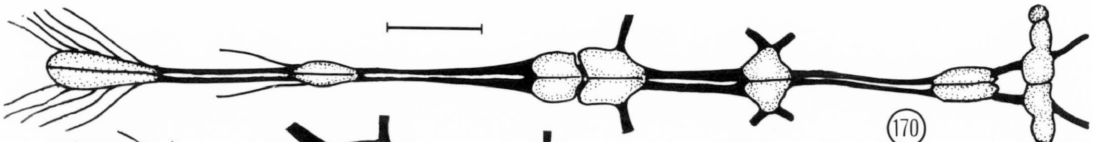
Fig. 176:- *Pissodes strobi* (Curculionidae).

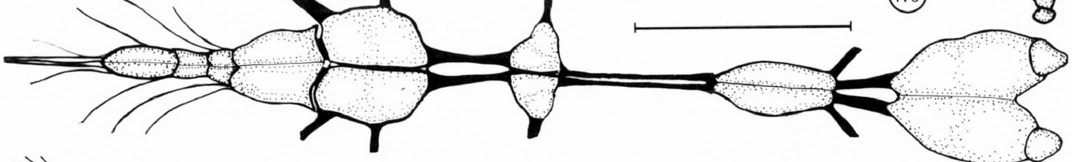
Fig. 177:- *Listronotus sp.* (Curculionidae).

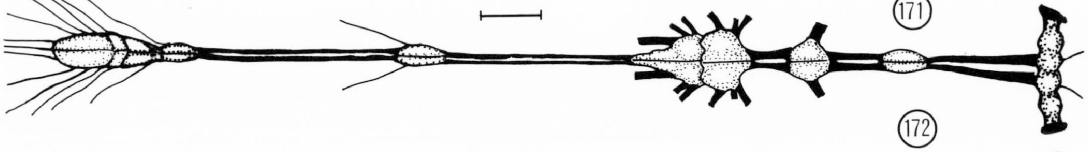
Fig. 178:- *Liparus sp.* (Curculionidae).

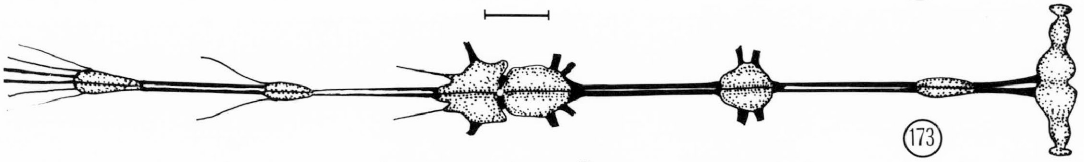
Fig. 179:- *Magdalis barbita* (Curculionidae).

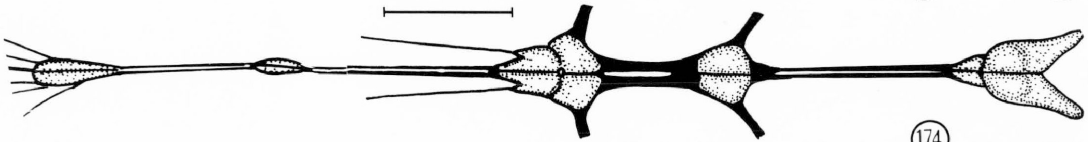
scale = .5 mm.

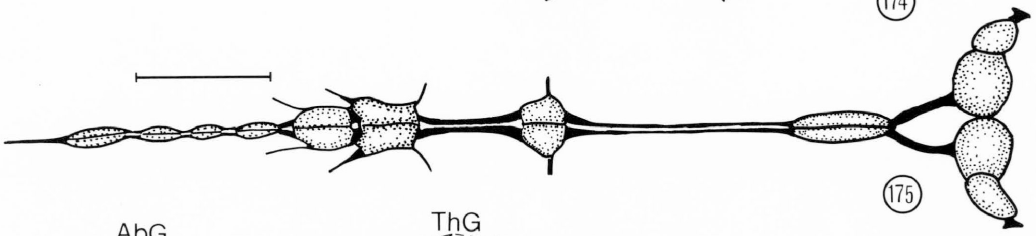

(170)

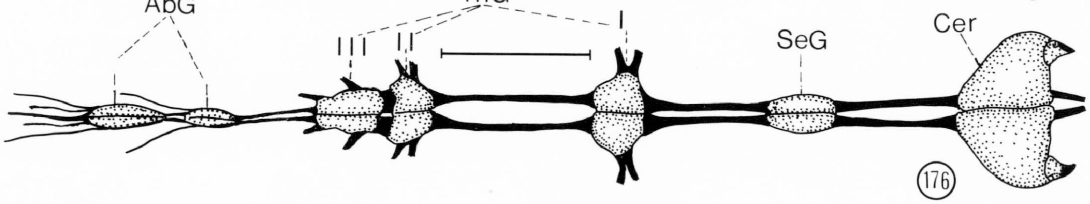

(171)


(172)

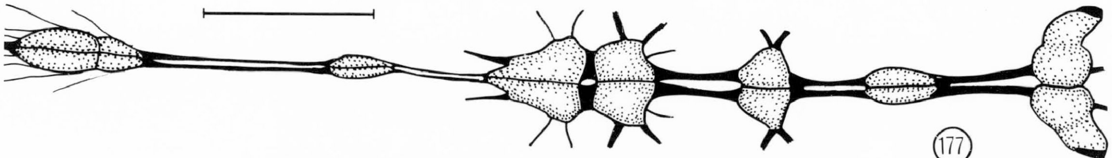

(173)

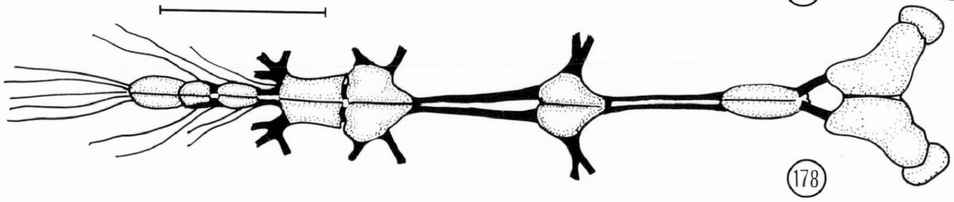

(174)

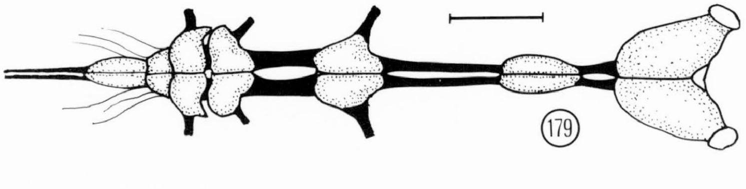

(175)



(176)


(177)


(178)


(179)

## Figures 180 - 184

## Hind Wings - Curculionoidea

Fig. 180:- *Cimberis elongatus* (Nemonychidae).

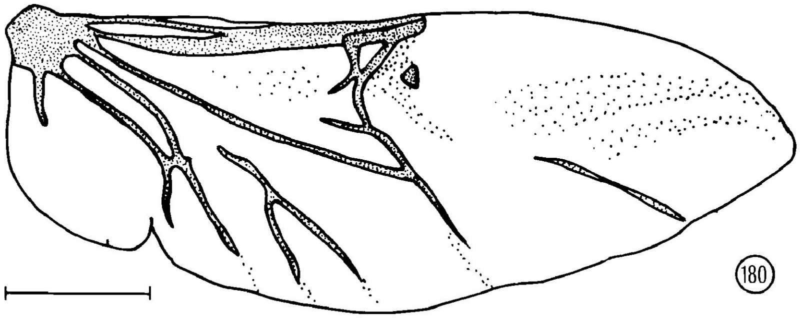
Fig. 181:- *Allandrus sp.* (Anthribidae).

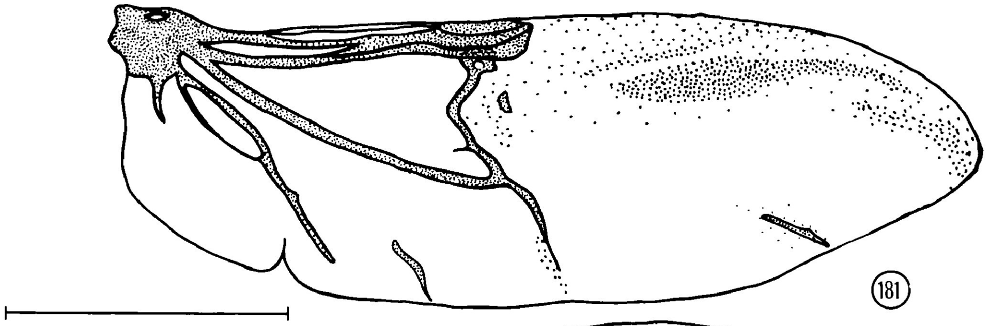
Fig. 182:- *Euparius marmoreus* (Anthribidae).

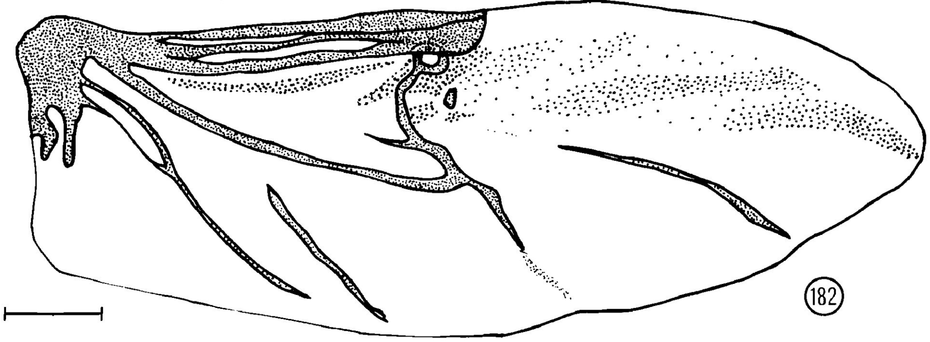
Fig. 183:- *Rhynchites bicolor* (Attelabidae).

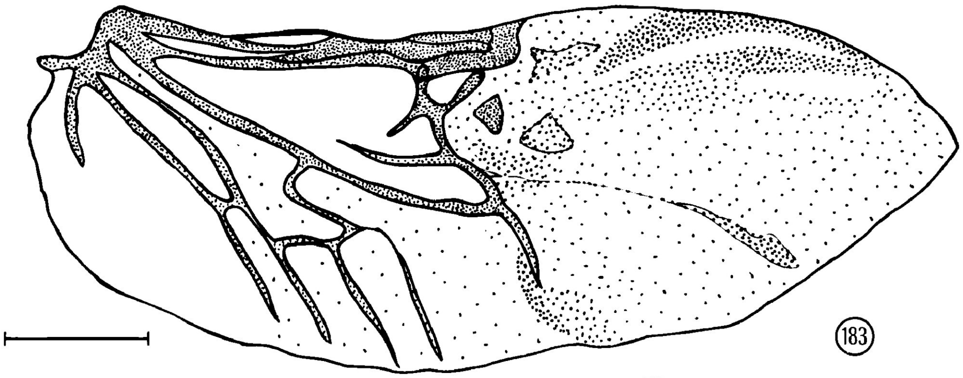
Fig. 184:- *Attelabus bipustulatus* (Attelabidae).

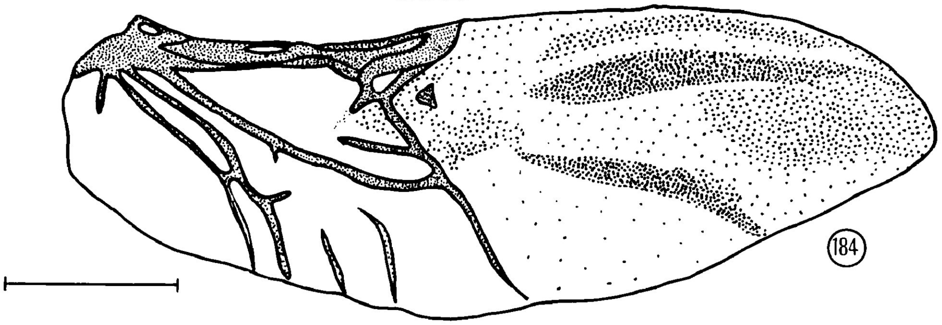
scale = 1.0 mm.


(180)


(181)


(182)


(183)

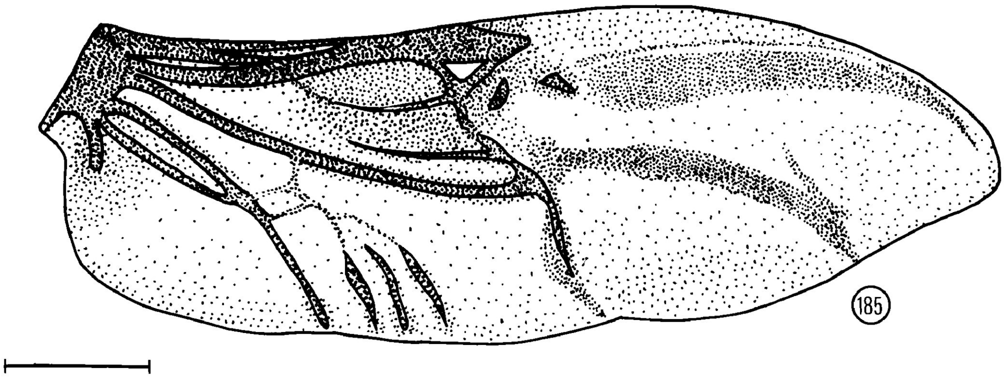

(184)

Figures 185 - 188

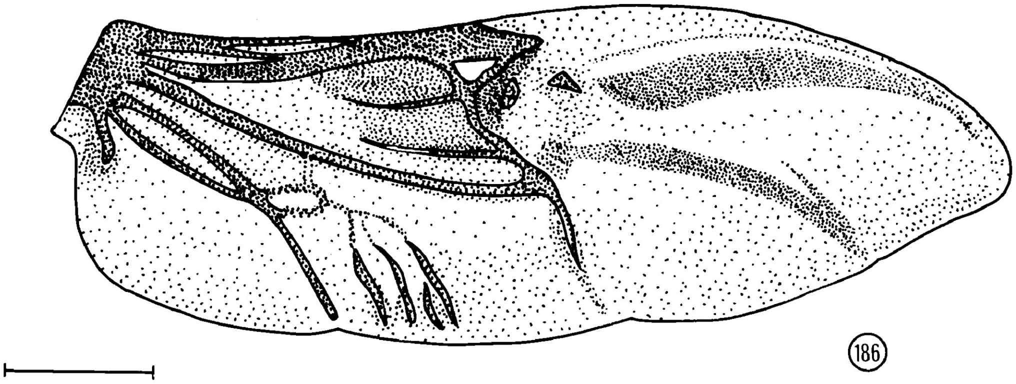
Hind Wings - *Ithycerus*

Variation in number and position of anal veins.

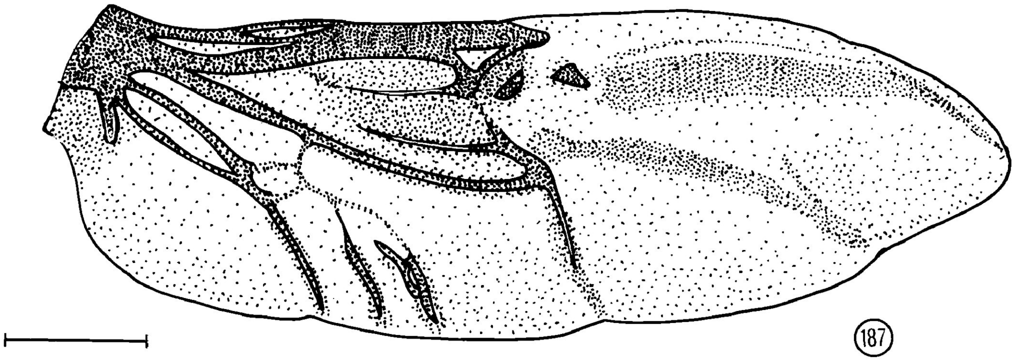
scale = 2.0 mm.



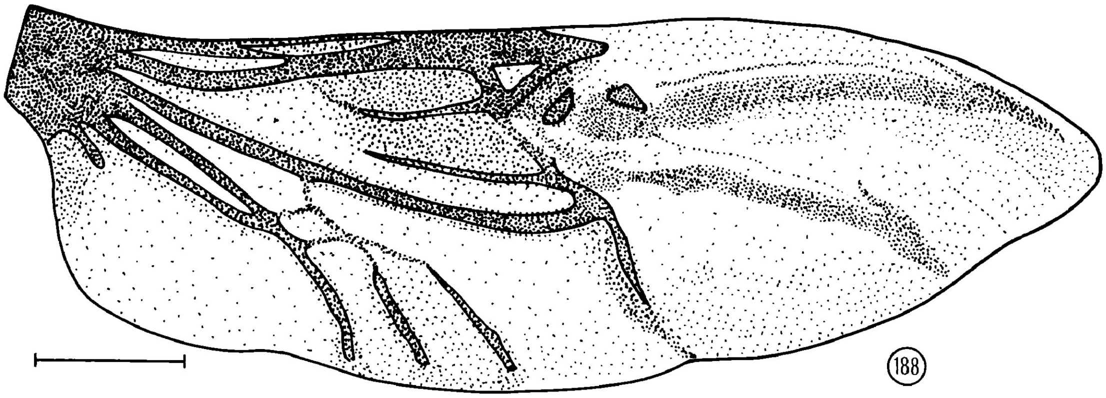
(185)



(186)



(187)



(188)

## Figures 189 - 193

## Hind Wings - Curculionoidea

Fig. 189:- *Arrhenodes minutus* (Brenthidae)

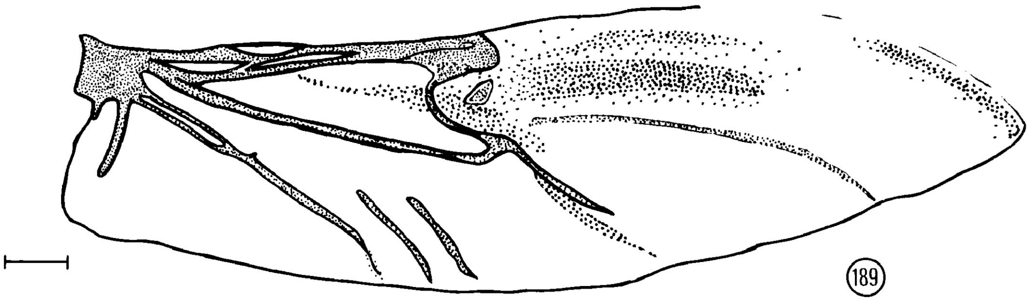
Fig. 190:- *Antliarrhinus sp.* (Antliarrhinidae)

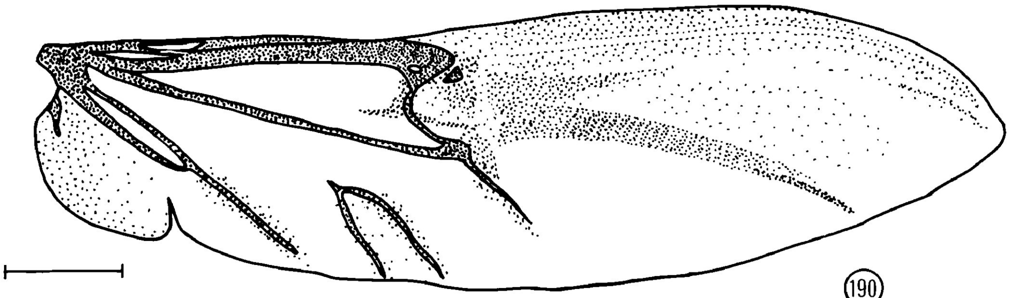
Fig. 191:- *Apion longirostra* (Apionidae)

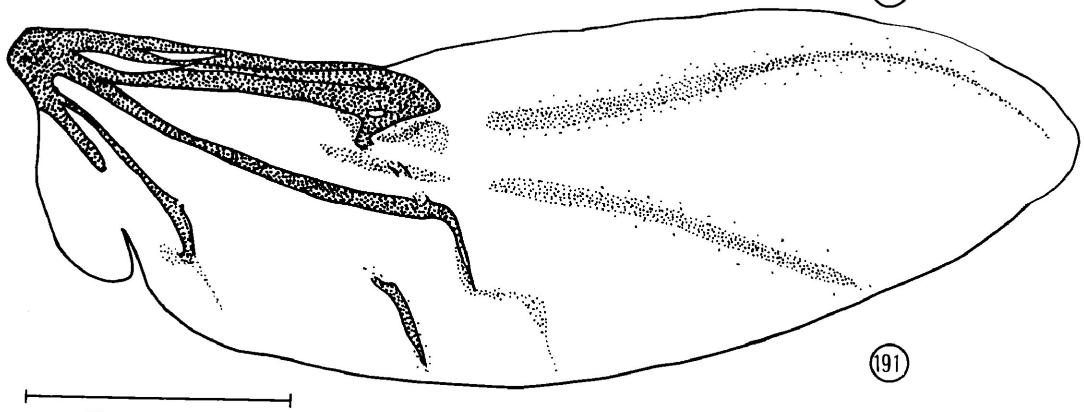
Fig. 192:- *Magdalis barbita* (Curculionidae)

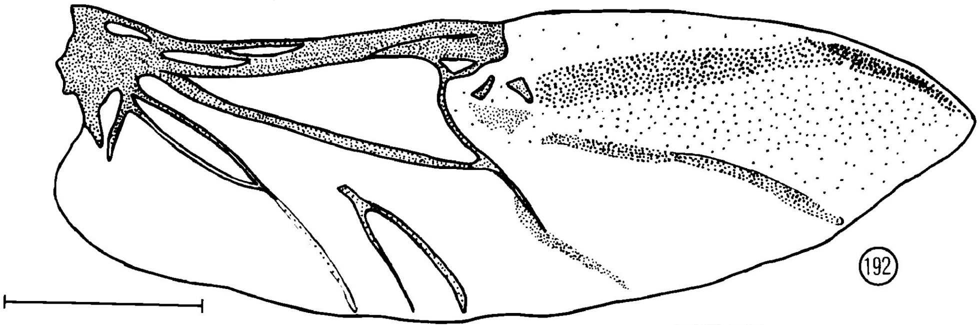
Fig. 193:- *Cossonus platalea* (Curculionidae)

scale = 1.0 mm.


(189)


(190)


(191)


(192)

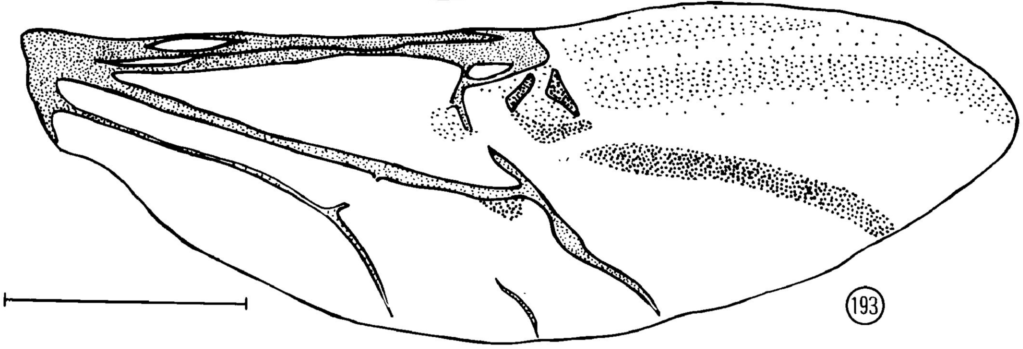

(193)

Figure 194

Distribution of *Ithycerus* in relation to the distribution of *Quercus alba* (White Oak).


NORTH AMERICA
0
500
MILES
Northern Grey Form ●
Southern Melanic Form ■
Quercus alba Dist'n ----

Fig. 194

Figure 195

Phylogenetic Relationships of Ithyceridae

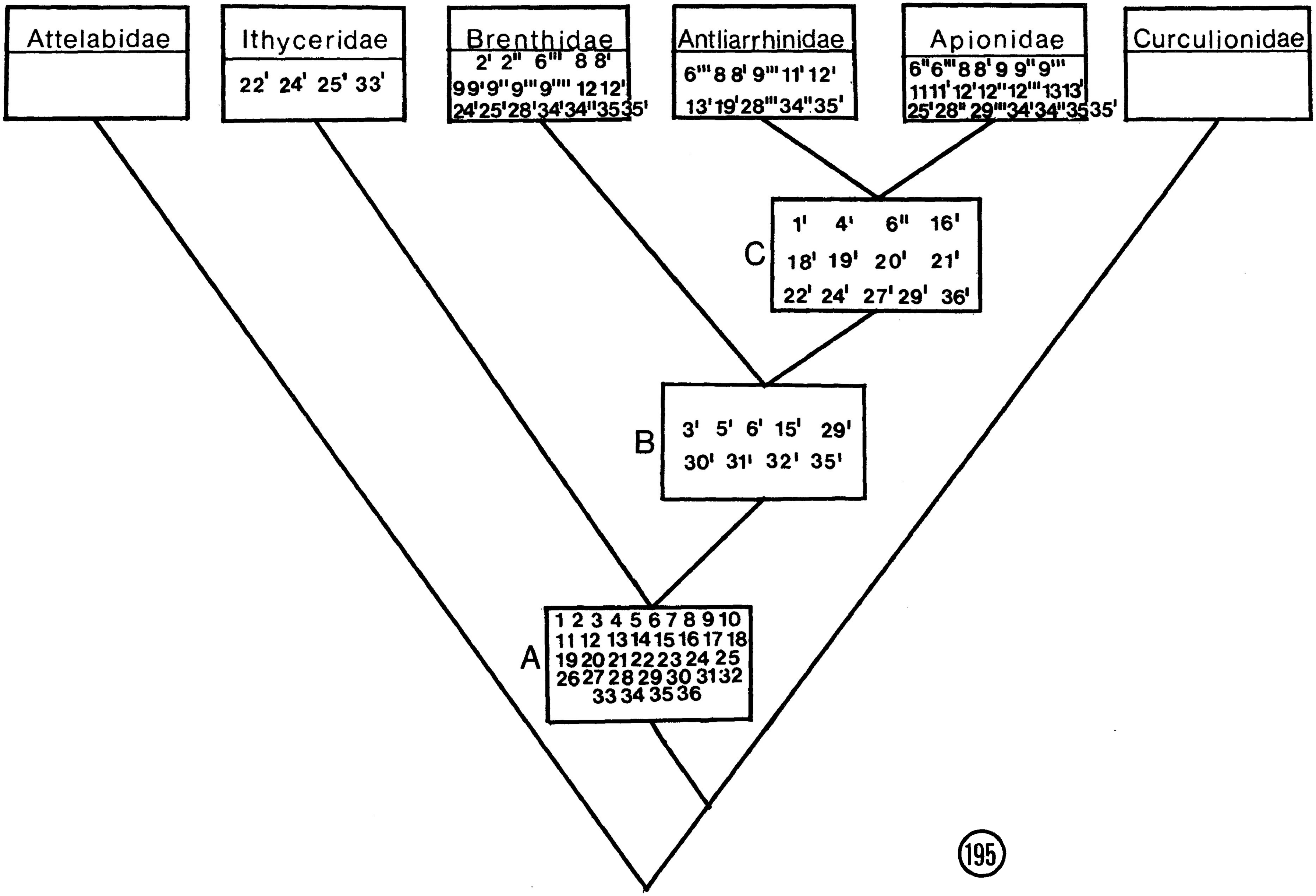
(after Sanborne)

Boxes indicate ancestral and shared derived character states.

A — Hypothetical ancestor

B — Hypothetical ancestor

C — Hypothetical ancestor

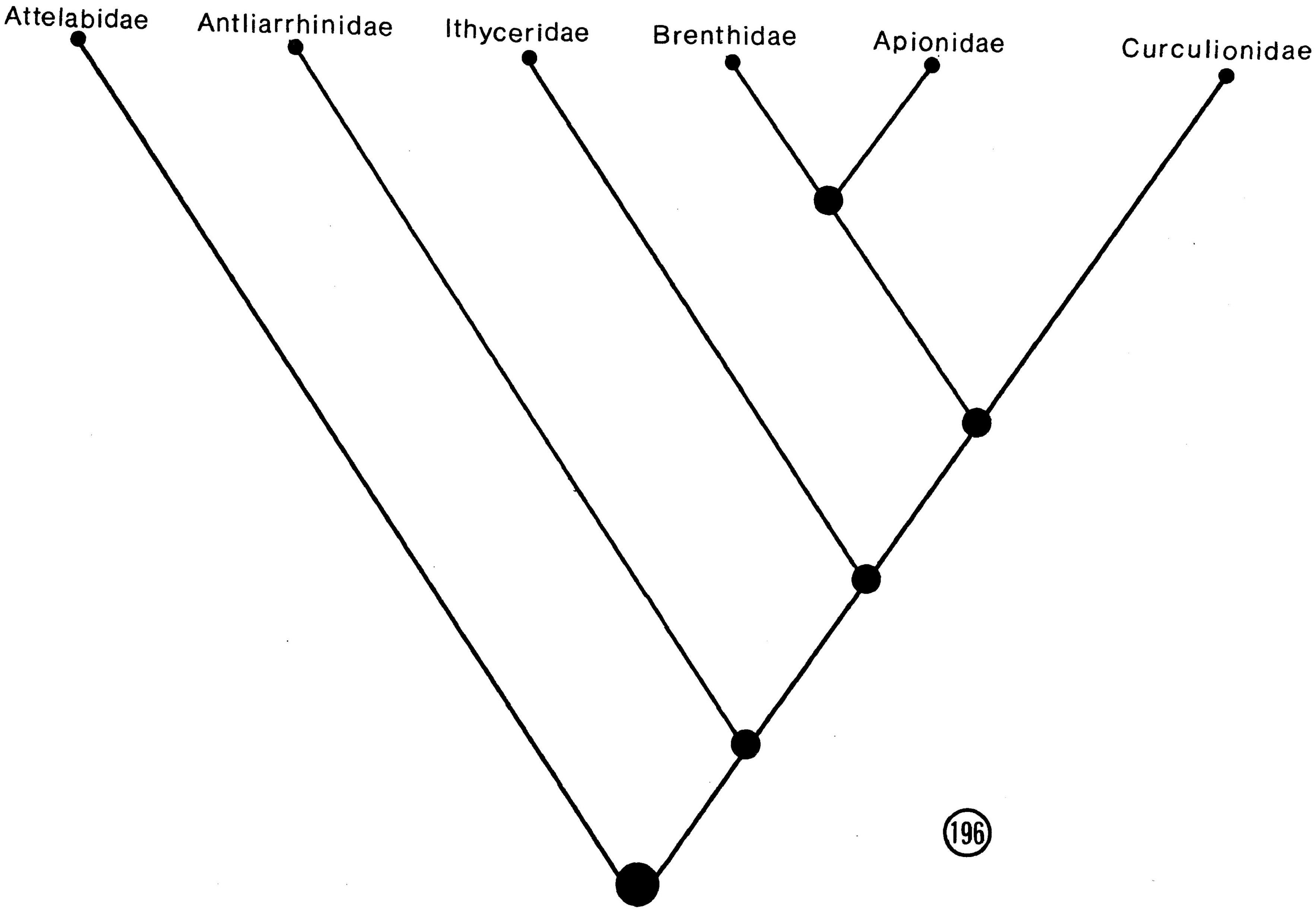

Attelabidae
Ithyceridae
22' 24' 25' 33'
Brenthidae
2' 2'' 6''' 8 8'
9 9' 9'' 9''' 9'''' 12 12'
24' 25' 28' 34' 34'' 35 35'
Antliarrhinidae
6''' 8 8' 9''' 11' 12'
13' 19' 28''' 34'' 35'
Apionidae
6'' 6''' 8 8' 9 9'' 9'''
11 11' 12' 12'' 12''' 13 13'
25' 28'' 29''' 34' 34'' 35 35'
Curculionidae
C
1' 4' 6'' 16'
18' 19' 20' 21'
22' 24' 27' 29' 36'
B
3' 5' 6' 15' 29'
30' 31' 32' 35'
A
1 2 3 4 5 6 7 8 9 10
11 12 13 14 15 16 17 18
19 20 21 22 23 24 25
26 27 28 29 30 31 32
33 34 35 36

(195)

Figure 196

Phylogenetic Relationships of Ithyceridae

(after Crowson)

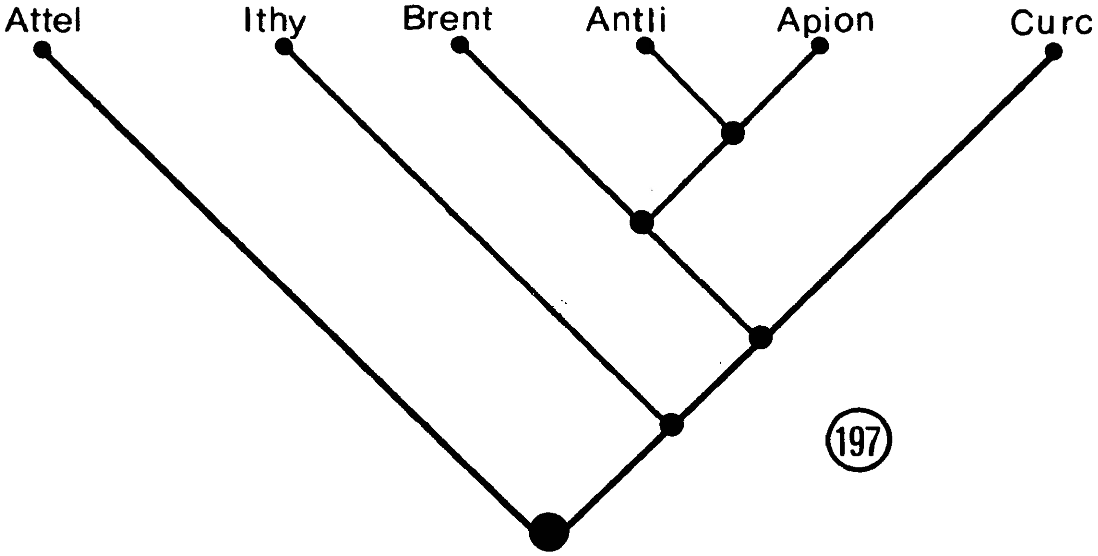

Attelabidae
Antliarrhinidae
Ithyceridae
Brenthidae
Apionidae
Curculionidae

(196)

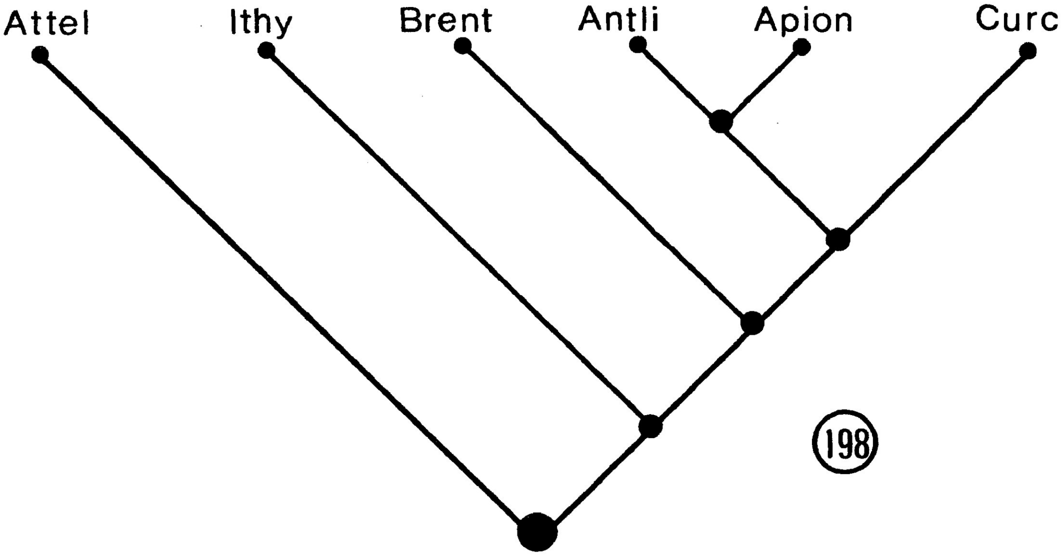
Figures 197 - 199

## Phylogenetic Relationships of Ithyceridae

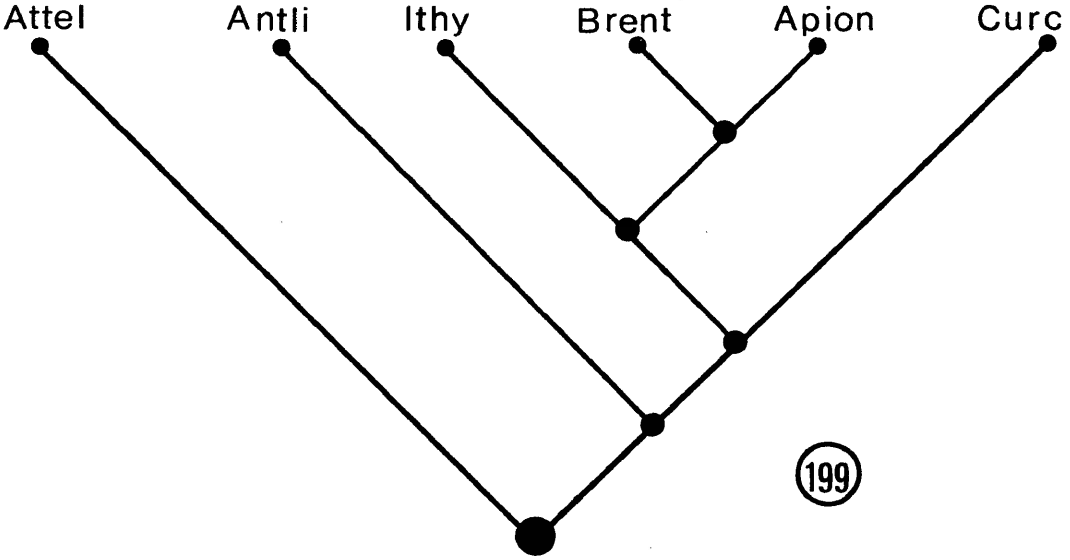
## Alternative Schemes


Attel
Ithy
Brent
Antli
Apion
Curc

(197)


Attel
Ithy
Brent
Antli
Apion
Curc

(198)


Attel
Antli
Ithy
Brent
Apion
Curc

(199)

Figure 200

Evolution of Larval Labral Sensilla

A — Hypothetical ancestor

B — Belidae

C — Nemonychidae, Anthribidae, Aglycyderidae,
Oxycorynidae, Attelabidae

D — *Sphenophorus* (Rhynchophorinae)

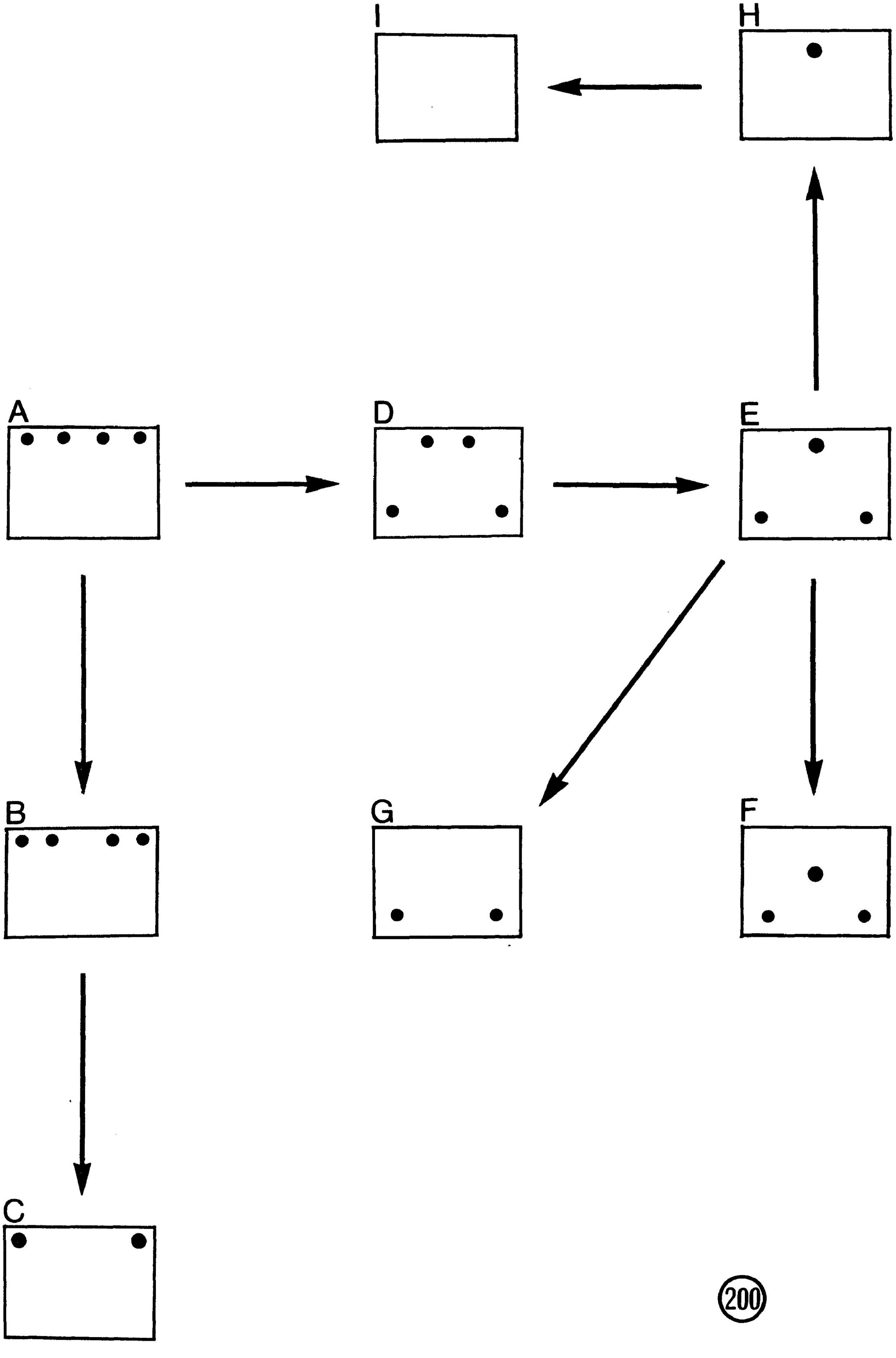
E — *Rhodobaenus* (Rhynchophorinae)

F — Scolytidae and Curculionidae

G — *Metamasius* (Rhynchophorinae)
and some other Curculionidae

H — *Dryophthorus* (Rhynchophorinae), Ithyceridae,
Brenthidae and some Apionidae

I — Antliarrhinidae and some Apionidae


I
H
A
D
E
B
G
F
C