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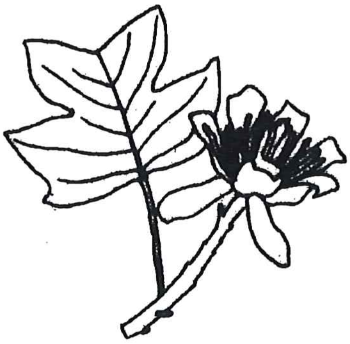

EVOLUTIONARY
MONOGRAPHS
4

BIOLOGY OF *ITHYCERUS NOVEBORACENSIS* (FORSTER) (COLEOPTERA) AND WEEVIL PHYLOGENY

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EVOLUTIONARY MONOGRAPHS 4

April, 1981

Received July 25, 1980; March 9, 1981
Initial price: $13.00
Initial price to individuals: $11.00
Pages 1-80, 33 plates
The editors thank W. Clark and D.R. Whitehead for help in evaluating this monograph.

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ABSTRACT

A detailed account of the biology of *Ithycerus* is given and includes life cycle, ecology, behaviour, distribution, geographic variation and zoogeography.

The larva and pupa of *Ithycerus* are described for the first time. Seven instars are reported with the possibility that more exist. The first instar larva of *Arrhenodes minutus* (Drury) and the final instar larva of *Antliarrhinus* are also described for the first time and compared with *Ithycerus*. The genus *Antliarrhinus* is given family ranking (Antliarrhinidae *stat. nov.)* and a diagnosis is provided. The digestive and reproductive systems, external genitalia and larval and adult ventral nervous systems of *Ithycerus* are described.

A history of the higher classification of *Ithycerus* is outlined and a discussion of the merits of maintaining family status (Morimoto, 1976) for the genus is given. Additional notes are given on the classification of the "higher weevils", which include all species which have the 1st and 2nd visible sternites solidly fused together while the 3rd, 4th and 5th remain more or less freely articulated. This is the 'curculionid type' abdomen of Morimoto (1962).

A phylogenetic scheme is presented for the five families examined in this study; Ithyceridae, Brenthidae, Antliarrhinidae, Apionidae and Curculionidae (excluding Platypodidae and Scolytidae). Ithyceridae is believed to be very closely related to Brenthidae. The phylogenetic importance of ventral nervous systems of adult and larval curculionoidea is discussed. Systems with 8 abd. ganglia, separated by long connectives, are considered primitive. An evolutionary sequence is postulated for the numbers and positions of setae and sensilla on the labra of larval Curculionoidea.

INTRODUCTION

The relationship of *Ithycerus noveboracensis (*Forster) to other Curculionoidea has been a matter of curiosity and concern for many years. Adult morphology provided few clues and this has resulted in many conflicting viewpoints. The problem was extensively discussed in a meeting of weevil specialists in Washington, D.C., August, 1976. It was felt that a suitable solution to the "mystery of the New York Weevil" might be found if the larva was discovered. I accomplished this through rearing experiments conducted in 1977. Further rearings to 1980 verified that oviposition and larval development occurs in the soil. This was further substantiated through field work in 1978 when four *Ithycerus* larvae were collected on the roots of *Fagus grandifolia* Ehrh. (American Beech) at Parkhill, Ontario. These discoveries contradict the observations of Riley (1871) who gave the first account of the biology of *Ithycerus*. He reported damage to the leaf 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, identified as *Ithycerus*. The larvae of *Ithycerus* are now known to possess legs.

The main purpose of this study is to provide an accurate account of the biology of *Ithycerus* with emphasis on its immature stages. It is my hope that the information will enable specialists to make comparisons with other weevil taxa so that they can form their own conclusions regarding the classification and phylogenetic relationships of *Ithycerus*.

The combined results and discussion is divided into four sections; Biology of *Ithycerus*, Morphology, Classification of the "Higher Weevils", and Phylogeny. The section on biology includes larval development, numbers of larval instars, adult longevity, flight period, feeding habits and associations with plants, mating and oviposition, grooming, predators and parasites, distribution, geographic variation and zoogeography of *Ithycerus*. The section on morphology includes descriptions of the egg larvae and pupa of Ithycerus, first instar larva of *Arrhenodes minutus* (Drury) and the final instar larva of *Antliarrhinus*, a diagnosis (in tabular form) comparing the larvae of these taxa, a diagnosis of the family Antliarrhinidae *stat. nov.*, descriptions of the digestive tracts (larvae and adults) of *Ithycerus*, reproductive systems and external genitalia of *Ithycerus*, and ventral nervous system (larvae and adults) of *Ithycerus*. The section on the classification of the "higher weevils" discusses the merits of maintaining family status for *Ithycerus*, with additional comments on Antliarrhinidae, Brenthidae, Apionidae and Curculionidae (excl. Platypodidae and Scolytidae). The section on phylogeny deals with the relationships between Ithyceridae and the four families listed above. A discussion is included on the phylogenetic importance of the ventral nervous systems (adults and larvae) of the Curculionoidea and finally, a scheme is presented to account for the evolution of the numbers and position of larval labral setae and sensilla (Curculionoidea).

The genus *Ithycerus* appears to be the most primitive extant member of the "higher weevils", based primarily on the characteristics of the immature stages. In view of this, it is felt that subsequent studies of larvae of these families must be based on comparisons with this unique genus.

LITERATURE REVIEW

The publication by Burke and Anderson (1976) deserves special mention here. It is a bibliography of all taxonomically important references dealing with the larvae and pupae of Curculionoidea occuring in the western hemisphere. It was indispensable in locating references relevant to this study.

The following list of references includes all those which were used to help determine character distributions: Boving and Craighead (1930), Van Emden (1938, 1946, 1950, 1952), Gardner (1932a, 1932b, 1934a, 1934b, 1935, 1936, 1938), Anderson (1941, 1947a, 1947b, 1948a, 1948b, 1952), Peterson (1951), Crowson (1955, 1967), Thomas (1957, 1967), May (1966, 1967, 1968), Muniz and Barrera (1969), Browne (1972), Ahmad and Burke (1972), and Clark, Burke and Anderson (1978).

It is necessary to list them this way because it was impossible to cite them properly in Table 8, where they belong. It would have been necessary to use multiple and repeated citations for the various character states and this would have unnecessarily enlarged and complicated the table. Other publications, and those above which were relevant to other parts of the study, are cited in the usual manner, in the body of the text.

MATERIALS AND METHODS

About 900 adults, 800 larvae and a single pupa of *Ithycerus* were examined. I collected 55 adults in two study areas, Parkhill Conservation Area, Parkhill, Ontario, and Pinery Provincial Park, Grand Bend, Ontario, and 2 adults at King Mountain, Old Chelsea, Quebec, Canada. All but 4 larvae were the offspring of these specimens. The other 4 larvae were collected on the roots of *Fagus grandifolia* Ehrh. (American Beech) at Parkhill. Other species of Curculionoidea examined in connection with this study are listed in Table 1. In addition, larvae of two species of Chrysomelidae, *Chrysomela* sp., *Calligrapha* sp., were also examined.

The following institutions and private collections kindly loaned specimens to me.

University of Kansas, Lawrence, Kansas, 66045, U.S.A.,
Peter D. Ashlock.

Illinois Natural History Survey, Urbana, Illinois,
61801, U.S.A., Donald W. Webb.

Henry and Anne Howden, 23 Trillium, Ottawa, Ontario, Canada.

Michigan State University, East Lansing, Michigan, 48824, U.S.A.,
Roland L. Fischer.

Virginia Polytechnic Institute and State University,
Blacksburg, Virginia, 24061, U.S.A., Michael Kosztarab.

Pennsylvania State University, Frost Entomological Museum, University Park,
Pennsylvania, 16802, U.S.A., S.W. Frost.

Clemson University, Clemson, South Carolina, 29631, U.S.A., John C. Morse.

University of Michigan, Ann Arbor, Michigan, 48104, U.S.A., Joan Miller.

Harvard University, Cambridge, Massachusetts, 02138, U.S.A., Alfred F. Newton.

University of New Hampshire, Durham, New Hampshire, 03824, U.S.A.,
Wallace J. Morse.

University of Minnesota, St. Paul, Minnesota, 550101, U.S.A., Philip J. Clausen.

Iowa State University, Ames, Iowa, 50010, U.S.A., Thomas A. Chandler.

Cornell University, Ithaca, New York, 14853, U.S.A., L.L. Pechuman.

Kansas State University, Manhatten, Kansas, 66506, U.S.A., H.D. Blocker.

University of Missouri, Columbia, Missouri, 65201, U.S.A., Wilbur R. Enns.

Purdue University, Lafayette, Indiana, 47907, U.S.A., A. Provonsha.

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Table 1. Adults and larvae of species of Curculionoidea (excluding *Ithycerus*) examined.

		N			
SPECIES	FAMILY	ADULTS	LARVAE	LOCALITY	COLLECTOR
Cimberis sp.	Nemonychidae	4		Constance Bay, Ont.	W. Brown
Euparius marmoreus (Olivier)	Anthribidae	15		Parkhill, Ont.	M. Sanborne
Euparius marmoreus (Olivier)	Anthribidae		3	Cartley, Quebec	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 Olivier	Apionidae	2		Waterdown, Ont.	M. Sanborne
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 (Peck)	Curculionidae	8		Constance Bay, Ont.	M. Sanborne
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

Iowa Insect Survey Collection, Iowa Wesleyan College, Mount Pleasant, Iowa, 52641, U.S.A., D.D. Millspaugh

Canadian National Collection, Biosystematics Research Institute, Ottawa, Ontario, K1A 0C6, Canada, Don Bright

R.A. Crowson, University of Glasgow, Glasgow, Scotland.

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.

Tree size was also a probable factor in adult distribution. 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. This maybe related to 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 food requirements were determined from rearing experiments done in 1977 on larvae reared from adults captured on King Mountain, Old Chelsea, Quebec. A search for larvae was also directed at the root systems of the tree species associated with the adults. However, trees selected in April and May, 1978, produced no larvae. I then began excavating trees on which newly emerged adults were found. 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. No larvae were found on White Oak roots at the Pinery site, however, their deep root systems took four to five times longer to expose 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. Subsequent searches around White Oak roots at the Pinery site revealed feeding damage identical to that seen in the laboratory but no larvae were found.

Rearing Techniques

Captured adults of *Ithycerus* were placed in rearing cages (Fig. 31) with up to 3 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. 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.

Female *Ithycerus* 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 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). Behaviour of the females indicated when they had deposited their daily production of eggs. Ovipositing females kept their heads lowered to the soil, probed small depressions with their rostra, 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 tried 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 of soil, and the containers were dampened with distilled water and stored at room temperature (ca. 22°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. 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 oviposition. 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 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 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.

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 root surfaces 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 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. These 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 fungal growth, probably due to exposure to light 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.

Illustrations

Photographs were taken with an Olympus OM-2 35 mm. camera equipped with a 50 mm. lens and a single flash. Scanning electron microscope photomicrographs were taken with a Cambridge Stereoscan 6000 equipped with a 35 mm camera. Drawings were made using Wild M5 dissecting and Wild M12 compound microscopes equipped with drawing tubes.

The system of naming larval structures and chaetotaxy follows that of Anderson (1947a) and Amhad and Burke (1972), *Ithycerus* pupa, Burke (1968), May (1967), and that of male and female reproductive systems and genitalia, Burke (1959), Clark (1977), and Hamilton (1979). The identity 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 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 it name, the *lateral cervical lobe*. 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 were cleared in hot 10% KOH and impregnated with 100% glycerine, then mounted in glycerine on ringed slides. The method allows detailed and rapid examintion of larvae.

Detailed examination of head capsules required that they be 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 the ventral side up.

Dissections of the digestive tracts and nervous systems 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 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. 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 was lifted away from the head capsule, stained in acid 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 unright 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 hindmost 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. 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 fuchsin and mounted on a glass slide in euparol.

Dissections of the genitalia of dried specimens were done by softening 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).

Measurements

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

Larval body lengths were taken by making three separate measurements along the division between the pleural and epipleural areas,in order to account for body curvature. 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 air tube *versus* width of the spiracular orifice were calculated for thoracic and abdominal spiracles. The anterior air tubes were measured because they are longer than the posterior air tubes. The widths of the spiracular orifices were made along their transverse axes between the inner margins of the peritreme. Thoracic spiracles and abdominal spiracles 1, 2 and 3 of both sides of each specimen were measured and a mean ratio of air tube 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 air tube bases to the outside margin of the peritreme.

Measurements of *Ithycerus* adults included head length, elytra length, pronotum length and width and ocular width. Numbers of yellow scales were counted. 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 and specimens 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 AND DISCUSSION

Biology of *Ithycerus*

Life Cycle

As indicated in Table 2, captive females oviposited continuously throughout the months of June and July. Eggs deposited in June and the first two weeks of July were much more viable than those laid in the last two weeks of July. Feeding was continuous from the time of eclosion (July-August) to April, indicating that winter diapause is facultative rather than obligate. Similar observations were made during a third rearing conducted from June, 1979 to April, 1980 when a single pupa was discovered. The average time to eclosion was 6 weeks, with no significant difference between eggs deposited in June or July. In contrast, eggs collected from the King Mountain, Quebec specimens hatched after 3 to 4 weeks. This is probably an adaptation to the shorter warm season of this region as compared to southwestern Ontario.

All available evidence points to a two year life cycle for *Ithycerus*. However, the precise timing of certain events, i.e., the advent and duration of pupation, and the exact number of larval instars is uncertain. Morphological evidence and direct observation of moulting strongly suggests a minimum of 7 instars. Furthermore, all moults through this stage were synchronous; the length of time for the entire culture to enter the next developmental phase being 3-5 days. However, the 6 specimens identified as 7th instars were observed to undergo an 8th, 9th and in a single instance (the sole survivor of the 1978-79 rearing experiment), a 10th moult. The question is whether these represent additional instars or were extra moults caused by some unknown factor such as a nutritional deficiency.

Table 2. Number of eggs and larvae collected from rearing experiments, 1978.

DATES OF OVIPOSITION	EGGS COLLECTION	TIME (DAYS) TO ECLOSION	TIME TO PEAK ECLOSION	NUMBER HATCHED	% HATCHED
VI-3-7	58	34-53	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-5-0	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
VII-3-22	247	-	-	0	0.0
Total	1997		Avg = 45	Total = 555	WA† = 46.1%

* The soil used in the bedding box was contaminated with eggs of a species of Tipulidae. Upon hatching, the larvae of these presumably destroyed a large number of *Ithycerus* eggs before being discovered.

† Weighted average

The following attempt at timing stages in the life cycle is based on observations compiled from 2 rearings conducted between 1978-1980, supplemented by meager information gathered through the collection of 4 wild larvae on roots of American Beech. It was assumed that the development times recorded (Table 3) under laboratory conditions correspond roughly to those under natural conditions. The consistency of observed events (i.e., synchronous moulting, size of larvae) seemed to indicate that natural cycles were occurring and therefore, the assumption appears reasonable.

Table 3. Development times for larval stages of *Ithycerus*.

STAGE	NO. OF DAYS 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
EGG - PUPA	225

Table 3 shows that the 7th instar was reached in a maximum of 179 days from eclosion (adding maximum no. of days in each stage). The majority of eggs hatched between July 23rd and Sept. 1st (Table 2). It was not known when the individuals identified as 7th instars eclosed during this 5 week period. I assumed that the time of eclosion of these individuals was ca. the middle of August. I also assumed that under natural conditions, feeding activity would end at the end of September in southwestern Ontario and resume again at the end of April. This would place the time to reach 7th instar around the end of August or early September the following year. The single pupa reared took ca. 225 days to develop (mid-August 1979 - March 24, 1980). The difference, then, between the 7th instar and the pupal stage was ca. 48 days. This is consistent with development times shown for the later instars in Table 3. Of the 4 wild larvae collected in late May 1978, 2 were identified as 7th instars. Furthermore, 2 teneral adults were collected about 1 week later.

The foregoing analysis, therefore, suggests that *Ithycerus* has a minimum of 7 instars; the second winter is spent as 7th instars; pupation occurs in May and June with emergence occurring in late May, all of June and at least part of July.

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 (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 shortest span for a male was 58 days. The longest surviving male lived for 81 days, and the average lifespan for 10 males was 70 days.

Flight Period

Adult *Ithycerus* are most abundant May through July, with a peak abundance in June. Emergence dates vary from north to south, as might be expected, with earlier times recorded farther south. The earliest dates of capture are April 10, Bethlehem, Pennsylvania; April 18, Arkansas; and April 26, Muncie, Indiana. The latest dates of capture are Sept. 4, Saugus, Massachusetts; Sept. 31, Indiana.

Predators and Parasites

There are nc recorded observations of predation of any life stages of *Ithycerus* except the probable destruction of eggs by the larvae of Tipulidae (Diptera) accidently introduced into rearing containers. Woodpeckers would be likely predators. I observed several species in Pinery Provincial Park knocking off loose scales of White Oak. This behaviour would expose adults hiding there.

The only recorded parasite of adults is a small tachinid fly, *Hyalomyodes weedii* Townsend, which has 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 a female collected on King Mountain, Old Chelsea, Quebec, Aug., 1971.

No egg or larval parasites are known.

Host Plants of *Ithycerus*

The genus *Ithycerus* has a relatively restricted host range in that they are regularly associated with species of three closely related families of woody plants, the Betulaceae (*Carpinus caroliniana* Walt., *Betula populifolia* Marsh.), Juglandaceae (*Juglans cinerea* L., *Carya cordiformis* (Wang.) K. Koch, *Carya ovata* (Mill.) K. Koch) and Fagaceae (*Fagus grandifolia* Ehrh., *Castanea dentata* (Marsh.) Borkh., *Quercus alba* L., *Q. macrocarpa* Michx., *Q. bicolor* Willd., *Q. coccinea* Muenchh., *Q. prinus* L. *Q. ellipsoides* E.J. Hill., *Q. borealis* Michx.). However, large numbers of adults are occasionally taken on introduced species of cultivated fruit trees such as 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, Washburn, 1902). Outbreaks have been recorded in South Carolina, Virginia, New York, Missouri and Minnesota. Because commercially grown fruit trees are fairly recent immigrants to this continent (ca. 200 years), this phenomena would have to be regarded as a secondary adaptation in feeding habits. It is interesting to note that collections from these trees are consistently earlier than for native hosts, with records in April and May. Collections from native hosts have generally been from June onwards. In spite of this, label data and my own collecting experiences indicate 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. Very few White Oaks were present in the Parkhill study area and equal numbers of adults were collected on American Beech and Bitternut Hickory. A few were also taken on Blue Beech (*Carpinus caroliniana* Walt.). This indicates that host preferences are affected by species composition and that White oak is not required to sustain populations of *Ithycerus*.

When comparing the distribution of *Ithycerus* with that of its host plants, it is interesting to note that all capture sites (except Ft. Coulonge, Que., and Chippewa County, Minnesota) lie within the range of White Oak. This is in spite of the fact that several host species occur outside this range (e.g. Bur Oak and American Beech). This may mean that the distribution of *Ithycerus* is limited by the same climatic conditions which limit White Oak.

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. 10-14). Washburn (1902) reports that leaves of plums are also eaten, and includes a photograph of adults clinging to partially skeletonized leaves. I tried to verify this on several occasions but without success. Having spent many hours watching *Ithycerus* feed, it is my opinion that they do not eat leaves.

Adult *Ithycerus* do not have a crop (Fig. 48) and the proventriculus consists only of eight rows of loosely aggregated setae (not illustrated). Consequently, all food material ingested is passed directly to the large midgut (Fig. 49).

Observations in the field and laboratory indicate that feeding does not occur when it is too hot or cold, and *Ithycerus* become inactive during these periods. 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 and phloem. The external bark is completely removed, exposing the inner 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 are formed from frass and exuvia mixed with soil. The change to new instars occurs at the end of tunnels, which are expanded. Occasionally, cells consisting of packed soil and exuvia were found away from the roots. The larvae of *Ithycerus* also lack 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 began sexual activity about 10 days after being placed in the rearing cages. Peak activity appeared to be reached after ca. 2 weeks.

There is no obvious courship 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 suggests 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 locating and mating with females.

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. On a number of occasions, I watched females trying to dislodge males by violently rocking from side to side, with little success. Once the long flagellum and transfer apparatus were in place, successful mating seemed assured.

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. 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. Using the 8th tergite and coxites, fecal matter was spread by drawing the tip of the abdomen back and forth over the egg. 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 (12 individuals observed).

Grooming in *Ithycerus*

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

The following cleaning movements were observed: (1) *Palpus Clean:* The palps appear to be chewed by the maxillae as described by Valentine (1973), 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.

Observations on grooming movements were as follows: (1) *Antenna Rub:* The ventral margins of the foretibia are rubbed along the dorsal surfaces of both antennae simultaneously. This was doen 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 tarsus of a hindleg were rubbed along the sides of the abdomen. (3) *Bilateral Foreleg Rub:* Two modes were recorded for this movement. The first and most common involved the rubbing of the tibia and tarsus of the forelegs below the head while the individual rested on a twig (Fig. 26). In the second mode, the tarsus and tibiae 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 tarsus 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 tarsus 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 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. This 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 tibia and tarsus 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 tarsus 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 tarsus were rubbed against the midtibia and tarsus on one side of the body while, at the same time, the tibia and tarsus 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.

Only four positioning movements (and their modes) were observed and include: (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.

Cleaning movements, except *palpus* and *foreleg clean*, appear to be absent in *Ithycerus*. This is probably due to the structure of the head and rostrum; 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.

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.

Table 4. Comparison of adult characters of three populations of *Ithycerus*. Pairs of 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	2.15	2.16	8.58	10.14	2.58	2.82	2.58	3.00	.84	.90	5	6
											(15)	(31)
MELANIC	2.16	2.58	9.60	11.60	3.00	3.24	3.00	3.36	1.01	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.

Distribution, Geographic Variation and Biogeography of *Ithycerus*

Figure 203 illustrates the known distribution of *Ithycerus*. In Canada, it is found in southern Ontario eastward through the St. Lawrence Valley to Montreal, Quebec. In the United States, it ranges from southern Minnesota to Arkansas and is recorded from all states east of the Mississippi River, except the state of Mississippi and southern Florida. In addition, I have not seen specimens from southeastern Texas or Louisiana. With the exception of southern Florida, *Ithycerus* probably occurs in all these areas because of the presence of its primary host, White Oak.

There are two distinct colour forms in three separate geographical regions (Fig. 203). A northern grey form exists in which there is low contrast between light and dark patches of pubescence. Two southern melanic forms (Ozarks, Southern Appalachians) were observed to have highly contrasted light and dark patches. The high contrast is produced by fewer yellow and a greater number of dark brown scales than are present in the northern grey form. The pubescence of the sourthern forms is also less dense than in the northern form and this exposes more of the dark exoskeleton, further enhancing the high contrast. Males of the Appalachian southern melanic form are consistently larger (Table 4) than the males of the other two forms. However, the Ozark southern melanic form differs from the grey form only in colour, and from the Appalachian form in having fewer yellow scales.

The geographic areas occupied by the two southern forms correspond to regions which are believed to have been refugia for organisms which survived the Pleistocene glacial periods. It is a situation very similar to the one described by Ross and Ricker (1971) in their study of the winter stonefly genus *Allocapnia*. Further collecting in areas connecting these regions is necessary to determine if there are populations which intergrade with these forms. If so, the differences noted are probably the result of environmental influences and do not reflect evolutionary divergence.

Morphology

Eggs of *Ithycerus*. Length 1.2 - 2.2 mm (Fig. 56) (10 specimens); $\bar{x}$ = 1.7 mm., subspherical, ca. 1.5 X longer than wide but variable; external surface of chorion formed of hexagonal facets with impressed borders (Figs. 57, 58); surface strongly punctate, with numerous aeropyles (Fig. 59). Eggs laid singly in soil, covered with fecal matter, pale yellow when first deposited, turning dark brown to black in one to two days.

Laying eggs singly has been observed in some species of broadnosed weevils such as *Otiorhynchus*, *Sitona* and *Alophus* (van Emden, 1950). The eggs of at least two species of *Otiorhynchus* darken with exposure to air as in *Ithycerus*. The eggs of *Barynotus* darken also, but are laid in batches (van Emden, 1950). The pigmentation may help conceal the eggs from predators and parasites. The habit of *Ithycerus* females covering eggs with fecal matter has not been reported in other species of Curculionoidea, although it has been observed in some Chrysomelidae (A. Howden, personal communication). This probably helps to further conceal the eggs and to protect against dessication.

I have not located 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.

First Instar Larvae of *Ithycerus* (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 ¼ 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., $\bar{x}$ = 2.8 mm; robust, strongly curved, cylindrical, dorsum strongly convex, sternum less strongly convex (Figs. 33, 61). Tuberclelike to spinelike asperites generally and rather densely distributed over entire body (Figs. 74-80, 82, 83); 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 (Fig. 33); width .60 - .72 mm., $\bar{x}$ = .68 mm., tapering posteriorly; margins only weakly converging toward mandibles from midpoint of head capsule (Fig. 34). Entire surface of epicranium without beaded microsculpture (Fig. 63). 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 (Figs. 34, 63). *Epicranial suture* about 3/4 as long as head capsule. *Endocarinal stuure* about 1/2 as long as anterior portion of frons; *endocarina* distinct, extending from posterior margin of head capsule to ca. the midpoint of the anterior portion of frons, broadest at posterior margin of head capsule. Setae of head capusle all rounded, never longitudinally ridged. *Antenna* completely enclosed by frontal area, supported by conspicuous frontal ridge; directed downwards toward mandible (Figs. 62, 66, 70); consists of membranous basal article (Figs. 65, 66), 1 large, subconical accessory appendage, ca. as wide as long, 1 large, elongate, bifurcate (rarely not, Fig. 67) accessory appendage, ca. as long as subconical appendage, 1 elongate, more or less sharply pointed seta, ca. 1/2 as long as bifurcate appendage, 3 shorter, blunt setae, and at least 2 obsolete setae (Fig. 67). *Frons* bears 5 pairs of setae and 2 pairs of sensilla (Figs. 34, 63); setae 1, 2, 3 long, 4 short, 5 long; upper sensilla of frons (Fig. 70) mesad between setae 1 and 3; lower sensilla between setae 3 and 4; diameter of lower sensilla ca. 2 X 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 pairs of setae and 3 pairs of sensilla (Figs. 34, 63), 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 pairs of long setae and 8 pairs 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* bears 2 pairs of setae and 3 pairs 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 pairs of minute setae and 2 pairs 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* ca. 4 X wider than long, bears 3 pairs of setae and 1 pair of sensilla (Figs. 34, 68); setae 3 short, 1/2 as long as setae 1 and 2; clypeal sensilla slightly anterior to clypeal setae 2. Tuberclelike asperities present on anterolateral corners. *Labrum* with 4 pairs of setae and a single basal sensillum (Figs. 68, 69) setae 1, 2 and 3 ca. equal length, moderately long; setae 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, ca. 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 ocrresponding to posterior margin of labrum. Tuberclelike asperities present on posterolateral corners of labrum. *Mandibles* large, somewhat elongated, triangular (Figs. 37, 62, 63), 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 on each. *Maxillary palpus* (Figs. 40, 72, 73) with 2 articles; apical article ca. 3/4 as long as basal article; bears 1 sensillum and 8 or 9 apical basiconic sensory papillae of equal length (Fig. 73) arranged in a circle around a shorter, wider central basiconic sensory papilla; free rodlike accessory process (Fig. 73) 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. *Labial palpus* (Figs. 41, 71) 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 ca. equal in length; spinelike asperities present on posterolateral corners of postmentum. *Glossa* (Fig. 41) bears 2 pairs of setae and 2 pairs of sensilla. THORAX - Narrows slightly towards head (Fig. 45); mesonotum and metanotum as wide as dorsum of abdominal segments 1, 11, wider than remaining abdominal segments (Figs. 74, 75). Dorsum of prothorax entirely covered by lightly pigmented, sclerotized *pronotal plate* bearing 9 pairs of setae and 2 pairs of sensilla (Figs. 45, 74); sensilla 1 mesad between pronotal setae 1 and 2; sensilla 2 laterad a short distance from pronotal seta 2 (only setae on one side of body described after Amhad and Burke, 1972), toward mid-dorsal line. *Lateral pronotal lobe* with 3 setae (Fig. 42). *Thoracic spiracle* intersegmental, between prothorax and mesothorax (Figs. 42, 50, 52, 54, 81) bicameral, with 11-13 annuli on each air tube; anterior air tube slightly longer than posterior air tube; anterior air tube averages 1.4 X longer than the diameter 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 of dense, short, flattened pointed asperities which are directed internally (Figs. 52, 54). *Predorsum* of meso and metathorax (Figs. 42, 45) bears 3 setae; seta 1 long, setae 2, 3 minute; *postdorsum* of meso and methathorax 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 metathorax 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. *Thoracic legs* present, 2-segmented (Figs. 44, 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 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 legs with conical, membranous projections at their apices which are bare of setae and lack sensilla. *Sternal areas* of thorax each bear 2 pairs 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 pairs of lateral, bicameral spiracles, each with 7-9 annuli on each air tube (Figs. 51, 53, 55, 78, 80); anterior air tubes 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 1-VIII each with 2 dorsal folds (Figs. 33, 43, 46, 75, 78); abdominal segments 1-IV each with an additional small fold, without setae, along the posterior of margin of the postdorsum, traversing the mod-dorsal line. *Dorsum* of segments 1-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 (Figs. 43, 78, 80). *Epipleura* of segments I-VIII each bear 3 setae; seta 1 short, setae 2, 3 long (Figs. 43, 80). *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* (Figs. 47, 76) 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. 82, 83), without setae; *lateral anal lobes* each bear 3 setae, seta 1 munute, 2, 3 short; ventral anal lobe without setae; inner surfaces of anal lobes bear numerous divided asperities having 2 or more spinelike projections (Figs. 82, 84) which grade into undivided asperities on the more exposed surfaces; anal slit transversely X-shaped; upper arms ca. 2 X longer than lower arms.

Larval Stages of *Ithycerus* Beyond First Instar

For the most part, the preceeding 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 very considerably due to inconcistencies 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 beween 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 intensity in each new larval instar, but there is apparently no measureable change in the extent to which specific structures are pigmented. The following larval features of later instars could be characterized and provided morphological criteria for separating instars. Seven larval instars are separated based on these features. Possible 8th and 9th and 10th instars were found but these moults may have been due to some nutritional deficiency. Additional rearings are needed to verify their existence.

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 air tube 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 air tubes 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 air tube 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 air tubes of spiracles .61 - .82 X as long as the width of the spiracular orifices, $\bar{x}$ = .72; spiracular orifices broadly elliptical; orifice ratio .85 - .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 air tube of spiracle .33 - .45 X as long as the width of the spiracular orifice, $\bar{x}$ = .40. ABDOMEN - Anterior air tubes of spiracles .42 - .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 air tube of thoracic spiracle .25 - .34 X as long as width of the spiracular orifice, $\bar{x}$ = .31. ABDOMEN - Anterior air tubes 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. HEAD - Width at widest point 3.3 - 3.8 mm., $\bar{x}$ = 3.5 mm. THORAX - Anterior air tube of spiracle .24 - .26 X as long as the width of the spiracular orifice, $\bar{x}$ = .25. ABDOMEN - Anterior air tubes 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 air tube of spiracular .17 - .23 X as long as the width of the spiracular orifice, $\bar{x}$ = .21 (Fig. 54). ABDOMEN - Anterior air tubes 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. If these were truly 8th instar, then, 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, possible tenth instar was identified but left undisturbed.

Pupa of *Ithycerus*

HEAD - (Fig. 89). *Vertex and frons* with a pair of very minute preorbital setae located medially between lower margin of eye cases and antennal insertions. Six pairs of supraorbital setae present; setae 1, 2, 3 ca. equal in length (as long as eye case), borne on tubercles; setae 4 very minute, located on upper posterior margins of eye cases, not borne on tubercles; setae 5, 6 minute, located posterior to setae 3; setae 1 ca. 2 X as thick near bases as setae 2 and approx. 1.5 X as thick as setae 3. One pair of postorbital setae present, ca. 1/2 as long as supraorbital setae. Frons with 1 pair of long frontal setae. *Rostrum* with 4 pairs of basirostral setae; setae 2, 3 as long as eye case; setae 1, 4 slightly longer than eye case, setae 4 ca. 2 X as thick as setae 3; all setae borne on tubercles. Genal setae absent. With 1 pair of distirostral setae, ca. 0.4 X as long as basirostral setae, borne on tubercles. One pair epistomal setae present, each seta as long as eye case. *Clypeus* bears 2 pairs of setae, each seta ca. as long as eye case. *Labrum* present, bears 5 pairs of setae; setae 1 ca. 1/2 as long as clypeal setae; setae 2, 3, 4, 5 minute; setae 4, 5 not borne on tubercles. *Mandible* bears 1 pair of very short, equal-size setae. Apical articles of *maxillary* and *labial palps* without setae or sensory papillae. Apex of *mala* bears 1 pair of rodlike setae. THORAX - (Fig. 92). All setae borne on tubercles except tarsal setae. *Pronotum* bears 2 pairs anteromedian setae; seta 1 minute, seta 2 short. Two pairs anterolateral setae; seta 1 minute, seta 2 moderately long. Bears 3 pair of posterior setae and 1 pair posterolateral setae, all moderately long. *Mesonotum* with 2 pairs of minute, predorsal setae. Four pairs of postdorsal setae present; setae 1 ca. 2 X longer than seta 4; setae 2, 3 ca. equal length, shorter than seta 4. Bears 2 pairs dorsolateral setae; seta 1 short, 1/2 as long as seta 2; seta 2 as long as PD seta 1. *Metanotum* with 2 pairs of predorsal setae; setae 1, 2 minute. Postdorsum with 4 pairs of long setae. Two pairs of dorsolateral setae present; seta 1 minute; seta 2 1/2 as long as PD seta 1. *Thoracic Legs* each with a pair of minute, sublateral setae, borne on apical tarsal segment (Fig. 86). *Elytra* with raised tubercles along intervals; the summits of the larger tubercles sclerotized and pigmented (Fig. 94). ABDOMEN - Figs. 86, 91, 92). Abdominal segments I-VIII with 2 dorsal folds, seg. IX apparently with only 1 fold. All dorsal setae borne on tubercles unless otherwise indicated. *Predorsum* (Abd. seg. I-VIII) with 2 pairs of setae. Seta 1 of abd. seg. I-VII minute: Seta 1 of abd. seg. VIII short. Seta 2 of abd. seg. I-VII very minute; Seta 2 of abd. seg. VIII almost indescernible. *Postdorsum* (abd. seg. I-VIII) with 4 pairs of setae. Setae 1, 3 of abd. seg. I-IV ca. 2 X longer than seta 2 of same,1/2 as long as setae 1, 3 of abd. seg. V. Seta 1, 3 of abd. seg. V ca. 3 X longer than setae 2, 4 of same, as long as setae 1, 3 of abd. seg. VI. Setae 1, 3 of abd. seg. VI, VII, VIII ca. 2 X longer than setae 2, 4 of same. Setae 1, 3 of abd. seg. VI slightly less than 1/2 as long as setae 1, 3 of abd. seg. VII. Setae 1, 3 of abd. seg. VII ca. as long as setae 1, 3 of abd. seg. VIII. Setae 1, 3 thicken progressively (measured at their bases) towards anus; setae 1, 3 of abd. seg. VI ca. 2 X thicker than setae 1, 3 of abd. seg. I but only 1/2 as thick as setae 1, 3 of abd. seg. VII. *Spiracular areas* of abd. seg. I-VIII each with 3 pairs of setae; seta 1 very long, seta 2 long, seta 3 minute. *Epipleurum* (Abd. seg. I-VII) with 3 setae; seta 1 longer than setae 2, 3. Abd. seg. VIII with 2 epipleural setae; seta 1 slightly longer than seta 2. *Pleural regions* of abd. seg. I-VIII each with 3 setae; seta 1 of abd. seg. I-VI ca. 5 X longer than seta 2; seta 1 of abd. seg. VII, VIII ca. 3 X longer than seta 2. *Sternal regions* of abd. seg. I-VII each with 1 pair of short sternal setae and 3 pairs of eusternal setae; eusternal setae 1, 2 minute, seta 3 very minute. Abd. seg. VIII bears 1 pair of short sternal setae; eusternal setae absent. *Predorsum* of *abd. seg. IX* bears 2 pairs of setae; seta 1 short, seta 2 minute. *Postdorsum* with 6 pairs of setae (setae 5, 6 probably homologous with spiracular setae of other segments). Setae 1, 2, 3 borne on sclerotized *posterior processes* (= pseudocerci of May, 1967). Setae 1, 4, 5 very long, 3 moderately long, 6 short. *Pleural region* (epipleurun + pleurum) bears 1 short seta. Sternal setae absent. Eusternal setae absent. *Anus* (Fig. 88) with a transverse slit. Dorsal and ventral lobes prominent; dorsal lobe ca. 2 X longer than ventral lobe; ventral lobe with 1 pair of minute setae.

Certain features of the pupa of *Ithycerus* are of great evolutionary interest. The most important of these is the presence of a distinct labrum, a structure not present in any of the "higher weevils" so far described. Mandibular setae are known only in the division of the Curculionidae known as the Adelognatha ('broadnosed weevils'). According to May (1967), these are associated with a 'deciduous cusp' which is present in most teneral adults of the 'broadnosed weevils'. I have examined only two teneral adults of *I. noveboracensis*. In these, the cusp was absent (lost burrowing to soil surface?). The important point is that the presence of the setae in *Ithycerus* would seem to indicate that the development of these cusps occurred early in the evolutionary development of the higher weevils (predating their development in the Adelognatha).

Other features which seem to attest to the primitiveness of *Ithycerus* are the larger numbers of setae found on pupal structures as compared with pupae of other "higher weevils".

First Instar Larva of *Arrhenodes minutus* (Drury). COLOUR - Body white; head, pronotal plate, 'shoulder patch' asperities, sternal plate, light yellow; anterior margin of frons, mandibular fossae, brown to dark brown; mandibles black; lower mouthparts, except premental sclerite, light yellow; premental sclerite, medium brown. BODY - Length 1.8 - 2.3 mm., $\bar{x}$ = 2.1 mm. (10 specimens), slender, elongate, moderately curved, cylindrical (Fig. 136). Abdominal segments VIII, IX swollen laterally (Fig. 136). Spinelike asperities (Fig. 129) 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. 128) and abdominal folds except sternum of abd. seg. I-VIII. HEAD - Free (Figs. 117, 136), width .39 - .46 mm., $\bar{x}$ = .41 mm., ca. 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. 140) 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* ca. 1/3 as long as head capsule. Setae of head capsule usually ridged longitudinally (Fig. 118). *Antenna* inset into frontal area (Figs. 117, 118); 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 sensilla (obsolete setae?). *Frons* large, ca. .7 X as long as wide (Figs. 116, 137), broadly triangular with anterior margins bent toward mandibles. Five pairs of frontal setae present; setae 1, 3, 4, 5 very long, setae 2 long; 2 pairs of sensilla present, sensilla 1 anterior to setae 1, sensilla 2 posterior to setae 3. *Dorsal epicranium* bears 5 pairs of setae (Fig. 137); setae 1 moderately long, 2, 3 long, 4, 5 very long; 3 pairs 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* bears 2 pairs of setae (Fig. 137); setae 1 short, setae 2 long; 2 pairs 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* bears four pairs of minute setae and 1 pair of sensilla (Fig. 137), posterior to setae 1. *Ventral epicranium* with 2 pairs of setae (Fig. 140); setae 1 very short, laterad of anterior corners of tentorial bar, setae 2 short, posterior to mandibular fossae; 3 pairs 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* ca. 3 X wider than long (Figs. 119, 120), anterior margin evenly arcuate, posterior margin fused to frons, frontoclypeal suture absent; bears 3 pairs of setae; setae 1 longer than setae 2 which are longer than setae 3; 1 pair of sensilla occur anterior to and mesad between setae 1, 2. *Labrum* as wide as long (Figs. 119, 120) with 3 pairs 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 (Figs. 119, 120, 121). *Epipharynx* bears

3 pairs of anterolateral setae, 4 anteromedian setae (Fig. 144); 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, a 3rd pair of sensilla occurs 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. 120, 145); bear 1 pair of equal length setae and 3 sensilla. *Maxillary palpus* (Figs. 141, 143) 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. *Labial palpus* (Fig. 142) 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; glossa bears 2 pairs of setae and 2 pairs 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 pairs of setae, setae 1 short, 2 long, 3 moderately long. THORAX - Slightly wider than abdomen (Fig. 136). *Pronotum* bears sclerotized plate with 6 pairs of setae and 2 pairs of sensilla, *lateral pronotal lobe* bears 1 pair of setae. *Thoracic spiracle* (Figs. 125, 138) bicameral, with 8-9 annuli on each air tube, 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, ca. equal in length, 3 spiracular setae, 1 short epipleural seta, and 1 moderately long pleural seta (Fig. 126); mesothorax bears triangular patches of interleafed, transversely flattened asperities on posterior margins of postdorsum (Figs. 122, 123). *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 (Fig. 126), 1 moderately long and 2 short. *Thoracic legs* present, short, 2-segmented (Fig. 127); 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 pairs of lateral, bicameral spiracles (Fig. 139), 4-5 annuli present on each air tube, anterior air tube longer than posterior. Segments I-VIII with 3 dorsal folds. *Egg bursters* present on spiracular areas of segments I-VIII, above spiracles. *Predorsum* of segments I-VII with 3 setae; segments VIII and IX bear 2 setae; seta 1 of segments I-VI short, 2, 3 minute; 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. 136). *Postdorsum* of segments I-IX with 4 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* of segments I-VI with 5 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. 131); seta 2 of segments II-VIII borne on egg burster (Fig. 130), 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. *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. 132, 133), 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 ventral longitudinal slit; internal surfaces of anal folds bear divided asperities (Fig. 135) which grade to undivided, spinelike asperities (Fig. 134) on more exposed areas.

Larvae of *Antliarrhinus* (as reconstructed from final instar larval skins).

BODY - Unable to ascertain size, shape from larval skin. Setae greatly reduced in length (visible only in compound microscope); chaetotaxy indeterminate from larval skins. Spinelike asperities generally but sparsely distributed over entire epidermis. Spiracles bicameral with annulated air tubes (Fig. 149); thoracic spiracles with 7-8 annulations per air tube; 7 pair of abdominal spiracles present, with 4-5 annulations per air tube, the air tubes very conspicuous (longer than the width of the spiracular orifice). *Thoracic legs* absent. Sclerotized *pronotal plate* absent. HEAD - Free, very small relative to body size (comparing surface area of head to that of larval skin) thinly sclerotized, unpigmented, except for mandibular fossae and mandibles. Entire epicranium lacks microsculpture. *Frontal sutures* meet articulating membrane of mandibles. *Ocelli* absent. *Endocarina* obsolete. *Epicranial setae* greatly reduced (Fig. 146), chaetotaxy indeterminate for the most part. *Ventral epicranium* (Fig. 148) with one pair of setae and one pair of sensilla. *Frons* forming an equilateral triangle (Fig. 147); bears 4 pairs of minute setae, 2 pairs of sensilla. *Antenna* consists of 1 elongate, blunt accessory appendage and 4-6 very minute setae (sensilla?); completely enclosed by frontal area (Fig. 147). *Clypeus* strongly divided (Fig. 147); bears 2 pairs of minute setae; sensilla absent. *Labrum* triangular; with 2 minute median setae (Fig. 147); labral sensilla absent. *Mandible* short triangular, strongly bidentate. *Epipharynx* bears 3 pairs equal length, anterolateral setae, 1 pair anteromedian setae, ca. 3/4 as long as anterolateral setae. One pair median setae present, ca. 2/3 as long as anterolateral setae, 1 pair epipharyngeal sensilla, located setae which are ca. as long as anterolateral setae (Fig. 154). *Labral rods* short, not extending beyond posterior margin of clypeus; somewhat triangular in shape, ca. 1/2 as wide as long at widest point (Fig. 154). *Hypopharyngeal bracon* thin, weakly sclerotized (Fig. 148). *Tentorial bar* weakly developed, thinly sclerotized. *Maxillary palpus* formed of a single article which bears an accessory appendage and a single sensillum (Fig. 153). Apex of article bears ca. 12 irregularly spaced sensory papillae. *Mala* with 5 ventral setae and 6 dorsal setae. *Stipes* bears 2 setae and 4 sensilla. *Labial palpus* formed of a single article which bears a single sensillum; apex of article with ca. 5 sensory papillae. *Glossa* (Fig. 152) bears 2 pairs of setae and 2 pairs of sensilla. *Prementum* with 2 pairs of setae; *premental sclerite* incomplete but with distinct lateral extensions. *Postmentum* bears 3 pairs of setae. ABDOMEN - Chaetotaxy uncertain but abdominal segments each with 2 dorsal folds.

PUPA - Pupal skins are available for study from the Canadian National Collection but these have not been examined. It is known that pupal ribbons are present.

Larval characters

Table 5 compares the main diagnostic features of the larvae of *Ithycerus*, *Arrhenodes* and *Antliarrhinus* and, therefore, serves as a brief summary of the preceeding descriptions. There are strong similarities shown between *Ithycerus* and *Arrhenodes* and these are discussed on page 37.

A few selected larval characters are discussed here in terms of their structure as related to function. Two striking features of *Ithycerus* larvae are the very large, heavily sclerotized head capsule and mandibles which are readily correlated with feeding habits. The head capsule houses a massive set of muscles which operate

Table 5. Comparison of diagnostic features of the larvae of *Ithycerus*, *Arrhenodes* and *Antliarrhinus*.

ITHYCERUS	ARRHENODES	ANTLIARRHINUS
Frontal sutures complete, meet articulating membrane of mandibles.	Frontal sutures complete, meet articulating membranes of mandibles.	Frontal sutures complete, meet articulating membranes of mandibles.
Endocarina distinct.	Endocarina distinct.	Endocarina not distinct.
Antenna supported by conspicuous frontal ridge.	Frontal ridge absent.	Frontal ridge absent.
Antenna bears 1 subconical accessory appendage, 1 elongate, bifurcate (usually) accessory appendage, 1 elongate, short seta, 3 very short, blunt seta, 2 obsolete seta.	Antennae bears 1 elongate subconical accessory appendage, 1 elongate, pointed, accessory appendage, 1 elongate, blunt seta. 2 obsolete setae.	Antenna bears 1 elongate blunt, accessory appendage, 4-6 minute setae.
3 ocelli.	Ocelli absent.	Ocelli absent.
Labrum with 4 pr. of setae single basal sensillum.	3 pr. of setae, 1 pr. setal pits, single basal sensillum.	1 pr. of setae, basal sensillum absent.
Labral rods extend beyond posterior margin of clypeus.	Labral rods do not extend beyond posterior margin of clypeus.	Labral rods do not extend beyond posterior margin of clypeus.
Epipharynx with 7 pr. anterolateral, 1 pr. submarginal lateral, 2 pr. anteromedian setae.	3 pr. anterolateral, 2 pr. anteromedian setae.	3 pr. anterolateral, 2 pr. anteromedian, 1 pr. median setae.
Mala with 17-18 dorsal seta arranged in evident row.	Mala with 18 dorsal setae arranged in evident row.	Mala with 6 dorsal seta.
Mandibles large, elongate-triangular, weakly bidentate at apices, 3 tooth-like processes at base of 1 pr. mandibular setae, 3 sensilla.	Mandibles large, short-triangular, bidentate at apices, 1 subapical tooth, each bears 1 pr. mandibular setae, 3 sensilla.	Mandibles small, short-triangular, strongly bidentate; each with 1 pr. of mandibular setae and at least one sensillum.
Thoracic spiracle intersegmental.	Thoracic spiracle intersegmental.	Indeterminate.
Abdomen with 8 pr. bicameral annulated spiracles.	Abdomen with 8 pr. bicameral, annulated spiracles.	Abdomen with 7 pr. bicameral spiracles.

the mandibles. The mandibles must be powerful in order to penetrate the tough outer layers of root bark to reach the nutrient high vascular cambium and phloem layers. 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 *Arrhenodes*. These larvae 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, sclerotized hypopharyngeal bracon.

The head capsules of *Antliarrhinus* larvae (Fig. 148) 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 relatively soft tissues inside cycad seeds. Many larvae of Curculionidae which feed on soft tissues such as those found in fruits, seeds and stems of many herbaceous plants appear to have similar reductions in the head capsules.

Another conspicuous feature of *Ithycerus* larvae is the presence of thoracic legs. These apparently serve no ambulatory function. They are well endowed with a stiff setae and numberous sensilla and therefore, probably have a sensory function. The legs of *Arrhenodes* are similarly developed though less conspicuous. Legs are absent in *Antliarrhinus* as they are in most other 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 *Arrhenodes* 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 larval tunnel completely and may present an armoured shield against the attacks of predators such as mites (early instars) or larger predators (e.g. Cleridae).

The inner surfaces of the anal folds of *Ithycerus* and *Arrhenodes* 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 are found on abdominal segments I-VIII on first instar larvae of *Arrhenodes*. 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 *Arrhenodes* 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 stridulation.

Family Antliarrhinidae *Stat. Nov.*

Adults (not illustrated except hind wing and nervous sys.) - BODY- Elongate, strongly dorsoventrally flattened in both sexes; glaborous, except for short, sparse setae generally distributed on body and along elytral intervals. HEAD - With single gular suture. Elongate-cylindric in females, elongate-squared in males, quite strongly constricted behind eyes in both sexes. Eyes round, prominent, laterally placed on head. Antenna geniculate, 12 segmented, with loose 4 segmented club; received near base of rostrum in females, at apical 1/3 in males. Rostrum 2 X as long as body in females (including head and thorax), 1/3 as long as body in males. Rostrum grooved to receive antennal scape in males, groove not apparent in females. Mandibles tridentate (as in *Apion*), move horizontally in males, vertically in females. Palpi rigid. Maxillary palpus consists of 2 articles. Labial palpus with single article. Postmentum shorter than prementum in both sexes (see Ting, 1936, for illustrations of mandible and discussion of mentum). THORAX - Pronotum more or less round, flattened. Prosternum with median triangular process along anterior margin; base of triangle raised above its apex and extends beyond anterior margin of prosternum; points where sides intersect with base of triangle rounded, nipplelike. Procoxae round, prominent, bases nearly contiguous. Mesosternum grooved laterally to receive femora of midlegs; grooves turn inward at but do not extend beyond inner margins of meta coxae. Mesocoxae round, prominent, separated by a distance ca. equal to width of single coxa. Metasternum is sloped along lateral margins, allowing hind femora to be pulled tightly into the body. Metacoxae round, prominent, separated by a distance ca. equal to 1.5 X the width of a single coxa. Femora of all thoracic legs strongly dilated, laterally compressed in males, not as pronounced in females; each with a broadly flattened median tooth on ventral margin; basal half of ventral margins of fore and midlegs of males with a row of soft, very close-set setae (femoral brush), femoral brush absent in females. Tarsal formula apparently 4-4-4; all tarsal segments with pads beneath; tarsal claws without pectination, not fused at their bases. Hind wing with distinct jugal lobe; R-s and median veins absent; radial cell round, very small; three anal veins present (Fig. 199). ABDOMEN - Five visible sternites; 1st and 2nd solidly fused, remaining three more or less freely articulated. First and 2nd sternites ca. 2 X as long as 3rd and 4th. Female pygidium without median sulcus. DIGESTIVE TRACT - Proventriculus absent (further details uncertain due to lack of fresh specimens). REPRODUCTIVE SYSTEMS - Females with 3 ovarioles per ovary, accessory gland present. Ovipositor as long as abdomen, sclerotized. Spermatheca 'C' shaped, with spherical 'head' (as in *Ithycerus*, Fig. 111). Transfer apparatus present in males, consists of pair of elongate 'comma' shaped sclerites. Cap piece of tegmen with elongate lateral lobes; apices of lobes setaceous. Tegminal strut long, broadly separated for more than 1/2 its length thus forming a 'y' shaped structure with long lateral arms connecting to basal piece of tegmen (in comparison, tegminal strut *Ithycerus* is long with short lateral arms connecting to basal piece). NERVOUS SYSTEM - Paired lobes of cerebrum directed anteriorly (Fig. 183). Subeosophageal ganglion situated very near cerebrum, separated from thoracic ganglia by long connectives. Two abdominal ganglia present, separated from thoracic ganglia and each other by long connectives.

Reproductive Systems of *Ithycerus*

Male Reproductive System - A pair of small, bilobed testes (Fig. 86); each lobe scalloped around edges and divided by septa into ca. 16 testicular follicles; when freshly removed, lobes 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. *External Genitalia* - Anterior portion of aedeagus consists of pair of broad median struts (Figs. 95, 96, 98) which fuse broadly posteriorly; a heavily sclerotized median apodeme-like extension runs posteriorly from bases of median struts to but not joining median lobe (Figs. 96, 98); two smaller, heavily sclerotized extensions project posteriorly from basolateral corners of median struts to 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. 96); basal piece of ring bears tegminal strut which projects anteriorly below apices of median struts of aedeagus. Ninth sternite (spiculum gastrale) consists of long, cylindrical apodeme which diverges posteriorly into two short rodlike extensions (Fig. 97); tips of extensions with thinly sclerotized projections for the attachment of membrane connecting ninth sternite to ninth tergite; ninth tergite (Figs. 104, 105) 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. 99, 101, 102, 103) consisting of two C-shaped, slotted sclerites; forms very long flagellum (Fig. 100); everted internal sac bears two sclerites, one dorsally and one ventrally, which may represent tenth tergite and sternite (Figs. 99, 100, 101); ventral sclerite small, with short posterior apodeme and two lateral lobes; dorsal sclerite large, with short posterior apodeme and two long, lateral lobes which curve inward posteriorly. Female Reproductive System - Ovaries paired, each with two ovarioles (Figs. 106, 107); terminal filaments unite to form suspensory ligaments which unite anteriorly aboe alimentary canal; ovariole pairs open into lateral oviducts; lateral oviducts converge posteriorly to form common oviduct. *External Genitalia* - Spiculum gastrale (Fig. 108) spatulate with truncated posterior margin; bears anterior apodeme which is ca. equal in length to posterior portion; with numerous minute ventral setae on posterolateral corners; tow larger setae arise medially just below posterior margin; median field circular, thinly sclerotized, transparent. Spermatnecal duct and gland each have separate insertion on globular 'head' of C-shaped spermatheca. 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.

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.

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

LARVAE - The ventral nervous system consists of suboesophageal ganglion, three thoracic ganglia and eight abdominal ganglia; seventh and eighth abdominal ganglia solidly fused (Fig. 175); abdominal ganglia extend posteriorly to anterior margin of eighth stermun; 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 from body which is ca. 2 X larger than abd. ganglia I-VI which are of equal size; thoracic ganglion 1 very large, elongated, separated from thoracic ganglion II by thick connectives a distance ca. equal to length of thoracic ganglion II; thoracic ganglion II ca. 1.5 X larger than thoracic ganglion III; separated from thoracic ganglion III by short, thick connectives; thoracic ganglion III ca. same size as abd. ganglion I; suboesophageal ganglion ca. 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. 181) 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 (true fifth, sixth, seventh and eighth); second and third abd. ganglia lie above third visible sternite; first abd. ganglion (= true abd. ganglion III equidistant from thoracic ganglion III (= thoracic ganglion III and true 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 four-sided, with three thick nerve branches arising from lateral margins on each side; first and second branches extend anterolaterally into thoracic cavity, third branch directed posterolaterally; thoracic ganglion I separated from thoracic ganglion II by very thick connectives a distance ca. 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 ca. 2 X as long as connectives between suboesophageal ganglion and thoracic gangion 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.

Classification of the "Higher Weevils"

In this context, the "higher weevils" include all species (adults) which have the 1st and 2nd visible sternites fused, the 3rd, 4th, and 5th remaining more or less freely articulated. This is the 'curculionid type' abdomen of Morimoto (1962). The genera *Ithycerus* and *Antliarrhinus* and the families Brenthidae, Apionidae and Curculionidae all possess such an abdomen as do Cyladinae, Platypodidae and Scolytidae (the latter 3 groups are not dealt with in this study).

I have chosen to take a conservative approach to the application of family names. This approach falls intermediate between those who would lump all the "higher weevils" in a single family (i.e. Curculionidae) and those who would prefer further splitting. I maintain separate family status for *Ithycerus* as proposed by Morimoto (1976) and elevate *Antliarrhinus* to the rank of family, as discussed below.

Crowson (1955) and Morimoto (1962) showed affinities between *Ithycerus* and Brenthidae based upon adult characteristics (Table 6). However, Morimoto (1976) separated *Ithycerus* from Brenthidae, raised it to the rank of a family (Ithyceridae) and placed it near Belidae (Table 6). He based this primarily on the structure of the abdominal sternum, which he described as 'anthribid type' (all sternites similarly inflected except 4th and 5th visible sternites which are deeply inflected). His observations were incorrect as it is clearly a 'curculionid type' abdomen as stated above.

It is not necessary to analyze character by character the differences between the larva of *Ithycerus* and those of Belidae (Figs. 156-168). The illustrations, my observations, and those of Vanin (1976) should be sufficient to show that no relationship exists between the two families as postulated by some authors (Leng, 1920, 1933; Ting, 1936; Bruhn, 1947; Morimoto, 1976). In fact, the unique combination of larval characteristics (Table 5) and the generalized nature of the pupa set *Ithycerus* apart from all known immature forms of Curculionioidea. Therefore, while I support the view that *Ithycerus* should be maintained in its own family, I do so on new evidence and place it among the "higher weevils".

Table 6. 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 (this paper)	Ithyceridae, near Brenthidae

The genus *Antliarrhinus* deserves similar treatment. Its relict distribution (South Africa), apparently primitive biology (develops in seeds of Cycads) and unique combination of primitive and highly specialized morphological characteristics (larvae and adults) are all viewed as evidence in support of elevating the genus to the rank of family, Antliarrhinidae *stat. nov.* within the higher weevils (see Phylogeny, pg. 37 and Fig. 203).

Phylogeny

The principles and methods of reconstruction of a phylogenetic system have been dealt with in detail by Hennig (1979) and Ross (1974). Relationships are inferred for Ithyceridae, Brenthidae, Antliarrhinidae *stat. nov.*, Apionidae, and Curculionidae (excl. Platypodidae and Scolytidae), based upon the determination of ancestral and derived states of adult and larval characters (emphasis is on the latter). This was done by ex-group comparisons with other Curculionoidea and, occasionally, other Coleoptera, and the identification of group trends. Ancestral states are inferred by assigning polarity to such trends.

A cladistic approach (relationships based upon extant groups) is used because of the meagre fossil record of the Curculionoidea and this creates several problems (not unique to weevil phylogeny). Convergence and/or parallelism are major problems, especially, when these become masked by the extinction of taxa with the resultant loss of character states (probably very common in taxa of high taxonomic rank, e.g. families). However, these adaptive events can usually be identified. Good examples of parallelism in the "higher weevils" are the reduction in the number of articles of the maxillary and labial palpi, and antennae of larvae. A more serious problem is that of 'reversal' where certain characters seemingly return to the 'ancestral' state with the result that polarity can be assigned erroneously. In reality, I believe that evolution cannot be reversed. The so-called 'reversals' are simply a special case of apomorphy; the 'ancestral' state arose from a pre-existing state and is, therefore, derived, by definition. A possible example of a 'reversal' in Curculionoidea is an increase in size resulting in the secondary elongation of connectives between the ganglia of the ventral nervous system (see pg. 39 for further discussion). Crowson (personal communication) feels that an increase in size could also lead to the reacquisition of veins in the hind wings to reproduce the ancestral state and cited *Ithycerus* (Figs. 194-197) as an example (see pg. 37).

For further discussion concerning the advantages and shortcomings of a cladistic approach see Cracraft and Eldredge (1979) and Van Valen (1978).

Once monophyletic taxa have been identified and ancestral and derived character states inferred, the next step is to express relationships between taxa in the form of 'sister-groups' (groups having a commonly shared derived state) (Hennig 1979). This step could not be strictly applied to the families studied here because of the apparent lack of such shared derived states. The best examples are the incomplete frontal sutures of larval Curculionidae (found in all known species) and the 'curculionid type' abdomen possed by all known species of "higher weevils". The latter feature is the strongest evidence for the monophyletic nature of the five families.

With these things in mind, a phylogenetic classification (Fig. 204) is postulated along with several alternative schemes (Figs. 205-208). The cladograms do not have a time base and therefore, the positions of the branching points only indicate the degree of relatedness. A summary of ancestral and derived states of selected characters is given in Table 7. Derived states of a particular character are identified by one or more superscript marks ('); thus, 2" indicates the second derived state of character 2 listed in the table.

Table 7. Comparison of selected larval and adult characters in the families Ithyceridae, Brenthidae, Antliarrhinidae, Apionidae and Curculionidae.

	CHARACTER STATES	
CHARACTER	ANCESTRAL	DERIVED
LARVAE		
Food Habits	Associated with woody plants mainly (1)	Associated with herbaceous plants mainly (1')
No. of Dorsal Folds on Abd. 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"), 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(9'), 2(9")
No. of Sensilla on Labrum	2(basal) (10)	1A(10'), 0A(10") 4(10"'), 3(10""), 2(10""') 1B(10"""), 0B(10"""')
No. of Sensilla on Clypeus	2(11)	0(11')

Cont'd.

Table 7 cont'd.

CHARACTER	CHARACTER STATES ANCESTRAL	DERIVED
No. of Setae on Clypeus	3 pairs (12)	2 pairs (12') 1 pair (12") 0 pair (12'")
Anterior Margin of Clypeus	Not divided (13)	Weakly to strongly divided (13')
Labral Rods	Present (14)	Absent (14')
Labral Rods	Long, extending beyond posterior margin of clypeus (15)	Short, not extending beyond posterior margin of clypeus (15')
Pairs of Setae on Frons	5 pairs (16)	Less than 5 pairs (16')
Pronotal Plate	Present (17)	Absent (17')
Frontal Sutures	Complete (18)	Incomplete (18')
Setae of Head	Epicranial setae long, conspicuous (19)	Epicranial setae somewhat to very reduced in length (19')
Postdorsum (Abd.)	Bearing 6 pairs of setae (20)	Bearing less than 6 pairs (20')
Ventral Nervous System	Abd. ganglia separated by distinct connectives, ganglia elongate (21)	Abd. ganglia not separated, connectives greatly reduced, ganglia moniliform (21')
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. Sys.	Present (25)	Absent (25')
Gular Sutures	Single (26)	
Cerebrum	Paired lobes transverse (27)	Paired lobes folded anteriorly, narrowly fused (27') Paired lobes folded anteriorly, broadly fused (27")
Ventral Nervous System	3 abd. ganglia, separated by long connectives (28)	2 abd. ganglia, separated by long connectives (28') Fusion of abd. ganglia to each other and thor. gang. (28") Ganglia separated by long connectives due to secondar elongation of abd. (28"')

Table 7 cont'd.

CHARACTER	CHARACTER STATES ANCESTRAL	DERIVED
Hind Wings	4 anal veins (29)	3 anal veins (29') 2 anal veins (29") 1 anal vein (29"')
Hind Wings	Median vein present (30)	Median vein absent (30')
Hind Wings	R-s vein present (31)	R-s vein absent (31')
Hind Wings	Radial cell large, triangular (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') 1 segmented (34") 0 segmented (34'")
Maxillary Palps	3 segmented (35)	2 segmented (35')
Maxillary Palps	Move horizontally (36)	Move vertically (36')
Abdominal Sternites	'Anthribid type' (37)	'Curculionid type' (37)

Ancestral states for Ithyceridae, Brenthidae, Antliarrhinidae, Apionidae and Curculionidae are postulated as follows:

LARVAE

Food habits - This was indirectly assessed. Weevil groups which are viewed as primitive on the basis of morphological features are, for the most part, associated with woody plants while more derived groups are usually associated with 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 - Not common among the Curculionoidea, these are deemed ancestral on the basis of ex-group comparisons with other families of Coleoptera.
Antennal Frontal Ridge - Not common among Curculionoidea, but believed to be ancestral on the basis of ex-group comparison with other families of Coleoptera.
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 - Two articles common in "higher weevils" with a trend to reduction. Therefore, less than 2 are considered derived, by ex-group comparison.
Number of Articles of Labial Palpus - Two articles occur most frequently and are deemed ancestral as determined by ex-group comparison.
Pairs of Setae on Labrum - Ex-group comparison with other families of Curculionoidea indicates a trend toward loss of pairs. Four pairs are deemed ancestral.
Number of Sensilla on Labrum - The presence of 1 pair of basal sensilla plus 4 pairs of labral setae is considered ancestral by ex-group comparison.
Clypeus - Two pairs of sensilla most commonly seen and are considered ancestral. Three pairs of setae commonly shared and are deemed ancestral. Ex-group comparisons indicate that an undivided clypeus is the ancestral state.

Labral Rods - Present in most Curculionoidea. Their presence is considered ancestral. Labral rods which extend beyond posterior margin of clypeus are believed to represent the ancestral condition, with a trend to reduction in length.
Frons - Five pairs of setae are ancestral with trend to reduction in number, as determined by ex-group comparison.
Pronotal Plate - Ex-group comparisons indicate that presence of a 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 except Curculionidae. This condition is considered ancestral.
Head Capsule - Ex-group comparisons indicate that conspicuous epicranial setae are ancestral, with trend to reduction in length.
Postdorsum (abdomen) - The presence of 6 pairs of setae is thought to be ancestral, with a trend to loss in number, as determined by ex-group comparison.
Ventral Nervous System - Long connectives between ganglia with ganglia longer than wide are determined to be ancestral by ex-group comparison. This may be complicated in a few instances by secondary elongation of the abdomen.
Egg Bursters - Determined to be ancestral, if present, by ex-group comparisons.

ADULTS

Antenna - Straight antennae of *Ithycerus* are considered ancestral. However, the presence of both straight and geniculate antennae in Brenthidae, Apionidae and Curculionidae and geniculate antennae in Antiarrhinidae suggests the possibility that reaquisition of straight antennae could have occurred in some instances.
Ovarioles - Ex-group comparisons indicate trend in loss of ovarioles. Three ovarioles are considered ancestral, by ex-group comparison.
Accessory Glands - Most Curculionoidea lack accessory glands in the reproductive systems of females, yet it is believed that their presence may be ancestral, 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 five families is derived with respect to those families possessing two gular sutures, ie., Belidae and its relatives but ancestral to the "higher weevils".
Cerebrum - Paired lobes of cerebrum transverse are ancestral, as determined by ex-group comparison.
Ventral Nervous System - All ganglia except second and third thoracic ganglia isolated by distinct connectives are ancestral, as determined by ex-group comparison. The 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, as determined by ex-group comparison.
Hind Wings - Presence of large, triangular radial cell is ancestral, as determined by ex-group comparison.
Hind Wings - Presence of well-developed jugal lobe is ancestral, as determined by ex-group comparison.
Labial Palps - Ex-group comparison indicates trend toward reduction. Presence of 3 articles is believed to be ancestral.
Maxillary Palps - Palps which move in horizontal plane are considered to be ancestral as determined by ex-group comparison. Three-segmented palps are ancestral with a trend to reduction in number.
Abdominal Sternites - The 'curculionid type' abdomen possessed by all known "higher weevils" is a shared derived feature as determined by ex-group comparison.

From the character states deemed to be derived on the basis of group trends and ex-group comparisons, the relationships of the five families studied are characterized as follows:

ITHYCERIDAE - This family appears to resemble most closely hypothetical ancestor A (Fig. 204) in possessing many ancestral characteristics and few derived ones. It is a relict group, occurring only in eastern North America.

The larvae possess 2-segmented legs as do the majority of the Brenthidae. These are considered to be ancestral and therefore, cannot be used in this context to establish a relationship. The chaetotaxy of most of the larval structures of both families are identical, particularily the epicranium and maxilla. The characteristics of these structures again only provide evidence for the primitive nature of the two families. It is in the larval labrum that we seem to find a truly shared, derived character. Larval *Ithycerus* and the more primitive members of the Brenthidae possess 4 pairs of labral setae and a single basal sensillum. This state is believed to be derived from an attelaboid ancestor having 4 pairs of labral setae and 2 basal sensilla, *via* the fusion of the sensilla.

The venation of the hind wing of *Ithycerus* (Figs. 194-197) is very attelabid-like (Figs. 192, 193). This and the large number of ancestral features are the reasons for placing Ithyceridae between Attelabidae and Brenthidae as the most primitive extant member of the "higher weevils".

BRENTHIDAE - The chaeototaxy 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 identical 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 venation (Fig. 198), particularly the shape of the radius, is the same type as in Antliarrhinidae (Fig. 199) and Apionidae (Fig. 200). The shape of the larval labral rods and chaeototaxy 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 (ca. 12) and arrangement of the basiconic sensory papillae of the maxillary palpi (not illustrated) of the larvae. For these reasons, Brenthidae is placed between Ithyceridae and the families Antliarrhinidae and Apionidae and shares a common ancestor with the latter two (Box C, Fig. 204).

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. 146-155) 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 of Apionidae.

The possession of an accessory gland in the female reproductive system, three ovarioles per ovary, association with cycads, and relict distribution are evidence of primitiveness 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 (Fig. 204).

An alternative arrangement (Fig. 205) 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 Antliarrhinidae are the result of convergent evolution. I believe that the lossess which resulted in two ovarioles per ovary occurred independently in Ithyceridae, Brenthidae, Apionidae and Curculionidae.

APIONIDAE - This family is believed to be very closely related to the Antliarrhinidae and indeed a strong argument could be made to place them together in the same family.

If this were done, it would probably be necessary to include the Brenthidae as well.

CURCULIONIDAE (excluding Scolytidae and Platypodidae) - Chaetotaxy of the larvae is very similar to that of Ithyceridae and Brenthidae; differences are primarily the result of reduction in numbers of setae. Perhaps the most fundamental difference between this family and the other 4 is in the frontal sutures of the larvae. In all species known, the sutures do not meet the articulating membrane of the mandibles. A traditional feature used to characterize this family is the presence of geniculate antennae in the adults of the vast majority of species. However, geniculate antennae are also found in Antliarrhinidae and some Apionidae. Though not included in the phylogenetic schemes presented, the tegmen of male Curculionidae is rarely bilobed in the majority of species, or, if present, the lobes are weakly developed. The tegmen of male Ithyceridae, Brenthidae, Antliarrhinidae, and Apionidae is distinctly bilobed. The venation in the hind wings of Curculionidae (Figs. 201, 202) show reduction from the ancestral attelabid-type.

In summary, the 5 families discussed are considered a monophyletic unit among the Curculionoidea. The most fundamental feature shared by all members of these families is the possession of the 'curculionid-type' abdomen of Morimoto (1962). Through *Ithycerus*, they are thought to be linked to the more primitive families by way of an attelabid-like ancestor possessing a single gular suture. It is possible that the phylogenetic schemes presented are somewhat artifical and therefore do not reflect the true nature of the relationships between the 5 families discussed. Alternative phylogenies are presented in Figs. 206-208 and reflect differences of opinion as to the positioning of the families Antliarrhindae and Curculionidae.

Ventral Nervous Systems and Phylogeny

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. The ancestral state of larval ventral nervous systems may have resembled that of *Listronotus* (Fig. 178). There are eight distinct abdominal ganglia, three distinct thoracic ganglia, suboesophageal ganglia and the cerebrum, all of which are separated by conspicuous connectives. Figs. 169 and 170 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 *Otiorhynchus* is probably a highly derived state (Fig. 177).

The values of these systems as phylogenetic indicators is incompletely known, 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. 179, 181, 182). 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 directed anteriorly yet remain essentially separate. A highly derived state is postulated for *Attelabus* (Fig. 180) and *Magdalis* (Fig. 188) in which there is extensive fusion of the anteriorly directed lobes.

Long connectives between the ganglia (Figs. 179, 181, 182) 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. 180 and 188 . However, long connectives are observed in nervous systems having anteriorly directed cerebral lobes. Such a condition is found in *Aglycyderes* and *Antliarrhinus*. 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*.

As with larvae, the value of adult nervous systems as phylogenetic indicators has yet to be proven. Again, 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 larval labral sensilla (Fig. 209). It is based on my own observations and on descriptions in the literature. I have invoked loss, migration and fusion to account for the various patterns observed. I am not advocating any particular phylogeny; the taxa named are used as examples only. However, it turns out that relationships at the family level are broadly defined by this scheme.

A hypothetical ancestor is postulated having 5 pairs of primary setae (the actual number maybe 6, this possibility will be discussed later). Loss of one or more pairs of these primary setae is thought to have resulted in the formation of sensilla (W.H. Anderson, personal communication). Specifically, the loss of 1 pair of primary setae is believed to have produced the pattern observed in Nemonychidae, Anthribidae, Oxycorynidae, Aglycyderidae and Attelabidae (Fig. 209,B). The result was the formation of a pair of basal sensilla. Fusion of this pair is believed to have produced the state observed in Ithyceridae, Brenthidae and some Apionidae (eg. *Nanophyes)* (Fig. 209,1). The next step in this sequence is the loss of this basal sensillum in some Apionidae and Antliarrhinidae (Fig. 209,J). Loss of a 2nd pair of primary setae is thought to have resulted in a labrum possessing 3 pairs of primary setae and 2 pairs of sensilla (Fig. 209,D), (eg. *Sphenophorus)*. A similar but independent event may have resulted in the formation of the belid labrum (Fig. 209,C). The patterns E, F, G, H are probably derived from D through loss and fusion of sensilla but with the maintenance of 3 pairs of primary setae.

Evidence for 6 pairs of primary setae is found in Belidae. The larval labrum (Fig. 159) bears 3 pairs of primary setae and 2 pairs of sensilla on the posterior region where 3 pairs of primary setae and a single pair of sensilla are present in the Nemonychidae and its allies. The anterior region of the belid labrum bears numerous pairs of (secondary?) setae where the 4th primary pair is located in Nemonychidae and its allies. These setae are virtually identical in structure and have identical insertions. It could be that a primary pair of setae is concealed here. It is therefore possible that Belidae have 4 pairs of primary setae and 2 pairs of sensilla. This implies that the larval ancestor had 6 pairs of primary setae. If so, the pattern observed in Nemonychidae and its allies can be interpreted as having been formed by the loss of a pair of sensilla. The question is whether or not Belidae should be placed in the pivotol position from which all other patterns are derived or as an end point of an independent evolutionary sequence as shown in Fig. 209. This may be answered when more belid larvae are found and described.

SUMMARY

(1) Methods are described for the collection and rearing of immature stages and adults of *Ithycerus*.

(2) Oviposition by *Ithycerus* occurs in the soil, presumably near host trees and larval development occurs on roots of host trees. Eggs are always covered with fecal matter.
(3) There is at least a two year life cycle for *Ithycerus* and there is probably no overwintering in the adult stage.
(4) Three closely related families of woody plants, Betulaceae, Juglandaceae and Fagacea, serve as primary hosts for *Ithycerus*. There is a preference for species of Fagaceae but large numbers of adults are occasionally reported on introduced species of fruit trees (Rosaceae) in early spring.
(5) Grooming behaviour in *Ithycerus* is described and several modes new for Coleoptera are reported.
(6) Evidence is presented for the presence of 3 geographic races of *Ithycerus;* a northern grey form, an Ozark melanic form, and a southern Appalachian melanic form.
(7) The eggs, larvae and pupa of *Ithycerus* are described. There appear to be at least 7 instars.
(8) The first instar larva of *Arrhenodes minutus* (Drury), (Brenthidae), and the final instar larva of *Antliarrhinus* sp. are described for the first time and compared with *Ithycerus*.
(9) The family Ithyceridae is maintained, based on studies of the immature stages.
(10) The genus *Antliarrhinus* is given family ranking (Antliarrhinidae *stat. nov.).*
(11) Adult and larval internal systems of *Ithycerus* are described and include reproductive systems and external genitalia, digestive tracts, and ventral nervous systems.
(12) A phylogenetic classification is presented for the families Ithyceridae, Brenthidae, Antliarrhinidae *stat. nov.,* Apionidae, and Curculionidae. Ithyceridae appears to be the most primitive of these families and is most closely related to Brenthidae.
(13) The five families studied all possess a 'curculionid type' abdomen and are therefore believed to constitute a monophyletic unit among the Curculionoidea.
(14) Ventral nervous systems are discussed in regard to their possible value as phylogenetic indicators. Systems with the paired lobes of the cerebrum transverse and ganglia (except 2nd and 3rd thoracic) separated by long connectives are considered primitive.
(15) An evolutionary sequence is postulated for the numbers of larval labral setae and sensilla. The hypothetical ancestor may have possessed 5 or 6 pairs of primary setae and no sensilla.

ACKNOWLEDGEMENTS

I extend my most sincere appreciation to Dr. Richard Freitag, Lakehead University, for his financial support of this project (National Science and Engineering Research Council Grant) and for sharing his knowledge of evolutionary matters. I thank Mrs. Anne Howden, Ottawa, Ontario for convincing me to do this study; her cautious approach to weevil studies helped me to avoid serious pitfalls. I am grateful to Professor R. A. Crowson, Glasgow University, United Kingdom for taking the time to answer my many letters and generously sharing his tremendous knowledge of relationships among the Coleoptera. I am particularly indebted to the Ausable-Bay field Conservation Authority for permission to conduct field studies in the Parkhill Conservation area in 1978 and 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, 1979. Special thanks go to Dr. Donald Whitehead and Dr. Don Anderson, U.S.N.M., Dr. Horace Burke, Texas A & M, Dr. Wayne Clark, Auburn University , for reviewing earlier drafts of this study and to Dr. W. H. Anderson, Snowhill, Maryland for his encouragement and suggestions.
In conclusion, I thank Judy Grenville, McMaster University, for her careful preparation of the final draft of this study.

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ABBREVIATIONS USED IN ILLUSTRATIONS

Larvae and Pupae - accessory appendage = ac ap, anterolateral setae - als, anteromedian setae = ams, anus = An, annulation = Anu, anal setae = Ans, antenna = ant, antennal setae = ants, alar setae = As, asperities = asp, air tube = AT, basirostral setae = baR, basal sensillum = bsl, clypeus = Cl, clypeal setae = Cls, clypeal sensilla = Clsl, cervical membrane = Cv, dorsal cervical setae ' Cvsd, lateral cervical setae = Cvsl, coxal setae = Cxs, dorsal epicranial setae = des, dorsal epicranial sensilla = desl, dorsal setae of maxilla = ds Ma, endcarinal suture = Enc, epipleural setae = Epls, epistomal setae = Epst, epicranical suture = ES, epipharyngeal sensilla = esl, eusternal setae = eus, femoral setae = Fms, frons = Fr, frontal setae = Fs, frontal sensilla = Fsl, glossal setae = Gls, glossal sensilla = Glsl, hypopharyngeal bracon = Hb, lateral epicranial setae = les, lateral epicranial sensilla = lesl, labral setae = Lbs, labral rods = LmR, lateral pronotal setae = lPrs, lateral mesonotal setae = ltMs, lateral metanotal setae = ltmt, lateral tergal setae = ltT, malar setae = Mas, mandibular setae = Ms, mandibular sensilla = Msl, mesothoracic leg = Mstl, metathoracic leg = Mttl, maxillary palpus = Mxp, Maxillary sensillum = Mxsl, ocellus = Oc, occipital foramen = OcF, orifice = Or, postdorsum = PD, postdorsal setae = PDs, pedal setae = Pds, posterior epicranial setae = pes, posterior epicranial sensilla = pesl, posterolateral pronotal setae = plP, pleural setae = Pls, postmentum = PM, postmental setae = PMs, posteromedian pronotal setae = pmP, postorbital setae = pO, posterior processes = PP, pronotum = Pr, predorsum = PrD, predorsal setae = PrDs, prementum = PrM, premental setae = PrMs, premental sensilla = PrMsl, preorbital setae = pr), pronotal setae = Prs, pronotal sensilla = Prsl, peritreme = Prt, prothoracic leg = Ptl, Submarginal lateral setae = Smls, supraorbital setae = sO, spiracle = Sp, spiracular setae = Sps, sternum = ST, sternal setae = STS, stipal setae = Sts, stipal sensilla = Stsl, tarsal setae = Ta, tentorial bar = TB, thorax = TH, ventral epicranial setae = ves, ventral epicranial sensilla = vesl, ventral setae of maxilla = vsMa.

Digestive System - gastric caeca = GC, proventriculus = Prov, rectum = Rec, rectal papillae = RP.

Reproductive Systems and External Genitalia - accessory gland = AcGl, basal piece of tegmen = bpt, bursa copulatrix = BC, common oviduct = COvid, eighth sternite = 8S, ejaculatory duct = Ejd, endophallus = Enph, flagellum = Flag, gonopore = Gpr, lateral oviduct = L)vid, lateral lobe = ll, median lobe = mel, median strut = mes, ovariole = Ovl, spermatheca = Spt, spermathecal duct = SptD, spermathecal gland = SptG, seminal vesicles = sv, tegmen = Teg, tegminal strut = tegs, testicles = Tes, transfer apparatus = TrAp, vagina = Vag, vas deferens = VD.

EXPLANATION OF ILLUSTRATIONS

Figs. 1-8: 1,3, male *Ithycerus;* 2,4, female *Ithycerus;* 5,6, male feeding; 7, mounted female feeding, position of male's hind legs indicated; 8, male, arrows indicate folded over eighth tergite and everted internal sac.

Figs. 9-16: 9, female *Ithycerus* ovipositing in soil; 10-14, feeding damage caused by *Ithycerus* adults to shoot bark, acorn buds and petioles, leaf buds, two year old growth, and leaf petioles; 15, mid-hindleg rub, third mode; 16, fore-midleg rub, first mode.

Figs. 17-24: 17-22, bilateral hindleg rub, complete sequence; 23, 24, bilateral antenna rub.

Figs. 25-32: 25, mid-hindleg rub, second mode; 26, bilateral foreleg rub, first mode; 27 fore-midleg, mid-hindleg rub; 28, bilateral fore-midleg rub; 29, bilateral mid-hindleg rub, second mode; 30, bilateral antenna rub; 31, cage used for rearing *Ithycerus* adults; 32, bedding boxes used for incubating *Ithycerus* eggs.

Figs. 33-37, 1st instar larva, *Ithycerus*: 33, lateral view of body; 34, dorsal view of head capsule; 35, ventral view of head capsule; 36, lateral view of head capsule; 37, mandible.

Figs. 38-41, 1st instar larva, *Ithycerus:* 38, epipharynx; 39, dorsal view of maxilla; 40, ventral view of maxilla; 41, labium. Scale = 0.1 mm.

Figs. 42-44, 6th instar larva, *Ithycerus:* 42, lateral view of thorax; 43, lateral view of abdominal segments 1, 11, 111; 44, mesothoracic leg, bold numbers with broken lines indicate coxal setae, bold numbers without lines indicate apical setae of basal segment, small numbers indicate apical setae of apical segment. Scale = 1.0 mm.

Figs. 45-47, *Ithycerus* larvae; 45, dorsal view of thorax, 7th instar; 46, dorsal view of abdomonal segments 111, 1V, 1st instar larva; 47, sternum of abdominal segments 1-V11, 7th instar larva.

Figs. 48-55; 48, digestive tract, 7th instar larva, *Ithycerus;* 49, digestive tract, adult *Ithycerus;* 50, thoracic spiracle, 1st instar larva, *Ithycerus;* 51, abdominal spiracle, 1st instar larva, *Ithycerus;* 52, thoracic spiracle, 3rd instar; 53, abdominal spiracle, 3rd instar; 54, thoracic spiracle, 7th instar; 55, abdominal spiracle, 7th instar, *Ithycerus*.

Figs. 56-61: 56, *Ithycerus* eggs; 57, chorion, SEM; 58, chorion, SEM; 59, microsculpture of single hexagonal facet of chorion, showing aeropyles; 60, egg, moments before eclosion 61, lateral view of body of 1st instar larva of *Ithycerus*, SEM.

Figs. 62-69, SEM micrographs of 1st instar larva, *Ithycerus:* 62, ventral view of head capsule; 63, frontal view of head capsule; 64, lateral view of head capsule; 65, antenna, 66, frontal ridge supporting antenna; 67, frontal view of antenna; 68, clypeus and labrum 69, basal sensillum of labrum.

Figs. 60-77, SEM micrographs, 1st instar, *Ithycerus:* 70, upper sensillum of frons; 71, labium and maxillae; 72, apical articles of maxillary and labial palpi; 73, maxillary palpus, showing free, rod-like accessory appendage; 74, pronotal plate; 75, mesonotum, metanotum, and 1st abd. seg.; 76, sternum, abd. seg. VI-IX; 77, prosternum, mesosternum.

Figs. 78-85, SEM micrographs, 1st instar larva, *Ithycerus:* 78, lateral view of abd. seg. V, VI; 79, meso, metathoracic legs; 80; spiracular area, abd. seg. V; 81, abd. spiracle, abd. seg. 1; 82, anus; 83, anus; 84, anal asperities; 85, spinelike asperities of body.

Figs. 86-90, Pupa of *Ithycerus:* 86, ventral view of body; 87, apex of femur; 88, ventral view of abd. seg. IX and anus; 89, frontal view of head; 90, labrum and mandible.

Figs. 91-94, Pupa of *Ithycerus:* 91, lateral view of body; 92, dorsal view of body; 93; dorsal view of abd. seg. IX; 94, dorsal view of right elytron.

Figs. 95-105, Reproductive system and external genitalia, *Ithycerus* male: 95, reproductive system; 96, aedagus; 97, 9th sternite; 98, tegmen; 99, ventral view of everted internal sac; 100, dorsal view of everted internal sac; 101, everted internal sac; 102, transfer apparatus; 103, transfer apparatus; 104, 9th sternite, dorsal; 105, 9th sternite ventral view, Scale = 1.0 mm.

Figs. 106-111, Reproductive system and external genitalia, *Ithycerus* female: 106, dorsal view of ovaries; 107, ventral view of ovaries; 108, 8th sternite = spiculum gastrale; 109, internal view of coxite and stylus; 110, external view of coxite and stylus; 111, spermatheca and associated structures.

Figs. 112-119, *Arrhenodes minutus:* 112, 114, male; 113, 115, female; 116, dorsal view of head capsule of 1st instar larva; 117, lateral view of head capsule, 1st instar larva; 118, antenna, 1st instar larva; 119, cylpeus, labrum, 1st instar larva, SEM.

Figs. 120-127, *A. minutus,* 1st instar larva, SEM micrographs: 120, frons, clypeus, labrum mandibles; 121, basal sensillum of labrum; 122, lateral view of thorax, 123, asperities; 124, 125, thoracic spiracle; 126, thoracic pleura and legs; 127, metathoracic leg.

Figs. 128-135, SEM micrographs, 1st instar larva, *A. minutus:* 128, divided asperities; 129 spinelike asperities; 130, 131, egg bursters; 132, 9th abd seg. and anus; 133, anus; 134, spinelike asperities on anal folds; 135; divided asperities on anal fold.

Figs. 136-140, 1st instar larva, *A. minutus:* 136, lateral view of body; 137, dorsal view head capsule; 138, thoracic spiracle; 139, abdominal spiracle; 140, ventral view of head capsule.

Figs. 141-147: 141-145, 1st instar *A. minutus;* 141, ventral view of maxilla; 142, labium; 143, dorsal view of maxilla; 144, epipharynx; 145, mandible. Figs. 146, 147, final instar larva of *Antliarrhinus* sp.; 146, ventral view of head capsule; 147, frons, clypeus, labrum, antenna. Scale = 0.1 mm.

Figs. 148-155, final instar larva, *Antliarrhinus:* 148, ventral view of head capsule; 149, abd. spiracle; 150, thoracic spiracle; 151, dorsal view of maxilla; 152, labium; 153, ventral view of maxilla; 154, epipharynx; 155, mandible. Scale = 0.1 mm.

Figs. 156-160, larva of unidentified Australian belid: 156, lateral view; 157, dorsal view of head capsule; 158, ventral view of head capsule; 159, labrum; 160, epipharynx.

Figs. 161-168, larva of unidentified Australian belid: 161, ventral view of maxilla; 162, labium; 163, dorsal view of maxilla; 164, lateral view of thorax, 165, proventriculus, 3 of 12 folds; 166, lateral view of 3rd abd. seg.; 167, 4th, 5th abd. sterna; 168 anus.

Figs. 169-178, ventral nervous systems, larval Chrysomelidae and Curculionioidea; 169, *Chrysomela* sp.; 170, *Calligrapha* sp.; 171, *Dendroctonus* sp (Scolytidae); Scolytidae; 173, *Curculio* sp.; 174, *Gymnaetron* sp.; 175, *Ithycerus;* 176, *Acanthoscelidius acephalus;* 177, *Otiorhynchus* sp.; 178, *Listronotus* sp.; Scale = 0.5 mm.

Figs. 179-188, ventral nervous systems, adult Curculionoidea: 179, *Euparius marmoreus* (Anthribidae); 180, *Attelabus bipustulatus* (Attelabidae); 181, *Ithycerus;* 182, *Arrhenodes minutus* (Brenthidae); 183, *Antliarrhinus;* 184, Scolytidae; 185, 186, 187, 188, *Pissodes strobi, Listronotus, Liparus, Magdalis* (Curculionidae). Scale = 0.5 mm.

Figs. 189-193, hind wings of Curculionoidea: 189, *Cimberis* (Nemonychidae); 190, *Allandrus* (Anthribidae); 191, *Euparius marmoreus* (Anthribidae); 192, *Rhynchites bicolor* (Attebalidae); 193, *Attelabus bipustulatus* (Attelabidae). Scale = 1.0 mm.

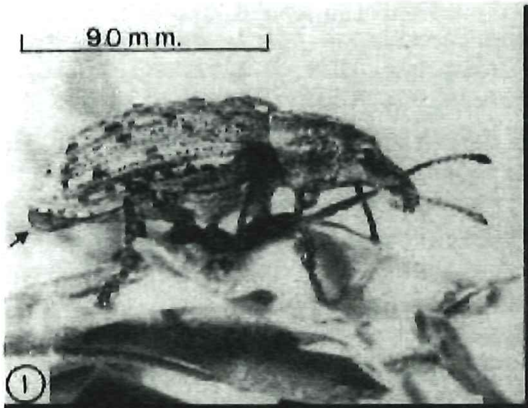
Figs. 194-197, hind wings of Curculionoidea: 194-197, *Ithycerus* (Ithyceridae). Scale = 2.0 mm.

Figs. 198-202, hind wings of Curculionoidea: 198, *Arrhenodes minutus* (Brenthidae); 199, *Antliarrhinus* (Antliarrhinidae); 200, *Apion longirostre* (Apionidae); 201, *Magdalis* (Curculionidae); 202, *Cossonus platalea* (Curculionidae). Scale = 1.0 mm.

Fig. 203: Distribution of *Ithycerus* in relation to the distribution of *Q. alba* (White Oak).

Figs. 204-205, phylogenetic classification of the "higher weevils": 204, after Sanborne, showing derived character states (from table 8); 205, after Crowson (personal communication).

Figs. 206-209: 206-208, alternative phylogenies; 209, evolution of larval labral sensilla and setae (Curculionoidea), A, hypothetical ancestor, B, Nemonychidae, Anthribidae, Aglycyderidae, Oxycorynidae, Attelabidae, C, Belidae, D, *Sphenophorus* (Rhynchophorinae), E, *Rhodobaenus* (Rhynchophorinae), F, Scolytidae and some Curculionidae, G, *Metamasius* (Rhynchophorinae), H, *Dryophthorus* (Rhynchophorinae), I, Ithyceridae, Brenthidae and some Apionidae, J, Antliarrhinidae and some Apionidae.



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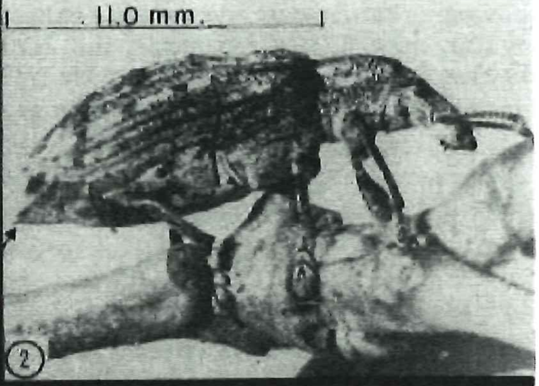

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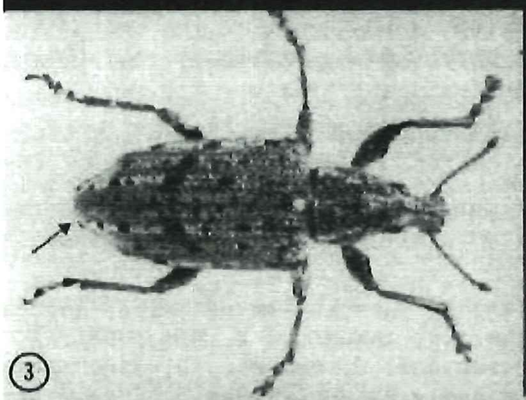
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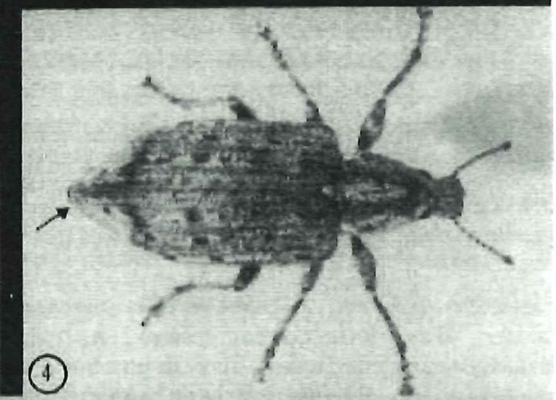
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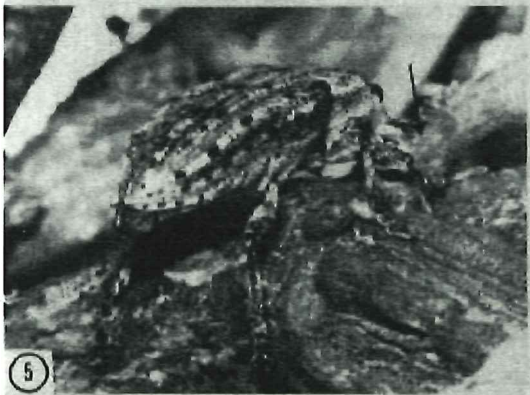
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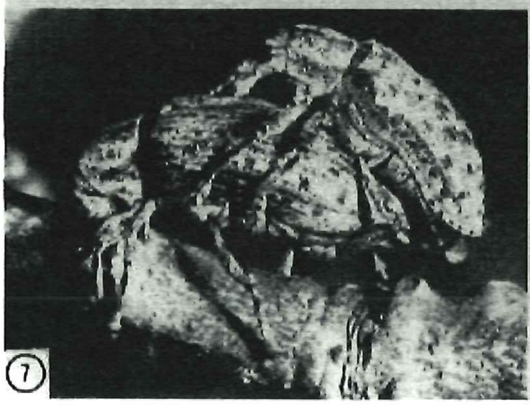
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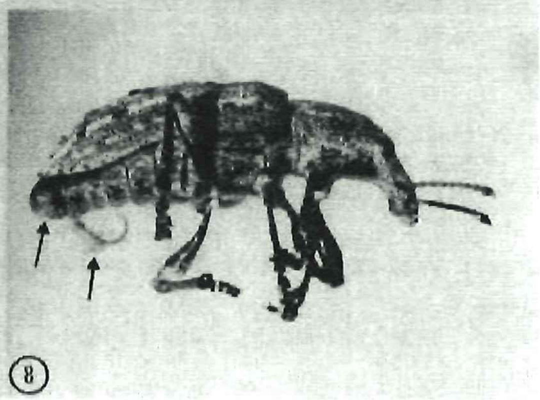
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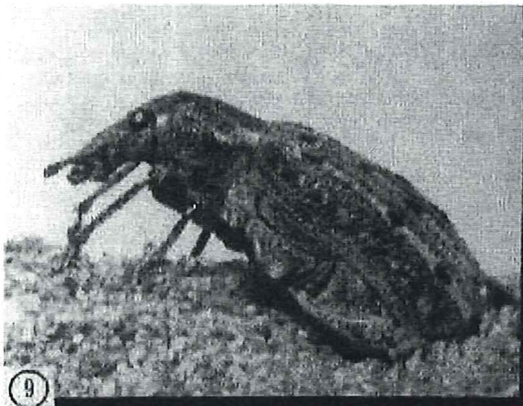
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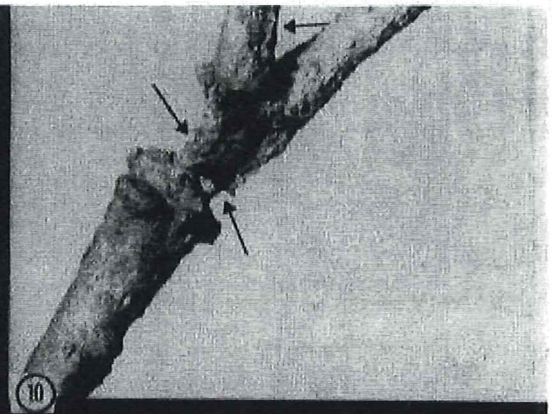
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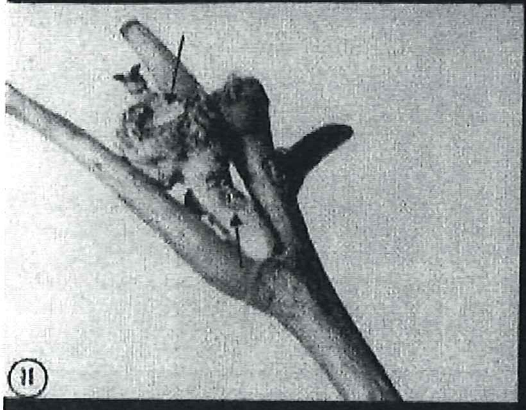
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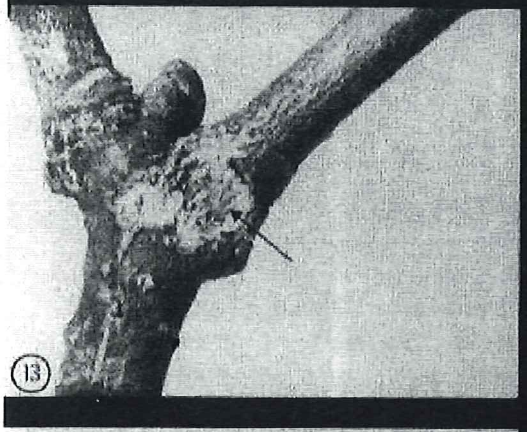
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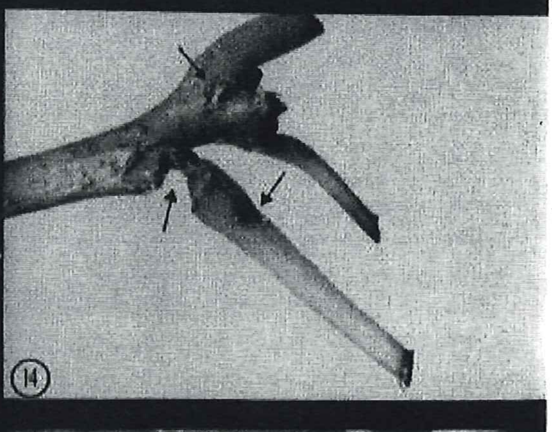
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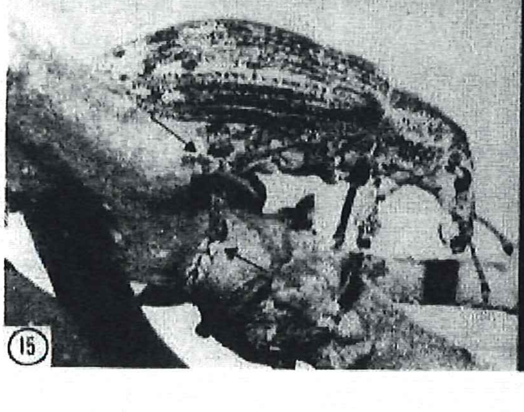
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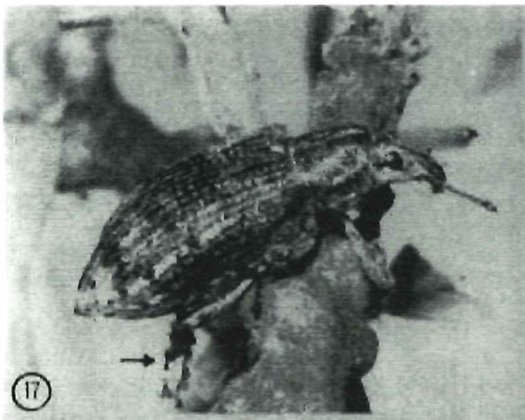

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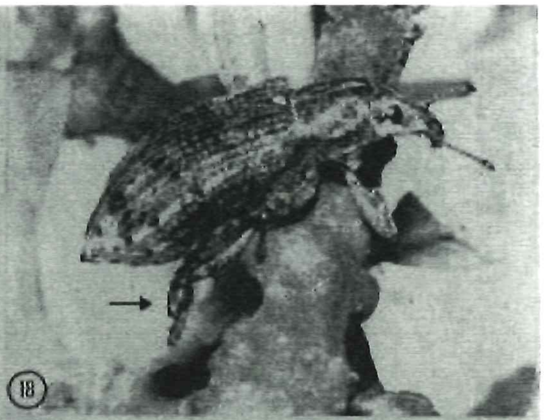

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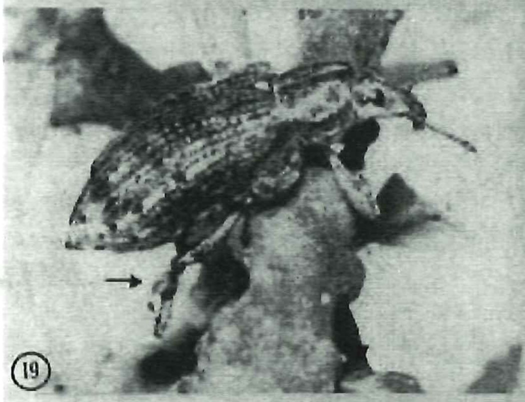

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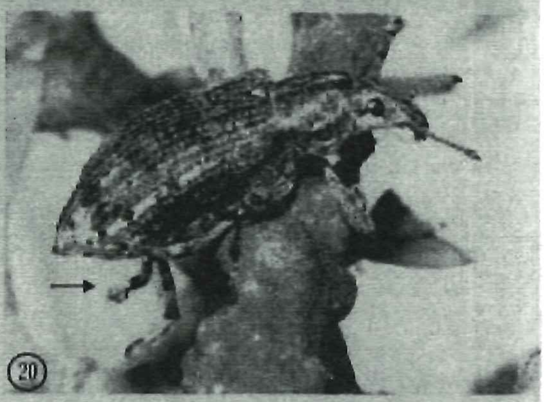

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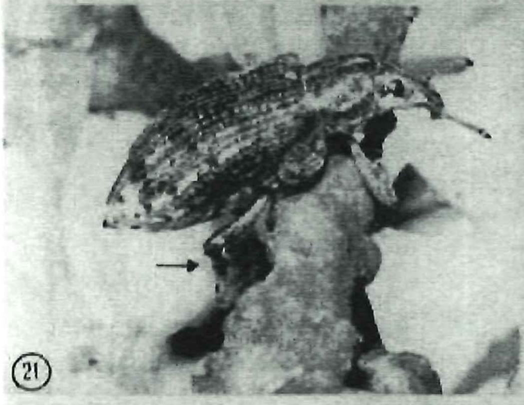

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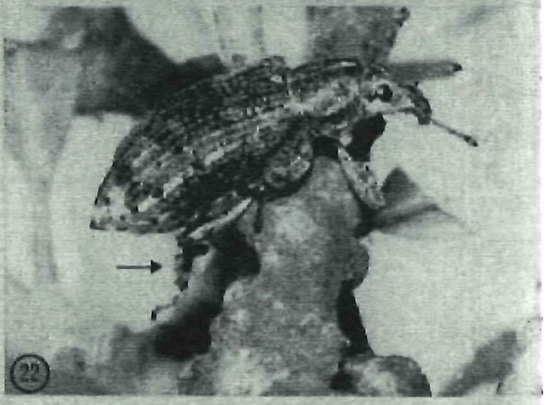

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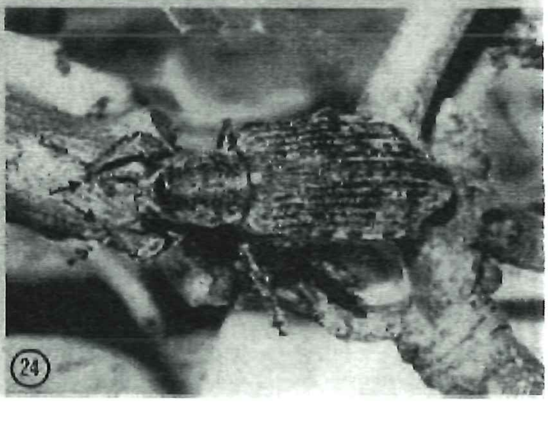

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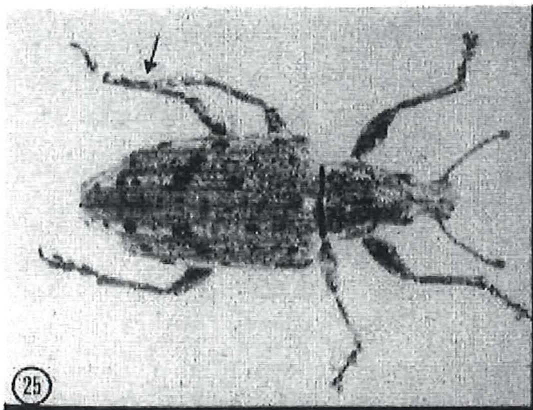
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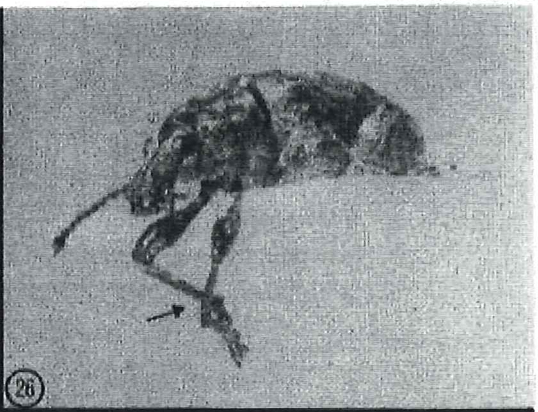
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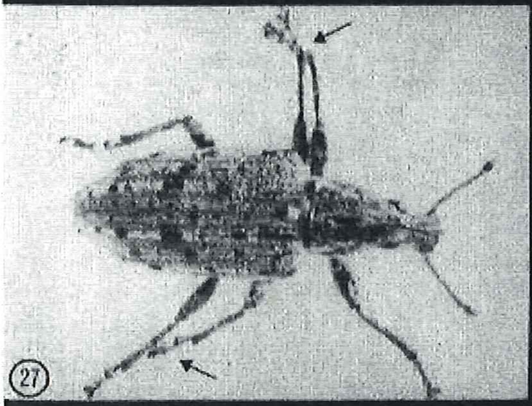
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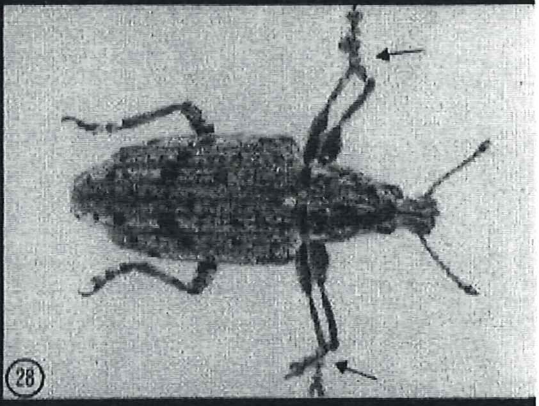
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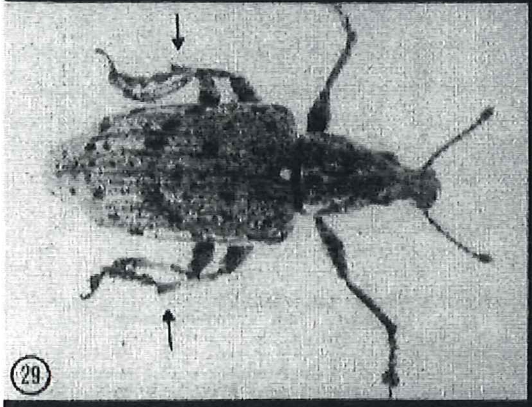
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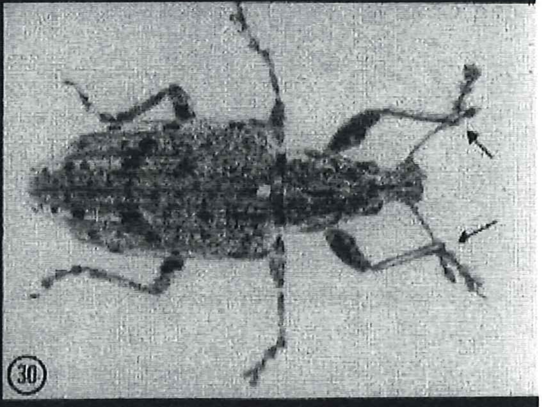
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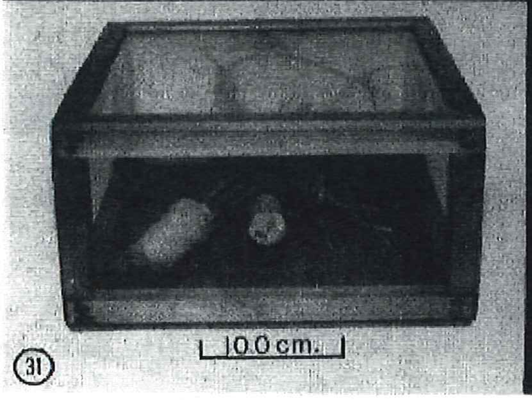

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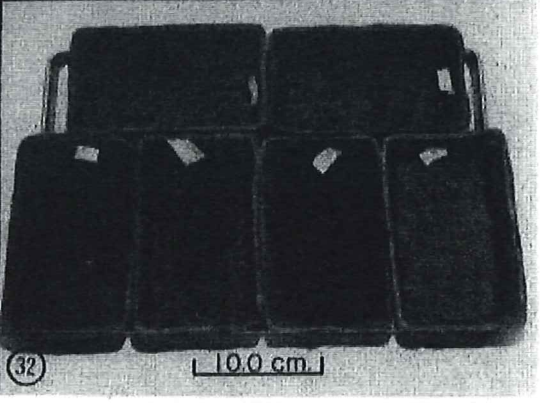

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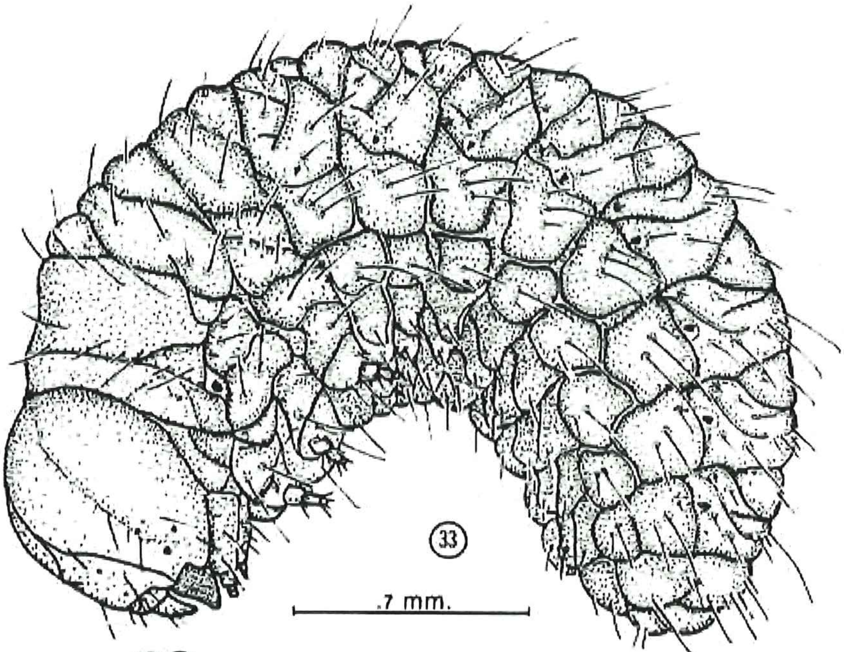
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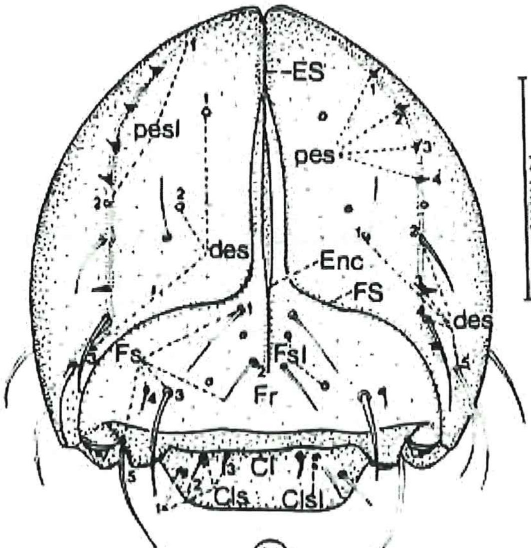
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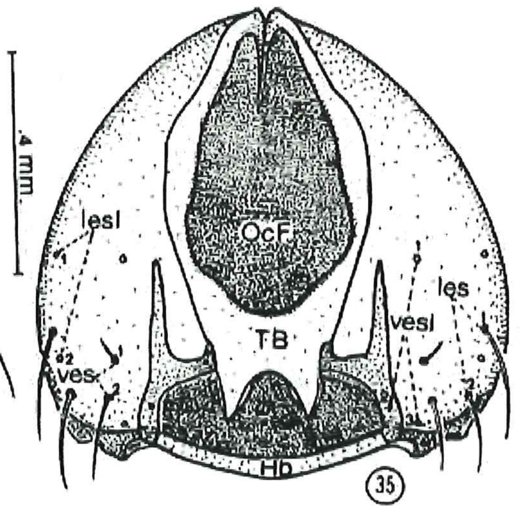
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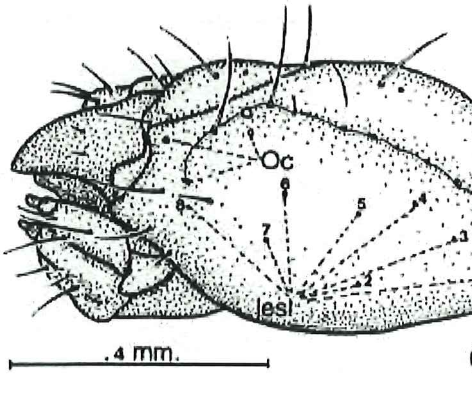
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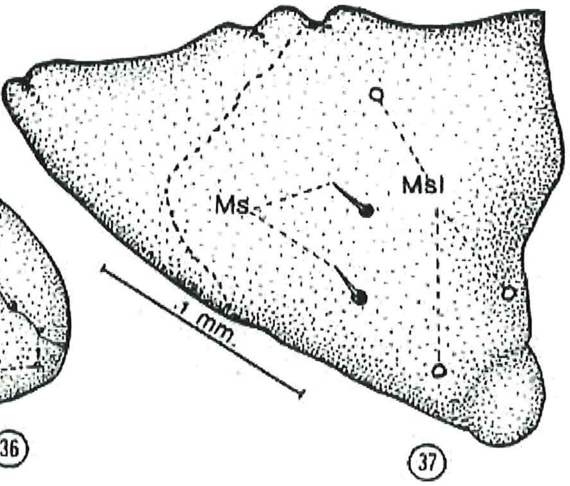
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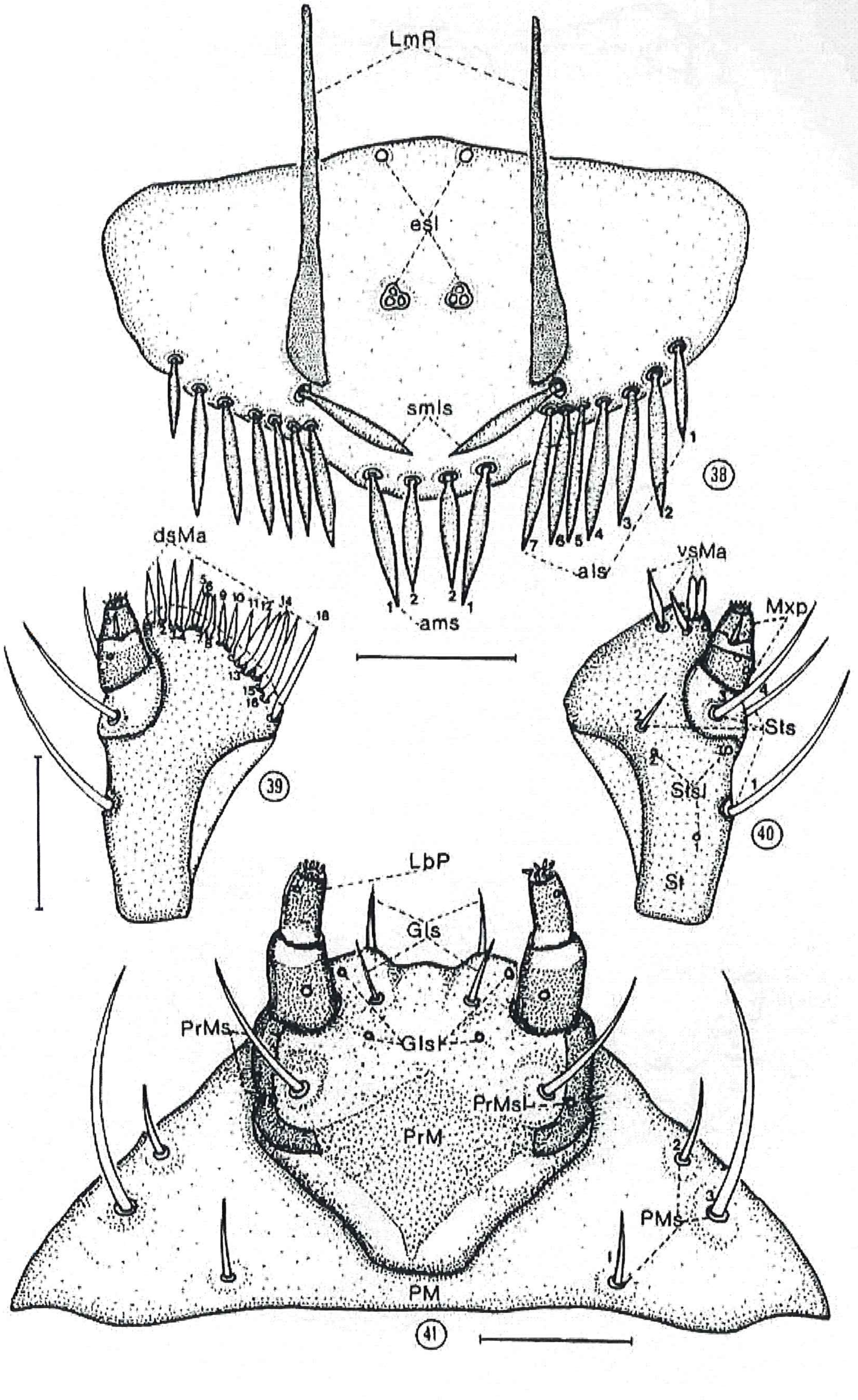
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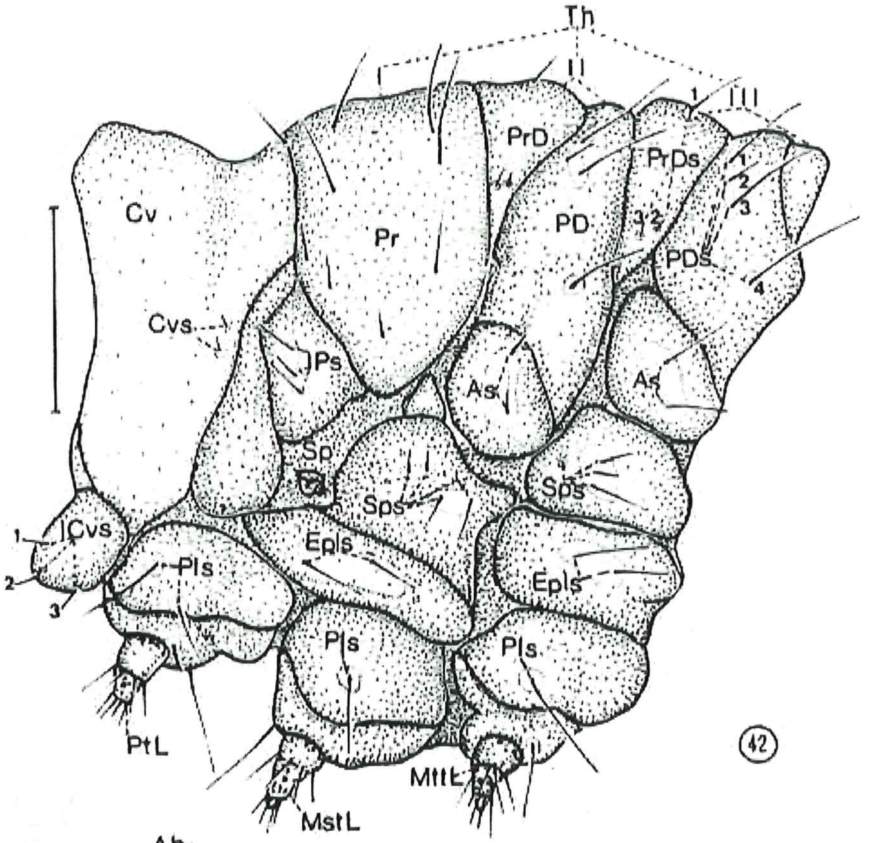
13
14
15
16
18
vsMa
Mxp
Sts
1
2
3
Stsl
St
LbP
Gls
Glsl
PrMs
PrMsl
PrM
PMs
1
2
3
PM

38

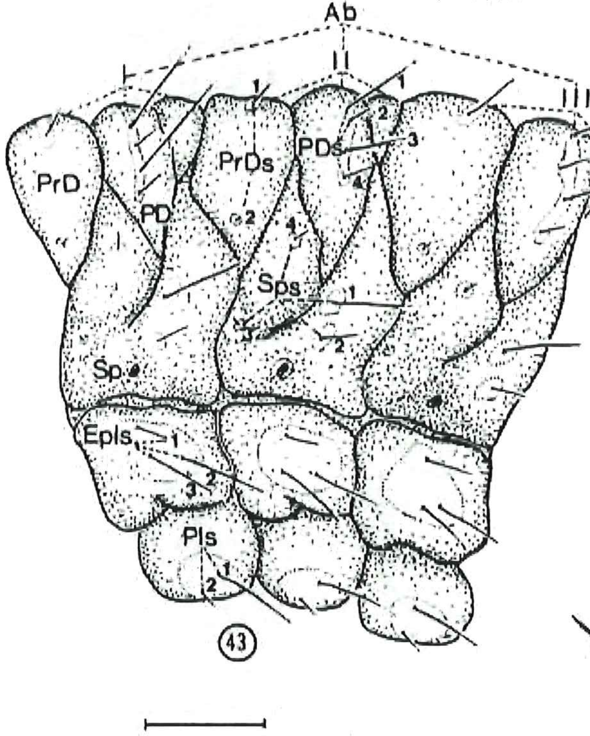
39

40

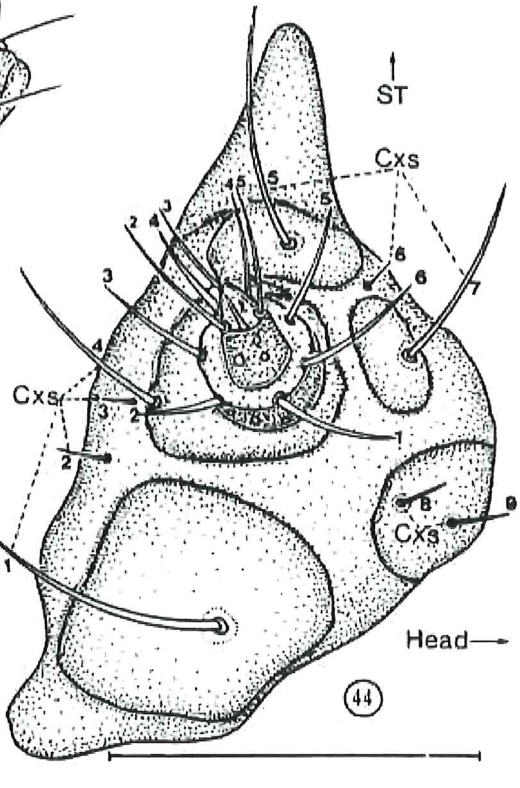
41


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

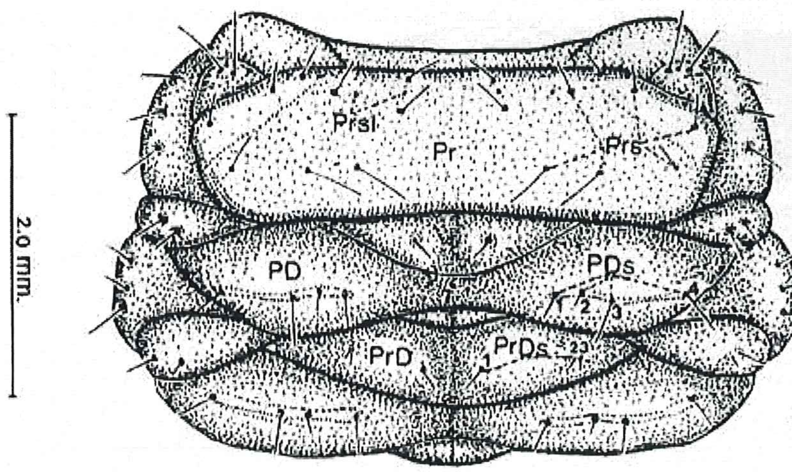
㊷


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

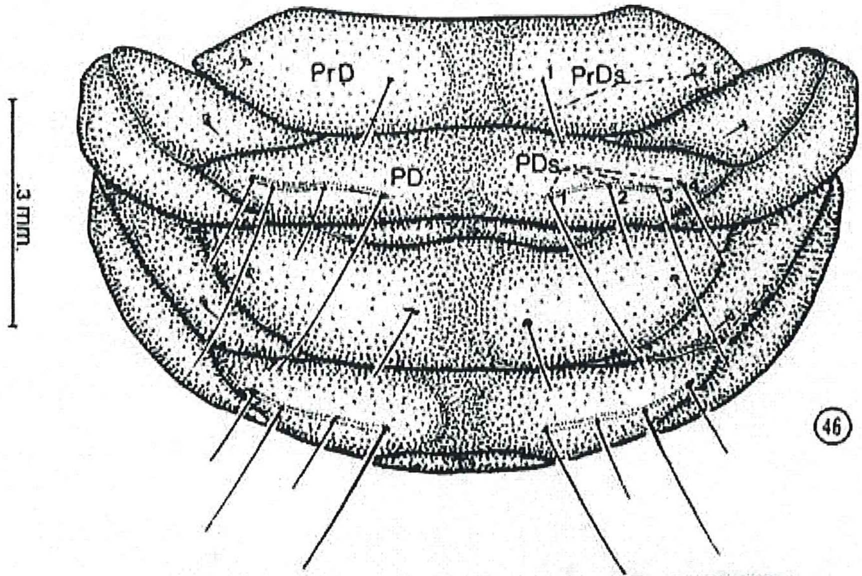
㊸


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

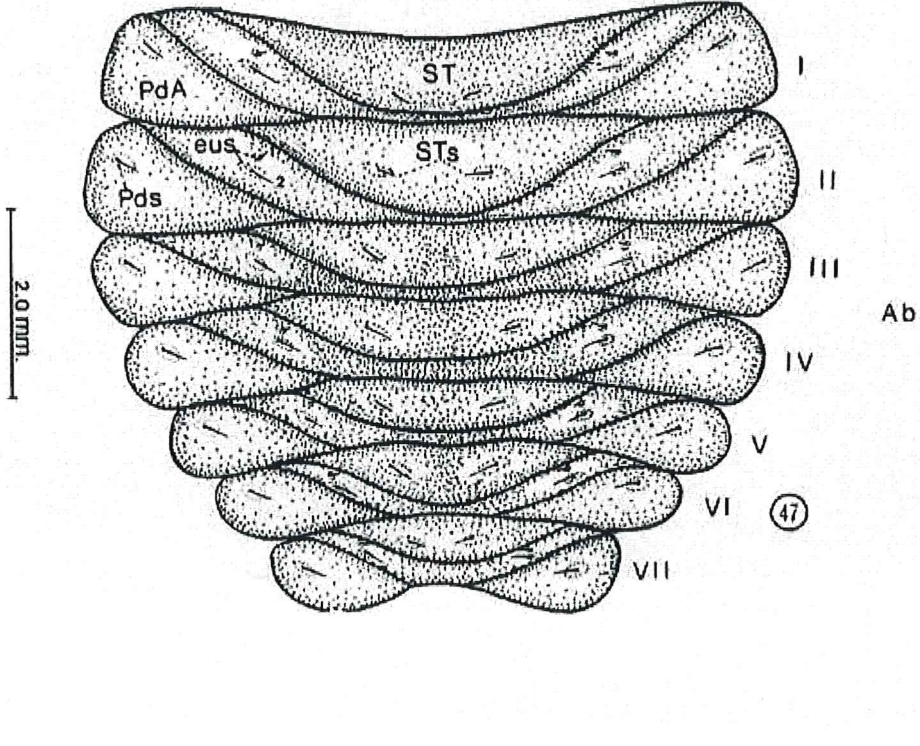
㊹


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

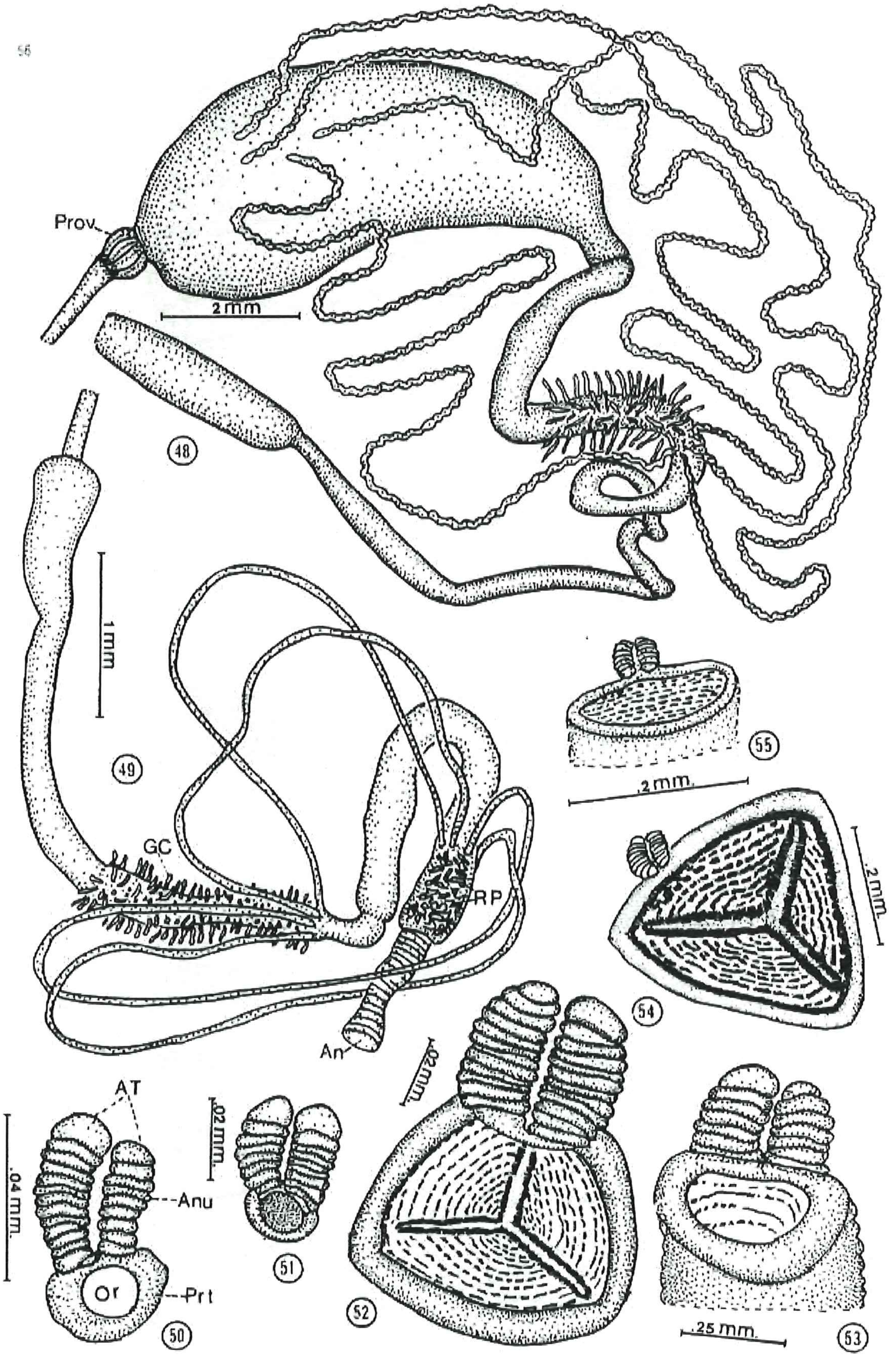
⑮

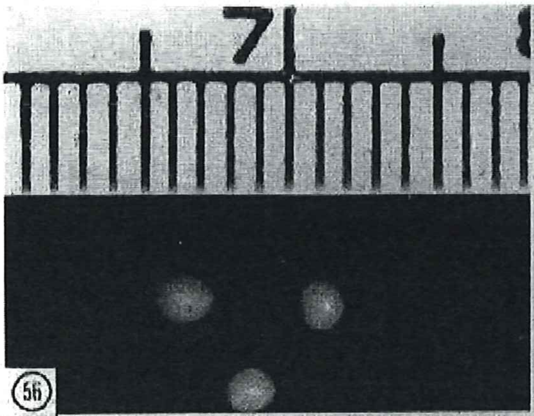

.3 mm.
PrD
PrDs
1
2
PD
PDs
1
2
3

⑯

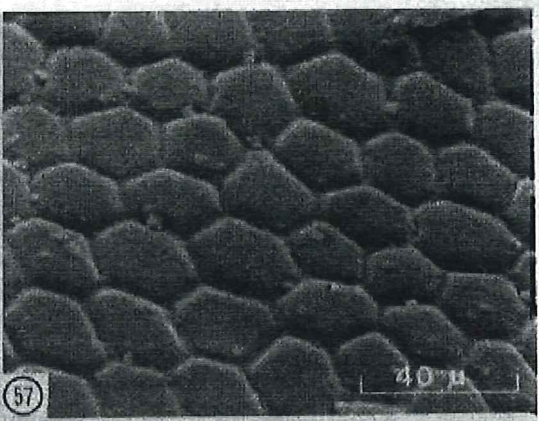

2.0 mm.
PdA
ST
I
eus
STs
2
II
Pds
III
Ab
IV
V
VI
VII

⑰

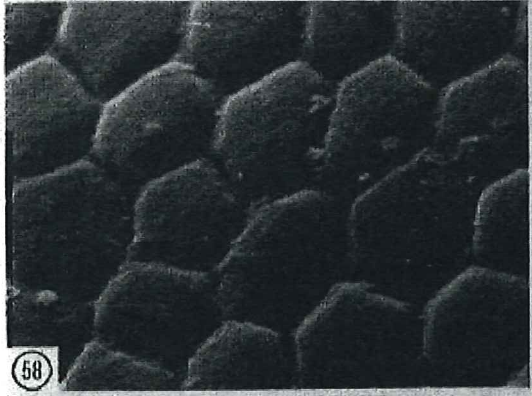

Prov.
2 mm
48
1 mm
49
GC
RP
An
55
.2 mm.
.2 mm.
54
.02 mm.
AT
.04 mm.
Anu
Or
Prt
50
.02 mm.
51
52
.25 mm.
53



(56)



(57)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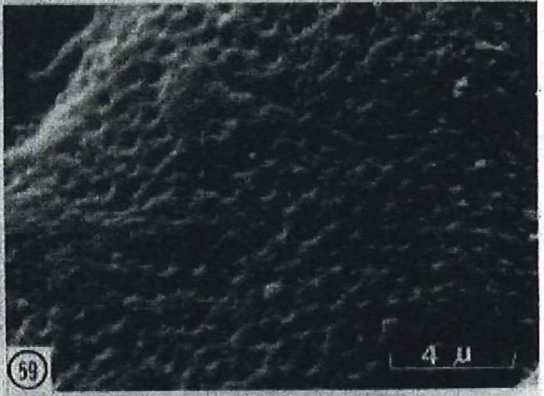
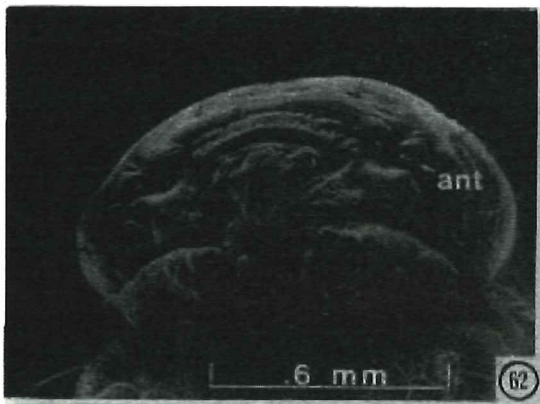


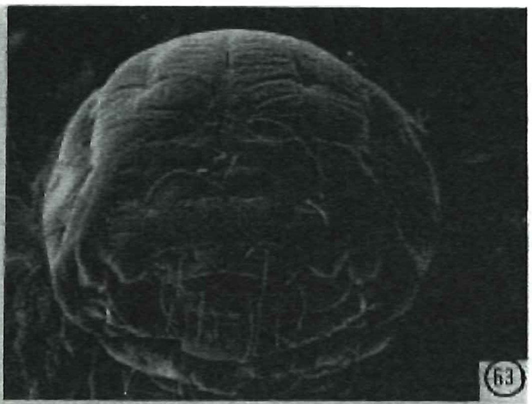
(59)

(60)

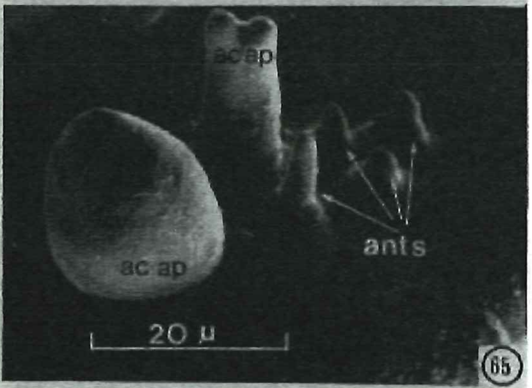
(61)



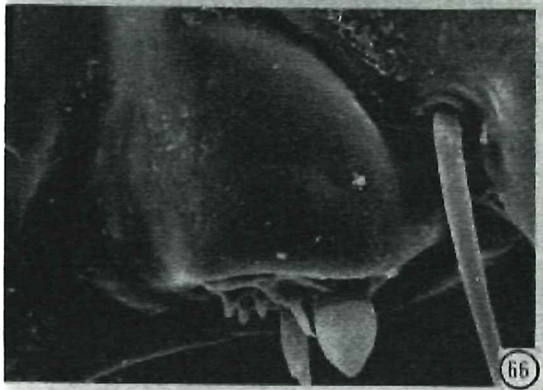
(62)

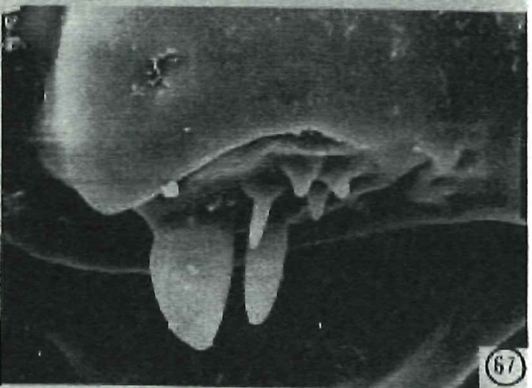

(63)

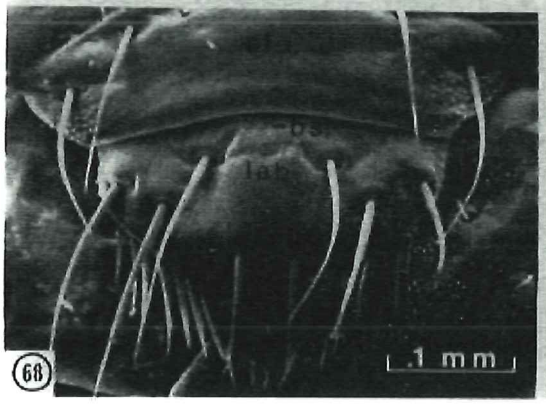
(64)



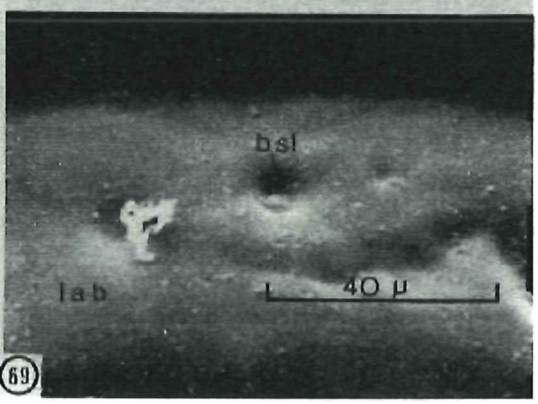
(65)


(66)

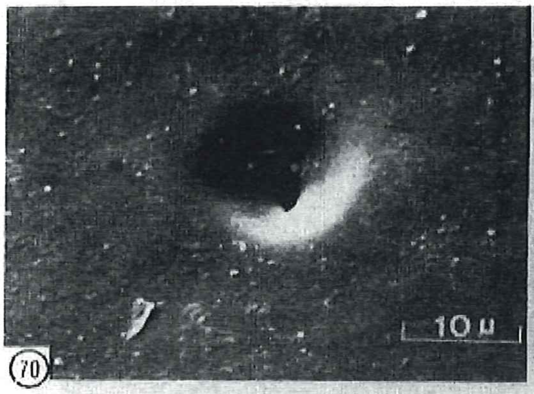

(67)

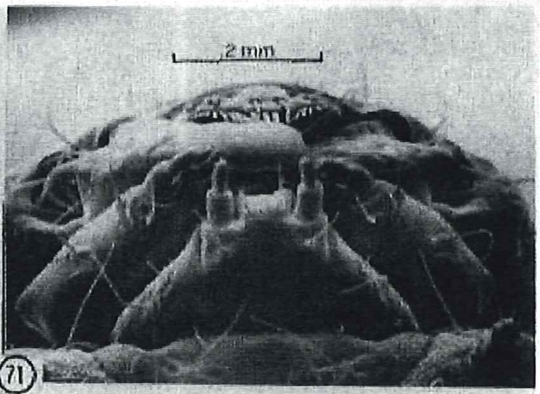


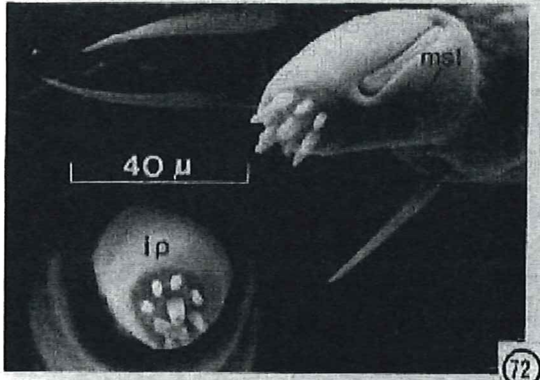
(68)

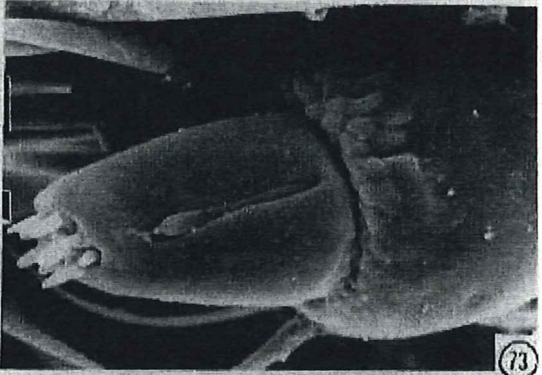


(69)


(70)


(71)


(72)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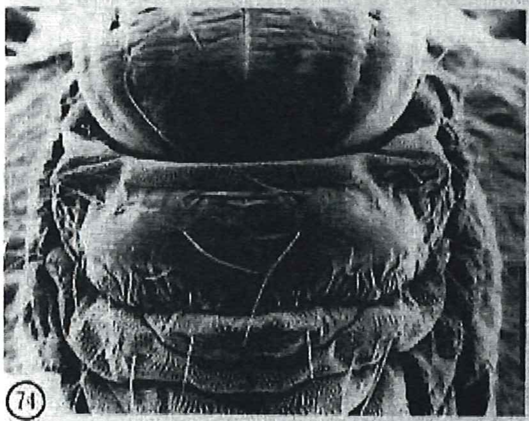
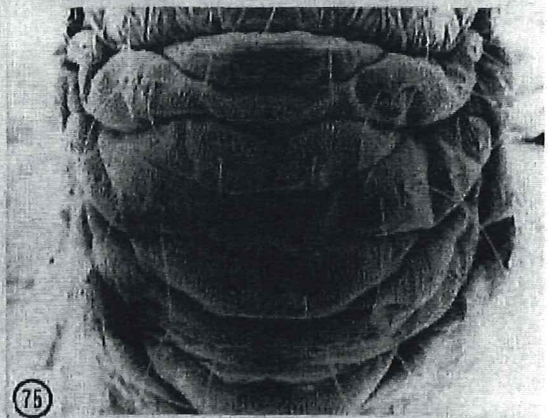
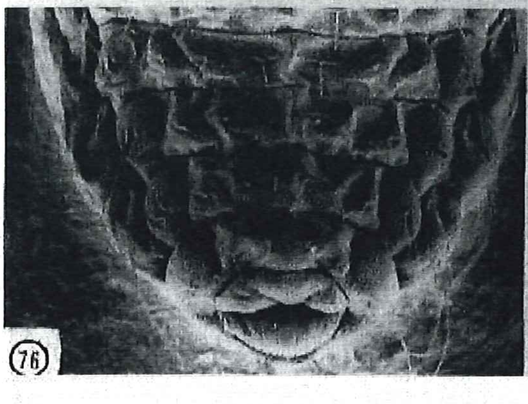
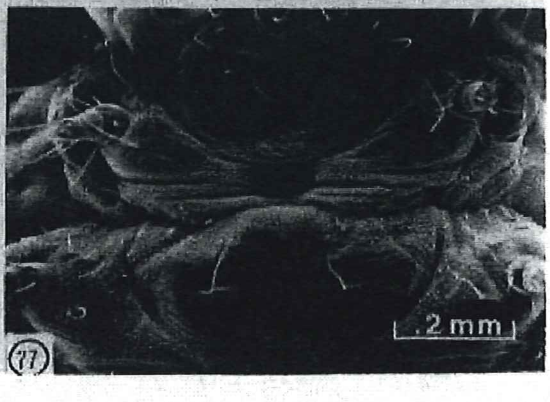
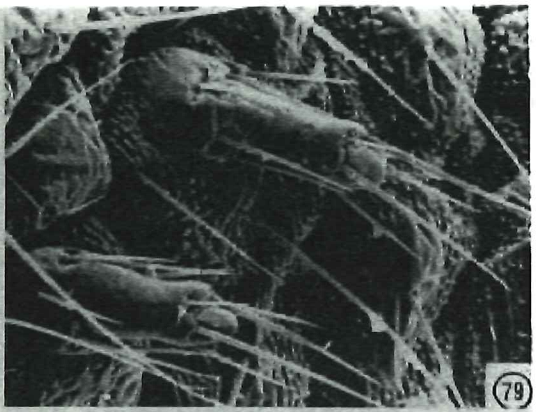

(74)


(75)

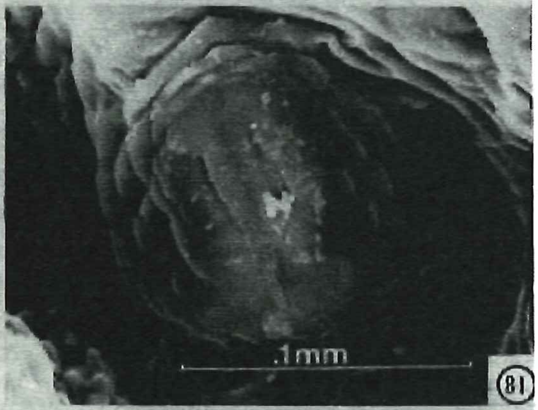

(76)

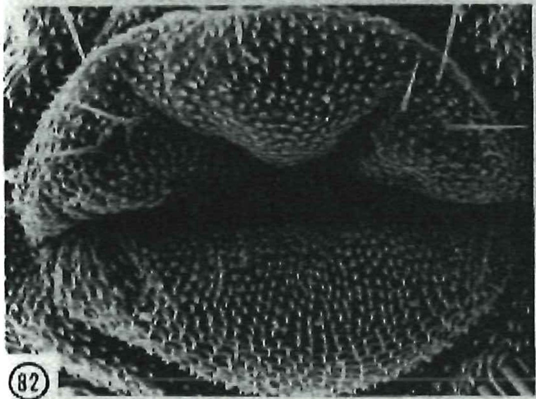

(77)

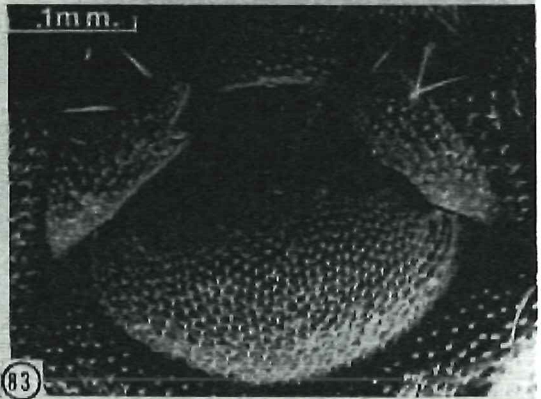

78

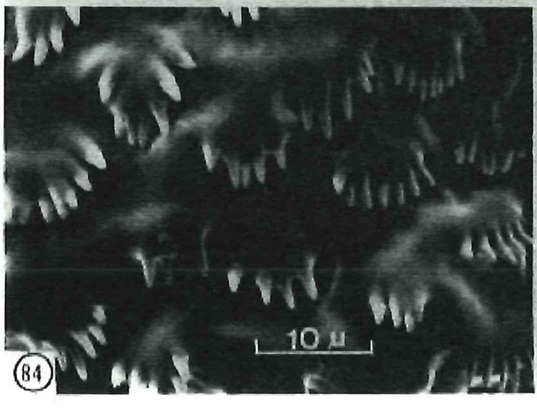

79

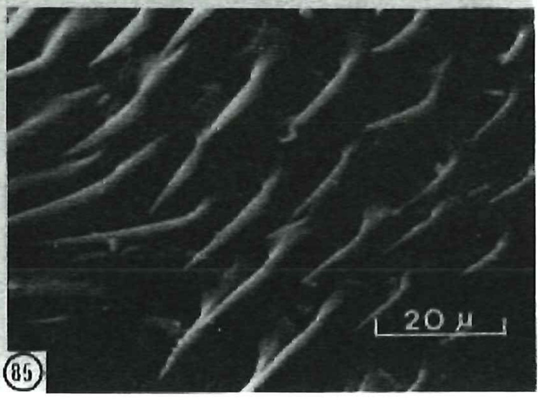

80

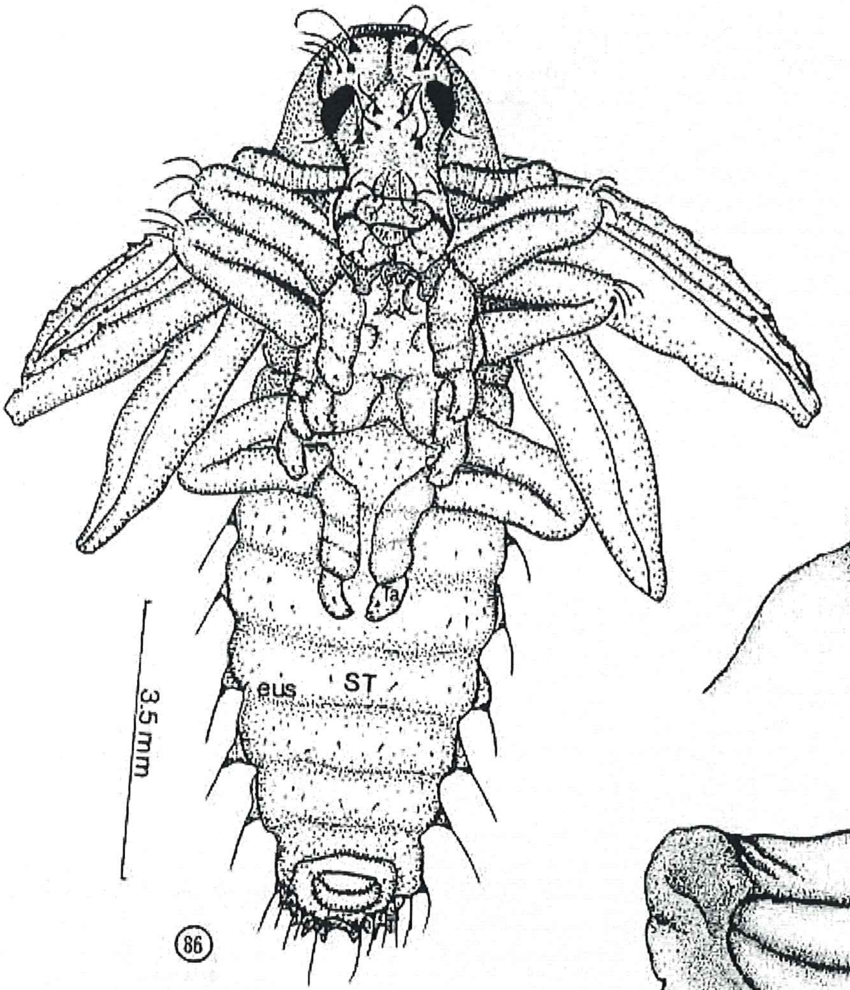

.1mm
81


82

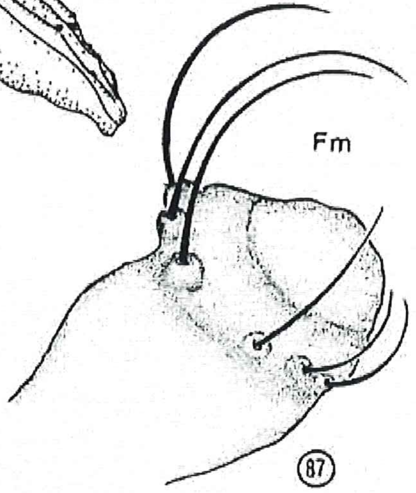

.1mm.
83


10 µ
84

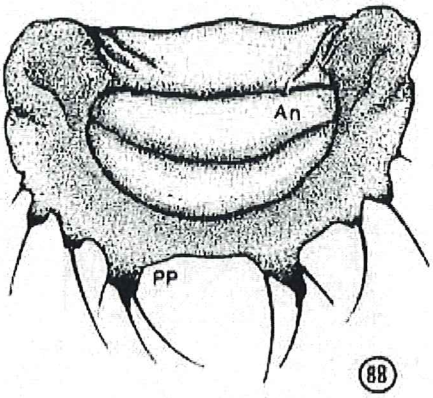

20 µ
85



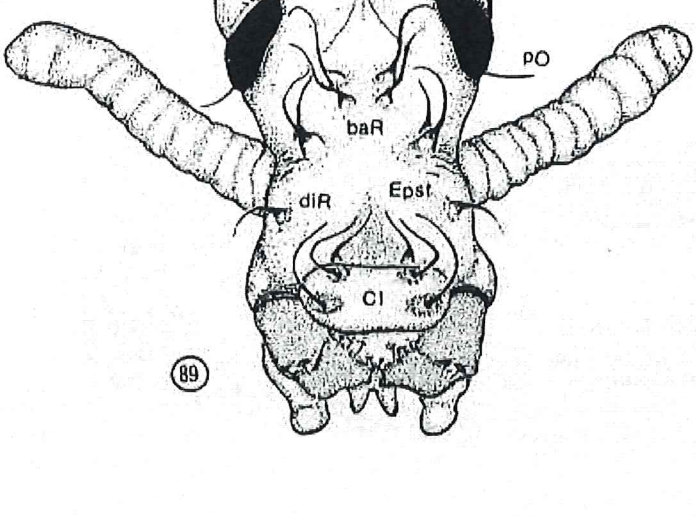
(86)



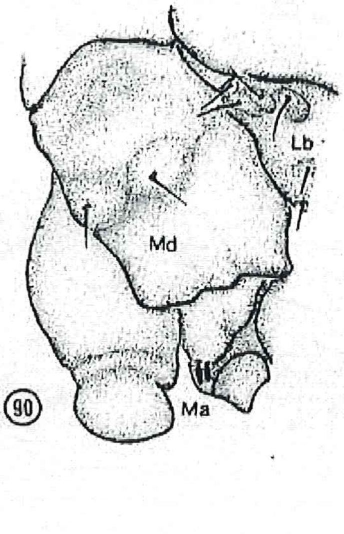
(87)



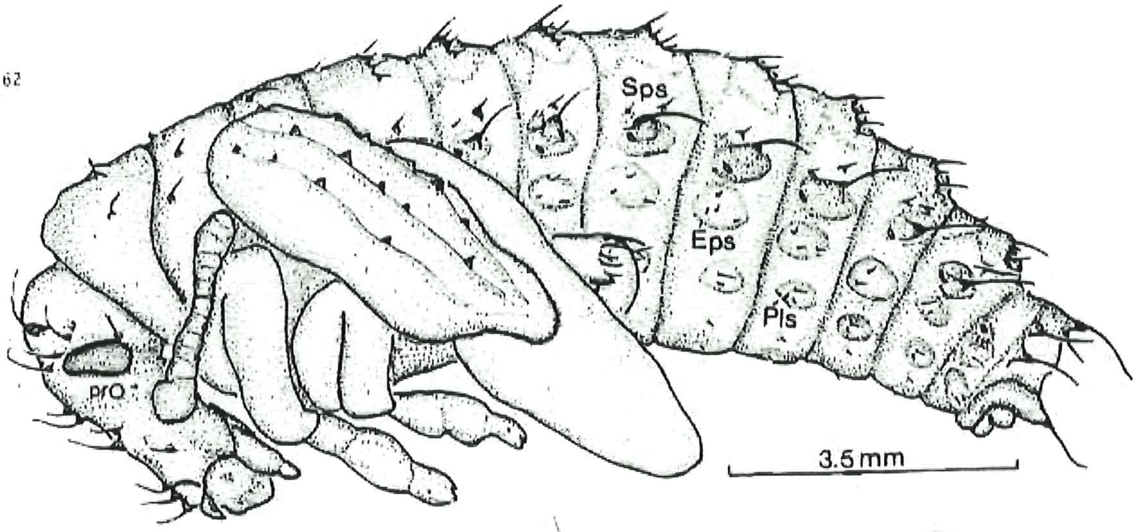
(88)



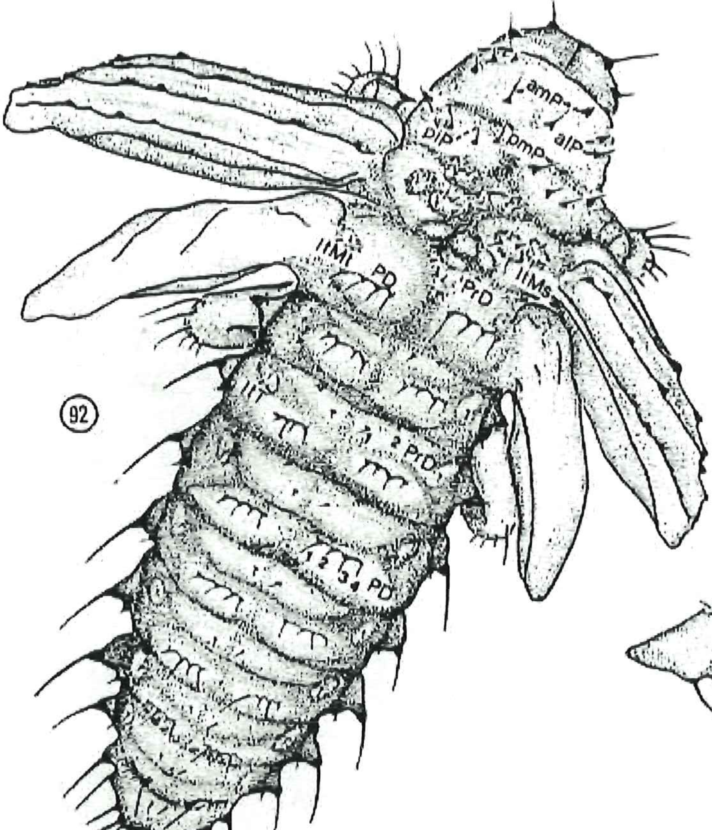
(89)



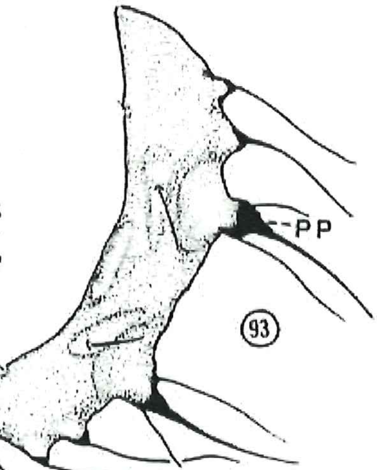
(90)


Sps
Eps
Pls
PrO
3.5 mm

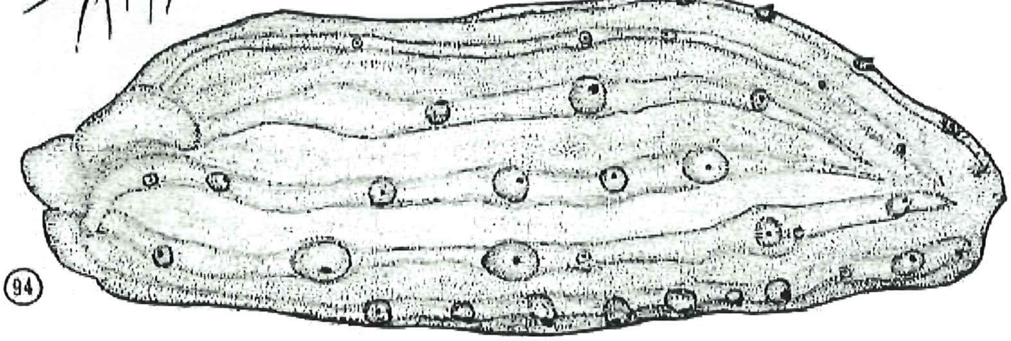
(91)


amP
plP
pmP
alP
IIMl
PD
PrD
IIMs
1
2
PrD
1
2
3
4
PD

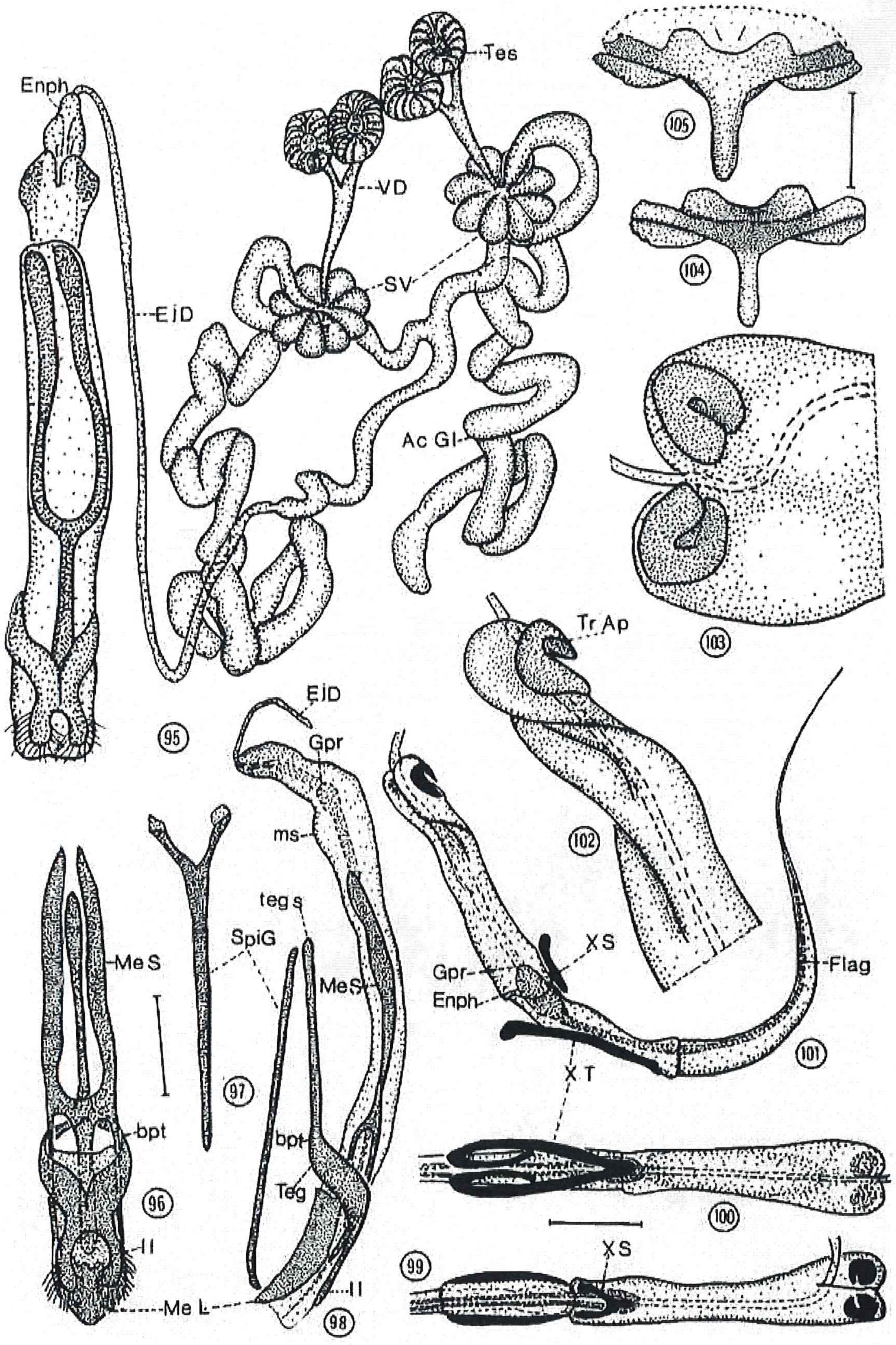
(92)

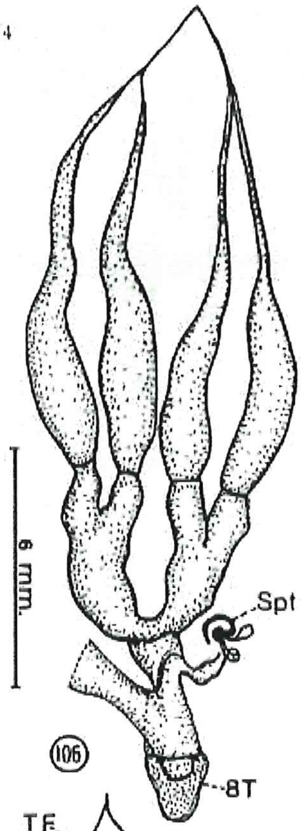

PP

(93)

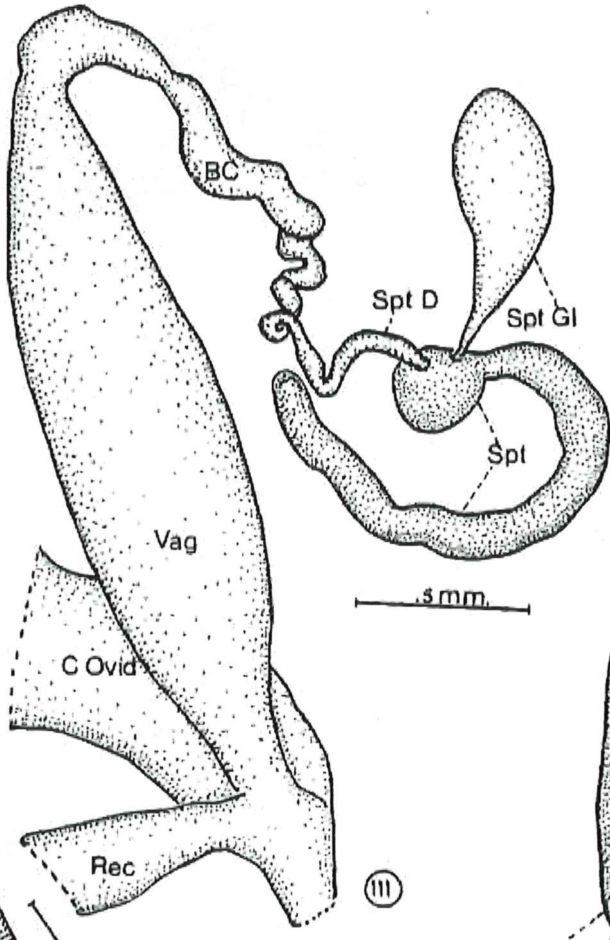


(94)

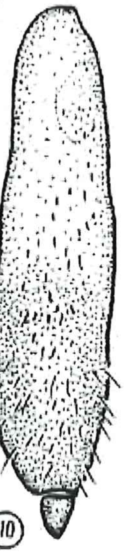

Enph
Tes
VD
SV
EjD
Ac Gl
95
105
104
103
Tr Ap
102
EjD
Gpr
ms
teg s
SpiG
Me S
MeS
bpt
96
97
bpt
Teg
II
Me L
II
98
XS
Gpr
Enph
Flag
101
XT
100
99
XS


6 mm.
Spt
8T

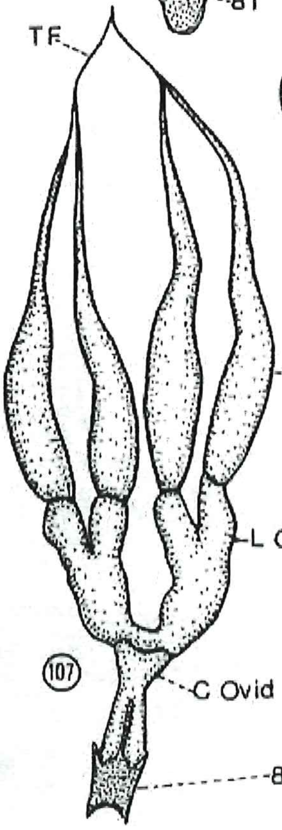
⑩⑥


BC
Spt D
Spt Gl
Spt
Vag
C Ovid
Rec
.5 mm.

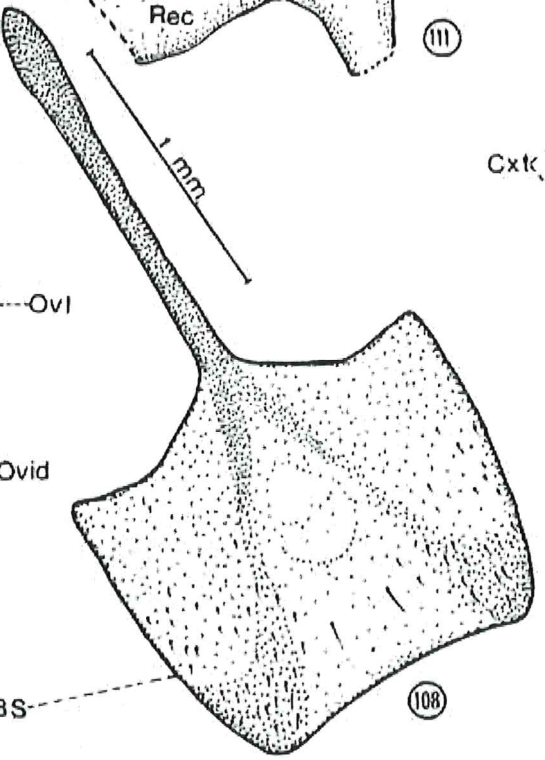
⑪



⑩

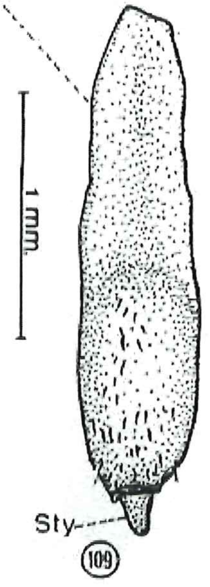

TF
Ovl
L Ovid
C Ovid
8S

⑩⑦

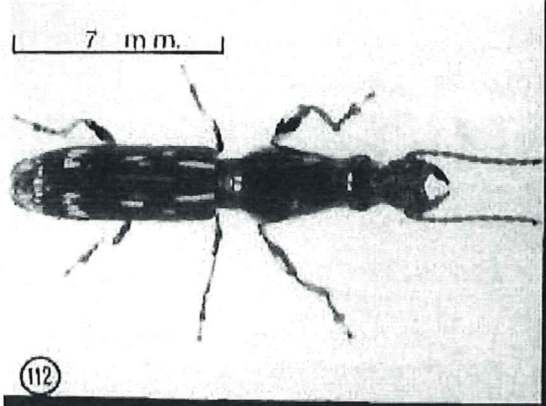

1 mm.

⑩⑧

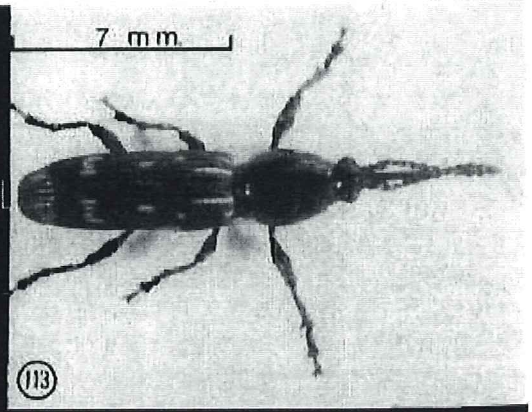
Cxt


1 mm.
Sty

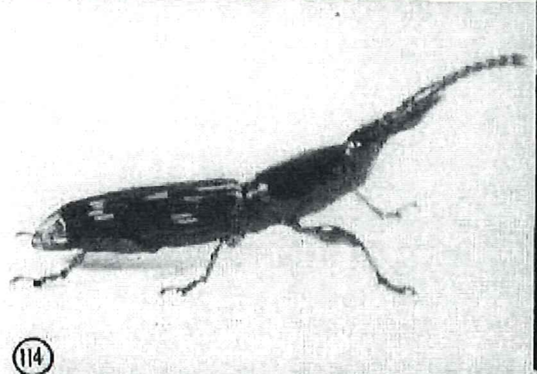
⑩⑨



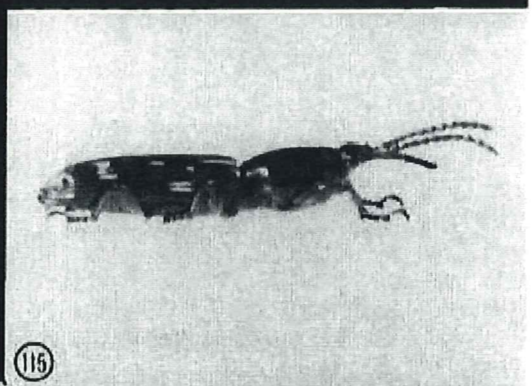
(112)



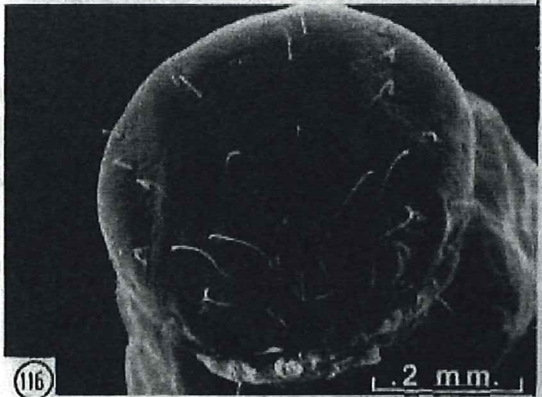
(113)



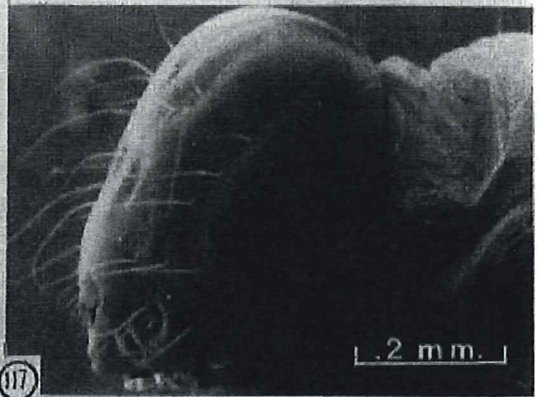
(114)



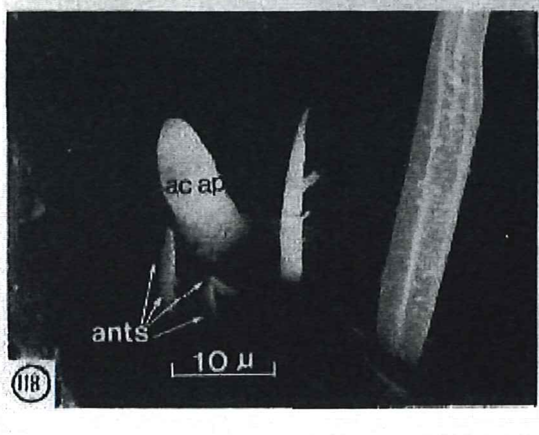
(115)



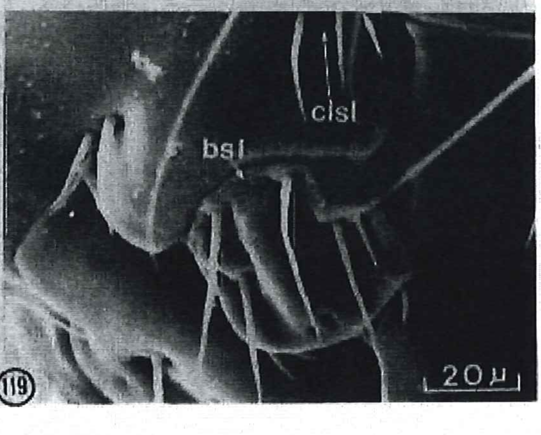
(116)



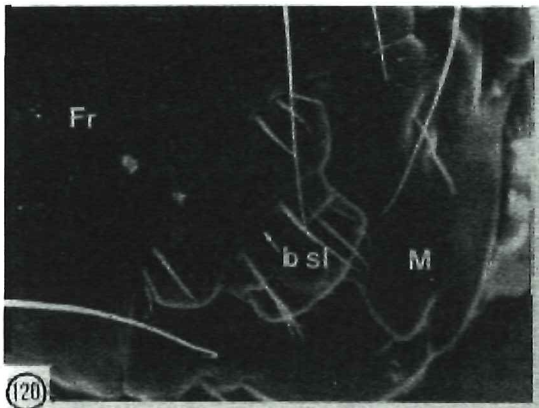
(117)

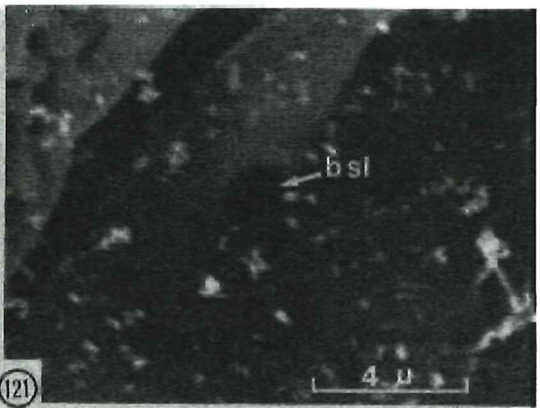


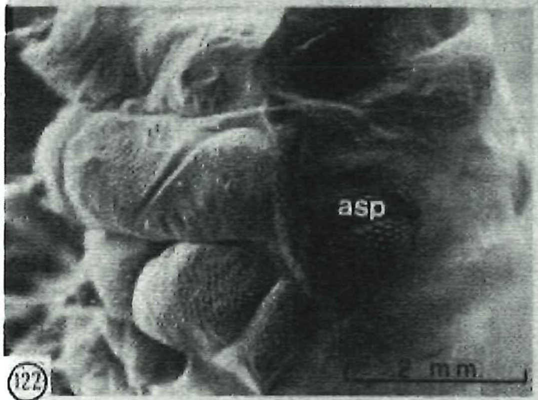
(118)

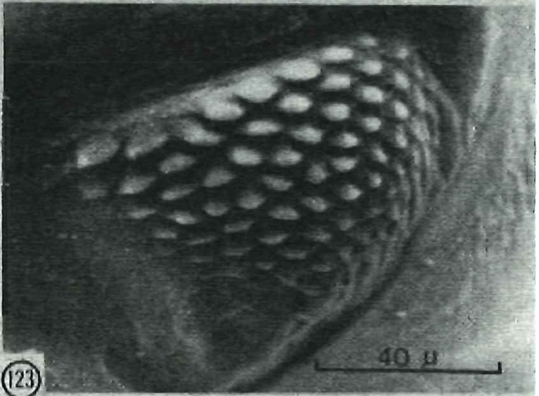


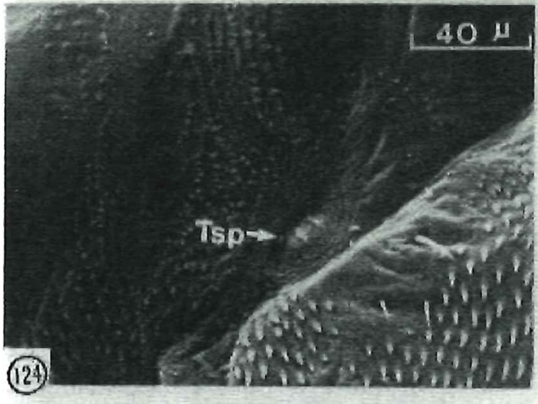
(119)

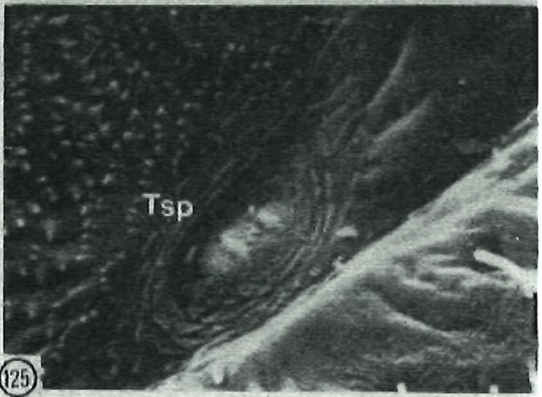

120

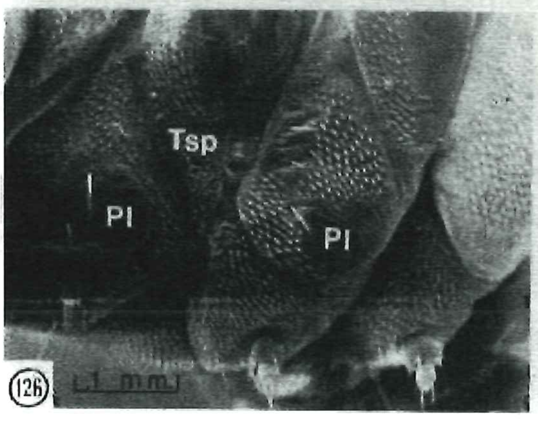

121

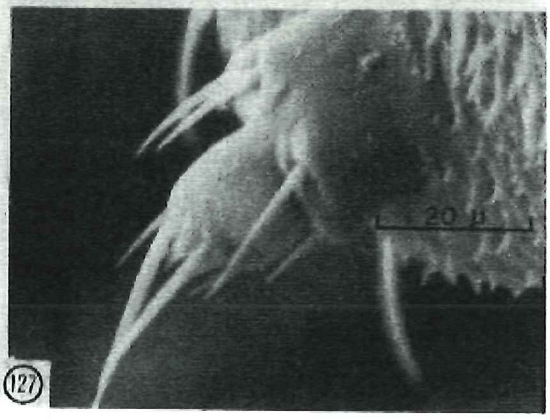

122

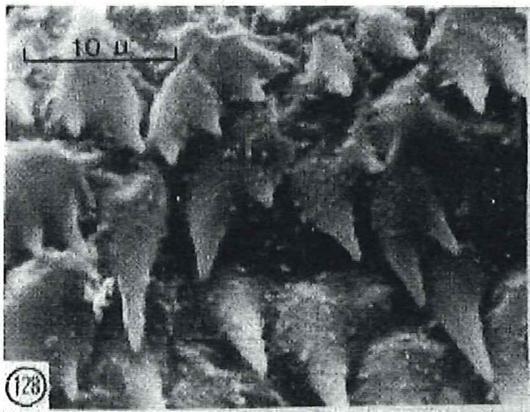

123


124

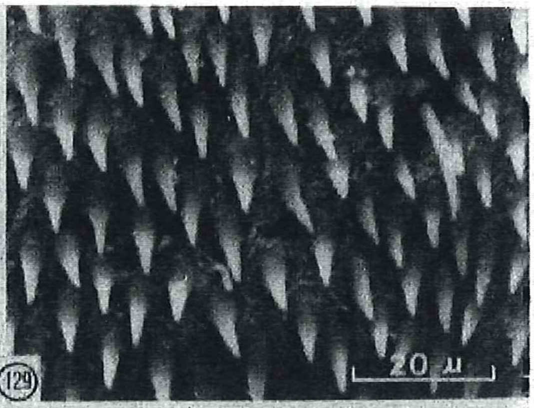

125


126

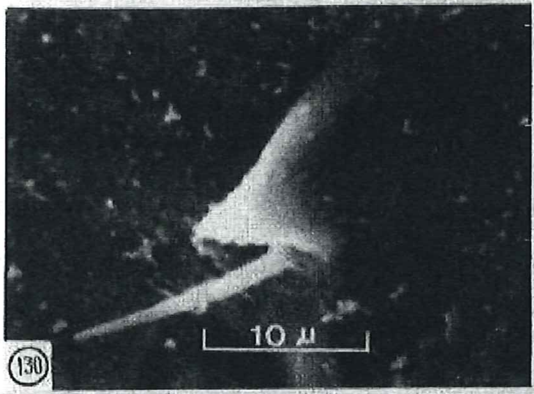

127



(128)



(129)



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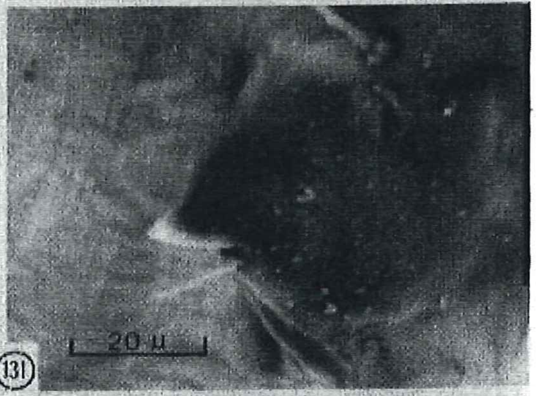

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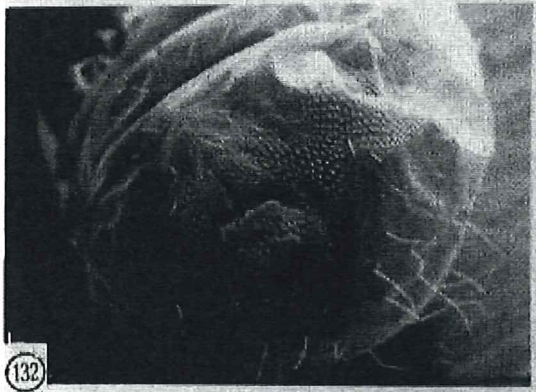

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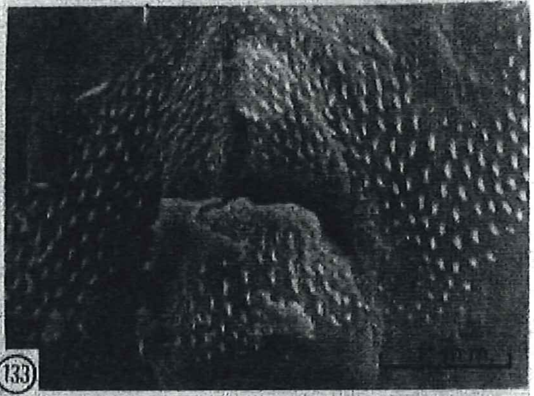

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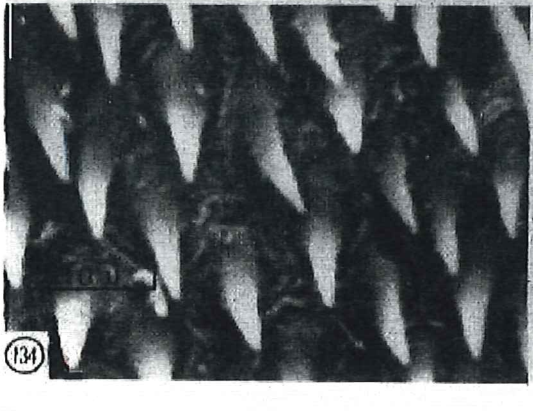

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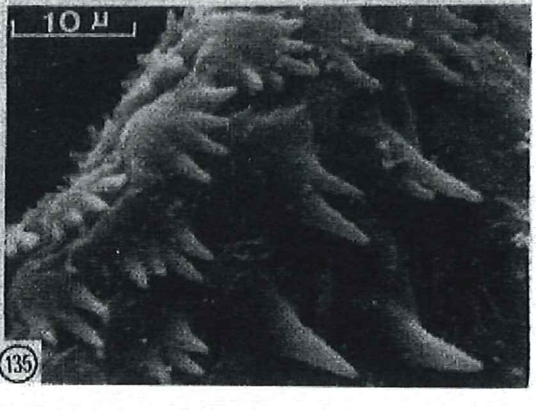

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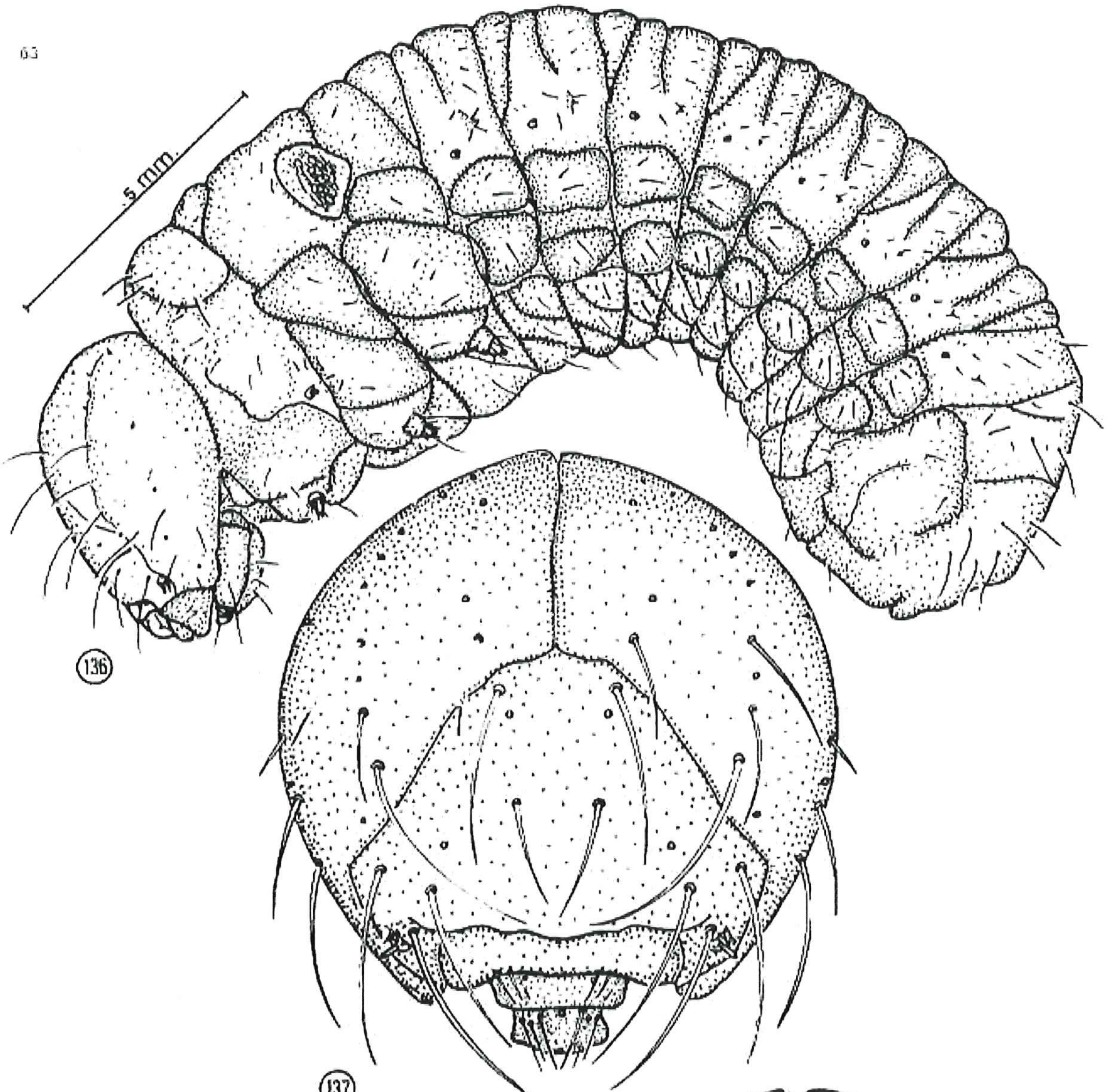

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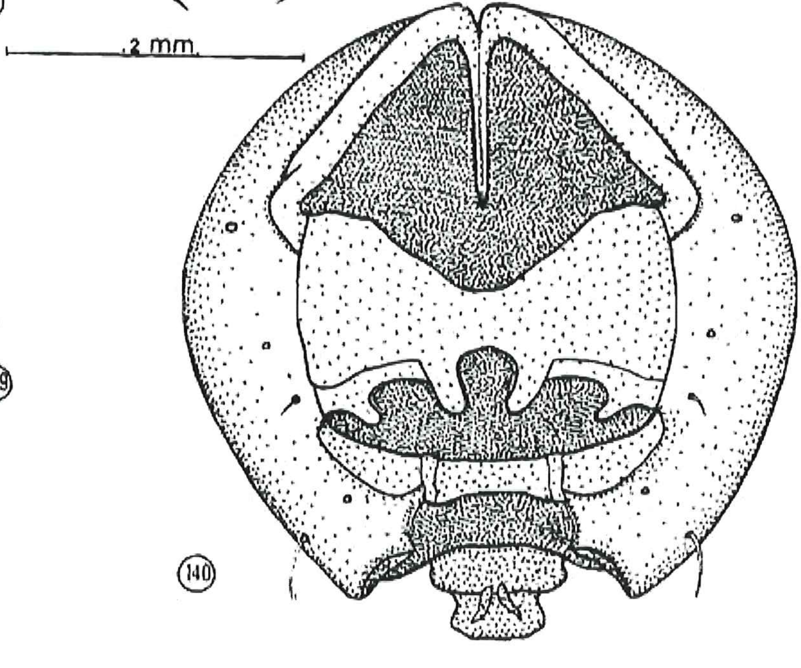

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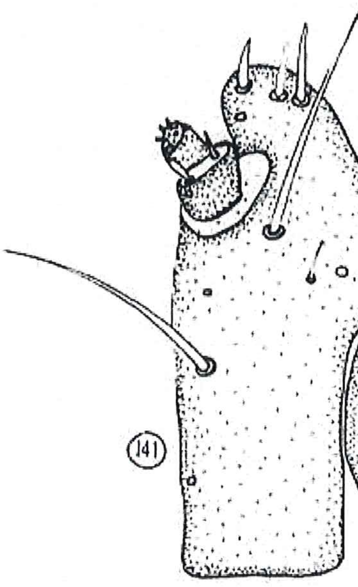
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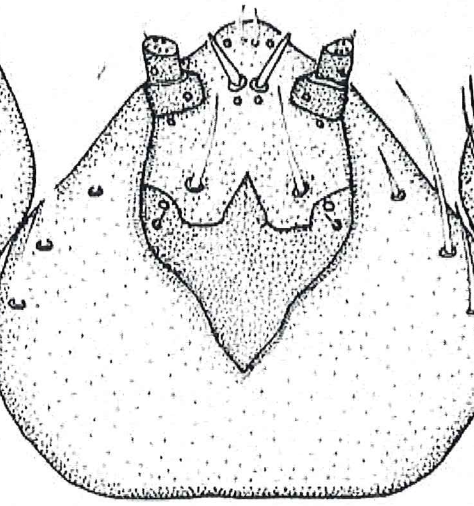
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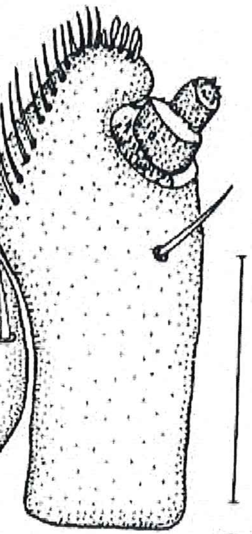
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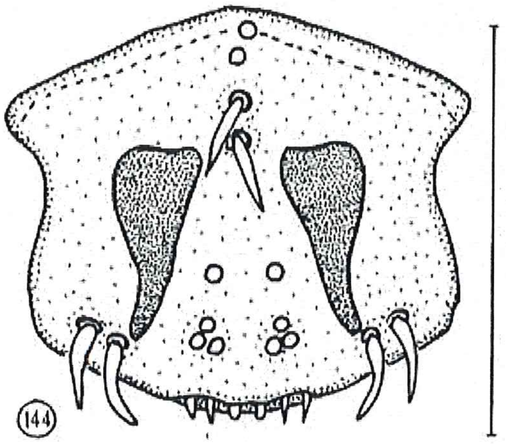
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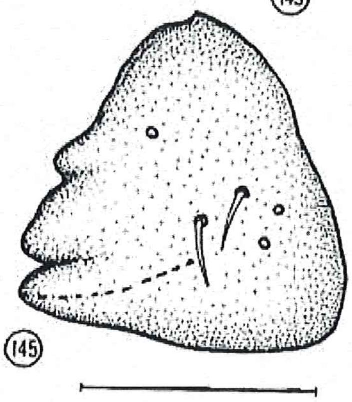
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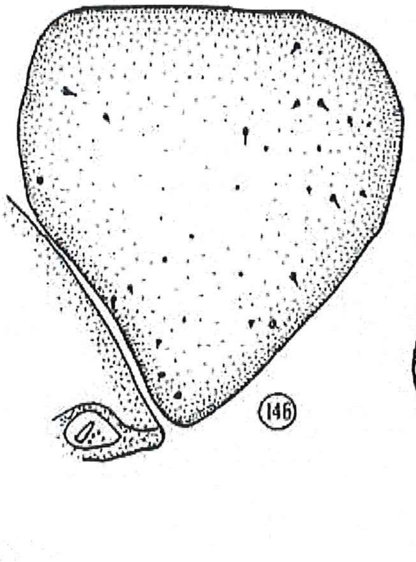
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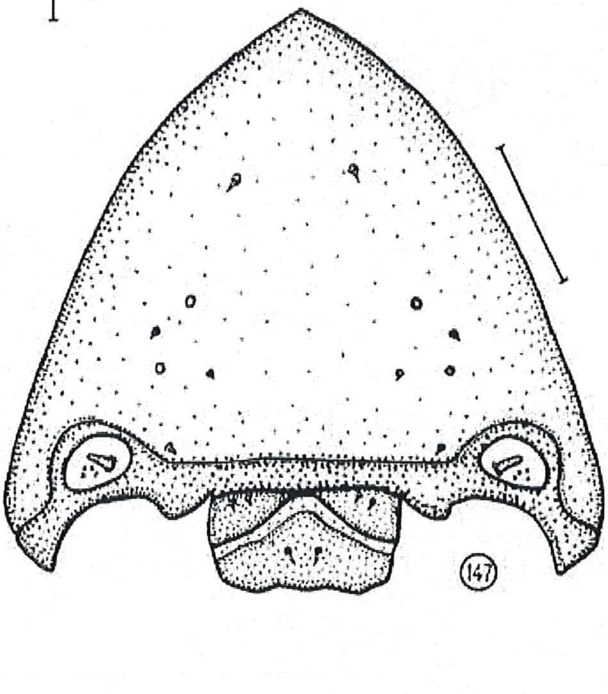
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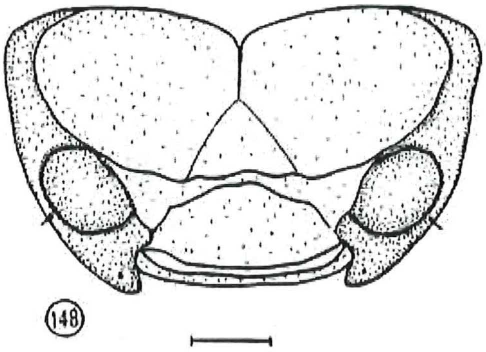
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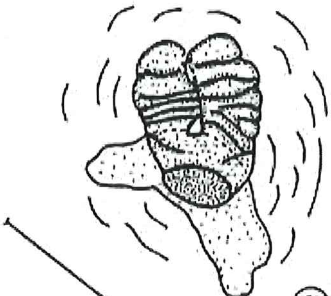
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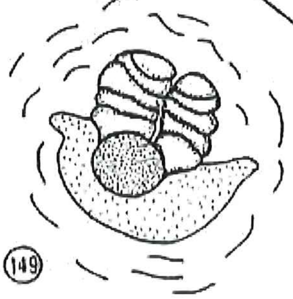
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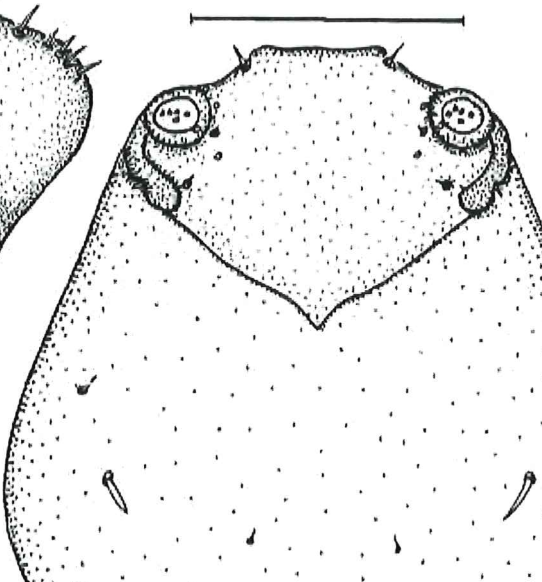
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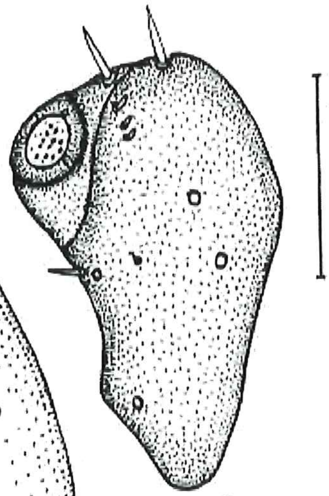
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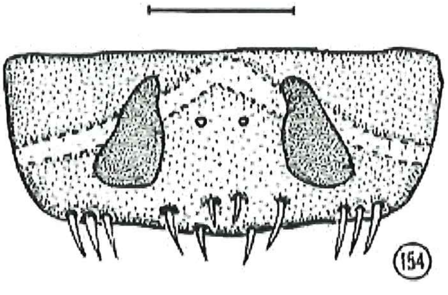
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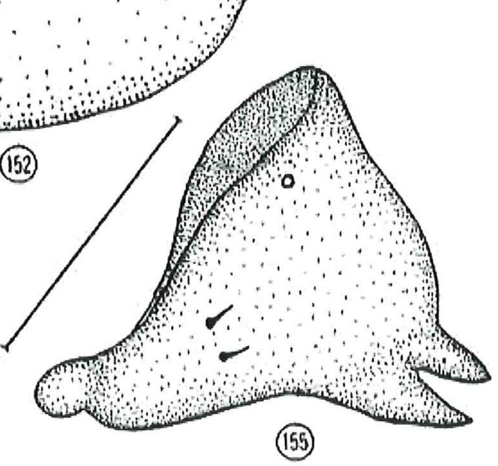
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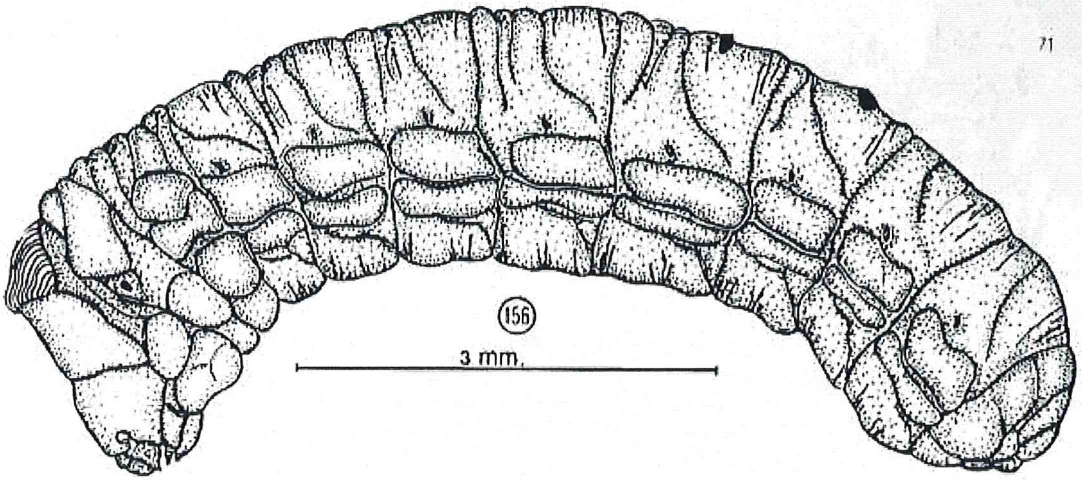

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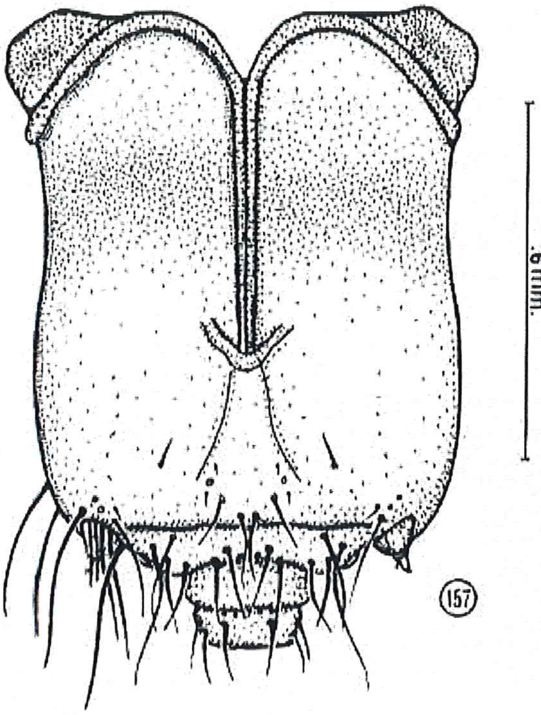

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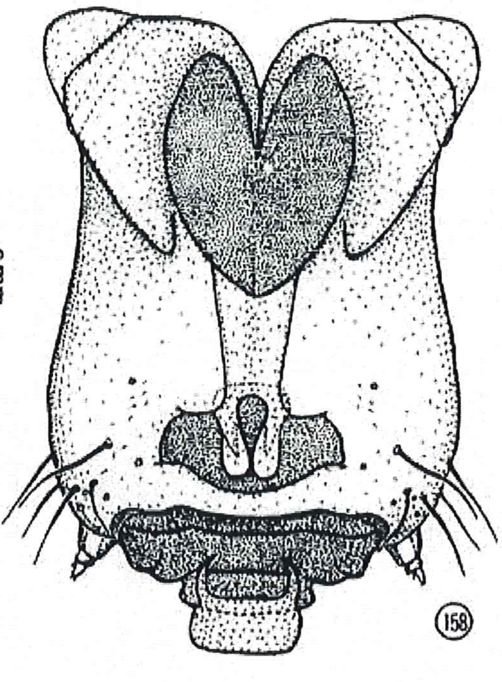

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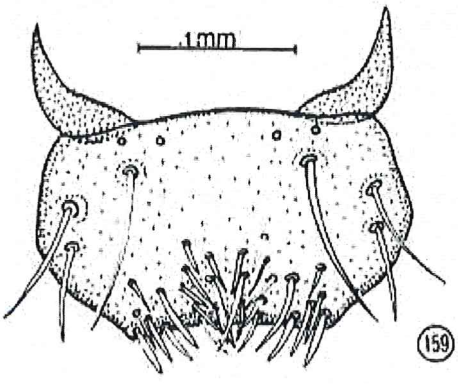

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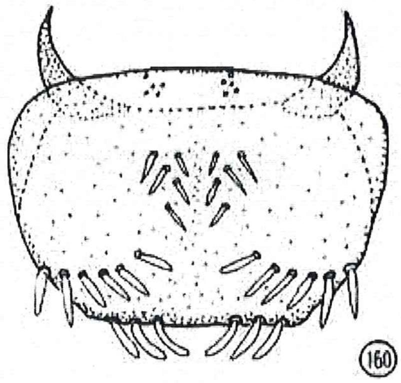

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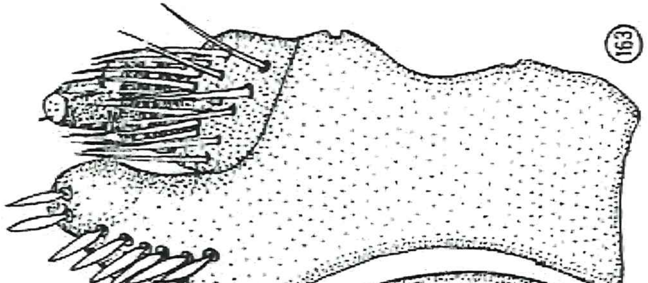

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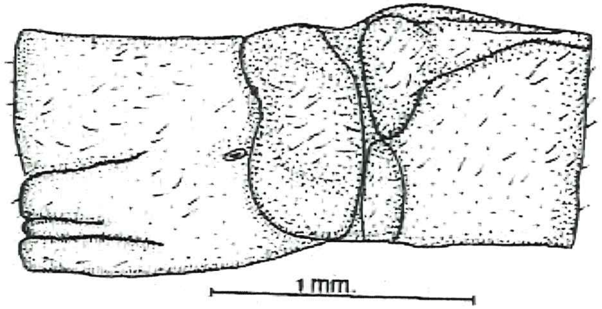

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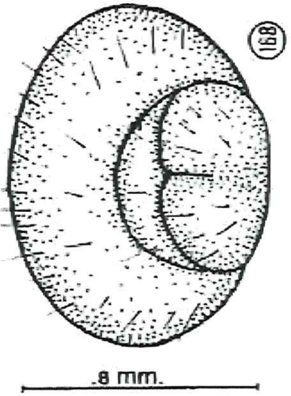

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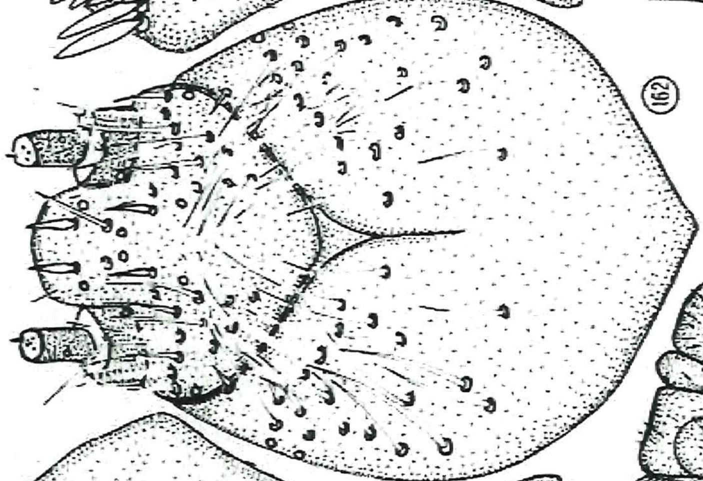

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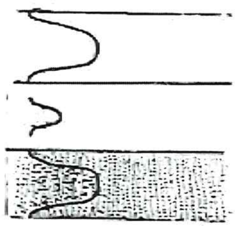

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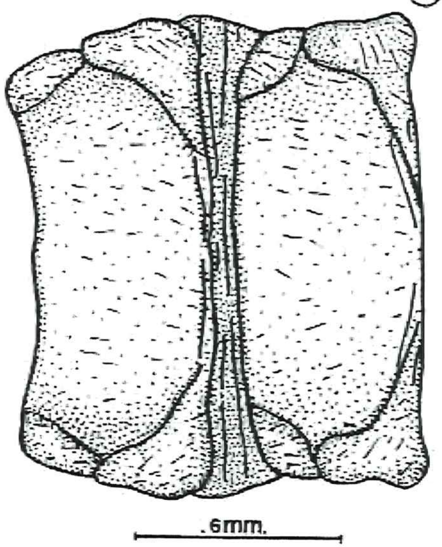

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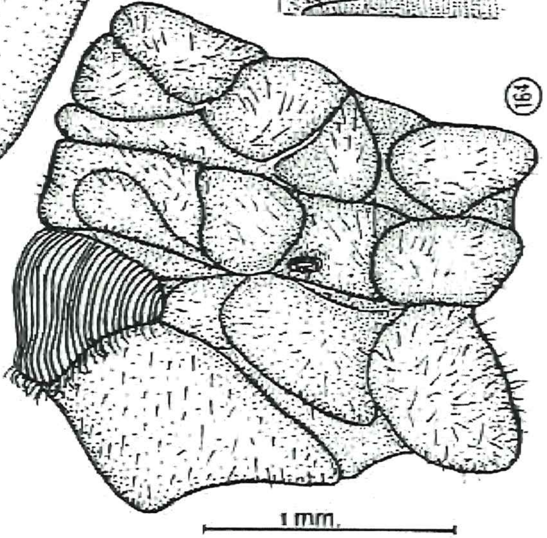

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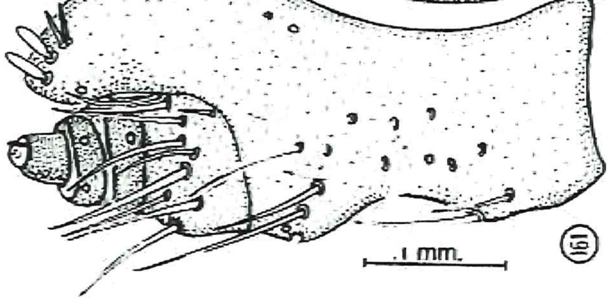

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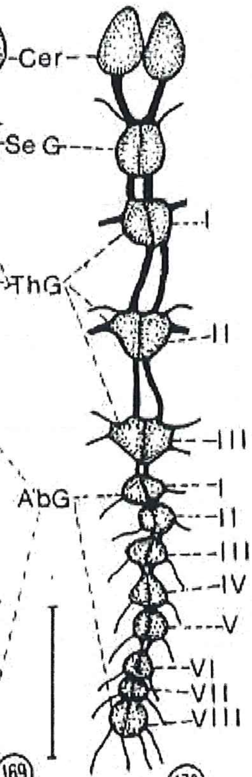

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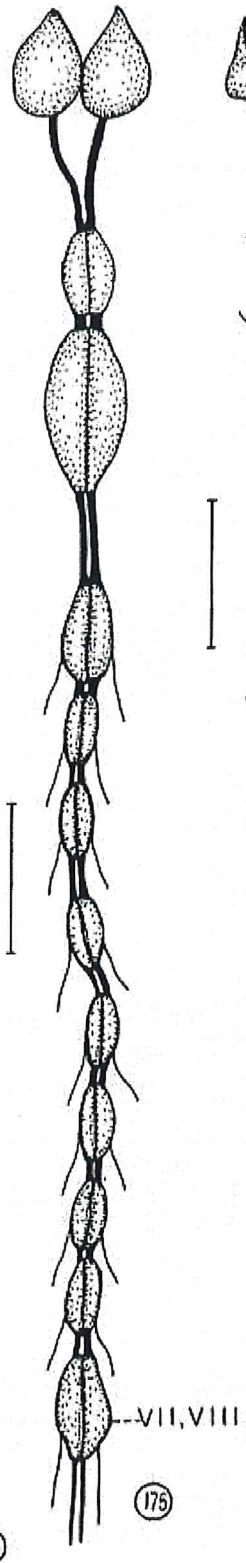

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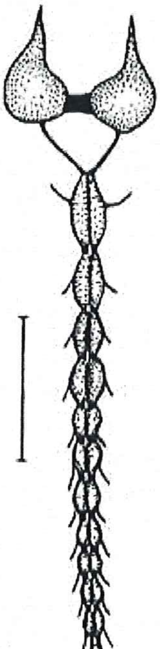
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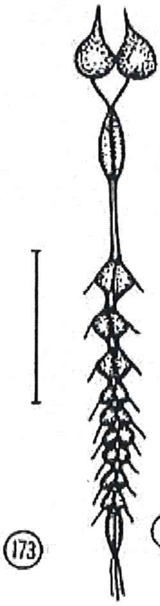
(178)


(173)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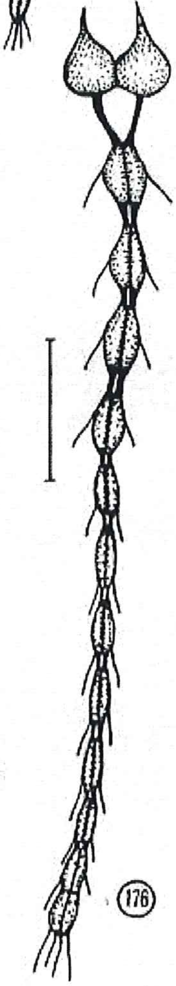
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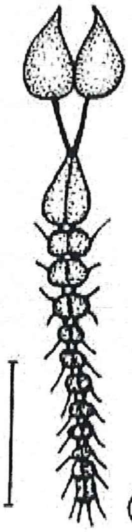
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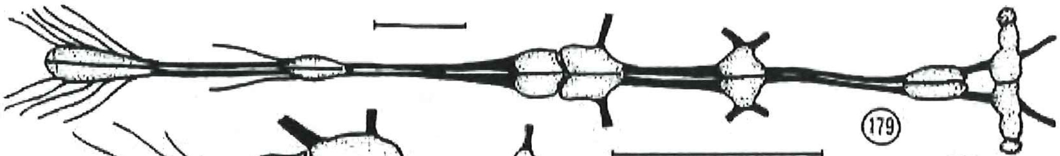
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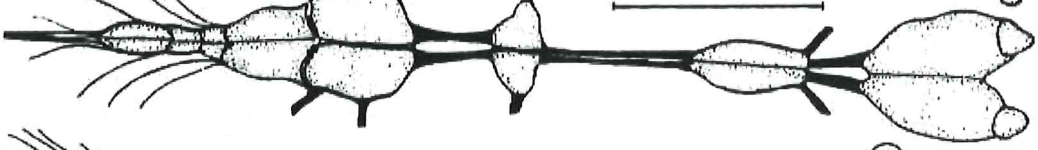
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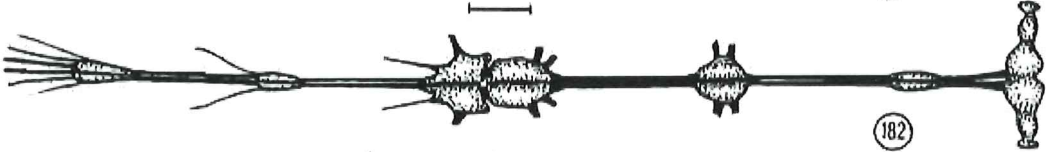
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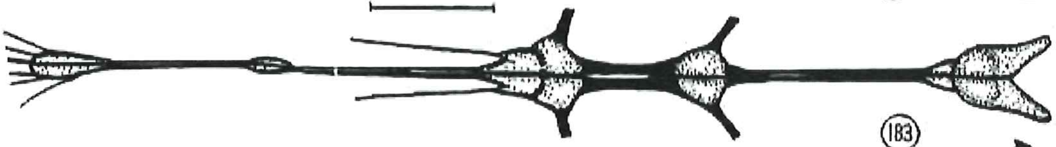
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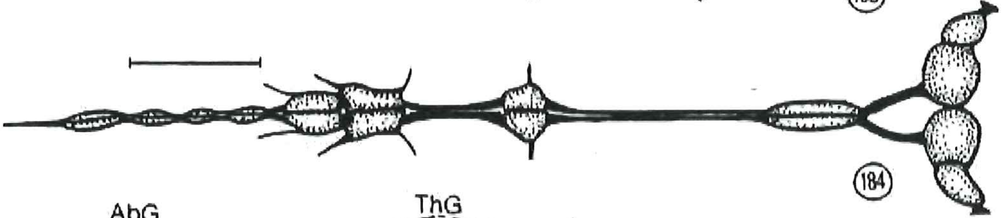
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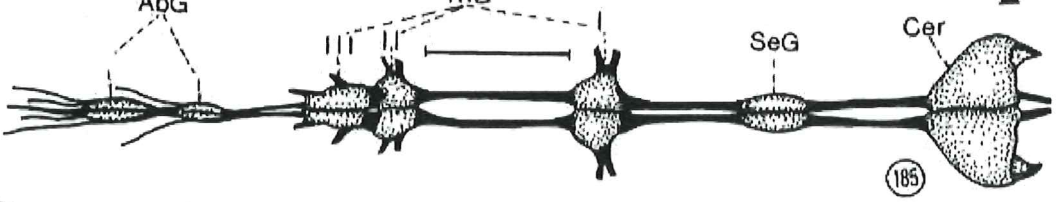

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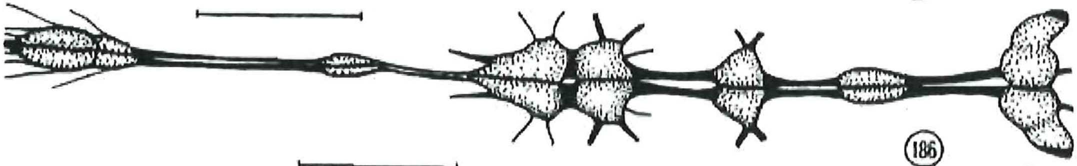
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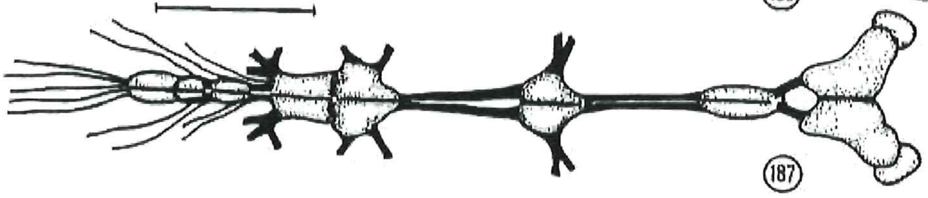
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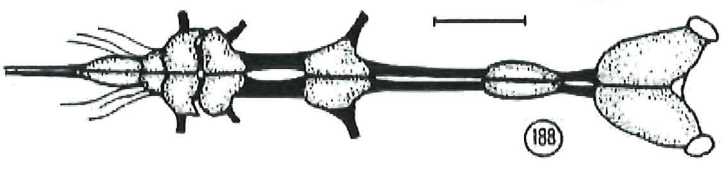
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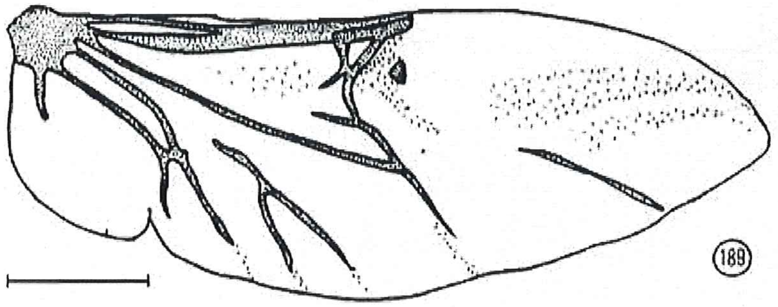

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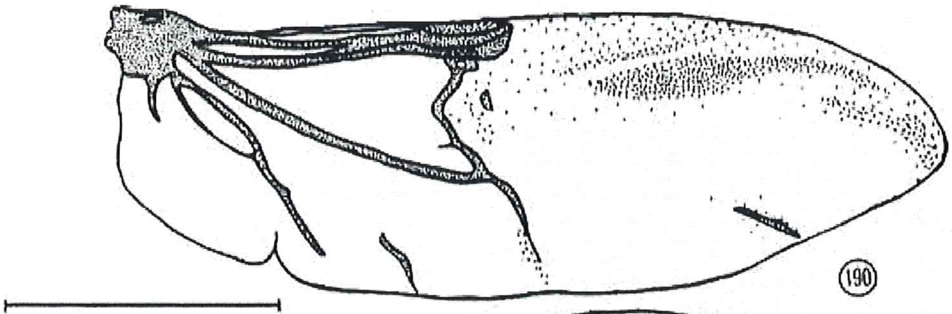

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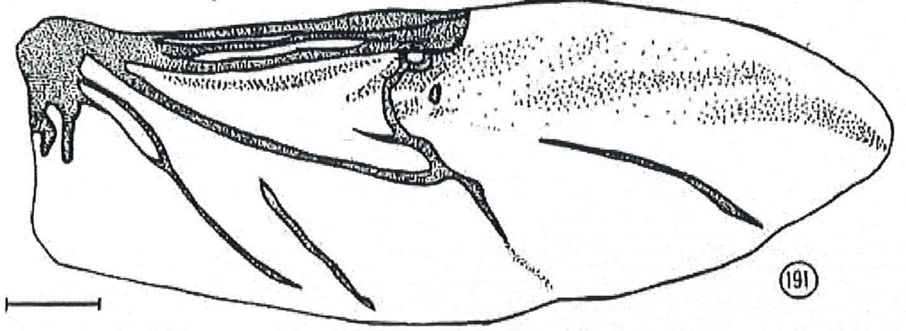

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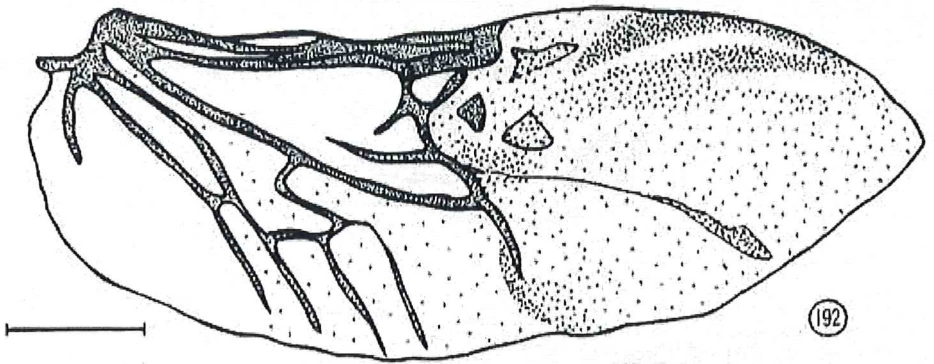

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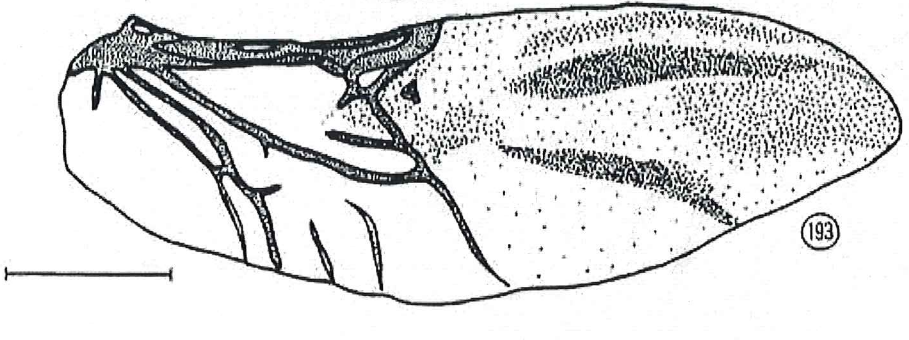

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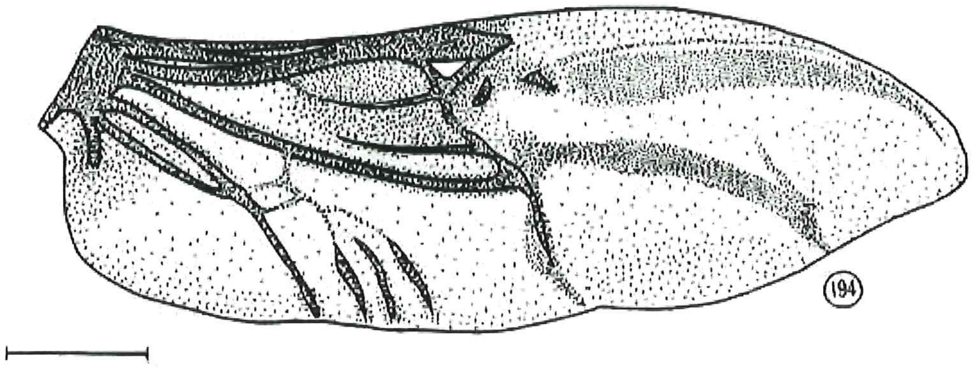

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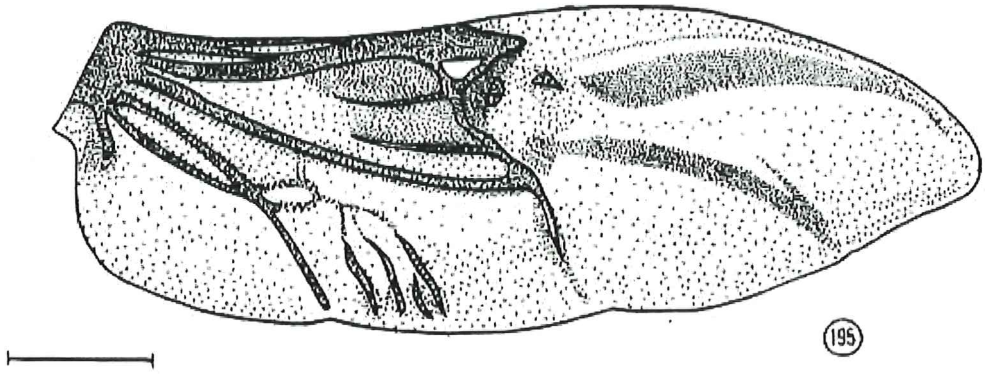

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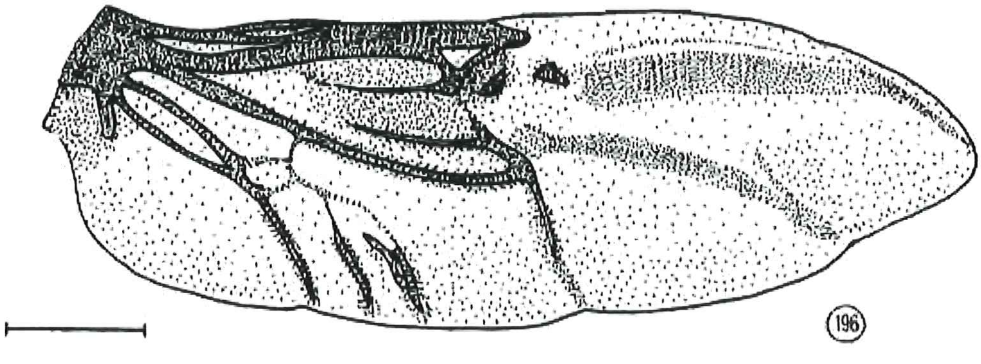

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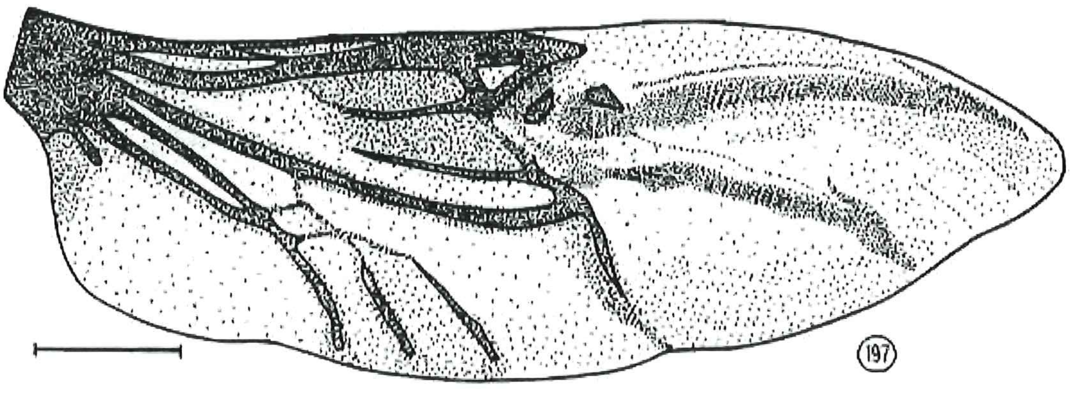

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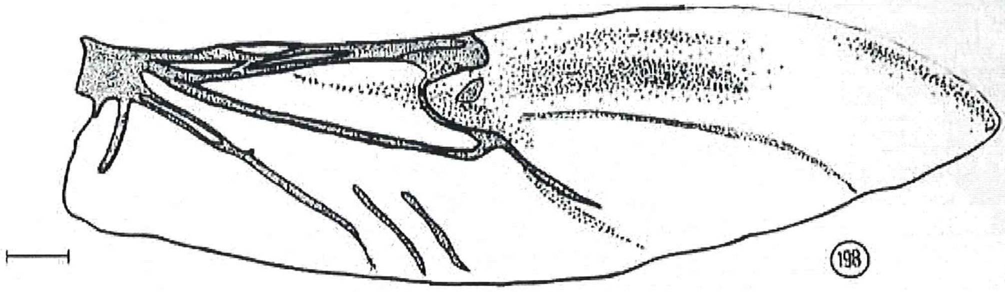

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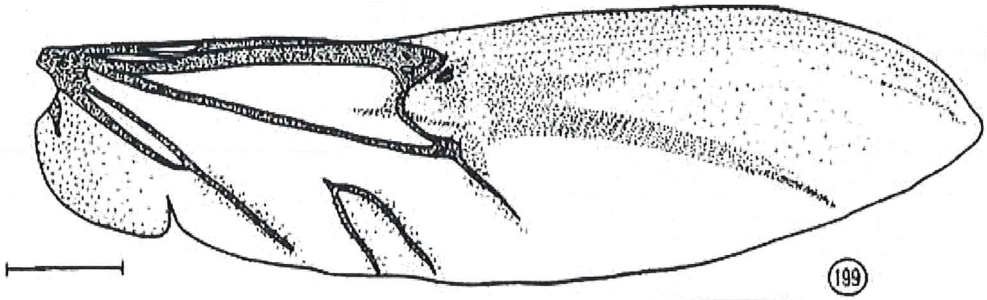

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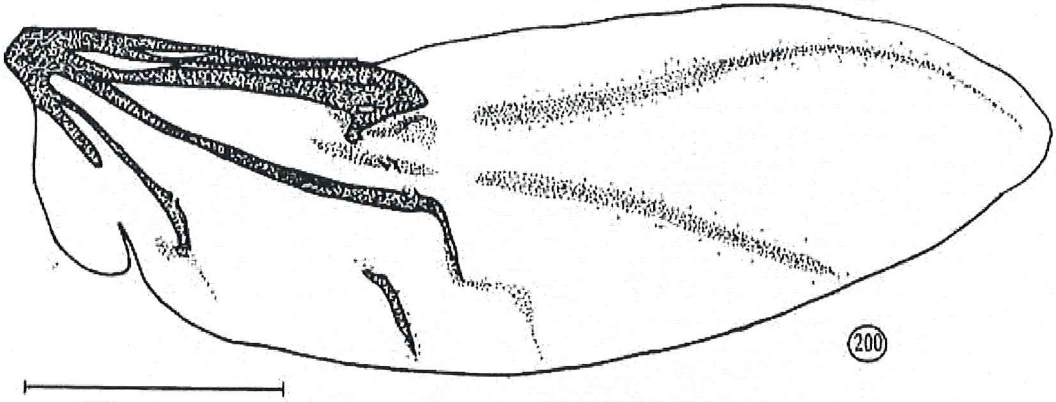

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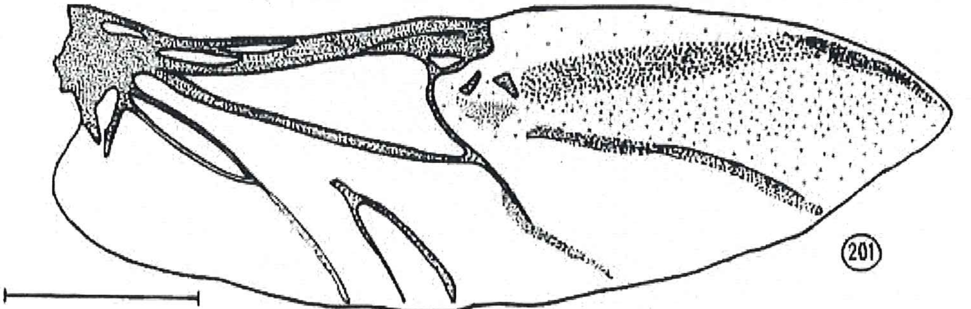

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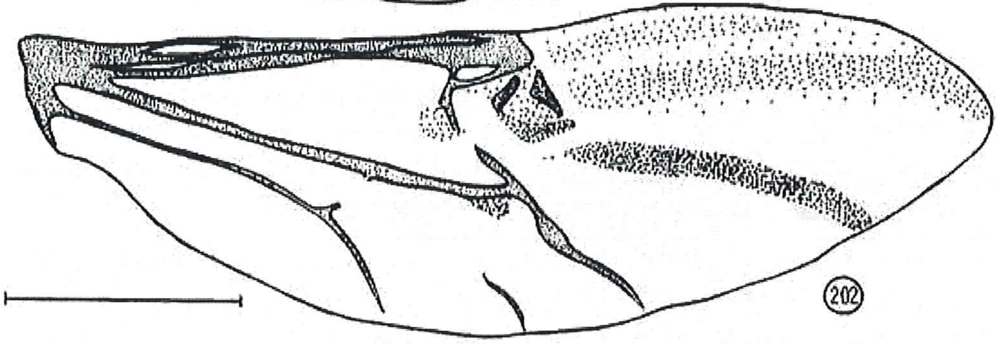
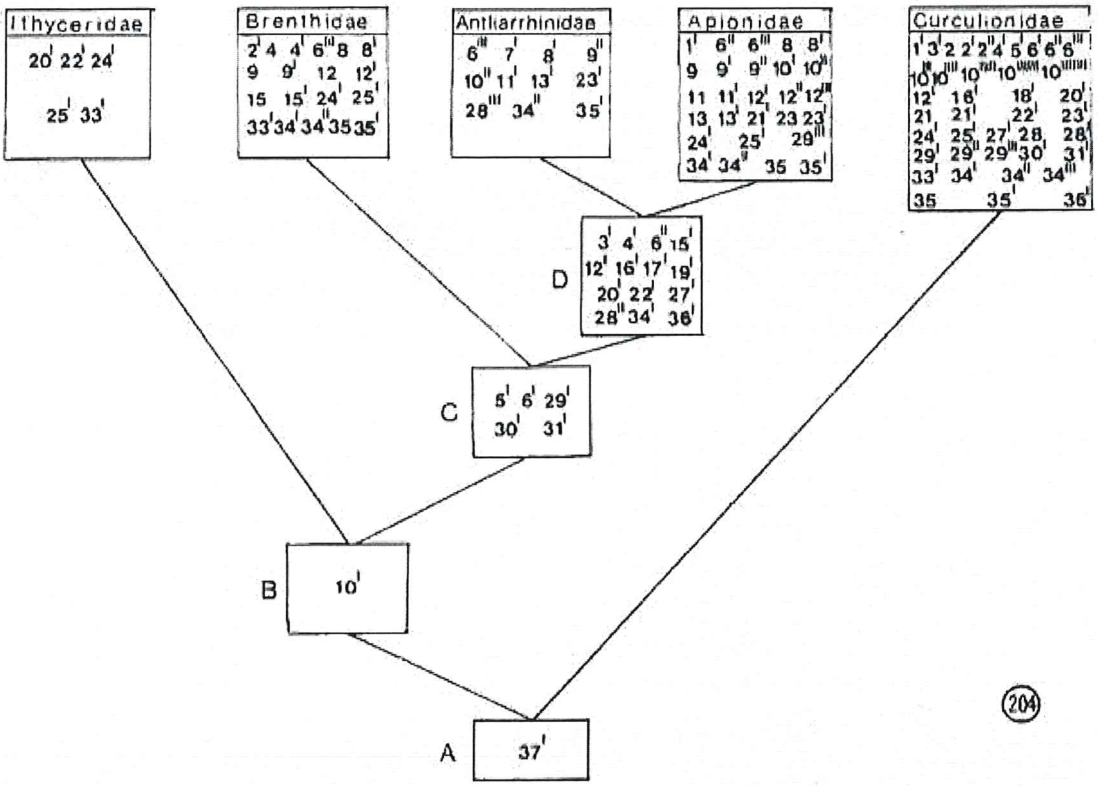
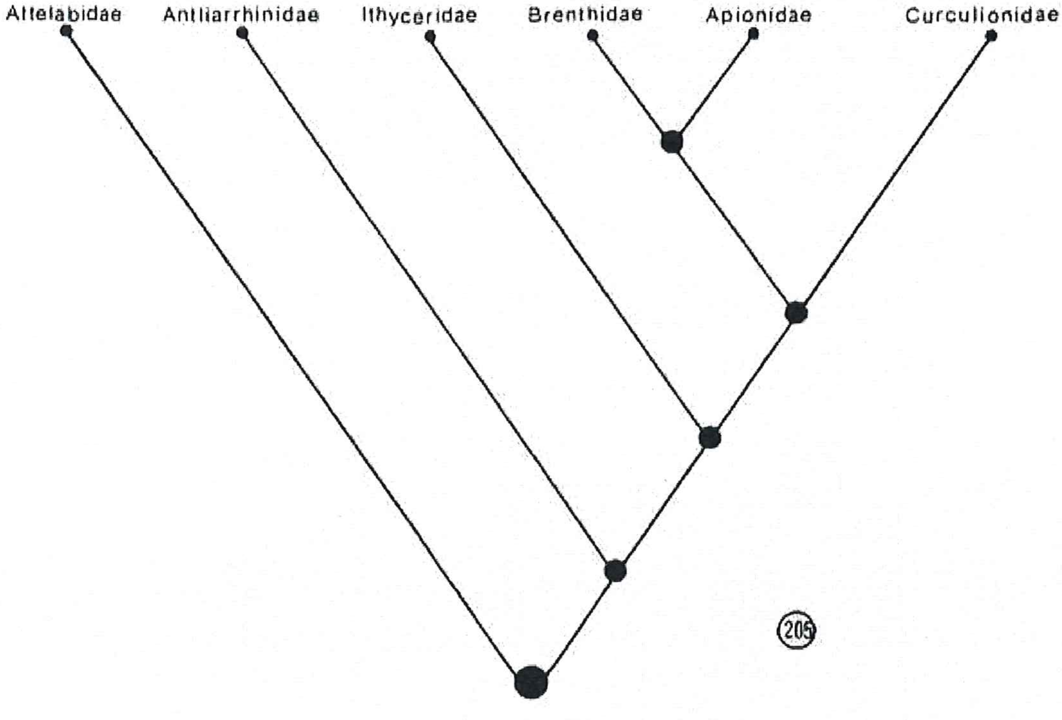


(202)

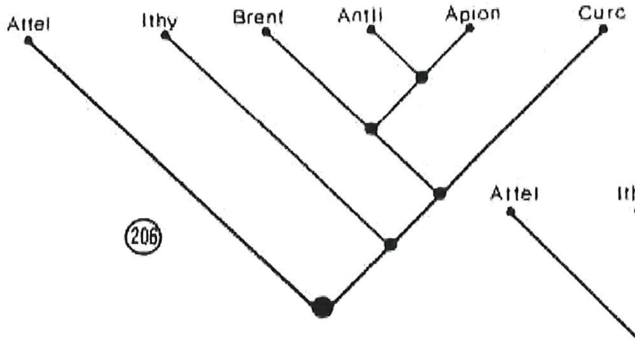

NORTH AMERICA
0
500
MILES
Northern Grey Form ●
Appalachian Form ■
Ozark Form ▲
203


Ithyceridae
20' 22' 24'
25' 33'
Brenthidae
2' 4 4' 6'' 8 8'
9 9' 12 12'
15 15' 24' 25'
33' 34' 34'' 35 35'
Antliarrhinidae
6''' 7' 8' 9''
10'' 11' 13' 23'
28''' 34'' 35'
Apionidae
1' 6'' 6''' 8 8'
9 9' 9'' 10' 10''
11 11' 12' 12'' 12'''
13 13' 21' 23 23'
24' 25' 28'''
34' 34'' 35 35'
Curculionidae
1' 3' 2 2' 2'' 4' 5' 6' 6'' 6'''
10'' 10''' 10'''' 10''''' 10'''''' 10'''''''
12' 16' 18' 20'
21 21' 22' 23'
24' 25' 27' 28 28'
29' 29'' 29''' 30' 31'
33' 34' 34'' 34'''
35 35' 36'
D
3' 4' 6'' 15'
12' 16' 17' 19'
20' 22' 27'
28'' 34' 36'
C
5' 6' 29'
30' 31'
B
10'
A
37'

(204)


Attelabidae
Antliarrhinidae
Ithyceridae
Brenthidae
Apionidae
Curculionidae

(205)



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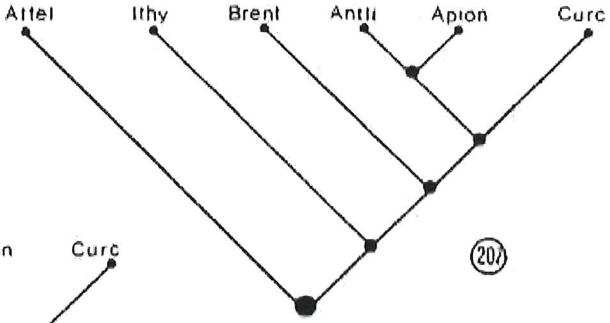
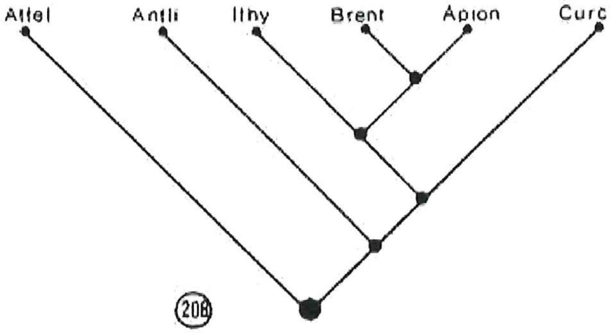


(207)



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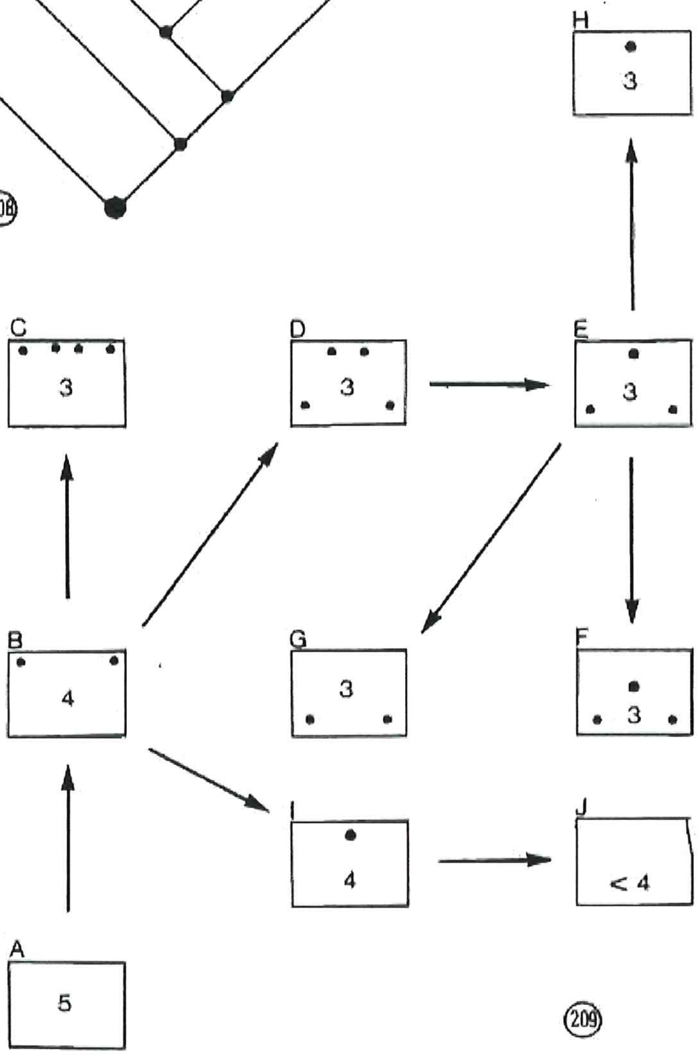

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