A COMPARATIVE STUDY OF THE EXTERNAL ANATOMY OF CONOPHTHORUS HOPKINS (COLEOPTERA: SCOLYTIDAE) WITH A TAXONOMIC INTERPRETATION OF SPECIES IN ONTARIO

by

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1. INTRODUCTION

The infestation of *Pinus* species in Ontario by species of *Conophthorus* Hopkins has been recognized for some time. Damage to the cones and shoots of eastern white pine, *Pinus strobus* Lamb., by *Conophthorus coniperda* (Schwarz) was noticed about 1884 (Harrington 1902a). Similar damage to red pine, *P. resinosa* Ait., due to *C. resinosae* Hopkins was reported by Harrington (1902a) to have been discovered several years later in 1887. Thomas and Lindquist (1956) and Herdy and Thomas (1961) have reported that shoots of jack pine, *P. banksiana* Lamb., are infested by *Conophthorus* species. The mining of Scots pine shoots, *P. sylvestris* Lamb., has also been mentioned by Thomas and Lindquist (1956), although the presence of *Conophthorus* species on this tree species does not seem to be extensive.

The beetles involved in the attacks on jack pine, according to Thomas and Lindquist (1956), were identified as *C. coniperda*, *C. resinosae*, *Conophthorus* possibly *coniperda*, and *Conophthorus* probably *resinosae*. The uncertainty in identification implied that further investigation was warranted. Certain details in the biology and ecology of *Conophthorus* reported in previous studies also suggested that identity of these species was uncertain. While the literature concerning these investigations has been reviewed and supplemented by personal observation, major emphasis has been placed on a detailed study of the adult anatomy, in an effort to resolve the taxonomic position of the species inhabiting jack pine in relation to *C. coniperda* and *C. resinosae*.

Throughout this report the beetles from *P. banksiana* will be referred to as *Conophthorus* "x".

2. THE GEOGRAPHICAL DISTRIBUTION OF *CONOPHTHORUS* SPECIES

The genus *Conophthorus* embodies seventeen known species. Fifteen of these occur on each of fourteen North American *Pinus* species, largely within the United States. The two remaining species are recent additions. *C. schwerdtfegeri* Schedl, was added to the genus by Schedl (1955) from *P. montezumae* Lamb. in Guatemala and *P. oocarpa* Schiede in Honduras. Wood (1962) described *C. mexicanus* from *Pinus* species in Mexico.

Three species of *Conophthorus* occur in Canada. *C. monticolae* Hopkins is found only in the cones of the western white pine, *P. monticola* Dougl. Its presence in the southern coast region of British Columbia, including Cowitiche (sic) Lake on Vancouver Island, and at Priest River, Idaho, was mentioned by Hopkins (1915a) and Keen (1958), and in Montana, Washington, and northern California by Ruckes (1963). Records of the Forest Insect Survey, Forest Entomology and Pathology Branch, Canada Department of Forestry, have indicated that *C. monticolae* was located on southern

Vancouver Island (presumably the Cowichan Lake record) (communication D. Evans 1960) and at Slocan, Crawford Bay, Salmo, and Trinity Valley on the mainland (comm. D.A. Ross 1960).

Blackman (1949) has stated that _C. coniperda_ "... occurs in Eastern Canada and as far south as North Carolina", while Swaine (1918) described its distribution as "... from Ontario to Nova Scotia, and southwards ..." Regional records of the Forest Insect Survey, Canada Department of Forestry, were checked during 1960 confirming the occurrence of _C. coniperda_ throughout Canada east of Manitoba.

Both _C. coniperda_ and _C. resinosae_ are apparently limited in their distribution to eastern North America (Table I) and probably occur throughout the range of their hosts, white and red pine respectively (Figures 1, 2).

The presence of _Conophthorus_ beetles in jack pine shoots was discovered in the vicinity of Lake Nipigon in northwestern Ontario in 1952 (Thomas and Lindquist 1956), at which time their known distribution was limited to Ontario. The host species is indigenous to most provinces of Canada, with the exception of British Columbia and Newfoundland, and occurs in Minnesota, Wisconsin, Michigan, and Maine, as well as in some widely scattered areas of New Hampshire, Vermont, Illinois, and Indiana (Figure 3). During 1962,

Table I. The geographical distribution of C. coniperda and C. resinosae, primarily from the literature.

	Location	Authority
C. coniperda	Ontario	Swaine (1909, 1918); Hopkins (1915a)
	Michigan	Schwarz (1895); Swaine (1909, 1918); Hopkins (1915a)
	New York	Swaine (1909)
	Maine	Hopkins (1915a); Godwin (1958)
	New Hampshire	Hopkins (1915a)
	Connecticut	Godwin (1958)
	Massachusetts	Schwarz (1895); Hopkins (1915a)
	Rhode Island	Hopkins (1915a)
	Virginia	Swaine (1909); Hopkins (1915a)
	Pennsylvania	Swaine (1909)
C. resinosae	Ontario	Swaine (1918); Blackman (1949); Lyons (1956)
	Quebec	Lyons (1956)
	Nova Scotia	Lyons (1956); Forest Insect Survey, comm. Forbes 1960
	Minnesota	Lyons (1956); Sandve (1957)
	Wisconsin	Lake States Forest Experiment Station (1963)
	Michigan	Lyons (1956); (1)
	New York	Blackman (1949); Lyons (1956)
	Maine	Hopkins (1915a); Blackman (1949)
	New Hampshire	Hopkins (1915a); Blackman (1949); Lyons (1956)

(1) Personal identification of C. resinosae collected in red pine shoots, Kalkaska county by P. Flink, October 1962.

specimens collected from jack pine shoots in Michigan were identified as _Conophthorus_ "x" by Dr. J.B. Thomas, Forest Insect Laboratory, Sault Ste. Marie, Ontario. In 1963, an additional specimen of _Conophthorus_ "x" was taken from a jack pine shoot at Gypsumville, Manitoba, by the Forest Insect Survey. Prior to this, the Forest Insect Survey apparently had no knowledge regarding the presence of _Conophthorus_ "x" in the other provinces of Canada where jack pine is known to occur, namely Alberta (comm. Brown 1960), Saskatchewan or Manitoba (comm. Prentice 1960), Quebec (comm. Martineau 1960) or in the Maritimes (comm. Forbes 1960). Dr. W.J. Carroll, Forest Entomology and Pathology Branch, Canada Department of Forestry (comm. 1960), could find no information of _Conophthorus_ species in Newfoundland, where jack pine does not naturally occur, but where both red and white pine are present.

The distribution of all species of _Conophthorus_ in Ontario is probably coincident with the range of their host trees. Lyons (1956) mentioned the prevalence of _C. resinosae_ in the area lying between Sault Ste. Marie, Ottawa, and Lake Simcoe, in particular. The Forest Insect Survey, Sault Ste. Marie, has recorded the occurrence of _C. resinosae_ and _C. coniperda_ at numerous points throughout the Province. The distribution of the jack pine infestation in Ontario has also been examined, and as pointed out earlier by Herdy and Thomas (1961), the host species in the forest districts including Port Arthur, Geraldton, White River, and Gogama have been particularly severely attacked. The presence of Conophthorus "x" at many other localities within the range of jack pine has also been established during subsequent surveys.

3. LITERATURE REVIEW AND HISTORICAL OUTLINE

Reference to either C. coniperda or C. resinosae, or to both species, has been made by Packard (1890), Harrington (1891, 1902a,b), Hamilton (1893), Schwarz (1895), Felt (1906), Swaine (1909, 1918), Hopkins (1915a), Doane et al (1936), Blackman (1949), Lyons (1956), Godwin (1958, 1959), Northeastern Forest Experiment Station (1958, 1959), and Henson (1961a,b, 1962).

The Conophthorus beetle was probably first collected in North America about 1850. The Fitch collection was reported by Hopkins (1915a) to have included a specimen of this genus bearing that date. Further specimens, Hopkins indicated, had been in the collection of Hubbard and Schwarz from 1877, that of Harrington at Ottawa in 1895, and since 1893 in the collection of Hamilton at Allegheny, Pennsylvania.

The early collectors were apparently confused as to the actual identity of the beetles collected. Some of this confusion, no doubt, arose as a result of an inadvertent error by LeConte. Schwarz (1895) revealed that some of a series of Scolytids, which he submitted to LeConte for identification in 1877, resembled specimens later reared by Hamilton from pine cones. According to Schwarz, LeConte had subsequently returned the material, identified as _Dryocoetes affaber_ Mannerheim. Similar beetles in other collections were reported by Schwarz to be labelled in this manner.

The initial observations on the activities of a _Conophthorus_ beetle have been credited to Harrington by Schwarz (1895). These observations conducted near Ottawa, were originally published by Packard (1890) as excerpts from a letter by Harrington to Packard. Later, publications by Harrington (1891, 1902a, b) followed. In his letter to Packard, Harrington related the discovery of the larva and adult of what he believed to be _D. affaber_, in small, undeveloped cones of red pine. Later in 1891, Harrington mentioned attacks by this beetle on white pine shoots and pointed out that both cones and shoots of red pine were infested with either _D. affaber_ or _Dryocoetes septentrionalis_ (sic) Mannerheim. In 1902 (a,b) he stated that both red and white were attacked by what was now known as _Pityophthorus coniperda_, causing abortion of the cones and prevention of seed development. His first collections of this beetle were reportedly from white pine on the

Gatineau, near Ottawa, in late May of 1884. At this time, he noticed injury to young terminal buds by a boring insect. It was this observation that led to his 1891 report on _D. affaber_. Near Aylmer, Quebec, in 1887, Harrington found red pine shoots and cones infested by a beetle he believed to be larger than those previously collected from hard, shrivelled, and underdeveloped white pine cones, but which was apparently determined as the same species. Once again, in 1901, Harrington reported examining white pine in the same locality as in 1884 and this resulted in the discovery of cones on the ground containing _P. coniperda_.

Hamilton (1893) concluded that a species of beetle he had taken from white pine cones at Sparrow Lake, Ontario, was similar to that mentioned in Packard's Report. He was convinced, however, that they were not a species of _Dryocoetes_, since specimens submitted to Hopkins and compared with _D. affaber_ as determined by Eichhoff had suggested to Hopkins that these insects might belong to an entirely different genus. Hamilton concluded that differences existed in the antennal club, tibiae, elytral striation and punctation, and in the color of the adults. He established that oviposition occurred during early summer; the infested cones dropped prematurely when only three to four inches long; larvae matured by late July; and that two or more mature adults were present in some cones by mid-September.

The original taxonomic description of C. coniperda as Pityophthorus coniperda by Schwarz (1895) was reported to be based on specimens collected at Marquette and Eagle Harbor, Michigan; Cambridge, Massachusetts, and Fortress Monroe, Virginia. Schwarz also mentioned having examined specimens collected in New York and Pennsylvania. In this material Schwarz was apparently able to recognize distinct differences, chiefly in the antennae and anterior tibiae, from that given in the generic description of Pityophthorus by Eichhoff. Also he noted that the adults of C. coniperda were larger, less elongate, and that their elytral declivity differed in structure from that of Pityophthorus. Schwarz considered the immediate erection of a new genus on the basis of this single species was not justifiable, particularly when, as he pointed out, other more diverse species had previously been readily accepted. However, Hopkins (1915a) placed this species in his newly constituted genus, Conophthorus, at its inception.

C. resinosae was described as a new species by Hopkins in 1915, with the female type, from red pine cones, in the Harrington Collection. Hopkins (1915a) gave its distribution as "Maine, New Hampshire, Ontario, Canada, in cones and shoots of Pinus resinosa".

4. COMPARATIVE LIFE HISTORIES AND BEHAVIOR OF *CONOPHTHORUS* SPECIES

To date, a number of species of the genus have been under investigation with respect to their life histories, habits and behavior. Those documented are: *Conophthorus lambertianae* Hopkins by Miller (1914, 1915), Struble (1947), and Ruckes (1957); *Conophthorus ponderosae* Hopkins by Miller (1914, 1915); *Conophthorus edulis* Hopkins by Little (1943); *C. resinosae* by Lyons (1956); *Conophthorus radiatae* Hopkins by Ruckes (1958) and Schaefer (1962, 1963); *C. coniperda* by Godwin (1958, 1959) and Henson (1961a,b, 1962); *C. monticolae* by Williamson (1961); and *Conophthorus* "x" inhabiting jack pine shoots in Ontario by Thomas and Lindquist (1956) and Herdy and Thomas (1961).

C. coniperda, *C. resinosae*, and *Conophthorus* "x" exhibit similar life histories, and with few exceptions, similar habits. Unfortunately, studies conducted on each species have been in different locations. *C. resinosae* was investigated by Lyons (1956) in central Ontario, while Godwin (1958, 1959) examined some aspects of *C. coniperda* near New Haven, Connecticut. The study on the jack pine-inhabiting species by Herdy and Thomas (1961) took place in northwestern Ontario. Under these circumstances the occurrence of certain events in the biology of these species (Table II) shows slight differences, which undoubtedly are minor variations, that can be attributed to local climatic conditions.

TABLE II. Occurrence & measurement of biological events in species of Conophthorus compiled from the literature.

EVENT	C. coniperda (New Haven, Conn.)	Conophthorus "x" (northwestern Ontario)	C. resinosae (central Ontario)
Adult emergence from overwintering sites.	April 21	May	May
Duration of oviposition period	May 19 to July	May 24 to July 16	mid-May to mid-July
Incubation period of eggs	not determined	estimated at 17 days	insectary reared in 16 days
Size of eggs in millimeters	0.75 ± 0.04 by 0.50 ± 0.04 Range 0.66-0.83 by 0.46-0.68	unpreserved 0.88 by 0.60. Range 0.70-1.19 by 0.44-0.84	preserved Range 0.86-1.02 by 0.53-0.79
Number of larval instars	2	2	2
Initial appearance of larvae in field	May 27	June 5	not determined
Duration of first instar	not determined	4-13 days in the insectary	estimated at 13 days
Duration of second instar	not determined	5-17 days in the insectary	estimated at 22 days
Size of larval headcap			
Instar I	0.33 ± 0.02	preserved 0.39 ± 0.03. Reared 0.36 ± 0.026	0.42 ± 0.003
Instar II	0.49 ± 0.02	preserved 0.54 ± 0.015. Reared 0.505 ± 0.026	0.61 ± 0.003
Initial appearance of pupae	July 10	in insectary on June 30. In field on July 4.	not determined
Duration of pupal period	not determined	6-13 days in the insectary	estimated at 19 days
Appearance of callow adults	July 17	July 8	mid-July

The emergence of overwintering adults of C. coniperda, C. resinosae, and Conophthorus "x", occurs within a period of a few weeks in each region. In Ontario, Lyons (1956) observed that C. resinosae began attacking the developing second-year cones and current year's shoots in May. Godwin (1958) established that C. coniperda began attacking second-year white pine cones about April 21, 1958, near New Haven. In jack pine, Conophthorus "x" has been known to begin mining shoots during May after emerging from vegetative buds on the ground (Herdy and Thomas 1961).

The initial mining activities during the early season may not be for oviposition, since Lyons (1956) found that "during the first few weeks the beetles feed individually and do not mate or oviposit." Godwin (1958) stated, "in many cones, no eggs are laid. In the weekly collections the percentage of cones containing no eggs ranged from 50 to 70 per cent, with the percentage decreasing as the season progressed." Herdy and Thomas (1961) merely indicated with respect to Conophthorus "x", that "a number of attacks in early May do not result in oviposition and may be feeding sites". These observations are also supported by those of Henson (1961a) who established that in C. coniperda "the gonads develop only after feeding."

The characteristic mining activities of C. resinosae in red pine cones were described by Lyons (1956), and these are essentially similar to those taking place in white pine cones, according to Godwin (1958), and in jack pine shoots (Herdy and Thomas 1961). Lyons (1956) observed that the female C. resinosae, sometimes exclusively, attacks the underside of the cone close to the petiole, making a tunnel into the rachis of the cone. Further mining then occurs along the longitudinal axis of the cone, throughout its length, with the development of niches in the sides of the mine into which eggs are placed and then surrounded with debris. The longitudinal dimension of the cone has been suggested by Lyons (1956) as the limiting factor in determining the number of eggs deposited in each cone. This number, he found, varied between one or two, but reached 10 or 11 in the larger cones. After oviposition, the female was observed to retreat from the cone through the axial tunnel, pausing to plug the entrance with debris and resin. An accumulation of resin and debris invariably occurs about the entrance hole of both cone and shoot mines, so that the attacks may be immediately identified.

White pine cones are attacked by C. coniperda, Godwin (1958) reported, at the junction of the cone and the petiole, with the initial penetration being so rapid that it is completed within an hour. The beetle then constructs a distal tunnel, placing eggs singly in lateral niches within the mine. After completing oviposition, Godwin found that the female simply mined through the apex of the cone to escape, rather than returning to the entrance as _C. resinosae_ had been observed to do by Lyons (1956). Godwin determined the seasonal average of eggs per cone to be three, but in northwestern Ontario, rearing _C. coniperda_ in white pine cones for anatomical studies has shown that fifteen or more eggs may be found in a single cone, with a range of three to ten common.

The mining behavior of _Conophthorus_ "x" is similar to that of the cone-mining species (Herdy and Thomas 1961). During the early attacks access to the interior of the shoot is gained through an entrance hole cut in the outer bark about three-quarters of an inch below the base of the current year's growth. Later in the season, when growth has progressed sufficiently, attacks may occur anywhere along the current shoots, although these are usually confined to within an inch or so of the base of the current bud. After penetrating through the bark, the beetle completely mines out the xylem of the stem, leaving the shoot supported by the undamaged portion of the bark. A mine, about one inch in length, is made distally through the center of the shoot, with eggs being placed in individual niches in the tunnel sides. After oviposition has been completed, the female is believed to escape from the shoot through the entrance, since exit holes were never found on any portion of the shoot above the tunnel entrance. The activities of the beetle kill the shoot, but when apical growth is sufficiently advanced, the most immediate effect is to cause it to wilt and droop. This provides an investigator with a readily perceptible sign of shoot infestation.

Jack pine shoots from an infested stand were collected and enclosed for the remainder of the season after oviposition had occurred during 1958 (Herdy and Thomas 1961). When dissected, they revealed that from one to seventeen progeny were produced in individual shoots, although the average was only 4.2. Dissection of 213 shoots in 1958 and 586 shoots in 1959, collected after oviposition, placed the average at 2.7 and 3.2 for the respective years, with the largest number of individuals recorded for a single shoot being twelve.

There are valid indications that individual beetles may make successive attacks during the infestation period. Lyons (1956) reported that one _C. resinosae_ female under observation successfully invaded four cones; three other beetles each mined three cones. Intervals of two to sixteen days, with a mean of 7.5 days, occurred during consecutive attacks. Godwin (1958) referred to successive infestations of four cones by some _C. coniperda_. At the beginning of the season he estimated an interval of eighteen days between successive attacks. This period was reduced to eleven and seven days respectively for the later infestations. Herdy and Thomas (1961) believed that individual _Conophthorus_ "x" mined a succession of jack pine shoots although this was not specifically established and the interval between consecutive attacks was not determined.

Although primarily associated with the infestation of developing second-year cones, _C. coniperda_ and _C. resinosae_ are also known to attack the shoots of their host, and _C. coniperda_ attacks the first-year cones as well. Attacks on white pine shoots, occurring at the upper six- to ten-foot levels, after the available cones had been mined, were observed by Godwin (1958). No mention was made of oviposition or brood production within these shoots. Reference to the infestation of _P. strobus_ shoots by _C. coniperda_ was made by Harrington (1891, 1902a), Hopkins (1915a), and Swaine (1918) prior to that of Godwin. Godwin (1958) also mentioned mining of white pine first-year conelets during the summer, but specifically stated that "no larval brood was found in any of these first-year cones." Mining of red pine shoots by _C. resinosae_, leading to brood production, has been reported by Lyons (1956), together with observations that occasional attacks on second-year jack pine cones had occurred.

Conophthorus "x" have been chiefly associated with infestations of jack pine shoots, although a limited number of attacks on cones have been found. Herdy and Thomas (1961) reported that only seven infested second-year cones of jack pine were found during two years of investigation. At least one of these cones is known to have yielded progeny. There is no evidence that first-year jack pine cones are ever attacked.

Other species of *Conophthorus* have revealed that strict preferences for oviposition sites are adhered to. *C. radiatae*, which attacks cones of the Monterey pine, *P. radiata* D. Don, in California (Ruckes 1958, Schaefer 1962), apparently relies on the developing second-year cones exclusively for brood production. Schaefer stated it "... occasionally attacks first-year conelets ... but principally mature 2-year-old cones. *C. radiatae* adults do not mine twigs ... No eggs are laid in the conelets." *C. monticolae* infests only the cones of *P. monticola* (Williamson 1961). In California, *C. lambertianae* normally attacks only the cones of sugar pine, *P. lambertiana* Douglas, for oviposition (Miller 1915, Ruckes 1957).

The host preference of *Conophthorus* "x" and *C. resinosae* was tested in 1958 at Black Sturgeon Lake Field Station. Ten cages were stocked with approximately two-foot lateral branch tips clipped from the host species and placed in moist sand, Six of the cages contained a combination of red, white, and jack pine shoots; four cages had only jack pine shoots. Some shoots supported mature or developing cones. Twenty C. resinosae adults were released into each of three cages containing the combination of shoots and four cages containing only jack pine shoots. Ten Conophthorus "x" from jack pine shoots were placed in each of the remaining three cages having a number of shoots obtained from the three host species.

C. resinosae readily attacked jack pine shoots ten times in one cage, with only one attack recorded on red pine; in another cage, two attacks resulted on jack pine shoots. None of the shoots were attacked in the third cage. No progeny was found in these three cages when the shoots were later examined. In cages containing only jack pine shoots, C. resinosae mined shoots in all four cages with resultant progeny; one mature larva and five pupae in one cage, and one small larva in another.

Conophthorus "x" made eleven attacks on jack pine and one on white pine in the three cages. Progeny developed only from the infested jack pine shoots; one nearly mature and six immature larvae were found in two of these cages.

This experiment, while by no means conclusive, suggests that at least under some circumstances, C. resinosae will mine jack pine shoots for oviposition sites and their larval progeny will develop on an alternate host species. Unfortunately, a method for determining the sex of living beetles was unknown at the time of this experiment and lack of results in some cages may have been due to the absence of one or other sex to initiate activities.

The duration of the subsequent stages in the biology of *C. coniperda*, *C. resinosae*, and *Conophthorus* "x" have been outlined in Table II.

The eggs of these species described by the various authors are ovoid or ellipsoid, pearl-white, and translucent. In size they range from 0.75 $\pm$ 0.04 mm. by 0.50 $\pm$ 0.04 mm., reported for *C. coniperda* by Godwin (1959), to 0.88 mm. by 0.60 mm., determined for *Conophthorus* "x" by Herdy and Thomas (1961).

The larvae of all species are very similar in external appearance and the description of *C. resinosae* by Lyons (1956) stating that they are " ... typically scolytid (being) apodous, soft-bodied, and white, with a light brown head" will suffice. Mature larvae construct a cell within the feeding mines in which pupation occurs.

After reaching the callow stage, the activities of *Conophthorus* adults are variable. *C. resinosae* emerges from brood cones 12 to 13 days after their initial appearance (Lyons 1956). On abandoning the cones, Lyons found that the beetles mined current year's red pine shoots near the base of the bud by tunnelling distally within them. The portion of the shoot with the vegetative bud above the entrance mine is eventually broken off, depositing the beetle on the ground. It is in this location that the beetles spend the winter. Lyons (1956) stated "no adults were found overwintering in dead cones although Keen states that these are the usual overwintering quarters for *Conophthorus* beetles."

C. coniperda adults seldom leave the brood cones until the following spring (Godwin 1958) and according to Henson (1961a), do not feed until this time.

Herdy and Thomas (1961) found that *Conophthorus* "x" abandoned the brood shoot during late summer to make additional attacks on current growth by mining near the base of the bud. Many shoots examined in late summer and fall were vacant, suggesting that several may be attacked before colder weather terminates activities. These beetles overwinter within mined buds on the tree which eventually fall to the ground, as in the case of *C. resinosae*.

Other species of *Conophthorus* exhibit minor deviations in post-emergence activities. Schaefer (1962) found that the majority of *C. radiatae* adults remain largely inactive in the brood cones until the following spring, although some feeding occurs on dead cone tissue during the interim.

A few adults emerge in the fall and winter to attack occasional first-year conelets or mature cones, with some individuals overwintering in these sites. This latter observation by Schaefer, agrees with the report of Ruckes (1958), who stated "there are two overwintering populations, one in the brood cones and one in the conelets."

Struble (1947) and Ruckes (1957) reported the presence of _C. lambertianae_ attacks on shoots of _P. lambertiana_ in the fall. _C. lambertianae_ enters the shoot just below the terminal bud and mines proximally in the center of the stem for one or two inches. The majority of these attacks were originally regarded merely as feeding sites since Struble (1947) reported that " ... examination late in the fall revealed that about 90% of the mined twigs were abandoned even though the flags were still attached to the affected trees." Ruckes (1957) found that "the beetle enters the twig at the base of the vegetative bud and mines only the current year's growth, remaining at the end of the burrow with its posterior toward the distal or bud end of the twig." Repeated examination of these shoots throughout the winter and early spring confirmed his suspicions that this was the overwintering site for some _C. lambertianae_. The remainder of the _C. lambertianae_ population spend the winter in the brood cones (Miller 1915, Struble 1947).

5. METHODS AND MATERIALS

The adult *Conophthorus* beetles used in this study were largely collected in mid-summer during the callow stage. Due to the distances between collection points, it was impossible to conduct this phase of the program without assistance. Considerable material was therefore assembled through the efforts of the Forest Insect Survey and several members of the Forest Insect Laboratory, Sault Ste. Marie, Ontario. Personal collections of *Conophthorus* "x" were made in stands located near Beardmore, Ontario, and in the general vicinity of Black Sturgeon Lake Field Station. *C. coniperda* and *C. resinosae* adults were also collected extensively in white and red pine stands near Sault Ste. Marie.

The *Conophthorus* beetles from individual shoots or cones were preserved in 70% alcohol within 22 x 6 mm. microvials, which were stored in larger 70 x 20 mm. rubber-stoppered homeopathic vials.

Microscopic slides of various anatomical structures were prepared using standard 25 x 72 mm. slides and one-half inch diameter cover slips. Structures of larger dimensions, such as the head capsule, elytra, and abdominal venter, required the support of microscopic slide chips placed beneath the cover slips to prevent crushing and distortion.

Both Hoyer's medium and Euparal were used in slide preparation. Since Hoyer's proved to be hygroscopic, it was found unsuitable when thick slides were prepared, as they tended to lose their permanence, becoming soft and mobile when subjected to humid conditions. Euparal displayed no similar tendency, becoming hard and permanent after the gradual application of heat for a short period.

Lactic acid was discovered to be useful for removing extraneous tissue from sclerotized structures, although at times prolonged immersion was necessary. However, material could be confined in lactic acid for extended periods without deleterious effects to the integument, while adipose and connective tissue disintegrated and could easily be removed.

Caustic potash was used as a clearing agent when specimens were deeply pigmented. Recently, Hokama and Judson (1963) described the use of commercial hair bleaching and conditioning agents, which appeared to yield material of superior quality to that obtained by the use of potash.

The linear measurements obtained in this study were secured by using an ocular micrometer and binocular microscope.

The illustrations presented were prepared through the use of the drawing aid (Thomas and Gardiner 1962) from material mounted on microscopic slides.

The method of presenting the results of this investigation has been to deal with the anatomy of the *Conophthorus* adults from each of the three host species, *P. strobus*, *P. resinosa*, and *P. banksiana* in rather general terms, pointing out specific differences when they occur. Unless direct reference has been made, it may be considered that the anatomy of all species concerned is wholly similar. To simplify the problem of illustration, *C. coniperda* was selected as the representative species, and except in instances where some area of difference exists, the diagrams were prepared from the female of this species alone. It was believed that this approach would eliminate repetition, which would be unavoidable, particularly if each species had been treated separately.

6. THE EXTERNAL ANATOMY OF THE ADULTS

The adults of *C. coniperda*, *C. resinosae* and *Conophthorus* "x" are typically scolytid in appearance (Figures 4a, b, 5a, b, 6a, b). They are cylindrical in shape and rather small (Tables III, IV), ranging in length from 2.25 to 3.70 mm. The overall length of the adult was taken as the distance, measured to the nearest 1/100 millimeter, from the anterior dorsal margin of the pronotum to a point vertically above the tip of the elytral apex.

Table III. Length of *C. coniperda* and *C. resinosae* adults as reported in the literature.

Species	Number of specimens measured	Length in millimeters Female	Range	Average	Authority
C. coniperda			2.50-2.90		Hopkins(1915a)
			2.7-3.3		Schwarz(1895)
			2.5-3.2		Swaine(1918)
C. resinosae		3.15	2.75-3.25		Hopkins(1915a)
	15		3.00-3.46	3.24	Lyons (1956)

Table IV. Overall length of *Conophthorus* adults in Ontario as determined in this study.

Species	Sex	Number of specimens measured	Mean	Standard deviation	Range	Standard error of mean
C. coniperda	male	100	2.83	0.193	2.35-3.21	0.019
	female	143	2.93	0.554	2.39-3.55	0.047
Conophthorus "x"	male	100	2.82	0.213	2.25-3.37	0.021
	female	100	2.94	0.517	2.50-3.32	0.052
C. resinosae	male	100	3.09	0.047	2.68-3.56	0.005
	female	100	3.22	0.197	2.68-3.70	0.020

The head was considered to be normally concealed within the prothorax and only those specimens in which there had been no undue elongation between the prothorax and mesothorax were selected. Generally, the females tend to be longer than the male of the same species. C. resinosae adults were found to be the longest and those of Conophthorus "x" among the smallest.

Mature adults are usually deep black in color throughout their sclerotized regions. Various other color ranges may be encountered depending on the maturity of the individuals, beginning with the light amber brown of the newly formed callow adult. In this respect, the time of year in which the collections are made is an important consideration to bear in mind. It is impossible to make specific determinations of the adult on the basis of color alone, since color seems to be chiefly associated with the state of maturity.

6.1 Head

The head of the Conophthorus adult consists of a completely sclerotized capsule or cranium which bears the usual associated head appendages. Typically it is prognathous in orientation. Generally the head capsule is largely concealed within the prothorax so that only the anterior portion bearing the appendages is visible. There appear to be no visible distinguishing features associated with the head capsule, such as special head capsule structure, shape, sculpture or furnishings, which might be interpreted as indicative of particular species of Conophthorus. However, the distribution of setae on the median facial area dorsal to the clypeus provides a means of identifying the sex of most individuals.

On the basis of DuPorte's (1960) interpretation of the cranium of Coleoptera, the head capsule of Conophthorus may be regarded as largely composed of the frontoparietal region. The occipital region appears to contribute only the postgenae and the postocciput. The gula and submentum may be represented either as individual sclerites or as the gulamentum.

The parietals (Figures 10 to 14) constitute the most extensive areas. They extend virtually from the oral to the occipital foramina and from the mid-cranial sulcus (Mcs) to the mid-ventral gular suture (Gls). Only narrow marginal areas surrounding the foramina are interposed. The oral foramen is encircled by the dorsal clypeus (Clp), lateral hypostomae and the mid-ventral submentum (Smt). The postocciput (Figure 13, Poc) lies about the occipital foramen. Its exact extent cannot be determined.

The cranium above the dorsal mandibular articulations (Dam) includes the vertex. Within this region is the clypeus and the indeterminate area of the epifrons. The frons has been eliminated from the facial area by the epifrons so that the parietals form the proximal boundary on the clypeus. The clypeus is but a narrow transverse marginal sclerite. The frontoclypeal suture could not be identified, but its relative position was estimated to lie between the anterior edges of the antennal sockets. Neither the anterior tentorial pits nor the anterior tentorial arms could be located. The anterior margin of the clypeus is infolded within the oral foramen with the dorsal mandibular articulations located on the lateral edges. The frontogenal sulci could not be recognized and the clypeus appears to merge into the postgenae. A pair of small lateral notches (Figure 10, Ln) are found on the anterior clypeal margin above each dorsal mandibular articulation. A notch on the median clypeal margin (Mn) appears similar, although not as extensive as the median notch referred to by Hopkins (1909) in *Dendroctonus valens* LeConte, and the serratus epistomalus of *Gnathotrichus* Eichhoff by Schedl (1931).

A low median ridge or carina (Ca) is located on the anterior margin of the facial region proximal to the clypeus. This low, longitudinal, and narrowly transverse, blunt-faced ridge has been mentioned by Schwarz (1895) in his description of *C. coniperda*. Schwarz described it as " ... a flattened tubercle on the clypeal margin which is continued posteriorly for some distance as a feebly elevated ridge." He pointed out its presence in the male and absence in the female. All specimens of *Conophthorus* examined in this study appeared to possess this ridge to some degree, although on some *C. coniperda* females it appeared particularly low.

Ventral to the dorsal mandibular articulations, the head capsule surrounding the oral foramen consists of the postgenae and the submentum, with the proximal region composed of the lower parietals or genae and possibly the mid-ventral gula. The posterior tentorial pits (Ptp) lie at the distal edges of what would appear to be the forked ends of the gular suture. These pits are most easily recognized in callow adults, although once their position has been established, they are distinguished with relative ease on most head capsules. The marginal portions of the postgenae lying between the ventral mandibular articulations (Vam) and the posterior tentorial pits are hypostomae. The hypostomae bear the ventral mandibular articulations, the maxillary articulations (Mxa) and the points of attachment of the hypopharyngeal bracon (Hphyb). The proximal edges of the hypostomae and the postgenae are marked by ridges beginning in the vicinity of the posterior tentorial pits. The occipital ridges (Ocr) extend to the ventral edges of the antennal sockets. Narrow depressions below the antennal sockets lying along the occipital ridges represent the antennal scrobes. The hypostomal ridges (Hstr) continue to the lateral edges of the ventral mandibular articulations.

The submentum (Figure 11, Smt) would appear to be a narrow sclerite partially inflected into the oral foramen on the mid-ventral edge of the cranium to which the labium is attached. Its proximal margin cannot be distinguished with certainty.

The remainder of the mid-ventral region lying between the submentum and the gular suture cannot be identified beyond suggesting that all or a portion might be the gula, a form of gulamentum or a hypostomal bridge. The gula could conceivably lie within the arms of the gular suture. Lateral boundaries which might further define the limits of a gula or gulamentum from those of the hypostomae are not apparent. It is quite possible that these may have been obliterated during evolutionary processes.

The proximal region of the head capsule encircling the occipital foramen is infolded and probably constitutes the extent of the postocciput. Two small median sclerites (Figure 13, Mscl) at the proximal end of the gular suture, together with a lateral area (Lata) on each side of the mid-cranial sulcus form the main points of attachment for the longitudinal muscles controlling movement of the head. An area of further sclerotization and light pigmentation (Scla) occurs immediately dorsad of the median sclerites filling in the ventral margin of the foramen.

The distal half of the cranium is setose and punctate. The anterior vertex, beginning distad of the mid-cranial sulcus and extending through the median region between the compound eyes, is lightly covered by an irregular distribution of various sized setae, many arising from shallow punctures. The most pronounced punctation occurs along the margin of the eyes and on the upper vertex. Both setae and punctures appear more closely congregated adjacent to the eyes. Facial setae are longest and more erect in the median anterior area, becoming shorter and sub-erect laterad. A particularly dense transverse line of sub-erect setae appear along the frontoclypeal margin. Most of these are of sufficient length to extend distally at least across the clypeus. The setae line continues ventrally past the antennal sockets to the posterior tentorial pits with the setae diminishing in size and concentration in the ventral region.

The remainder of the ventral cranium has a scattering of setae on each gena and in the narrow triangular median area between the posterior tentorial pits. Genal setae occur from the ventral margins of the eyes to gular suture in a triangular area extending almost to the occipital foramen. Most are short and slender, but approximately three, situated between the eyes and the occipital ridges, and those of the median area, are of considerable length. Punctation is relatively inconspicuous in the ventral region of the cranium.

A small median space, extending dorsally from the clypeus in male Conophthorus of all species, exhibits a consistent lack of setae. The similar area on the female cranium is setose. This dimorphic characteristic seems sufficiently constant that it may be employed to distinguish between sexes (Figures 16a,b).

The entire proximal portion of the cranium posterior to the compound eyes and normally concealed within the prothorax is largely free of setae and punctures.

Internal strengthening ridges are basically confined to the anterior ventral cranial region surrounding the oral foramen where they assist in reinforcing the bases of the appendicular articulatory processes. The cranial dorsal edge seems to require no additional support other than provided by the infolded margin of the clypeus and a generally thicker cranial wall. The only internal ridge of the vertex is that of the mid-cranial sulcus. This extends ventrad as an attenuated process along the course of the sulcus. The tentorium has apparently been suppressed. The posterior tentorial arms are vestigial; the anterior arms could not be located, and apparently they too, have atrophied.

The most prominent internal processes include the gular ridges (Figure 15), occipital inflection (Oci), and the processes (anti) extending about the ventral edges of the antennal sockets. The gular ridges extend longitudinally through the cranium as a trough-like structure rising dorsad from the gular suture. Posteriorly the gular ridges are confluent with the postocciput and narrow portions lying along their dorsal edges may be inflections of this region. The anterior edge of each ridge follows the gular suture to the vicinity of the posterior tentorial arms. There the dorsal edge unites with the occipital inflection. The occipital inflection continues dorsally where it divides, one arm becoming fused with the posterior edge of the ventral mandibular articulation, the other extending to the process at the lower edge of the antennal socket. The ventral edge of each socket is encircled by the antennal inflection extending from the anterior margin of the eye to the posterior edge of the dorsal mandibular articulatory process.

The compound eyes are located antero-laterally on the head capsule. Each is composed of a large number of facets arranged in a sub-elliptical shape. Schwarz (1895) described the eyes of C. coniperda as " ... large, acutely, but not deeply emarginate in front." An emargination, occurring on the anterior margin below the median line, appears roughly equivalent to one-half the width of the eye at this point. A very shallow indentation also occurs on the posterior margin for some distance directly opposite the anterior emargination. The overall length appears slightly less than one-third that of the head capsule and more than twice the width of the eye at the dorsal margin.

6.2 Head appendages

6.2.1 Antennae

The antennae (Figure 17) are geniculate and clavate, arising from sockets or fossae located immediately cephalad of the anterior emargination of the compound eyes and caudad of the base of the dorsal mandibular articulations.

The antenna has been divided into a number of distinct regions for purpose of reference. Snodgrass (1935) and DuPorte (1950) refer to the antennal scape, pedicel (or pedicil of DuPorte), and the flagellum or clavola. There have been however, some minor differences in the terminology and antennal divisions employed by others. For example, Hopkins (1909) described the antenna of D. valens and Pissodes strobi (Peck) as composed of the scape, funiculus, and the club. Hopkins' funiculus included the pedicel. The same divisions were used by Schedl (1931) for Gnathotrichus although the funiculus was known as the funicle, and by Kaston (1936) in his work on H. rufipes. The description of Hylobius warreni Wood by Warren (1960) recognized the pedicel as a distinct region of the antenna exclusive of the funicle. The antennae of Scolytidae have a very prominent distal or club region, which may be considered as distinct from the immediately proximal funicle. The pedicel is similarly rather clearly set off from the remainder of the funicle by virtue of its size and shape so that the antennal divisions employed by Warren (1960) may be warranted.

The antennae of C. coniperda have been described by Schwarz (1895). Those of the species of Conophthorus examined in this study appear similar. They are composed of nine segments which may be divided into four basic regions. These are: the scape (Scp), pedicel (Pdc), funicle (Fnc), and the club (Cl). The scape and pedicel are single segments; the funicle is made up of four and the club composed of three.

In its normal position on the head capsule, the posterior surface of the antenna is orientated toward the caudal end of the insect; the anterior surface is directed anteriorly. The posterior surface, particularly that of the funicle and club, is flattened, the anterior rounded or convex. The dorsal and ventral edges of flattened segments form acute or attenuated surfaces, otherwise the segments are approximately cylindrical.

The antennal scape comprizes approximately one-half the overall length of the antenna. Viewed from the lateral aspect it appears club-shaped. Near the base, a deep notch occurs on the dorsal surface at the point where it passes through the external rim of the antennal socket. Distal to this notch, the scape is expanded on both the dorsal and ventral margins, gradually becoming enlarged and rounded to the apex, which is slightly narrowed. Below the notch, the base of the scape is produced into a bulbous condyle, bearing on its dorsal surface, a small depression into which the antennifer is seated. Although the scape is comparatively free of setae, a number of considerable length are dispersed about the distal half of the anterior surface.

The pedicel, the second segment of the antenna, is situated medially on the broadly rounded apex of the scape. It is equal to the combined lengths of the first two segments of the funicle. The base is narrow with the apex considerably wider. Both the dorsal and ventral margins are expanded distad beyond a point slightly more than one-third the distance from the base. The dorsal margin is sharply curved, the ventral one less so, to produce the distal enlargement. The apical margins are rounded with the surface flattened. At least six relatively long setae are situated about the pedicel below the apex.

The four-segmented funicle is approximately twice the length of the pedicel. The first segment is the longest and does not quite equal the combined lengths of the remaining three. Both the apical and proximal portions are expanded beyond a narrow constriction near the base. The apex is approximately twice the width of the base. The dorsal and ventral margins are straight, though tapering outwardly beyond the constriction. Only one short seta occurs on this segment.

The second funicular joint is quite compressed in its longitudinal dimension, being only slightly larger than one-half the length of the first. The base is slightly narrower than the apex. Both the dorsal and ventral margins are rounded outwardly from the base. At least three long setae are located about the circumference of the segment near the midpoint.

At the apex, the third segment of the funicle is almost twice as broad as it is long. Its narrow base is situated medially within the distal end of the proximal segment. The dorsal and ventral margins expand gradually from the base, with the dorsal edge rather straight and the ventral rounded toward the apex. The apical edges are produced quite sharply laterad. Two setae, one on each of the dorsal and ventral margins, are located near the uppermost angles. The length of the dorsal seta exceeds the transverse dimension of the segment.

The fourth or terminal segment of the funicle is shaped similarly to the third. It is slightly larger transversely, with the base narrower than the apex. A number of long setae, generally in excess of six, are located about the circumference at the segmental midpoint.

The antennal club is greatly enlarged in comparison to the funicle. It is flattened antero-posteriorly. In length it is equivalent to that of the combined pedicel and funicle. The club is divided by two rather indistinct sutures into three segments, the smallest being the basal one, the apical the largest. Location of the sutures may be estimated from the positions of a series of relatively long setae extending around the upper edges of the first two segments. The apex of the third or apical segment is covered by a sparse arrangement of setae equivalent in length to those outlining the sutures. The anterior surface of the club appears to possess slightly more setae than the posterior surface.

6.2.2 Mandibles

The mandibles are situated anteriorly on the head capsule so that they enclose the dorsal region of the oral foramen. Held as they are normally, a portion of the proximal dorsal surface of each mandible is concealed beneath the margin of the clypeus, and the apices of the teeth, or the entire teeth of one mandible overlap those of the other. Each mandible articulates with the head capsule at the dorsal and ventral articulations. Lateral movement is obtained by means of a large adductor muscle (Adm) attached mesad and a smaller abductor (Abm) laterad (Figure 18b). The mandible is rather stout and strongly constituted with its interior hollowed in a large sinus. In the mature adult, the mandible is deep black in color similar to other sclerotized areas.

The mesal edge of the mandible is dentate. The teeth include two distal or incisoral, the apical (Apt) and sub-apical (Sapt), having sharply pointed apices. A single proximal molar (Mol) tooth appears almost bilobed, being impressed or grooved medially to form an articulatory surface for the tooth of the opposite mandible. The dorsal lobe of the molar tooth is rounded, but the ventral is produced acutely on the mesal edge.

The proximal or basal end of the mandible is quite broadly expanded, particularly ventro-laterally, becoming roundly narrowed mesally. It bears a number of emarginations, impressions and processes which are engaged in the articulation of the mandible with the head. The proximal dorsal margin is rather deeply emarginate medially to form the dorsal condyle (Dcon). The cephalic edge of the condyle is raised in a ridge, then sharply depressed to form a shallow semi-circular impression to receive the dorsal mandibular process of the head. The proximal internal edge of this impression is reinforced by the infolded margin which extends from the meson laterad as a transverse process. Another emargination occurs on the meson at the base of the molar tooth. No special significance is assumed by this notch beyond the fact that the mandibular adductor is attached about its margin. Between the dorsal condyle and the lateral edge of the mandible lies the anterior condyle (Acon). Ventrad of this process, the narrow elongate lateral impression, articulating with the lateral edge of the ventral mandibular articulatory process of the head, extends anteriorly.

A small, but variable number of setae, probably never exceeding six, of comparative moderate size, arise from the distal end of this groove. On the proximal ventral, or inner margin of the mandible, the remainder of the ventral mandibular articulation is engaged in the ventral impression (Vimp), lying between the ventral condyle (Vcon) and a median process (Mpro).

The dorsal surface of the mandible is rounded or convex and bears a median fossa (Mf), a prominent transverse ridge (Tr), and two sensillae (sen) (Figure 18a). A number of setae, generally in excess of those found in the lateral impression, arise from the oval median fossa. The transverse ridge is relatively low, but sharply elevated, and extends from the median edge of the dorsal condyle, proximad of the fossa, then mesally above the median region of the molar tooth. This ridge represents the distal boundary of the proximal mandibular area normally concealed within the head capsule. A sensilla occurs laterad on each side of the median fossa to complete the complement of surface structures.

The ventral or inner surface of the mandible is slightly concave, with several ridges crossing its area (Figure 18b). One, the ventral apical (Vapr), extending from the apical tooth, branches about the edge of the ventral impression. The sub-apical (Vsapr), though much less extensive, extends basally from the sub-apical tooth. A third, the molar, is produced laterad from the mesal edge of molar tooth sharply across its base. The remainder of the ventral mandibular surface is comparatively smooth.

6.2.3 Maxillae.

A pair of maxillae are based on the lower margin of the oral foramen ventral to the mandibles and immediately dorsal to the labium. They enclose much of the ventral oral foramen below the mandibles and lateral to the labium. Each maxilla articulates with a notched process on the hypostoma ventral to the lower mandibular articulation.

The maxilla (Figure 19) is composed of a proximal cardo, a more distal stipes (St), a dorsal lacinia (Lc), and a ventral three-segmented palpus (Plp). It was impossible to identify an area associated with the galea. The palpiferal area (Plf) appears rather indistinct and is assumed to be a small, less highly sclerotized, lightly pigmented region at the base of the palpus.

The cardo is a small basal sclerite articulating proximally with the maxillary process on the hypostoma. The remainder of the maxilla, through the stipes, is broadly hinged to the distal cardinal margin. Most of the dorsal surface of the cardo is given to muscular attachments, as is the proximal outer stipital area.

Through rotation and flexure, these surfaces may be drawn together. In this position, the cardo lies perpendicularly across the base of the stipes and is largely concealed by the ventral stipes and the edge of the head capsule.

Examined in ventral aspect, the cardo appears elongate. The distal end is truncate; proximad where the cardo passes through the narrow articulatory process, it is constricted and emarginate. Two muscle-bearing processes are present at the base of this region. The ventral surface of the cardo is smoothly sclerotized, with the edges roundly produced over the margins onto the dorsal area. The dorsal cardo lacks sclerotization due to the extensive muscular connections covering this area. A few setae, to which Schedl (1931) referred as "cardol setae," occur on the distal edge of the ventral cardinal surface.

The stipes lies between the edge of the hypostoma, the ventral surface of the mandible and the labium. Proximoventrad it is connected to the cardo; distad to the lacinia. Ventrally the palpiferal area and palpus are located on its margin.

The stipital region is a median, roughly rectangular, portion of the maxilla. Laterad each surface is a flattened expanse. The outer lateral surface, lying adjacent to the hypostoma and the mandible, is gradually inclined toward the dorsal margin. A portion of its proximal area, which is flexed against the cardo, lacks sclerotization, and in addition, pigmentation is absent from a further small adjoining median area as well. The mesal surface is produced almost perpendicularly dorsad. The dorsal margin of the stipes is attenuated. Ventrally the stipes is narrow with the edges rounded into the lateral surfaces.

The lacinia is a laterally flattened dorsal lobe broadly joined to the distal stipes. Although the proximal margin is indistinctly set off from the stipital area, in some mounted specimens the whole lacinial region appears noticeably more lightly pigmented than the stipes. Ventrad the lacinia is separated from the palpus by a narrow median space.

The dorsal edge of the lacinia is thinly produced, with a row of approximately twelve, long, flattened, sword-shaped setae (Lct) extending along the outer lateral margin distad from the stipes. Hopkins (1909) and Kaston (1936) have called these setae lacinial teeth. The remainder of the outer surface is glabrous, having only a group of long, slender setae at the distal edge above the palpus. The mesal surface is uniformly covered by a series of short, stout setae which tend to become longer in the distal region.

A small, rectangular, lightly pigmented area of the maxilla, immediately proximal to the palpus, was assumed to represent the palpiferal region. The base of the palpifer is only slightly wider than that of the first palpal segment and they are approximately equal in length. The proximal margin is outlined on both lateral surfaces by a row of setae extending along the distal edge of the stipes.

The maxillary palpus extends along the distal edge of the maxilla ventral to the lacinial lobe. It is composed of three segments. All have broad bases which appear to be invaginated medially within the apex of the preceding segment. The basal segment is the largest, being approximately equal in length and width, and exceeding one-half the combined lengths of the remaining two segments. Two long setae project anteriorly from the ventral edge, with several additional smaller ones located on the lower surfaces. The second segment is smaller than the first. At least three setae, not as long as those of the basal segment, are found on the ventral surface. The terminal segment is elongate and just exceeds the first in length. No setae are present on its surfaces, but a number of pore-like depressions may represent sensillae. A series of small structures on the apex may be similar to papillae identified by Thomas (1957).

6.2.4 Labium

The labium is situated between the maxillae, astride the meson, on the ventral oral foraminal margin. It consists of a proximal postlabial sclerite, the submentum, adnate on the ventral wall of the cranium, and a free distal prelabium. The submentum has been previously mentioned in connection with the structure of the cranium. The prelabium (Figures 20a,b,c), hinged to the distal edge of the submentum, consists of a basal prementum (Prmt), bearing a pair of three-jointed labial palpi (Lplp) located distad of the lightly pigmented palpiger region (Plg), and a median dorsal ligula.

The prementum, constituting the largest region of the prelabium, is narrowly elongate. The ventral surface is flatly rounded laterad, narrowed throughout most of the median region, but expanded both basally and distad. The lateral surfaces are rather concave through the median area. Basally the prementum bears a median dorsal process, and two smaller projections occur on the ventro-lateral angles. These processes apparently assist in hinging the labium to the submentum. At least six slender setae are present on the distal portion of the ventral surface. Additional setae extend from the distal margins of the lateral surfaces, outlining the proximal edge of the palpiger.

The ligula is a smoothly rounded lobe situated on the dorsal prementum. Basally it appears confluent with the surface of the prementum, as a thin structure beginning in the region beyond one-third of the distance from the basal edge. Distad it becomes considerably thicker dorso-ventrad. In dorsal aspect it tapers gradually cephalad, being rather sharply projected between the bases of the labial palpi at the apex. The ligula apparently lacks direct connection with the surface of the palpiger. The dorsal ligual surface bears a number of moderately long, anteriorly directed setae in the distal region, but more proximally this surface is thickly covered by a series of short, stout, bristle-like setal structures.

Mounted specimens of the prelabium exhibit a less heavily pigmented region lying across the distal end of the prementum. It is this area that was assumed to represent the palpiger. In length, the ventral dimension of the palpiger is approximately one-half that of the first palpal joint, but dorsad it is protracted more extensively toward the base of the prelabium. No setae are based directly on the palpiger.

The three-jointed palpi based laterally on the palpiger are directed anteriorly. The base of each segment is invaginated within the median apical end of the previous one. The apex of the terminal joint is rounded. Each segment is approximately twice as long as it is wide. The first is the largest. The second and third are nearly equal in length, but the latter is more slender. Setae are confined to the ventral surfaces. At least three of varying length are found on the distal region of the first segment, two shorter ones occur medially on the second, and one or more near the base of the third. At least four papilla-like structures occur on the apex of the terminal joints.

6.2.5 Hypopharynx

The hypopharynx (Figure 21) is a small triangular-shaped, lightly-sclerotized median lobe, suspended within the preoral cavity between the lower mandibular articulations, ventral to the mandibles and distal to the mouth. The proximal margin is attached dorsad along the anterior edge of the pharynx. Laterad, the base of the hypopharynx is connected at the proximal edges to the mesal angles of the ventral mandibular articulations by the hypopharyngeal bracon (Hopkins 1909, Thomas 1957), and ventrally, by a membraneous area to the margin of the cardines.

The narrowly truncate apex is nearly bilobate as a result of a shallow median groove extending caudad along the ventral surface. The surface of the groove is covered by a series of minute, broad-based spines, projecting anteriorly; the largest being on the lateral edges. The remainder of the ventral and the entire dorsal surface is uniformly invested in a series of thin, longitudinal ridges.

6.3 Thorax

6.3.1 Prothorax

The prothorax comprizes about one-third of the overall length of the adult. It forms a sclerotic ring (Figures 22, 23), in which the tergal, pleural, and sternal elements are united with almost indistinguishable boundaries. The anterior foramen opens cephalo-ventrally due to the projection of the anterior pronotal margin beyond that of the prosternum. The head capsule moves freely within the anterior foramen and often lies concealed beneath the pronotum. Posteriorly, the prothorax has no firm connections with the mesothorax other than are provided by the intersegmental membrane. The margin of the posterior foramen overrides portions of the mesonotum, the bases of the elytra, and the mesosternum. In area, the prothoracic venter or prosternum is only about one-third as large as the pronotum.

The pronotum is nearly equal in its median longitudinal and basal transverse dimensions. Viewed from the dorsal aspect (Figures 25a,b), the sides appear less than parallel. They are broadly rounded basally, becoming slightly constricted about the apical margin, so that anteriorly, the pronotum is only wide enough to accommodate the head. A fringe, consisting of numerous minute, closely-arranged, flattened, five to seven-pointed, scale-like structures, extends along the edge of the anterior pronotal margin from the dorsum ventrad, to completely encircle the foramen. The basal margin of the pronotum is shallowly depressed, smooth, and free of punctures and setae, but for two, more or less rows of setae along the very caudal edge. One of these rows forms a posteriorly-directed, setal fringe encompassing the margin of the foramen. The anterior row is composed of more or less erect setae, which only border the edge of the pronotum, and fail to extend further ventrad than the lateral pronotal margins. Laterally a sharp ridge (bsr) (Figure 22) extends anteriorly a short distance along each side of the pronotum as a continuation of the upper edge of the proximal margin. More anteriorly the pronotal setal-punctation pattern terminates along the line of this ridge through the area to within one-quarter the distance to the anterior foramen. Within the remaining area, lying on the margin of the anterior foramen, setae and punctures appear indiscriminately. Whether this ridge and line of discontinuity mark the boundary between pronotal and propleural elements is a matter of conjecture.

Punctures, setae, and tubercles in concentric series, cover most of the surface of the pronotum. The exception is a small median space located near the basal margin, extending longitudinally for over one-third of the pronotum. It is approximately one-sixth as wide as long. The surface of the space appears smooth, without punctures or setae. A very low, longitudinal elevation may extend along the meson.

The anterior median portion of the pronotum has a series of rather low, flattened, truncate tubercles set in front of many setae. On the anterior margin, a single row of tubercles is separated from those more posterior by a small transverse area lacking tubercles, but displaying both setae and punctures. Setae and punctures cover the remaining areas to the basal margin.

Two aspects of the pronotum have been mentioned, in conjunction with other characteristics, by Hopkins (1915a) in his descriptive key to the genus, as a means of distinguishing between certain species of Conophthorus. These are, the width of the anterior pronotal margin, the "front"; and the degree of refinement in the pronotal punctures. Pronotal punctation does not seem to have significance in C. coniperda, C. resinosae, or Conophthorus "x". In *C. coniperda* (Figure 25b), the lateral pronotal edges appear more acute, with more pronounced emarginations when viewed from the dorsal aspect. These features tend to reflect a narrower pronotal apex than is apparent in specimens of the latter two. A broader anterior margin is suggested in both *C. resinosae* (Figure 25a) and *Conophthorus* "x" by more nearly parallel lateral margins and less emphatic emarginations. However, it is extremely difficult to make conclusive predictions on the basis of these apparent differences, since they are relatively minute, not clear-cut, and subject to distortion by the attitude in which the specimens are examined and perhaps influenced by the size of individual specimens.

The extent to which the pleura are involved in the structure of the prothorax is difficult to establish due to the lack of features outlining their boundaries. Lines of discontinuity in the upper prothorax are believed to mark the union of the notum and pleura. The ventral pleural margins appear less distinctive, but seem to lie in the regions dorsal to the coxal cavities. Other workers, Hopkins (1909) on *D. valens*, and Schedl (1931) working with *Gnathotrichus*, appear to have experienced less difficulty in formulating boundaries and identifying pleural sclerites. Hopkins was able to recognize pleural areas in *D. valens* which he designated as preepisternal,

episternal and epimeral. Remnants of the pleuronotal suture and differences in surface texture enabled Schedl to determine that three similar areas exist in Gnathotrichus. However, Kaston (1936) found in H. rufipes that "it is not possible to delimit epimeral or episternal areas as in Dendroctonus and Gnathotricus (sic)." This latter condition seems to exist in Conophthorus also, for here, definitive pleural sclerites cannot be identified; instead, the entire pleural regions appear to be unified composites.

Approximately one-half of each pleuron is covered by moderate punctation and small setae, the remainder is smooth. Punctation, although not as coarse or concentrated as on the pronotum, continues ventrally along the anterior foraminal area and posteriorly above the coxal cavities. The posterior pleural region is relatively free of both punctures and setae. An extension of the long setal fringe from the notum may be noticed on the edge of the posterior foraminal margin.

The prosternum (Figures 23, 24) is indistinguishably fused with the ventral margins of the propleura. In Conophthorus, as in Gnathotrichus of Schedl (1931), the area between the coxal foramina is concave. Small, adjacent transverse anterior and posterior areas, lying on the margins of the respective anterior and posterior foramina are on the same level as the propleura. Mesad each transverse area is produced between the bases of the coxae to form anterior (Aip) and posterior (Pip) intercoxal processes.

Four transverse divisions of the sternum were recognized by McLeay in 1830, and according to Hopkins (1909), these were designated as the presternum, sternum, sternellum, and poststernellum. These terms were applied in Dendroctonus by Hopkins (1909) and also by Kaston (1936) in H. rufipes. Schedl (1931) named only the anterior and posterior marginal elements of Gnathotrichus, calling them, the sternal and poststernal areas; the median coxal area was merely labelled as the coxal cavity.

The prosternum of Conophthorus bears a prominent suture, the sternacostal (scs), extending transversely between the mesal edges of the coxal foramina. A similar suture was mentioned, but unidentified by Kaston in H. rufipes, and appeared unlabelled in an illustration of the prothoracic venter of G. sulcatus LeConte by Schedl (1931). The sternacostal suture divides the prosternum of Conophthorus into two,more or less, equal areas. Following Snodgrass (1935) and DuPorte (1959), these would be known as the basisternum or basisternite (Bs) and sternellum (Sl)(Figure 23). Adjacent anterior and posterior marginal areas cannot be regarded as separate sclerites, as they lack features which might differentiate them from the main sternal elements. In the light of this discussion, the prosternum of Conophthorus may be simply considered as a eusternum consisting only of a basisternite and sternellum.

The prosternum is only sparsely setose. A few setae occur on the apex of the anterior intercoxal process and others extend along the caudal edges of the acetabula. The setal fringe from the notum continues ventrad across the edge of the posterior foramen, and the scale-like structures of the anterior foraminal margin extend across the meson.

Internal marginal sclerotizations appear on the ventral edges of both the anterior and posterior foramina. These extend dorsad to nearly the pronotum before merging into the propleura. The anterior inflection is fused caudad along the edge of the sternacosta. The edges of these marginal thickenings are associated with intersegmental membranes connected to the prothorax.

A pair of sternal apophysis (SA) may be recognized on the anterior sternum anterior to the mesal ends of the sternacosta (sca).

6.3.2 Mesothorax

The mesothorax is the smallest segment of the thorax. Within it, the tergal, pleural, and sternal regions are extensively sclerotized, but not as thoroughly unified as in the prothorax. Extensive sclerotic connections between the mesothorax and the next caudal segment, the metathorax, occur only in the venter. The notum and pleura are largely joined to adjacent metathoracic regions only by small sclerotic processes or through intersegmental membranes. There is, of course, no direct sclerotic attachment with any portion of the prothorax.

Much of the mesonotum may be concealed by the pronotum, with the exception of a small median caudal area. Small portions of the lateral mesonotum are covered by the elytra when these are closed. Most of the mesopleura and all of the mesosternum, other than the portion engaged in the coxal cavities, are exposed at all times.

The mesonotum (Figures 26,27) is located medially between the bases of the elytra and the dorsal mesopleura. Only membranous connections or minute sclerotic areas of contact occur between it, the metanotum, and the mesopleura. The mesonotum is roughly rectangular and only slightly wider than long.

Three sclerotic regions, representing the prescutum (Prsc), scutum (Sct), and scutellum (Scl), enter into its composition. The anterior-most sclerite, the prescutum, occupies the largest surface area. The scutum consists of two small sclerites situated on the latero-posterior prescutal margins. Between the scutal sclerites, on the median posterior margin of the prescutum, is the scutellum. The scutellum is divided by the scutellar suture (ss) into an elevated portion (eScl), which is invariably exposed; and a depressed area (dScl), normally concealed by the elytra when they are in repose. There is no evidence of a postscutellum.

The prescutum comprises approximately two-thirds of the surface area of the mesonotum. Along the meson it is bisected by the median notal sulcus (mns) (Figure 27), which forms a low internal inflection. Only the prescutal anterior, and portions of the antero-lateral margins, are free of association with other notal sclerites. The antero-lateral angles are attenuated in the prealar arms (Pra). In the mid-lateral region, the margins are produced ventrad in alar bridges (Albr) meeting the mesopleura in the vicinity of the pleural wing processes. The posterior margin is separated from the scutellum by the scutoscutellar suture (vs).

The prealar arms are similar to processes that have been illustrated by Hopkins (1909) in _D. valens_; Schedl

(1931) in Gnathotrichus; Kaston (1936) in H. rufipes; and Warren (1960) in Hylobius. Schedl and Kaston employed the term clavicola in their designation of these processes, apparently after Berlese (Schedl 1931). Kaston has described the clavicola as long, thin, acute processes, formed from the prescutum in conjunction with the lateral prephragma. This conclusion seems to have been reached by Hopkins and Schedl as well. Warren indicated they were prealar arms. In Conophthorus, the prealar arms are reinforced by a sclerotization extending beneath the entire anterior prescutum. This gives them the bipartite appearance described by the earlier authors.

The surface of the prescutum is marked by a series of setae issuing from moderately large punctures distributed over most of the median area. Both punctures and setae become smaller and more numerous laterad, but the more ventral portions of the prescutum are smooth.

An extensive endodorsum or internal plate-like sclerotization underlies the anterior prescutum. This sclerotic formation may be the antecostal prephragma, although it bears little semblance to the typical phragmatal structure. Hopkins (1909), Schedl (1931), and Kaston (1936) have referred to mesonotal prephragma in their respective investigations. In *Gnathotrichus*, Schedl described the wide anterior prescutal ridge as a prephragmal remnant. Kaston identified the ridge underlying the prescutum in *H. rufipes* as the prephragma. Warren (1960) commented that a similar structure in *Hylobius* was a ridge or bridge common throughout Coleoptera. In *Conophthorus*, the plate-like formation is fused along the anterior prescutal margin and also laterad, from the prealar arms to the alar bridges. It extends mesad at a slight caudal angle (indicated by the dotted line on Figure 27), becoming broadest ventrad the median notal inflection with which it is united. Caudad it reaches over one-half the length of the prescutum before joining a median anteriorly-directed process from the prescutal inflection. Additional thickening occurs along the caudal edge of the sclerotization, extending mesad as a tapering strut from the base of the prealar arms and the alar bridges. This latter marginal strengthening ridge gives the posterior region a darker appearance and to casual observation suggests the entire structure may be limited to this region.

The posterior prescutum is also strengthened by a pair of inflections extending from the alar bridges caudad along the prescutal sutures. Mesad these continue beneath the median notal sulcus anteriorly a short distance as a thickened process before uniting with the anterior sclerotization.

The two small, oval, lateral scutal sclerites are situated between the margins of the latero-posterior prescutum and the depressed scutellum. Dorsad they are bounded by the prescutum; postero-ventrad by the scuto-scutellar suture. Cephalad the prescutal alar bridges pass ventrad along their margins. The remaining portion of the outer lateral scutal margins are free of sclerotic attachment. Normally when the elytra are in repose, the scutal sclerites are concealed beneath them.

The outer lateral edges of the scutal sclerites form two processes. Slender scutal extensions (ph), pass postero-ventrad beneath the axillary cords at the anterior edges of the scutellum, to meet the metanotum in the only sclerotic connections between the mesonotum and the meta-thorax. These lateral processes have been designated, rather unsatisfactorily, as pleural hooks by Schedl (1931) and Warren (1960). Hopkins (1909) and Kaston (1936) called them lateral arms of the postphragma. The scutal sclerites meet the first axillary sclerites of the elytra along the proximal portion of the alar bridges (NP). The surface of the scutal sclerites appear flatly concave as a result of being situated below the margins of the surrounding sclerites. It is free of setae and punctures.

The scutellum consists of two small sclerites located on the posterior edge of the mesonotum separated transversely by a scutellar suture. The upper or elevated portion is a large, somewhat triangular, median lobe, produced caudad in a narrow process, bluntly rounded at the apex. Ventrad of this tergite, the depressed scutellum extends along the caudal edge of the mesonotum as a narrow sclerotic strip between the scutal sclerites. The anterior regions are narrowed about the margins of the scutum to form the axillary cords.

The surface of the narrow dorsal scutellar process is uniformly covered by setae of moderate length arising from prominent individual punctures. In addition, the anterior region of the upper scutellum is traversed by a distinct line, marking the location which the posterior pronotal margin occupies on the mesotergum. The surface of the depressed scutellum is smooth, lacking setae and punctures.

Each mesopleuron is composed of two principal sclerites (Figures 28,29). The largest, the anterior episternum (Eps_2), is separated from a narrow posterior epimeron (Epm_2), by a distinct pleural suture (PlS). In addition to the two conspicuous pleurites, a narrow marginal sclerotization fused on the infolded cephalic edge of the episternum and wholly within the body cavity, may represent the preepisternite (Figure 29, $Peps_2$). There appear to be no further major subdivisions of these primary sclerites.

Dorsad, two processes appear to encompass the upper median edges of the episternum, the pleural ridge, and the epimeron. Designation of these elements is in doubt. Hopkins (1909) labelled processes on the upper pleuron of D. valens as the pleural claviculus, with the anterior and posterior processes, the clavicle and coracoid condyles respectively. Both of these processes appear to originate on the episternum. Schedl (1931) referred to the entire region as the pleural clavicola, with the preepisternal element as the clavicolar-disk. In H. rufipes, Kaston (1936) described a clavicle process on the preepisternum and a coracoid process on the dorsal epimeron. Snodgrass (1935) pointed out the presence of epipleurites in this area. The anterior or episternal, being the basalare; the posterior or epimeral, the subalare. Between them, the pleural ridge supports the wing process. This is essentially the view of DuPorte (1959) also. Warren (1960) indicated the presence of a basalare lobe on the dorsal anepisternum of Hylobius, and caudad, a small rounded sclerite he believed to be the subalare, situated in the membranous area between the notum and pleuron.

The preepisternite of Conophthorus does not appear to form a part of these dorsal mesopleural processes. The processes are confined to the episternum and epimeron, and probably originate from the pleural ridge as wing processes. A shallow depression, whose function was not determined, occurs on the anterior median angle of the episternum dorsad of the preepisternite (Figure 28). More caudad, an extensive concave impression extends through the remainder of the episternal margin to the pleural ridge, rising medially as the clavicle condyle (cl). When the elytra are in repose, the costal head of the elytron rests within the concavity provided at the base of this process. Another condyle (cor) extends from the apex of the pleural ridge and the edge of the epimeron. The second axillary sclerite of the elytral pteralia appears to articulate on the surface of this sclerotization, and it is this point of the mesopleuron that is approached by the alar process of the scutum. Both the basalare or basalar plate and the subalare or subalar plate appear to be absent from the mesopleuron of Conophthorus or are represented by above processes.

The episternum occupies over three-quarters of the mesopleural surface area. It is rather rectangular, although the dorsal margin is considerably shorter than the ventral; and the anterior, more or less perpendicular while the posterior is inclined caudally toward the venter. The anterior margin is roundly folded within the body aperture. The upper posterior margin is invaginated in a deep trough-like depression, with the cephalic edge of the invagination protruding caudally over the pleural sulcus. This depression provides room for the basal portion of the elytral costal margin. Ventrad, the remainder of the episternal caudal margin is marked by the conspicuous line of the pleural sulcus extending to the coxal foramen.

The pleural inflection (PIR) is recognized as a low ridge on the interior surface of the posterior mesopleuron (Figure 29). Ventrad it terminates at the upper edge of the coxal foramen in a thickening representing the pleural coxal process (Plcxp). An additional ridge extends anteriorly from this process, dorsad along the edge of the coxal foramen, to within one-half the distance of the anterior mesothoracic margin. This is believed to be the pleuro-sternal inflection (PlSi). Anteriorly it is closely approached by a narrow projection of the united presternal-preepisternal margins, as well as being combined with the sternal apophysis (SA). It marks the relative position of the pleurosternal line. Anteriorly, the pleurosternal line is indicated by an inflection directed to the venter from union of the preepisternal and presternal margins.

A marginal sclerite, adjacent to the episternal anterior infolded surface, is believed to constitute the preepisternite. This sclerite lies entirely caudad of a line, barely discernible, bearing the intersegmental membrane. Dorsally the preepisternite is fused into the episternal margin, extending along the inner edge to the pleural inflection. The upper anterior angle of the preepisternite bears a small internally-directed apodeme (apo). Ventrad the preepisternite meets the base of the presternite (Prs) and the margins continue caudad to the sternal apophysis. The united preepisternite and the presternite is known as the prepectus. The episternal surface, except for the anterior infolded margin and a small caudo-ventral region above the coxa, is irregularly punctured. Moderate punctations of the median area bear the largest setae.

The epimeron is a narrow posterior marginal sclerotization in the mesopleuron (Epm_2, Figures 28, 29). Extending along the pleural sulcus, it forms a postcoxal bridge (Pc) ventrad, but fails to continue dorsad as an appreciable sclerite, only as a slight semi-membranous element. In the median area the epimeron is narrowly emarginate to accommodate the mesothoracic spiracle (Sp_2). Ventrad, the postcoxal bridge is narrowly rounded and articulates with the mesosternum in the clavicula (Clav) (Schedl 1931). The posterior epimeral margin is grooved for nearly one-quarter of its distance to permit the articulation of the metepisternal margin on its surface. The lower epimeral surface is extensively sclerotized, pigmented, and covered with minute punctures. Only light sclerotization and pigmentation occur on the dorsal region which is impunctate.

The mesosternum is situated ventrally between the mesopleura. Three of its margins are immovably united with other sclerites. Laterally each margin is enclosed, largely by the episternum, although the epimeron engages the postero-lateral angle. The posterior margin is fused with the metasternum throughout its length, as well as being in contact with the epimera laterad.

A basisternite (Bs_2) and sternellum (Sl_2) appear to be visibly distinguishable in the structure of the mesosternum (Figures 30,31). These sternites are separated by a fairly discernible line which has been interpreted as the sternacostal suture. The sternacosta (Figure 31, sca) extends transversely between the bases of the sternal apophyses (SA). It passes immediately below the anterior rim of each acetabulum, caudally toward the meson, dividing the eusternum into two sclerites of approximately equal area. The basisternite is almost completely exposed at all times, but the sternellum is generally concealed by the coxae. Further external sternites are not apparent in the mesosternum. A narrow marginal sclerotization, caudad of the anterior basisternal margin and entirely within the body cavity, was assumed to be the presternite (Prs). The presternite has been previously discussed in connection with the prepectus.

The basisternite is irregularly shaped. The anterior margin is nearly straight and dorsad becomes rounded into the presternite. Laterad the basisternal margins expand about the coxal cavities to the bases of the pleural sulci. These lateral sternal expansions have been designated as exocoxal areas by Hopkins (1909) and Kaston (1936). A narrow elongation of the basisternal caudal margin is produced between the acetabula to form the anterior portion of the intercoxal process (aicp). The remainder of the posterior margin lies immediately below the anterior rim of the coxal cavities.

A considerable portion of the basisternal surface, particularly the median area from the anterior margin to the intercoxal process, is covered with a series of minute punctures, many bearing short setae. Two small antero-lateral areas and most of the exocoxal regions are smooth, generally lacking both punctures and setae. A number of longer setae occur in a row extending along the anterior rim of the coxal cavities. The entire surface of the anterior intercoxal process is rather densely setose.

The remaining mesosternal sclerite, the sternellum, is largely concerned with the formation of the coxal cavities. Only a narrow marginal portion, extending across the caudal edge of the mesosternum on the posterior rim of the acetabula is excepted. Mesad, this strip is projected anteriorly between the coxal cavities, forming the caudal section of the intercoxal process. The apex of this process is rounded, grooved, and loosely engaged by the hollow terminus of the anterior section. This arrangement permits a certain degree of flexibility to this region of the sternum. The entire intercoxal process is elevated in a median arch extending over the inner surface of the cavities. A small rounded aperture joins the two compartments. Laterad the sternellum meets the pleural sulci in firm connections on the outer margin of the coxal foramina. Articulatory surfaces of the sternellum and epimera meet at the calvicula. Much of the surface of the coxal cavities is minutely pitted. No setae occur on the surface of the posterior intercoxal process.

The interior surface of the mesosternum is dominated by the sternal apophyses (Figure 31, SA). These are a pair of extensive apodemes based at the lateral terminations of the sternacosta. Each apophysis consists of a slender process, directed anteriorly at the base, but rising dorso-laterally toward the mesopleuron, which it does not appear to contact. The base of each sternal apophysis is joined by the anterior end of the pleurosternal inflection at a point approximately one-half of the distance to the anterior mesosternal margin. The median area between the junction of the pleurosternal inflection and sternal apophysis is enclosed by a lighter sclerotic integument extending upward from the lateral exocoxal surface. A further flattened sclerotization occurring in the median region of the anterior edge increases the muscle-bearing capacity of each apophysis.

6.3.3 Metathorax

The metathorax is the largest thoracic segment in total surface area. In length it is exceeded only by the notum of the prothorax. Individual metatergites are generally more extensive than those of the mesonotum, and in addition, a postnotal plate is present. To provide greater flexibility, the degree of sclerotization within the metanotum appears to have been considerably reduced as compared with that exhibited in the pleura, sternum, or in the mesotergum. Several additional internal ridges have been incorporated into its structure as well. The metapleura have been modified, so that the component pleurites occupy a horizontal rather than a vertical plane, as was evident in the mesothorax. Unification, reduction, or modification of the metasternum has been thorough, making the identification and extent of its constituents difficult.

Situated between the mesothorax and the abdomen, the metathorax is closely associated with adjacent segments. Anteriorly, the alinotum is connected to the mesotergum through the prealar arms and pleural hooks. Pleura and sterna are closely integrated ventrad. Both the metathoracic notum and upper pleura extend slightly cephalodorsad over the mesopleura. The mesonotum is retracted caudally against the metatergum, with the elevated scutellum produced well over the anterior margin of the scutellar groove. The depressed scutellum extends dorsally over the surface of the prescutum until it lies against the anterior margin of the metanotal scutum. Caudad the alinotum meets the postnotal plate at two points. The postnotum and remnant first abdominal tergum are united at the antecostal suture, bringing the dorsum of the metathorax and the abdomen together. Ventrally the metasternum projects posteriorly well beneath the second abdominal tergum, No sclerotic union occurs between the metathorax and the abdomen in the pleural or sternal regions.

The metanotum (Figures 32, 33) is the most extensive region of the metathorax. Much of its surface area is occupied by an expansive scutum (Figure 32) (Sct_3), essentially composed of two large lateral sclerites. In conjunction with the scutal sclerites, there is also a narrow anterior prescutum ($Prsc_3$) which is partially membranous; a median scutellum composed of the scutellar groove (Sclg) and a posterior sclerite (Scl_3); and a postscutellum or postnotal plate (PN_3). This latter tergite bears a pair of large phragmata (Ph_3).

The anterior-most sclerite of the metanotum is the prescutum. Medially it is represented by a thin sclerotic strip, the dorsal edge of the antecosta (Ac), and a posterior membranous area, referred to by Schedl (1931) and Warren (1960) as the anterior membrane (Amb). Laterally the prescutum expands into a pair of triangular processes known as the prealar arms (Pra) (Warren 1960), anterior prealar processes (Schedl 1931) or the lateral arms of the prephragma (Hopkins 1909, Kaston 1936).

The prealar arms are rather compressed anteriorly and curve ventrad to meet the mesonotal pleural hooks. Caudad, prescutal or transverse sutures (ts) separate the prealar processes from adjoining scutal lobes lying on the postero-lateral margins. Since the prescutal margin has been partially inflected beneath the anterior edge of the scutal lobes, the transverse sutures actually appear to be located within the prominent grooves situated between the sclerites. Examination of this region of the inner metanotum reveals the presence of two short diagonal lines undoubtedly representing the transverse sutural inflections. The antecosta extends ventrally as a transverse plate between the prealar arms. On the ventral margin it bears a slight median notch.

The surfaces of both the sclerotic and membranous elements of the prescutum appear smooth; undisturbed by either punctures of setae. The anterior membrane is completely unpigmented, in contrast to the tergites which are darkly colored in the mature individuals.

The metathoracic scutum covers over one-half of the surface area of the alinotum within its two lateral sclerites. The anterior margin is elevated well above the prescutal surface. A median sclerotization, the scutellar groove, located between the scutal lobes, has generally been accepted as an anterior extension of the scutellum. The actual median boundaries of the scutum are the scuto-scutellar sutures (vs). Laterally the scutal margins are produced into the notal wing processes (ANP, PNP).

Each scutal lobe might be recognized as a composite of three distinct regional elements. These include a large median area, a small antero-lateral sclerite, and a rather narrow longitudinal lateral region, sometimes referred to as the lateral impression (Hopkins 1909, Schedl 1931).

The antero-lateral sclerite is a small, triangular area, separated from each main scutal lobe by the intra-scutellar suture (Figure 32, iss), as designated by Warren (1960) in Hylobius. Kaston (1936) previously determined this to be the location of the prescutal suture in H. rufipes. He was in agreement with the suggestion of Hopkins (1909) that the anterior sclerites were probably prescutal rather than portions of the scutum. In Conophthorus, the position of the prescutal sutures has already been decided as the inflection between the prealar arms and the anterior margin of the scutal lobes. Besides, the anterior notal wing processes are clearly products of these anterior lobes, a function to which the scutum is unquestionably dedicated.

The anterior edge of each anterior scutal sclerite appears to be fused with a pair of small, irregularly-shaped sclerites, one of which extends anteriorly along the edge of the prealar arm. These sclerites appear to occupy the positions, designated by Schedl (1931), as the anterior and posterior prescutellar disks. Perhaps one or both bear some relationship to the sclerite more commonly known as the tegula.

The main scutal lobes are outlined medially and posteriorly by the scuto-scutellar sutures, anteriorly by the elevated margin, and laterally by the broadly-rounded ridges. The scuto-scutellar suture extends along, and slightly lateral to each margin of the scutellar groove. Beginning near the anterior edge of the scutum, it runs caudally before turning sharply, but smoothly, along the posterior edge and proceeding laterally above the posterior margin of the alinotum. It terminates at a point approximately one-half the distance to the lateral impressions.

The median anterior margin of each scutal sclerite is directed caudad from the junction with the intra-scutellar suture. Sharply elevated above the surface of the prescutal anterior membrane, it consists of a slender, but strongly sclerotized ridge (Figure 33, asr). The ridge from each sclerite extends beneath the scutellar groove. It fuses on the inner surface of the groove with a short median extension continuing anteriorly from a pair of prominent internal strut-like sclerotizations (VR) crossing diagonally beneath the scutal sclerites. These struts are marginal thickenings of the V-shaped ridges accompanying the scuto-scutellar sutures. Due to their position in Conophthorus, they appear less obviously associated with these sutures. Examination of the inner alinotal surface reveals each ridge is connected by a thin, triangular, plate-like sclerotization inflected from the suture, completely underlying the median posterior portion of each scutal sclerite.

The lateral impressions of the scutum are flattened marginal regions (Figure 32). Bordering medially on a suture (iss_2) Warren (1960) designated as a second intra-scutellar, each impression extends caudad toward the posterior edge of the alinotum. Cephalo-mesally a steeply rounded ridge assists in outlining the extent of each region. Beginning at the caudal edge of the anterior notal process, the ridge passes through the junction of the intra-scutellar suture. The lateral margins of the scutal sclerites then extend directly caudad to form the posterior notal wing processes (PNP).

Hopkins (1909) believed the area of the lateral impressions, involved in the posterior notal processes, to be a portion of the scutellum. This appears contrary to the opinion that the notal processes are of scutal origin

(Snodgrass 1935, DuPorte 1959). The posterior margin of the scutal sclerite is difficult to establish in <u>Conophthorus</u>, nevertheless, most of the lateral impression could arbitrarily be regarded as scutal, as readily as scutellar, in the absence of more convincing characteristics.

The surface of the scutum is essentially smooth, except for a few punctures on the lateral scutal ridges on the latero-posterior margins. A number of setae issue from a shallow emargination at the junction of the intrascutellar sutures. The s cutal sclerites are darkly colored with the exception of the lateral impressions which, even in mature individuals, are only lightly pigmented.

The metathoracic scutellum comprises the median region of the alinotum. It is composed of a scutellar groove and a posterior scutellar sclerite of undetermined area. The scutellar groove (Figure 32, Scl_2) is a narrow, trough-like structure, impressed below the level of the scutum and the remainder of the scutellum. A faint line extends through the meson. Kaston (1936) has pointed out the function of the scutellar groove in connection with " ... the reception of the sutural margins of the elytra." The scutellar groove extends from the anterior margins of the scutum caudally almost reaching the posterior edge of the alinotum. Its lateral edges are outlined by the costae or parapsidal ridges (Figure 33, co) (Kaston 1936). More laterally the scuto-scutellar sutures flank the scutellar groove for most of its length. Caudad, the scutellar groove becomes less impressed before terminating at the level of the posterior scutellar margin.

The remainder of the scutellum consists of a posterior area (Figure 32, Scl_3) lying between the scutal sclerites and the posterior margin of the alinotum. The lateral edges of the posterior scutellum are difficult to establish, but the region within the confines of the scuto-scutellar sutures is most certainly scutellar. Axillary cords extend from the edges of the alinotum laterad to the alar membranes. The surfaces of both the scutellar groove and posterior scutellum are smooth.

The endodorsum of the alinotum is extensive (Figure 33). Already described in connection with the various tergites, it consists of the ridges of the anterior scutal margin, the intra-scutellar sutures, the costae, and the V-shaped scuto-scutellar ridges.

The metathoracic postscutellum or postnotal plate is a narrow transverse sclerotization extending across the posterior metanotum (Figure 32). Connected to the alinotum by narrow sclerotic processes at two points laterad the median, it consists of two main elements; an acrotergite

(PN_3) and an antecosta (Ac), separated by a faintly visible line, the antecostal suture (acs). The acrotergite is narrow medially, becoming expanded laterally beyond each point of fusion with the alinotum. Its lateral margins continue ventrally to lie adjacent to the metepimera in postalar extensions (Pa). The antecosta consists of a narrow median ventral plate which is expanded laterally into a pair of large triangular phragmata (Ph_3). The phragmata are directed caudo-ventrally, with their apices reaching the vicinity of the metendosternite in the mid-pleural region. Muscular ligaments connect these structures. The remainder of the first abdominal tergum is united to the postnotal plate along the edge of the antecostal suture. A pair of large spiracles, associated with the first abdominal segment, are located in the conjunctiva caudad the postalar bridges.

Each metapleuron has only limited areas of contact with the notum and abdomen; often their association is only through intervening conjunctivae. Direct physical contact does occur with the adjacent mesopleuron and sternum, although here too, union through direct fusion of sclerites is extremely limited. The metepisternum articulates quite freely with both the margins of the mesopleuron and sternum. Dorsad the prealar and postalar processes approach the metapleuron closely, but besides this, the pleuron and notum have a mutual relationship with the wing. Basal alar processes articulate with the clavicle and coracoid processes (Hopkins 1909, Schedl 1931, Kaston 1936) or the basalare and wing processes (Snodgrass 1935, Warren 1960) of the pleuron and through the axillary sclerites with the notum. Only caudo-ventrally, where the metepisternum is continuous with the sternum, are two sclerites firmly united.

The metapleuron is composed of two primary regions, a lower metepisternum (Eps_3) (Figure 28) and an upper metepimeron (Epm_3), separated by the pleural sulcus (PlS). The pleural suture follows a sinuous course from the antero-dorsal angle to the postero-ventral margins as it divides the pleuron into two roughly triangular areas. The episternum has considerably more area and is entirely sclerotized; the epimeron is extensively membranous dorsally.

The episternum extends to all four metapleural extremities. Ventrally it is in contact with the entire margin of the sternum, anteriorly it borders on the mesopleuron, dorsad forms the clavicle or the basalare process, and caudad unites with the sternum. The ventral episternal margin lies on the pleurosternal line. Besides being rather heavily sclerotized, this edge is also flattened and narrowly inflected internally. The anterior angle has been produced into a sharply projected process (sh) which Schedl

(1931) and Warren (1960) called the sternal hook. The sternal hook meets the edge of the clavicula, an emargination of the mesosternum. Near the caudal end, the margin is fused in a single sclerotic point of union with the sternum. The remainder of the ventral margin articulates freely on the metasternum.

The anterior edge of the episternum is unattached to the mesopleuron except through a conjunctiva. The lower margin meets the shallowly-grooved edge of the mesopleuron, with the episternal margin being similarly channelled in the median region for reception of the mesepimeron. Dorsad the anterior edge of the episternum continues into the clavicle process. Caudad the episternum is produced antero-dorsad in the clavicle or basalare process and outlined from the cephalo-dorsal to the caudo-ventral angles by the pleural sulcus. The clavicle process connects through a short alar membrane with the costal head of the wing, and it is with this region, that the prealar arm articulates. The area between the clavicle and coracoid processes is often semi-membranous in appearance. A small apodeme arises at the base of this region. Angling from the anterior edge of the coracoid process as an inconspicuous line, the pleural sulcus becomes more prominent ventrad. It also produces an extensive internal ridge which is partially twisted from its horizontal plane in two regions, so that the sulcus and inner edge of the ridge do not appear to coincide. As a result of these convolutions, the episternal margin is carried dorsad into the epimeron in one region, and more caudally, the epimeron appears to overlap the episternal margin. Ventrally the pleural ridge terminates in a small coxal process. This process is largely located on the postepimeron, which in turn, meets the metacoxa. In the median region, one edge of the pleural sulcus seems to extend anteriorly a short distance marking the base of a small impression on the dorsal margin of the episternum.

The episternum appears to consist of a single pleurite, although there is some indication that it may be otherwise. Differences in surface texture between the dorsal and ventral regions, and a faint line visible in some mature, deeply-pigmented specimens, suggests that a median longitudinal division separating the episternum into a dorsal anepisternum and a ventral katepisternum may have been present at some time. However examination of the internal surface of the pleuron failed to reveal any semblance of a ridge which could be associated with this line.

In conjunction with the episternum, a large, triangular, internal sclerotic plate (Figure 28, Ba) occurs beneath the anterior dorsal region of the metapleuron. A portion of this sclerite extends beyond the cephalic margin of the episternum with a posterior section further visible caudad the epimeron. Dorsad and ventrad it is attached to the inner anterior episternal surface by chitinous tendons (Hopkins 1909). Various associations have been suggested for this sclerotization. Hopkins (1909) called it the clavicle disk, stating "... (it) evidently represents one or both of the paraptera of certain other insects and belongs to the prepleura." To Schedl (1931), it was the pronator or muscle disk. Kaston (1936) unequivocally stated it was the anterior or episternal parapteron or epipleurite, which he pointed out, Snodgrass had labelled as the basalare. Warren (1960) took exception to these views and called it the preepisternum in Hylobius. The basalare is, according to Warren, a portion of the anterior pleural wing process. Both the suggestions of Hopkins, Schedl, and Kaston, that this sclerite is an epipleurite, and that of Warren, that it is the preepisternum, seem plausible. However Snodgrass (1935) clearly stated, that although there is generally but one basalare and one subalare per segment, each is sometimes doubled. This may be the case in these Rhynchophora, and if so, would satisfy both theories to a certain degree.

The surface of the episternum has two shallow impressions and is roughly punctate and sparsely setose ventrally.

One impression, occurring in conjunction with the pleural sulcus in the mid-dorsal region, has already been mentioned. Generally, two, short, widely separated setae are found within its base. The other impression is located in the antero-ventral region above the sternal hook. It extends as a rather conspicuous triangular groove at an angle towards the pleural sulcus. The caudal edge is particularly marked by a moderate internal ridge. Most of the lower episternum is roughly pitted with large, shallow punctations interspersed ventrad with minute punctures. A few setae occur near the lower anterior margin on the sternal hook, and at the caudal-ventral angle. The dorsal episternum is basically smoother, as well as lacking the typical dark pigmentation of the lower area.

The epimeron forms the dorso-posterior region of the metapleuron. Ventrally it is separated from the episternum by the pleural suture. Dorsally it approaches the metanotum and abdominal tergum. Posteriorly the epimeron meets the abdominal hypopleurite as a small, triangular sclerite, the postepimeron (Figure 28, emp_3).

The epimeron proper is only lightly pigmented and not as highly sclerotized, particularly dorsally, as either the episternum or the postepimeron. Two main sclerotic components separated by an intervening area of lighter pigmentation and almost membranous appearance may be recognized.

The first encompasses the base of the coracoid process and extends narrowly caudad above the pleural sulcus to the postepimeron. The second forms a circular, disk-like sclerotization near the posterior margin of the metapleuron. Schedl (1931) is believed to have mislabelled this latter area as "structure of the episternum."

The first sclerite covers the largest area of the epimeron; the second only a minor portion. Dorsad in the coracoid process and along the pleural sulcus, the former is fairly well sclerotized and pigmented. Medially it is extremely narrowed by the slight dorsal expansion of the episternum. Caudad it extends over the episternal margin before terminating in a dorsal expansion on the posterior edge of the pleuron. Numerous minute punctations occur on the lower surface bordering on the pleural sulcus. The second epimeral sclerite has a smooth surface, with generally lighter pigmentation, lacking both punctures and setae.

A branch of the pleural sulcus separates the post-epimeron from the epimeron proper (Schedl 1931). This sulcus extends across the narrow cephalic edge of the postepimeron, cutting it off from the dorsal expansion of the anterior epimeron. On its dorso-caudal margin, a small hooked process is apparent. This is the postepimeral hook (Figure 28, pepmh) (Schedl 1931, Warren 1960) which articulates in the clavicula of the abdomen. The surface of the postepimeron is highly pigmented and sclerotized, resembling the episternum in this respect. A few setae occur on its lower margin, with numerous small punctures dotting the remainder of its surface.

The subalare (Sa), the epipleurite associated with the epimeron, is a small, circular disc lying in the conjunctiva near the edge of the scutum beneath the posterior notal wing process.

Situated between the metapleura, the mesosternum and the abdominal venter, the metasternum has the general appearance of a large rectangular plate (Figure 30). Its lateral margins are parallel, the caudal edge almost straight, except in the median region. The anterior margin is irregularly composed due to the imposition of the mesocoxae in this region. The metasternum of Conophthorus closely resembles that of Gnathotrichus materiarius Fitch as illustrated by Schedl (1931).

The anterior metasternal margin has been rather difficult to establish. It is regarded as the line extending transversely across the sternum from the caudal edges of the clavicula to the intercoxal process, immediately posterior to the rim of the mesocoxal cavities. This is contrary to the opinion of Schedl (1931), who apparently believed this boundary was represented by the actual caudal rim of the coxal cavities. The narrow marginal sclerite which was formed between the edges of the acetabula and the slightly more posterior line, was in his estimation, the metasternal presternum. Hopkins (1909) and Kaston (1936) failed to provide many details on the metasternum during their respective investigations of D. valens and H. rufipes, so that very little precedent exists. The metasterna of Hylobius described by Warren (1960) apparently differs from that of Conophthorus in the structure of the sternellum.

The metasternum of Conophthorus is composed of a large, rectangular basisternite (Bs_3, Figures 30, 31), and a slender posterior median projection, the metendosternite (Mes) of Crowson (1938, 1944), which appears to be a remnant of the furcasternite. Two short transverse lines (scs), extending across the median edge of the basisternal posterior margin, are apparently the sternacostal suture. Only the ventral portion of the metendosternite is normally visible; the remainder is concealed between the coxae and the abdomen. These must be either removed or flexed in order to disclose the remaining metendosternal structures.

The basisternite is large, exceeding the area of either the mesosternum or the prosternum. The anterior margin is deeply emarginate about the posterior edge of the mesocoxae with the median region produced anteriorly in a short intercoxal projection. Although the line marking this edge of the basisternite is clearly visible across most of the sternite, examination of the internal surface failed to disclose any evidence of an internal ridge. The lateral basisternal margins have been produced both dorsally and laterally to form longitudinal grooves in which the ventral edges of the metepisterna repose. The dorsal processes form low longitudinal internal marginal ridges. On the outer edges, the lateral processes are almost serrate. Near the caudal end, the lateral margins unite with the lower metepisternal edges in thin sclerotic connections. The posterior margin of the basisternite is infolded, forming a narrow marginal strip extending mesally from the lateral angles. Most of this infolded portion lies flatly against the inner surface of the sternum, but in the median region, it is produced almost perpendicularly. At the meson, a short longitudinal line, the longitudinal suture (Figure 30, ls) (Crowson 1944), marks the location of an internal ridge supporting the infolded basisternal margin on the inner surface of the sternite. Schedl (1931) described the transverse marginal portion as the sternellar area in Gnathotrichus.

The surface of the basisternite is slightly elevated from the lateral margins to the meson and impressed immediately anterior to, but not between, the metacoxae. Most of the surface is uniformly, but not thickly, covered with moderately long, posteriorly-directed setae. The meson, being glabrous, is excepted, and only a number of short setae occur sparsely over the caudal edge of each impression.

The median caudal process, extending from the posterior margin of the basisternite dorsally between the coxae, is the metendosternite or the furca of Snodgrass (1935) (Figures 31, 34). Anteriorly it is firmly united to the basisternite by a rather thickly constituted basal region. A short, antero-ventral groove (mg) normally occupied by the median intercoxal process of the abdomen, occurs on the meson. Laterad a small articulatory condyle (mcxc) meets the sternartis of each coxa. The stalk (mstk) of the endosternite continues dorsad, narrowly at first, then expanding considerably before forming two lateral transverse arms (lta) above the metacoxae. Both the stalk and arms have a low internal central ridge which supports a thin flange on each side.

At approximately one-half the distance to the apex of each arm, a small, antero-ventrally directed apodeme (apd) occurs. Each arm is thinly flattened at the apex for further muscular attachment and a small tendon extends to each phragma of the metanotal postscutellar plate.

As well as providing a source of muscular attachment, the metendosternite appears to function as a structural framework engaged in forming a septum across the lower region of the posterior metathorax. Conjunctival membranes stretched between the dorsal edge of the coxae and the lateral metendosternal arms complete its formation.

6.4 Thoracic appendages

6.4.1 Prothoracic, mesothoracic, and metathoracic legs.

The thoracic legs are basically similar in size and structure (Figures 35, 36, 37). Each is composed of the segments; coxa (Cx), trochanter (Tr), femur (Fm), and tibia (Tb); with five tarsomeres (Tar), and a pretarsus (Ptar). The coxa displays the only apparent variation in shape; the remaining segments are similar in each leg.

The procoxae are situated within the acetabula of the prosternum so that their mesal surfaces are almost contiguous. Each coxa (Figure 38) is slightly longer than wide and subglobose in outline when viewed in anterior aspect. The outer surface is smoothly rounded, tending to become slightly concave dorsal to the base of the trochanter. The mesal edge is slightly emarginate near the distal end of the coxa. A considerable number of long, widely-spaced setae cover the anterior median surface. This pattern composed of shorter setae, passes distally along the ventral coxa to extend over the posterior surface from the outer edge to the median. The remainder of the coxal surface is smooth.

The distal coxa has two circular apertures on its surfaces. A trochanteral fossa (trf) occurs on one surface, and directly opposite, a small opening for the tip of the articulatory condyle of the trochanter (atrc). The trochanteral fossa bears an impressed rim in which the inner surface is partially recticular. The procoxa, differs from the mesocoxa and the metacoxa, in having the trochanteral fossa on the posterior surface. In the latter two coxae, this aperture is located on the anterior surface.

The base of the procoxa is sharply constricted on both the outer and mesal edges before passing through the coxal fossa into the sternum. This proximal region constitutes the basicoxite (Bcx). It is generally said to be separated from the coxa proper by the basicostal sulcus (Snodgrass 1935, DuPorte 1959), but in <u>Conophthorus</u> this suture is not evident. Instead, a low external elevation circumscribing the segment appears to mark the distal edge of the basicoxite. The outer proximal edge of the basicoxite is produced in an articulatory process (art). The apex of this condyle is in contact with a large, sclerotic strut (Figure 35, st), extending to the inner surface of the pronotum. A small region on the anterior dorsal surface of the articulatory condyle bears a number of short setae.

The mesocoxae are separated by the intercoxal process which projects ventrally between their mesal edges so that they are subcontiguous. The mesocoxa (Figure 39) is nearly ovate, with its length exceeding the width. Both the outer and mesal edges appear smoothly rounded in anterior aspect. The trochanteral fossa is located on the anterior surface of the distal coxa. Dorsad to the fossa, the surface is flattened and smooth to accommodate the mesofemur which may be flexed against it. The anterior surface from the median to the meson, the outer surface, and the outer portion of the posterior surface, are covered by widely spaced setae, those of the posterior surface of smaller size.

The mesocoxal basicoxite is very similar to that of the procoxa. Once again, the proximal outer margin is produced into an articulatory process with a number of short setae occurring in a compact area on the anterior surface, as on the procoxa. There is no indication of an internal strut, similar to that articulating with the procoxal basicoxite, occurring in the mesothorax.

The metacoxa (Figure 40) displays the most diverse structure. Each coxa extends across one-half of the caudal edge of the metasternum from the metepisternum to the metendosternite. Mesally the coxae are separated by the narrow base of the metendosternite. There is no indication of a basicoxite in connection with the metacoxa, but two small artes processes, the sternartis (Figure 37, st), on the mesal edge, and the coxartis (co) from the proximal outer margin, provide the articulatory condyles. Transversely elongate, the width of each coxa is exceeded more than twice by the length. The proximal margin is slightly folded, but a narrow elongate opening remains across the end of the coxa, allowing certain muscles to enter its interior. The anterior surface is shallowly concave throughout the median transverse region, with a single row of setae issuing from punctures located on the upper margin of this impression. The coxal suture (cxs) traverses the outer half of the anterior surface from a point near the coxartis. A thin, dorsally-directed internal ridge accompanies the suture. The distal edges of the anterior and posterior surfaces, the postero-mesal, and the antero-mesal surface about the trochanteral fossa are setose. The setae are generally widespread and moderately long; many arise from punctures.

The second segment of the leg, the trochanter (Figure 41), is the smallest of the limb segments. Roughly triangular, it is slightly longer than broad, and antero-posteriorly flattened. The basal portion, an articulatory condyle (Trac), comprising over one-half the length, is confined to the interior of the coxa. A thin, inseparable covering, produced at the outer distal edge in a distinctive ridge (trcr), encloses the entire condyle in a cone-like sheath. This covering may be the inner ring of the coxal fossa described by Schedl (1931). The narrow base of the articulatory condyle rests on the margin of the small circular aperture opposite the trochanteral fossa, forming a monocondylic articulation which allows partial rotary movement to the trochanter. The broader distal region of the trochanter (Dtr) is normally exposed. Its distal margin is immovably united with the proximal edge of the femur along the diagonal trochanter-femoral suture (trfms) which is clearly evident on both surfaces. The anterior distal surface of the protrochanter and the posterior surfaces of the meso- and metatrochanter are produced in a ridge (trr), identified by Schedl (1931) as the basicosta of the trochanter, which forms an articulatory surface with the rim of the coxal fossa. The opposite surfaces of the distal trochanter, that is, the posterior surface of the protrochanter and the anterior surfaces of the meso- and metatrochanter, are flattened, with sparse numbers of setae occurring on these areas. A particularly long seta occurs on the distal mesal edge of the trochanter adjacent to an acutely raised process located on this margin.

The femur (Figure 42) is the largest segment of the leg, equalled in length only by the tibia. It is elongate, being approximately three times as long as broad. Rather flattened antero-posteriorly, the mesal and outer edges are narrowly rounded. The median anterior surface of the profemur and the outer one-half of the meso- and metafemoral posterior surfaces adjacent to the trochanter, and at times flexed against the coxa, are free of setae. The opposite surface of each femur is covered by relatively long, widely placed setae. Over the remaining surface area, such as the lateral margins, the setae are shorter in length. The distal end of the femur is notched to receive the tibial base. Both the inner anterior and posterior surfaces bear articulatory processes to form a dicondylic articulation with the tibia. The mesal edge of the distal femur is produced into two thinly, flattened processes, the "wing-like extensions" of Schedl (1931). Between these lateral processes, a narrow concavity extends proximad to allow the base of the tibia to rest against the femur. A stout median tooth (mt) occurs between the processes on the distal edge of this groove.

The tibia is slender, equalling the femur in length. Basally it is narrow, being less than one-half of the width of the apical end. The anterior and posterior surfaces of the proximal tibia are produced in a pair of condyles which articulate with the femur. Immediately distad, the mesal surface is carried into a deep notch, with the marginal edges raised into flattened processes. This notch engages the femoral tooth when the tibia is flexed against it. On the mesal edge the tibia expands at a point beyond one-third of the distance from the proximal end. This edge is rounded, with the protibia bearing numerous closely packed, bristle-like setae on its surface. The meso- and metatibia have fewer setae of larger size in this same region. The outer margin of the tibia is relatively straight, flatly rounded, with numerous irregularly placed, low serrations from which long setae issue. The anterior and posterior surfaces of the tibia are clothed with long, widely spaced setae. Three prominent marginal teeth protrude from sockets located on the outer margin and the tibial apex (Figure 43). In addition, a larger, curved, apical tooth (apt) is situated at the apex of the mesal edge. Between the apical and the third marginal teeth, a deep socket (skt) occurs in the distal edge of the tibia for reception of the first tarsal joint.

The tarsus (Figure 44) consists of five sub-segments or tarsomeres having a combined length exceeding about one-half that of the tibia. Each tarsomere is supported in the socket provided in the distal edge of the preceding joint. The base of the first tarsomere is located within the apex of the tibia. Arranged in descending order of length, the tarsomeres follow the sequence: five, one, three, two, and four. The first three tarsomeres are rounded, narrowed basally, becoming uniformly expanded distally beyond the median. A number of long setae occur about the distal margins of sub-segments one and two, with the second being more abundantly endowed. The mesal surface of the third tarsomere is covered by a brush-like grouping of slender setae, having peculiar concavely-flattened apices. The fourth tarsomere is narrowed basally, becoming enlarged apically. On the outer apical margin, it bears a deep emargination which receives the base of the fifth. Its surface is smooth and lacks setae. The sparsely setiferous fifth tarsal joint equals the combined lengths of the second and third tarsomeres. On its mesal edge it is emarginate and produced into a socket which engages the base of the pretarsus.

The pretarsus consists of paired claws and an arolium. The claws are narrow, becoming expanded medially beyond their bases, and curved at the apices. The arolium is oval, flattened, with a finely grooved ventral surface. The pretarsus can be partially retracted within the cavity provided in the apex of the fifth tarsomere.

6.4.2 Mesothoracic wings or elytra

The elytra are extensive sclerotized structures covering most of the dorsal and lateral regions of the mesothorax, the metathorax, and the abdomen, when in repose. Each elytron is connected to the mesonotum and the mesopleuron through an alar membrane extending to the processes of the basal region. A transverse elevation sets off a small, proximal, triangular basal region from the larger distal area of the elytron. Disregarding the basal region, which is almost entirely concealed by the posterior prothorax, the remainder of the elytron occupies approximately two-thirds of the overall longitudinal dimension of the adult. The most conspicuous elytral features are the longitudinal rows of punctures.

The basal region of the elytron is essentially composed of two distinct areas. The most prominent is the triangular elytral base which is separated from the large distal region by the transverse elevation. More or less appended to the proximal anal margin, is a smaller membranous area bearing the axillary sclerites.

The base of the elytron is constituted by the projected heads and proximal portions of the wing veins. Of these, the costa and subcosta have combined in the most prominent process. This process approaches the mesonotal prealar arm, the edge of the scutum, and the clavicle process of the mesopleuron, quite closely. Near the sutural margin, the anal vein forms a lesser promontory. On the dorsal surface of the elytron, between the costal-subcostal and anal processes, lies a small, narrowly elongate, less heavily sclerotized, impressed area, bounded proximally by a small sclerite. This impression consists of a small, circular, setal bearing area (Figure 45, teg), and a larger, more lightly sclerotized region situated immediately posterior. The setal bearing area at the anterior end of the impression is immediately adjacent to the base of the subcostal vein. The setae on its surface are short, stout, and cover the entire area. In Gnathotrichus, Schedl (1931) referred to a similar area as the tegula. If his interpretation is correct, then it would appear that this sclerite has been displaced from its more customary position, which is generally suggested as anterior to the base of the costal vein.

The remaining portion of the basal impression has not received much previous mention in the literature, although both Hopkins (1909) and Schedl (1931) appear to have interpreted the marginal area as an axillary sclerite. While Hopkins referred to it as the radial plate in *D. valens*, Schedl is believed to have labelled a similar area in *Gnathotrichus* as the third axillary. The remainder of the dorsal surface, extending to the transverse elevation, is smooth, with only a few minute setae distributed over it.

The ventral surface of the anterior basal region is raised in the costal- subcostal process. However, the largest area, chiefly underlying the dorsal impression, is deeply emarginate, almost to the base of the transverse elevation. The axillary membrane extends across the emargination to the apical edge, where it is connected to the base of the elytron. This emargination is believed to receive the folded axillary region when the elytron is flexed against the thorax.

Two less prominent structures are located on the ventral surface as well. One, a small opening or fossa, located on the anterior edge of the emargination, appears to function as an aperture for the trachae of the elytron. The purpose of the other structure, a moderate impression situated between the emargination and the anal edge of the elytron, was not determined.

A very small, triangular sclerite is located in the membranous area between the ventral edge of the costal head and the antero-dorsal angle of the mesepisternum. Hopkins (1909), with some reservation, referred to a similar sclerite in D. valens as the clavicle disc, believing it represented a modification of an epipleurite.

The axillary region of the elytron (Figure 45) is not as extensive as that of the metathoracic wings. However, in addition to the presence of the first, second, and third axillaries, there is also a fourth axillary sclerite which is absent from the hind wing pteralia. The median plate (mp) is represented by a narrow sclerite located adjacent to the midpoints of the second and third axillaries.

The axillaries are narrow and irregular in shape. The first (1Ax) is situated transversely across the anterior portion of the axillary region. Its anterior edge is located near the base of the subcostal head. A slender posterior region straddles the edge of the anterior notal process of the mesoscutum. The second axillary (2Ax) is much smaller than the first, and overrides a portion of the first axillary sclerite. A ventral process from the proximal margin of the second axillary approaches the pleural wing process of the mesopleuron. The third (3Ax) sclerite is situated transversely across the posterior margin of the axillary region. It is narrowly elongate and curved from the mid-point toward both ends. The proximal anterior edge lies adjacent to the second and fourth axillaries. A small, rectangular, lightly sclerotized area, located proximally between the second and third axillaries represents the fourth (4Ax) axillary sclerite.

The distal region of the elytron is broadly rounded from the sutural to the costal margins. The inner surface, underlying the sutural margin has been produced into a narrowly rounded process for approximately one-quarter of the distance, from the basal region toward the apex. This ventral elevation is believed to represent the anterior portion of the anal trachea. When the elytron is closed over the dorsum, this process occupies the metathoracic scutellar groove. The costal margin of the elytron lying adjacent to the sternum is sinuate, and a shallow, but particularly noticeable emargination occurs immediately dorsal to the metathoracic leg. A light external thickening on this edge of the elytron appears to provide additional strength to this margin.

The sutural margins are designed to unite along their edges. Each is slightly elevated before becoming sharply impressed ventrally. The inner layer of the elytron has been produced mesad along the margin to form a lamellar ledge bearing numerous minute transverse striations on its surface. Both elytral ledges appear wider in the declivity than more anteriorly, where they are less conspicuous.

In addition to the lamellar ledge, the left elytron also has a narrow groove extending between the ledge surface and that of the upper margin. This groove receives the right elytral ledge, effecting a tongue and groove union. This relationship has been illustrated by Hopkins (1909) for *D. valens* and by Warren (1960) for *Hylobius*. Kaston (1936) pointed out its existence in *H. rufipes* also, but Schedl (1931) does not mention its occurrence in *Gnathotrichus*.

Two structures located on the sutural margin and one occurring on the inner lateral surface near the costal margin are believed to assist in retaining the elytra of *Conophthorus* locked in position over the dorsum. The first of these, located on the surfaces of the lamellar ledges near the apex, simply consists of a small depression on the left elytron which engages a raised process from that of the right. This mechanism appears similar to the processes described in *Gnathotrichus* by Schedl(1931). A second device occurs on the anterior portion of the sutural margin near the basal region. Kaston (1936) mentioned its presence in H. rufipes where it is considerably more elaborate. In Conophthorus, the dorsal edge of the left elytral lamellar ledge bears a small depression which engages a small process produced from the edge of the elytral ledge of the right.

Another locking mechanism, the wing lock (Schedl 1931), may be found on the inner surface of the lateral region of the elytra. In Conophthorus, this device consists of a small raised sclerotic flap issuing from the elytral surface above the costal margin. This structure engages the post-epimeral hook provided by the antero-dorsal margin of the combined anterior abdominal hypo-pleurites. Warren (1960) mentioned the presence of an apparently slightly different mechanism in Hylobius.

An additional thinly raised process occurs on the inner surface of each elytron near the anterior edge of the costal margin. This process becomes lodged in the triangular impression located on the antero-ventral edge of the metepisternum, dorsal to the sternal hook. The purpose of these structures has not been determined.

A particular feature of the elytron is the declivity. When viewed from the lateral aspect, the declivity at the meson begins as a broadly rounded slope beyond one-half the distance from the proximal end of the elytron and continues at a gradient to the apex. The degree of slope and shape of the declivity, as displayed by _C. coniperda_, constitutes a minor variation from that encountered in either _C. resinosae_ or _Conophthorus_ "x" (Figures 7,8,9). Schwarz (1895) stated of _C. coniperda_ "... declivity moderately steep, at middle slightly flattened." The word "middle" is ambiguous, since it might mean in the center of the transverse dimension of the elytron, as well as the central portion of the declivity taken at the meson. However, it is considered that the latter interpretation was implied. In lateral aspect, the angle of the declivity in _C. coniperda_ is much more acute and generally flatter than that of _C. resinosae_ and _Conophthorus_ "x". The declivity in these latter individuals is basically more rounded, as well as being produced at an angle closer to ninety degrees. While the declivity of _C. coniperda_ appears to display this minor variation from that occurring in _C. resinosae_ and _Conophthorus_ "x", in which it is similar in appearance, its application as a taxonomic character would be difficult.

Apart from the degree and shape of the declivity, the structure of the elytra was generally similar in those individuals examined. Immediately lateral to the sutural margin, each elytron is slightly raised, and a number of granulations occur near the apex, in conjunction with the setae located there. Laterally, beyond this area, the declivity becomes smoothly surfaced through a narrow space. This is bounded more laterally by another, wider elevation, that fails to extend fully to the costal margin, merging instead latero-caudally into the surface of the elytron. Remaining is a flattened area at the base of the elevation, which extends anteriorly along the costal margin from the apex.

The most prominent feature of the elytron are the punctures. These are basically arranged in longitudinal, uniseriate rows, beginning at the basal elevation and extending parallel to the sutural and costal margins to the vicinity of the apex. Each Conophthorus elytron examined bore nine rows of punctures which were slightly impressed, more or less uniformly dense, and essentially uniseriately arranged. These rows have been known as striae. A minute seta rises from each strial puncture.

Commencing at the sutural margin and alternating with the striae are the punctures of the interspaces, the interstriae or the interstitial series. These are generally not in impressed rows but occur on the smooth surface of the interspace. The interstitial punctures are less regularly uniseriate, frequently less dense in arrangement, and often smaller than those of the striae. In addition, the interspacial series almost invariably have a long, sub-erect seta issuing from each puncture. At least nine rows of interstitial punctures occur on each elytron as well, but near the costal margin and at the basal elevation, this basic pattern is interrupted by confused punctation. Often the strial and interstitial series cannot be readily determined. On the declivity, the more dorsal rows join those extending from the vicinity of the costal margin, forming a continuous unbroken series. One row, the fifth strial, near the middle of the elytron, is unpaired. In addition to this, the second interspace is not punctured on the median space of the elytral declivity.

The characteristics of the elytral punctures were employed by Hopkins (1915a) as the chief basis for separation of a number of species of Conophthorus including C. coniperda and C. resinosae. C. coniperda, as described by Schwarz (1895), has "... regular rows of moderately coarse, not closely-set punctures, the first row, and often one or two of the outer rows, slightly impressed posteriorly; first and second intervals very sparsely uniseriately punctured, sometimes nearly smooth, the other intervals with regular series of punctures so that the interstitial series can hardly be distinguished from the striae; narrow basal margin of the elytra irregularly punctured ...." According to Hopkins (1915a), all species in the genus Conophthorus with the exception of one, C. edulis, have the "elytral declivity with stria 1 not punctured, 2 and 3 approximate and faintly punctured, interspace 3 rarely without granules." However, this statement cannot be accepted as a valid interpretation of the characteristics of C. coniperda, C. resinosae, or Conophthorus "x", since all specimens of these species examined unquestionably had the elytral declivity with stria one, two, and three punctured and to the same degree. The chief means of separating C. coniperda from C. resinosae lies in Hopkins' statements splitting the second division of the genus into two subdivisions. Accordingly, C. coniperda has "elytra with strial and interspacial punctures unequal in size and density, those of the interspaces smaller and sparsely placed, especially on the dorsal area." C. resinosae has "elytra with strial and interspacial punctures equal or subequal in size and density on dorsal and lateral areas." Hopkins further pointed out that C. coniperda has "elytra with strial punctures in obscure rows on lateral area ... punctures of elytra distinct, those of striae rather dense ... declivity with interspaces

1 granulate, pubescence moderately long, erect ... black, shining." C. resinosae meanwhile, was described further, as having "elytral punctures coarse, impressed ... interspaces 3 of elytral declivity with distinct granules, the declivity not strongly impressed ... elytra with strial punctures confused on dorsal area ... declivity with interspace 1 granulate ... dull black."

Thomas and Lindquist (1956) have reported the identification of Conophthorus from jack pine as C. coniperda and C. resinosae, as well as Conophthorus possibly coniperda and Conophthorus probably resinosae. Most of the Conophthorus from jack pine examined in this study had elytral punctations characteristic of C. resinosae. Some tendency toward intermediateness between C. resinosae and C. coniperda was also apparent. To determine whether there is any taxonomic significance in the number of punctures occurring on the elytra, the number of punctures in the second interstrial series of the left and right elytron of 24 female Conophthorus from each host tree was counted. Analysis of variance revealed a significant difference (Table V). The "t"-test was employed to establish whether a significant difference in the mean number of punctures of the second interstria of the left elytron occurred between particular species. A noticeable difference was found at

Table V. Analysis of variance on the second interstrial punctures, left elytron of *C. coniperda*, *C. resinosae*, and *Conophthorus* "x".

	Sum of squares	d.f.	Mean square	F ratio	
Means	880.88	5	176.18	$F: \frac{176.18}{13.43}:$	13.12
Within	1933.68	144	13.43		
Total	2814.56	149		$F_{.95(5,144)}:$	2.28

Table VI. The summation of results of a "t"-test on the second interstrial punctures of the left elytron of *C. coniperda*, *C. resinosae*, and *Conophthorus* "x".

Comparing	d.f.	Calculated "t"	Given "t" values at different levels of signifance			
			$t_{.95}$	$t_{.975}$	$t_{.9875}$	$t_{.995}$
C. resinosae with *C. coniperda*	148	5.947	1.66	1.98	2.27	2.62
C. resinosae with *Conophthorus* "x"	148	2.204				
C. coniperda with *Conophthorus* "x"	148	3.948				

all levels of significance when C. resinosae was compared with C. coniperda and for C. coniperda compared with Conophthorus "x". It was significant at the 5% and 2.5% levels when C. resinosae was compared with Conophthorus "x". These results are summarized in Table VI.

6.4.3 Metathoracic or hind wings

The metathoracic or hind wings are rather large (Figure 46), exceeding the overall length of the adult in their longitudinal dimension. When not engaged in actual flight, they are concealed beneath the elytra, being laid flatly against the dorsum. To accomplish this, they are twice folded in the distal region, longitudinally, as well as transversely.

Basally each wing is narrow, becoming broader toward the apical or outer margin, so that distad its breadth is approximately one-third that of the overall length. The costal margin is sinuate. The apex is rounded to the edge of the anal margin. A lobe, resembling a jugum, is present in the proximal anal region. Pteralia, composed of the first (1Ax), second (2Ax), and third (3Ax) axillary sclerites, and a median plate (mp), occupy the basal or axillary region. Here, too, the bases of the costal (C), subcostal (Sc), radius, media (M), cubitus (Cu) and anal veins are located. The distal portion of the wing is membranous with rather sparse and weak venation.

The axillary sclerites (Figure 47) are well developed and defined. The first axillary is the largest. It is rather an elongate, irregularly-shaped sclerite, produced antero-laterally in a condyle which meets the base of the subcosta. Anteriorly, it is narrowly separated from the anterior notal process and the edge of the scutum. Its posterior edge is emarginate. The second axillary sclerite lies posterior to the distal margin of the first, with only a narrow median membrane separating them. This sclerite is roughly triangular in shape, with the anterior margin exceeding the width of the posterior edge. There appears to be no significant connections between this sclerite and the wing veins. Ventrally an acute process from the proximal margin pivots on the coracoid process of the pleuron. The third axillary is also narrow and elongate. Its proximal margin is partially adjacent to the posterior notal process. On its anterior distal edge an acutely curved elongation, which might bear some association with the weak anal veins, forms the anterior margin of a small anal fold in the wing. The chief function of the third axillary sclerite appears to be concerned with the flexation of the wing. There is no evidence of a fourth axillary sclerite. The median plate lies adjacent to the second and third axillaries. It is roughly triangular in outline. Although there is no indication of a median division, the distal, rather rectangular region, is more highly sclerotized than the remainder of its area.

Only in the proximal region of the wing is the venation moderately developed. Even so, the costal vein is short, extending only a very slight distance distally. The base of the costal vein is connected to the clavicle process of the metepisternum by a minute projection of the ventrocaudal edge. The subcosta appears to approach the costa near its base, but contact between them is limited. A number of setae, not exceeding six, are located in a line on the caudal edge of the costal vein near its distal end.

The subcosta equals the costa in length. The proximal portion is convoluted in a spiral, and near the base it is in contact with a condyle of the first axillary sclerite. Analysis of the elements associated in the structures at the base of the subcosta is difficult due to confusion resulting from its grotesque composition. Schedl (1931) pointed out some elaborate relationships between the basal elements in this region of Gnathotrichus. In Conophthorus, it would appear that the radial vein has entered into this structure as well. A large triangular process, situated dorsal to the subcostal base, meets the first axillary sclerite and more distally appears to be narrowly connected to the radial vein.

The radial vein is approximately twice as long as the subcostal. Its base is curved posteriorly to lie beneath that of the subcosta. Distally it terminates at the median fold (Hopkins 1909, Schedl 1931, Kaston 1936, Warren 1960) in two branches. Only one branch appears in the distal region of the wing. Hopkins (1909) and Schedl (1931) referred to such a vein as the R_2, but Kaston (1936) and Warren (1960) have designated similar veins in their investigations as the R_3. A number of setae, in excess of six, are uniformly placed on the anterior edge of the radial vein near the median fold, with a single seta occurring on the outer margin of the vein, also immediately adjacent to this fold.

The medial vein originates near the radius in the area distal to the median plate. It extends distally to the ventral region of the median fold, then curves sharply posterior to the anal margin. Kaston (1936) and Warren (1960) appear to have indicated this vein as the cubitus. Hopkins (1909) and Schedl (1931) believed it to be the median. A distal branch has been labelled by all these authors as the medial. A vein, of similar characteristics to one determined by Hopkins (1909) and Schedl (1931) as the cubitus, appears faintly in the region distal to the third axillary sclerite. It extends toward the anal margin. Two slightly pigmented areas posterior to this latter vein may represent the remnants of the anal veins.

The distal region of the wing has at least two prominent longitudinal folds. The most anterior, appears to be the scutellar fold (sf), as designated by Warren (1960) and Kaston (1936). It lies just anterior to the R_2 vein. Another fold follows the M_1 vein.

Two transverse folds also occur. Of these, the median (mf) is the most prominent. The other takes place in the membranous distal area of the wing and is not marked. A small anal area of flexation is also present in the basal region.

The anal margin, from the apex to the jugum, has a fringe of widely, although uniformly spaced, spine-like structures which have been called setuale by Kaston (1936).

6.5 Abdomen

The abdomen is composed of seven partial or wholly visible external segments in the female and eight in the male. Each segment is theoretically constituted by a tergum (T), a pair each of epipleurites (Ep) and hypopleurites (Hp), and a sternum (S). However, the unification of some regional elements with those of other segments, and the reduction or absence of others, has altered the actual appearance of some abdominal segments from the basic plan. The entire abdominal dorsum is normally concealed beneath the elytra and at least partially covered by the metathoracic wings as well, except of course, when these are opened, as during flight.

The composition and relationship of each of the segmental regional elements follows a basic pattern. The tergum is rather lightly sclerotized and generally is not as heavily pigmented as the sternum. Each tergum is separated from preceding and succeeding terga by membranous conjunctivae. The sterna, on the other hand, are highly sclerotized and pigmented, as well as being either fused, or closely fitted to those adjacent. The epipleurites are small, lightly sclerotized and very lightly-pigmented, lateral sclerites supporting the spiracles. Like the sterna, with which they are indistinguishably fused on their ventral margins, the hypopleurites are both highly sclerotized and heavily pigmented.

The most anterior tergum of the abdominal dorsum (Figure 48, T1) is distinctly divided transversely by a membranous conjunctiva into an anterior acrotergite (atg) and an almost membranous but pigmented posterior tergite. The acrotergite of this tergum is more extensive than that of any of the remaining segments since it functionally represents an integral part of the metathorax which is known as the postnotal plate. The terga of segments two to six are essentially similar in shape, although generally reduced in size, particularly in transverse dimension, toward the caudal end of the abdomen.

The shape of the seventh tergum is coincident with the sex of the adult (Herdy 1959). Previously, Kaston (1936) showed this relationship to be valid in H. rufipes. The male seventh tergum (Figure 49) is similar in appearance to the preceding terga, resembling an inverted trapezoid, with the caudal margin extending squarely across the end of the tergum. The caudal margin is reinforced by being carried ventrad and anteriorly in a narrow semicircle. A line of small, flattened triangular projections lie along the edge of the margin, with scale-like processes produced distally into five or six acute tips, protruding from between the bases of adjacent projections. The remainder of the surface, except for the anterior one-third, is minutely punctured, with small, broad, sword-shaped setae issuing from occasional punctures. The anterior region is only lightly sclerotized and pigmented, with an absence of punctation, but with very minute setae distributed uniformly over the surface.

The female seventh tergum (Figure 50) differs from that of the male in the shape of the caudal margin, its greater size and posterior surface furnishings. The female tergum is much larger than that of the male, having almost equal transverse and longitudinal dimensions. The caudal margin is produced in an acute semi-circle rather than squarely cut-off as in the male. The edge is nevertheless directed ventrally to strengthen the margin of the tergum. A small portion of the posterior tergum is more highly sclerotized and pigmented than the anterior region. Long setae issue from the bases of low flattened serrations, covering this surface of the tergum. Much of the anterior surface has minute punctures and sword-shaped setae as in the male. The remaining anterior one-third is similarly but lightly sclerotized and pigmented.

The eighth tergum is only externally visible in the male. The female eighth is completely covered by the seventh. The male tergum (Figure 51) is greatly reduced in size in comparison to the anterior terga. The lateral margins are produced smoothly from the cephalic region so that the caudal edge is almost semi-circular. Both the lateral and posterior margins are folded ventrad for additional strength. The caudal half of the surface is deeply pigmented and covered with numerous punctures and long setae. The anterior portion is for the most part, only lightly pigmented.

The female eighth tergum bears some semblance to the male counterpart in both size and shape. Differences exist in the shape of the anterior margin, the degree of sclerotization and in the abundance and type of surface furnishings. The tergum has only moderate lateral sclerotic regions with the median surface area almost membranous and completely lacking in pigment. The caudal portion bears a number of low flattened serrations which are the only furnishings found on its surface.

Although the abdominal dorsum has seven or eight visible terga according to sex, the composition of the venter appears limited to only five clearly visible sterna (Figure 52) in each. These sterna represent segments three to seven, as indicated by Hopkins (1909) for *Dendroctonus* and Kaston (1936) in *H. rufipes*. However, in addition, Hopkins was able to determine that the sterna of segments one and two, in *Dendroctonus*, were fused to the anterior margin of the third sternum. Faintly visible lines on the surface of the metacoxal cavities and extending across the intercoxal process of *Dendroctonus* have been suggested by Hopkins to represent the disengaging sutures. Similar, faintly visible sutures (?S) in *Conophthorus* may be determined by examining the surface of the anterior sternum.

Sternum three, with sterna two and one, probably represents the most diverse structure in the abdominal sternum. Sterna one (?S1) and two (?S2) are components of the inner wall of the metacoxal cavities. Sternum three appears as a narrow transverse sclerite situated between adjacent sterna. The suture between sterna two and three lies just caudad to the metacoxal cavities. Sternum two forms a narrow ledge outside the cavities, meeting sternum three caudad, and anteriorly constituting the greatest portion of the inner wall, as well as the complete intercoxal process. The remaining portion of the inner wall of the metacoxal cavities, a narrow rim on the anterior margin, is the component of sternum one. Sternum one also appears to form the smaller inner intercoxal process within the coxal cavity.

Sterna three and four are inseparably fused, although a clearly visible former suture plainly delimits the boundaries of these sterna. The point of union between these sterna is relatively weak in the callow adults, so that separation along this line could be affected by the application of slight pressure with a sharp instrument. In the mature adults, the points of contact are more firmly set, so that it is virtually impossible to initiate separation in this region.

Sterna four, five, six, and seven are relatively similar in shape, although here, as in the dorsum, the progressive reduction of sternal size is evident towards the caudal end of the abdomen. Sternum seven is elevated in the median region to allow the posterior margin to make contact with the edge of the final exposed abdominal tergum. The posterior margin of sternum four overlaps the anterior margin of sternum five and this pattern in which the preceding sternum covers the margin of the succeeding sternum is continued caudad.

The sterna of all segments are highly sclerotized and deeply pigmented. With the exception of sterna one and two, located in the coxal cavities, the surfaces of the remaining sterna are covered with irregular distributions of punctures and backward projecting setae. Particularly conspicuous setae are found on sterna four, five, six, and seven.

Seven pairs of functional abdominal spiracles (Sp) are evident in both sexes. The first six pairs are situated on the epipleurites; the remaining or seventh, is located on the antero-lateral portion of the seventh tergum. An eighth pair, apparently rudimentary, are faintly visible in the male eighth tergum, but the female tergum bears no such evidence.

The number of functional pairs of abdominal spiracles in Rhynchophora appears quite variable as suggested by Warren (1960). He stated that Hopkins, 1911, reported seven pairs in Pissodes. Hopkins (1909) found eight pairs in Dendroctonus. Kaston (1936) indicated only six functional pairs in H. rufipes and Schedl (1931) recognized seven in Gnathotrichus. The possibility of rudimentary spiracles is not without precedent since Schedl (1931) mentioned the rudiments of an eighth pair in the male Gnathotrichus and Warren (1960) described a rudimentary eighth pair on the female Hylobius. Kaston (1936) stated that the seventh pair in H. rufipes were nonfunctional.

The hypopleurites are rather small, rectangular sclerites indistinguishably fused with the dorso-lateral margins of the sterna Those of segments one to four are united to form one composite hypopleurite on each margin of the sternum, with faintly visible sutures outlining their boundaries. The anterior dorsal margin of the first hypopleurite engages the lateral wing lock of the elytra. The remaining hypopleurites of segments five, six, and seven are free along both of their anterior and posterior margins.

All of the hypopleurites have a smooth, highly sclerotized and deeply pigmented surface ventrad of a line extending from the postero-dorsal edge of hypopleurite four and continuing through hypopleurite five and through the median regions of numbers six and seven. Above the line, the hypopleurites are only lightly sclerotized and pigmented. No setae are apparent on the surface of any hypopleurite.

6.6 Male genitalia

The male genitalia is composed of a number of sclerotized and partially or wholly membranous elements associated in the structures designated by Snodgrass (1935, 1957) and Kaston (1936) as the phallus (Figure 53). At times, the phallus has also been referred to as the penis by Schedl (1931) and the aedeagus or male genital tube by Lindroth and Palmen (1956) and Warren (1960). In *Conophthorus*, the phallus is situated to the right of the meson, immediately beneath the seventh abdominal tergum. A cursory inspection reveals at least four main components, the phallobase, the aedeagus, the endophallus and the spicule. Confusion is inevitable when any attempt is made to homologize the terminology that has been employed to designate its respective elements.

The outermost or ectal element is a sclerotic ring-like structure encircling the proximal region of the aedeagus. This structure has been commonly referred to as the tegmen by Hopkins (1915b), Kaston (1936), Lindroth and Palmen (1956), and Warren (1960); as the perameren by Schedl (1931) after Verhoeff, and according to Schedl, as the gabel by Lindeman. Undoubtedly this structure is the phallobase of Snodgrass (1935, 1957).

The phallobase in Conophthorus is a narrow circular structure having a prominent ventral proximally directed arm or apodeme. Some specimens also appear to have two much smaller proximal mid-lateral apodemes, but these structures are apparently reduced or vestigal in others. The main circular element (bp) has been called the pars basalis or basal piece by Lindroth and Palmen (1956) and the basal piece by Warren (1960). The ventral apodeme (mab) was known as "an apodemal process" by Hopkins (1915b), the metula by Schedl (1931) apparently after Fuchs; the tegminal strut by Kaston (1936), and the manubrium by Lindroth and Palmen (1956) and Warren (1960). The purpose of the phallobase seems to have been determined by Hopkins (1915b) as that of an apodeme essential for the attachment of certain muscles concerned in the movement of the aedeagus and certain other components.

Schedl (1931) pointed out that the penis (phallus) of Gnathotrichus is covered by an "outer layer" formed by " ... a membranous tube in which the inner cover (the aedeagus of Snodgrass 1935) slides forward and backward. A ringlike part of this tube (the phallobase) is heavily chitinized, and when dried specimens are used only this structure is obtained." A thin membranous sheath envelops the aedeagus of Conophthorus, extending from the phallobase over the distal edge of the aedeagus and continues caudally as a tube-like structure to the ventral surface of the eighth tergum, where it terminates at the genital opening.

The main portion of the phallus was known as the body by Hopkins (1915b), the inner covers by Schedl (1931) after Fuchs, and according to Schedl, as the penis tube by Nusselin. Kaston (1936) has referred to it as the median lobe; Lindroth and Palmen (1956) as the penis or median tube, and Warren (1960) as the penis. It was called the aedeagus by Snodgrass (1935, 1957).

The aedeagus in Conophthorus is a small rather cylindrical, incompletely sclerotized, bilaterally symmetrical structure. The latero-dorsal, lateral, and ventral surfaces consist of a single sclerotized plate which is separated dorsally along the meson by a narrow, but varying, unsclerotized area. Hopkins (1915b) designated the lateral surfaces as the lateral folds. Schedl (1931) was able to distinguish in the "inner covers" of Gnathotrichus, the lateral, laminae dorsales and the ventral, laminae ventrales. The latero-ventral and ventral surfaces of the aedeagus in Conophthorus are slightly constricted throughout the median region. The ventral surface, in particular, also appears less deeply pigmented through the median region. A short suture originates on the caudal margin in the mid-ventral region, extending a short distance proximad. The dorsal, lateral, and ventral distal surfaces have a number of widely placed punctures, called sensory pores, by Hopkins (1915b) and Schedl (1931). The distal end of the aedeagus is enclosed by a pair of curved triangular "end plates" (Hopkins 1915b) or parameres (Snodgrass 1935). These end plates are connected to the dorsal edge of the endophallus. The proximal end of the aedeagus is unsclerotized, but completely filled instead, with muscle fibers and associated tissues. It is through this region of the aedeagus that the ductus ejaculatoris enters to meet the endophallus.

The remainder of the aedeagus is composed of two long slender apodemes (aed apo) extending proximad from the antero-lateral margins of the ventral surface. These curve dorsad from independent bases to become united by a narrow median dorsal sclerotization, the transverse band (tb) of Hopkins (1915b), or the jugum or Steg of Fuchs, according to Schedl (1931). The apodemes have been known as the body apodemes or femora by Hopkins (1915b). Schedl (1931), in the text dealing with Gnathotrichus, has called them, the peduculi penis, but the illustrations are labelled as the femora penis, apparently after Verhoeff. To Snodgrass (1957) they were merely the aedeagal apodemes.

The aedeagus encloses the endophallus (Figure 54), which according to Snodgrass (1935) contains the opening of the ejaculatory duct, the gonopore (gpr), at the apex. The endophallus of Conophthorus consists of a curved membranous structure occupying a median position in the aedeagus. The dorsal end is forked into two large lobes; one lobe rests against the upper edge of each end plate, and it appears that the endophallus pivots at this point. Pressure everts the distal and ventral end of the endophallus, which is really the penis (pen), through the opening created between the end plates. The distal or lower half of the endophallus in encircled by a looser membranous sheath (mns) which appears to contain the ejaculatory duct extending caudad from the proximal regionn of the aedeagus. The ejaculatory duct enters the penis at the base of the encircling sheath and may be seen passing distally at the junction of the two mediums. A small opening may be noticed at the apex of the penis.

Lying in various positions along the right side of the phallus is a slender curved and forked rod-like structure. This is the spicule (Figure 55) of Hopkins (1915b) and Warren (1960); the spiculum gastrale of Kaston (1936), and mistakenly it is believed, as was mentioned by Kaston, it was called the spiculum ventrale by Schedl (1931). The proximal portion of the spicule is curved to fit over the cephalic end of the phallus, usually well above the apices of the aedeagal apodemes. The slender median region lies against the right side of the phallus. The distal end is orientated so that the aedeagus is partially enclosed by the forks. The smaller lateral apex (mp) has been designated as the lateral or minor prong by Hopkins (1915b). Kaston (1936) has observed in _H. rufipes_ that the prongs "... are attached by thin muscle strands to the eighth sternite." The cephalic end of the spicule in _Conophthorus_ is fastened to the left dorsal margin of the phallobase by a slender muscular connection. In the distal region, the spicule is attached to the membranous covering of the aedeagus, and also, by other connections, to the surface of the eighth tergum. According to Hopkins (1915b), the spicule is another apodeme associated with muscles concerned in the movement of portions of the inner phallus, but it would appear more likely to be associated with the movement of the phallus through the genital aperture.

7. GENERAL DISCUSSION AND CONCLUSIONS

A thorough anatomical study has not provided any criteria to identify the *Conophthorus* species inhabiting jack pine shoots, nor added materially to the characteristics for separating *C. coniperda* and *C. resinosae*. The characteristics of the elytral punctures enables the separation of these two species, as outlined by Hopkins (1915a), but does not establish the identity of *Conophthorus* "x". A qualification of Hopkins' system, using the mean number of punctures in the second interstria of the elytron, increased the reliability which may be placed on this character for the identification of *C. coniperda* and *C. resinosae*, and also suggests that *Conophthorus* "x" may be more closely related to the latter species, if it is not in itself allopatric.

Other anatomical features, such as the shape of the pronotum and the slope of the elytral declivity, have also indicated a closer morphological relationship between *C. resinosae* and *Conophthorus* "x". However these two characteristics are difficult to measure and assess. *C. coniperda* and *Conophthorus* "x" are inseparable on the basis of length alone.

Certain diverse ecological trends which tend to reflect individuality are apparent from previous investigations.

C. coniperda, for instance, appears to confine brood rearing exclusively to white pine cones, overwintering only in the brood cones, and failing to feed (Henson 1961a) prior to overwintering. C. resinosae invades both shoots and cones of red pine to rear brood, but also feeds in red pine shoots before overwintering exclusively in the vegetative buds which fall to the ground (Lyons 1956). Occasional broods of C. resinosae have been mentioned by Lyons (1956) to have also occurred in second-year cones of jack pine. Conophthorus "x" has not been known to attack many jack pine cones, relying almost exclusively on the shoots for feeding, oviposition, and overwintering sites (Herdy and Thomas 1961).

Other species of Conophthorus have shown further trends. C. lambertianae, as C. coniperda and C. resinosae, utilized both cones and shoots of its host, P. lambertiana, but attacks the shoots only in the fall, to overwinter within them (Struble 1947, Ruckes 1957). C. monticolae (Williamson 1961) and C. radiatae (Ruckes 1958, Schaefer 1962) are believed to limit their activities specifically to cones for both brood rearing and overwintering sites.

Failure to locate many jack pine cones infested by Conophthorus "x" (Herdy and Thomas 1961) would suggest that infestation of these cones was limited. The unlikely possibility that jack pine cones are for some reason unacceptable must also be considered. Unacceptibility may be due to either some physiological nature of the cones or the behavior of the beetles. Schaefer (1962) stated for C. radiatae "mature cones are not suitable for attack in late summer and fall as the tissues have become extremely hard and would be unsuitable as a food source for the larvae." This is probably true of jack pine cones also. However, in the spring and early summer when oviposition is occurring, jack pine cones appear no different than those of P. resinosa and could provide a suitable source of food for larvae. During the investigation of the seasonal development of Conophthorus "x", jack pine cones were sliced and the larvae reared on this medium. No unusual effects were noticed. In California, Ruckes (1963) has demonstrated that species of Conophthorus larvae may be reared on cones of Pinus, other than those of the host species. At the present time, the scarcity of attacks by Conophthorus species on jack pine cones cannot be adequately explained.

Struble (1947) pointed out that the significance of the twig-mining habit of C. lambertianae was not understood. Further he stated, "among other scolytids, notably Phloesinus, and certain buprestids, twig feeding by adults is required for sexual maturity. This might be presumed to be the case with Conophthorus". Since Struble's observation, Lyons (1956), Ruckes (1957) and Herdy and Thomas (1961) have found that twig or shoot mining in the late summer usually leads to the ultimate overwintering of the *Conophthorus* within this niche. However, the observation by Struble (1947) and Herdy and Thomas (1961) that many shoots are abandoned after mining, suggests that overwintering sites may not be the prime objective of some species. If, as Struble suggested, twig mining is necessary for attaining maturity, this still does not explain why this activity is not engaged in by all species of *Conophthorus*. Both Ruckes (1958) and Schaefer (1962) found that *C. radiatae* fails to mine shoots of *P. radiata* at any time. This has also been observed by Williamson (1961) for *C. monticolae*. Henson (1961a) finds that gonads of *C. coniperda* develop in the spring after feeding in white pine cones without apparent prior mining of white pine shoots. Godwin (1958) reported that shoot mining occurs only after the available cones have been attacked.

Generally it must be said, that no firm conclusion has been reached on the basis of this study to suggest that the species of *Conophthorus* occurring in jack pine may not be a combination of *C. coniperda* and *C. resinosae* as reported by Thomas and Lindquist (1956), a form of *C. resinosae*, or a separate species. However, there is little evidence to support the involvement of *C. coniperda*. Current knowledge of *C. coniperda* suggests that in its behavior, the adult restricts oviposition exclusively to white pine cones. Two other species of *Conophthorus*, *C. radiatae* and *C. monticolae*, exhibit a similar restrictive selection of oviposition sites, both infesting only the cones of their hosts. *C. coniperda* does not leave the brood cone during the summer but remains in this site over the winter without feeding. It appears to attack even white pine shoots only after the available cones have been infested. The characteristics of its elytral punctures tend to allow its separation from both *C. resinosae* and *Conophthorus* "x". The shape of the pronotum and the slope of the elytral declivity also tend to imply that there is some area of dissimilarity between *C. coniperda* and these latter species.

There appears to be more area of similarity between *C. resinosae* and *Conophthorus* "x". *C. resinosae* mines red pine shoots and cones, producing brood in both. It abandons brood sites in summer to attack vegetative shoots, apparently to feed. *Conophthorus* "x" fails to attack many cones of jack pine but the remainder of its habits are similar to those of *C. resinosae*. The characteristics of their elytral punctures are also similar, although separation on the basis of the mean number of punctures per interstria may be acceptable. Some difference is indicated in their mean overall length as adults, although their ranges overlap considerably.

Further investigation into the ecological aspects of these *Conophthorus* beetles appears warranted, particularly to establish if they express an affinity for alternate hosts and whether or not any degree or form of reproductive isolation exists. Conceivably, additional information from studies on other species could also assist in providing a solution to this problem.

8. SUMMARY

The external anatomy of adult *C. coniperda*, *C. resinosae*, and the *Conophthorus* species inhabiting jack pine shoots has been examined to establish whether populations of the latter are taxonomically similar or different from the former two species. Although no anatomical features were found to permit unqualified identification of populations of the latter, the characteristics of the elytral interstrial punctures provide some basis for partial determinations. The shape of the pronotum and the slope of the elytral declivity are also mentioned as possible characteristics which appear to exhibit some differences, particularly if *Conophthorus* "x" and *C. resinosae* are compared with *C. coniperda*.

A review of the literature pertaining to the development of the immature stages, and the biology and behavior of the adults, has pointed out areas of similarity and difference which could prove to be taxonomically significant with further investigation.

9. ACKNOWLEDGMENTS

The assistance of many Forestry technicians in the Department of Forestry, Sault Ste. Marie, Forest Insect Laboratory, who aided in the collection of *Conophthorus* material is gratefully acknowledged and appreciated. The advice and consideration of several Research Officers of this Laboratory, particularly Dr. J.B. Thomas, may also be mentioned with sincere thanks. I am indebted to the officials of the Forest Entomology Branch of the Department of Forestry for providing the time to pursue this project. The photographs were prepared by Mr. D.C. Anderson, Forest Insect Laboratory. Reproductions of these, and the remainder of the illustrative material, were provided by the Biographic Unit of the Department of Agriculture, Ottawa.

10. BIBLIOGRAPHY

Blackman, M.W. 1949. The bark beetles, p.328. In Insect enemies of eastern forests. U.S. Dept. Agr. Misc. Publ. 657.

Crowson, R.A. 1938. The metendosternite in Coleoptera: a comparative study. Trans. R. Ent. Soc. Lond. 87. Part 17, 397-413.

________. 1944. Further studies on the metendosternite in Coleoptera. Trans. R. Ent. Soc. Lond. 94. Part 2, 273-310.

Doane, R.W., E.C. Van Dyke, W.J. Chamberlin, and H.E. Burke. 1936. Forest insects, p.115-117. McGraw-Hill Book Company Limited, New York.

DuPorte, E.M. 1959. Manual of insect morphology. Reinhold Publishing Corporation, New York, 244pp.

________. 1960. Evolution of cranial structure in adult Coleoptera. Can. J. Zool. 38: 655-675.

Felt, E.P. 1906. Insects affecting park and woodland trees, p.751. New York State Mus. Mem. 8(2).

Godwin, P.A. 1958. White-pine cone beetle-life history study. Northeastern For. Expt. Sta., Div. For. Res., Quart. Rept. (4): 1-3.

________. 1959. White-pine cone beetle-life history study. Northeastern For. Expt. Sta., Div. For. Res., Quart. Rept. (1): 2-4.

Hamilton, J. 1893. List of Coleoptera taken at Sparrow Lake, Ontario. Can. Ent. 25: 279.

Harrington, W.H. 1891. Notes on a few Canadian Rhyncophora. Can. Ent. 23: 26-27.

________. 1902a. Notes on *Pityophthorus coniperda* Schwarz. Can. Ent. 34: 72-73.

________. 1902b. Note on insects injurious to pines, p. 114-117. Ent. Soc. Ont. 33 Rept.

Henson, W.R. 1961a. Laboratory studies on the adult behavior of Conophthorus coniperda (Schwarz) (Coleoptera:Scolytidae). I. Seasonal changes in the internal anatomy of the adult. Ann. Ent. Soc. Amer. 54: 698-701.

_____________. 1961b. Laboratory studies on the adult behavior of Conophthorus coniperda (Schwarz) (Coleoptera:Scolytidae). II. Thigmotrophic aggregation. Ann. Ent. Soc. Amer. 54: 810-819.

_____________. 1962. Laboratory studies on the adult behavior of Conophthorus coniperda (Schwarz) (Coleoptera:Scolytidae). III. Flight. Ann. Ent. Soc. Amer. 55: 524-530.

Herdy, H. 1959. A method of determining the sex of adult bark beetles of the genus Conophthorus. Bi-Mon. Prog. Rept. For. Biol. Div. Can. Dept. Agr. 15(3): 1.

__________ and J.B. Thomas. 1961. The seasonal development of a species of Conophthorus Hopkins (Coleoptera: Scolytidae) in the shoots of jack pine, Pinus banksiana (Lamb.), in Ontario. Can. Ent. 93: 936-940.

Hokama, Y. and C.L. Judson. 1963. A new bleaching technique with possible general use in entomology. Ann. Ent. Soc. Amer. 56: 407-408.

Hopkins, A.D. 1909. Contributions toward a monograph of the scolytid beetles. I. The genus Dendroctonus. U.S. Dept. Agr. Tech. Ser. 17, Part 1, 1-164.

_____________. 1915a. A new genus of scolytid beetles. Jour. Wash. Acad. Sci. 5: 429-433.

_____________. 1915b. Contributions toward a monograph of the scolytid beetles. II. Preliminary classification of the superfamily of Scolytoidea. U.S. Dept. Agr. Tech. Ser. 17, Part II, 165-232.

Kaston, B.J. 1936. The morphology of the elm bark beetle, Hylurgopinus rufipes (Eichhoff). Conn. Agr. Expt. Sta. Bul. 387: 613-650.

Keen, F.P. 1958. Cone and seed insects of western forest trees. U.S. Dept. Agr. Tech. Bul. 1169: 46-58.

Lake States Forest Experimental Station 40th Annual Report, 1963. p.51. For. Ser., U.S. Dept. Agr. St. Paul 1, Minn.

Lindroth, C.H. and E. Palmen. 1956. Coleoptera, pp.69-76. In Taxonomist's glossary of genitalia in insects, ed, S. L. Tuxen. Munsgarrd, Copenhagen.

Little, E.L. 1943. Common insects on pinyon (Pinus edulis). Jour. N.Y. Ent. Soc. 51: 239-252.

Lyons, L.A. 1956. Insects affecting seed production in red pine. Part I. Conophthorus resinosae Hopk. (Coleoptera:Scolytidae). Can. Ent. 88: 599-608.

Miller, J.M. 1914. Insect damage to the cones and seeds of Pacific coast conifers. U.S. Dept. Agr. Bul. 95: 1-7.

__________. 1915. Cone injury to sugar pine and western yellow pine. U.S. Dept. Agr. Bul. 243: 1-12.

Northeastern Forest Experimental Station Annual Report. 1958. p.37-38. U.S. Dept. Agr., For. Ser. Upper Darby, Pa.

__________. 1959. p.40. U.S. Dept. Agr., For. Ser. Upper Darby, Pa.

Packard, A.S. 1890. Fifth report of the United States entomological commission. Insects injurious to forest and shade trees, p.810.

Ruckes, H. 1957. The overwintering habit of the sugar-pine cone beetle. Jour. Econ. Ent. 50: 367-368.

__________. 1958. Some observations on the Monterey pine cone beetle, Conophthorus radiatea Hopkins (Coleoptera: Scolytidae). Ann. Ent. Soc. Amer. 51: 214-215.

__________. 1963. Cone beetles of the genus Conophthorus in California. Pan. Pacific Ent. 39: 43-50.

Sandve, J.R., ed. 1957. Consolidated insect survey report Minnesota. Minn. Dept. Agr., Div. Plant Industry, St. Paul.

Schaefer, C.H. 1962. Life history of _Conophthorus radiatae_ (Coleoptera:Scolytidae) and its principal parasite, _Cephalonomia utahensis_ (Hym:Bethylidae). Ann. Ent. Soc. Amer. 66: 569-577.

______________. 1963. Factors affecting the distribution of the Monterey pine cone beetle (_Conophthorus radiatae_ Hopkins) in Central California. Hilgardia 34: 79-103.

Schedl, K.E. 1931. The morphology of the bark beetles of the genus _Gnathotrichus_ Eichh. Smiths. Misc. Coll. 82: 1-88.

______________. 1955. Die Kiefern-Borkafer Guatemalas. 145. Bietrag zur Morpholige und Systematik der Scolytoidea, p.28-29. Zeit. f. angew. Ent. 38: 1-48.

Schwarz, E.A. 1895. Description of the pine-cone-inhabiting scolytid. Proc. Ent. Soc. Wash. 3: 144-145.

Snodgrass, R.E. 1935. Principles of insect morphology. McGraw-Hill Book Company, Limited, New York, 667pp.

______________. 1957. A revised interpretation of the external reproductive organs of male insects. Smiths. Misc. Coll. 135(6). 60pp.

Struble, G.R. 1947. Twig damage in sugar pine caused by the cone beetle. Jour. For. 45: 48-50.

Swaine, J.M. 1909. Catalogue of the described Scolytidae of America, North of Mexico, p.134. New York State Mus. Bul.

______________. 1918. Canadian bark-beetles. Part II. A preliminary classification with an account of the habits and means of control, p.92-93. Dom. of Can. Dept. of Agr. Ent. Br. Bul. 14, 143pp.

Thomas, J.B. and O.H. Lindquist. 1956. Notes on bark beetles and associated insects feeding in pine shoots. Bi-Mon. Prog. Rept. For. Biol. Div. Dept. Agr. 12(4): 2.

______________. 1957. The use of larval anatomy in the study of bark beetles (Coleoptera:Scolytidae). Can Ent. Sup. 5, 45 pp.

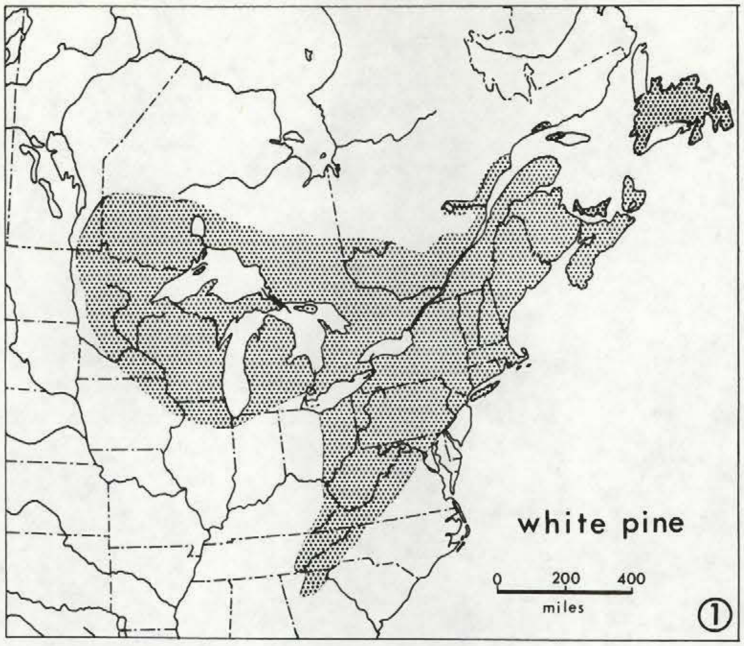
Thomas, J.B. and L.M. Gardiner. 1962. A new drawing aid. Can. Ent. 94: 218-220.

Warren, G.L. 1960. External anatomy of the adult of *Hylobius warreni* Wood (Coleoptera:Curculionidae) and comparison with *H. pinicola* (Cooper). Can. Ent. 92: 321-341.

Williamson, D.L. 1961. The biology of *Conophthorus monticolae* Hopkins in northern Idaho (Coleoptera:Scolytidae). (Unpublished M.Sc. thesis. University of Idaho, Moscow, Idaho).

Wood, S.L. 1962. Miscellaneous taxonomic notes on Scolytidae (Coleoptera). Great Basin Nat. 22: 76-82.

Figure 1. Botanical range of white pine.
Figure 2. " " " red pine.
Figure 3. " " " jack pine.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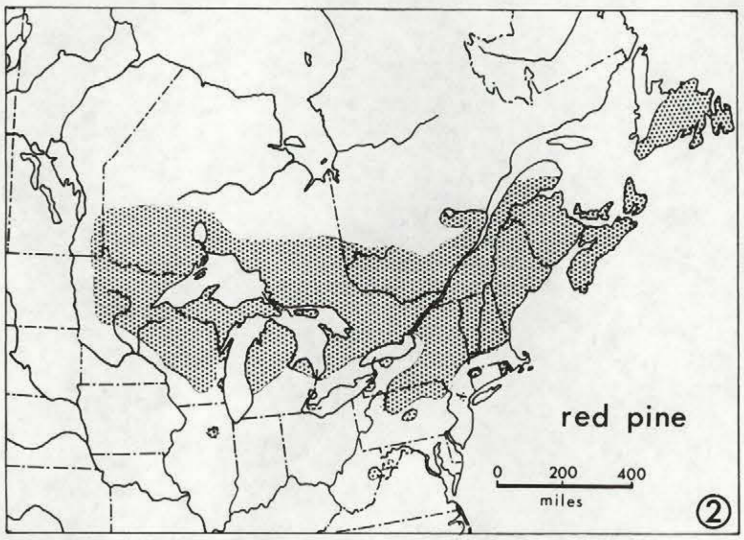
red pine
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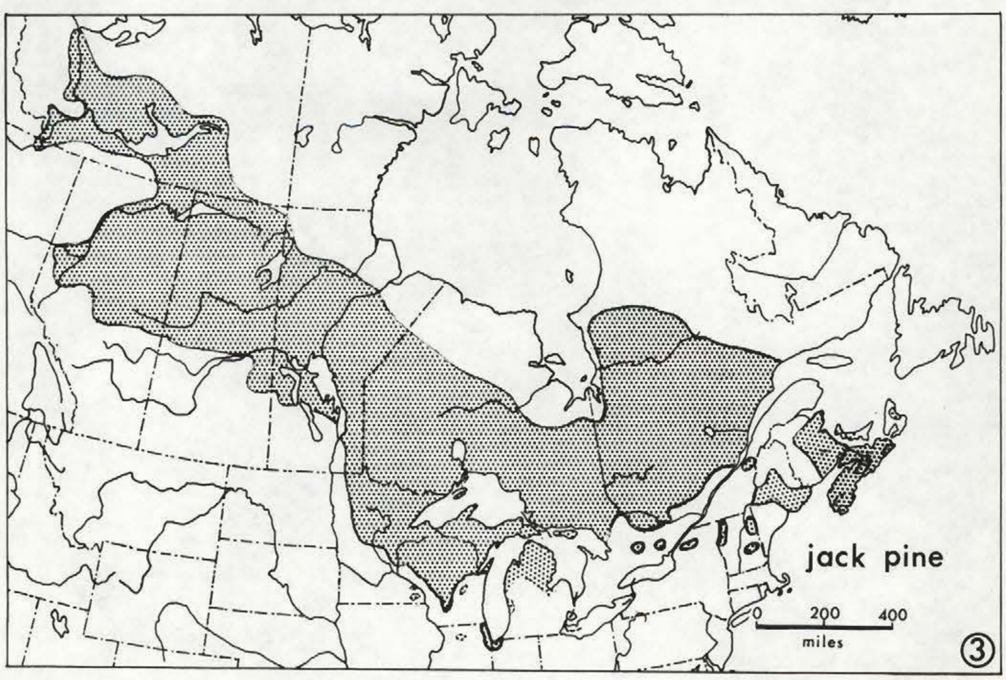
jack pine
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Figure	4a.	Lateral aspect of	*C. coniperda* adult.
"	5a.	" " "	*C. resinosae* adult.
"	6a.	" " "	*Conophthorus* "x" adult.
Figure	4b.	Dorsal aspect of	*C. coniperda* adult.
"	5b.	" " "	*C. resinosae* adult.
"	6b.	" " "	*Conophthorus* "x" adult.
Figure	7.	Dorsal aspect of the elytra,	*C. coniperda*.
"	8.	" " " " "	*C. resinosae*.
"	9.	" " " " "	*Conophthorus* "x".

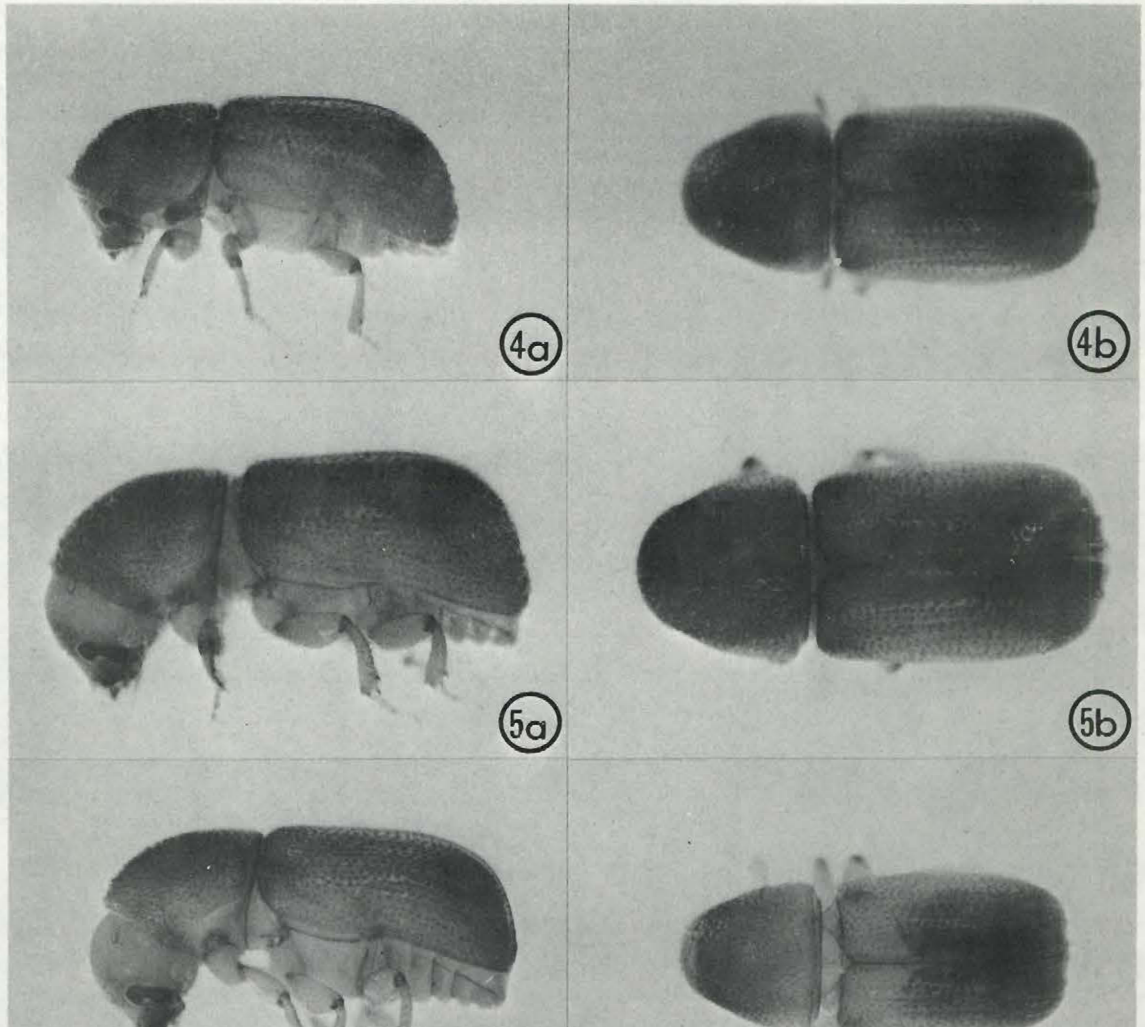
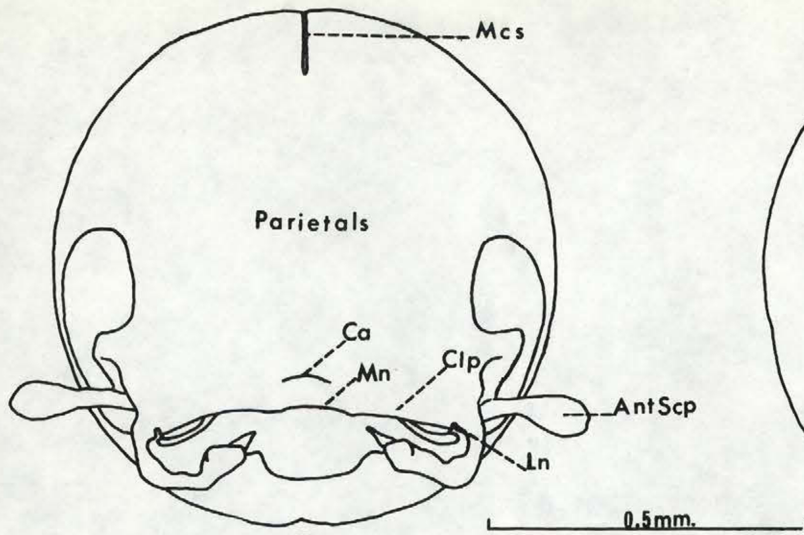

4a
4b
5a
5b
6a
6b
7
8
9

Figure 10. Anterior dorsal aspect of the head capsule.
" 11. " frontal " " " " "
" 12. Ventral aspect of the head capsule.
" 13. Posterior " " " " "
" 14. Lateral " " " " "
" 15. Internal view of lateral aspect of the head capsule.

Anti	antennal inflection
Ant Scp	antennal scape
Ca	carina
Clp	clypeus
Dam	dorsal articulation of the mandible
Gls	gular suture
Hphyb	hypopharyngeal bracon
Hstr	hypostomal ridge
Lata	lateral area
Ln	lateral notch
Mcs	mid cranial sulcus
Mn	median notch
Mscl	median sclerite
Mxa	maxillary articulation
Oci	occipital inflection
Ocr	occipital ridge
Par	parietal
Poc	postocciput
Pta	posterior tentorial arm
Ptp	posterior tentorial pit
Scla	semi-sclerotic area of posterior head capsule
Smt	submentum
Vam	ventral articulation of mandible



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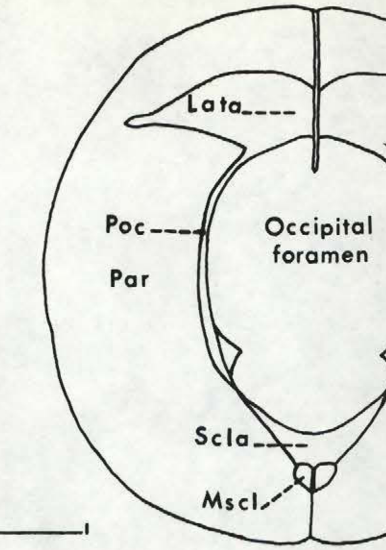

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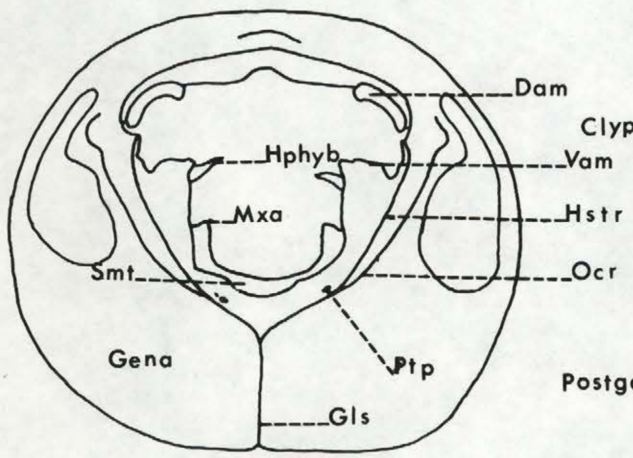

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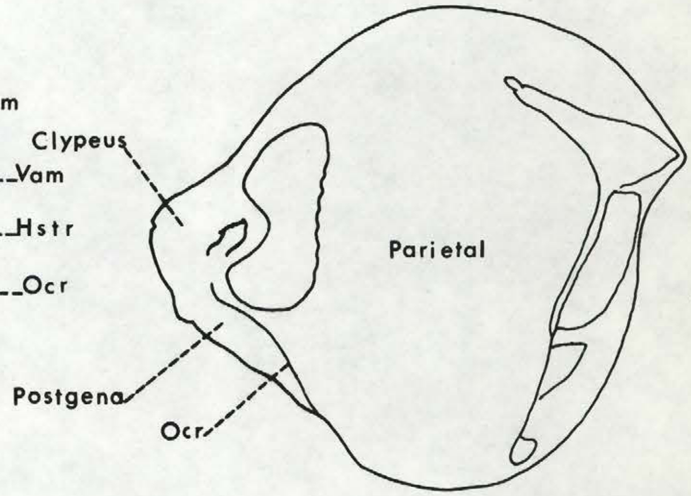

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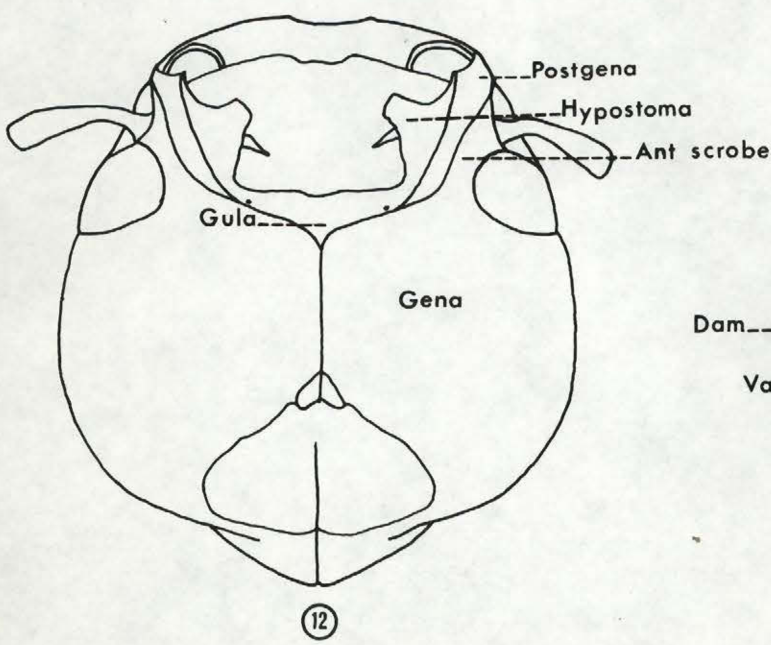

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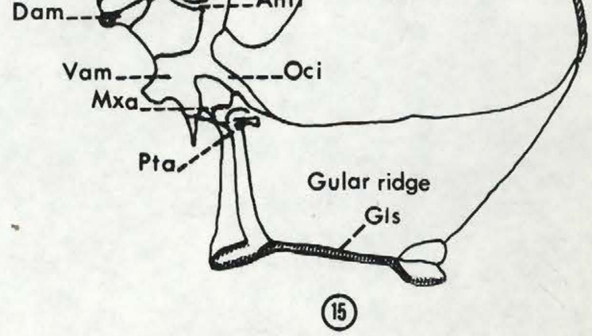

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Figure	16a.	Setal pattern on frontal area of male head capsule.
"	16b.	" " " " " " female head capsule.
"	17.	The antenna.
"	18a.	Dorsal aspect of the mandible.
"	18b.	Ventral aspect of the mandible.
"	19.	The maxilla.
"	20a.	Dorsal aspect of the labium.
"	20b.	Lateral " " " "
"	20c.	Ventral " " " "
"	21.	" " " " hypopharynx.
"	22.	Lateral aspect of the prothorax.
"	23.	Ventral " " " "
"	24.	Internal " " " prosternum.

Abm	abductor muscle
Acon	anterior condyle
Adm	adductor muscle
Aip	anterior intercoxal process
Apt	apical tooth of mandible
Bs	basisternum
Bsr	basal ridge of pronotum
Cl	club
Dcon	dorsal condyle
Fnc	funicle
Lc	lacinia
Lct	lacinial teeth
Lplp	labial palpi
Mf	median fossa
Mol	molar tooth
Mpro	median process of ventral surface of mandible
Pdc	pedicel
Pip	posterior interooxal process
Plf	palpifer
Plg	palpiger
Plp	palpi
Prmt	prementum
Sa	sternal apophysis
Sapt	subapical tooth of mandible
Sca	sternacosta
Scp	scape
scs	sternacostal suture
sen	sensilla
Sl	sternellum
St	stipes
Tr	transverse ridge of mandible
Vapr	ventral apical ridge
Vcon	ventral condyle
Vimp	ventral impression
Vsapr	ventral subapical ridge

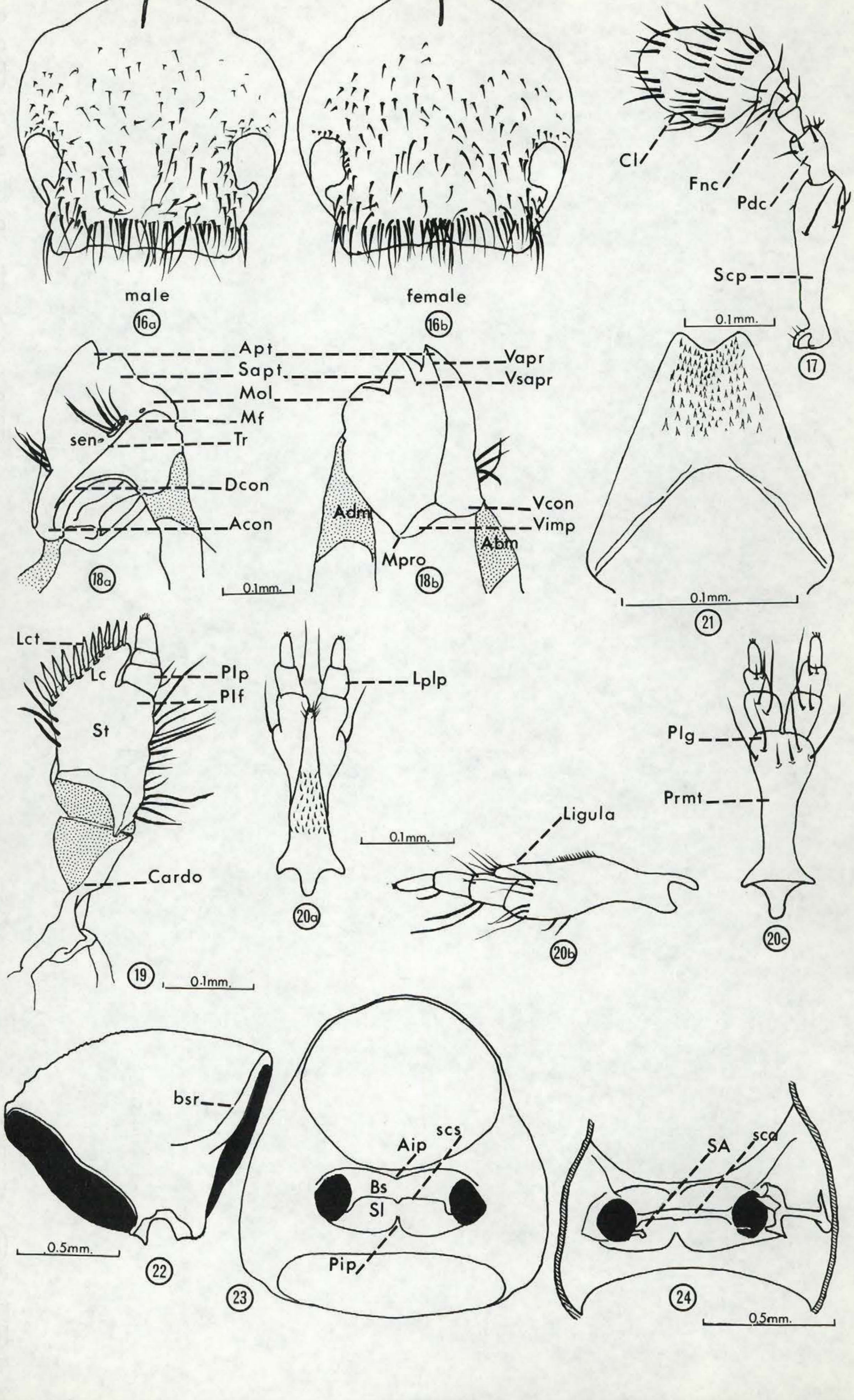
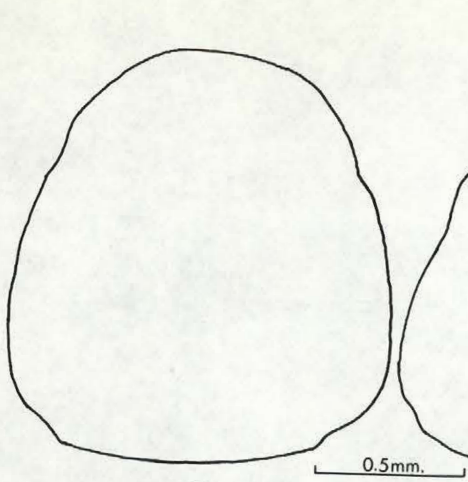

male
16a
female
16b
Cl
Fnc
Pdc
Scp
0.1mm.
17
Apt
Sapt
Mol
Mf
sen
Tr
Dcon
Acon
Vapr
Vsapr
Adm
Mpro
Vcon
Vimp
Abm
18a
18b
0.1mm.
21
0.1mm.
Lct
Lc
Plp
Plf
St
Cardo
19
0.1mm.
Lplp
20a
0.1mm.
Ligula
20b
Plg
Prmt
20c
bsr
0.5mm.
22
Aip
scs
Bs
Sl
Pip
23
SA
sca
24
0.5mm.

Figure	25a.	Pronotal outline of C. resinosae from dorsal aspect.
"	25b.	" " " C. coniperda " " "
"	26.	Lateral aspect of mesonotum.
"	27.	Dorsal " " "
"	29.	Internal aspect of mesopleuron.
"	32.	Dorsal aspect of metanotum.
"	33.	Internal aspect of metanotum.
"	34.	The metendosternite.

Ac	antecosta
Acs	antecostal suture
Albr	alar bridge
Amb	anterior membrane
ANP	anterior notal wing process
Apd	apodeme
Asr	anterior scutal ridge
cl	clavicle condyle
co	costa or parapsidal ridge
cor	coracoid condyle
dScl	depressed portion of scutellum
Epm_2	mesepimeron
Eps_2	mesepisternum
eScl	elevated portion of scutellum
iss	intra-scutellar suture
iss_2	second intra-scutellar suture
issr	intra-scutellar ridge
lta	lateral arm
mcxc	metendosternal articulation with coxa
mg	median groove
mns	median notal sulcus
mstk	median stalk
NP	notal process
Pa	postalar extension
Pc	postcoxal bridge
$Peps_2$	preepisternite
ph	pleural hook
Ph_3	metathoracic phragmata
Plcxp	pleuro-coxal process
PlR	pleural inflection
PlS	pleural sulcus
PlSi	pleuro-sternal inflection
PN_3	postscutellum
PNP	posterior notal process
Pra	prealar arm
Prs	presternite
Prsc	prescutum
$Prsc_3$	metathoracic prescutum
SA	sternal apophysis
Scl_3	metathoracic scutellum
Sclg	scutellar groove
Sct	scutum
Sct_3	metathoracic scutum
ss	scutellar suture
ts	transverse suture
VR	v-shaped scuto-scutellar ridge
vs	scuto-scutellar suture



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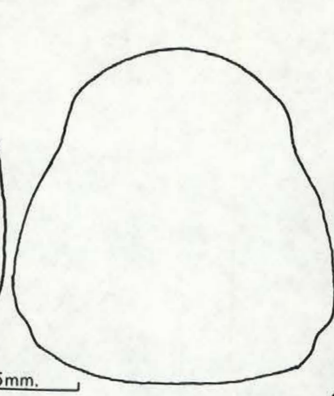

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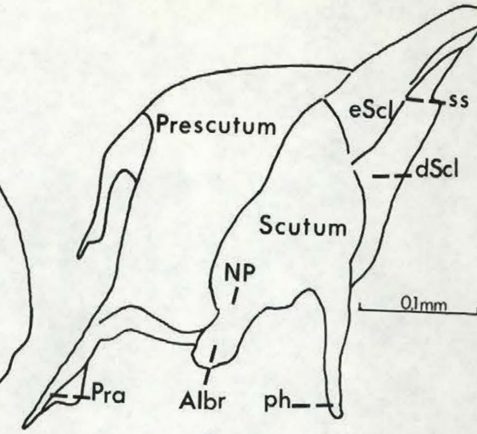

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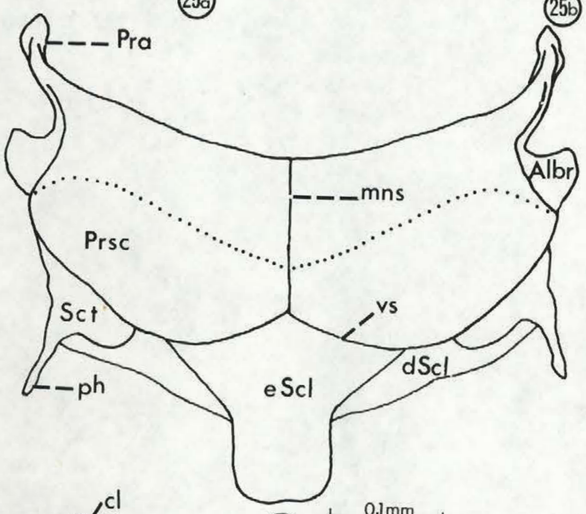

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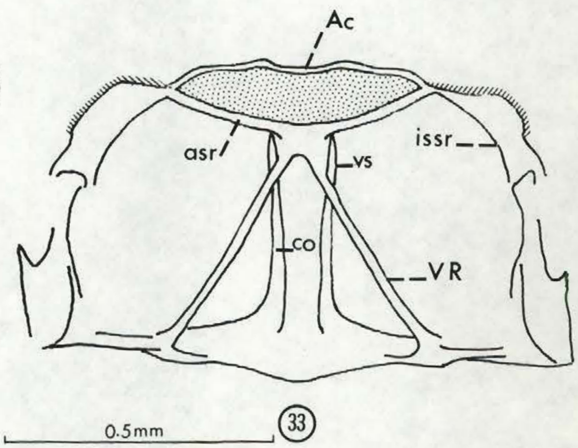

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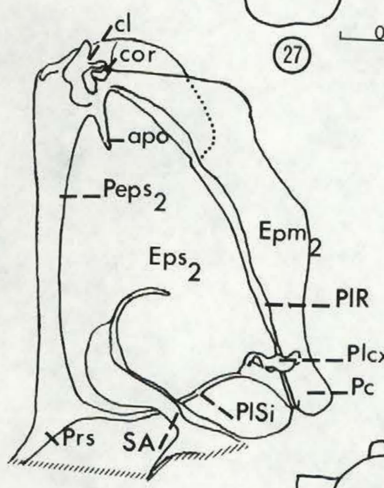

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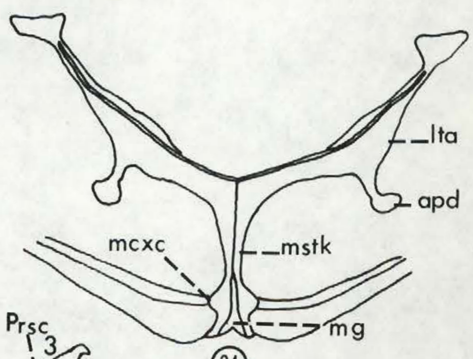

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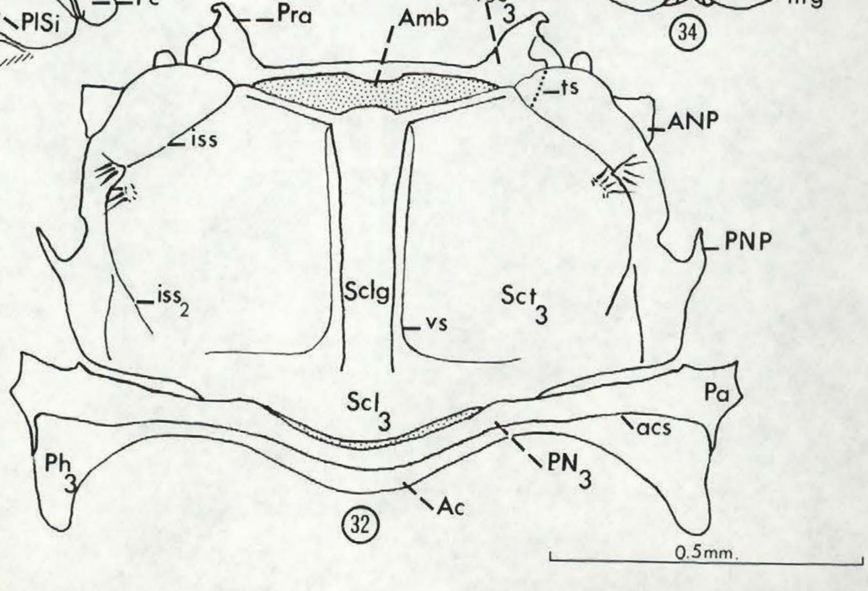

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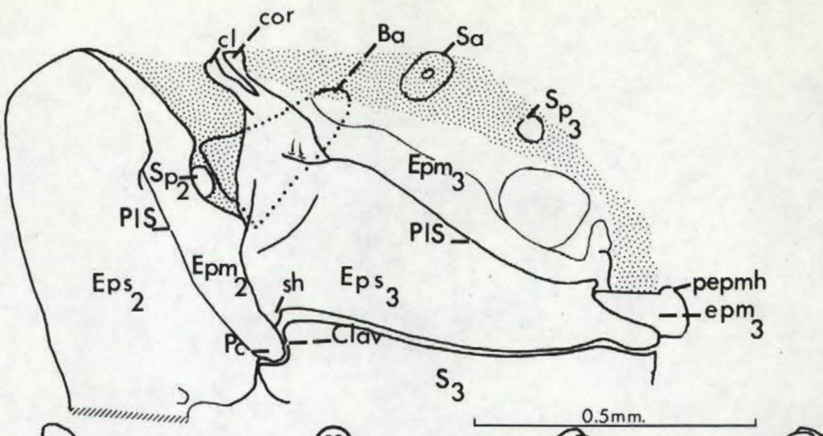
Figure 28. Lateral aspect of meso- and metapleura.
" 30. The meso- and metasternum.
" 31. Internal aspect of the meso- and metasternum.
" 35. The prothoracic leg.
" 36. " mesothoracic leg.
" 37. " metathoracic leg.
" 38. " procoxa.
" 39. " mesocoxa.
" 40. " metacoxa.

aicp	anterior intercoxal process
art	articulation of basicoxite
atrc	fossa for articulatory condyle of trochanter
Ba	basalare
Bcx	basicoxite
Bs_2	mesothoracic basisternum
Bs_3	metathoracic basisternum
cl	clavicle condyle
Clav	clavicula
co	coxartis condyle
cor	coracoid condyle
Cx	coxa
cxs	coxal suture
Epm_2	mesepimeron
epm_3	postepimeron
Epm_3	metepimeron
Eps_2	mesepisternum
Eps_3	metepisternum
Fm	femur
ls	longitudinal suture
Mes	metendosternite
Pc	postcoxal bridge
pepmh	postepimeral hook
Plcxp	pleuro-coxal process
PlS	pleural sulcus
PlSi	pleuro-sternal inflection
Prs	presternite
Ptar	pretarsus
S_3	metathoracic sterna
SA	sternal apophysis
Sa	subalare
sca	sternacosta
scs	sternacostal suture
sh	sternal hook
Sl_2	mesothoracic sternellum
Sp_2	mesothoracic spiracle
Sp_3	metathoracic spiracle
stc	sternartis condyle
st	strut
Tar	tarsomere
Tb	tibia
Tr	trochanter
trf	trochanteral fossa



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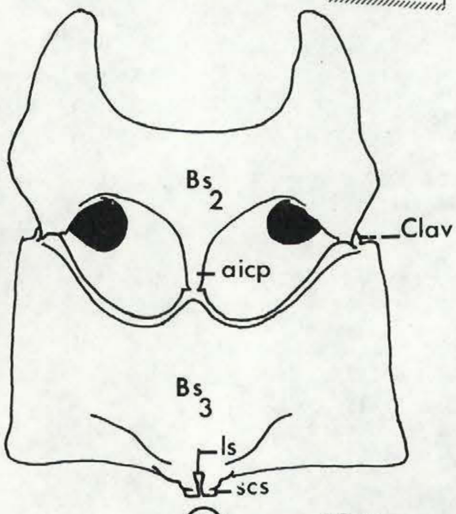

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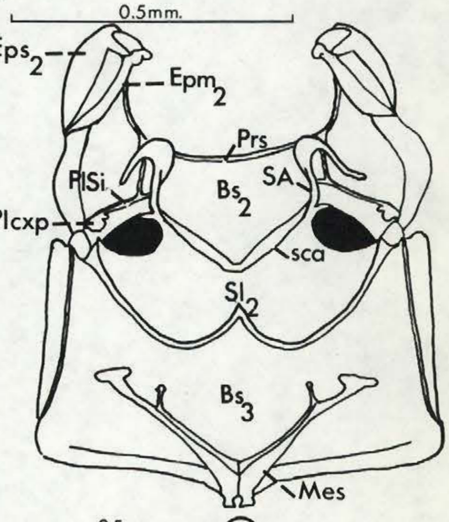

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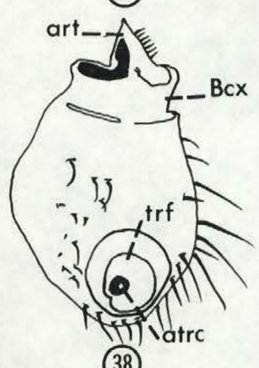

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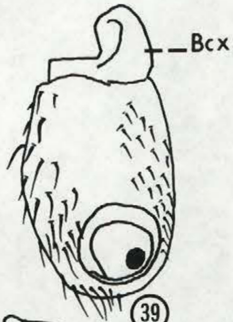

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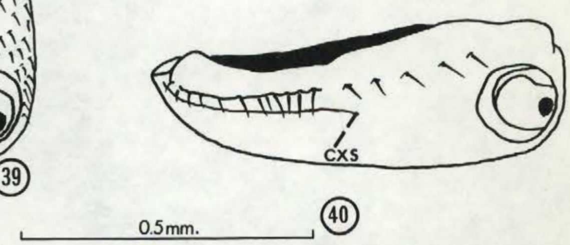

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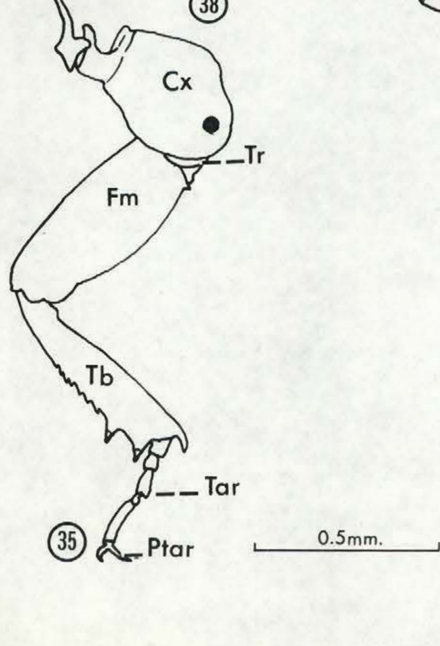

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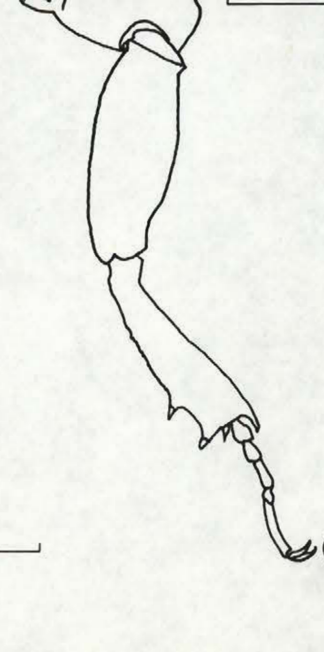
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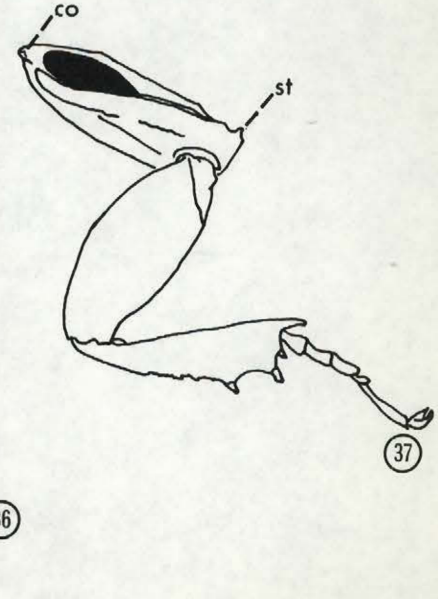

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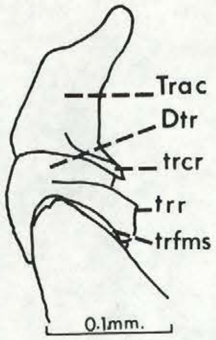
Figure 41. The trochanter.
" 42. The femur.
" 43. The tibia.
" 44. The tarsomeres and pretarsus.
" 45. Axillary region of the elytron.
" 46. The hind wing.
" 47. Axillary region of the hind wing.

ANP	anterior notal process
apt	apical tooth of tibia
1Ax	first axillary sclerite
2Ax	second " "
3Ax	third " "
4Ax	fourth " "
C	costal vein
Cu	cubital vein
Dtr	distal portion of trochanter
M	medial vein
M_1	distal branch of medial vein
mf	median fold
mp	median plate
mt	median tooth of femur
PNP	posterior notal process
R_2	distal branch of radial vein
Sc	subcostal vein
sf	scutellar fold
skt	socket of tibia
teg	tegula
Trac	trochanteral articulatory condyle
trcr	outer trochanteral ridge
trfms	trochanteral-femoral suture
trr	trochanteral ridge



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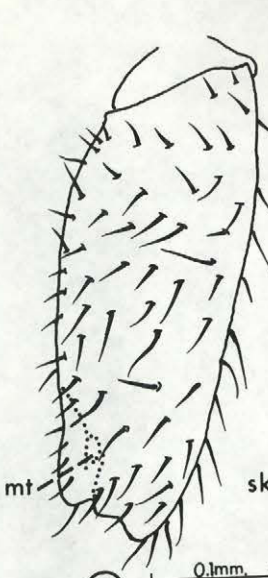

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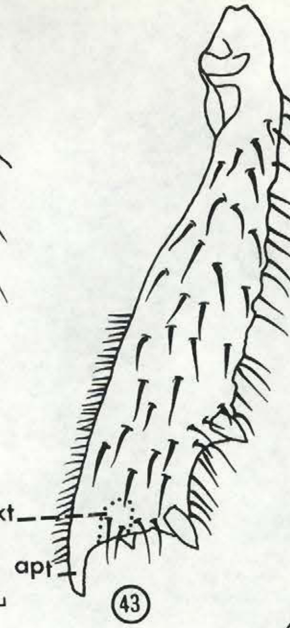

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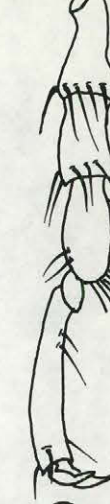

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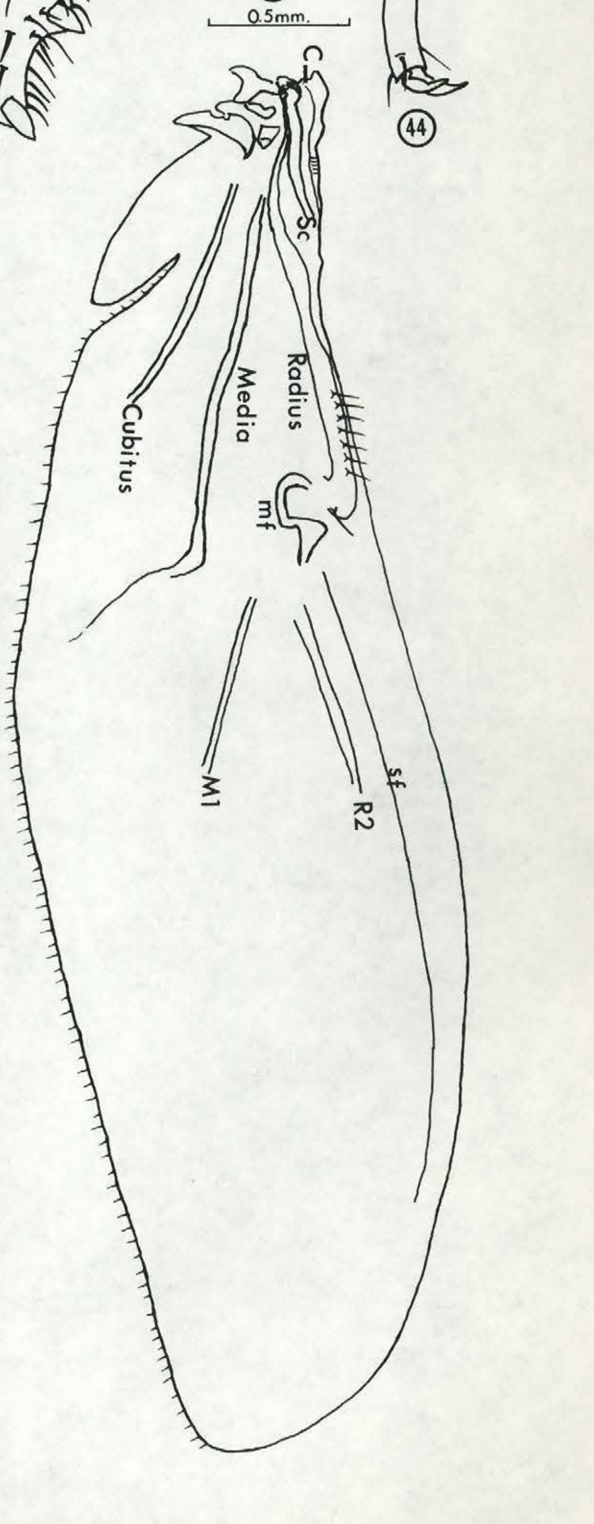

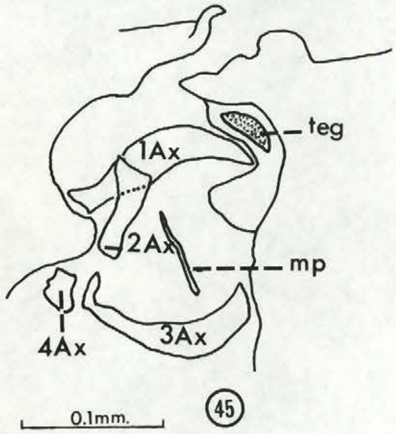

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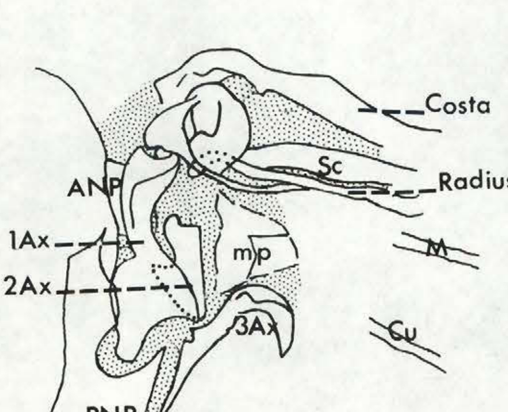

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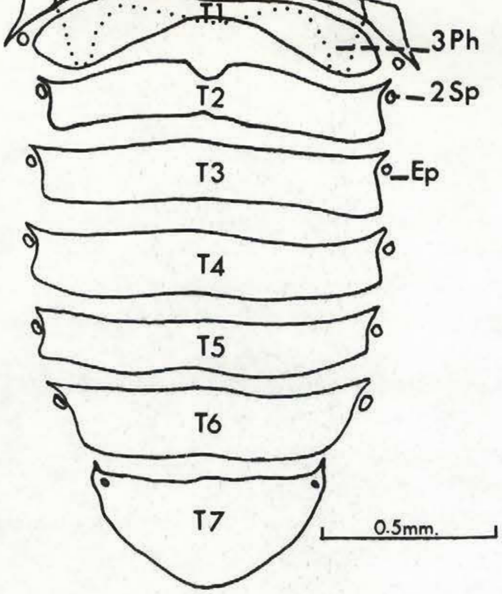
Figure 48. The abdominal terga.
" 49. Male tergum seven.
" 50. Female tergum seven.
" 51. Male tergum eight.
" 52. The abdominal sterna.
" 53. Lateral aspect of the phallic structures.
" 54. The endophallus.
" 55. Lateral aspect of the spicule.

aed apo	aedeagal apodeme	pen	penis
atg	acrotergite	3Ph	metathoracic phragmata
bp	basal piece	S	sternum
Clav	clavicula	?s	abdominal sternal suture
Ep	epipleurite	?S1	abdominal sternum one
gpr	gonopore	?S2	abdominal sternum two
Hp	hypopleurite	2 Sp	second abdominal spiracle
mab	manubrium	T	tergum
mns	membranous sheath	tb	transverse band
mp	minor prong of spicule		



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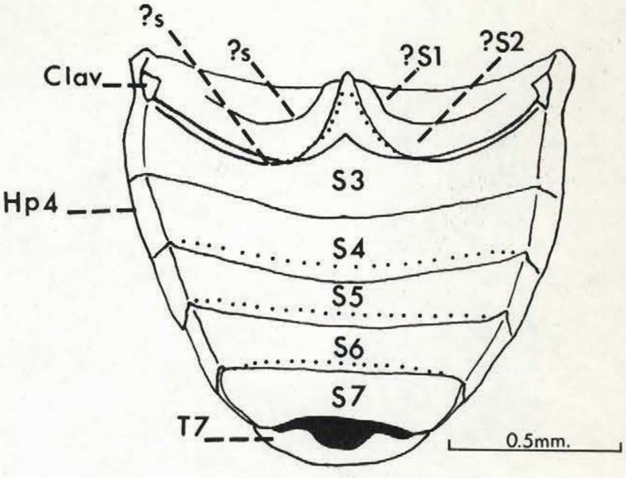

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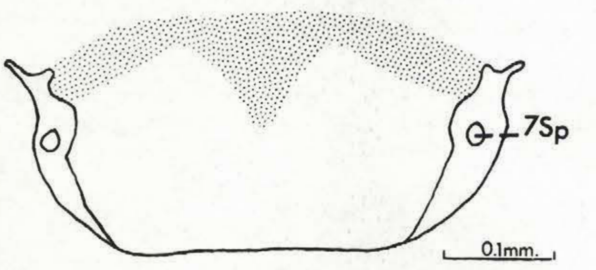

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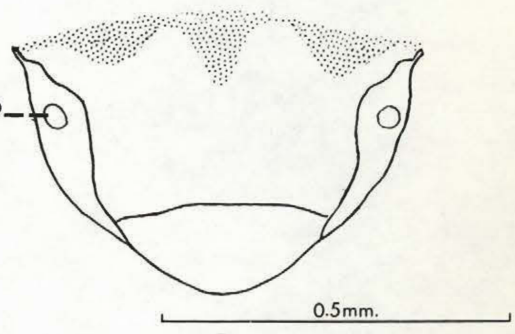

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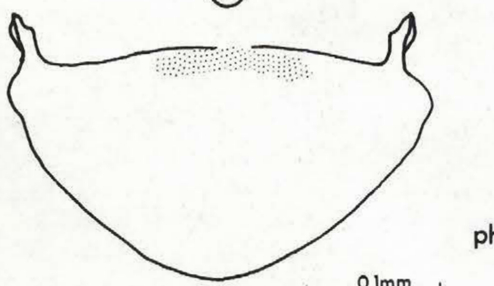

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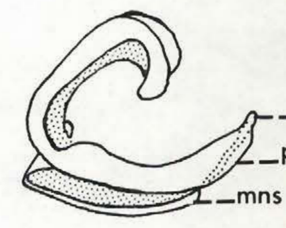

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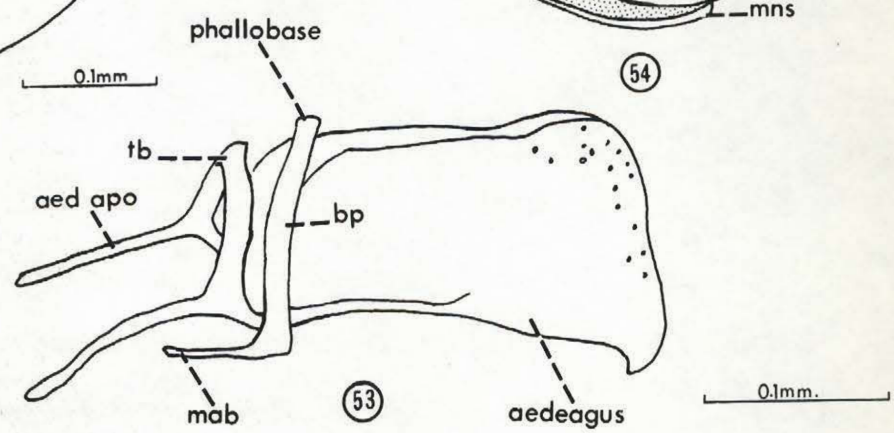

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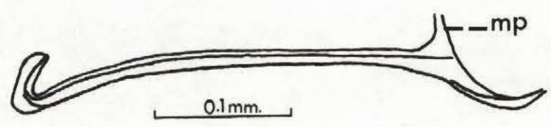

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