

SHORT TITLE

BARK BEETLES AND ASSOCIATED INSECTS IN  
PINE LOGGING SLASH

PART I - BARK BEETLE DEVELOPMENT AND ASSOCIATED INSECTS  
IN WHITE AND RED PINE LOGGING SLASH

PART II - EXTERNAL ANATOMY OF Ips pini (Say) (COLEOPTERA:IPIDAE)

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## I. INTRODUCTION

Logging slash constitutes an environment supporting a particular association of insects and other arthropods. Initially, the species of insects in the community are governed by the character of the slash, that is, the tree species, thickness of bark, and size of tops. The condition of the slash changes with the passage of time, the rate of change being directly affected by bark beetles and wood borers which initiate the ingress of wood-destroying fungi. As the environment changes, those species, for which the habitat is no longer suitable, drop out, leaving in the association of animals only those which can exist under the new conditions. The succession of communities of animals inhabiting slash, logs, dying and dead trees has been shown by Adams (1915) and Savely (1939) to continue until the wood has disintegrated completely.

The community of insects and other arthropods invading red and white pine logging slash during the first summer following winter logging has been examined during this study. One object of the study was to determine the importance of the development of broods of various species of bark beetles in the subsequent establishment of other arthropods in the community. Wherever possible, from original observations or from works of other authors, the role of each species in the particular environment has been indicated. Seasonal history notes have been prepared for each species of bark beetle found in the slash.

Ips pini (Say) was one of the most important and abundant species in the establishment of a faunal community in red and white

pine slash. The external anatomy of this species was studied as a contribution to the morphology of the Ipidae and constitutes part II of this paper.

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Specialists in the Unit of Systematic Entomology, Division of Entomology, Department of Agriculture, Ottawa, identified the insects. Dr. H. H. J. Nesbitt, Carleton College, Ottawa, identified the mites, and Dr. S. I. Auerbach, Northwestern University, Evanston, Illinois, the centipedes.

## II. REVIEW OF IMPORTANT LITERATURE

The role of insects and other arthropods in logs, slash, dead and dying trees, has been the topic of many papers. A few of the more important ones are reviewed briefly.

In an attempt to draw attention to the importance of bark beetles in the destruction of timber, Hopkins (1893) published a catalogue of West Virginia Scolytidae and their enemies. The value of the catalogue is enhanced by notes on tree and shrub species attacked, habits of the insects, and associated forms. Later, Hopkins (1899) published the results of an investigation into the cause of unhealthy conditions of spruce and pine in West Virginia from 1880 to 1893. He attributed the destruction of the timber to outbreaks of Polygraphus rufipennis (Kby.) and Dendroctonus frontalis Zimm. Habits of all species of associated insects were discussed.

Blackman and Stage (1918) published an account of insects bred from dying and decaying larch, Larix laricina (DuRoi) K. Koch, including notes on their biology and feeding habits and the associations formed about each of the principal borers. Forty-four species of borers and associated insects were found breeding in larch. The same authors published, in 1924, an account of the succession of insects in dying, dead and decaying hickory, Carya glabra (Mill.). Sweet, following primary attacks of the hickory bark beetle, Eccoptogaster quadrispinosus Say. The insects were collected and reared over a period of six years during which time the condition of the wood ranged from green or recently dead to almost completely disintegrated. It was found that there was a definite succession of species from season to season until the wood had disintegrated.

One of the most extensive contributions on this subject is a paper by Savely (1939) presenting detailed results of a survey



of animals in dead pine and oak tree trunks in various stages of decay, and a study of the relationship of certain species to their environment. About 95 species of animals were found in pine logs which had been cut one year, this number decreasing through successive years as the wood disintegrated. In the oak logs, the number of species increased from 50 in the first year to 96 in logs which had been on the ground over three years. The primary invaders in logs of both species were phloem and sapwood feeders, followed by predaceous and parasitic forms associated with the borers and a group feeding upon fungi or decaying animal and vegetable matter. In succeeding years, the number of phloem and sapwood feeders was reduced and the bulk of the animals were mycetophagous or saprophytic and predaceous.

Graham (1925) recognized the felled tree trunk as an ecological unit having "a definite succession of organisms as the chemical and physical character of the wood changes during the process of disintegration and decay". It was found that the distribution of the xylophagous forms was governed by the moisture and subcortical temperature of the logs.

Howden and Vogt (1951) recognizing the conspicuous absence of information on the ecology of standing dead trees, investigated the insect associations in standing dead pine trees, Pinus virginiana Mill., in the succession forest from an old field to an oak-hickory climax type in Maryland. One hundred and eighty-four species were collected on and beneath the outer surface of the bark. In recently dead trees, the community was centred around the bark beetles, while after six months, cerambycids and buprestids became the dominant

species. Several years later, termites became the most abundant and later were partially replaced by saprovores.

A number of insects were found in association with Ips pini (Say) by Clemens (1916). Most of the species were predaceous or parasitic and few other associates were recorded. A comprehensive report of bark and ambrosia beetles in North Carolina has been prepared by Beal and Massey (1945), including insects found in association with the various scolytids. DeLeon (1934) published an annotated list of parasites, predators and other associated fauna of the mountain pine beetle, Dendroctonus monticolae Hopk., in western white pine and lodgepole pine. About twenty species of Ipidae are mentioned with considerable data on natural enemies.

### III. FOREST COMPOSITION OF THE STUDY AREA

The investigation was carried out in pine cutting operations on the shores of Lake Kipawa, near Laniel, Quebec, at 47 degrees north latitude and an elevation of approximately 884 feet above mean sea level. While the forest in the vicinity of Lake Kipawa and in the upper Ottawa valley is in the Algonquin-Laurentides section of the Great Lakes-St. Lawrence Forest Region of Halliday (1937), it is adjacent to the southern limits of the Boreal Forest Region and this is reflected in the tree species represented. The forest is mixed coniferous, white pine, Pinus strobus L., and red pine, P. resinosa Ait. being the dominant species. Jack pine, P. banksiana Lamb., occurs on burned-over tracts, while white spruce, Picea glauca (Moench.) Voss., black spruce P. mariana (Mill.) B.S.P., and balsam

fir, Abies balsamea (L.) Mill., are mixed with the pines. White cedar, Thuja occidentalis L., yellow birch, Betula lutea Michx., and black ash, Fraxinus nigra Marsh., occur together in low areas and swamps. Bigtooth aspen, Populus grandidentata Michx., and white birch, Betula papyrifera Marsh., constitute a high percentage of the stand close to the shore in cut-over areas. Farther inland, these species are more scattered among the conifers.

#### IV. METHODS

Logging of red and white pine has been carried on for the past several years around Lake Kipawa, thereby providing a yearly supply of fresh breeding material for large populations of bark beetles. Cutting seldom begins before the middle of October which precludes the possibility of insects entering the slash before the next spring. Twenty-five stumps and an equal number of tops of each of the two species of pine were chosen for periodic examination. These were identified by metal tags. Every three or four days, a small section of bark was removed from three stumps of each species and from butt, centre, and branches of the same number of tops. Periodically, sections of bark, showing the average stage of development of the galleries of Ips pini and Pityogenes hopkinsi, were removed carefully from the tops and photographed to record pictorially the progress of these two species. These species were selected because they were the only two of importance which left distinctive engravings in the slash for their entire life history.

Samples of all insect and animal life found in the slash were preserved in 70 per cent alcohol, or placed in cardboard pill boxes for further study. The collections included all species found crawling or landing on the slash, and pupae found under the bark or in the humus at the base of the stumps. Examination of the slash was conducted in a manner which would provide a reasonably accurate sample of all species represented in the community. Notes were made on cases of predation or parasitism as well as general feeding habits of as many species as possible. To supplement observations made on the feeding habits of some of the adult and larval forms in the field, further studies were made under laboratory conditions. Sections of bark, duplicating as closely as possible the condition of the material in which these forms were collected, were placed between two sheets of glass, four inches square. The insects to be studied were placed on the bark, and the glass sheets held together by elastic bands. To prevent evaporation and keep the insects from escaping, cotton was packed around the edges of the bark between the glass. By moistening the cotton, it was possible to keep the bark from drying out excessively. Bark beetle larvae and other insects were offered as food and their acceptance or rejection of the prey was recorded.

#### V. ECOLOGICAL ASSOCIATION OF SPECIES

Approximately 138 species of insects and other arthropods were collected from 100 collection points in the experimental area. Only an approximation of the total number of species represented in

the community can be given, owing to the number of immature forms, particularly in the order Diptera, which could not be identified to species or, in many cases, even to genus. The species were distributed as follows: Chilopoda 3, Arachnida 7, Insecta 128. The class Insecta was represented by the following orders: Collembola 4, Psocoptera 1, Hemiptera 1, Homoptera 1, Lepidoptera 4, Coleoptera 62, Hymenoptera 18, Diptera 37.

The species collected during the season are listed in Appendices I and II. Appendix I contains those species which occurred frequently enough to form a definite part of the community. On the other hand, about sixty species (Appendix II) were collected on the outer bark surface or foliage, or rarely within or under the bark. In most cases, isolated specimens were not considered to have any obligate relationship to the slash or the community within it. Evidence was insufficient to classify, according to feeding habits, those specimens which occurred only rarely under the bark. Wherever possible, an indication of their probable host relationship, taken from references in the literature, is given in Appendix II.

Active associates in the community were segregated according to their feeding habits into four groups as follows: I, phloem and sapwood borers; II, fungus, frass and detritus feeders; III, parasites; IV, predators. The number of species in these groups occurring in the stumps and tops of both species of pine is shown in Plate I. Relatively more parasites were recovered from white pine than red pine stumps, although the same hosts occurred in proportionate numbers in both. A similar situation was apparent in the tops. The number of secondary

insects, group II, was greater in the stumps of both species, than in the tops, owing to several factors. Species common to the litter and humus, such as elaterids, probably find it easier to enter the stumps than the tops which are usually raised up off the ground. Moisture conditions in the stumps are also more suitable for supporting a larger fauna. Finally, larvae of the bark beetles, Orthotomicus caelatus, Hylurgops pinifex and Dendroctonus valens feed gregariously, thereby providing large, compact quantities of boring dust and other debris under the bark. This appears to be preferred as a breeding medium by many species of Diptera.

The species comprising groups I to IV and the periods during which they were present are shown on Plates II and III for tops and stumps respectively. Food chain relationships are indicated by code numbers applied to individual species. Intervals, during which various stages of the more important species were present, are also shown and an indication of the increase and decline of the population is given by broken lines. This is merely to indicate a trend in development and is not supported by a sample of the actual population at any one time. Ips pini, I. chagnoni and Dryocoetes americanus were found too infrequently in the stumps to enable the individual stages to be shown on the graph. Because of the concealed habits of the ambrosia beetles, only the overall periods covering their presence in the stumps is indicated.

Ips pini and Pityogenes hopkinsi had second broods during the summer but their identification in the slash was very difficult. Consequently, the lines on the graph representing these species cover

a longer period than normally required to complete development of one brood. Second broods were also common for Hylurgops pinifex and Orthotomicus caelatus but overlapping was less confusing because of their different location in the stumps. The occurrence of second broods for these two species is shown on Plate III.

As shown in these plates, the species of bark beetles and borers differed between the tops and stumps. The scolytids in the tops were identical, with the exception of Pityogenes plagiatus, which occurred in red pine only. Ips pini and Pityogenes hopkinsi were present in both, although the latter occurred only rarely in red pine. Eight species of bark and ambrosia beetles were present in the stumps compared with three in the tops. Only one, Ips pini, occurred in both and it was of minor importance in the stumps. The presence of ambrosia beetles in the stumps may be attributed to moisture conditions being more suitable for the culture of fungi eaten by the beetles. Many of the tops are raised off the ground and have thinner bark causing more rapid drying and making them unsuitable for the growth of the fungi. This argument is strengthened by the fact that the ambrosia beetles did attack the thicker-barked logs in skidways.

The emphasis in these studies has been placed on the development of the initial community of arthropods rather than on an attempt to define clearly a succession of species. However, examination of Plates II and III does reveal a trend toward succession. The bark beetles were the first to enter the slash and with many the population of immature forms reached a peak during

the first half of the season. Shortly after, a second group of borers of the families Cermabycidae, Buprestidae, Pythidae and Curculionidae entered the logs. With the possible exception of species of Pythidae, borers of the second group were not dependent upon the activities of the bark beetles to gain an entry into the stumps and tops.

The insects in group II invaded the slash after the bark had been loosened by the bark beetles and borers. The staphylinid, Atheta sp., was one of the first to appear, entering through the bark beetle holes soon after they were made. However, the bulk of these insects did not appear until the first brood of bark beetles and the other borers had loosened the bark. These species were still present on September 17 indicating that they might be expected to form an important part of the community in the following season.

Predators and parasites followed closely the establishment of the broods of bark beetles. There are two classes of predators. First, are those, such as ants and centipedes, which do not remain in the community continuously but leave and return or are replaced by others of the same species. The second class of predator forms a more integral part and spends all or nearly all of its life in the community. Species of the families Cleridae, Histeridae, Tenebrionidae and Staphylinidae are predaceous in both larval and adult forms. Larval forms of the first three families were most abundant when the immature stages of the bark beetles were present. However, staphylinid larvae and adults were still abundant in mid-September and apparently carry over into the next season.

Unfortunately, observations could not be continued beyond



September 17th and it is therefore impossible to state definitely what species overwintered in the slash. By that date, very little activity was apparent in those species still under the bark and it is reasonable to assume that they would hibernate there.

## VI. NOTES ON IMPORTANT SPECIES OF THE COMMUNITY

The information in Plates II and III (see also Appendix I) is supplemented by the following notes on each species. The bark beetles are considered to be most important in the development of the community, and consequently have been treated in more detail than the other species. Personal observations have been augmented, in many cases, by references to the literature.

### A. GROUP I. PHLOEM AND SAPWOOD BORERS

#### ORDER COLEOPTERA

#### FAMILY IPIDAE

#### Dendroctonus valens Lec.

The red turpentine beetle, the largest known bark beetle, was usually found in the lower parts of the stumps although a few specimens were found in the upper half of the stump. Egg galleries were frequently extended several inches below ground level. The species is monogamous, each pair carving a slightly curving egg gallery which may be branched, but which retains a general vertical direction. The eggs are deposited, several layers thick, in grooves

cut into the sides of the gallery and covered with boring dust. On hatching, the larvae feed in congress, destroy all the phloem as they move forward and leave the space behind packed with reddish-brown frass and boring dust.

The first galleries were found in the stumps on May 30 but eggs were not found until June 5, followed by the first larvae on June 15. Eggs and larvae were present in nearly all galleries until August 1 when eggs were last noted. The larvae were still in the feeding area when the last examination was made therefore the overwintering habits of this beetle for this area are unknown. It seems very possible that they overwinter in immature as well as adult stages, and this habit was reported by Hopkins (1909).

Dryocoetes americanus Hopk.

Prior to 1915, this species had been confused with the European species, Dryocoetes autographus Ratz., and references in the literature to the latter beetle in North America can be interpreted as applying to D. americanus.

Dryocoetes americanus was relatively rare in the slash, occurring too infrequently to permit the seasonal history to be worked out. It was first collected on July 26 from the brace roots of a white pine stump and three days later in the roots of a red pine stump. Two small, irregular galleries were uncovered in which the eggs were deposited singly in niches. The attack on the stumps was late in the season after the first brood of other bark beetle species had almost completed development. This may account for

their attack on the roots since nearly all the available space in the main area of the stumps had been occupied by broods of Orthotomicus caelatus, Hylurgops pinifex, Dendroctonus valens and by cerambycid larvae. While D. americanus occurred rarely in the pine slash, it was well established in the trunk of a white spruce tree which had been blown over in the spring. There is a possibility that the pine stumps were alternate hosts for second broods.

When first observed, this species was associated with the second broods of H. pinifex and O. caelatus. A few beetles of the family Nitidulidae, Epuraea sp., were found in the galleries of D. americanus.

Gnathotrichus materiarius (Fitch)

Trypodendron bivittatum (Kby.)

Both species of ambrosia beetles confined their attacks to the stumps where moisture conditions were most suitable for the propagation of their food. The fungus, on which the beetles feed, grows on the sides of the tunnels causing a black stain to penetrate the wood. The spores are carried on the hairs of the body and under the elytra, and may also be ingested and later excreted in a viable condition. When new host material is entered, the spores brush off the body or are excreted in the frass and the fungus begins to grow on the tunnel walls if conditions are favourable. Hubbard (1897) concluded that each species of ambrosia beetle was limited to a specific fungus, irrespective of the host tree. The use of different host trees by the same species of beetle is not too surprising since the most important factor is the finding of conditions suitable for the

propagation of the fungus.

The adult beetles bore through the bark and into the sapwood, pushing out light-coloured boring dust. The main tunnel proceeds directly into the stump and at intervals there are branches which usually follow the annual growth rings. Eggs are deposited in small niches cut into the upper and lower sides of the main and branch tunnels. The larvae feed on the fungus, enlarging the egg niches until typical larval cradles are constructed in which pupation and transformation to the adults occur.

The seasonal history of the ambrosia beetles was not followed closely because of their concealed habits. Both species were boring into the bark and wood when the first examination was made on May 23. T. bivittatum is larger in cross-section than G. materiarius, consequently the tunnels of the two species are distinguishable. By July 19, all stages of G. materiarius, from egg to newly transformed adults, were present, a condition which persisted for the remainder of the season. On the other hand, T. bivittatum had almost disappeared from the slash by the end of July. Tunnels of this species became plugged with a thick, white fungus growth which, at times, protruded from the entrance holes. This growth of fungus apparently choked the tunnels and prevented their further use by the beetles.

The relationship of the ambrosia beetles to other insects in the community appeared to be unimportant. On several occasions larvae of Glioschrochilus sanguinolentus and of a species of staphylinid were found entering the tunnels, but no cases of actual predation were observed.

Hylurgops pinifex (Fitch)

This species was found in both red and white pine stumps and, on two occasions only, in the thick-barked areas of white pine tops. The stumps were the preferred breeding sites probably because the moisture conditions and bark thickness more closely approximated those in the lower parts of standing trees. H. pinifex is monogamous and, in the latitude of the study area, produced one and a half broods but only one generation a year. The brood chambers are simple, nearly straight galleries proceeding either up or down from the entrance holes which were cut on a slant through the bark. There is usually a short branch just inside the entrance hole and another at the end of the gallery, probably used as turning niches. Blackman (1919) gives 70 mm. as the average length of the galleries, with a range of 50 to 85 mm. Eggs are deposited either in pockets or long grooves along the sides of the gallery, grooves being more common. From two to six eggs may be placed in each pocket whereas, in the grooves, there may be several rows of closely packed eggs. On hatching, the larvae fed gregariously. Pupation and transformation to adults took place in cells hollowed out of the bark by the larvae.

The seasonal history of the development of this species was as follows. On May 23, the beetles had commenced galleries in the stumps and deposited a number of eggs. The middle third of the stump appeared to be preferred, but as the number of attacking beetles increased, the areas above and below were used. The first larvae appeared between June 5 and 9. The larval period was quite long, the first migration of larvae into the bark for pupation occurring on July 26. Pupae were collected on July 29 but newly transformed

adults were not found until the middle of August. The egg laying period of the parent beetles extended over a considerable time, and eggs were still present on July 22. Consequently, the succeeding stages of development were proportionately extended. By July 19, galleries, with eggs and larvae of the second brood, were found in the roots, often several inches below ground level. The broods had not developed to maturity by September 17 and first generation pupae and adults were also present in the upper areas of the stumps at that time. It appears, therefore, that this species overwinters in immature and adult stages at Laniel.

The galleries of this beetle were associated with those of O. caelatus, D. valens and occasionally I. chagnoni and I. pini. Immature stages were attacked by larvae and adults of staphylinids, histerids and nitidulids. Small beetles of the genus Epuraea, family Nitidulidae, were nearly always present in the galleries but were not predaceous. The second brood galleries were favourite locations for syrphid larvae.

Ips chagnoni Sw.

This is the larger of the two species of Ips collected from the slash and is readily distinguished from I. pini by the five pairs of declivital teeth in contrast to four pairs on I. pini. The galleries were confined to the stumps, the nuptial chambers being located near the top with usually two, or occasionally three, egg galleries paralleling each other in a downward direction. The eggs were laid singly in niches along the sides of the galleries, and the larvae mined mostly in the bark, scarring the sapwood slightly.

This species was not very abundant and observations indicated that there was only one brood and one generation a year in the slash.

Associated with I. chagnoni were Orthotomicus caelatus, Hylurgops pinifex and Dendroctonus valens. The immature stages were attacked by nearly all species of predators found in the stumps.

Ips pini (Say)

This beetle occurred chiefly in the tops of the red and white pine slash, although occasionally in the stumps of both species. In white pine tops, it preferred the rough, thick-barked areas near the butt end. The smooth, thin-barked regions farther up the main stem and in the branches were occupied by Pityogenes hopkinsi. A transition zone occurred between rough and smooth bark in which there was competition between the two species. As the number of attacks by I. pini increased, the adults were forced to use more unfavourable sites and to encroach upon territory formerly occupied solely by P. hopkinsi. However, the entrance holes were usually located in the slightly roughened, thicker bark where branches joined the main stem. Contrasting with the separation of the species in white pine, in red pine, I. pini occupied all the main stem, and the larger branches as well. This may be attributed to the presence of rough scaly bark over the entire red pine top which enables the beetles to secure a firm purchase at any place for cutting entrance holes.

The developmental rate of the first brood was essentially the same in white and red pine. Stages in the progress of the bark

beetle broods and the consequent deterioration of the inner bark of white pine are shown in Figures 1 to 4. On May 23, the parent beetles had made entrance holes and constructed nuptial chambers in the inner bark. Progress within the next week was very rapid, each male being joined by several females which began the egg galleries which are shown with egg niches on the sides in Figure 1. The eggs were deposited singly in small niches cut into both sides of the galleries and packed with boring dust to retain the contour of the walls, thereby preventing damage from the adult beetles. Observations showed that the female completed one niche, deposited an egg and packed it in solidly, before proceeding to extend the gallery and make the next niche. The larvae were first found on May 30 and by June 2 were present throughout nearly all the slash (Fig. 2). The eggs nearest the nuptial chambers, being the oldest, hatched first and consequently the larval mines were longest in the vicinity of the nuptial chambers during the early developmental period. As the eggs continued to hatch, the larvae from adjacent galleries approached each other and were forced to deviate from a straight course to find food (Fig. 3). Excessive crowding of galleries frequently results in starvation of many of the larvae. Pupae were found in one top on June 15 and generally throughout the slash by June 19. One newly transformed adult was found on June 19 and another on June 22. By June 30, the adults of the first brood could be found in nearly all the tops.

Within the space of 30 to 35 days, during which time one brood of I. pini developed, the fresh, white phloem was converted into a ragged, chewed mass of boring dust, larval frass and fragments



of bark. The colour of the inner bark was stained to a dark brown and fungus growth had commenced. The new adults made food galleries usually extending from the pupal cells as seen in the upper left of Figure 4, and then cut holes to the outside of the bark. The sudden appearance of these led to the erroneous conclusion that general emergence had occurred. However examination of the bark revealed most of the young beetles still present. They fed with their heads pointed into the bark and used the holes for disposing of accumulations of frass. A close examination showed a fringe of dark-coloured frass clinging to each hole.

While new adults were generally present in all the tops by June 26 to June 30, they did not migrate from either white or red pine to different parts of the slash or to other trees until July 29. On that date, short, new adult galleries were found in the smaller branches of red pine tops and in the upper portions of the white pine trunks which formerly had probably been too hot for larval development. Cutting of brood galleries by new adults was never observed at this time and it is therefore concluded that there was only one generation a year. The parent beetles probably produced more than one brood a year because eggs, larvae, and pupae, were present together in the slash for too long a period to have originated from one brood. On June 27, new brood galleries were discovered in the top branches of red pine slash. Since first generation adults were then only beginning to transform from the pupal stage, it is most unlikely that any of these galleries were the work of the new beetles. It was also noticed that a large white spruce tree, which had been blown over in the spring, and which previously had been free from attack by I. pini, contained

many new galleries of this species. As final evidence, two red pine blocks, in which adults of I. pini were working, were caged with sections of freshly cut white pine logs. On June 27, brood galleries were found in the fresh material indicating that some of the beetles had migrated from the former breeding site.

Overwintering habits of I. pini at Laniel were not definitely determined. Unfortunately, observations in the area were started after spring emergence of the adult beetles occurred. Slash, in which broods of these beetles had developed in the summer, was examined as late as October 9, and a few adults, in an inactive condition, found under the bark of the tops and stumps, might have overwintered there. An examination of the litter and humus beneath the slash did not reveal any adults. According to Leach, Orr and Christensen (1934), in Minnesota, the pupae and a portion of the adults hibernated under the bark and some of the young adults hibernated in the soil. However, Orr (1935) amended this conclusion and stated that in Minnesota I. pini hibernated in the litter and duff rather than under the bark of trees. Clemens (1916) stated that in the region around Ithaca, New York, the beetles tunneled into the bark and hibernated in the trees in which they had developed.

Ips pini, being the most abundant beetle in the tops, was subject to the greatest number of attacks by predators. All but two species of the hymenopterous parasites recovered from the tops were found in the pupal cells of this species.

Orthotomicus caelatus (Eichh.)

This beetle was found in the stumps of both species of pine. The adults are polygamous, and several brood galleries radiate from each nuptial chamber. Many of the first entries into the stumps are made by boring down between the bark and wood. Later, the beetles bore directly through the bark. The galleries are short and curved with from two to six eggs deposited in pockets cut into the sides. With so many larvae feeding in a congested area, individual larval mines were not maintained and soon the larvae appeared to feed in congress, resulting in the almost complete destruction of the phloem.

Adults were present on May 23 and in three days, galleries with eggs were found. The upper area of the stumps was preferred by the first brood. The first larvae appeared on June 2 and when mature they bored into the sapwood or occasionally into the thick bark, to a depth of one to two mm. to construct pupal cells. By July 12, all stages, from egg to newly transformed adults, were present. Egg laying was extended over several weeks with a corresponding spread in the appearance of succeeding stages. Thus eggs were still present in some galleries when adults appeared in the pupal cells. The young adults fed between the bark and wood and within the bark. By July 15, second brood galleries were started lower in the stumps, the majority of them in the roots. Larvae were first noted in these galleries on July 26. The position of these galleries in the roots and lower areas possibly may be attributed to the destruction of all available food in the upper two-thirds of the stump by first broods of O. caelatus, Hylurgops pinifex and by the larvae of the cerambycid, Stenocorus inquisitor.

Adults in an inactive state were found under the bark on September 17 and a few adults were found in the spring in stumps which had supported broods of O. caelatus the previous year. Therefore, it is possible that part of the adult population overwinters in the stumps.

All stages of this beetle with the possible exception of the more protected pupae were attacked by predators. Histerid beetles in particular appear to attack this species and, as early as June 2, a few days after the galleries were started, Platysoma coarctatum and Platysoma sp., were found in the galleries. The early destruction of many individuals of this species of bark beetle may be attributed in part to the fact that they are among the first to enter the stumps. They were also attacked by adults and larvae of Thanasimus dubius and Enoclerus nigripes rufiventris, and the staphylinids Nudobius cephalus and Quedius spp. Glischrochilus sanguinolentus was an active predator in both larval and adult stages. On one occasion a pseudoscorpion was observed carrying away an adult beetle.

Pityogenes hopkinsi Sw.

Pityogenes hopkinsi occupied most of the space in the thin-barked areas of white pine tops, and was found occasionally in the small branches of red pine tops. It competed with Ips pini for space in the transition zone from rough to smooth bark, galleries of the two species intermingling.

Progress made by the beetles is recorded photographically in figures 5 to 8. By May 23, many entrance holes had been bored through the outer bark, nuptial chambers constructed, and the males

were each joined by two to six females. The egg galleries were cut transversely across the bark by the females, an arrangement which enabled the larvae to mine with the bark fibres rather than across them. Eggs were deposited singly in niches along the sides of the galleries (Fig. 5). The galleries were extended rapidly and by June 5, the first larvae hatched from the eggs nearest the nuptial chambers (Fig. 6). Competition between larvae of P. hopkinsi and Ips pini is apparent in Figures 6, 7 and 8. Larval mines from different galleries approached and passed between each other (Fig. 7), the available food was consumed, and the inner bark almost completely destroyed in the process (Fig. 8). The first pupae were found on June 15, and pupation was general by June 26. The larvae mined almost entirely within the bark except in very thin-barked twigs, where the larval mines as well as the egg galleries scored the sapwood. Pupation usually took place in the bark, but in very thin-barked twigs, the mature larvae bored into the sapwood and pupation took place in small holes in the wood. Young adults of the first brood appeared by July 15. The feeding period for the young adults before emergence varied from one to several weeks. Blackman (1915) found that, if the bark of the host remained moist, the beetles continued to feed in it for a longer period than if it dried out. There is adequate time in the Lanier area for a second brood to develop, however most of the breeding space in the white pine tops was occupied by the first brood. Consequently, in only a few cases were new brood galleries discovered in white pine. On July 22, new brood galleries were found in red pine tops, and it is probable that some of these resulted from beetles migrating from white pine.

Blackman (1915) prepared a valuable account of the life history of P. hopkinsi. According to Blackman, this species overwinters in the host tree as larvae, pupae and young adults, with the majority in the adult stage. Examination of white pine tops on September 17 revealed mostly pupae and young adults under the bark and in the sapwood, which would appear to confirm part of Blackman's findings.

The associates of this species were Ips pini, Monochamus scutellatus, a staphylinid, Atheta sp., and predators of the families Cleridae, Histeridae and Staphylinidae. Larvae of the fly, Empis sp., were found in the larval mines but it is not known if they were predaceous.

Pityogenes plagiatus (Lec.)

This species was found in small numbers in the small branches of red pine tops. The beetles are polygamous, the males excavating the entrance hole and nuptial chamber before being joined by two to six females. The eggs were laid singly in niches along the sides of the egg galleries which radiated in all directions from the nuptial chambers. The niches were irregularly placed in contrast to the even spacing of those of P. hopkinsi. The work of the two species could be separated readily by the engravings, those of P. plagiatus being more irregular than those of P. hopkinsi. Also, the entire engraving scored the sapwood, possibly due to the thin bark on the smaller branches.

The first adults were found in the branches on May 30 and the egg galleries were well developed by June 5. The first larvae appeared on June 12, continuing to feed until pupation which began

on July 26. The new adults fed under the bark and it is possible that they overwintered in the branches as they were still present on September 17. Since the egg galleries were well established by the middle of June, there may be more than one brood a season. However, the beetle was not abundant enough to permit sufficient observations to clarify this point.

Other borers associated with P. plagiatus were Ips pini, occasionally P. hopkinsi, and Monochamus spp. Clerid larvae were found in the galleries.

#### FAMILY CERAMBYCIDAE

##### Asemum atrum Esch.

Adults of this species appeared early in the season in the bark crevices of the stumps. The larvae were recovered from beneath the bark June 26 and were still present on September 17. This species is a shallow borer, the larvae mining through the sapwood leaving the tunnels filled with frass and powdery boring dust.

##### Monochamus notatus (Drury)

##### " scutellatus (Say)

Separation of the larvae is difficult, therefore the two species are discussed collectively as far as their activity in the slash is concerned.

The adults of M. scutellatus began to emerge from the

previous year's slash about June 12, followed by M. notatus two to three weeks later. This indicates that each generation requires one year in the Laniel area that is one year less than is required in standing balsam fir, Abies balsamea (L.) Mill., in the Lake Nipigon region of Ontario (Belyea, 1951). The adults of both species gnawed slits in the bark in which to deposit their eggs, the larvae hatching from these eggs feeding on the phloem and sapwood. The eggs appear to be deposited indiscriminately throughout the bark area of the tops and consequently, the larvae were in close association with the broods of Ips pini, Pityogenes hepkinsi and P. plagiatus. Until the larvae began to penetrate the wood, they were constantly in competition with these bark beetles for space and food. The cerambycid larvae frequently ate completely through the space occupied by broods of bark beetles, and when actual destruction of the larvae did not occur in this manner, the Menochamus feeding in the phloem and sapwood reduced the amount of food available for the bark beetle larvae. The borers began to penetrate the wood toward the end of July and by August 1, one larva was found to have tunnelled to a depth of two inches. By September 17, many larvae were four inches deep and had started to move toward the surface of the log. Not all the larvae were in the wood, a number were still between the bark and sapwood.

In addition to the three above mentioned species of bark beetles associated with these borers, numerous small staphylinids of the subfamily Aleocharinae, probably species of Atheta, were found in association with the cerambycid larvae. Parasitic flies, Eutheresia trivittata, were reared from puparia found in the pupal cells of the borers.



Stenocorus inquisitor (L.)

Adults of this beetle were numerous during the last week in May, and larvae appeared in the middle of June. The species confined its attacks to the stumps and the larvae fed entirely between the bark and sapwood. The mature larvae construct cells of shredded bark between the bark and sapwood in which to pupate. Craighead (1950) states that this species overwinters in the bark as adults and a similar observation is reported by Knull (1946). The very early appearance of the adults in the Laniel area would seem to indicate that some adults overwinter. However, by September 17 of one year and October of the succeeding year, larvae in an inactive state were still under the bark. Examinations as early as May 23 of slash attacked the previous year, revealed many pupal cells with larvae still within them, while others were empty. It seems probable that many individuals of this species overwinter as larvae at Laniel.

The larvae of S. inquisitor were heavily parasitized by Eutheresia nipigonensis ? Curr., a large fly of the family Tachinidae. Many puparia of this parasite were recovered in the spring from the pupal cells of the wood borer.

FAMILY PYTHIDAE

Pytho americanus Kby.

Pytho sp.

The larvae of both these species fed on the bark fibres and possibly on the boring dust in the galleries of the bark beetles.

Feeding habits of the adults were not established. The larvae were found in association with all species of Ipidae, with the exception of the ambrosia beetles, soon after the bark had been loosened. However, they were not restricted to the galleries alone but were found any place where the bark was loose enough for them to move about. They overwintered as larvae, completing their development the next season in the same habitat. Pupation took place between the bark and wood and, on several occasions, a crude sort of pupal cell similar to that of the cerambycid Stenocorus inquisitor, was built. Certain species of this genus are apparently predaceous. DeLeon (1934) found Pytho planus Herbst. in the galleries of the mountain pine beetle, Dendroctonus monticolae Hopk., and reported it to be occasionally predaceous.

#### FAMILY CURCULIONIDAE

##### Pissodes spp.

Two species of Pissodes similar in appearance to Pissodes strobi (Peck), but differing greatly in habit, were recovered from the stumps and tops of the slash. In the stumps, the larval borings started very close to the ground and in certain cases even in the larger roots. The larvae fed upward beneath the bark and, when mature, constructed pupal cells in the wood, using the wood fibres chewed out of the cells, to cap them over, forming chip cocoons. Some of the larvae completed development in one season and emerged as adults, while others overwintered as prepupae, pupating and emerging as adults the following spring. The species were associated with

Dendroctonus valens, Hylurgops pinifex, and Orthotomicus caelatus in the stumps, and with Ips pini in the tops. A parasite, Eubadizon sp., was recovered from the chip cocoons.

FAMILY BUPRESTIDAE

Larvae of Unidentified spp.

Adults of eight species of this family (listed in Appendix II) were collected in relatively large numbers on the slash. Contrary to expectations, buprestid larvae did not constitute an important part of the community under the bark. Larvae of unidentified species of buprestids were collected from only two red pine tops during the season.

B. GROUP II. FUNGUS, FRASS AND DETRITUS FEEDERS

ORDER COLLEMBOLA

FAMILY ENTOMOBRYIDAE: Tomocerus sp.

Unidentified genus

FAMILY PODURIDAE: Unidentified genus

FAMILY SMINTHURIDAE: Sminturus sp.

Sometime after the bark beetle broods have started their development, environmental conditions appear suitable for an influx of various species of Collembola. The above-noted species were collected from under the bark and although no direct evidence of their feeding habits were obtained, they have been classed as commensals.

ORDER PSOCOPTERA

Unidentified spp.

Unidentified psocids were collected from the outer bark of the slash and later from beneath the loosened bark. Feeding habits were not determined although they did not molest insect material offered to them. Imms (1948) states that psocids, which occur out-of-doors, live on fragments of vegetable matter, particularly fungi and lichens.

ORDER COLEOPTERA

FAMILY ELATERIDAE

Agriotes fucosus (Lec.)

Ampedus sp.

Ctenicera triundulata Rand.

Limonius aeger Lec.

Melanotus sp.

Unidentified larvae

Adults of the above-noted species were collected on and under the bark of the stumps, and reared from pupae dug out of the humus at the base of the stumps. Feeding habits of the adults were not determined. Elaterid larvae, unidentified but probably the immature stages of at least some of the above-noted species, were found in the humus around the stumps and under the bark. They were frequently found in areas devoid of other insects and presumably fed upon organic matter. According to Craighead (1950), the elaterids are predominantly vegetable feeders on the soft tissues under bark and

in decayed wood. However, a few are predaceous as confirmed in this study. A few larvae kept in rearing tins fed at times on larvae and pupae of Ips pini and Hylurgops pinifex. The pupae appeared to be favoured by most of the elaterids over larvae, possibly because they were more inactive. The elaterid larvae were also cannibalistic. Kirk (1922) reported that a number of species of Elateridae found in the galleries of wood-boring larvae were predaceous on the wood borers. Limonius aeger was collected by Glen (1950) in Saskatchewan from forest litter but no feeding habits were given. Morris (1951) found that larval Elateridae fed upon immature stages within cocoons, and emerging adults of the European spruce sawfly, Gilpinia hercyniae (Htg.).

#### FAMILY NITIDULIDAE

##### Eपुरaea sp.

Small brown beetles, Eपुरaea sp., inhabited the galleries of Hylurgops pinifex, Ips pini and Orthotomicus caelatus. Feeding habits of the adults were not determined, but the larvae were observed feeding on fungi, boring dust and other debris in the galleries. Craighead (1950) considers that species of the genus Eपुरaea are sap feeders occurring between the bark and wood of dead trees.

#### FAMILY RHIZOPHAGIDAE

##### Rhizophagus sp.

These small beetles were collected from the galleries of Ips pini, Hylurgops pinifex and Orthotomicus caelatus. As far as could

be determined from observations in the field and laboratory, the adults are not predaceous. They did not feed upon any larvae offered to them but rather chewed the decaying bark. Contrary to these findings, DeLeon (1934) found that both adults and larvae of Rhizophagus procerus (Csy.) were predaceous on the larvae and eggs of Dendroctonus monticolae Hopk.

FAMILY STAPHYLINIDAE

Atheta sp.

These small staphylinids were extremely numerous in the galleries of Ips pini, Pityogenes hopkinsi, and in the tunnels of Monochamus scutellatus. The adults were first observed immediately after the nuptial chambers and the egg galleries of the bark beetles were started, later entering the tunnels of M. scutellatus. Careful observations in the laboratory revealed that both the larval and adult stages fed upon boring dust, fungi and fragments of bark in the galleries. Fungus growing on dead pupae and adults of I. pini was eaten, but not the bodies of the insects.

ORDER DIPTERA

FAMILY CECIDOMYIIDAE

Aprionus sp.

Holoneurus sp.

Unidentified larvae

Larvae of the genera Aprionus and Holoneurus and of four

unidentified genera were collected from the moist phloem of the inner bark surface. Feeding habits were not observed in the field, but the collections were made from sections of bark not in direct contact with bark beetles or other insects. Laboratory observations confirmed that they were not predaceous. They appeared to feed on the juices in the decaying bark. Clausen (1940) mentions that members of this family are predaceous chiefly on mites. According to Webber (1950), larvae of an unidentified species have been collected from galleries of Hylurgopinus rufipes (Eichh.).

FAMILY CERATOPOGONIDAE

Forcipomyia simulata Wal.

Forcipomyia sp.

Many specimens of F. simulata were collected as larvae and pupae from under the bark of a red pine top. They lived gregariously and although broods of Ips pini were present, the Forcipomyia larvae did not feed on them. Feeding appeared to be on the plant juices. Four larval specimens, identified as a species of Forcipomyia, were collected at the same time. Clausen (1940) states that the habits of the larvae are little known. They appear to fall into the classification of commensals in the community in the slash.

FAMILY COENOMYIIDAE

Xylophagus fasciatus Walk.

Xylophagus sp.

Larvae of these species were collected from under the bark of red and white pine stumps. They appeared late in the season after

most of the bark beetles emerged, overwintered in the larval stage, and completed their development the second season. To check the feeding habits of this species, more mature larvae were collected from slash attacked the previous year. Some of the larvae were kept in a vial with boring dust and other debris from under the bark but without any noticeable animal matter for food. Although not provided with any additional food, they pupated and emerged after about one month. A second group was placed on bark between two sheets of glass and was supplied with larvae of Ips pini, Hylurgops pinifex and other larvae of the order Diptera, but was not predaceous. The larvae kept moving back and forth over the bark and finally died. Clausen (1940), Curran (1934) and Peterson (1951) state that the larvae are predaceous on other insects.

#### FAMILY EMPIDIDAE

##### Empis sp.

Larvae belonging to this genus were recovered in large numbers from under the bark of the slash. They were associated with Dendroctonus valens, Hylurgops pinifex, Ips pini and Pityogenes hopkinsi but remained under the bark after the majority of the beetles had emerged. They fed upon pupae of Ips pini and H. pinifex in the laboratory and also on the decaying bark. Under the bark, they were frequently located where there were no other insects available for food. From these observations, it was concluded that they were both scavengers and predators. Curran (1934) states that the larvae of Empididae may be found in decaying vegetation, under bark and in streams. Melander (1902) believes all larvae are



predaceous, while Clausen (1940) states that the adults are predaceous upon small insects and the larvae are either predators or scavengers.

FAMILY LONCHAEIDAE

Lonchaea sp. probably watsoni Curr.

The larvae of this species were extremely numerous under the bark in the boring dust and other fragments of bark. They did not feed upon any insects offered to them, and in many cases they were located in areas apparently devoid of other insects. On September 17, the larvae were still present and they may overwinter as such. In the spring, collections were made from one-year-old slash and by that time, the larvae had pupated and adults emerged from the brown puparia shortly after they were brought into the laboratory. According to Webber (1950), the larvae may be either scavengers or predators.

FAMILY PHORIDAE

Megaselia iroquoiana Mall.

A number of adult flies identified as M. iroquoiana emerged from a piece of white pine bark held between two glass sheets. The adults were left between the glass and in a few days numerous larvae of this species were seen feeding on the dead body of a larva of Xylophagus fasciatus which was on the bark. They were feeding actively on the soft tissues inside the larval skin of the host and eventually only the integument of the larva remained. They subsequently ate larvae of Ips pini, Hylurgops pinifex and of the families Cerambycidae and Curculionidae which

were provided. A braconid parasite, Aphaereta sp., was observed ovipositing in the Dipterous larvae.

Some of the adult flies, along with the braconid, were transferred to a vial with a crushed cerambycid larva. Frequent matings occurred between the flies and, the day after they were transferred, eggs were deposited on the sides of the vial and on the body of the cerambycid. These hatched in one day and the larvae began feeding on the dead cerambycid larva. The braconid oviposited in the larvae and subsequently four specimens of the parasite were recovered. The adult flies also sucked at the fluids alongside the dead borer larva. They also fed on larvae of the families Cleridae and Elateridae, and other dipterous larvae and adults. Pupation took place in the last larval skin.

#### FAMILY SCIARIDAE

##### Plastosciara sp.

Larvae and pupae of a species of Plastosciara were frequently found under the bark of the stumps. They were in compact masses and appeared to feed on the juices of the decaying bark and possibly on fungi.

##### Scaptosciara myrmecophila Frey.

Large numbers of adults of this species emerged from a small rearing jar filled with boring dust scraped from under the bark of the slash. Larvae or pupae were not observed as the material had been collected for another purpose and was not suspected of having

minute Diptera hidden in it. Consequently no feeding habits were recorded. They apparently are not predaceous or parasitic on bark beetle larvae as these were absent from the material.

Sciara sp.

Only larvae of this genus were found beneath the bark of white pine. The larvae were small, whitish and remained massed on a thin slimy web spun over the area. They did not eat any insect food offered.

FAMILY STRATIOMYIIDAE

Neopachygaster maculicornis (Hine)

Zabrachia polita Coq.

Unidentified larvae

Larvae of these species were collected from many of the galleries of Ips pini, Hylurgops pinifex, Dendroctonus valens, and in the boring dust and fragments of phloem beneath the bark. They are apparently both scavengers and predators. A number of specimens were placed on bark containing galleries and some pupae and dead adults of Ips pini. The stratiomyiid larvae were observed feeding on a pupa and on a dead adult of I. pini. Larvae and pupae of H. pinifex were also eaten. Frequently, they appeared to be feeding directly on the phloem. Curran (1934) states that the larvae are either predaceous or feed on decaying vegetation and bark.

FAMILY SYRPHIDAE

Genus nr. Brachyopa

Larvae of a genus near Brachyopa were collected from the galleries of Hylurgops pinifex and Dendroctonus valens in the stumps. They were found in the ends of the galleries which were filled with a slimy residue. It is not known whether they were predaceous on the immature stages of the bark beetles. All bark beetles had disappeared from galleries where these larvae were found. If they are predaceous, they must revert to feeding on the wood or sap since they continue to exist in the galleries. Metcalf (1913) describing the feeding habits of Syrphidae in Ohio, states that the larvae feed on living plant tissues or sap, decaying wood, decaying organic matter or excrement, and also on soft-bodied insects.

C. GROUP III. PARASITES

ORDER HYMENOPTERA

FAMILY BRACONIDAE

Aphaereta sp.

The first specimen was observed ovipositing in the larvae of a dipterous scavenger, Megaselia iroquoiana. Subsequently, four specimens of the parasite were recovered from the puparia of the fly.

Coeloides sp.

A large number of cocoons from which a species of Coeloides emerged, were collected from the pupal cells of Ips pini in red and white pine tops.

Eubadizon sp.

Three specimens of a species of Eubadizon were recovered from the chip cocoons of a weevil identified as a species of Pissodes. These weevils were active in the stumps and tops of both species of pine.

FAMILY PTEROMALIDAE

Pachyceras eccoptogastris Ratz.

Numerous specimens of this parasite were recovered from the galleries of Ips pini in white pine tops, while others were collected ovipositing on bark infested with I. pini. Three species of Dendroctonus, three of Ips, and Orthotomicus caelatus are listed by Peck (1951) as hosts. Of this group of hosts, I. pini and O. caelatus occurred in the habitat under study.

Rhopalicus pulchripennis (Cwfd.)

Cocoons of this species were collected from the pupal cells of Ips pini. Adults were collected while they were ovipositing in the bark of the white pine tops. Peck (1951) lists a number of bark beetles and borers as hosts, none of which were recovered in the red and white pine slash.

Rhopalicus tutela (Walk.)

Cocoons of this parasite were found in the pupal cells of Ips pini in white pine tops along with those of R. pulchripennis.

One adult was captured on the outer bark of a white pine top. Peck (1951) lists as hosts of this parasite, Pissodes notatus (F.) and P. strobi (Peck). There is apparently only one other Canadian record of R. tutela (personal communication, O. Peck, Unit of Systematic Entomology, Ottawa).

ORDER DIPTERA

FAMILY MUSCIDAE

Phaonia harti. Mall.

Larvae and pupae of this species were recovered from the pupal cells of Stenocorus inquisitor, a cerambycid found in the stumps. The parasite fed internally leaving only the larval integument and head capsule of the host.

FAMILY TACHINIDAE

Eutheresia nipigonensis ? Curr.

" trivittata Curr.

E. nipigonensis was recovered from the pupal cells of Stenocorus inquisitor, while E. trivittata was parasitic on the same borer and also on Monochamus scutellatus. The immature forms of S. inquisitor were heavily parasitized. In one-year-old slash examined in the spring, the parasite larvae were frequently found still feeding within the larval skin of the cerambycids. According to Peterson (1951), the larvae are parasitic on the larvae of many insects including wood boring beetles.

D. GROUP IV. PREDATORS

CLASS CHILOPODA

Nampabius n. sp.

Geophilus probably rubens

Centipedes belonging to the above-noted genera were found on and under the bark after it had been loosened by the bark beetles. One record was obtained of a centipede of the genus Nampabius carrying away a pupa of Orthotomicus caelatus and it is probable that they are facultative predators on bark beetles and other small animal life in the slash. Centipedes occupy a permanent place in the forest floor fauna and migrate to the slash when opportunities for obtaining food are presented.

CLASS ARACHNIDA

Pseudoscorpions were frequently observed crawling over the bark and later entering the bark beetle galleries. Several records were obtained of these animals capturing both larvae and adult bark beetles, therefore they should be classed as facultative predators. Undoubtedly, they captured insects other than bark beetles which occurred in the slash.

Mites appeared shortly after the bark beetle galleries were started and soon were present in all the galleries and elsewhere beneath the bark. They were found attached to the bodies of nearly all species of bark beetles and, consequently, were carried with them to new hosts. It was not possible to determine if they were parasitic on the beetles or merely used them as a means of getting

from one host to another. Species belonging to three separate genera were collected from galleries in the bark and from the bodies of the bark beetles. On the other hand, one species was found in the galleries of Ips pini only, while a species was collected from the body of this bark beetle and not from the galleries. It has been pointed out by Rust (1933) that the economic value of mites as agents of control of bark beetles has never been realized. He observed mites feeding on the eggs and larvae of Ips oregoni (Richh.) in yellow pine and estimated that they destroyed 10 to 85 per cent of the eggs. Blackman (1915) reports that a mite, Seius pomi Parrot, found in the galleries of Pityogenes hopkinsi Sw., was predaceous on all stages of this bark beetle. Mites were present in the slash during the entire period when observations were made, but only one record of their feeding on a pupa of Ips pini was obtained.

ORDER COLEOPTERA

FAMILY CLERIDAE

Enoclerus nigripes rufiventris Spin.

Thanasimus dubius (Fab.)

Adults of these species were active predators of adult bark beetles, and the larvae were similarly predaceous on the bark beetle larvae. The adults appeared about the same time as the beetles were moving to fresh host material and, therefore, were in a position to inflict considerable damage. The clerid larvae appeared soon after the first bark beetle larvae and fed on Ips pini, Pityogenes hopkinsi, Dendroctonus valens, Orthotomicus caelatus, Hylurgops pinifex, and



probably on the larvae of other associated insects as well. When mature, they mined out into the bark and constructed a pupal cell near the surface. The adults on emergence cut openings to the outside.

Clerids have received considerable attention owing to their aggressiveness in preying on other insects. T. dubius is reported by Balduf (1935) as attacking and feeding on all kinds of bark beetles in spruce and pine. Fiske (1907) states that this species ranks among the most important predators of Dendroctonus frontalis Zimm., and also feeds on other insects. The activities of T. dubius and of Enoclerus are highly praised by Boving and Champlain (1920), who list the former as a predator of bark beetles of the genera Ips, Dendroctonus and Polygraphus, as well as other borers in coniferous trees. Hopkins (1899) was so impressed with the predaceous habits of clerids that he made a trip to Germany to collect specimens of Clerus formicarius L., an active predator of scolytids in Europe. One thousand adults and pupae of this species were released in Virginia in 1892 to help combat an outbreak of Dendroctonus frontalis. However, in 1893, the bark beetle epidemic subsided due to some unknown cause and the results of the experiment were never assessed. Several species of clerids are listed by Hopkins (1893) in a catalogue of West Virginia Scolytidae, including an undetermined species predaceous on Tomicus pini (now Ips pini).

The adult clerids were themselves attacked by other members of the insect community in the pine slash at Kipawa Lake. Several instances were noted of a large ant, Camponotus herculeanus, feeding upon adults of both species,

FAMILY ELATERIDAE

The predaceous habits of larvae of this family have been discussed along with their scavenger habits under section VI B.

FAMILY HISTERIDAE

Platysoma coarctatum Lec.

Platysoma sp.

These species were predaceous against all stages of bark beetles, the adults entering the galleries very shortly after they had been started. The majority of these predators were found in the galleries of Orthotomicus caelatus and Hylurgops pinifex in the stumps. Those in the tops were feeding on all stages of Ips pini and Pityogenes hopkinsi. The larvae completed development in August and pupated between the bark and sapwood, transforming to adults the same year. They apparently overwinter in the adult stage between the bark and sapwood as examination of the slash in later September revealed a number of adults still present. Baldur (1935) published a long list of the insects preyed upon by histerid beetles. Struble (1930) published an account of the life cycle and habits of Platysoma punctigerum (Lec.) in which he states that the larvae feed upon any bark beetle larvae available, as well as other predators, scavengers and inquilines; occasionally they are also cannibalistic. Schedl (1932) records P. coarctatum as a predator of Ips pini.

FAMILY NITIDULIDAE

Glischrochilus sanguinolentus Oliv.

This beetle was predaceous in both the larval and adult stages. The larvae were recovered from the galleries of all species of bark beetles occurring in the stumps. In the laboratory, the larvae ate the immature stages of Ips pini, Hylurgops pinifex, Dendroctonus valens and the larvae of a Syrphid fly. When other forms of food were scarce, they became cannibalistic. The adults fed upon larvae and pupae of I. pini and H. pinifex, but apparently fed upon plant juices and fungus growth as well, since they were seen chewing on decaying bark and fungi growing in the galleries. The larvae pupated in the humus and soil around the bases of the stumps in association with larvae of the family Elateridae.

FAMILY STAPHYLINIDAE

Nudobius cephalus Say

This is one of the largest staphylinids found in association with the bark beetles. Complete feeding habits were not determined for this species, but one instance of it feeding on an adult of Orthotomicus caelatus was noted. According to Chamberlin (1939), all species of Nudobius are predaceous as far as known.

Quedius spp.

Two or more species of this genus were found under the bark in association with bark beetles and other insects. Three

adults of one species kept in the laboratory fed upon larvae and pupae of Ips pini and Hylurgops pinifex offered to them. Larvae reared from this species died before definite feeding habits could be determined. Larvae of another species of the genus Quedius were very abundant beneath the bark but were difficult to keep alive in the laboratory. One record was obtained of one of the larvae feeding on a pupa of Ips pini.

FAMILY TENEBRIONIDAE

Corticus sp.

Adults and larvae of this species were collected from the galleries of Ips pini, Hylurgops pinifex, Orthotomicus caelatus and elsewhere beneath the bark. The larvae were predaceous on the immature stages of bark beetles and were also cannibalistic. One larva ate the pupa of another of the same species and then took over its pupal cell. An adult was seen feeding on the pupa of H. pinifex. There appear to be two colour phases in the larvae. In one phase, the transverse markings on the dorsal surface of the abdominal segments are a light brown and the entire body has a pale appearance. In the other case, the markings are darker, almost black. The larvae of each colour phase were found together under the bark, appeared to have the same food habits and acted similarly in all respects. On emergence, the adults all appeared identical and were identified as the same species of Corticus.

Tenebrionids under the bark of beetle-infested trees have been reported as scavengers and as predators. DeLeon (1934) reports

that Hypophloeus parallelus is a predator of Dendroctonus monticolae Hopk. Blackman (1915) considers that H. tenuis Lec. is apparently predaceous on adults of Pityogenes hopkinsi. Craighead (1950) reports that Struble tested the beetles with fungi and found the adults and larvae of Corticus to be entirely phytophagous.

ORDER HYMENOPTERA

FAMILY FORMICIDAE

Camponotus herculeanus (L.)

These large ants were very numerous on and under the bark of the stumps. As the bark became loosened by the activities of the bark beetle broods, they were able to get beneath the bark and prey upon the immature stages of the beetles and insects associated with the bark beetles. On two occasions, ants were noticed with adult clerid beetles, Thanasimus dubius, in their mandibles. When ants of this species were placed in a jar with adults of T. dubius, the clerids were promptly killed.

ORDER DIPTERA

FAMILY EMPIDIDAE

Empis sp.

The predaceous habits of the larvae of this fly have been discussed with its scavenger habits under section VI B.

## VII. SUMMARY

1. The community of insects and other arthropods, established in white and red pine logging slash during the summer following winter cutting, was examined.
2. Approximately 138 species were collected, distributed as follows: Chilopoda 3, Arachnida 7, Insecta 128, (Collembola 4, Psocoptera 1, Hemiptera 1, Homoptera 1, Lepidoptera 4, Coleoptera 62, Hymenoptera 18, and Diptera 37).
3. Active associates in the community are listed in Appendix I. About 60 species, which were casual visitors to the slash or which occurred so rarely under the bark that their ecological position could not be determined, are listed in Appendix II.
4. Species having an integral part in the community were segregated into the following four groups according to their known or probable feeding habits; I, phloem and sapwood feeders; II, fungus, frass and detritus feeders; III, parasites and IV, predators.
5. Three species of bark beetles occurred in the tops compared with eight in the stumps. Ips pini, the only species of bark beetle found in both stumps and tops, was of minor importance in the stumps. Pityogenes hopkinsi was present in tops of both species but only occasionally in red pine. The third species in the tops, Pityogenes plagiatus, was specific to red pine. The species of bark beetles in the stumps were equally represented in both red and white pine.
6. Most of the species in the community fell into Group II,

a situation true of both stumps and tops.

7. The parasites were mostly hymenopterous, with few from the order Diptera. The greatest number of predaceous species was recovered from the bark beetle galleries in white pine tops.

8. There were two classes of predators. First, those such as ants and centipedes, which did not remain in the community continuously but left and returned or were replaced by others of the same species. The second class of predator formed a more integral part and spent all or nearly all of its life in the community. The majority of the predators were of this second class.

9. Although the period during which observations were made, May 23 to September 17, was too short to define clearly a succession of species, trends toward succession were indicated. The community was centred chiefly around the activities of the bark beetles which were the first to attack the slash. Borers of the families Cerambycidae, Curculionidae and Pythidae followed the bark beetles but, with the possible exception of borers of the family Pythidae, were not dependent upon them for access to the slash. Parasites and predators accompanied the bark beetles and borers, followed by species in Group II which were dependent on the bark beetles and borers to initiate the development of suitable environmental conditions. Species in Group II were still present on September 17 after most of the bark beetles had left and might be expected to form an active part of the community in the slash the following season.

10. The situation outlined in paragraph 9 above has been portrayed graphically in Plates II and III, and supplemented by notes on the species concerned. The bark beetles were considered to be most important

in the development of the community, and consequently were treated more extensively than other species. Personal observations have been augmented in many cases by references to the literature. The apparent feeding habits of certain species observed during this study have not always agreed with reports on the same species or genera made by others.



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APPENDIX I - SPECIES ASSOCIATED IN THE COMMUNITY

SPECIES	LOCATION IN SLASH				STAGE
	WHITE PINE		RED PINE		
	STUMP	TOP	STUMP	TOP	
<u>GROUP I. PHLOEM AND SAPWOOD BORERS</u>					
<u>ORDER COLEOPTERA</u>					
<u>FAMILY IPIDAE</u>					
<u>Dendroctonus valens</u> Lec.	X		X		A,E,L
<u>Dryocoetes americanus</u> Hopk.	X		X		A,E,L
<u>Hylurgops pinifex</u> (Fitch)	X		X		All
<u>Ips chagnoni</u> Sw.	X		X		All
<u>Ips pini</u> (Say)	X	X	X	X	All
<u>Orthotomicus caelatus</u> (Eichh.)	X		X		All
<u>Pityogenes hopkinsi</u> Sw.		X		X	All
" <u>plagiatus</u> (Lec.)				X	All
<u>Gnathotrichus materiarius</u> (Fitch)	X		X		All
<u>Trypodendron bivittatum</u> (Kby.)	X		X		All
<u>FAMILY CERAMBYCIDAE</u>					
<u>Asemum atrum</u> Esch.	X		X		A,L

APPENDIX I cont'd.

SPECIES	LOCATION IN SLASH				STAGE
	WHITE PINE		RED PINE		
	STUMP	TOP	STUMP	TOP	
<u>Monochamus notatus</u> (Drury)		X		X	A,L
" <u>scutellatus</u> (Say)		X		X	A,L
<u>Stenocorus inquisitor</u> (L.)	X		X		A,L
<u>FAMILY PYTHIDAE</u>					
<u>Pytho americanus</u> Kby.	X	X	X	X	A,L
<u>Pytho</u> sp.	X	X	X	X	A,L
<u>FAMILY CURCULIONIDAE</u>					
<u>Pissodes</u> spp.	X	X	X	X	A,L,P
<u>FAMILY BUPRESTIDAE</u>					
Larvae of Unidentified spp.		X		X	L
Adults of eight species were found on the slash but only two records of larvae in the slash were obtained. (See Appendix II)					



APPENDIX I cont'd.

SPECIES	LOCATION IN SLASH				STAGE
	WHITE PINE		RED PINE		
	STUMP	TOP	STUMP	TOP	
<u>GROUP II. FUNGUS, FRASS AND DETRITUS FEEDERS</u>					
<u>ORDER COLLEMBOLA</u>					
<u>FAMILY ENTOMOBRYIDAE</u>					
<u>Tomocerus</u> sp.	X	X	X	X	A
Unidentified sp.	X	X	X	X	A
<u>FAMILY PODURIDAE</u>					
Unidentified sp.	X	X	X	X	A
<u>FAMILY SMINTHURIDAE</u>					
<u>Sminthurus</u> sp.	X	X	X	X	A
<u>ORDER PSOCOPTERA</u>					
Unidentified sp.	X	X	X	X	A
<u>ORDER COLEOPTERA</u>					
<u>FAMILY ELATERIDAE</u> (Refer to Group IV)					
<u>Agriotes fucosus</u> (Lec.)	X		X		A
<u>Ampedus</u> sp.	X		X		A

APPENDIX I cont'd.

SPECIES	LOCATION IN SLASH				STAGE
	WHITE PINE		RED PINE		
	STUMP	TOP	STUMP	TOP	
<u>Ctenicera triundulata</u> Rand.	X		X		A
<u>Limenius aeger</u> Lec.	X		X		A
<u>Melanotus</u> sp.	X		X		A
Unidentified spp.	X		X		L
<u>FAMILY NITIDULIDAE</u>					
<u>Eपुरaea</u> sp.	X		X		A,L
<u>FAMILY RHIZOPHAGIDAE</u>					
<u>Rhizophagus</u> sp.	X		X		A
<u>FAMILY STAPHYLINIDAE</u>					
<u>Atheta</u> sp. probably	X	X	X	X	A,L
<u>ORDER DIPTERA</u>					
<u>FAMILY CECIDOMYLIDAE</u>					
<u>Aprionus</u> sp.	X				L,A

APPENDIX I cont'd.

SPECIES	LOCATION IN SLASH				STAGE
	WHITE PINE		RED PINE		
	STUMP	TOP	STUMP	TOP	
<u>Holoneurus</u> sp.	X	X	X	X	L
Larvae of Unidentified spp.	X	X	X	X	L
<u>FAMILY CERATOPOGONIDAE</u>					
<u>Forcipomyia simulata</u> Wal.				X	L,P
<u>Forcipomyia</u> sp.				X	L
<u>FAMILY COENOMYIIDAE</u>					
<u>Xylophagus fasciatus</u> Walk.	X		X		A,L
<u>Xylophagus</u> sp.	X		X		L
<u>FAMILY EMPIDIDAE</u>					
<u>Empis</u> sp. (Refer to Group IV)	X	X	X	X	A,L
<u>FAMILY LONCHAEIDAE</u>					
<u>Lonchaea</u> sp. probably <u>watsoni</u> Curr.	X	X	X	X	A,L,P

APPENDIX I cont'd.

SPECIES	LOCATION IN SLASH				STAGE
	WHITE PINE		RED PINE		
	STUMP	TOP	STUMP	TOP	
<u>FAMILY PHORIDAE</u>					
<u>Megaselia iroquoiana</u> Mall.	X	X	X	X	A,L,P
<u>FAMILY SCIARIDAE</u>					
<u>Plastosciara</u> sp.	X		X		L,P
<u>Scaptosciara myrmecophila</u> Frey.	X	X	X	X	A
<u>Sciara</u> sp.	X	X			L
<u>FAMILY STRATIOMYIIDAE</u>					
<u>Neopachygaster maculicornis</u> (Hine)	X	X	X	X	L
<u>Zabrachia polita</u> Coq.	X				A,L
Larvae of Unidentified sp.	X	X	X	X	L
<u>FAMILY SYRPHIDAE</u>					
Genus nr. <u>Brachyopa</u>	X		X		L

APPENDIX I cont'd.

SPECIES	LOCATION IN SLASH				STAGE
	WHITE PINE		RED PINE		
	STUMP	TOP	STUMP	TOP	
<u>GROUP III. PARASITES</u>					
<u>ORDER HYMENOPTERA</u>					
<u>FAMILY BRACONIDAE</u>					
<u>Aphaereta</u> sp.	X	X	X	X	A
<u>Coeloides</u> sp.		X		X	A,P
<u>Eubadizon</u> sp.	X				A,P
<u>FAMILY PTEROMALIDAE</u>					
<u>Pachyceras eccoptogastris</u> Ratz.	X				A
<u>Rhopalicus pulchripennis</u> (Cwfd.)	X			X	A,P
" <u>tutela</u> (Wlk.)	X				A
<u>ORDER DIPTERA</u>					
<u>FAMILY MUSCIDAE</u>					
<u>Phaenia harti</u> Mall.	X				A,P

APPENDIX I cont'd.

SPECIES	LOCATION IN SLASH				STAGE
	WHITE PINE		RED PINE		
	STUMP	TOP	STUMP	TOP	
<u>FAMILY TACHINIDAE</u>					
<u>Euthersia nipigenensis</u> ? Curr.	X				A,P
" <u>trivittata</u> Curr.		X			A,L,P
<u>GROUP IV. PREDATORS</u>					
<u>CLASS CHILOPODA</u>					
<u>Geophilus</u> probably <u>rubens</u>	X		X		A
<u>Nannobius</u> n. sp.	X	X	X	X	A
<u>CLASS ARACHNIDA</u>					
<u>ORDER AGARINA</u>					
<u>Amoetus</u> sp.	X	X	X	X	A
<u>Atomus</u> sp.	X	X	X	X	A
<u>Eugamasus</u> sp.	X	X	X	X	A
<u>Suidasia</u> sp.	X	X	X	X	A

APPENDIX I cont'd.

SPECIES	LOCATION IN SLASH				STAGE
	WHITE PINE		RED PINE		
	STUMP	TOP	STUMP	TOP	
<u>ORDER PSEUDOSCORPIONIDA</u>					
Unidentified sp.	X	X	X	X	A
<u>CLASS INSECTA</u>					
<u>ORDER COLEOPTERA</u>					
<u>FAMILY CLERIDAE</u>					
<u>Enoclerus nigripes rufiventris</u> Spin.	X	X	X	X	A,L,P
<u>Thenasimus dubius</u> (Fab.)	X	X	X	X	
<u>FAMILY ELATERIDAE</u>					
(Refer to Group II.)					
<u>FAMILY HISTERIDAE</u>					
<u>Platysoma coarctatum</u> Lec.	X	X	X	X	A,L,P
<u>Platysoma</u> sp.	X	X	X	X	A,L,P

APPENDIX I cont'd.

SPECIES	LOCATION IN SLASH				STAGE
	WHITE PINE		RED PINE		
	STUMP	TOP	STUMP	TOP	
<u>FAMILY NITIDULIDAE</u>					
<u>Glischrochilus sanguinolentus</u> Oliv.	X		X		A,L,P
<u>FAMILY STAPHYLINIDAE</u>					
<u>Nudobius cephalus</u> Say	X	X	X	X	A,L
<u>Quedius</u> spp.	X	X	X	X	A,L
<u>FAMILY TENEBRIONIDAE</u>					
<u>Corticus</u> sp.	X	X	X	X	A,L
<u>ORDER HYMENOPTERA</u>					
<u>FAMILY FORMICIDAE</u>					
<u>Camponotus herculeanus</u> (L.)	X	X	X	X	A
<u>ORDER DIPTERA</u>					
<u>FAMILY EMPIDIDAE</u>					
<u>Empis</u> sp. (Refer to group II.)					



APPENDIX II. SPECIES NOT FORMING AN INTEGRAL PART OF THE COMMUNITY

SPECIES	LOCATION IN SLASH				STAGE	REMARKS
	PW		PR			
	S	T	S	T		
<u>CLASS CHILOPODA</u>						
<u>Linotenia chionophila</u> (Wood)		X			A	One specimen only collected under the bark
<u>CLASS ARACHNIDA</u>						
<u>ORDER ARANEAE</u>						
Unidentified spp.	X	X	X	X	A	From the outer bark surface and under bark.
<u>CLASS INSECTA</u>						
<u>ORDER HEMIPTERA</u>						
Unidentified nymphs	X	X	X	X	N	Under bark scales and in galleries of <u>Ips pini</u> .
<u>ORDER HOMOPTERA</u>						
<u>FAMILY ACHILIDAE</u>						
<u>Epiptera confusa</u> Beirne			X		N,A	Four immature stages collected from under bark.
<u>ORDER LEPIDOPTERA</u>						
<u>FAMILY GEOMETRIDAE</u>						
<u>Protoboarmia porcelaria indicataria</u> Wlk.	X				P	Hibernating in bark crevice; defoliators McGuffin (1943)

APPENDIX II cont'd.

SPECIES	LOCATION IN SLASH				STAGE	REMARKS
	PW		PR			
	S	T	S	T		
<u>Semiothisa granitata</u> Guen.		X			P	Hibernating in bark crevice; defoliators McGuffin (1943)
<u>FAMILY NOCTUIDAE</u>						
<u>Platyperigea multifera</u> Wlk.		X			P	Hibernating in bark crevice.
<u>FAMILY OLETHREUTIDAE</u>						
<u>Petrova gemistrigulana</u> Kft.				X	L,P	Larvae mine in the scaly outer bark of red pine; not restricted to slash.
<u>ORDER COLEOPTERA</u>						
<u>FAMILY BUPRESTIDAE</u>						
<u>Buprestis maculativentris</u> Say	X	X	X	X	A	Adults of all these species were captured on and about the slash. It was thought that the larvae would be an important com- ponent of the community beneath the bark, but only two records of larvae were obtained in red pine tops during the season.
" <u>nutallii</u> (Kby.)	X	X	X	X	A	
" <u>striata</u> (Fab.)	X	X	X	X	A	
<u>Chalcophora virginiensis</u> (Drury)	X	X	X	X	A	
<u>Chrysobothris</u> sp.	X	X	X	X	A	
<u>Dicerca punctulata</u> (Schön.)	X	X	X	X	A	
" <u>tenebrosa</u> (Kby.)	X	X	X	X	A	

APPENDIX II cont'd.

SPECIES	LOCATION IN SLASH				STAGE	REMARKS
	PW		PR			
	S	T	S	T		
<u>FAMILY CANTHARIDAE</u>						
<u>Cantharis</u> sp.		X			A	Collected on the bark; adults partly predatory and partly phytophagous, Balduf (1935)
<u>FAMILY CARABIDAE</u>						
<u>Bothriopterus luczoti</u> (Dej.)		X			A	One specimen collected in bark crevice.
Unidentified spp.		X			L	Larvae of two genera collected in the moist bark at the base of a stump.
<u>FAMILY CERAMBYCIDAE</u>						
<u>Acanthocinus pusillus</u> Kby.		X			A	Two specimens only, one on the slash and one from pupal cell in a top.
<u>Acmaeops proteus</u> (Kby.)				X	A	One adult collected on a stump.
<u>Anoplodera mutabilis</u> (Newm.)		X			A	Two specimens captured on the slash.
<u>Evodinus monticola</u> (Rand.)		X			A	One adult collected on the top.
<u>Monoctamus mutator</u> Lec.		X			A	One adult collected on the top.
<u>FAMILY CHRYSOMELIDAE</u>						
<u>Syneta pilosa</u> Brown		X		X	A	Two specimens collected from the bark.

APPENDIX II cont'd.

SPECIES	LOCATION IN SLASH				STAGE	REMARKS
	PW		PR			
	S	T	S	T		
<u>FAMILY CURCULIONIDAE</u>						
<u>Hylobius congener</u> D.T.	X				A	Two adults from litter at the stump base.
<u>Hylobius</u> sp.	X				A	One adult from in the bark.
<u>Podapion gallicola</u> Riley				X	A,L	Cause galls on the small twigs of red pine and are present before cutting.
<u>FAMILY HISTERIDAE</u>						
<u>Plegaderus</u> sp.	X				A	Two adults collected from under the bark.
<u>FAMILY LAMPYRIDAE</u>						
<u>Lucidota</u> sp.				X	A	One adult from the outer bark; adults usually predaceous (Craighead, 1950).
<u>FAMILY LYCIDAE</u>						
<u>Celetes basalis</u> Lec.				X	A	One adult from under the bark scales; occasionally predaceous (Craighead, 1950)
<u>FAMILY MORDELLIDAE</u>						
<u>Anaspis</u> sp.				X	A	One adult from the bark.
<u>FAMILY ORTHOPERIDAE</u>						
<u>Sacium</u> sp.	X				A	One adult collected under the bark.

APPENDIX II cont'd.

SPECIES	LOCATION IN SLASH				STAGE	REMARKS
	PW		PR			
	S	T	S	T		
<u>FAMILY STAPHYLINIDAE</u>						
<u>Siagonium</u> sp.		X			A	One specimen found in the gallery of <u>Ips pini</u> .
<u>ORDER HYMENOPTERA</u>						
<u>FAMILY BRACONIDAE</u>						
<u>Atanycolus anocomodis</u> Cush.		X			A	One adult collected from the bark surface.
<u>Coeloides dendroctoni</u> Cush.		X		X	A	Collected while ovipositing on tops infested with <u>Ips pini</u> and <u>Pityogenes hopkinsi</u> .
<u>Spathius</u> sp.		X			A	One specimen collected from the bark surface.
<u>Triaspis</u> sp.		X			A	Two specimens collected from the bark surface.
<u>FAMILY EURYTOMIDAE</u>						
<u>Eurytoma</u> sp. nr. <u>atripes</u> Gahan		X			A	Collected from the outer bark surface.
" " " <u>cleri</u> Ashm.		X			A	" " " " " "
<u>FAMILY ICHNEUMONIDAE</u>						
<u>Neurateles</u> sp.		X			A	One adult collected on the bark surface.
<u>FAMILY PLATYGASTERIDAE</u>						
Unidentified sp.		X			A	One adult collected from under the bark.

APPENDIX II cont'd.

SPECIES	LOCATION IN SLASH				STAGE	REMARKS
	PW		PR			
	S	T	S	T		
<u>FAMILY PTEROMALIDAE</u>						
<u>Dinotiscus</u> sp. possibly new		X			A	From outer bark surface.
<u>Tomicobia tibialis</u> Ashm.		X			A	One specimen collected from the gallery of <u>Ips pini</u> .
<u>ORDER DIPTERA</u>						
<u>FAMILY BIBIONIDAE</u>						
<u>Bibio</u> sp. nr. <u>slossonae</u> Cock.		X			P	Two adults reared from pupae found in the bark. Larvae are scavengers (Peterson, 1951)
<u>FAMILY CECIDOMYIIDAE</u>						
<u>Joannisia</u> sp.		X			A	One specimen only from the bark surface.
<u>Winnertzia</u> sp.		X			A	One specimen only from the bark surface.
<u>FAMILY CYRTIDAE</u>						
<u>Pterodonita flavipes</u> Gray		X			A	One specimen collected on the bark; a parasite of spiders (Clausen, 1940, King, 1916).
<u>FAMILY DOLICHOPODIDAE</u>						
<u>Medeterus</u> sp.		X		X	A	Adults collected while ovipositing in bark infested with <u>Ips pini</u> and <u>Pityogenes hopkinsi</u> ; predaceous (DeLeon, 1934).

APPENDIX II cont'd.

SPECIES	LOCATION IN SLASH				STAGE	REMARKS
	PW		PR			
	S	T	S	T		
<u>FAMILY EMPIDIDAE</u>						
<u>Drapetis</u> sp.		X			A	One specimen from the bark surface.
<u>FAMILY ORITIDAE</u>						
<u>Pseudotrephitis corticallis</u> (Loew.)		X			A	One specimen from the outer bark; occasionally predaceous (Clausen, 1940)
<u>FAMILY SCATOPSIDAE</u>						
Unidentified larva		X			L	One specimen only from under the bark; larvae breed in decaying animal and vegetable matter (Curran, 1934)
<u>FAMILY SCIARIDAE</u>						
<u>Plastosciara</u> n. sp.		X			A	One adult collected from the outer bark.
<u>Scaptosciara</u> n. sp.		X			A	One adult collected from under the bark.
<u>FAMILY TIPULIDAE</u>						
<u>Gnophomyia tristissima</u> O.S.		X			A,P	Emerged from pupae found under the bark.

Symbols used in Appendix II

S - stump	A - Adult
T - top	E - Egg
Pw - white pine	L - Larva
Pr - red pine	N - Nymph
	P - Pupa

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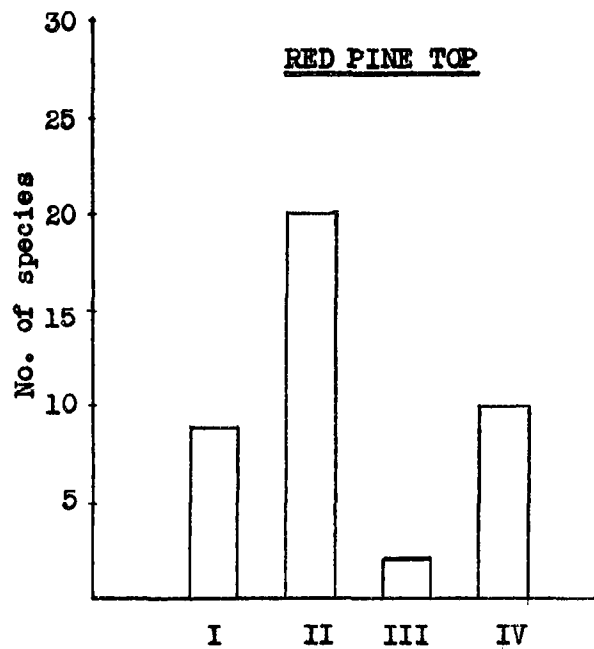
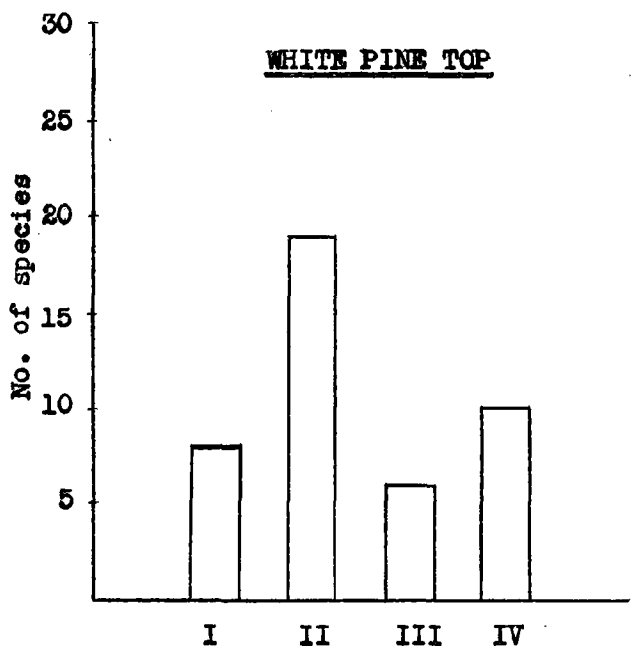
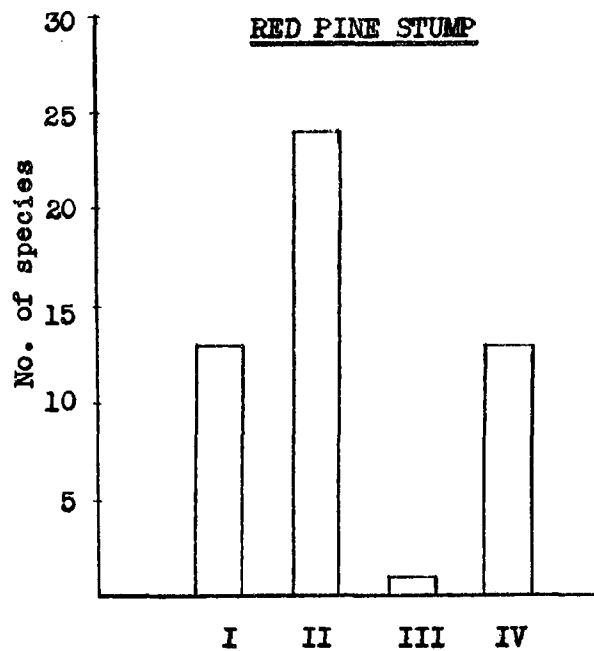
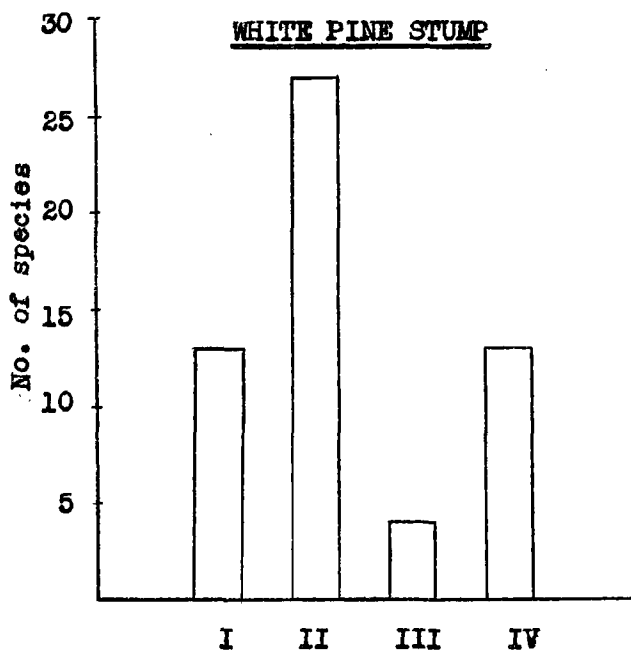
PLATES I TO VII TO PART I

PLATE I

PLATE I

- Upper left - - Number of species in the community in white pine stumps grouped according to feeding habits.
- Upper right - - Number of species in the community in red pine stumps grouped according to feeding habits.
- Lower left - - Number of species in the community in white pine tops grouped according to feeding habits.
- Lower right - - Number of species in the community in red pine tops grouped according to feeding habits.

GROUPING OF SPECIES BY FEEDING HABITS



- I - Phloem and sapwood borers
- II - Fungus, frass and detritus feeders
- III - Parasites
- IV - Predators

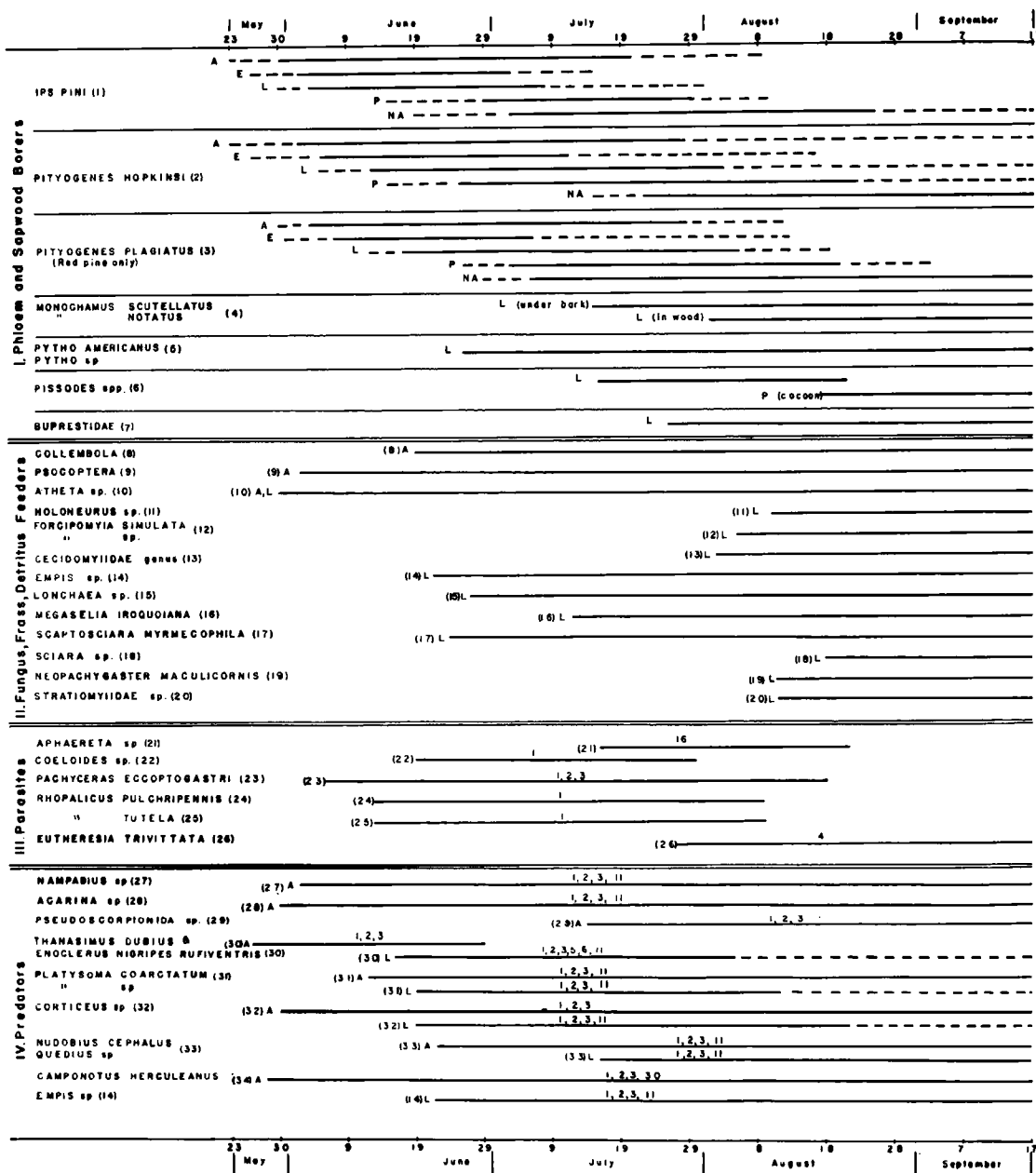
PLATE II

PLATE II

Ecological association of species in the community in red and white pine tops.



**SPECIES ASSOCIATED IN RED AND WHITE PINE TOPS**



**LEGEND**

- A - ADULTS
- E - EGGS
- L - LARVAE
- P - PUPAE
- NA - NEW ADULTS
- 20 - SECOND BROOD

PLATE III

PLATE III

Ecological association of species in the community in red  
and white pine stumps.

SPECIES ASSOCIATED IN RED AND WHITE PINE STUMPS

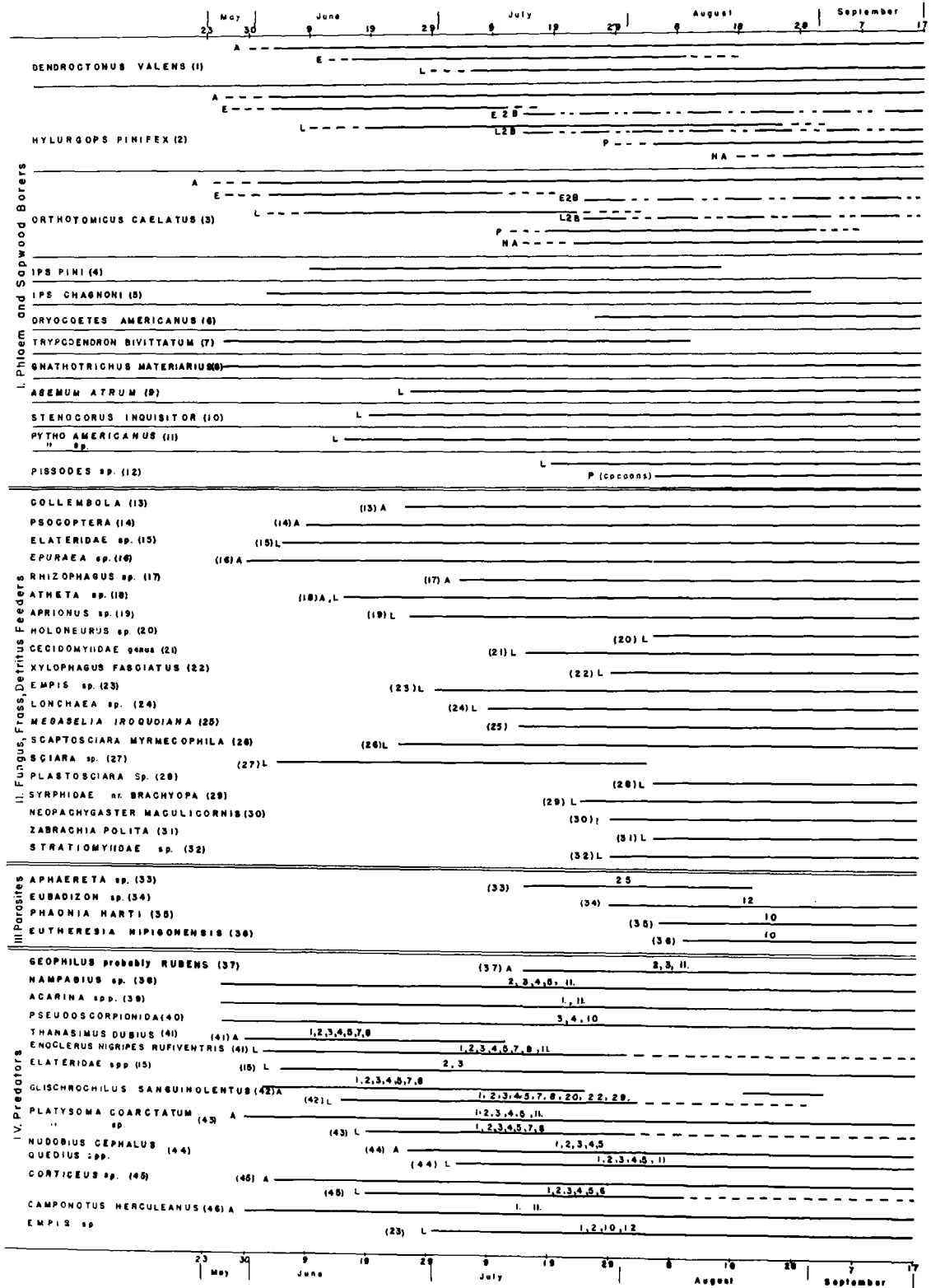


PLATE IV

PLATE IV

Fig. 1 - Egg galleries of Ips pini in white pine tops on May 26.

Fig. 2 - Egg galleries of Ips pini in white pine tops on June 2.



PLATE V



PLATE V

Fig. 3 - Egg galleries of Ips pini in white pine tops on June 12.

Fig. 4 - Galleries of Ips pini in white pine tops on June 30.



PLATE VI

Fig. 5 - Galleries of Pityogenes hopkinsi in white pine tops on  
May 26.

Fig. 6 - Galleries of Pityogenes hopkinsi in white pine tops on  
June 5.

PLATE VI

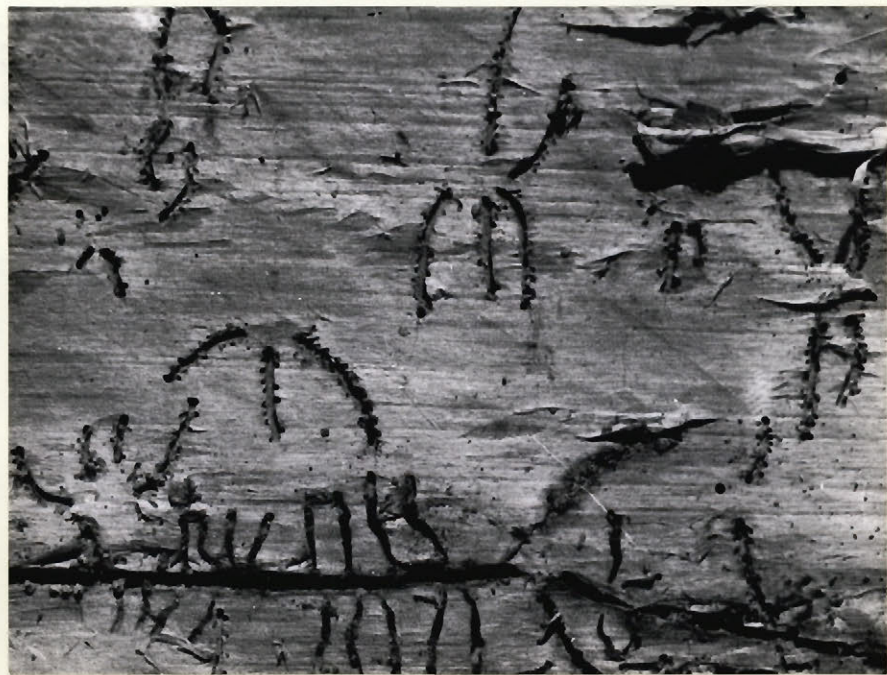


PLATE VII

Fig. 7 - Galleries of Pityogenes hopkinsi in white pine tops on June 19.

Fig. 8 - Galleries of Pityogenes hopkinsi in white pine tops on June 22.

PLATE VII





PART II

EXTERNAL ANATOMY

OF

Ips pini (Say)

(COLEOPTERA: IPIDAE)

## I. INTRODUCTION

As discussed in Part I of this paper, Ips pini (Say) normally cannot be classed as a primary insect pest. However, in view of its relative importance in preparing the way for the establishment of an animal community beneath the bark of red and white pine slash, this beetle has been selected for further study. Furthermore, any addition to the limited number of papers now available concerning the anatomy of bark beetles should be considered of importance.

A review of the literature reveals the need for more attention being directed toward this important group of insects, particularly in the field of anatomy. Hopkins (1909) published, as part of a series entitled, "Contributions toward a monograph of the Scolytid beetles", a paper on the genus Dendroctonus. This included the anatomy of Dendroctonus valens Lec. A second part of this series was published in 1915 by the same author and dealt with a preliminary classification of the superfamily Scolytoidea. Included in this paper were comparisons of those structures found to be of value in taxonomy. The morphology of the genus Gnathotrichus Eichh. was discussed by Schedl (1931). In 1936, Kaston published an account of the morphology of Hylurgopinus rufipes (Eichh.). Finally, Fuchs (1911) brought out a paper on the morphology of the genera Ips DeGeer and Pityogenes Bedel. Unfortunately this last paper does not cover as wide a scope as the title indicates. The comparative anatomy of the male genitalia and the abdomen of the two genera comprise the greater part of the paper. The anatomy of I. pini has never been described to my knowledge. An account of the habits and stages of the beetle was published by Clemens (1916), but no detailed anatomical

drawings were included.

## II. SYSTEMATIC POSITION

The eastern pine engraver, Ips pini (Say), belongs to the order Coleoptera, suborder Rhynchophora, family Ipsidae, subfamily Ipinæ (Swaine, 1909). The genus was formerly described as Bostrichus in 1777 and as Tomicus in 1807. The generic name Ips had been applied to a group of beetles in the family Nitidulidae. However, the synonymy as worked out by Swaine (1909) gives priority to the name Ips erected in 1775 by DeGeer. The original description of I. pini was made by Say (1826) under the genus Bostrichus according to Swaine (1909).

## III. GENERAL DESCRIPTION OF ADULT

Fully mature adults are dark brown to black in colour, with a light covering of hairs over the body. Normally the head is entirely or almost concealed from above by the pronotum. The antennae are characterized by sutures on the anterior faces only of the clubs. The anterior of the pronotum is roughened by several concentric rows of asperities. The punctures on the elytra are arranged in definite striae.

Like all Ips species, the declivity is sulcate and continued into an apical shelf or plate. The armature of the declivity consists of four teeth on each side of the sulcus. In the females, the second and third teeth are acute and joined basally. The third tooth in the male is longer, more rounded, and frequently bent downward. This is a fairly reliable secondary sexual characteristic.

There is no significant difference between the lengths of the males and females. Based on measurements of 100 specimens of each sex, the length of the body from the front of the head to the end of the apical plate was found to be  $3.63 \pm .23$  mm. for males and  $3.64 \pm .20$  mm. for females.

#### IV. DETAILED DESCRIPTION OF THE ADULT

##### A. THE HEAD

In its normal position, the head is retracted into the prothorax leaving only a small area exposed (Figs. 1, 2 and 3). The head capsule is globular in form, the widest point being just anterior to the coronal suture (Fig. 7). The caudal part of the head is attenuated into a V-shaped wedge. Conforming to the characteristics of most rhynchophorous heads, many of the head regions are completely fused and devoid of limiting lines or sutures. The structure of the head capsule shown in figures 7, 8, 9, 10 and 11 is described in detail in the following sections.

##### 1. LABRUM, CLYPEUS

Neither the labrum nor the clypeus are represented as distinct sclerites. Elements of one or of both may be included in the epistomal and frontal areas.

##### 2. EPISTOMA

Bordering the dorsal part of the oral foramen, there is a slightly raised, narrow region which may be designated as the epistoma

(Fig. 7). The lateral margins are produced into protuberances over the articulation of each antennal scrobe. The ventral surface of the epistoma is inflected inwards. It is weakly divided into a median and two lateral sections (Figs. 9 and 10). The epistoma strengthens the dorsal rim of the oral foramen providing support for the mandibles. The dorsal articulatory processes of the mandibles are borne on the lateral sections. In certain genera, notably Dendroctonus, the epistoma is a prominently developed process. Hopkins (1909) uses this feature to separate the genus Dendroctonus from other genera of the subfamily Hylesininae.

### 3. FRONT

The frons is not marked off by sutures. Schedl (1931) considers that two slightly raised lines originating at the upper margins of the antennal grooves, are remnants of the frontal sutures in the heads of Gnathotrichus retusus Lec. and G. materiarius Fitch. With this evidence, he designates an area of the front of the head in these two species as the frons. These sutures are not present in the head of I. pini. The frontal area of the head dorsal to the epistoma and between the eyes bears a number of small asperities from which setae arise. There is a transverse row of larger tubercles immediately dorsal to the epistoma.

### 4. PARIETALS

In generalized insects, the two parietals are those regions of the head bounded anteriorly by the frontal and frontogenal sutures, and posteriorly by the occipital suture. That part of the parietal

dorsal to the compound eye is the vertex while the ventral portions beneath the eyes are the genae. With the absence of the head sutures, the parietal region in I. pini, however, can only be indicated in a general way. A portion of the coronal suture separating the two parietals is visible on the top of the head capsule (Fig. 7).

#### 5. GENA

The dorsal limit of the gena may be considered as being in the area level with the upper edge of the eye. The gena extends ventrally to the median gular suture (Figs. 7 to 11).

#### 6. OCCIPITAL REGION

Because of the absence of the occipital suture, the occipital region of the head is not clearly defined. The caudal area of the head is drawn out into a V-shaped structure with the apex of the "V" pointing posteriorly (Figs. 7, 8 and 11). A suture, which I have called the post-occipital suture, marks the sharp edges of this region of the head. Beginning at the caudal extremity of the head on the dorsal side, the suture passes anteriorly along the edges of the "V" until the posterior region of the head in the same plane as the occipital foramen is reached. The suture then begins to descend, curving mesally until it reaches a point at the dorso-lateral angle of the foramen. From this point it follows the edge of the foramen until the two sides of the post-occipital suture converge in the median gular suture.

In figure 9, a suture "a" is shown crossing the endoskeleton of the head anterior to the ventral edge of the occipital foramen. I interpret this suture as marking the original limit of the edge of the

occipital foramen where it is inflected into the head. In the majority of specimens examined, the definitive posterior of the head appeared to be continued ventrally in this suture.

The occipital foramen is completely enclosed by the sclerotized cranium. The edges of the foramen are inflected into the head capsule, joining with the gular apodemes to increase the rigidity of the head.

#### 7. GULA

The gular area is not represented in the head of I. pini. A single median gular suture separates the genae (Figs. 8 and 10). Schedl (1931) describes two gular sutures very close together in the genus Gnathotrichus. This condition, which is very rare in Rhynchophora, provides a definite median gular area in that genus. Hopkins (1909) located a pregular sclerite in the genus Dendroctonus. Kaston (1936) similarly described a pregular area in the head of Hylurgopinus rufipes. This sclerite is not present in I. pini.

#### 8. HYPOSTOMA

The hypostomal sutures diverge from the median gular suture and extend to a point between the eye and the articulation of the antenna (Figs. 8 and 10). An internal apodeme corresponds to each hypostomal suture. The areas anterior to these sutures are the hypostomal areas which bear the ventral articulations of the mandibles as well as the maxillary articulations. Each hypostoma extends mesally to form a hypostomal bridge between the submentum and the gular suture (Fig. 10). Anterior to the hypostomal suture, a line

extends from the lateral angle of the ventral articulation of the mandible, continuing across the hypostomal bridge to a corresponding point on the other side (Fig. 10). Hopkins (1909) in the genus Dendroctonus, calls this line the hypostomal suture, and the posterior suture, the pre-genal suture. This anterior line in I. pini appears to be only the crease where the hypostoma is inflected inward.

#### 9. TENTORIUM

The endoskeleton of the head is known as the tentorium. In generalized structure, the tentorial body consists of anterior and posterior arms arising as invaginations of the cranial walls. In certain insects, the tentorium also includes a pair of dorsal arms arising from the anterior arms.

Stickney (1923) was able to observe a pretentorium in Dendroctonus, but not in any other members of the Rhynchophora. He believed the pretentorium was rudimentary in Scolytus, but because of the difficulty of making a dissection showing the pretentorium intact, the same could not be said of the other genera. The presence of frayed ends suggested to him that all of the pretentorium had not been seen. A similar difficulty was found in dissecting the head of I. pini. The anterior tentorial pits are not visible externally. Internally, the rudiments of the anterior tentorial arms are visible in the region of the dorsal articulation of the mandibles (Figs. 9 and 10). The posterior tentorial pits presumably would be located in the area where the hypostomal suture and gular suture meet. However, there is not sufficient evidence to indicate the location definitely. Internally, the posterior arms could not be identified.



The most prominent structures inside the head capsule are two broad sclerotized plates which are elevated above the ventral cranial region (Fig. 9). Medially, these plates appear to arise from the ridge formed by the invagination of the gular region. Posteriorly, they are fused with the ventral rim of the occipital foramen. The line of fusion is marked by the transverse suture referred to in the description of the post-occipital region of the head. Anteriorly, the plates are slightly constricted and unite with the strong apodemes bracing the submentum. Posterior to the submentum, a narrow sclerotized bridge unites the two lateral plates (Fig. 9).

The structures described above may form a portion of the body of the tentorium, or they may be secondary invaginations of the head for attachment of the strong muscles of the gnathal appendages. A more detailed study of the heads of many specimens in different genera of Scolytidae is required to determine the exact structure of the tentorium.

## 10. APPENDAGES OF THE HEAD

### a. Antennae.

The antenna consists of a long basal segment, the scape, a funicle composed of five segments, and a club (Fig. 12).

The scape is slender, slightly curving to the base where there is a sharp bend or elbow, the scrobe. The scrobe articulates in a socket or fossa at the lateral area of the head between the eye and the base of the mandible. The lateral area of the epistoma forms a slight protuberance over the antennal scrobe. The scape is almost

equal in length to the funicle and club combined.

The funicle is five segmented. The basal segment is longer than any of the remaining four segments.

The club is oval in outline. In a lateral view (Fig. 14), it is seen to be narrower at the distal end than at the base. The posterior face is entire (Fig. 13). The anterior face is divided by what appear to be two sinuate sutures (Fig. 12). However, under high magnification, what appear to be sutures are not sutures in the strict sense of the word. The anterior face bears three sclerotized or corneous areas. The first is basal and has a sinuate upper edge. A row of setae is borne along this upper edge. There is also a transverse row of setae near the base. The area between the basal and second sclerotized regions has a pitted surface. It is this narrow region which appears to be a suture under lower magnification. The median sclerotized area is also sinuate and bears a row of setae along its upper edge. The distal point of this region reaches about the midpoint of the length of the club. From this point to the tip of the club, the surface is pitted, with the exception of a small curved sclerotized region in the centre. This final sclerotized area does not approach the sides nor is it as definite in outline as the basal and median areas.

#### b. Mouth Parts.

(1) Epipharynx. There is no true epipharynx in I. pini as defined by Snodgrass (1935), who states that it is a median lobe sometimes present on the posterior surface of the labrum or clypeus.

Packard (1898) states that the term epipharynx was first used by Savigny in 1876. He applied it to the membranous lobe located on the dorsal surface of the preoral cavity just anterior to the true mouth opening in the honey-bee. Réaumur (1740) observed and described a structure in the honey-bee and bumble-bee which he called "la langue". His descriptive remarks were that it closed the opening into the oesophagus and was applied against the palate. According to Packard (1898), this structure represented the epipharynx and had that name bestowed upon it by Savigny in 1876. In I. pini, a membranous structure (Fig. 10), attached ventrally to the median area of the inflected epistoma, continues dorsally into the lining of the oesophagus. This membranous structure is the epipharyngeal wall and bears a number of setae on the inner surface.

(ii) Hypopharynx. The hypopharynx is a partially membranous structure suspended in the preoral cavity by tendons from a pair of hypopharyngeal bracons (Fig. 10). These are sclerotized processes arising from the inner surfaces of the hypostoma near the ventral articulation of the mandible (Fig. 9). The hypopharynx has a sclerotized ring on the anterior surface and is partially sclerotized on the dorsal surface.

(iii) Labium. The submentum of the labium is a bifid process fused with the hypostoma (Fig. 10). Internally, it is supported by two braces rising from the sides of the hypostomal bridge (Fig. 9). The remainder of the labium is a compactly fused structure. The mentum occupies three quarters of the total length of the labium (Figs. 17, 18, and 19). The base of the mentum articulates with the

submentum and has a basal foramen.

The glossae and paraglossae are absent as distinct elements. The dorsal anterior part of the labium, the ligula, is elliptical in shape and bears a large number of stiff setae (Figs. 17 and 18).

The palpi are three-segmented. The first and second segments are equal in length. The distal joint is smaller than each of the other two. The palpifers supporting the palpi are not marked off as distinct areas of the labium.

(iv) Maxillae. Each maxilla consists of a distinct, basal cardo, a median area composed of the fused stipes, palpifer, galea and lacinia, and a distinct palpus (Figs. 15 and 16).

The cardo is a stout basal segment broadly hinged to the remainder of the maxilla. The basal portion of the cardo is produced into two lateral angles for the attachment of muscles. It articulates with the maxillary process borne on the hypostoma (Fig. 9).

The main body of the maxilla is broader than long consisting of stipes, palpifer, galea and lacinia. The area articulating with the cardo may be considered to be a part of the stipes. The palpifer is fused with the stipes and bears the three-segmented palpus. The galea and lacinia are fused to each other and to the stipital area of the maxilla. The inner edge of the apical lobe of the lacinia and galea adjacent to the palpus, is continued downward for a short distance by a suture visible on the ventral surface only (Fig. 15). The edge of the lobe adjacent to the palpus is more

heavily sclerotized than the remainder of the maxilla. Hopkins (1909) considers that this sclerotized band in the genus Dendroctonus is the galea. Schedl (1931) is of the opinion that a shallow emargination in the tip of the lobe indicates the dividing line between the galea and lacinia in the genus Gnathotrichus. Kaston (1936) does not separate a distinct galea but indicates an area which he calls the subgalea in Hylurgopinus rufipes. It is apparent that the maxilla has become too fused to indicate distinct elements clearly. A number of these diverging opinions might be clarified through a comparative study of the maxillae of many genera.

The lacinia is armed on the ventral, inner edge with a row of very stout teeth (Fig. 15). There is an opening on the dorsal surface near the base of the stipital area for the passage of muscles. The ventral surface of the main body of the maxilla bears a large number of long setae (Fig. 15).

The three segments of the palpi are connected by membrane which allows slight movements. The palpi are relatively short, being about one third the total length of the maxillae.

(v) Mandibles. The mandibles are stout, heavily sclerotized structures well suited to their task of cutting through bark and wood. The shape and structure of the mandibles can be seen in figures 20, 21, 22 and 23. The cutting edge is wedge shaped with several distal teeth and a basal molar area. The outer face of the mandible bears three setae. Two of these are grouped and are called

the dorsal setae. The remaining one is known as the lateral bristle (Figs. 21 and 23).

The dorsal articulation with the cranium is a complex mechanism of condyles and fossae as shown in figures 21 and 23. These structures articulate with corresponding fossae and condyles supported by the epistomal area (Fig. 10). The ventral point of articulation is simply constructed and articulates with the ventral articulatory point on the hypostoma (Figs. 9 and 10). Attached to each mandible are strong sets of adductor and abductor muscles. The muscles are attached to large discs connected to the mandible by tendons.

## B. THORAX

The prothorax, mesothorax and metathorax, are all represented in the thorax of I. pini. The prothoracic segment is distinct from the remainder of the thorax. The mesothorax and metathorax are united to form the pterothorax. The union is not as rigid as in some beetles, being partially membranous between the mesonotum and metanotum. The pleural regions are also partially united by membranous conjunctivae. The mesosternum and metasternum, however, are completely fused around the coxal cavities of the mesothoracic legs.

### 1. PROTHORAX

The prothorax is a hollow cylinder formed by the complete fusion of dorsal, pleural and ventral areas. When the beetle is at rest, the prothorax almost entirely conceals the head and the anterior

of the mesotergum (Fig. 3). It is slightly more than one third the total length of the insect. Viewed from above, the prothorax is broadly rounded anteriorly. The sides are sub-parallel, widening to the posterior. The posterior edge is broadly rounded. From a lateral aspect, the front of the pronotum is sharply oblique while the posterior area is only slightly oblique (Fig. 1).

From the anterior margin of the prothorax to a point on the summit midway on the overall length and laterally to a point over the coxal cavities, the surface is roughened by a number of asperities arranged in concentric rows. Each asperity is more or less triangular in shape, the sharp, raised angle being pointed posteriorly. As the beetle cuts the entrance hole and galleries, the asperities serve as a brace holding the body in position against the thrust of the mandibles. The remainder of the dorsal and pleural areas have numerous small punctures over the surface. The anterior of the prothorax consists of a large circular opening, the lateral and ventral edges of which are reflexed into the inside. The ventral entothoracic fold reaches a point over the anterior walls of the coxal cavities. The membrane connecting the head to the prothorax is attached along this inner rim. The edge of the anterior foramen is lined with a fringe of short hairs. The edges of the posterior foramen, which is smaller than the anterior opening, are folded in on all sides. The ventral edge is folded in to a point over the posterior walls of the coxal cavities (Fig. 44). The intersegmental membrane is attached to the inner edge of the infolded rim. The mesothoracic pair of spiracles are situated in small sclerites in the inter-segmental membrane. When the prothorax is in its normal position, the spiracles are covered.

The prothoracic tergum is not marked by any lines or sutures. The pleural areas are similarly devoid of distinct sclerites or sutures with one exception. On the outer rim of the coxal cavity there is a minute, slightly projecting piece which is more heavily sclerotized than the remainder of the pleural area. There is an indication of a small suture starting at this point on the coxal rim and proceeding dorsally and anteriorly for a short distance (Fig. 43). Internally, a small fold is visible lying against the inner pleural wall. Basally it is connected to the outer rim of the coxal cavity and is fused to the pleural wall for a short distance as it proceeds in a dorsal direction. It narrows to a sharp triangular point which leaves the pleural wall and projects in over the coxal cavity (Fig. 44). This point would appear to be the pleural apophysis and accordingly the remainder of the structure should contain anteriorly the episternum and posteriorly, the epimeron. There is no evidence of an internal pleural ridge. The short outer suture described previously may be the vestiges of the pleural suture.

The greater part of the sternum has been depressed to form the walls of the coxal cavities. The anterior sternal area is formed into a short median intercoxal process (Fig. 43). The coxae are contiguous since the intercoxal process does not extend completely between them. Internally, a sternal apophysis arises at the inner edge of each coxal cavity (Figs. 44 and 45). A sternacostal ridge extends between the two sternal apophyses (Fig. 45). Outwardly, the position of this ridge is marked by a transverse suture, the sternacostal suture, dividing the sternal area within the coxal depression (Fig. 43).



## 2. MESOTHORAX

### a. Notum

The mesonotum is partially concealed by the posterior margin of the pronotum and by the bases of the elytra (Fig. 3). The correct interpretation of the anatomical structure of the mesonotum is complicated by the modifications in form which have occurred in this area. The anterior, posterior and lateral margins are depressed and folded. From the sutures still visible two or more interpretations of the structure might be taken. The explanation given here is my opinion of the position and form the various components of the mesonotum have taken. A comparative study of examples from different genera of Scolytidae and between orders would be of great interest. The results of such a study might invalidate some of the conclusions set forth here.

The anterior half of the notum is broadly rectangular. The posterior half is triangular, the apex of the triangle being the raised lobe of the scutellum (Fig. 46). The anterior portion is folded ventrally and proceeds posteriorly so that it now lies below the definitive anterior of the notum (Fig. 47). This ventral fold is supported by a median carina extending from the anterior margin to the anterior point of the scutellum (Fig. 47A). The position of the internal carina corresponds to an external median suture dividing the scutum longitudinally (Fig. 46).

A line or suture crosses the ventral fold (Fig. 47). The intersegmental membrane joining the pronotum and mesonotum is attached along this line. It is possible, therefore, that it does not represent

a true suture but indicates only the line of adhesion of the membrane. If it is considered a suture, it may be the transverse suture separating the prescutum from the scutum. Snodgrass (1935) has stated that a prescutal area behind the antecostal suture is well developed in the mesothorax of Coleoptera. Appended to the posterior edge of the ventral fold are two phragmata. Between these phragmata and the transverse suture there is no indication of an antecostal suture. An alternative interpretation of this area is thus presented. The transverse suture may be the antecostal suture, the area posterior to it bearing the phragmata becoming the expanded acrotergite. The prescutal area would then be inseparable from the scutum.

On the dorsal surface, the median longitudinal suture appears to divide posteriorly. A curving suture proceeds laterally to where the edge of the notum is folded ventrally (Fig. 46). This is the scuto-scutellar suture separating the scutum and scutellum. In mature adults, the path of the suture is obscured by pigmentation. However, in specimens in which only partial pigmentation has occurred, the suture is quite evident. The sculpture of the scutum also differs from that of the scutellum and this can be used to orientate these two regions. The surface of the scutum is punctured while that beyond the scuto-scutellar suture is smooth.

The lateral margins of the scutum are curved ventrally. The marginal depression is continued posteriorly along an oblique line proceeding medially and continuing into the scutellar region (Fig. 46). The folds in the posterior region of the scutum and scutellum which have apparently taken place, at least in part, to accommodate the closing of the elytra, obscure the details of this region. However, several

valid landmarks are present. The anterior lateral angle of the scutum is produced into a process against which the base of the elytron articulates. This is the anterior notal wing process. A posterior notal wing process is also well developed on the margin of the scutum. The third wing axillary articulates with this process (Fig. 46). Beginning at the anterior lateral margin of the scutum, a suture is visible along the depressed sides (Fig. 46). The suture makes a slight curve following the line of the posterior notal wing process before proceeding mesally toward the median elevated part of the scutellum. The suture appears to separate the lateral depressed areas of the scutellum from the scutum. However, the exact course of this suture is difficult to follow owing to the folding of the posterior part of the scutum and the scutellum. This suture may be the reversed notal suture described by Snodgrass (1935) as occurring in the thorax of certain insects.

The posterior lateral angles of the scutum are prolonged into tapering arms or processes (Figs. 46 and 47). The ends of these processes unite with the anterior arm of the prescutum of the metanotum and fold back into a shallow groove in the prescutum. These two points form the only sclerotized union between the mesonotum and the metanotum. The remainder of the union is membranous.

The scutellum has a median elevated portion and two lateral depressed regions. The lateral angles of the scutellum are continued into the axillary cords of the wing membranes (Fig. 46). The posterior edge of the scutellum is folded ventrally and anteriorly, forming what Snodgrass (1935) describes as a posterior reduplication. Beneath the scutellum there is a triangular fold which is partially supported on

the median carina (Figs. 47 and 47A). This may be part of the scutellum or the scutum or may contain elements of both.

Hopkins (1909) with the genus Dendroctonus, Schedl (1931) with the genus Gnathotrichus and Kaston (1936) with Hylurgopinus rufipes, have interpreted the structure of the mesonotum differently. The large dorsal plate of the notum which I consider the scutum is termed the prescutum in their papers. The scutum is represented by the depressed areas below the prescutum anterior to the scutellum and by two lateral lobes anteriorly fused with the prescutum. In I. pini, the presence of a definite scuto-scutellar suture would seem to prove that the greater part of the dorsal surface is occupied by the scutum and not by the prescutum. The interpretation of the remainder of the mesonotum requires clarification by comparative studies of other species.

b. Pleuron.

The mesopleuron has been greatly strengthened by the infolding of the anterior and posterior edges. The episternum is a prominent sclerite comprising nearly the entire visible portion of the pleuron (Figs. 1 and 58). The anterior edge is folded in to form a strong rim. A narrow sclerite, the preepisternum (Fig. 59) is cut off this edge. Only a very little area of this sclerite is exposed beyond the episternum (Fig. 58). The episternum is fused ventrally with the mesosternum, the line of fusion being marked externally by a suture (Figs. 1 and 2). The pleural suture near the posterior of the pleuron separates the episternum and epimeron (Fig. 58). The suture is continued ventrally into the pleural coxal process but disappears externally as it approaches the dorsal edge of the pleuron (Fig. 58). This is due to the infolding of the pleuron. In a posterior aspect, the suture can be traced into the pleural wing process. A strong internal

pleural ridge extends from the pleural coxal process to the pleural wing process (Fig. 59). The pleural apophysis projects inward dorsal to the pleural coxal process. The epimeron is fused posteriorly and ventrally with the metepisternum and metasternum. The wing process is distally notched into two projections (Figs. 58 and 59). Hopkins (1909) in the study of the genus Dendroctonus, named the anterior of these the clavicle process and the posterior one, the coracoidal condyle.

A small triangular sclerite is situated in the membrane anterior to the preepisternum (Fig. 58). It is attached by tendon to the base of the elytron and assists in wing movements. According to Snodgrass (1909) this sclerite is the preparapterum. Since then Snodgrass (1935) refers to this sclerite as the basalare.

c. Sternum.

The mesosternum consists of a simple plate (Fig. 49) the anterior edge of which is reflexed inward for added rigidity (Fig. 51). The posterior lateral angles are produced into excoxal pieces laterad of the coxal cavities and meeting the anteriorly projecting angles of the metasternum. The median sternellar area unites with the anteriorly produced median area of the metasternum by a type of ball and socket joint. An external sulcus separates the two sterna. The walls of the coxal cavities are completely fused between the mesosternum and metasternum.

The sternal apophyses arise from invaginations in the suture joining the mesosternum and the episternum. Apophyseal pits mark the positions of the invaginations (Fig. 2). Internally, the apophyses

are greatly developed into leaflike expansions approaching the pleural apophyses (Fig. 51).

### 3. METATHORAX

#### a. Notum

The metanotum is completely concealed by the elytra in a closed position (Fig. 3). Details of the structure from an inner and outer aspect are shown in figures 53 to 57. A prescutum, scutum, scutellum and postnotum can be distinguished.

The prescutum consists of a narrow transverse median bar (Fig. 54) with a deeply inflexed margin (Fig. 53). Well developed phragmata are appended to the ventral edge. The lateral areas of the prescutum are expanded and fused to the anteriorly projecting lobes of the scutum. The extreme lateral areas have been reflexed beneath the scutal lobes (Fig. 56). The anterior notal wing process is a development from the prescutum (Figs. 53, 54 and 56). The prescutum is separated medially from the scutum by membrane. At the two points of fusion of the scutum and prescutum, the latter is developed into two prominent anterior arms (Figs. 53 and 54). Each arm projects in an antero-ventral direction with the extreme tip fused with the lateral arm of the scutum of the mesonotum. The arm or process of the mesonotum from the point of union rests in a shallow groove in the antero-dorsal face of the prescutal process. It is lifted out of this groove during movements of the thoracic segments.

Laterad of the prescutal arm are two points of muscular attachment. One is referred to as the anterior disc (Figs. 53, 54 and 56). The other is a large circular disc from which a muscular tendon passes to the pleural wing process of the pleuron (Figs. 54 and 56).

The scutum and scutellum are combined into a broad sclerite. The integument is sclerotized although retaining a certain flexibility to assist in wing movements.

The scutum is divided into two large lateral areas by the scutellum (Fig. 54), each area being divided again into two regions by an outer groove. Internally, an oblique ridge marks off this area. Hopkins (1909) considers that the anterior areas are part of the prescutum in Dendroctonus valens. Kaston (1936) agrees with Hopkins and calls the same area in Hylurgopinus rufipes the prescutal lobes. Schedl (1931) in his study of the morphology of the genus Gnathotrichus, opposes this opinion. He considers that this area is more likely to be part of the scutum than of the prescutum. Similarly, in I. pini, there is no sound evidence for separating the anterior regions from the scutum. The infolded ventral area alone appears to belong to the prescutum. On the lateral margin of the scutum, a topographical area, the lateral emargination, is weakly defined (Fig. 54). The posterior notal wing process is borne on the lateral emargination. The anterior margin of the scutum along the line of union of the membranous area of the prescutum is depressed. Internally, a strong transverse ridge is developed along this line (Fig. 56).

The scutellum forms a median depression which divides the scutum into halves. The trough of the scutellar groove extends beyond the anterior margin of the scutum. The inner edges of the elytra fit into the scutellar groove forming a part of the locking mechanism of the anterior wings. The scutellar sutures (Fig. 54) curve outward and approach the posterior limit of the notum midway to the lateral margin.

Strongly developed apodemes (Fig. 56) mark the course of the scuto-scutellar suture on the internal surface of the notum. The posterior limits of the scutellum are not distinguished from the scutum. As a result of this, the axillary cords appear to arise from the scutum instead of the scutellum.

The postnotum is joined to the scutum and scutellum by a membranous conjunctiva except for two points near the posterior limits of the scutellar apodemes. At these two points, direct fusion between sclerotized plates has occurred (Fig. 54). The median area of the postnotum is a narrow transverse bar bearing ventrally the postphragmata (Fig. 55). The lateral areas are expanded into prominent arms which extend ventrally into the body cavity approaching the metendosternite. Strong muscles originating on the scutum are inserted on the postnotal arms. A small triangular process on the outer margin of the postnotum (Figs. 54 and 55) forms a partial ring around the first abdominal spiracle.

b. Pleuron.

The metapleuron is divided by a horizontal pleural suture into a dorsal epimeral area and a ventral episternum (Fig. 48). The episternum has been modified to effect a close union with the sternum and also to assist in locking the elytra closed. As described in the section on the sternum, an outer process at the anterior ventral angle and an inner process at the ventral angle, assist in uniting the sternum and episternum. The episternum also bears a horizontal groove and ridge on its outer surface (Fig. 48). At the anterior end, the ridge is produced into a rounded, dorsally projecting process which,



together with the ridge, fit into corresponding concavities along the outer margin of the elytron. The posterior dorsal angle of the epimeron also fits into a shallow concavity of the anterior lateral margin of the abdominal sternum thereby locking the two together.

The pleural suture is evident internally as a strong ridge continuing into a distinct wing process at the dorsal anterior angle (Fig. 48). Hopkins (1909) calls this the coracoid process. Anterior to the coracoid process, there is a similar arm which Hopkins designates as a clavicle process. A large muscle disc is supported on the inner side of the anterior process. Snodgrass (1909) describes how, in Dendroctonus valens, the base of the preparapterum bearing the muscle disc has become fused with the front of the episternum to produce the effect of a double wing process. It would appear that a similar condition exists in the metapleuron of I. pini.

The metathoracic spiracle is located in the membranous conjunctiva between the mesopleuron and metapleuron.

#### c. Sternum

The metasternum is a broad rectangular plate. The median anterior margin is projected forward where it unites with the sternellar area of the mesosternum (Fig. 49). The anterior margins are concave and are completely fused with the posterior margins of the mesosternum to form the walls of the mesocoxal cavities. The sternum is divided longitudinally by a median line which is quite definite at the posterior but which becomes less evident as it proceeds cephalad (Fig. 49).

The union of the sternum with the episternum is effected by a special method. The lateral margin of the sternum is folded in to form a narrow groove, the outer rim of which is serrated (Fig. 51). The ventral margin of the episternum is acute and has a sharp, hooked process at the anterior ventral angle and a small process at the internal, postero-ventral angle (Fig. 48). The sternum and episternum fit together with the union being made more secure by the two processes described.

The posterior margin of the sternum is inflexed near the midline forming a fold on the inner surface (Fig. 51). The sternum shows a remarkable development of the sternal apophyses. These have been carried inward by an invagination of the sternellar area to form the metendosternite (Figs. 50 and 52). This consists of a "Y" shaped structure, hinged to the sternellar area by an interlocking mechanism. Two furcal arms are carried inward on the stem of the "Y". A comparative study of the metendosternite in Coleoptera has been made by Crowson (1938, 1942). The metendosternite of I. pini is similar to that of Ips typographus (L) described by Crowson. The endosternite serves for the attachment of a number of muscles. The exterior surface of the sternellar area receives the projecting intercoxal piece of the abdomen (Fig. 2).

#### 4. APPENDAGES OF THE THORAX

##### a. Legs.

The three pairs of legs show slight structural differences which will be discussed. The details of the form and structure are shown in figures 24 to 42.

(1) Coxa. The coxa of the prothoracic leg is sub-globose, being flattened on the ventral side. The two coxae are contiguous and occupy nearly the entire ventral area of the prothorax. The basicostal suture cuts off a dorsal rim, the basicoxite. On the ventral surface near the inner margin there is a conical impression or fossa in which the trochanter articulates. The walls of the fossa slope down from an outer rim to an inner rim located at approximately half the depth of the fossa (Fig. 30). In the side of the coxa opposite the mouth of the fossa, there is a small opening in which the distal end of the trochanter articulates (Fig. 31). This appears to be covered by membrane only.

The mesothoracic coxae are essentially similar in structure to those of the prothorax (Figs. 34 and 35). The coxae are separated by a narrow sternal piece formed from the mesosternum and metasternum. The basicoxite is produced into a rounded condylar surface (Fig. 35) which articulates with the inner surfaces of the sternum and pleuron. Anterior to the basicostal suture a shallow groove provides a guide for the antero-posterior rotary movement of the coxa.

The metathoracic coxae are transversely elongated, situated in deep coxal cavities. The coxae are separated by an intercoxal process formed by the fusion of two or more abdominal sterna (Fig. 2). The axis of movement is transverse, allowing for an antero-posterior rotation. The inner angle of the coxa (Figs. 32 and 33) articulates with the metasternum near the median suture. The lateral ventral angle of the metepisternum fits into a shallow depression in the outer angle of the coxa (Figs. 32 and 33) forming the pleural articulation

with the coxa. The inner ventral area of the coxa is invaginated forming a cone-shaped depression (Fig. 32). The inner rim of the invagination is expanded into a flange which articulates with a groove on the trochanter. The basicostal suture is discernible on the dorsal side of the coxa beginning at the pleural articulation. It follows the inflected rim of the coxa bending down to meet the circular depression with which the knob on the trochanter articulates. From this point, it can be traced dorsally to the point of articulation of the coxa with the metasternum (Fig. 33). The suture marks the inflected rim of the coxa along the ventral surface. The narrow sclerite set off by the basicostal suture is the basicoxite (Fig. 33) which is inflected to form a rim around the anterior face of the coxa. A transverse impression is apparent as an external line on the ventral surface of the coxa (Fig. 32). A large internal ridge (Fig. 33) on which muscles are inserted, corresponds to the external impression.

(ii) Trochanter. The trochanters on the prothoracic, mesothoracic and metathoracic legs are similar in construction. The detailed structure of the prothoracic trochanter alone has been shown in figures 40, 41 and 42.

The trochanter is closely attached to the femur. On the ventral side, a deep trochantero-femoral groove (Figs. 40 and 41) separates the femur and trochanter. On the dorsal side, the distinction between these two elements of the leg is by a suture only (Fig. 42). The base of the trochanter is an enlarged ring which rests against the outer rim of the fossa in the coxa. The condylar part of the trochanter is cone shaped with a small apical knob. Dorsal to the basal ring-like structure, the surface of the condyle is

molded into a fossa and ridge. These articulate with the flange on the inner ring of the coxal fossa permitting a swivel motion to the leg. The small apical knob fits into the circular opening on the inner wall of the coxa, opposite the fossa.

(iii) Femur. The femur in all three pairs of legs has the same general structure (Figs. 24 to 29). It is the largest segment of the leg. The prothoracic femur is compressed in an antero-posterior direction, while the compression in the mesothoracic and metathoracic legs is dorso-ventral. The distal end of each femur bears two inner, circular fossae into which the condyles of the tibia fit to make the hinging mechanism. The lateral surfaces of the femur are projected to form a rim on the outside of the condylar mechanism. These rims, together with a groove in the ventral surface of the femur close to the tibial joint, permit the tibia to be flexed closely against the femur.

(iv) Tibia. The tibia is slightly shorter in length than the femur. It is narrow at the base and widened distally. The basal portion is slightly curved to permit the tibia to be closed against the femur. The outer margin of the tibia is serrated and toothed. The inner apical margin is produced into a tibial spur or tooth (Figs. 24 to 29). The prothoracic tibia bears three teeth set in sockets. Two of these are marginal and the third is sub-apical (Figs. 24 and 25). Both the mesothoracic and metathoracic tibiae have three marginal teeth and one sub-apical tooth (Figs. 26 to 29).

The prothoracic tibia has a deep longitudinal groove on the antero-dorsal surface into which the tarsus can be fitted (Fig. 25). The tarsi of the mesothoracic and metathoracic legs can be folded back against the tibiae, but the grooves to receive them are shallow and inconspicuous.

The proximal end of the tibia is developed to provide a dicondylic hinge with the femur. Each side bears a half-circular condyle (Figs. 37, 38 and 39) which fits into a corresponding, half-circular fossa in the femur. The femora-tibial hinging mechanism is shown in figure 36.

(v) Tarsus. The tarsus in all three pairs of legs is five segmented (Figs. 24, 26 and 28). Segment one is about one and half times the length of each of the second and third segments. The fourth segment is very small and cylindrical in form, not dilated as in certain genera. The distal segment is nearly equal in length to the first four combined. It is slightly curved and bears at its distal end the paired ungues of the pretarsus.

b. Wings.

(1) Mesothoracic wings. The mesothoracic elytra when closed provide a sclerotized shield over the metanotum and abdomen (Fig. 3). The sides are parallel for two thirds of the length of the elytra. They are slightly narrower in width than the pronotum. The posterior third of each elytron slopes obliquely downward and is extended into a flattened plate-like structure at the extreme posterior. The sloping region is referred to as the declivity and the flattened extension as the apical plate. The margin of the

declivity on each elytron bears four teeth (Fig. 3). The upper or first tooth is very small and pointed. The second and third teeth are the largest of the four. In the female, the second and third teeth are united basally and are of equal size. In the male, the third is longer than the second and is frequently bent downward and inward. This is a secondary sexual characteristic in I. pini.

The outer surface of the elytron bears a number of punctures arranged in longitudinal rows or striae (Fig. 4). There are nine striae numbered, for reference purposes, outward from the sutural margin. The intervals between striae are referred to as interspaces and are numbered from one to ten. The striae are definite on the main part of the elytron but become confused and irregular on the declivity.

The elytra, when in a closed position, are tightly locked together. The sutural margins are developed into a tongue and groove interlocking process (Fig. 6). The expanded rim of the left elytron appears slightly wider than that of the right. When the wings are together, the rim of the left goes beneath the right elytron. The basal, sutural margin of each elytron bears an expanded rim (Fig. 4) which hooks into the acute margins of the scutellar groove of the metanotum. The area between the rim and the outer surface of each elytron is serrated thereby forming a sutural wing lock when the wings are closed and the serrations intermesh. As a further means of holding the outer wings tightly to the body, the costal margin bears a groove, called the costal groove, which fits over a ridge on the metepisternum (Fig. 48). The costal groove is expanded at

two points, one anteriorly, and one just beyond the middle of the groove (Fig. 4). The anterior depression receives a special locking device borne on the metepisternum (Fig. 48). A process borne on the posterior angle of the metepimeron (Fig. 48) fits into the posterior depression in the costal groove.

It was found that when the elytra were removed from the insect and dried in the air, the veins became filled with air. After the wings were immersed in glycerin or water, the courses of the main longitudinal veins could be traced fairly accurately under the microscope. Five of the main veins are represented in the elytron, occupying interspaces 1, 3, 5, 7 and 9 (Fig. 4). Two of the anterior veins unite near the wing base and enter the articulatory head of the elytron as one. Hopkins (1909) found three veins in D. valens entering the basal articulation. He contends that the articulatory head has been formed from the fused bases of the costal, subcostal and radial veins. Since only two veins are apparent in I. pini, these have been considered to be the subcosta and radius. It is possible that the costal vein may be represented in the extreme margin. The remaining three veins I have considered to represent the media and cubitus one and two.

The axillary sclerites assisting in the wing articulation are located in the axillary membrane (Fig. 46). From the position of the axillaries, it appears that the first axillary, which typically articulates with the anterior notal wing process, is not represented. The second axillary is closely attached to the base of the elytron, articulating with the articulatory head of the wing and with the third axillary. The latter articulates directly with the posterior notal wing process. The posterior part of the axillary membrane



contains three sclerites. A long and narrow plate parallels the axillary cord. A very small sclerite adheres closely to the inner end of this plate forming an articulation between this plate and the third axillary. A third plate is located between the outer angle of the third axillary and the longer plate.

(ii) Metathoracic wings. The metathoracic wings are membranous in contrast to the sclerotized elytra. The wings are twice the length of the elytra but are folded and withdrawn completely beneath the outer wings when at rest. They are elliptical in shape with a cleft in the anal margin forming an anal lobe.

The venation in the wing of I. pini represents a wide departure from typical wing venation pattern. Forbes (1922) made an extensive study of the wing venation in Coleoptera, however, the venation of the Scolytidae was not discussed. It is stated that the higher Rhynchophora are highly modified in connection with their peculiar wing folding. Graham (1922) also made a study of the venation of Coleoptera. He concluded that one of the most striking modifications to the venation in the posterior wings of Coleoptera was a pushing back toward the base of the wing of the primary venation and the substitution of secondary thickenings in the apical area. Such a condition appears to have occurred in I. pini (Figs. 5 and 54).

The veins in the basal half of the wing are heavily sclerotized. The costa and subcosta are fused at the base with the head of the costa projecting beyond the subcosta. A tendon or short muscle connects the costal head to the muscle disc on the anterior edge of the metanotum. The costa and subcosta are separated by membrane for

a short distance and then fuse again. The base of the subcosta articulates with the second axillary sclerite. It is fused at one point with the medial vein and then joins the marginal, costal and subcostal complex ending at the middle of the wing. The fusion of the costal, subcostal and radial veins provides a rigid, sclerotized bar along the anterior margin of the first half of the wing. The media is a strong vein from the base to the middle of the wing where it bends sharply to reach the posterior margin of the wing. Following the media, there are two veins united at the base. The posterior vein is much shorter and in some specimens was almost rudimentary. These veins represent the first and second branches of the cubitus. The anal veins are represented by a short sclerotized area along the anal margin and a small vein articulating with the third axillary.

In the centre of the wing where the major fold occurs, there is a small sclerite which is joined to the radius by a slightly sclerotized region (Fig. 5). The outer half of the wing contains what appears to be two veins reaching to the margin of the wing. Close examination shows that they are not the strongly sclerotized structures as is the case in the basal veins. They appear more as secondary thickenings on the surface of the wing for the purpose of support following the withdrawal of the primary veins into the basal half of the wing. Anterior to the first of these secondary thickenings and joined to it at the outer angle of the wing, there is a transparent line which may represent the position of an earlier vein (Fig. 5). Presumably this would be a branch of the radius. This line appears as though it might mark the line of folding of the wing. However, the wing does not fold along this line.

The axillary membrane connects the wing to the metathorax. The first, second and third axillary sclerites are located in the membrane. The first axillary articulates with the anterior notal wing process. The second axillary articulates dorsally with the radius and laterally with the first axillary. The third axillary articulates with the posterior notal wing process and dorsally with the inner medial plate. There are two medial plates hinged together in the centre to permit folding and flexing of the wing. The medial and cubital veins are articulated to the medial plates.

### C. ABDOMEN

The abdomen is comprised of eight segments. When the elytra are in the closed position, the sterna only are visible ventrally. Removal of the elytra reveals eight terga (Fig. 61). The first six are lightly sclerotized allowing considerable flexibility. The tergum of the first segment has a transverse membranous strip through the centre. All the segments are connected by transverse, membranous conjunctivae. The terga of segments seven and eight are more heavily sclerotized in places. Number seven overlaps the eighth segment. The anterior margins of the seventh and eighth terga of the males and females are scolloped forming three membranous areas separated by sclerotized projections (Figs. 63, 64, 65, 67, 68 and 69). The posterior edge of the eighth tergum is inflected ventrally forming a transverse fold (Figs. 65 and 69).

The membranous areas differ slightly in shape between the males and females. However, the differences are too slight and

inconsistent to be used as criteria for differentiating between the sexes. Hopkins (1909) and Schedl (1931) found sexually distinct structures in the seventh and eighth terga of Dendroctonus valens and in the genus Gnathotrichus respectively. The chief characteristic was a bifid stridulating process on the posterior margin of the seventh tergum in the male. Kaston (1936) also found a stridulating scraper on the seventh tergum of the male in Hylurgopinus rufipes.

The first seven segments each bear a pair of spiracles. Those of the first segment are large and surrounded by a peritreme, located in the extreme, antero-lateral margin of the tergum. The remaining six pairs of spiracles are smaller and are located in the sclerotized areas of the terga at the anterior dorsal margin adjacent to the longitudinal conjunctivae. These spiracles open directly through the terga and are not surrounded by peritremes.

The ventral sclerites of the abdomen are heavily sclerotized in contrast to the more flexible terga. There are five exposed segments of the abdomen in ventral and lateral views (Figs. 1 and 2). The most anterior, exposed segment is number three. Sterna three and four are separated by a curving suture (Fig. 60) which is not always clearly evident, thereby making the first visible segment appear extremely wide. The two sterna are not movable on each other. Sterna, four, five, six, and seven are connected by slightly curved sutures which permit the flexing of these segments. Internally, there are phragmata between segments four, five, six and seven. The suture between the third and fourth sterna has no complementary internal

ridge except for a very slight one on the lateral areas. The median internal area is devoid of any indication of a ridge.

The median anterior area of the third sternum is projected into a wedge-shaped, intercoxal process (Figs. 60 and 62). The apex of this process fits into a groove on the median posterior edge of the metasternum thereby separating the metacoxae (Fig. 2).

The posterior and median walls of the metacoxal cavities are formed from the sloping anterior portions of the abdominal sternum. There is a faintly indicated suture (Fig. 60 and 62) which traverses the coxal wall. Therefore, there are elements of the first three abdominal sterna in the coxal wall. This suture may separate the second sternum from the third, in which case, one and two are completely fused. On the other hand, it may separate one from two with the suture between two and three gone. Apparently, elements of all three anterior sterna are involved.

The lateral anterior angles of the ventral abdominal surface are formed into small cup-shaped depressions into which the posterior angles of the metepimeron fit, locking the abdomen and the thorax together at that point.

The eighth sternum is not externally apparent in either the male or female. By raising or removing the seventh and eighth terga, the eighth sternum is exposed (Figs. 66, 70 and 71). In the male, it is reduced to a narrow curved sclerite attached by a membrane to the inflexed posterior edge of the seventh sternum (Fig. 66). In the female, the position is the same, although the shape of the sternum is different. The median area of the sternum is formed into a projecting lobe (Figs. 70 and 71).

D. EXTERNAL MALE GENITALIA

The genitalia of a number of species of bark beetles have been studied by Hopkins (1909, 1915), Fuchs (1911) and others. The genitalia of several species of Ips have been figured by these authors but not that of I. pini.

The entire genital structure is withdrawn into the body. There are no periphallic structures. The main body of the penis or the aedeagus is a tubular, sclerotized sheath (Figs. 72 and 73). The posterior half consists of a dorsal and ventral lobe connected by membrane. The dorsal lobe shows evidence of having been formed by the union of two lobes. There is a shallow, membranous emargination at the posterior from the anterior of which a faint line or suture extends to the anterior margin. A line or suture extends posteriorly from each lateral angle of the anterior portion of the aedeagus to meet the median suture (Fig. 73). Two long, sclerotic apodemes extend forward into the body from the anterior of the aedeagus. They are hinged to it by tendons or ligaments. A curved rod or spicule, (Figs. 72 and 73) lies alongside the aedeagus and is connected to it by membrane and ligaments.

Surrounding the aedeagus is a sclerotized collar or ring which is produced anteriorly on the ventral side into a long hook or apodeme (Figs. 72 and 73). Snodgrass (1935) calls a similar structure in other Coleoptera the phallobase. Hopkins (1915) calls it the tegmen.

A long sclerotized tube or rod, a seminal rod, as it is called by Hopkins, passes through the hollow cylinder of the aedeagus. The tip bears a small terminal hair or flagellum. The structure of the rod is shown in figure 74. It consists of an open trough formed by the rolled edges of the rod. This would appear to be the endophallus or part of the endophallic structure described by Snodgrass (1935). The ejaculatory duct joins the anterior end of the rod.

#### V. CONCLUSIONS

The anatomy of Ips pini, like that of the members of the Rhynchophora generally, presents a highly complex structure. The detailed study of one species usually brings many of the problems of interpretation of structures to the forefront. Unfortunately, it does not go far toward reaching an acceptable explanation as to how or why certain parts are modified in a particular way. This can only be achieved through a comparative study of representatives of many genera and families in the light of present day morphological principles. However, I do not feel that the value of an isolated study such as this is lessened too much by its limitations, in view of the noticeable gap in the literature on the morphology of the Scolytidae.

Several specific points worthy of further investigation have been brought to my attention. Very little is known of the structure of the tentorium of the bark beetles. The head capsules of Dendroctonus valens, Hylurgops pinifex and Orthotomicus caelatus were compared to that of Ips pini for reference only, but even this

sketchy examination revealed structural modifications between them. The sutures and shape of the post-occipital region of the head offer an additional opportunity for valuable study and these two points might be incorporated into a detailed investigation of the head capsule of the Scolytidae. Finally, the interpretation of the mesonotum of Ips pini raised several points requiring further detailed examination. This too, I believe, could and should be enlarged to a comparative study of the mesonotum of bark beetles as a whole.

## VI. SUMMARY

1. The external anatomy of Ips pini (Say) has been studied and figured.
2. The structure of this beetle presented morphological problems beyond the scope of this paper, but which should receive further attention.
3. The head capsule is a compact structure in which the tentorium and sutures of the post-occipital region presented difficulties in interpretation.
4. The prothorax has been modified into a sclerotized cylinder in which the dorsal, pleural and sternal areas are completely fused. The sutures separating these areas have disappeared.
5. The mesothorax and metathorax have retained more or less distinct dorsal, pleural and sternal areas. The mesonotum has been highly modified by folding of the anterior and posterior areas and is difficult to interpret. A comparative study of many species is required before a satisfactory explanation can be given.



6. The venation of the membranous hind wings has been modified by the withdrawal of the main veins into the basal section. Secondary thickenings strengthen the apical section of the wing.

7. The abdominal terga are membranous and completely concealed by the elytra when they are in a closed position. The sternum is sclerotized with only five visible segments, the first of these being number three. Fusion of segments one, two and three has occurred.

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PLATES I TO IX TO PART II

PLATE I

PLATE I

- Fig. 1. Lateral aspect of adult with legs and wings off.  
Fig. 2. Ventral aspect of adult with left elytron removed.  
Fig. 3. Dorsal aspect of adult.  
Fig. 4. Inner aspect of right elytron.  
Fig. 5. Metathoracic wing.  
Fig. 6. Posterior of elytra showing the interlocking flanges.

- A - Anal vein  
ANT - Antenna  
ABD - Abdomen  
AP - Apical plate  
C - Costa  
CUL1 - Cubitus 1  
CUL2 - Cubitus 2  
CX - Coxa  
CXC - Coxal cavity  
EL - Elytron  
EPM - Epimeron  
EPS - Episternum  
LB - Labium  
M - Media  
MD - Mandible  
MX - Maxilla  
R - Radius  
SC - Subcosta  
SCL - Scutellum  
SCT - Scutum  
SP2 - Metathoracic spiracle  
STN - Sternum  
TH1 - Prothorax  
TH2 - Mesothorax  
TH3 - Metathorax  
a - Intercoxal process  
b - Anterior wing locking process  
c - Sutural groove and wing lock  
d - Posterior wing locking process  
e - Costal groove of elytron  
f - Secondary thickenings of the wing

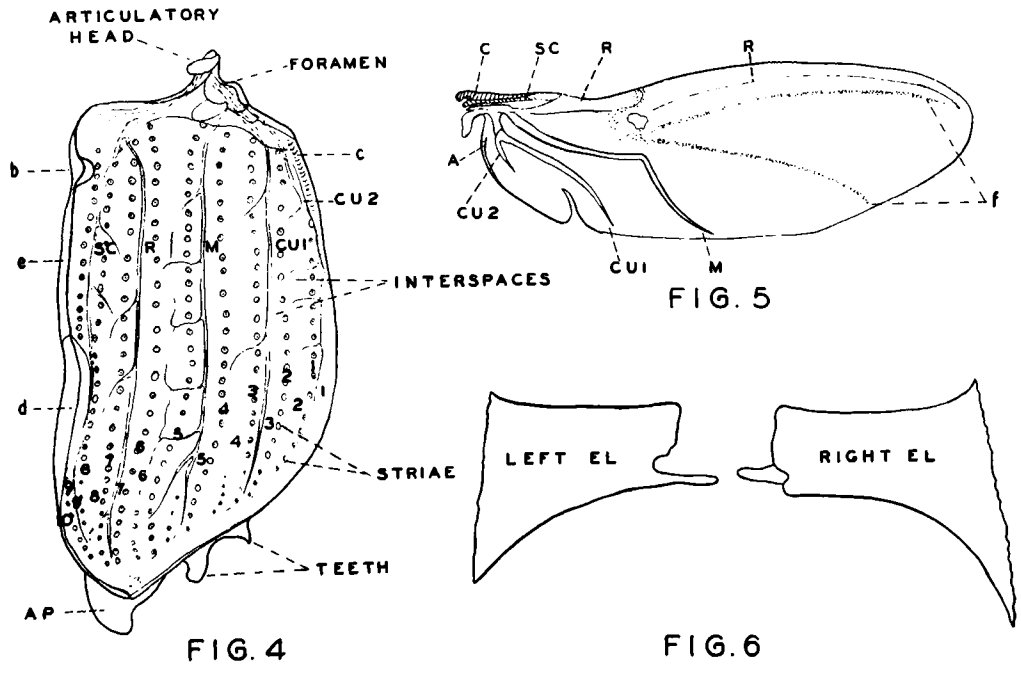
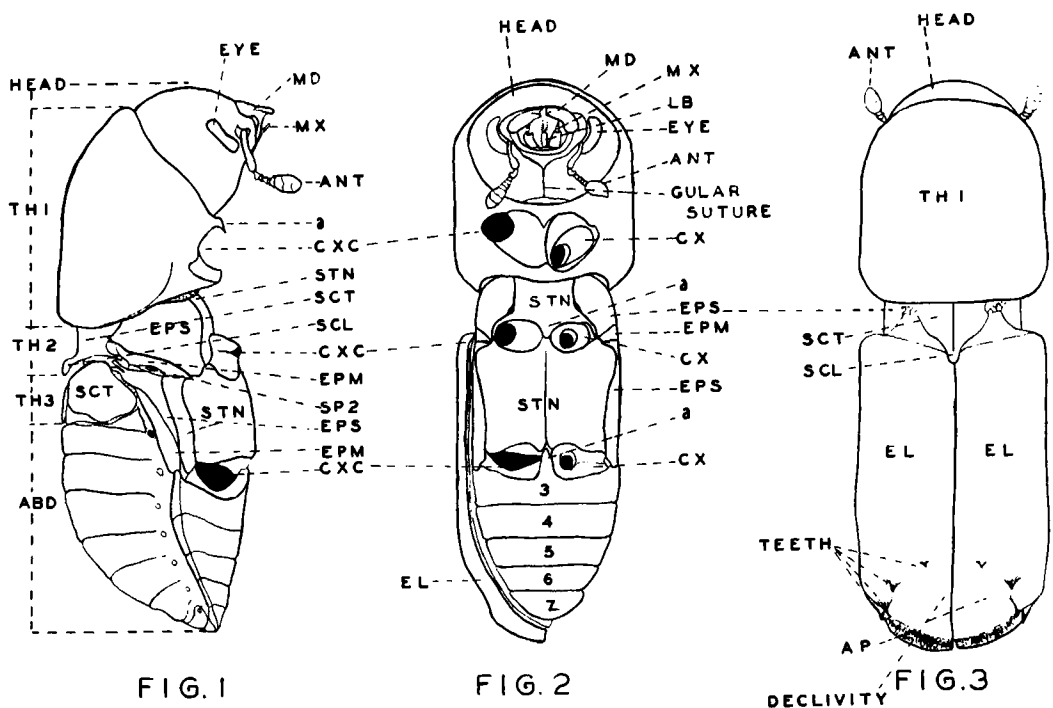




PLATE II

- Fig. 7. Dorsal aspect of the head.  
Fig. 8. Occipital region of the head.  
Fig. 9. Inner aspect of the ventral region of the head.  
Fig. 10. Ventral aspect of the head.  
Fig. 11. Lateral aspect of the head.  
Fig. 12. Anterior aspect of the antenna.  
Fig. 13. Posterior face of the club and the distal segment of the funicle of the antenna.  
Fig. 14. Lateral aspect of the club of the antenna.

- ANT - Antenna  
AT - Anterior tentorial arm  
CS - Coronal suture  
EPS - Epistoma  
GE - Gena  
HB - Hypostomal bridge  
HPHY - Hypopharynx  
HS - Hypostomal suture  
HST - Hypostoma  
LB - Labium  
MD - Mandible  
MX - Maxilla  
OC FOR - Occipital foramen  
POS - Post-occipital suture  
PRTL - Parietal  
SCL - Sclerotized  
SCP - Scape  
SMT - Submentum  
VX - Vertex  
a - Transverse suture marking the inflected edge of the occipital foramen.

PLATE II

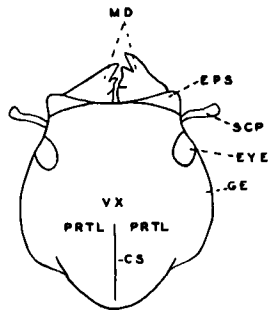


FIG. 7

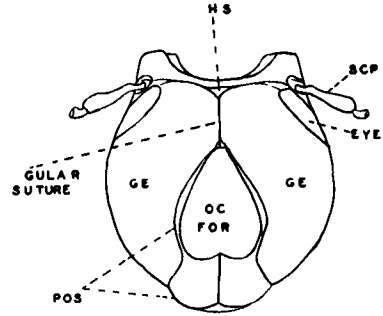


FIG. 8

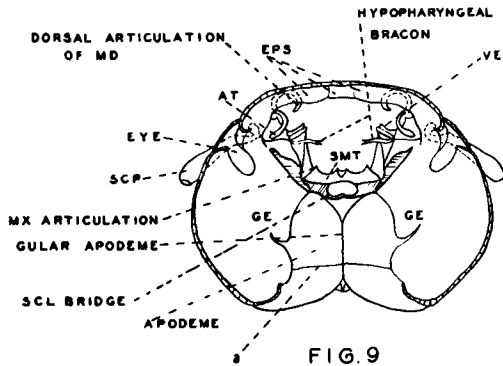


FIG. 9

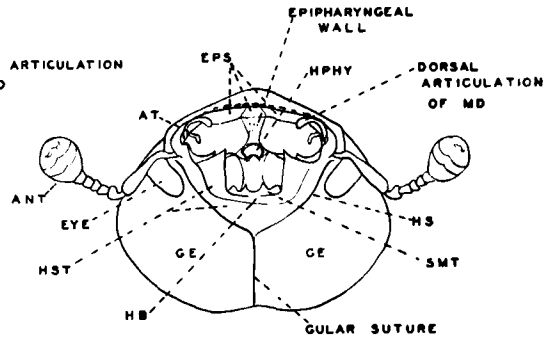


FIG. 10

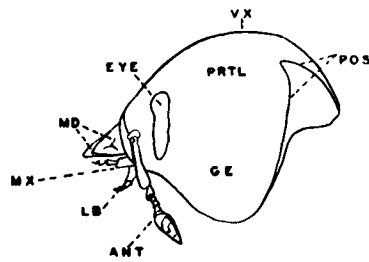


FIG. 11

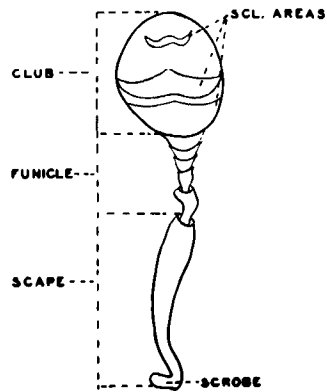


FIG. 12



FIG. 13

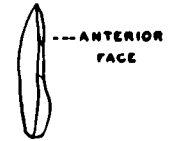


FIG. 14

PLATE III

- Fig. 15. Ventral aspect of right maxilla.  
Fig. 16. Dorsal aspect of right maxilla.  
Fig. 17. Lateral aspect of labium.  
Fig. 18. Dorsal aspect of labium.  
Fig. 19. Ventral aspect of labium.  
Fig. 20. Inner postero-dorsal aspect of mandible.  
Fig. 21. Antero-dorsal aspect of mandible (Reverse of Fig. 20).  
Fig. 22. Inner face of right mandible.  
Fig. 23. Outer face of right mandible (Reverse of Fig. 22).

CD - Cardo  
E Disc - Extensor disc  
E Tendon - Extensor tendon  
GA - Galea  
LC - Lacinia  
LIG - Ligula  
MT - Mentum  
PLP - Palpus  
R Disc - Retractor disc  
R Tendon - Retractor tendon

PLATE III

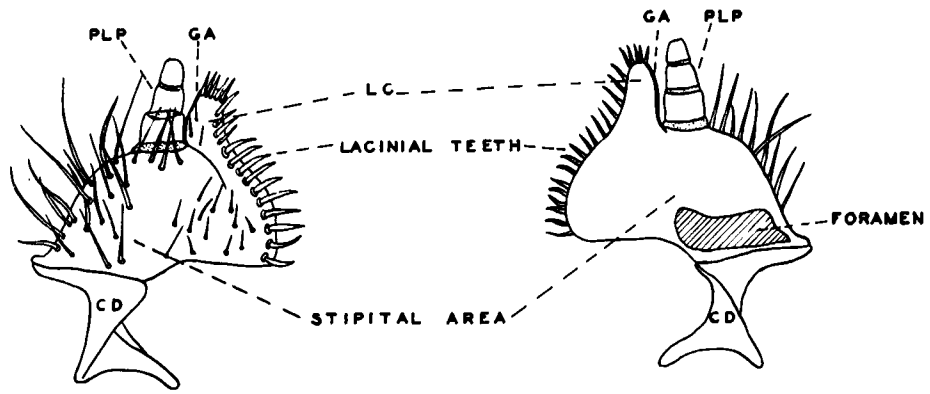


FIG. 15

FIG. 16

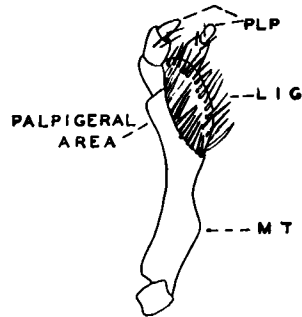


FIG. 17



FIG. 18

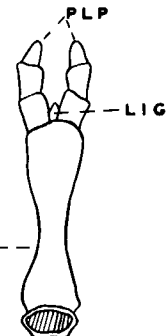


FIG. 19

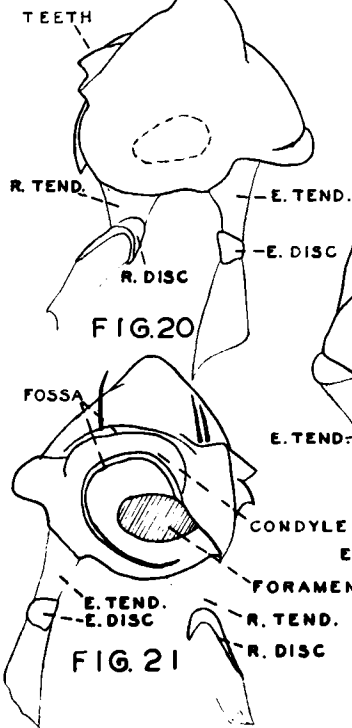


FIG. 20

FIG. 21

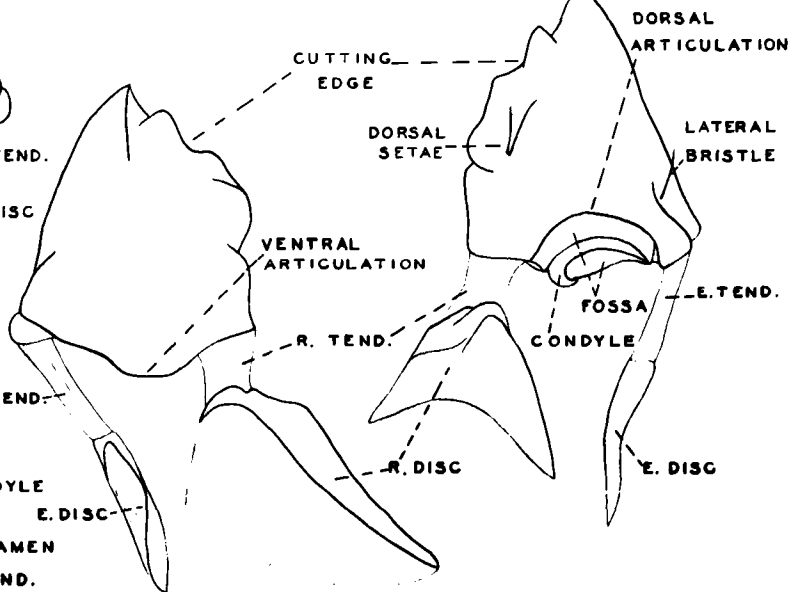


FIG. 22

FIG. 23

PLATE IV

- Fig. 24. Postero-dorsal aspect of right prothoracic leg.  
Fig. 25. Antero-ventral aspect of right prothoracic leg.  
Fig. 26. Dorsal aspect of right mesothoracic leg.  
Fig. 27. Ventral aspect of right mesothoracic leg.  
Fig. 28. Ventral aspect of right metathoracic leg.  
Fig. 29. Dorsal aspect of right metathoracic leg.

BCS - Basicostal suture  
BCX - Basicoxite  
CX - Coxa  
FM - Femur  
TAR - Tarsus  
TB - Tibia  
TR - Trochanter  
UN - Ungues

PLATE IV



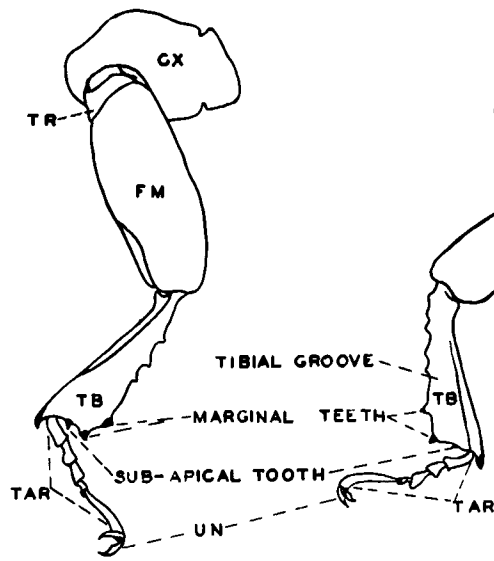


FIG. 24

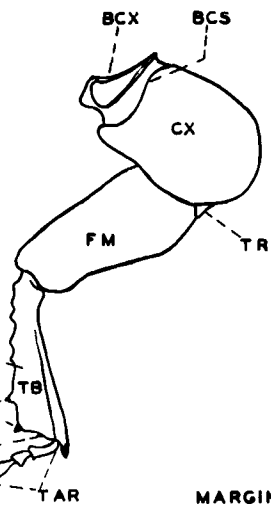


FIG. 25

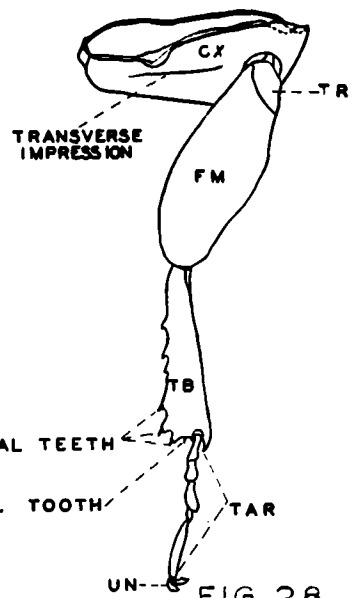


FIG. 28

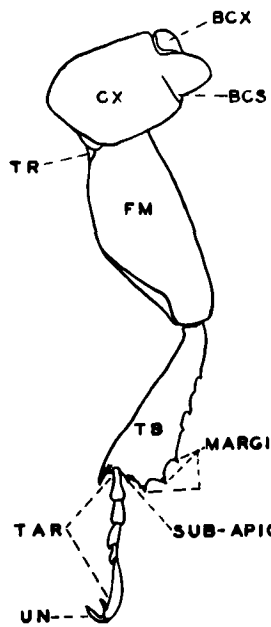


FIG. 26

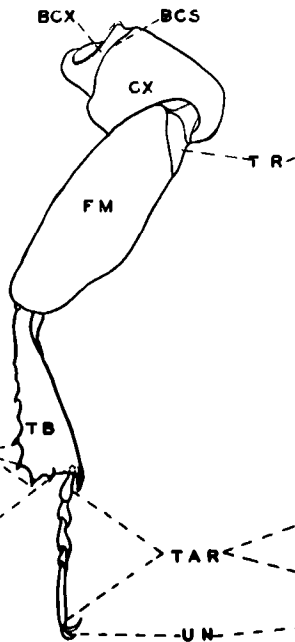


FIG. 27

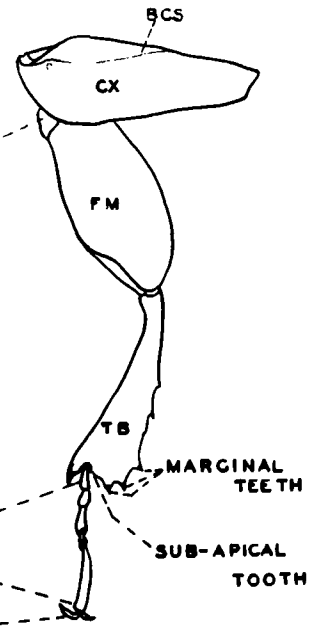


FIG. 29

PLATE V

- Fig. 30. Ventral aspect of prothoracic coxa.  
Fig. 31. Dorsal aspect of prothoracic coxa.  
Fig. 32. Ventral aspect of metathoracic coxa.  
Fig. 33. Inner anterior aspect of metathoracic coxa.  
Fig. 34. Ventral aspect of mesothoracic coxa.  
Fig. 35. Dorsal aspect of mesothoracic coxa.  
Fig. 36. Hinging mechanism of femur and tibia.  
Figs. 37,  
38, 39. Dicondylic articulatory process of the tibia.  
Fig. 40. Ventral aspect of the prothoracic trochanter.  
Fig. 41. Lateral aspect of the prothoracic trochanter.  
Fig. 42. Dorsal aspect of the prothoracic trochanter.

BCS - Basicostal suture  
BCX - Basicoxite  
FM - Femur  
TB - Tibia  
TR - Trochanter

PLATE V

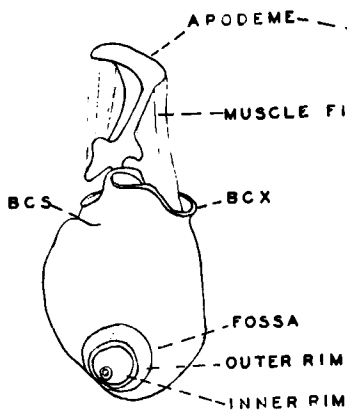


FIG. 30

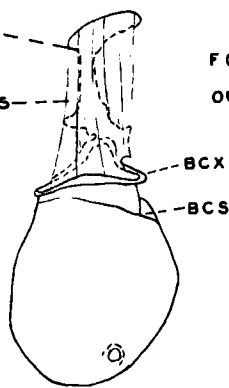


FIG. 31

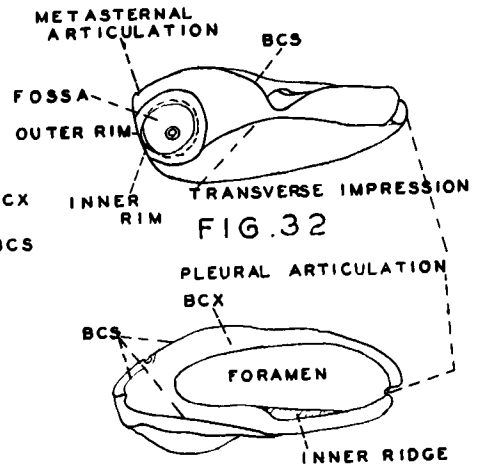


FIG. 32

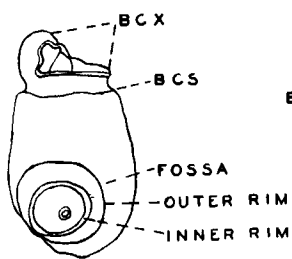


FIG. 34

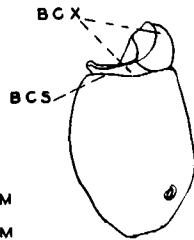


FIG. 35

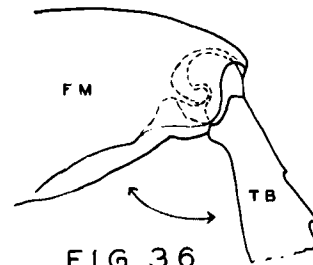


FIG. 36

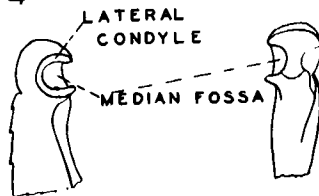


FIG. 37



FIG. 38

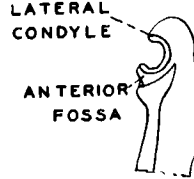


FIG. 39

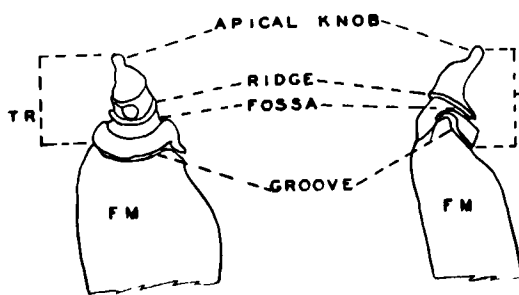


FIG. 40



FIG. 41

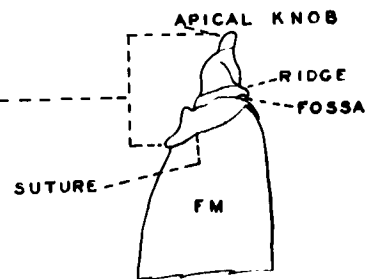


FIG. 42

PLATE VI

- Fig. 43. Ventral aspect of prothorax.  
Fig. 44. Inner aspect of sternal area of prothorax.  
Fig. 45. View through the posterior of the prothorax.  
Fig. 46. Dorsal aspect of mesonotum, pteralia and base of right elytron.  
Fig. 47. Inner aspect of the mesonotum.  
Fig. 47A. Sagittal section of the mesonotum showing the median carina.  
Fig. 48. Outer aspect of the metapleuron.  
Fig. 49. Ventral aspect of the mesosternum and metasternum.  
Fig. 50. Posterior aspect of metendosternite.  
Fig. 51. Inner aspect of the mesosternum and metasternum.  
Fig. 52. Anterior aspect of metendosternite.

- 2AX - Second axillary  
3AX - Third axillary  
AXC - Axillary cord  
ANP - Anterior notal wing process  
CXC - Coxal cavity  
EPM - Epimeron  
EPS - Episternum  
MS - Median Suture  
PH - Phragmata  
PLA - Pleural apophysis  
PLS - Pleural suture  
PNP - Posterior notal wing process  
PRSC - Prescutum  
RD - Posterior reduplication  
RVS - Reversed notal suture  
SA - Sternal apophysis  
SCL - Scutellum  
SCT - Scutum  
STN - Sternum  
TS - Transverse suture  
VS - Scuto-scutellar suture  
WP - Wing process  
a - Anterior ventral angle  
b - Anterior process for wing locking mechanism  
c - Part of the process for the wing locking mechanism

PLATE VI

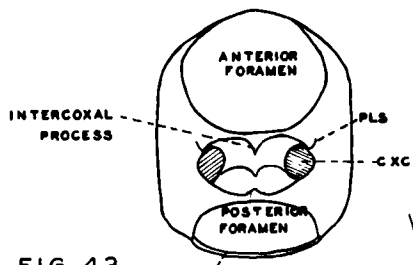


FIG. 43

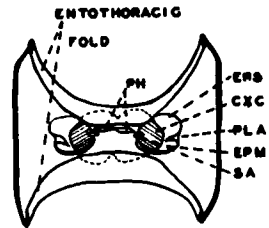


FIG. 44

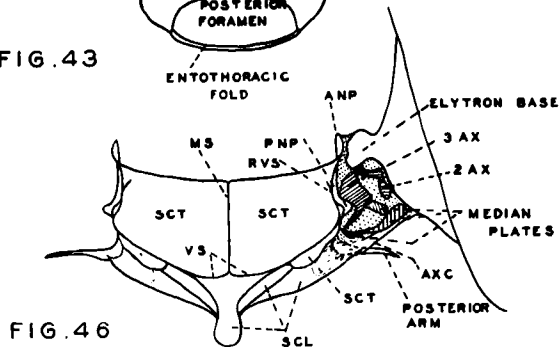


FIG. 46

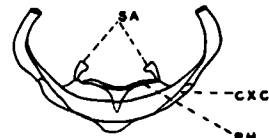


FIG. 45

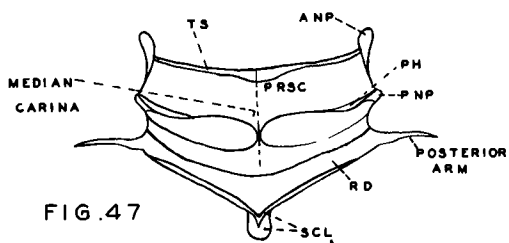


FIG. 47

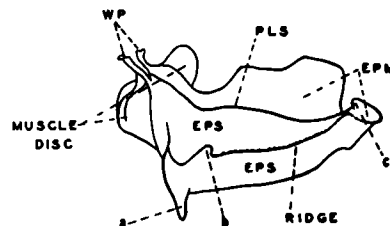


FIG. 48

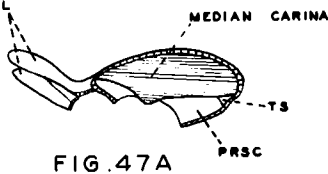


FIG. 47A

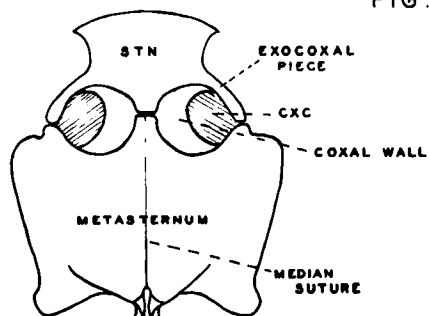


FIG. 49

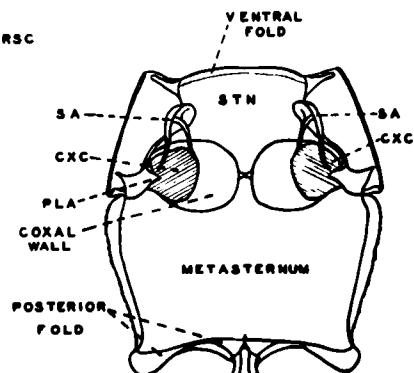


FIG. 51

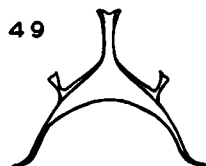


FIG. 50

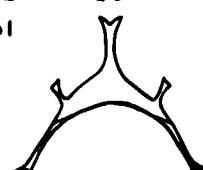


FIG. 52

PLATE VII

- Fig. 53. Anterior aspect of prescutum.  
Fig. 54. Dorsal aspect of metatergum.  
Fig. 55. Posterior aspect of postnotum.  
Fig. 56. Inner aspect of metatergum.  
Fig. 57. Inner aspect of postnotum.  
Fig. 58. Outer aspect of mesopleuron.  
Fig. 59. Inner aspect of mesopleuron.

- A - Anal veins  
ANP - Anterior notal wing process  
AX1 - First axillary  
AX2 - Second axillary  
AX3 - Third axillary  
BA - Basalare  
C - Costa  
CU1 - Cubitus 1  
CU2 - Cubitus 2  
EPM - Epimeron  
EPS - Episternum  
M - Media  
MP - Median plate  
HI - Phragmata  
PLA - Pleural apophysis  
PIR - Pleural ridge  
PLS - Pleural suture  
PN - Postnotum  
PNP - Posterior notal wing process  
PRE-EPS - Pre-episternum  
PRSC - Prescutum  
R - Radius  
SC - Subcosta  
SCL - Scutellum  
SCT - Scutum  
VS - Scuto-scutellar suture  
WP - Wing process  
a - Anterior muscle disc  
b - Circular muscle disc  
c - Sclerotized process in front of first abdominal spiracle  
d - Anterior arm



PLATE VII

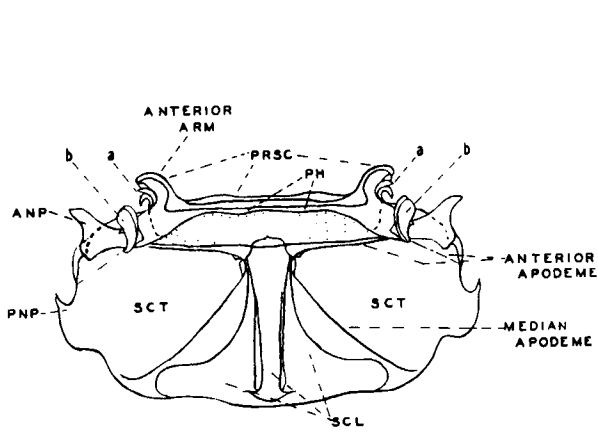
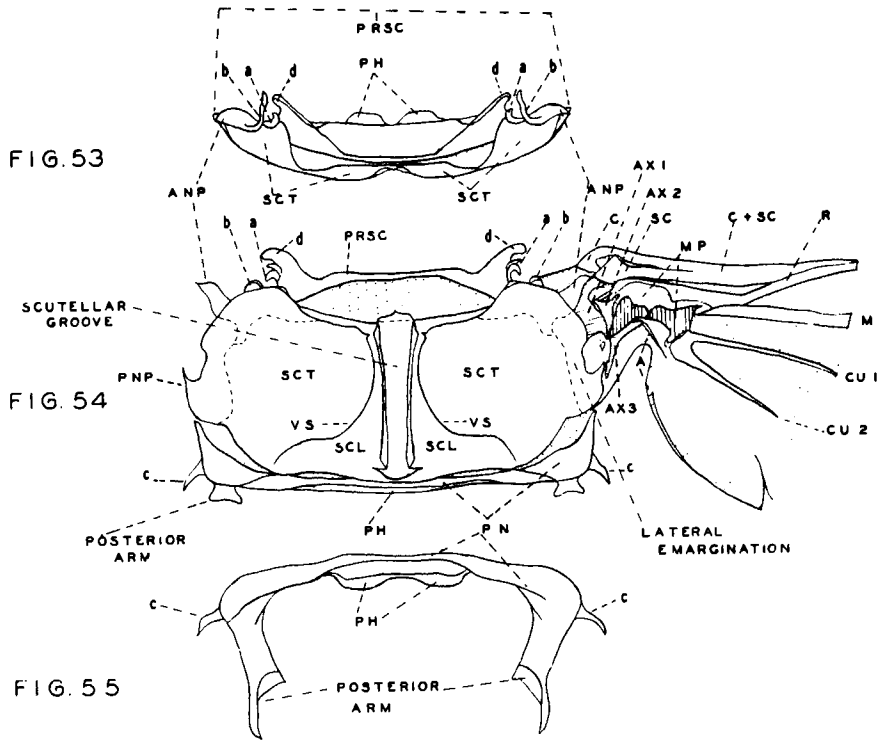


FIG. 56

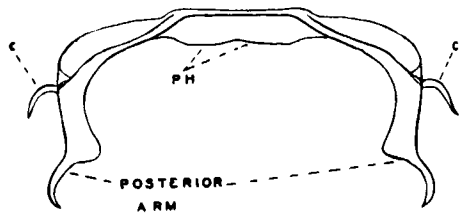


FIG. 57

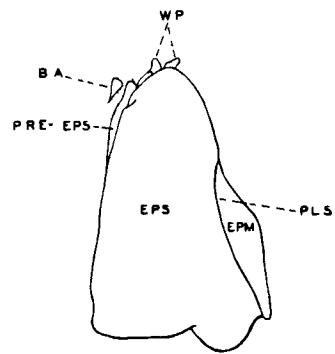


FIG. 58

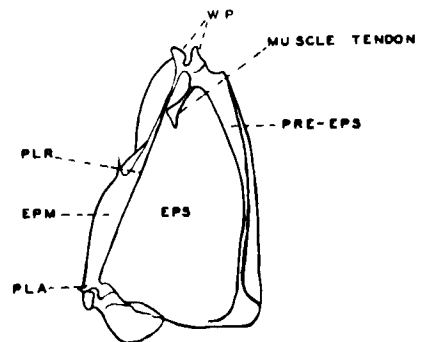


FIG. 59

PLATE VIII

- Fig. 60. Ventral aspect of abdomen.  
Fig. 61. Dorsal aspect of abdomen.  
Fig. 62. Lateral aspect of abdomen.  
Fig. 63. Dorsal aspect of terga 7 and 8 of male.  
Fig. 64. Outer aspect of tergum 8 of male.  
Fig. 65. Inner aspect of tergum 8 of male.  
Fig. 66. Inner aspect of sternum 7 showing the position of sternite 8 of male.  
Fig. 67. Dorsal aspect of terga 7 and 8 of female.  
Fig. 68. Dorsal aspect of tergum 8 of female.  
Fig. 69. Inner aspect of tergum 8 of female.  
Fig. 70  
and 71. Inner aspect of sternum of female showing the position of sternum 8.

S       Sternum  
SP       Spiracle  
T       Tergum

PLATE VIII

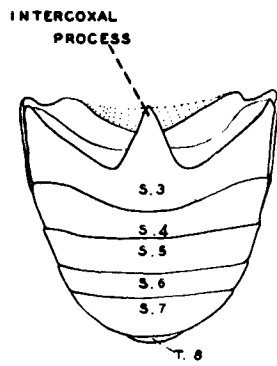


FIG. 60

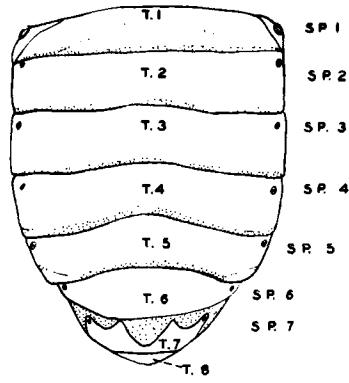


FIG. 61

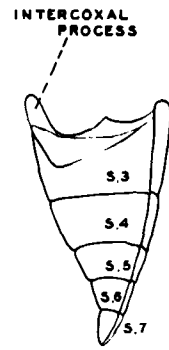


FIG. 62

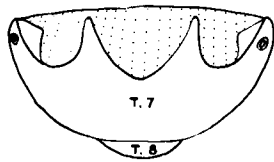


FIG. 63

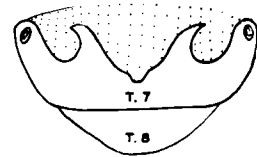


FIG. 67

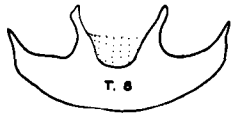


FIG. 64



FIG. 68

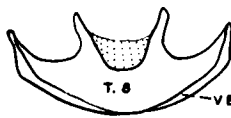


FIG. 65



FIG. 69

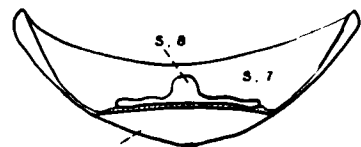


FIG. 70

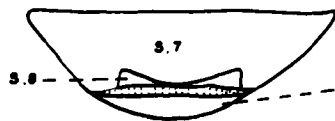


FIG. 66



FIG. 71

VENTRAL INFLECTION

VENTRAL INFLECTION

PLATE IX

- Fig. 72. Ventral aspect of the external male genitalia.  
Fig. 73. Dorsal aspect of the external male genitalia.  
Fig. 74. Enlargement of a section of the seminal rod.

PLATE IX

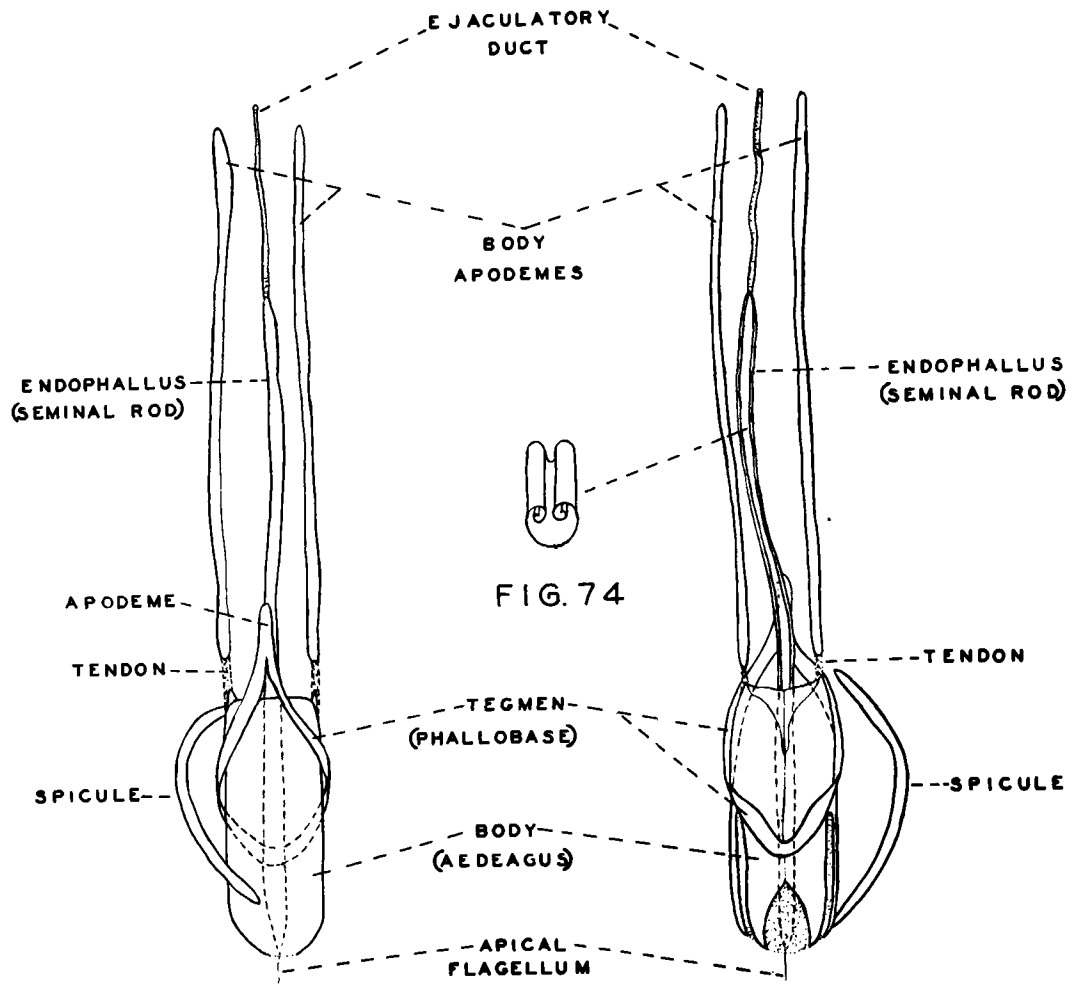


FIG. 74

FIG. 72

FIG. 73