BIOLOGY OF

IPS PERTURBATUS EICHHOFF

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by

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A THESIS

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INTRODUCTION

Of all the injurious insects,the Scolytidae are certainly among those which were most thoroughly studied by entomologists.For all that,however,about the only thing we know on the majority of those insects,is what has been written in the original description.Indeed,in America,apart from some species belonging to the genus Dendroctonus which have been quite well worked out,most of the others were rather considered as of secondary economic importance and their study has been neglected. We cannot foretell,however,if certain species,actually considered as secondary might not,eventually,owing to certain conditions of environment or for other reasons,become of great economic importance.Thus,during the year of 1934,the Québec Government gave to the companies a reduction on stumpage for trees killed by insects.I was recently told,however,that the grantees of the large forest limits of the Gaspé Péninsula,which are heavily infested by the European spruce sawfly,were not able to get that reduction on stumpage because the trees,although very badly defoliated by the sawfly,were not"killed" as mentionned in the order-in-council.On the other hand,last summer I found some trees which,after a severe defoliation by the sawfly,were killed by *Ips perturbatus* attacks.Although these insects were certainly not primarily responsable for the death of the trees, they have played a very important rôle and they might, in the following years, enable the grantees to cut with a reduction all the trees attacked by the sawfly, which otherwise would not actually have been killed.

The object of this study was therefore to obtain more knowledge on one of these Scolytidae considered as a secondary bark-beetle. Very little is actually known on the biology of Ips perturbatus. I do not have, however, the presumption to solve all the questions which might be raised concerning the habits of this species; Ips perturbatus has a two year life-cycle, and most of the work presented in this paper, was done in one year during my spare time while engaged in other problems for the Dominion Entomological Branch. Nevertheless, this study will certainly bring to light much information which will be of help in the pursuit of further work.

The writer desires to acknowledge the assistance and advice given by Mr. E. B. Watson who has been engaged in bark-beetle biological studies for several years. I wish to thank Dr. Melville Du Porte and Mr. J. J. de Gryse who carefully read the manuscript and made many corrections and suggestions. The author is also indebted to Dr. J. M. Swaine for general information on the habits of Scolytidae, to Mr. G. S. Walley who kindly identified a parasitic species, and to Mr. M. L. Prebble who provided the records on temperature and precipitation.

I.-HISTORY

The following abstract of the literature shows that, except for a few short papers published during the last ten years and dealing with the biology of *Ips perturbatus*, all the information found in the literature is of taxonomic character only.

1868.- Eichhoff, W. (9).

Original description, page 274.

Tomicus perturbatus, new species. Oblongus, cylindricus, subnitidus, thorace breviter ovato postice fortiter punctato; elytris sucrenato-striatis, stria suturali profundiore pone medium fortiter rugulóso-punctata, interstitiis convexiusculis laevibus apice oblique truncatis, truncatura excavata spatio punctato nitido, margine laterali utrinque 4-dentato, dente 3° majore a primo minimo remoto, margine apicali longe elevato.- Long. 2½ Lin.- Patria: Ameré. bor.

1876.- Leconte, J.L. (14).

Described *Tomicus hudsonicus* (synonym) as a new species from Hudson Bay Territory. Differentiated from *Ips pini* by much larger punctures on the elytral striae, and the tooth of the fifth interspace with a tendency to become thicker and curved.

In appendix no II, under the title "Unrecognized species", he places Ips perturbatus Eichh. and quotes verbatim Eichhoff's description.

1878.- Eichhoff, W. (10).

Revised description of Ips perturbatus.

1878.- Hubbard, H. G. & Schwarz, E. E. (13).

Tomicus hudsonicus recorded from Marquette, Michigan

1909.- Swaine, J. M. (22).

Reference to literature only. He classifies I. perturbatus and I. hudsonicus as two different species, giving for habitat all America borealis to the first one and only Hudson Bay and Utah region to I. hudsonicus

1916.- Blatchley, W. S. & Leng, C. W. (4).

Quotes verbatim Leconte's description, recognizing Tomicus hudsonicus as a distinct species closely allied with Ips pini Say, I. perroti Sw. and I. interruptus Mannh. In their key they do not mention Ips perturbatus

1918.- Swaine, J. M. (23).

Gives taxonomic characters; secondary sexual character: "male with third declivital tooth more acutely pointed."

Tomicus hudsonicus syn. of Ips perturbatus.

Host tree: White spruce

Distribution in Canada, see "Geographical distribution".

1920.- Leng, C. W. (15).

Reference only. Tomicus hudsonicus syn. of Ips perturbatus.

1924.- Swaine, J.M. (24).

A paper on the control of Dendroctonus piceaperda, but the author also gives a short account of the life-history of the secondary bark-beetles which work with Dendroctonus. Among these, is included Ips perturbatus.

1924.- Swaine J.M., & Craighed, F.C. (25).

A paper on the Spruce Budworm. Under the heading "secondary insects associated with the Budworm," the authors give a very brief description of Ips perturbatus and its habits.

1927.- Watson, E.B. (26).

Notes on hibernation. Studying Ips perturbatus in Algoma district, Ontario Watson observed that this species over-wintered in the adult stage; the beetles leave their host in the fall and hibernate in the moss or in the debris on the ground.

1928.- Watson, E.B. (27).

The paper treats of Dendroctonus piceaperda, but there is also a short account of Ips perturbatus. In the Frater district, the infestation is confined to trees killed by Dendroctonus the previous year. Winter is always passed in the adult stage and hibernation takes place in the ground. Some beetles cut two sets of tunnels during the same season. Pupation in the first brood takes place in July but the young beetles do not leave their host until fall. Second brood also mature to adult stage before winter.

II.-SYSTEMATIC POSITION OF THE SPECIES

Order COLEOPTERA

Family Scolytidae
syn. Ipidae

Head concealed above by the pronotum; anterior tibiae widened distally................................subfamily Ipinae

Head visible from above; anterior tibiae with the sides nearly parallel..................................all other Scolytidae

Subfamily Ipinae

Elytral concavity toothed; the concavity of the declivity separated from the apical margin of the elytra by the strongly produced, horizontal, plate-like, acute apical margin of the declivity...............................Genus Ips DeGeer

Elytral declivity generally without teeth, but if these are present the declivity has always the apical margin only slightly produced, the plate dividing the declivital apex from the elytral apex, when present oblique and very short...all other Ipinae

Genus Ips DeGeer, 1775
syn.-1777-Bostrichus Fab.
" 1807-Tomicus Lat.

Declivital margin with four teeth, the third tooth cylindrical;

the discal interspaces impunctuate except near the declivity; pronotum not longer than wide...............*Ips perturbatus* Eichh.

Declivital margin with 3 to 6 teeth. When 4 teeth are present the third tooth is compressed and emarginated at the tip, and all the interspaces are punctured uniseriately except near the declivity...................................all other *Ips*

Ips perturbatus Eichhoff, 1868. Type.-Eggers Coll. Stulburg, Germany.
syn.-1876- *Tomicus hudsonicus* Leconte.

III.-GEOGRAPHICAL DISTRIBUTION

Eichhoff (1868), in the original description of *Ips perturbatus*, gives for the geographical distribution all Amer. bor. Swaine (1909) mentions for the species the same rather undetermined distribution, and he confines the synonym *Ips hudsonicus* to Hudson Bay and Utah region.

Leconte (1876) described *Tomicus hudsonicus* as a new species from Hudson Bay Territory.

Hubbard & Schwarz (1878), referring to *Tomicus hudsonicus*, record it from Marquette, Michigan.

Swaine (1918) gives a definite and exact account on the distribution of this species in Canada: "Newfoundland, Quebec, Ontario and across Canada, extending north of the prairies in Sasketchewan and Alberta to the Peace River and through Northern British

Columbia into the Yukon...", and he makes this statement which sums up the entire question:" It apparently follows the northern range of its host tree. He also states that :" Back's Bostrichus typographus Fabr., taken on the Great River Fish, was probably this species".

IV.-HOST TREE AND HOST SELECTION

A. - Host-Tree

In the Gaspe Peninsula, Ips perturbatus attacks only the white spruce killed or much weakened generally by Dendroctonus piceaperda Hopk., or less often by Diprion polytomum Hartig. They enter the upper part of the trunk the year following the Dendroctonus attack; thus, during the summer 1934, Ips were found on trees infested by Dendroctonus in June and July 1933.

Although at the decline of a Dendroctonus outbreak, Ips are often as numerous as the former, they are not found in the upper part of every tree killed by Dendroctonus. Indeed, if the latter species is present on more than half of the total length of the trunk, the bark then seems to be to dry, and the portion of the trunk free from Dendroctonus is generally infested by Dryocoetes affaber Mannh. (see table-1, trees no. 9,12) In other cases, although the upper part of the tree presents the suitable conditions for Ips infestation, the examination of such trees reveals the presence of Polygraphus rufipennis Ky. only (table-1, trees no. 7,8,10,11). This is due to the fact that often Polygraphus enter the tree during the same year as Dendroctonus. Simpson ('29) reports that at Fredericton, P. rufipennis breed three times during the same summer, in June, July and at the end of August. In Gaspe, the number of broods was not determined for this species, but many adults are also seen flying at the end of August. At that time of the year, they enter the trees infested by Dendroctonus in June of the same season, so that when Ips emerge the following spring, their place in many trees suitable for attack is already taken by Polygraphus rufipennis.

Twelve trees killed by Dendroctonus were cut and the trunks were examined to gain a general idea of the distridutionof secondary bark-beetles on the different portions of the trunk, and the type of trees preferred by each species, especially by Ips perturbatus. Table 1 shows the distribution of the different species of bark-beetles on those trees.

Each zone does not end abruptly; between each of them there is an intermediate zone of one to three feet long where the species of the two adjacent zones intermix.

Where Ips Perturbatus and Ips borealis are mixed together on the same portion of the trunk as in trees no. 1.2. and 4, I. perturbatus is always the predominent species.

Table -I- shows that Ips perturbatus

Table No. 1

Distribution of secondary bark-beetles on the trunk of white spruce killed by <u>Dendroctonus</u> <u>piceaperda</u>.

Tree No.	D.B.H. in inches	Total length in feet	Dendr. zone in feet	Other secondary bark-beetles
1	13	61	28	Ips pert., Ips borealis and Dr. affaber 14', dia.9"-6"; Ips borealis only 24', dia.6"-1".
2	8	48	16	Ips pert.and I.borealis 18',dia. 6"-4";Ips borealis 12',dia.4"-1'
3	12	72	22	I.pert.14', dia.8"-6";I.borealis 10', dia.3"-1";P.rufipennis 26'.
4	11	69	26	I.pert. and I.bor.28',dia.8"-3"; I.borealis 13', dia.3"-1".
5	12	67	27	I.pert.22',dia.8"-4"; I.borealis 16', dia.4"-1".
6	9	66	13	I.pert.32',dia.7"-4";I.borealis 18'; last 3',Pityophthorus sp.
7	11	65	30	Polygraphus rufipennis 33'.
8	10	55	20	Polygraphus rufipennis 32'.
9	10	51	31	Dryocoetes affaber 18'. (tree very dry).
10	11	75	34	Polygraphus rufipennis 39'.
11	12	74	25	Polygraphus rufipennis 47'.
12	11	68	40	Dryocoetes affaber 25'.

attack generally the portion of the trunk situated between the diameters of 8 and 4 inches. In the upper part, their distribution is limited by the thickness of the bark which is too thin for them. We might be inclined to believe that just the opposite condition limits their distribution on the lower part, but this is not the case however, and if Ips are rarely found at the base of the trunk, it is due to the fact that they generally go to trees killed by Dendroctonus, i.e. trees having the base already infested when Ips enter them. But in some other cases, for instance, where the trees are almost completely defoliated by Diprion polytomum, Ips is found at the base of the trunk. Thus on July 17th, many Ips perturbatus tunnels were found at the D.B.H. on a tree of about 10 inches diameter which, although much weakened by the saw-fly attacks, still bore green needles even on the lower branches. A more careful examination of the same tree, made on August 29th, revealed the presence of Ips perturbatus for, at least, the first 40 feet of the trunk. Other secondary scolytids, such as Ips borealis Sw., Dryocoetes affaber Mannh. and Trypodendron bivittatum Ky. were conjointly inhabiting the same portion of the trunk, but in much smaller numbers. On August 30th, many other saw-fly trees were examined and three of them were found severely infested by Ips perturbatus for the first 20 basal feet of the trunk. These trees were dead by that time, but they were certainly alive in the spring since it was still possible to see at the top of the tree the new foliage which was, at the end of August, of a yellowish color.

We may conclude that in general Ips perturbatus follows

Dendroctonus distribution, being noticeable one or two years after the appearance of *Dendroctonus*. When the *Dendroctonus* outbreak is at its peak, *Ips* have not yet reached their maximum number; they arrive at it only when *Dendroctonus* is on its descending trend. By that time, they are probably as numerous or even more numerous than *Dendroctonus*, but the decrease of the latter means also a decrease in the number of trees on which *Ips* are able to live; so that their diminution will be as rapid as that of *Dendroctonus*. In Gaspe, however, a very interesting and particular case seems to occur. Last summer (1934), while *Dendroctonus* were at their decline, *Ips* were probably at their maximum density; the number of trees infested by *Dendroctonus* not being sufficient for them, many attacked the white spruce severely defoliated by the saw-fly. As the trunk of these trees was absolutely free from *Dendroctonus*, *Ips* entered them at the very base and their population per tree was doubled. Therefore, it appears that in the absence of trees killed by *Dendrontonus*, those defoliated by the spruce saw-fly would be in a condition suitable to *Ips perturbatus*. This case, however, is peculiar to the Gaspé Péninsula where two outbreaks, namely *Dendroctonus piceaperda* and *Diprion polytomum*, exist concurrently. For this reason, it should be very interesting to follow the progress of *Ips perturbatus* in that particular district.

B. - Host-Selection

Many trials were made to develop broods of *Ips perturbatus* on healthy white spruce, balsam and black

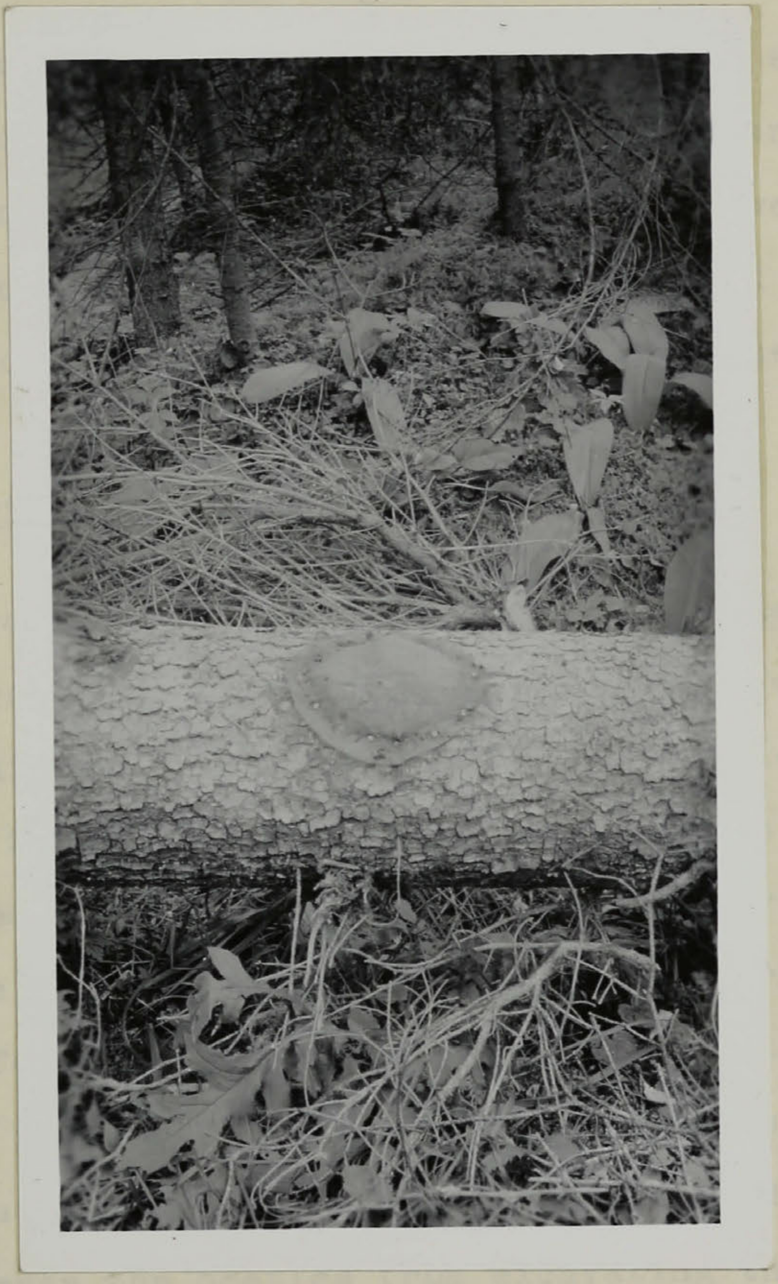

fig. 1.- Ips perturbatus, showing cage used for host-selection experiments.

spruce, the two latter species presenting the conditions which should have been the most favorable for the development of the insect. Most of these experiments, however, failed to produce positive results.

The cages used for these experiments (fig.1.) were made of wire screen and had a circular shape of about 6 inches in diameter. Many tacks were nailed around the edge of the cage in such a way that no interstices were left where the beetles could escape. Consequently, they had either to die there or to feed on the tree and develop a new colony.

Experiments.

A.- On healthy white spruce, (*Picea canadensis* Mill.)

1.) Two groups of about twenty beetles each were caged on two healthy white spruce on June 27th. Examination of these cages on August 29th, showed many entrance-tunnels but no female had succeeded in cutting an egg-tunnel. They were all drowned out by the flow of resin or they were submerged by the latter and were found at the beginning of the egg-tunnel.

Ips perturbatus cannot breed on a healthy white spruce; the large amount of resin produced by the injured tree prevents the beetles from excavating the egg-tunnel.

B.- On balsam, (*Abies balsamea* Mill.)

1.) On June 10th, about 20 beetles were placed on a tree blown down by the wind during the previous winter. On July 12th, many entrance-holes were seen on the bark, but none of the entrance-tunnels reached the cambium. In one case only, a female had started to cut an egg-tunnel of about 1/4 of an inch long, but did not deposit any eggs and the beetle was found dead in the tunnel.

2.) Another experiment made on a standing balsam failed to produce any result.

It seems certain that Ips perturbatus cannot live on balsam; not on account of the resin, since in the first experiment on this species the tree had been dead for several months and there was no resin production. The tree, is inherently unfit for Ips development.

C.- On black spruce, (Picea mariana Mill.)

1.) About 20 beetles, caged on June 27th on a healthy black spruce cut many entrance-tunnels but were quickly driven back or submerged by the flow of resin.

2.) On June 28th, two days after a black spruce 7 inches in diameter had been cut, ten Ips perturbatus were caged on it. The beetles entered under the bark, three of them excavated egg-tunnels about two inches long and were still living when the cage was opened on August 30th, but none of these females had laid any eggs.

3.) Twenty-five Ips perturbatus were caged on the 30th of June on a black spruce 7 inches in diameter and heavily injured by Diprion polytomum; the defoliation amounted to about 75%. Many beetles cut their entrance-tunnels, and when the tree was examined on August 28th, a few had excavated egg-tunnels about an inch long, but all had been drowned eventually by the resin flowing in the galleries.

4.) On July 1st, twenty-five beetles were placed on a standing black spruce,which was dry on one side. The defoliation, which was nearly total,— only few green needles remaining at the top of the tree— was also due to the ravages of the spruce saw-fly. The females cut their egg-tunnels, laid eggs which hatched, and the larvae lived all summer. But on September 1st, when the cage was opened, these larvae were still quite small and seemed to be struggling very hard for their subsistence. It is probable that they would not have been able to reach the adult stage before the advent of the first snow.

These experiments on black spruce indicate that Ips perturbatus cannot live on a healthy tree or on a tree partly defoliated by Diprion polytomum. They can, however, excavate their egg-tunnels and the larvae will be able to live on a tree much weakened and almost completely defoliated by the spruce saw-fly, but it is doubtful whether the larva could reach the adult stage. Even Dendroctonus piceaperda in certain districts do not, under natural conditions, breed on the black spruce; Thus, Watson ('28) reports that in Algoma district, Ontario, Dendroctonus is never found on black spruce. In Gaspé, however, the same author occasionnally found a few black spruce killed by Dendroctonus and, as Ips perturbatus generally breed on the same trees as Dendroctonus, it is possible that they might succeed in living on dying or dead black spruce, but the percentage of mortality among the larvae would be very high and, in nature, no Ips colony has ever been found by the writer on this species of tree.

V.- THE INSECT AND ITS LIFE HISTORY

A. - Description of the Insect

1.) Egg.

When first deposited, the eggs are opaque and milky white in colour. They are elliptical in form, with one side rounded and the other very slightly concave in middle (Pl. II, fig. 1.). They measure on the average 1.06 mm. in length by 0.68 mm. in width.

2.) Larva.

The larva is a cylindrical, footless grub, with the body transversely wrinkled, curved and tapered towards the rounded posterior end (Pl. I, fig. 1.). Just after hatching, and during all its feeding period, the larva is whitish; the head is yellowish and the teeth of the mandibles dark brown. When newly hatched the larva is just a little longer than the egg and the head, which is spherical, is about as long as the rest of the body, measuring 0.53 mm. in length, while the total length is not over 1.1 mm.

When full- grown, about a month after hatching, the larvae are of a pinkish cream or flesh colour but after completing the pupal cell, they stop feeding, void excrement, and become snowy white in colour; the larva is then referred to as the prepupa. During their development and especially in the last stage, the larvae are so distended by the amount of fat they have accumulated that the segmentation is very indistinct. The length of the full-grown larvae varies from 5.1 to 5.5 mm., while their greatest width as measured on the thorax, is about 1.70 mm. In the last stage the head-width is 0.93-0.94 mm.

Owing to the limited time at my disposal, no regular collection of larvae and, consequently, no head measurements were made to obtain information on the number of larval stages. The number of larval stages varies greatly among the Scolytidae; Prebble ('33) found four larval stages for <u>Dendroctonus simplex</u> Lec. and three for <u>Pityokteines sparsus</u> Lec., while Blackman and Russo, working respectively on <u>Pityogenes hopkinsi</u> Sw. and <u>Chaetoptelius vestitus</u> Fuchs, found that the larvae pass through five stages before they reach the pupal stage.

3.) <u>Pupa</u>.

The newly formed pupae are snowy white, but later on, before they change to adults, they become light yellow in colour. They vary in length from 4.67 to 5.07 mm., while the width is about 1.87 mm. The elytra are generally half opened, but when the pupa grows older they lie on the side of the abdomen leaving the dorsal part uncovered. The abdomen itself terminates in two brown-tipped horns (Pl.I, fig.2).

A constant number of brown setae is always present on the head, thorax and abdomen of the larva and pupa. A nomenclature has been devised for those setae by Russo ('26) and was modified by Schedl ('31). Those found on the pronotum of the pupa are illustrated on Pl. II, fig. 2. The others are not discussed here.

4.) Adult.

Just after emergence from the pupal skin, the young adult is of a creamy colour; it starts to feed almost immediately and takes, then, a yellow colour which becomes light brown by the time it is ready to leave the tree in the fall. The following spring, the young adult is of a dark brown colour when it emerges from the ground, and during the summer it becomes blackish.

The length of the beetle varies from 4.6 - 4.85 mm. The elytra are of about the same width as the pronotum, which measures 2.0 - 2.1 mm. in length and is almost exactly as long as wide. The elytral disc averages 2.5 mm. in length; it is excavated behind and possesses four teeth on each side (Pl. I, fig. 3, 4).

The following technical description is from Dr. Swaine ('18) page 109: "Antennal club with arcuate sutures; length 4.0 - 5.5 mm., stout, elytral disc little longer than the pronotum; striae usually impressed, with interspaces convex; pronotum very short and stout, not longer than wide; declivital teeth stouter; 1st two interspaces granulate, punctate, hairy to the base; the pronotum sparsely, finely punctured behind; the pubescence erect, abundant; the profile of the elytral suture on the disc strongly arcuate."

B.- Life History.

Like most Insects, Ips perturbatus passes through four distinct stages during its life-history. These are the egg, the larva, the pupa and the adult. The adult, which is a small brownish or blackish beetle, flies throughout the first half of the summer. It usually attacks the middle and upper portion of the trunk of white spruce killed by Dentroctonus the previous year, but occasionally it goes to white spruce heavily defoliated by the spruce saw-fly. The adults hibernate in the moss and emerge from the ground the following spring, at the beginning of June, to enter trees attacked by Dendroctonus. The male cuts the entrance-tunnel through the bark, then, builds the nuptial chamber which lies partly in the bark and partly in the wood. He is soon joined by one to four females, each of which digs her own egg-tunnel between the bark and the wood, The female deposits each egg in a separate niche along the sides of the gallery. From these eggs, larvae hatch and feed on the inner bark for about a month, i.e. until full-grown; then, they excavate the pupal cells and transform to pupae. The first pupae appear at the beginning of August and in from 9 to 14 days, they change to adult beetles. The latter feed for 1.½-2 months, leave the tree through exit holes and fall to the ground to hibernate in the moss. The adults live for nearly two years;

they mature in the fall, hibernate in the ground, emerge the following spring, and during this first summer the females may cut two sets of egg-tunnels. They overwinter a second time, lay their eggs again the following spring and die during the summer.

VI.-BIONOMICS

A. -Adult-

1.) Teneral Period.

A tree, infested by *Ips perturbatus* in early June, was cut at the beginning of July, and examined about twice a week by removing a small piece of bark. The first newly transformed adults were found on July 30th, but they were few in number. On August 1st and 2nd, however, about 25% of the pupae had reached the adult stage. The young beetles feed very extensively;they obtain their food solely from the fiber of the bark, changing it to a kind of brown dust and leaving the larval mines and pupal cells almost unrecognizable.

On August 4th, a log of three feet long obtained from the tree under observation, was placed two feet above the ground and a mat, surrounded with "tanglefoot", was placed underneath to catch the beetles as they emerged. It was thought then that they would feed for a month or so and, subsequently, would leave their host by the beginning of September. However, they did not leave the log until September 22nd. This proves that the young adults feed for about seven weeks, nearly two months, before they emerge from their host. Of course, this statement applies only to the young beetles which reach the adult stage early in August. If the pupae transform to adults only at the beginning of September, as some do, they can not feed much more than a month before the advent of the first snow ~~and~~ at which time they leave their host; these younger beetles can be recognized the following spring by their color which is of a paler brown.

Occasionally some pupae do not reach the adult stage until the middle or at the end of September. In this case, the young beetles are still very immature at the time of the first snows and since they are unable to hibernate in the tree they die during the winter. Formerly, from cursory observations the belief was held (Swaine '18) that the young adults could emerge from their host towards the end of July, and that there were two generations a year or at least one and a partial second, but the above study indicates that such is not the case in the Gaspé Péninsula.

2.) <u>Emergence from host-tree and hibernation</u>.

Many Scolytidae, such as <u>Dendroctonus</u> and <u>Dryocoetes</u>, pass the winter as larvae or adults in their host-tree under the bark. Others as <u>Ips perturbatus</u> and <u>I. borealis</u> leave their host in the fall and hibernate on the ground in the moss. This habit, however, is not common to all the species of the genus Ips; thus Ips longidens, like Dendroctonus, hibernates in the larval or adult stage under the bark where they had matured from the eggs (Blackman '19).

It was believed for a long time that Ips perturbatus, like many Scolytidae, pass the winter in their host-tree. To the best of my knowledge, Watson ('27) was the first and the only worker to give the correct information on the hibernating place of this species. Working in Algoma district, Ontario, he found that they overwinter as adults, after leaving their tunnels in September and October to hide in the ground.

With few exceptions, the same habit obtains in the Gaspe. The larvae in general reach the adult stage between the first week of August and the beginning of September. As said before, the young beetles feed for 1½ - 2 months and then drill through the bark to make an orifice, or "exit-hole" of the same diameter as that of the entrance-hole bored a few months previously by the parent beetles. In winter, a tree which was severely infested by Ips perturbatus during the summer, is completely free of living insects belonging to this species. The young beetles, which have matured too late in the fall to leave their host before the fall of the first snow, are always killed by the low winter temperature and are found dead under the bark the following spring.

Early in the spring, large numbers of beetles can easily be found in the moss beneath the tree attacked by them during the previous year. Many beetles are also found in the detritus scattered on the ground; under the bark of fallen trees, in the crevices of old stumps or any other obstacles which stop the insects in their fall before they reach the ground. Some are even present in old Dendroctonus tunnels at the base of the infested tree.

In general, it can be said, that the beetles leave their host-tree in the fall to hibernate in the ground. However, if a tree infested by Ips perturbatus is cut during the summer, although the majority of the adults will leave the tree in the fall, quite a few will hibernate in their host and emerge from it the following spring. This was observed last spring when I found several living adults under the bark of a tree attacked by Ips perturbatus the previous year and cut during the same summer. The same phenomenon was also observed in another tree presenting exactly the same conditions. Believing, then, that even in standing trees few adults might succeed to stand the winter in their host, I immediately cut two trees infested by Ips during the previous year, however not a single living beetle was found in either of them. It may be assumed, that in standing trees these insects leave their host in the fall, because they can not resist the low temperatures of the open during the winter, and they shelter themselves under the snow where the minimum temperatures are much higher than in the open. It is probably for this reason, that when an infested tree lies on the ground, the adults which have not left the tree before the advent of the first snow, succeed in hibernating in their host tree.

fig. 2.- Wooden frame(on which a mat was nailed) used for records of <u>Ips perturbatus</u> emergence in the fall.

In order to secure exact information as to the time of exodus of the young beetles from their host, a large mat was nailed on a wooden frame (fig. 2.), constructed by the middle of the summer at the base of a tree attacked by Dendroctonus and subsequently infested by Ips perturbatus. The frame formed a square of 8'x 8', and the small joists on which the mat (consisting of factory cotton) was nailed, were two feet above the ground. A band of tanglefoot two inches wide surrounded the mat, while another band was also placed on the mat, just around the base of the tree to prevent the beetles from climbing the trunk, in a third band of tanglefoot surrounding the tree itself and placed at one foot above the mat. This third band was used to discover if the adults, when they leave their exit-hole, simply fall down from the tree or crawl down the trunk as some of Mr. Watson's observations in Ontario seemed to indicate.

This mat was constructed by the end of August (23rd), and was examined at least twice a day, generally at 11.45 a.m. and 5 p.m. Table II shows the daily emergence from August 24rd to September 28th.

The young adults began to abandon their host in appreciable numbers on September 23rd. However, the great majority probably emerged only at the beginning of October. As I was forced to leave the district by September 28th, the daily examinations had to be discontinued.

Although no young beetles left their host

Table -II-

Emergence period of <u>Ips perturbatus</u> in the fall.

Date	Old parent beetles	Young adults
Aug. 24	26	-
" 25	10	-
" 26	4	-
" 27	5	-
" 28	2	-
" 29	1	-
" 30	2	-
" 31	7	-
Sept. 1	-	-
" 2	1	-
" 3	-	-
" 4	14	-
" 5	6	-
" 6	1	-
" 7	2	-
" 8	1	-
" 9	-	-
" 10	1	-
" 11	-	-
" 12	1	-
" 13	1	-
" 14	-	-
" 15	-	-
" 16	2	-
" 17	1	-
" 18	-	-
" 19	10	-
" 20	3	1
" 21	3	2
" 22	-	-
" 23	4	6
" 24	1	6
" 25	-	7
" 26	2	15
" 27	4	14

before September 20th, the emergence records for each day are given from August 23rd to show that there is, during the entire summer, a more or less continuous emergence of the old black parent beetles. At the end of August, however, these beetles do not go to new trees to lay more eggs as they do in July; they merely hide themselves from the light in the folds of the mat. The old beetles leave their tunnels before the young adults simply because they have been feeding during the entire summer.

No beetles were found on the band of tanglefoot placed on the mat around the tree or the one surrounding the trunk of the tree itself. It can therefore be assumed, that the insect does not crawl down the trunk but simply lets itself drop to the ground. On leaning trees, however, it might be possible, as suggested by Mr. Watson, that the beetles crawl down the trunk from the exit-hole.

The number of beetles which left the tree after September 20th, is certainly greater than what is indicated by the records. The action of the wind and the rebounding of the insect from one branch to another may cause it to fall much farther from the trunk than four feet. Nevertheless, the table gives a good idea of the beginning of the emergence and its rate of increase.

It was also discovered that these insects, although very small, could after a few hours of struggle pass through a band of tanglefoot two inches wide; this was the reason for inspecting the mat twice a day and sometimes oftener at the end of September. The majority of the beetles were found in the folds formed at the corner of the mat. For the above two reasons, in the construction of apparatus of that kind for the study of bark-beetles, a board 2" to 3" wide should be nailed around the mat, and the beetles being more easily caught in such a device since they would hide themselves under the board. A narrow band of tanglefoot on the board would increase the efficiency of the trap.

3.) Spring emergence.-

Ips perturbatus emerges in the spring as soon as the snow has disappeared and the ground is thawed.

Two emergence cages were constructed to follow the period of emergence. One of the two, Cage A, was built on the slope while the other, cage B, was set in the valley. These cages (fig.3) measured 2' long X 2' wide x 2' high, and were placed at the base of a tree. The cheese cloth covering was kept in place by tacks only half nailed to each corner-post to facilitate its daily removal for the liberation of the beetles. As soon as they come out of the ground, the beetles, attracted by the light, go to the top of the cage and gather in the folds of the cheese cloth especially at the upper corners where they were collected at the end of every after-noon.

The results obtained from these cages seem to show that other factors being equal, the beginning of the emergence period varies with the topography of the

fig. 3.- Ips perturbatus, showing spring emergence cage.

site, being earlier on the east slope than in the valley; thus in cage A, the first beetles emerged from the ground on June 3rd, while in the valley they were not observed until June 8th, i.e. five days later. It is quite possible that the daily period of insolation being longer on the east slopes than in the valley may produce this accelerated or delayed emergence.

Table III shows the length of the emergence period in the valley and the number of Ips perturbatus collected every day in cage B. The temperature and precipitation records for every day are also included in order to show the relation which exists between these two factors and the emergence.

It can be seen from Table III that the emergence is intimately connected with the factor of precipitation. The temperature also influences the emergence period, but to estimate this influence properly, temperature records should also be taken under the moss within the cage. However, such records were not available, due to lack of thermometers. The second week of July was very warm but at that time all the beetles had emerged from the ground, since none were found in the cage after July 11th.

One may wonder if the larvae which hatch from eggs laid by females emerging as late as July 11th, will reach the adult stage early enough to leave their host before the advent of the first snow. This is dealt with in detail further on, but it can be said here that the progeny of parent beetles caged on July 9th reached the adult stage by September 7th.

Table -III-

Emergence period of Ips perturbatus in the spring.

Date	Emergence	Precipitation	Mean temperature at 4' from the ground[1]
June 8.	44	-	43.25
" 9.	-	Trace	43.25
" 10.	64	-	53.00
" 11.	-	0.30	50.85
" 12.	-	rain	51.85
" 13.	-	rain	46.40
" 14.	-	rain	45.15
" 15.	-	0.68	45.55
" 16.	-	-	48.25
" 17.	46	-	52.00
" 18.	-	0.09	54.40
" 19.	31	-	58.20
" 20.	-	0.70	49.85
" 21.	43	-	54.70
" 22.	-	0.30	53.30
" 23.	-	-	52.45
" 24.	20	1.98	57.25
" 25.	-	0.04	55.30
" 26.	-	-	53.25
" 27.	2	-	51.00
" 28	7	-	54.10
" 29	-	0.55	55.80
" 30	-	-	52.75
July 1	16	-	52.30
" 2	-	0.74	57.00
" 3	-	0.04	55.80
" 4	8	0.38	57.45
" 5	11	0.06	55.25
" 6	4	-	61.75
" 7	-	0.48	61.50
" 8	1	-	55.70
" 9	9	-	57.55
" 10	4	-	56.65
" 11	3	-	62.30

[1]e mean temp. was obtained by taking the average between the max. d min. temperature for every day.

4.) Entrance-hole and entrance-tunnel.-

Ips perturbatus tunnels are not as a rule mixed with those of Dendroctonus except on a small section of the trunk in the intermediate zone. Their entrance-holes are easily differentiated from those of Dendroctonus by the well known resin-tubes, found around the entrance-holes of Dendroctonus but never present around those of Ips perturbatus since the latter attack the trees only when they are partly dry. Furthermore, the entrance-holes of Dendroctonus are much larger than those of Ips, the former being 3.0 to 3.5mm. in dia. while the latter measure only 2.0mm. in diameter.

Quite often Ips perturbatus and Ips borealis share the same portion of the trunk and, to the uninitiated, their entrance-holes are difficult to differentiate since they are almost of the same size. The entrance-hole of Ips borealis is somewhat smaller and has an average diameter of about 1.3mm while, as already said, that of Ips perturbatus measures 2.0mm.

The entrance-tunnel passes through the bark and leads to the nuptial chamber; its length varies, with the thickness of the bark. On a standing tree these tunnels are always directed upward at an angle of 45 degrees. The diameter of the entrance-tunnel, and that of the egg-gallery, is just large enough to admit the cylindrical body of the beetle. The entrance-tunnels of Ips perturbatus are always cut by the males. Soon after the first beetles had emerged last spring, I opened a number of tunnels and wherever only one beetle was present, it was removed and preserved in alcohol for sex determination at some later date. On 17 tunnels thus opened and found to contain only one adult in the nuptial chamber all specimens proved to be males.

5.) Nuptial chamber.-

As stated in a previous chapter, the male cuts the entrance-tunnel, excavates the nuptial chamber, and is then joined by one to four females, each mining its own egg-tunnel. The nuptial chamber is the central part of this subcortical dwelling place, where all the passages, formed by the egg-galleries, radiate from it; it is more or less triangular or suboval in shape and of a quite constant size. The base of the isosceles triangle measures about 8mm. and its height varies from 12 to 14mm. The triangular shape is most striking in a triramous engraving, each egg-gallery beginning at an angle of the geometrical figure (PI. IV,fig.I). In a uniramous or biramous engraving, the nuptial chamber is more sub-oval in shape (PI.IV,fig.2,3). As Dr. Swaine ('18) writes, the chamber is used for several purposes: "It serves as a temporary storage room for boring dust thrust into it by the females working in the egg-tunnels; it is also used by the beetles for turning or reversing their position, particularly by species which cut no ventilation-tunnels; and it is used regularly for copulation. With polygamous species the male spends nearly all his time in the nuptial chamber and in the entrance-tunnel".

6.) Excavation of the egg-tunnel and food-tunnel.-

Several beetles were caged on June 10th and three days later, when the cage was opened, the examination of the tunnels already started showed that one female had mined her egg-tunnel to a length of 15 mm. and had excavated 5 egg-niches on one side of it. This shows that as soon as the female has entered the nuptial chamber and copulated, she begins to cut the egg-gallery and deposit eggs. This egg-gallery is made partly in the wood and partly in the bark. In a biramous or triramous engraving, the egg-tunnel opposite the entrance-tunnel is generally cut by the female which was the first to enter the nuptial chamber. Evidence of that is seen in uniramous engravings where the single egg-tunnel is always situated opposite the entrance-tunnel. this is also confirmed by the fact that in polygamous engravings, the egg-gallery opposite the entrance-tunnel frequently contains more eggs than the others, probably because these eggs are laid by a young female, which is laying her first set of eggs and, consequently, had entered the tree right after emergence early in the summer.

When a female has laid her first batch of eggs, she needs a period of feeding before starting to cut a second egg-tunnel. For that, she simply continues to mine and prolong the egg-tunnel which then takes the name of food-tunnel or "food burrow".

Some experiments were undertaken to know the rate at which the females bore their egg-tunnels, and at the same time obtain information on the length of the egg stage. Many beetles were put in cages of the type illustrated in figure 1; the tunnels cut by these beetles were examined every three days and the distance excavated was measured. Sixteen cages were constructed, each of them containing from 8 to 10 adults. In some engravings the beetles being disturbed, left their tunnels; others were killed when the cages were opened. In many tunnels, however, I was able to keep track of the work done by the females for a period of over a month. As expected there is a great variation in the distance excavated by the same female from one day to another, or by one female as compared with another. Some females mined only 13 to 14mm. in 3 days, while others mined over 22mm. in the same period of time. Certain tunnels were left undisturbed for a month and when they were opened after that period, I found some measuring 100 to 120mm., while others had a total length of only 40 to 50mm. These great variations, observed from one tunnel to another, are chiefly due to the different conditions found by the insect under the bark, such as notches, etc. But the daily variations in the length excavated by one female are mainly explained by differences in temperature, the insect being less active on cold days.

The information obtained on the egg stage is dealt with in another section of this paper.

7.) Egg-niches.-

The female of Ips perturbatus deposits her eggs singly in small notches or "niches" which she makes on each side of the egg-tunnel. These niches seen from above have a triangular appearance but from the side they are cup-shaped. The lumen of the niche is of about 1.25mm. long, while the depth varies from 1.0 to 1.25mm. If we compare these proportions with the size of the egg, which is 1.06mm. long by 0.68mm. thick, we find that the niche is much larger than the egg (PI. II,fig.3). This is necessary, however, since the egg is not simply deposited loosely in the niche, but is surrounded and packed with dust by the female. This dust does not project into the egg-tunnel but simply fills the niche in such a way that the sides of the egg-tunnels remain smooth.

Very often especially at the beginning of the egg-tunnel, there is only a short distance between adjacent niches. The niches are almost contiguous, and, as a matter of fact, I have counted as many as 20 egg-niches in 1½ inches. Since the opening averages 1.25mm., there is not more than a space of 0.5mm. or even less between two consecutive niches.

A peculiar and very interesting case is found when two egg-tunnels of different engravings are adjacent, being separated by less than ¼ of an inch as in PI. IV,fig.2,3,. In this case, the female which is the last to start the egg-tunnel (PI. IV,fig.2b) does not cut any egg-niches on the side contiguous to the other tunnel i.e. the right side in PI. IV,fig. 2b, probably because she is aware of the other female burrowing in the adjacent tunnel. Tunnels of that kind with all or most of the egg- niches constructed on one side of it and none or merely a few here and there on the other side were often found.

Occasionally, although the egg-tunnel may be quite long, the egg-niches are not numerous and are widely separated one from the other. This may be due to the fact that the female which excavated this egg-gallery was an old adult, which had already laid one or two sets of eggs before, and consequently had its power of reproduction much reduced. However, this subject requires further study.

8.) Ventilation-tunnels.-

These are burrows placed at irregular intervals in the roof of the egg-gallery and perpendicular to it. They may extend to or near to the surface of the bark or even only half-way through it. There is no rule for their distribution and number; sometimes in a long egg-gallery of three to four inches only one or two are present, while in other short galleries four or five may be found very near one another. (Pl. IV, fig. 1,2,3).

There are different opinions on the purpose of these tunnels, which are present in the egg-gallery of many species of Scolytidae. Some authors believe that they serve only for the aeration of the egg-tunnel. Barbey ('25) agrees with Chewyreuv that they serve the purpose of the nuptial chamber and he calls them "encoches d'accouplement" or copulation niches. He writes that: "Chewyreuv, ayant observé des Scolytides et Hylesines mis en élevage sous vitres, a pu constater que ces cavités n'avaient d'autre but que de permettre au mâle de s'accoupler pendant le forage de la gallerie de ponte". Dr. Swaine('18) states that they are used as "turning-niches" for the female while she lays her eggs and as storage-places for boring-dust. Hopkins('15) believes that they serve for ventilation of the gallery and as storage-places. There is probably some truth in all these statements. They may serve for ventilation but not exclusively for that purpose since some of them do not go through the bark. Furthermore, unlike the _Dendroctonus_ galleries, which often contain a mixture of resin and dust packed in the egg-tunnel, the _Ips_ galleries are, as a rule, always kept clean and have good aeration from the entrance-tunnel. It is also probable that the so-called ventilation-tunnels may serve for copulation as claimed by Chewyreuv and Barbey or as turning-niches while the female lays her eggs. But, if this be their only purpose, it is difficult to understand why some should be found even in the food-tunnels where no eggs are laid. Even in these food-tunnels they do not always serve for ventilation or as an opening to eject dust since some of them end bluntly in the bark. There is probably something more to be known about these tunnels.

9.) Fertility and longevity.-

It seems to be quite a common habit for many scolytid females to excavate more than one egg-tunnel in the same season. Dr. Swaine('25) states that apparently *Ips perturbatus* and *Ips borealis* Sw. cut two egg-tunnels in the same summer. Watson('28) wrote that *Dendroctonus piceaperda* Hopk. lays two sets of eggs in the same season. Simpson('29) records *Polygraphus rufipennis* Ky. as cutting three egg-tunnels in the same year and a fourth one the following spring before they die; he also found ('29a) that the female *Dendroctonus simplex* Lec. lays three sets of eggs during the same season. De Leon & Bedard('34) working on *Dendroctonus monticolae* Hopk. found that two egg-tunnels are also cut by the females during the same summer.

To gather further information on that point sofar *Ips perturbatus* Eichh. is concerned, a log of 12" diameter by 3' long and heavily infested by *Ips perturbatus* on June 4th and 5th, was caged on July 5th with another log 7" in diameter by 39" long, obtained from a tree blown down by the wind the previous winter and free of any kind of bark-beetle attack. At that time (the beginning of July), the beetles were well established in the infested stick and some eggs had already hatched. These two logs when peeled on September 5th, revealed 42 egg-tunnels in the fresh stick while the original infested log contained 106 egg-tunnels.

The result indicates then that 40% of the females left the original stick and entered the fresh one to lay a second set of eggs. In reality the percentage, however, should be much higher than that since the infested log was not caged until a month after the original infestation and it is very probable that some females had already left the log when the latter was placed in the cage. Moreover, some females after they had completed their first egg-tunnel, might have come out and started to cut a second egg-gallery on the same log instead of entering the fresh stick. Nevertheless, the experiment shows that a high percentage of the females, if not all, lay two sets of eggs in the same season.

Many old parent beetles — differentiated from the young by the black colour — leave their host tree in the fall to pass a second winter in the ground. Thirty-six of these old black beetles, were kept separately in the moss to determine if they would die during the winter or emerge again the following spring and lay more eggs. Of these beetles, thirteen were living the following spring(1934). On June 4th, they were placed in three holes of ½" square, made in the bark of a log of spruce obtained from the top of a tree attacked by Dendroctonus the previous year; each hole was covered with celluloid and fastened to the bark with adhesive tape. When the log was examined on August 9th, two egg-galleries were found, one containing eight egg-niches and the other ten; the progeny at that time were pupae and full-grown larvae. All the old parent beetles were dead in the galleries. The reason why only two egg-tunnels were excavated, may be partly attributed to the fact that only a small proportion of the surviving beetles were of the female sex.

The conclusions of these experiments are:

1.) That the females of <u>Ips perturbatus</u> lay two sets of eggs during the same season.

2.) That the reproductive power of the female is greatly reduced following the second period of hibernation.

3.) That the adult stage in some instance lasts nearly two years, the old parent beetles hibernating in the ground the second year to lay a third set of eggs and die during the summer.

10.) <u>Relation between fecundity and proportion of sexes in the engravings.</u>-

If the bark of a tree infested by <u>Ips perturbatus</u> is removed we find numerous nuptial chambers, each of them used as rallying-place for two, three or even four females each mining her own egg-tunnel.

Between the middle of July and the beginning of August two trees were peeled and studied to have an exact idea of the proportion of the females in these different types of brood burrows and the average number of eggs laid per gallery for each type. Often the egg-tunnels of two different engravings unite and are mixed over a part of their length; this occurs chiefly when the density of attack is

Table -IV-

Results of the study of 87 engravings of <u>Ips perturbatus</u>

a.) Tree no. 1:-Tree examined between July 13th and July 15th.
37 engravings or 70 egg-tunnels yielding a total of 2138 eggs.

Type of engraving	%	Average no. of eggs per engraving	Average no. of eggs per egg-tunnel	Average length of the egg-tunnel
Uniramous engrav.	40.5	37.7	37.7	2.92
Biramous engrav.	32.4	60.8	30.4	2.66
Triramous engrav.	24.3	86.4	28.8	2.66
Quadriramous eng.	2.7	101.0	25.25	2.25
Average		58.68	32.80	2.75

b.) Tree no. 2:-Tree examined between Aug. 6th and Aug. 10th.
50 engravings or 95 egg-tunnels yielding a total of 2614 eggs.

Uniramous engrav.	34.0	35.00	35.00	3.25
Biramous engrav.	46.0	62.40	31.20	3.01
Triramous engrav.	16.0	75.00	25.00	2.83
Quadriramous eng.	4.0	75.48	18.87	2.20
Average		55.62	31.00	3.00

c.) Total average:- 87 engravings or 165 egg-tunnels yielding a total of 4752 eggs.

Uniramous engrav.	36.8	36.2	36.2
Biramous engrav.	40.2	61.8	30.9
Triramous engrav.	19.6	79.8	26.6
Quadriramous eng.	3.4	86.4	21.6
Average		57.0	31.8

high. Except such engravings as were not distinctly separated one from the other, all those occurring on definite portions of the trunk were studied.

Table IV, presents in summary the various data derived from a careful study of 87 engravings. It can be seen from the figures presented in this table that a.) the biramous engravings are the most commonly found, b.) the average number of eggs per egg-tunnel decreases with the number of females per engraving, c.) the number of eggs per egg-tunnel average, on the whole, approximately 32.

Tree no 2 was studied two weeks later than tree no 1. During this period the females were feeding all the time, increasing consequently the length of the egg-tunnels in the second tree. This explains why the average length of the egg-tunnels is higher in the latter tree and also why the total average length was not included in part "c" of the table.

As just said the highest average number of eggs per egg-tunnel is found in the uniramous engraving; the average decreases as the number of females per engraving increases. The decrease in the fecundity is not, however, directly due to the proportion of the sexes in the brood burrows since small numbers of eggs were sometimes found even in uniramous engravings. The reason is to be found in the fact that in brood burrows of two, three or four egg-galleries, the probabilit~~ies~~y is two to four times greater that one of

Table -V-

Number of egg-niches per egg-tunnel in the different types of engravings.

Number of eggs per egg-tunnel	Occurrence in the different types of engravings.							
	Uniramous engraving		Biramous engraving		Triramous engraving		Quadriramous engraving	
	No	%	No	%	No	%	No	%
1 to 10	0	0	2	2.8	3	6.0	1	8.4
11 - 20	1	3.1	10	14.1	10	20.0	6	50.0
21 - 30	6	18.8	23	32.4	22	44.0	3	25.0
31 - 40	17	53.1	19	26.8	9	18.0	2	16.6
41 - 50	5	15.7	8	11.2	6	12.0	0	0
51 - 60	2	6.2	5	7.1	0	0	0	0
61 - 70	1	3.1	4	5.6	0	0	0	0

female will be excavating her second or even third egg-tunnel, i.e. that she will have her reproductive power greatly reduced(see paragraph 9, on fertility and longevity). We also know that the male after he has constructed the nuptial chamber early in the spring, is soon joined by the females. In a uniramous engraving there is more chance that this first and single female, which joins the male at the beginning of the season, will be laying her first batch of eggs and, consequently, able to produce the maximum number of eggs. Table V shows that large number of eggs per egg-tunnel was not limited only to the uniramous engravings, although on the whole the females under monogamic conditions produce more eggs than under conditions of bigamy or polygamy.

Sixty-nine eggs is the greatest number of eggs observed in one egg-tunnel and was found in a biramous engraving, while the smallest number was six eggs found in a branch of a triramous engraving. Table V shows that the majority of the uniramous engravings contain between 31 and 40 eggs; the biramous 21-40, while the average for the triramous lies between 21 and 30, and only between 11 and 20 for the quadriramous engravings.

11.) Numerical relation of sexes.-

From what has been observed in the brood burrows, there are nearly two females to one male. However, the dissection of 500 young beetles, obtained from the same portion of a tree, revealed about an even number of males and females, namely

242 females and 258 males or 48% and 51.6%.

Blackman ('15) working on Pityogenes hopkinsi Sw., explains this anomaly between the actual counts and what is found in the brood burrows by two factors:a.) Some males die bachelors in their nuptial chamber not succeeding to attract any female,b.) the male is preyed upon by predaceous birds and insects while he is making the entrance-tunnel or he may be washed from his burrow by beating rain. There is probably some truth in Blackman's statements, but these factors alone can certainly not explain the disproportion of nearly two females to one male found in the brood burrows of Ips perturbatus. It is also doubtful that they could explain the disproportion, which is sometimes even greater, in the brood burrows of all the polygamous species of bark-beetles. Although I have stripped the bark of many Ips perturbatus trees and examined hundreds of engravings, I can not recall ever having found even a single burrow containing a male by himself; the proportion of these bachelor burrows, however, should be quite high to explain, even only in part, the disproportion of 2 or 3 females to 1 male found in brood burrows of polygamous species. With regard to the second factor, insofar as Ips perturbatus is concerned, the influence of predaceous birds and insects amounts to almost nothing; Ips perturbatus is usually found where Dendroctonus occurs, and the woodpeckers which are the most effective predaceous birds are much more busy working on the comparatively big and plump Dendroctonus larvae than on small Ips mining their entrance-tunnel in the upper part of the tree.

It appears to me that this disproportion of the two sexes in the brood burrows of polygamous species of Scolytidae could be readily understood if we generalize two facts common to many polygamous species:a.) that among polygamous scolytids, the entrance-tunnel is excavated by the male, b.) that the female lays more than one set of eggs during the same season. Many authors such as Nusslin ('13), Blackman ('15), Escherich ('23) and others have noted that among the polygamous species, the entrance-tunnel is cut by the male. On the other hand, as said in a previous paragraph (9), many workers have also observed that among certain species of Scolytidae the female cuts more than one egg-tunnel during the same season. The observations made by the writer on <u>Ips perturbatus</u> in Gaspé Péninsula show that these two statements hold for the species. From all these observations we may legitimately conclude the following: The male digs the entrance-tunnel and is soon joined by the female who cuts the egg-tunnel and lays one complement of eggs. When the first egg-tunnel is completed, this female feeds for a while and then leaves that particular brood burrow to start a second egg-tunnel elsewhere. She can not, however, like <u>Dendroctonus piceaperda</u> or other monogamous species, cut her own entrance-tunnel and she has to look for one already made by a male. It generally happens, then, that she finds the latter already established with one or two females, but apparently the male readily receives this new arrival.

Therefore, although the total number of males and females is about even, Ips perturbatus practice polygamy because each female cuts two egg-tunnels during the same season and must rely on the good-will of the male for the excavation of an entrance-tunnel. As the latter digs only one of these entrance-tunnels at the beginning of the summer, we arrive at an approximation of two egg-tunnels per engraving.

B. - Egg

The length of the egg stage, as the length of all the following stages, varies with the temperature under which development occurs. The first beetles began to emerge last spring on June 3rd and 4th. Some were noted on a log on the 4th of June, but most of the tunnels opened at that time contained only one adult, always a male. On the 5th many females entered the tunnels and started to lay their eggs on June 6th and 7th. The tunnels on that particular log were examined every two days, but the first larvae were not found until June 24th. Hence, the eggs laid at the beginning of June took from 17 to 18 days to hatch.

The period of oviposition lasts about a month and half, from the beginning of June to the middle of july. The period of incubation for eggs laid in July was not observed, but the daily temperature in July being higher than in June, the period of incubation should not extend over two weeks.

C. - Larva

1.) Larval mines.-

The larvae excavate their mines in the inner layers of the bark only. They do not make any incrustation in the wood as do the females when they cut their egg-tunnels. Each larva burrows its own mine and the mines are always distinctly separated one from the other. They are filled with a dark-brown frass which the larvae leave behind them as they progress in their work. When the bark is removed from the tree, this frass makes the larval mines very conspicuous and easy to follow. They are more or less perpendicular to the egg-gallery for the greater part of their length but towards the end they are often directed upwards.

At their base the larval mines are almost linear, but they increase in width as the larva grows and when the latter is full-grown the mine is nearly 2.0mm. wide. (Pl. III, b) There is a great variation in the length of the mines; some measure only 40mm., while others are as long as 80 to 90mm. They are generally longer when the density of the population is low; thus if only a few beetles are caged on a log, the tunnels may reach 90mm., but if the tree is heavily infested, the larval mines are rarely longer than 60mm.

2.) Length of the larval stage.-

The appearance of the first larvae was observed on June 24th, and since some pupae were found on July 21th, we may conclude that the larval stage lasts about four weeks. As the temperature at the end of June is about the same as that of the end of August in Gaspé Peninsula, the length of the larval stage does not vary much, whether the eggs be laid early or late in the summer.

D. - Pupa

When full-grown, the larva makes the pupal chamber or pupal cell and then ceases to feed. This pupal cell, which is generally located at the end of the larval mine, is an oval cell with rounded ends (Pl. III, d.). It is constructed entirely in the bark and is about 3mm. wide x 6mm. long and 1.5mm. deep.

The first pupae were noticed last summer on July 21st. At that time many full-grown larvae, ready to pupate and easily recognized by their milky white color, were taken from a log and placed in a tin box between two moist pieces of bark. Four of these larvae pupated on July 25th. They were then removed and transfered on another piece of bark in a pupal cell previously made by other larvae. That bark was also kept on wet moss in a tin box and the piece of wood, which was originally covered by the bark, was fitted exactly and placed on top; thus the pupae were kept as nearly as possible under natural conditions. One of these pupae reached the adult stage on August 2nd, and the others on the following day.

The same observations were repeated at the end of August on full-grown larvae, which had developed from eggs laid at the beginning of July. Six of these larvae pupated on August 23rd and reached the adult stage on the following dates:

September	5th	1 larva
"	7th	4 larvae
"	8th	1 larva.

These two observations made at different times during the summer show that at the end of July the pupal stage lasts only 8 to 9 days, while by the end of August and the beginning of September, the daily average temperature being much lower, the pupal stage may be as long as 14 to 16 days.

E. - Complete Duration of the Post-Embryonic Development

Many beetles were caged at different periods of the summer and left undisturbed for 1½ to 2 months. When the tunnels made by these beetles were examined at the end of this period, most of the young were only full-grown larvae or pupae. They were then allowed to complete their development to the adult stage. In this manner, exact data were obtained as to the length of time required for the complete developmental cycle.

On June 3rd, many beetles were observed entering a log lying on the side of the road. This log was well exposed to the action of the sun. On July 29th, the first beetles to be seen that summer were found on that log, but they were not very numerous before the beginning of August.

The beetles obtained from the emergence cages on July 9th, were caged on a tree blown down by the wind the previous winter. When their tunnels were opened a month and half later (Aug. 20th), many full-grown larvae were found; these larvae pupated on August 23rd and reached the adult stage on September 7th.

These two experiments, with others not mentioned here made at different times throughout the summer, show that the duration of the post-embryonic development is about the same, approximately two months, whether the eggs be laid at the beginning of either June or July. The length of the larval stage is also the same (four weeks) in both cases. The pupal stage, however, is much longer towards the end of the summer than in beginning, being respectively 14 days and 9 days. Consequently, although no experiments were conducted for the late brood, the incubation period must be shorter at the beginning of July than in early June when the temperature is still quite low on certain days.

Table VI is a résumé which gives an approximate idea of the length of each stage in the early and late broods.

Table -VI-

Biographical dates on the early and late broods of 1934 in Gaspé Péninsula.

Early brood:

June 3rd and 4th............	Males enter the tree.
June 5th and 6th............	Females lay their first eggs.
June 24th..................	Appearance of the first stage larvae.
July 21st..................	Few larvae have reached the pupal stage.
July 29th and 30th.........	Larvae which pupated on July 21st reach the adult stage.

Late brood:

July 9th...................	Males and females caged on a tree.
July 10th..................	Females caged on July 9th lay their first eggs.
July 25th..................	Eggs hatch.
August 23rd................	Appearance of the first pupae.
September 7th..............	Young adults.

VII. - POPULATION IN A SINGLE TREE AND MORTALITY

The number of beetles breeding in an infested tree varies directly as the area of the tree harbouring Ips perturbatus. If the latter, instead of being the only species occupying the upper part of the trunk, is mixed with Ips borealis Sw. and Dryocoetes affaber Mannh., its number may be reduced to a minimum, sometimes less than 1000. However, in certain cases where the weakened condition of the tree is due not to Dendroctonus but to Diprion polytomum, Ips perturbatus may occupy the total area of the trunk and the number of larvae reaching maturity will, probably, be over 50000. This is, however, a case particular to the Gaspe Peninsula where two outbreaks, the Spruce Saw-fly and Dendroctonus piceaperda, occur presently. In general the portion of the trunk infested by Ips perturbatus varies between 15 and 30 feet and the number of beetles reaching maturity is of 10000 to 20000.

The most exact manner of obtaining information on the population of a tree infested by Ips perturbatus would be to peel carefully the whole tree under observation and make an exact count of the beetles found under the bark. It is possible, however, to have quite precise data by stripping the bark only on certain sections of uniform length and uniformly spaced. Owing to the limited time I had at my disposal, the latter method was the one followed **for the** population study.

The tree used had a total length of 66 feet and a D.B.H. of 9 inches. The distribution of the different species of bark-beetles under the bark of the trunk was, from the base to the top, as follows:

Dendroctonus zone: 13 feet long; dia. at the lower part, 9 inches; dia. at the upper part, 7 inches.

Ips perturbatus zone: 32 feet long; dia. at the lower part, 7 inches; dia. at the upper part, 4 inches; average circumference, 18 inches; total superficies, 48 feet.

Ips borealis zone: 18 feet long; dia. at the lower part, 4 inches; dia. at the upper part, 1 inch, i.e. 3 feet from the top.

Pityphthorus sp. zone: the last three feet.

On the portion of the trunk infested by Ips perturbatus, three sections, A, B and C representing the lower, middle and upper part of the infested portion, were cut. Their dimensions were:

Section A: 2 feet long x 20 inches circumference; cut at 9 feet from the base of Ips perturbatus zone, i.e. at 22 feet from the D.B.H.

Section B: 1 foot long x 16 inches circumference; cut at 17 feet from the base of <u>Ips perturbatus</u> zone, i.e. at 30 feet from the D.B.H.

Section C: 2 feet long x 15 inches circumference; cut at 22 feet from the base of <u>Ips perturbatus</u> zone, i.e. at 35 feet from the D.B.H.

These three sections being cut, the bark was carefully removed and an exact count of the egg-tunnels, egg-niches, larvae, pupae, young adults, parasites, etc., was made.

Among the different methods of analysing bark-beetle population, the one proposed by Golovjanko and later modified by Iljinsky seems to be the most suitable. These two quantitative methods of special population studies with many others are very well summarized in a paper by J.J. de Gryse ('34).

Using, with few modifications, the system of symbols devised by Iljinsky, the analysis of the above population study shows the following interesting facts:

A. - Number of egg-tunnels per square foot = 501[1]

M. - Number of egg-niches " " " = 1225

O. - Number of young adults " " " = 502

b. - Density of attack $= \frac{A}{1 \text{ square foot}}$ = 50

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[1] All these figures are obtained from section B only, since this is the only one where all the egg-niches were counted.

d. - Average number of eggs per egg-tunnel $= \frac{M}{A} = 24$

c. - Average number of young beetles per egg-tunnel $= \frac{O}{A} = 10$

f. - Percentage of mortality $= \frac{100(d - c)}{d} = 58.33$

The high percentage mortality "f" is the most striking character of all these data. This high percentage is almost entirely due to the factor "b", density of attack. Golovjanko was also of that opinion when he stated in his conclusions: "A decrease in, "b" is followed by (1) an increase in the number of larval tunnels; (2) an increase in the percentage of larvae successfully completing their development....." Illjinsky also shows conclusively that the density of attack is in itself a factor affecting the favourableness of the environment.

There are two reasons why a high density of attack of Ips perturbatus reduces the progeny of the families to less than half its original number: (1) The scarcity of food; in fact, it would be quite impossible for the progeny of 50 females per square foot laying a total of 1225 eggs thus giving an average of 9 larvae to the square inch, to reach maturity in such a restricted space. Some will necessarily die by starvation. (2) The other reason for this high percentage of mortality lies in the fact that when the density of attack is high the condition represented in Pl.IV, fig. 3a, is often found; that is to say, the egg-tunnels are very near one another, almost contiguous. In such a case, what evidently happens, is that when the young larvae of the egg-tunnel "3a" of Plate -IV- have fed until they reach the egg-tunnel 2b(Pl. IV.); they try to go through it, but the hardened dust which is deposited in the egg-niches on one and sometimes both sides of the tunnel "2b" will prevent the young larvae from crossing the second egg-tunnel and causing them to die at that point by starvation.

All the data obtained from this population study and not indicated in the previous figures are summarized in table VII.

It can be readily seen that the estimates for this particular tree give a total number of 2448 egg-tunnels or beetle families and 58800 eggs out of which a total of only 22512 larvae reached maturity.

Owing to the large number of egg-niches per square foot, those of section B only were counted and from this section the figures giving the percentage of mortality were obtained.

It should be noticed that the average number of living pupae and adults is lower at the upper part of the trunk (section C) than at the lower and middle parts, where we found the optimum conditions for _Ips perturbatus_. The thinner bark of the upper section makes the conditions less favourable for its development.

The item "dead adults and pupae" includes

Table -VII-

Population study of Ips perturbatus on white spruce.

Section	Living adults and pupae	Dead adults and pupae	Coeloides	egg-tunnels	egg-niches	young adults per egg-tunnel	% of mortality
A. (2'x 20"=3⅓f^2)	1737	104	75	189		9	
Average per f^2	521	31	21	57			
B. (1'x 16"=1⅓f^2)	669	91	21	67	1633	10	58.33
Average per f^2	502	68	16	50	1225		
C. (2'x 15"=2.5f^2)	956	53	91	115		8	
Average per f^2	384	21	36	46			
Tot. aver. per f^2	469	40	25	51		9	
Tot. popul. of the tree	22512	1920	1200	2448	58800		

chiefly the pupae, since more than 50% of the progeny had reached the adult stage when the work was done. Moreover, most of the deaths were caused by Coeloides dendroctoni Cushman which generally kill the full-grown larva and pupa. The number of dead pupae and adults in section B is much larger than in the other two sections; the higher percentage of mortality in this case was caused by a white fungus surrounding the pupal cells and killing the pupae. This fungus, however, was confined to only a small part of section B.

VIII. - PARASITES AND PREDATORS

As a general rule parasites do not play a role of great importance as factor of natural control of Ips perturbatus. And as can be seen by table VII of the previous chapter, although Coeloides dendroctoni Cushm. is about the only and certainly the most important parasite of Ips perturbatus, the percentage of mortality which might be attributed to it is not over 5.3%. On some trees these parasites seem to be concentrated more or less in spots, and under certain pieces of bark of about 6" x 10", groups of 15 to 20 cocoons were found.

Coeloides dendroctoni is also about the most important parasite of Dendroctonus piceaperda; it seems however to prefer Ips perturbatus, probably because Ips generally breeds in the upper part of the trunk where the bark is thinner and, oviposition easier. This seems to be confirmed by the fact that Coeloides is always more numerous on a Dendroctonus tree with rather thin bark. Thus these parasites are generally found in greater number on a tree 9" to 12" in dia. than on one 18" to 20" in diameter.

It should be mentioned that the Coeloides dendroctoni associated with Ips perturbatus although identical with the species feeding on Dendroctonus piceaperda, is however smaller than the latter in all its stages of development (larva, pupa and adult), probably because its host is also smaller.

Besides Coeloides dendroctoni, a few small Chalcids, which had reached the adult stage when collected at the end of August (29th), were also found in the course of the population studies. These parasites were identified by Mr. C. S. Walley as belonging to the genus Pachyceras, family Pteromalidae. The species of this genus seem to be associated with many different bark-beetles; thus De Leon ('34) records the species Pachyceras eccoptogastri as a primary parasite on Dendroctonus monticolae Hopk. The species found in the Gaspe Peninsula, however, is not common and seems to be of very little importance as a parasite of Ips perturbatus.

Although some predaceous insects may attack Ips perturbatus, none was noticed by the writer.

Among the predaceous birds, the woodpeckers, which are so effective on Dendroctonus are of very small importance as control agents of Ips perturbatus. This is understood if we consider that the woodpeckers are chiefly active in winter time when Ips are hidden in the ground and safe from their attacks. It is true that they could feed on them in the summer time, but since Ips perturbatus is usually closely connected with Dendroctonus piceaperda, the woodpeckers prefer to feed on the latter species. However, since Ips perturbatus can breed on heavily defoliated saw-fly trees and reach outbreak proportions even in the absence of Dendroctonus, the woodpeckers may in such circumstances exercise a measure of control. But actually such control, if any, must be very limited and sofar no trace of woodpecker work has ever been found when the trees were cut in the fall.

Therefore it may be asserted that parasites and predators are of secondary importance as control factors of Ips perturbatus. The only effective check on its increase is the absence of food, i.e. the absence of trees possessing the degree of weakness and dryness required to render them suitable as breeding places for the species. Consequently, the decrease of primary outbreaks caused by Dendroctonus piceaperda or by Diprion polytomum will be the only adequate factors in ending an Ips perturbatus outbreak.

SUMMARY.

Ips perturbatus generally follows *Dendroctonus* distribution and breeds on white spruce killed by *Dendroctonus* the previous year. In Gaspé, however, *Ips perturbatus* has been found inhabiting the trunk of white spruce heavily defoliated by *Diprion polytomum* Hartig.

The beetles could not be induced to breed either on living or dead balsam; on healthy white spruce and black spruce. In nature, they have never been found by the writer on dying black spruce, but under cage conditions the females cut their egg-tunnels, lay eggs and the larvae live all the summer. It is doubtful, however, whether they could reach the adult stage before the advent of the first snow.

The first newly transformed adults were found on July 30th. They feed very extensively upon the inner layers of the bark for a period of 1½-2 months and leave their host by the end of September and beginning of October to hibernate in the ground or in the detritus scattered on the ground.

The winter is always passed in the adult stage; no larvae or pupae have ever been observed to hibernate successfully. In winter time, a standing tree infested by *Ips perturbatus* during the summer, is always free of living insects belonging to this species. However, when the infested tree lies on the ground the adults succeed in passing the winter in their host, probably because they are protected by the snow from the low temperature prevailing above the snow-line.

The period of emergence from the ground in the spring 1934 lasted over a month i.e. from June 8th to July 12th.

The entrance-tunnel, which is always cut by the male, passes through the bark and leads to the nuptial chamber. On a standing tree the entrance-tunnels are generally directed upwards.

The nuptial chamber, as well as the egg-tunnel, lies partly in the bark and partly in the wood. It has a triangular or sub-oval appearance.

As soon as the female has entered the nuptial chamber and copulated, she begins to cut the egg-gallery and deposit eggs. These eggs are placed in small niches which are cut on each side of the egg-tunnel. At the beginning of the tunnel the niches are almost contiguous and as many as 20 egg-niches have been counted in 1½ inches.

In the roof of the egg-tunnel and placed at irregular intervals are short burrows extending near or through the bark and called ventilation-tunnels. The uses of these tunnels are varied and there are many opinions on their purpose.

Experiments made on the fertility and longevity of the beetle indicate that 1.) The females of Ips perturbatus lay two sets of eggs during the same season, 2.) The reproductive power of the female is greatly reduced following the second period of hibernation, 3.) The adult stage in some instance lasts nearly two years, the old parent beetles hibernating in the ground the second year to lay a third set of eggs and die during the summer.

The study of nearly hundred engravings revealed that a.) There are one to four egg-tunnels to each engraving, but the biramous engravings are the most commonly found, b.) The average number of eggs per egg-tunnel decreases as the number of females per engraving increases, c.) The number of eggs per egg-tunnel average, on the whole, approximately 32.

Although a polygamous species, the dissection of 500 young adults obtained from the same portion of a tree revealed about an even number of males and females viz., 52% males for 48% females. The disproportion of the sexes in the engravings is probably due to the fact that while one female may cut two egg-tunnels during the same season, she must rely on the male for the excavation of the entrance-tunnel and the latter cuts only one entrance-tunnel during the summer.

In early June the incubation period lasts

17 to 18 days, but in July the daily temperature being higher the egg stage should not extend over two weeks.

The larvae excavate their mines in the inner layers of the bark only. There are great variations in the length of these mines; some measure 40 mm., others 90 mm., but the average is about 60 mm. the length of the larval life is about four weeks.

The full-grown larva transforms to pupa in the oval pupal chamber. During the summer 1934, pupae were found on July 21st. and reached the adult stage 8 to 9 days later. But at the end of September the pupal stage may be as long as 14 to 16 days.

Analysis of a population study made on a white spruce representing 48 feet of tree superficies attacked by *Ips perturbatus* produced the following results: 2448 egg-tunnels, 21512 young beetles, 58800 egg-niches and a mortality rate of 58.33%. Overcrowding is mostly responsable for this high mortality.

Parasites and predators play a rôle of minor importance as factors of natural control. *Coeloides dendroctoni* Cushm. is the most important parasite of *Ips perturbatus*, but apparently does not kill more than 5% of the larvae and pupae. Few representatives of a *Pachyceras* species were also found. No trace of woodpecker control has ever been found by the writer on *Ips perturbatus*.

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A. R. Gobeil.

PLATE -I-

<u>Ips</u> <u>perturbatus</u> Eichhoff.

Fig. 1.- Larva. Magnified 7 dia. (Original).

Fig. 2.- Pupa. Magnified 7 dia. (Original).

Fig. 3.- Dorsal view of the adult. Magnified 20 dia. (After Swaine, D. C. D. A. Pamphlet 48 n. s.)

Fig. 4.- Adult, showing the declivital teeth of the elytra. Magnified 20 dia.(After Swaine, D. C. D. A. Pamphlet 48).

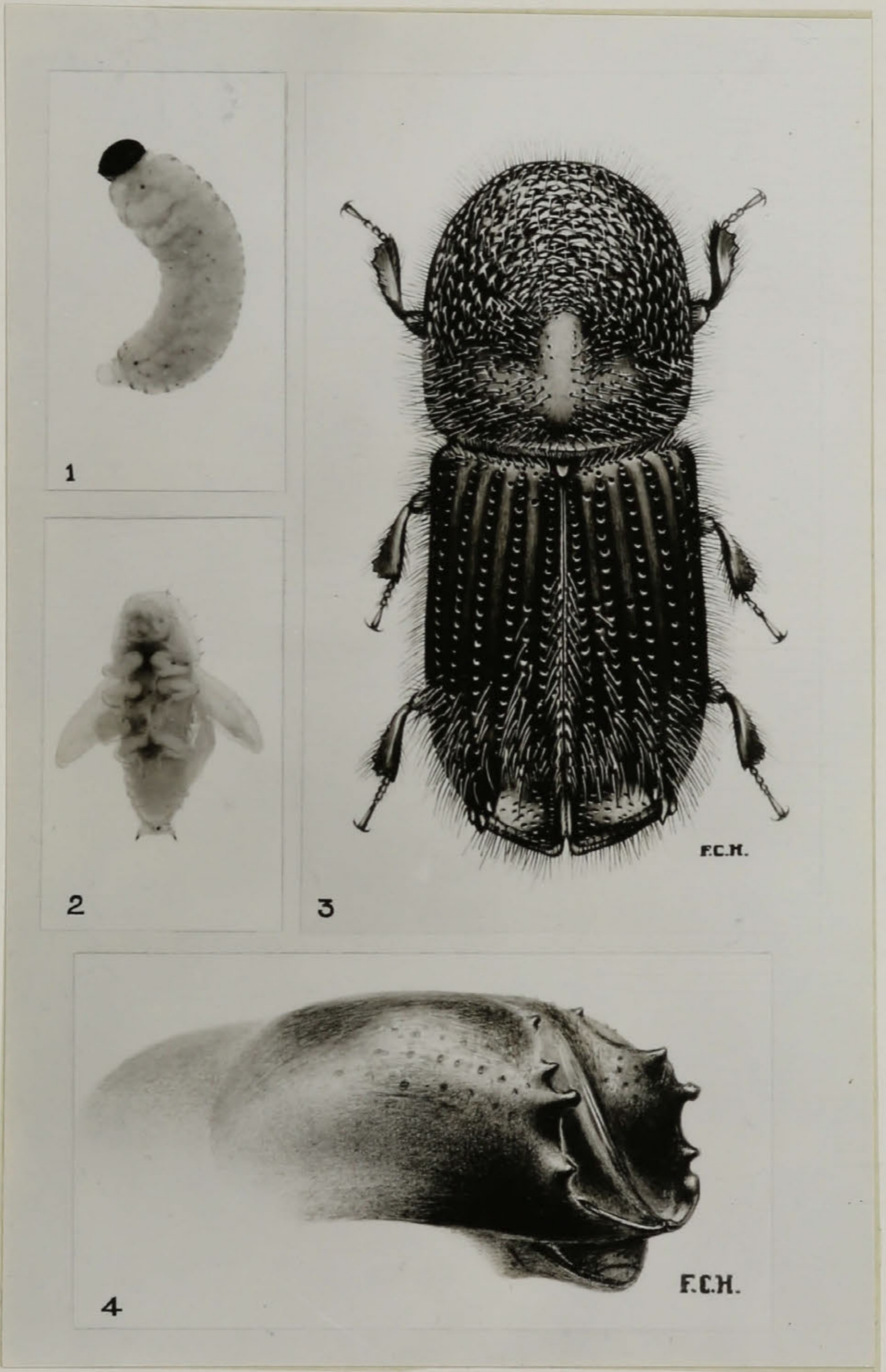

PLATE -1-

PLATE-II-

<u>Ips</u> <u>perturbatus</u> Eichhoff.

Fig. 1.- Egg. Magnified 25 dia. (Original).

Fig. 2.- Pronotum of pupa showing the arrangment of the setae. 1.) Protergal setae, 2.) medio-tergal setae, 3.) latero-tergal setae, 4.) postergal setae. Magnified 15 dia. (Original).

Fig. 3.- Section of egg-tunnel showing the egg-niches with the eggs in situ. Magnified 10 dia. (Original).

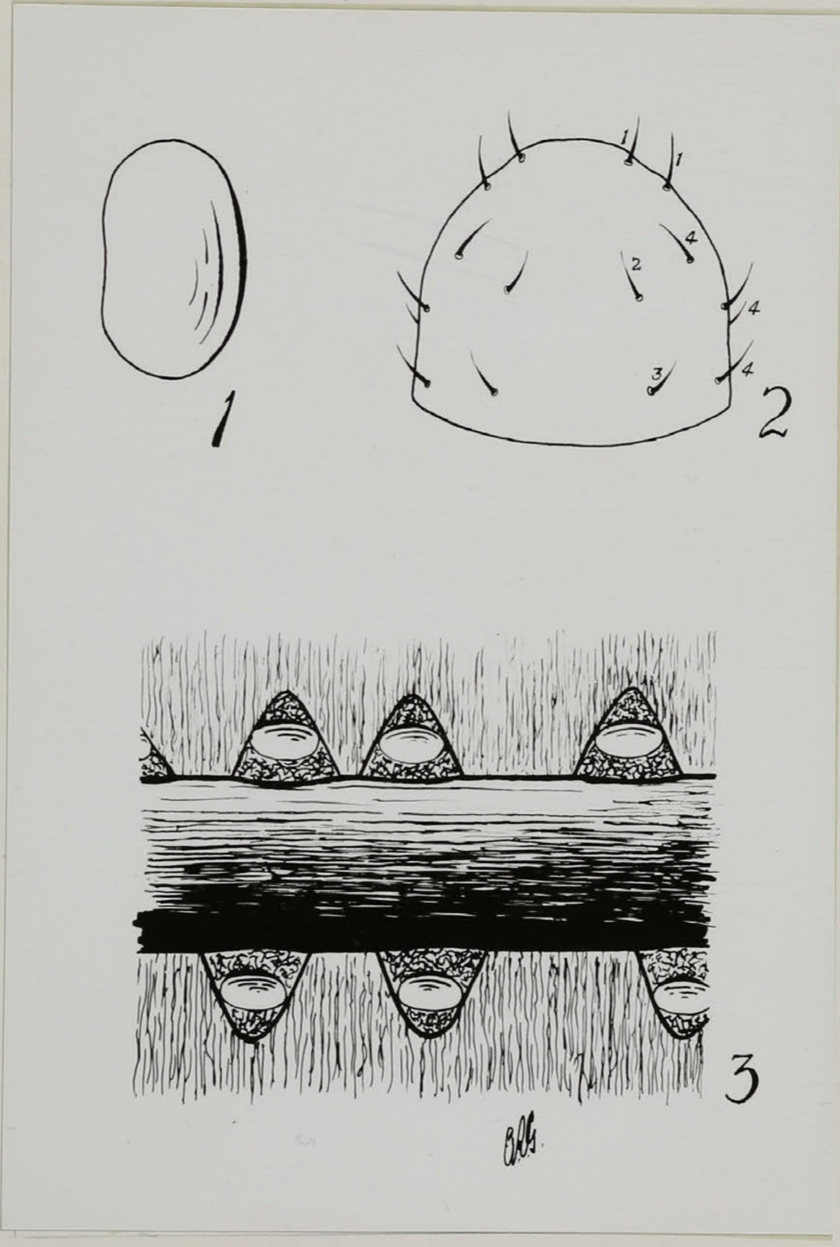

PLATE -II-

PLATE -III-

Ips perturbatus Eichhoff.

General appearance of engraving with two egg-tunnels. Natural size. (Original).

a.- nuptial chamber.

b.- larval mine.

c.- entrance-tunnel.

d.- pupal cell.

e.- ventilation-tunnel.

f.- egg-niche.

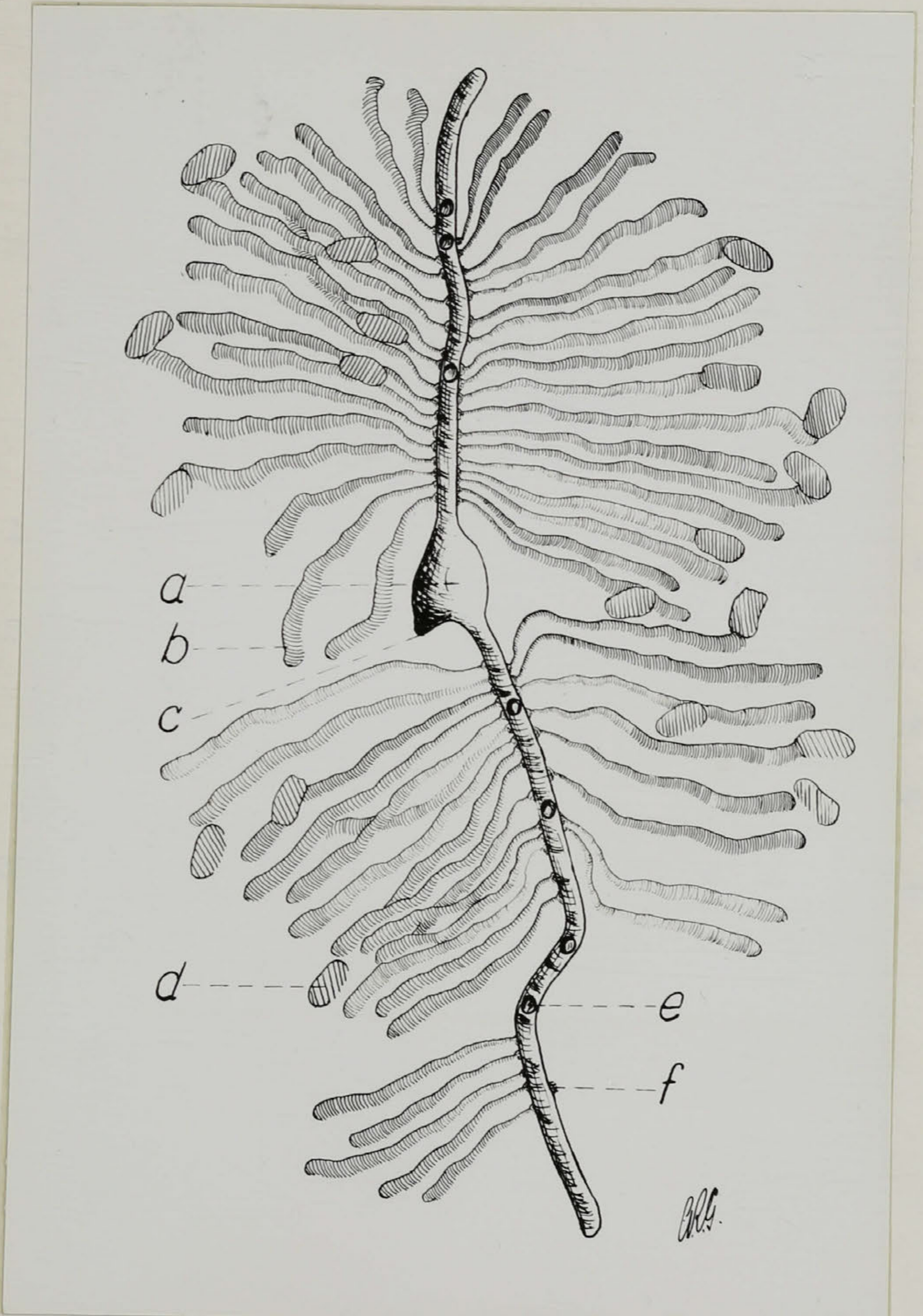

PLATE -III-

PLATE -IV-

Ips perturbatus tunnels.(Original).

All natural size.

Fig. 1.- Engraving with three egg-tunnels, a, b, and c, (Triramous).

Fig. 2.- Engraving with two egg-tunnels, a and b. Note that there are only 3 egg-niches on the right side of tunnel b. Explanation on page 37. (Biramous).

Fig. 3.- Engraving with one egg-tunnel, a. (Uniramous).

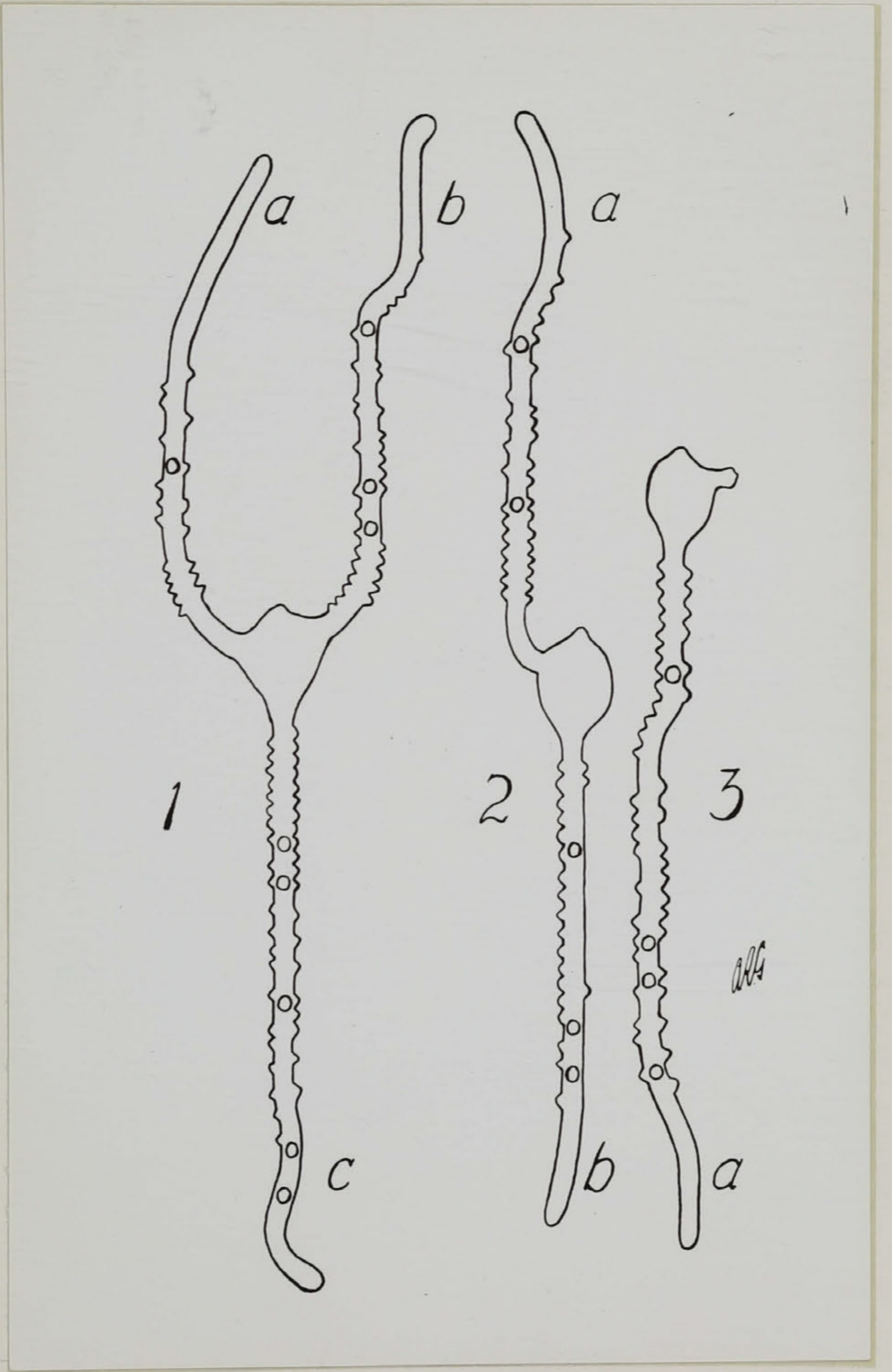

PLATE -IV-