ECOLOGICAL NOTES ON THE *SIREX* WOOD WASPS AND THEIR PARASITES.

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(PLATES I–VI.)

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1. Introduction.

The following notes on the ecology of the *Sirex* wood-wasps and their parasites have been collected during a period of several years. In 1927 the Imperial Institute of Entomology received a request from Dr. David Miller, Government Entomologist of New Zealand, for parasites for the control of *Sirex noctilio*, a species of wood-wasp which had become established in New Zealand and was rapidly increasing in the coniferous forests in that country.

The preliminary investigations were carried out by Dr. J. G. Myers, of Farnham House Laboratory, in collaboration with Dr. R. N. Chrystal, of the Imperial Forestry Institute, Oxford. While the investigations were in their early stages Dr. Myers left Britain to take up duties in Trinidad in 1928. After that date all subsequent investigations on behalf of the Imperial Institute of Entomology were carried out by the present writer under the direction of Dr. W. R. Thompson, Superintendent of Farnham House Laboratory. Dr. Chrystal carried out entirely independent biological investigations at Oxford. The results of his researches and those of Dr. Myers have been published in a series of papers.

The large-scale operations carried out on behalf of Farnham House Laboratory afforded exceptional facilities for the study of the ecology of the wood-wasps and their parasites, and much useful information about their inter-relationship was collected. It is felt that the publication of the data is desirable in order to supplement what has already been written on the subject.

2. Duration of the Life-cycle of the Sirex Wood-wasps and their Parasites.

The *Sirex* wood-wasps are probably familiar to all those who are interested in the study of nature. Four species normally occur in Britain : *Sirex gigas*, L., *S. cyaneus*, F., *S. noctilio*, F., and *S. juvencus*, L. Other species are sometimes introduced in imported timber, but have not been recorded as breeding species.

In a paper by Dr. R. N. Chrystal (1928) the late Dr. James Waterston gave some systematic notes on British wood-wasps. These notes should be consulted by those interested in the determination of the various species.

Sirex gigas, L., is a very conspicuous yellow and black insect, while the other three species are all of a dark metallic blue colour and are very similar in general appearance. Formerly all three blue wood-wasps were known to foresters and others generally interested in forest insects as *Sirex juvencus*, L., but Dr. Waterston has shown that the blue wood-wasp most common in Britian is *Sirex cyaneus*, F., and that *Sirex juvencus*, L., and *Sirex noctilio*, F., are comparatively rare insects.

Sirex gigas and *S. cyaneus* occur in most coniferous woods throughout Britain but are never very numerous unless local conditions are exceptionally favourable for their increase. Both species are attacked by two Hymenopterous parasites, an Ichneumonid, *Rhyssa persuasoria*, L., and a Cynipid, *Ibalia leucospoides*, Hochenw. A brief outline of the life-cycle of these insects is given below.

(*a*). *Life-cycle of* Sirex.

The normal life-cycle of both *Sirex gigas* and *S. cyaneus* extends over a period of three years from the egg to the adult stage, but development is sometimes retarded and the adult insects may not emerge from the timber until several years have elapsed. Most coniferous timbers are used for breeding purposes, but perhaps silver fir, spruce, larch and pine are the most frequent hosts.

The eggs are laid during the summer from the end of June onwards, in a short oviposition hole in the outer layers of the wood. During the first winter the tiny larvae may be found burrowing in tunnels running almost at right-angles to the oviposition hole at first, later they begin to burrow deeper into the wood, and during the second summer they are often about 1½ inches below the surface ; as the larvae develop they burrow towards the pith, and during the second winter they may be found about half-grown. Plate I, fig. 1, shows half-grown *Sirex* larvae burrowing in the region of the pith in a small silver fir log during the second winter of their development. The larvae continue to burrow during the whole of the following summer, and as they become full-grown they turn outward and burrow towards the surface. During the third winter they are to be found lying full-grown in chambers near the surface of the wood ready to pupate (Plate I, fig. 2). The frass-filled burrows formed during the previous summer are shown in Plate I, fig. 3. The larvae pupate in the spring, usually from ½ to 2 inches below the surface of the wood. Plate II, fig. 1, shows a female *Sirex cyaneus* pupa in the pupal chamber.

In longitudinal section, the exit tunnel made by *Sirex cyaneus* is only slightly curved, while that of *Sirex gigas* is generally very strongly curved, describing almost a complete quadrant.

Plate II, fig. 2, shows a female *Sirex gigas* adult in the pupal chamber ready to emerge. The adult wood-wasps begin to emerge in June ; the males frequently emerge first, but are seldom seen after they leave the timber, as they spend most of their time among the crowns of the trees. The females are often seen ovipositing in logs or standing trees. Large, over-mature, standing trees which are slowly dying from the top downwards often support a colony of wood-wasps for a long period of years, the region of infestation increasing from year to year as additional portions of the tree become suitable for breeding purposes.

Two and sometimes three generations of *Sirex* larvae may be present in the same piece of timber. The length of the duration of the *Sirex* larval stage is of considerable importance as will be seen when dealing with the inter-relationship of the host and parasites and the percentage of parasitism.

Discussing the exit holes of *Sirex*, Dr. Chrystal states " J. H. Fabre in an essay entitled ' The Problem of *Sirex* ' has described how in *S. augur* the larva, when full-grown, lies lengthwise in the tree not far from the centre of the trunk. In this position metamorphosis takes place and the adult insect, on emerging, is faced with the problem of cutting its way out through the wood in which it is a prisoner. In the vertical plane in which it lies this is a difficult task for the heavily armoured adult, which is incapable of bending the body freely. The task is accomplished, according to Fabre, by the construction of an exit gallery which is the wide arc of a circle whose lower extremity is connected with the larval tunnel, and whose upper extremity is prolonged in a straight line which ends at the surface with a perpendicular or slightly oblique incidence. The wide connecting arc, which enables the insect to adjust its position gradually, is a curve which Fabre has shown approximates as nearly as possible to the circumference of a circle, and the construction of which is a constant feature of the species even over lengths that sometimes exceed four inches. These remarkable observations by the great French naturalist have not been duplicated in the case of *Sirex cyaneus.*"

The above remarks are quoted because of their general interest with reference to the difference in the shape of the exit tunnels formed by the various species of *Sirex*, and also because of their special interest in relation to problems of insect behaviour.

After discussing Fabre's description of the exit tunnel of *Sirex augur*, Dr. Chrystal described by way of contrast, the exit tunnel formed by *Sirex cyaneus*, and states that in nearly every case he examined " the pupal cell was so constructed that the adult was afforded a perfectly straight forward passage to the outside, whether it chose to proceed in an oblique or horizontal direction." He gives the average depth of the pupal chamber as being from $\frac{3}{4}$ to $\frac{1}{2}$ an inch, but says that in many cases, especially in male pupae, the pupal cell lies less than $\frac{1}{4}$ inch from the exterior. The present writer has noticed that *S. cyaneus* larvae seem to prefer the sapwood when burrowing in larch and the larval tunnel is in consequence generally near the surface. Plate V, fig. 3, shows the pupal chamber of *S. cyaneus* in larch timber with the remains of an adult female. This specimen was parasitised by *Rhyssa* and the full-grown parasite larva is seen *in situ*. When, however, *S. cyaneus* breeds in large silver fir, the larvae burrow to a considerable depth and the length of the exit burrow is correspondingly long. Examples are seen on Plate II, fig. 1, Plate IV, fig. 2, and Plate VI, fig. 2. In each case it will be seen that the tunnel is not perfectly straight, but shows a slight curve, although it bears no strong resemblance to the exit tunnel of *S. augur* as described by Fabre.

Dr. Chrystal's studies were confined almost entirely to *S. cyaneus* material, consequently he makes no reference to the shape of the exit tunnels of *Sirex gigas*, which differ considerably from those of *S. cyaneus* and bear a very strong resemblance to the tunnels of *S. augur* as described by Fabre, except that the upper extremity is not prolonged into a straight line. Two *Sirex gigas* exit tunnels are shown on Plate VI, fig. 1. It will be seen that each tunnel described a complete quadrant, although the angle of incidence with the surface of the timber is slightly different. The shape of these exit tunnels is typical for *S. gigas*. The photograph is of special interest because it shows two exit tunnels converging to one exit hole, a rather unusual occurrence. The *Sirex* adult from the lower tunnel emerged first, as is shown by the presence of the bark frass in the tunnel. In the absence of this exit hole the last half inch of the second *Sirex* tunnel would normally have been produced in an almost horizontal direction, but the tunnel is seen to be strongly curved downwards at this point, as if the insect had deliberately burrowed in that direction in order to avail itself of the existing exit hole. The explanation appears to be that the lower portion of the second *Sirex* tunnel would be the first point of intersection with the first tunnel, and as there would be a breach in the wall of the second tunnel formed at this point, the course of the insect would be automatically deflected owing to the peculiar manner in which the insect is propelled forward during the process of boring the tunnel. At the end of the last abdominal segment there is a long, pointed, spike-like process which is thrust against the side of the completed part of the tunnel and used as a lever to propel the body of the insect forward and thus assist the legs which are in a very cramped position within the narrow tunnel. This tail-like organ can be seen in Plate II, fig. 2. The pointed process is much more strongly developed in the female wood-wasp than in the male, and although it is much shorter than the ovipositor, like the latter organ, it differs in length in each of the British species. The last segment of the wood-wasp larva is also furnished with a sharp spike which is used in the same way. It is doubtful whether the insect would be able to bite its way through the wood without the assistance of this organ.

In his Presidential Address to the Entomological Society of London in 1932, Dr. H. Eltringham F.R.S., in discussing the insect's powers of biting its way through wood and even lead remarked : " This power of biting seems to cease on emergence into the open air, since a *Sirex* cannot, or at any rate does not, bite its way out of a match box."

It will be seen from what has been said, that when confined in a wooden box too large to allow this organ to be brought into use, the insect is unable to "keep its nose to the grindstone" and bite its way out, but it does not lose its power of biting.

In the previous quotation it is stated that the adult *Sirex augur* is faced with the " problem " of cutting its way out of the timber, and it is explained that in order to do so the insect described an arc, thus changing its position from a vertical to a horizontal plane. If the tree is felled the " problem " may be further complicated by the fact that the insect in the pupal chamber will then be in a horizontal position instead of vertical. The problem is, however, supposed to be solved in exactly the same way by all specimens of that particular species, except that in the case of a felled tree the exit tunnel will be bored only in a horizontal plane if the insect decides to emerge from the side of the log and vertically if it chooses to emerge from the upper side. This statement infers mental process and choice of course of action on the part of the insect, presumably based on a knowledge of its position relative to the shape of the tree and the position in which the latter may be either standing or lying. It is clear, however, that each individual *Sirex* adult must perform the task without any knowledge of the external shape or position of the object forming the medium in which it is boring.

Whether the pupal chamber of *S. augur* is actually formed lengthwise in the tree as described by Fabre, *i.e.*, in the direction of the long axis of the stem, and parallel with the pith and the bark, the present writer is not in a position to say, as he has no personal knowledge of the habits of this species, but this is certainly not the case with the pupal chambers of *S. gigas* and *S. cyaneus*. In both species the larvae turn outwards towards the bark as seen in Plate I, fig. 2, and the greater part of the curved exit tunnel is bored by the full-grown larva before the pupal stage is reached. Plate II, fig. 1, shows a female *S. cyaneus* pupa in the pupal chamber. Plate IV, fig. 1, shows a *S. gigas* pupal chamber containing a *Rhyssa* pupa. In the case of *S. cyaneus* the larva often turns outward at a distinct angle, as seen in Plate IV, fig. 2, but

S. gigas generally forms a definite curve. It will be seen, therefore, that in these two species the adult insect is not confronted with the problem of getting from a vertical to a horizontal position, as the greater part of the task has been performed by the larva. It may, however, be argued that this is merely handing the problem back a stage to the larva for solution, and that the case for mental process is all the more complex, since the larva has not only to solve the geometrical exit problem, but has also to visualise the future requirements of the heavily chitinised adult insect. The writer does not consider that Fabre actually attributed reasoning powers to the insect and he personally is convinced that no such mental process is involved and the process is entirely a mechanical one. Plate I, figs. 1 and 3, show that during the feeding stage the larvae wander at random through the timber, the rate of their forward progress being determined by their food requirements. During this period it is essential that the timber be gnawed into very tiny particles in order to obtain the food on which the larva subsists. This would be facilitated by gnawing at the ends of the long fibres in the wood rather than by biting off splinters from the sides of these fibres. When, however, the feeding period is finished and the only remaining urge is the formation of a chamber in which to lie, biting off tiny particles is no longer absolutely necessary, and as boring is now the only task, the act of biting off larger particles of the long fibres tends to turn the tunnel in a transverse direction as the tunnel is more easily enlarged when working across the grain of the timber. By the time the resting chamber has reached the required dimensions the tunnel has assumed the shape of a curve, after pupation a continuation of this curve, or even a straight tunnel, will bring the insect to the surface.

If the above explanation is correct, it will probably be found that the greater part of the curved portion of the exit tunnel of *Sirex augur* is formed by the larva and not by the adult insect as stated by Fabre.

Scheidter (1923) states that in Germany, *S. gigas* and *S. augur* attack the biggest stems, whereas *S. juvencus* and *S. noctilio* prefer poles, probably because their short ovipositors cannot pierce thick bark ; *S. augur* pupae were found at a depth of 4¾ inches from the surface. Dissections showed that females of *S. augur* contain an average of over 1,000 eggs each. In *S. noctilio* the number is about 400. Dissections made by Dr. Chrystal indicate that the number of eggs in *S. cyaneus* is between 300 and 400 on an average.

(*b*). *Life-cycle of* Ibalia leucospoides, *Hochenw.*

The biology and post-embryonic development of *Ibalia leucospoides* have been described in great detail by Dr. R. N. Chrystal (1930).

The observations of the present writer confirm those of Dr. Chrystal, so far as the life-cycle of *Ibalia* is concerned, but his conclusions as regards the relative efficiency of this parasite as compared with *Rhyssa*, and their inter-relationship with the host, differ considerably. This subject will be discussed in detail later. Only an outline of the life-cycle of *Ibalia* will be given here ; the reader is referred to Dr. Chrystal's excellent paper for a full description of the insect and its biology.

The life-cycle of *Ibalia* extends over a period of three years. The *Ibalia* adults begin to energe towards the end of July, but are most numerous in late August and early September. At this time they may be seen ovipositing in trees in which *Sirex* have recently oviposited.

The ovipositor of *Ibalia* does not project beyond the end of the abdomen, as is the case in many other Hymenopterous parasites, but lies coiled within the body. The insect is highly specialised and is unable to attack the host larva by boring through the bark and timber. The oviposition hole of *Sirex* has first to be located, *Ibalia* then lowers her ovipositor into the *Sirex* oviposition hole and inserts her eggs within the eggs or recently hatched larvae of *Sirex*. Each *Ibalia* larva develops as an internal parasite until the third larval stage is reached. When more than one parasite larva is present the supernumerary larvae are destroyed at this stage, and the survivor then emerges and devours the remains of the host larva ; this period of development as an internal parasite occupies about two years. After emerging from the *Sirex* larva during the second summer, the *Ibalia* larva remains as a fourth-stage larva within the *Sirex* tunnel until the spring of the following year. It then pupates and emerges from the tree. The adult insect bores an exit hole through the timber and bark. It has been mentioned that *Sirex* larvae normally burrow towards the pith during the first year of their development, but when *Sirex* larvae have been parasitized by *Ibalia* they do not follow the normal course ; at first they begin to burrow into the timber, but as the parasite begins to develop the *Sirex* larva changes its course and tends to burrow outwards towards the bark, so that the tunnel formed by a parasitized *Sirex* larva is much nearer the surface than that of an unparasitized larva. Plate III, fig. 1, shows three *Sirex* tunnels, two of which represent the normal course of unparasitized *Sirex* larvae and one which shows the course taken by a *Sirex* larva parasitized by *Ibalia.* In this case, however, all three *Sirex* larvae have been parasitized by *Rhyssa* when they were one year old. Plate III, fig. 2, shows the tunnels of three *Sirex* larvae which were parasitized by *Ibalia.* Two of these tunnels contain fourth-stage *Ibalia* larvae resting during the third winter ready to pupate in the spring. The one in the centre contains a *Rhyssa* larva showing that one of the three original *Ibalia* larvae was subsequently parasitized by *Rhyssa.*

(*c*). *Life-cycle of* Rhyssa persuasoria, *L.*

The life-cycle of *Rhyssa* is completed in one year. The adults begin to emerge in the spring and may attack the host larvae at any time throughout the summer, as, unlike *Ibalia,* they do not attack the eggs and first stage larvae of the host, but locate the *Sirex* larvae which have completed one or more years development. Having located the position of the *Sirex* larva by means of the antennae, *Rhyssa* proceeds to bore a hole with her ovipositor, penetrating the bark and timber until the host larva is reached. The egg is then laid upon the host larva within its tunnel. The statement still repeated by some authors, that *Rhyssa* sometimes reaches its host by inserting its terebra along the burrows of the latter, is incorrect.

As *Sirex* normally takes three years to complete its development, it will readily be seen that one generation of *Sirex* may produce three generations of *Rhyssa.* This subject will be referred to again when discussing the inter-relationship of the host and its parasites. Plate III, fig. 1, shows the first generation of *Rhyssa* which are the result of *Sirex* larvae being parasitized when one year old. Plate III, fig. 2, shows a *Rhyssa* larva of the second generation, as although the host in this case was *Ibalia* it corresponds to a *Sirex* larva two years old. Plate III, fig. 3, also shows a *Rhyssa* larva of the second generation. In this case the host was a *Sirex* larva, two years old, which would normally have spent the winter as a full-grown larva and emerged as an adult in the following summer.

The discrepancy in the size of the *Rhyssa* larvae is due to the size of the host. One-year-old *Sirex* larvae and *Ibalia* larvae produce very small *Rhyssa* adults, while two-year-old *Sirex* larvae produce fairly large *Rhyssa,* and full-grown *Sirex* larvae produce very large *Rhyssa.*

Plate IV, fig. 1, shows the pupa of a third generation *Rhyssa.* In this case the host was a full-grown *Sirex* larva which was in the pupal chamber ready to pupate. Plate IV, fig. 2, shows an adult female *Rhyssa* tunnelling the exit hole from pupal chamber of *Sirex.* When the *Sirex* infested logs are very large the *Sirex* larvae may be out of reach of *Rhyssa* during the second summer, but when the timber is under 3 inches in diameter the *Sirex* larvae are within reach of large specimens of *Rhyssa* during the whole period of their development and in such cases parasitism by *Rhyssa* is very high and few *Sirex* escape destruction.

Even in the third year, when *Sirex* has completed its development and is about to merge, the adult insect is often parasitized by *Rhyssa* while actually burrowing the xit tunnel, as is shown in Plate V. fig. 3.

. The Collection of Sirex Parasites for Shipment to New Zealand.

The first attempt at large-scale collection of the parasites was carried out in orth Devon during the season 1928–29, the writer having studied the *Sirex* con-litions in that area during the previous year. During the summer of 1928 forty reeding-places were prepared consisting of *Sirex* infested logs, about 30 tons of this aterial being used. The logs were so arranged that the parasites could readily gain ccess to all parts of the surface and so parasitize the *Sirex* larvae. These logs were ft in the woods until the autumn and were then hauled to a central depot, where they ere crosscut into short lengths and dissected to obtain the parasite larvae. This ethod proved successful, 1,753 *Rhyssa* larvae and 113 *Ibalia* larvae having been ollected from this material. During the examination of the logs much useful nformation was obtained, not only with reference to the life-cycle of *Sirex* and its arasites, and their inter-relations, but also as to the most productive type of logs. his information proved extremely valuable during the season 1930–31 when ollections were carried out on a much larger scale.

During the autumn of 1930 a survey was made with the object of locating suitable ollecting areas. A large area of blown spruce in Montgomeryshire was visited and he presence of numerous *Rhyssa* ovipositors observed sticking in the bark of these rees indicated that this parasite had been actively engaged in oviposition during the ummer. Two other estates, one in Bedfordshire and one in Wiltshire, were found o be suitable localities for the collection of parasites, not because *Sirex* was abnormally bundant, but simply on account of the extensive areas of mixed woodlands of the ype usually found on large private estates. On both these estates individual oniferous trees, some of which were over-mature or had been damaged by wind, ghtning or fungi, were found to support communities of *Sirex*, and each infested tree cted as a focus for the parasites.

During this season's work 6,458 *Rhyssa* larvae and 572 *Ibalia* larvae were collected om the three areas, bringing the total collections to 8,211 *Rhyssa* and 685 *Ibalia*. f these 7,830 *Rhyssa* and 382 *Ibalia* were shipped to New Zealand.

The collection of this large number of specimens of what had hitherto been egarded as very rare insects was a laborious task ; several hundred *Sirex*-infested rees were felled and crosscut into short lengths, each length of timber was then arefully split into small pieces and examined in detail. Over a hundred tons of *irex*-infested timber was dealt with in this way, and in order to avoid transportation f the timber to the Laboratory, the greater part of the material was cut up and xamined in the forest.

. The Inter-Relationship of Sirex and the Parasites.

The detailed examination of such a large amount of material provided unique pportunity for the study of the inter-relationship of *Sirex* and its parasites. The ata collected explained much that could not previously be understood ; they also rovided much new knowledge about the biological control of *Sirex*.

During the early stages of the investigation each log or tree examined seemed to roduce an entirely different set of conditions, and there appeared to be little hope of orrelating the data, but as the work proceeded it became evident that the apparently ontradictory data were rapidly being supplemented and gaps being filled.

Before the completion of the work it was possible to construct a complete picture f the *Sirex* biological complex. The knowledge gained was extremely useful in electing material during the later stages of the work and will greatly simplify the ork in future should further supplies of *Sirex* parasites be required.

Standing trees were found to yield the best results. Logs lying on the ground seldom contained more than one generation of *Sirex*, as the bark often becomes loose and they are then unattractive. Once the *Sirex* larvae have become established in a log, they are generally able to complete their development before the timber becomes too decayed.

Sirex-infested logs remain attractive to *Rhyssa* as long as they contain any *Sirex* larvae or pupae, although the log may have ceased to be attractive for *Sirex* oviposition.

The sequence of events in a log infested by *Sirex* is as follows :—The eggs of *Sirex* may be laid at any time from June throughout the summer. The *Sirex* eggs or first-stage larvae may be parasitized by *Ibalia* during the summer provided that the attack by the parasite is made before the *Sirex* larvae have begun to burrow tunnels in the timber, but as *Ibalia* does not normally appear until towards the end of July or later, it is possible for the very early batches of *Sirex* larvae to escape parasitism by *Ibalia*. If the *Sirex* larvae escape parasitism by *Ibalia* at this stage, they are immune from the attack of the parasite throughout the rest of their development, as *Ibalia* is unable to bore holes through the timber with its ovipositor. The eggs of *Sirex* are quite useless to *Rhyssa*, and the *Sirex* larvae during the early stages are equally useless, and although *Sirex* larvae may be attacked by *Rhyssa* at any time during the first summer, they are too small during that period to form suitable hosts, and both the *Sirex* larva and the parasite larva perish.

During the whole of the second summer the *Sirex* larvae are liable to be parasitized by *Rhyssa*. The *Sirex* larvae which were parasitized by *Ibalia* in the first summer lie nearest to the surface and therefore run the greatest risk, as they can be reached by small *Rhyssa* females, while unparasitized *Sirex* often can only be reached by large specimens of *Rhyssa*. Plate III, figs. 1 and 3, show the depth to which *Rhyssa* may reach with her ovipositor. *Sirex* larvae which have been parasitized by *Rhyssa* cease to burrow and are devoured by the parasite larvae. The latter are unable to burrow in the wood and remain in the same spot until ready to emerge as adults in the following summer. The adult *Rhyssa* emerges from the log during the third summer and the exit hole may be found in the log. During the third summer the *Sirex* larvae which escaped *Rhyssa* during the second summer may be parasitized unless they have burrowed too deep into the timber, as sometimes happens in large logs.

In the case of *Sirex* larvae which were originally parasitized by *Ibalia*, the parasite larvae emerge during this period and devour the remains of the host larvae, leaving only the empty skin. The *Ibalia* larvae then rapidly complete their development and remain in the *Sirex* tunnel until the fourth summer, when they pupate, and the adults emerge from the log, as also do the unparasitized *Sirex*, both species having completed their three year life-cycle. The second generation of *Rhyssa* also pupate and emerge. It will be seen, therefore, that during the fourth summer the *Sirex*, *Ibalia* and second generation of *Rhyssa* emerge from the log, leaving exit holes. All the *Sirex* do not escape ; during the spring and early summer they are liable to be parasitized by *Rhyssa* either in the full-grown larval stage, the pupal stage, or even the adult stage, thus producing a third generation of *Rhyssa* which emerge from the log during the fifth summer. Plate IV, fig. 1, shows a third generation *Rhyssa* pupa in the *Sirex* pupal chamber. Plate IV, fig. 2, shows an adult *Rhyssa* of the third generation boring its exit hole from the pupal chamber of *Sirex*.

Table I indicates what a log may be expected to contain in either summer or winter over a period of four years when only one generation of *Sirex* is concerned.

By examination of the contents of a log it is now possible to state accurately whether the log is being examined in the first, second, third, or fourth year of *Sirex* infestation.

Very small standing trees or poles seldom support more than one generation of *Sirex*, if they are heavily infested during the first year. If the diameter of the pole is less than 3 inches the percentage of parasitism may be very high, owing to the fact that the *Sirex* larvae are unable to get out of reach of *Rhyssa* at any stage. These small poles were generally found to be very productive. The small section of timber seen standing on the large log in the top right-hand corner of Plate V, fig. 2, contains exit holes of 14 *Rhyssa* and only one *Sirex*. This section was only 3 inches in length by 2½ inches in diameter and was cut from the base of a small, standing silver fir pole within 6 inches of the ground.

TABLE 1.

Period	*Sirex*	*Ibalia*	*Rhyssa*
1st Summer ...	Oviposits.	Parasitizes some of the *Sirex* eggs.	—
1st Winter ...	Larvae begin to burrow.	Internal parasite.	—
2nd Summer	Larvae about one-third grown.	Internal parasite.	Parasitizes *Sirex* larvae, some of which may contain *Ibalia* larvae.
2nd Winter ...	Larvae about half-grown burrowing towards pith (Plate I, fig. 1).	Larvae feeding as internal parasites.	Larva full-fed lying in gallery of *Sirex* ; Plate III, fig. 1, shows two *Rhyssa* larvae which have fed on unparasitized *Sirex* larvae and one *Rhyssa* larva which has fed on a *Sirex* larva previously parasitized by *Ibalia*.
3rd Summer	Larvae about two-thirds grown.	Larvae emerge from *Sirex* host in the spring and destroy remains of the host.	1st generation of *Rhyssa* pupate and emerge from log. *Rhyssa* parasitizes *Sirex* and *Ibalia* larvae giving rise to the 2nd generation of *Rhyssa*.
3rd Winter ...	Larvae are nearly full-grown and are burrowing towards the surface (Plate I, fig. 2).	Larvae full-grown lying in *Sirex* galleries. Plate III, fig. 2, shows two unparasitized *Ibalia* larvae and a *Rhyssa* larva which has fed on *Ibalia*.	Larvae, 2nd generation are full-fed (Plate III, fig. 3).
4th Summer	Pupate and emerge.	Pupate and emerge.	2nd generation pupate and emerge. *Rhyssa* parasitizes *Sirex* pupae and *Ibalia* pupae.
4th Winter ...	—	—	*Rhyssa* larvae 3rd generation with remains of *Sirex* pupa. *Rhyssa* larvae with remains of *Sirex* adult.
5th Summer	—	—	*Rhyssa* 3rd generation emerge (Plate IV, figs. 1, 2).

Very large trees show a wide range in the conditions governing the degree of parasitism. In the thick part of the stem the percentage of parasitism is often very low, owing to the fact that the *Sirex* larvae are out of reach of *Rhyssa* during the second summer and remain out of reach until the spring of the year in which the adults are due to emerge. A few pupae and full-grown larvae are then parasitized (Plate IV, fig. 1), but in large logs many of the pupal chambers are too far from the surface to be reached by the ovipositor of the parasite (Plate II, fig. 2), although the adult *Sirex* are often parasitized as they approach the surface.

The small section in the left-hand top corner (Plate V, fig. 2), is from a large silver fir, the surface of which measures only 5 inches by 2½ inches and contains the exit holes of 8 large *Sirex* and only 1 *Rhyssa*. On the other hand, the upper portions of these large trees show a very high percentage of parasitism. An 8 ft. length, 4 inches in diameter at the thick end and 2 inches in diameter at the thin end, broken from the top of a large silver fir in Devon, yielded 91 *Rhyssa* larvae and only 15 *Sirex* larvae. A small piece 6 inches in length and only 1½ inches in diameter which broke off the tip of the same piece contained 7 *Rhyssa* larvae and no *Sirex*, making a total of 98 *Rhyssa* and 15 *Sirex* in a piece of timber 8 ft. 6 ins. in length and less than 3 inches average diameter. Another similar piece gave 65 *Rhyssa* larvae and 23 *Sirex* larvae.

In the Bedfordshire area a small piece which had been broken from the top of a large silver fir contained 125 *Rhyssa* larvae. In this case every *Sirex* larva had been parasitized. This piece was only 6 ft. in length, was less than 4 inches in diameter at the thick end and tapered to 1½ inches at the thin end. A small silver fir on the same estate 30 ft. in length by about 4 inches average diameter was found to have been entirely missed by *Rhyssa* but was heavily parasitized by *Ibalia*. This tree contained 95 *Ibalia* larvae and 25 *Sirex* larvae, but only one generation of *Sirex*, and reference to the tables showing the rate of development clearly indicates that the log was examined at a stage corresponding with the third year of infestation. Both the *Sirex* and *Ibalia* adults would normally have emerged from the log during the following summer. This was the only tree found in any of the four areas which showed a high percentage of parasitism by *Ibalia*, but this is doubtless because it was the only tree examined in which no *Rhyssa* larvae were found. Many examples afforded strong evidence that *Ibalia* is normally heavily super-parasitized by *Rhyssa*. It seems probable that some of the remaining *Sirex* and a large proportion of the *Ibalia* would have been parasitized by *Rhyssa* during the following summer before the adults were ready to emerge.

A silver fir on the Wiltshire estate 55 ft. in length by 6 inches average diameter yielded 459 *Rhyssa* larvae, 29 *Ibalia* larvae and 139 *Sirex* larvae. In this case two generations of *Sirex* larvae were present, and it is unfortunate that the *Sirex* larvae were not dissected as it is almost certain that a number of them would have been found to contain *Ibalia* larvae, and a more accurate and higher percentage of parasitism would have been obtained. In this case also, the population was liable to be further attacked by *Rhyssa* during the following summer. It will be seen, therefore, that the actual percentage of parasitism would have been much higher than the above figures indicate.

These five cases cannot be regarded as typical examples. They represent the highest percentages of parasitism found in several hundred trees examined.

TABLE II.

Locality	Host tree	*Sirex*	*Rhyssa*	*Ibalia*
Devon ...	Silver fir	15	98	—
Devon ...	Silver fir	23	65	—
Bedford ...	Silver fir	—	125	—
Bedford ...	Silver fir	25	—	95
Wilts	Silver fir	139	459	29
	Totals	202	747= 69·61 per cent.	124= 11·55 per cent.

The five cases taken together show that of a total of 1,073 *Sirex* larvae 871 (81 per cent.) had been parasitized. The figures cannot be regarded as final, however, since the remaining 202 *Sirex* larvae were still liable to be parasitized by *Rhyssa* during the early part of the following summer before they emerged as adults, and the exceptionally large number of *Rhyssa* adults which would emerge from this small amount of material increases the probability that a large proportion of the *Sirex* larvae would be parasitized. These figures serve to show that under conditions which are favourable to *Rhyssa* the percentage of parasitism may be very high. Where the conditions are unfavourable, owing to the diameter of the log in which *Sirex* may be breeding, the percentage of parasitism may be very low. Nevertheless, no cases were found where colonies of *Sirex* had entirely escaped attack by both parasites.

The following is a summary of the number of each species obtained from the various localities:—

TABLE III.

Season	Locality	*Rhyssa*	*Ibalia*
1928–29 ...	North Devon ...	1,753	113= 6·05 per cent.
1930–31 ...	Montgomeryshire ...	3,792	210= 5·53 ,, ,,
1930–31 ...	Bedfordshire ...	713	247=34·64 ,, ,,
1930–31 ...	Wiltshire	1,953	115= 5·88 ,, ,,
	Totals ...	8,211	685= 7·70 per cent.

These figures show a close resemblance in the proportion of *Rhyssa* and *Ibalia* found in the Devon, Montgomeryshire and Wiltshire areas, as compared with the Bedfordshire area, but as the 95 *Ibalia* found in one small tree represent approximately two-fifths of the total collected in the whole area, this largely accounts for the difference.

The above figures do not represent the true ratio of the *Rhyssa* and *Ibalia* population, because while all the *Rhyssa* larvae were collected, only full-grown *Ibalia* larvae were collected. It must be remembered that the *Ibalia* larvae are internal parasites during the early stages and many of the *Sirex* larvae under two years of age contained *Ibalia* larvae, but at the time it was considered that these larvae would be useless for shipment, and they were thrown away and are not therefore included in the number of *Ibalia* larvae collected. At a later date the writer collected some of these parasitized *Sirex* larvae and kept them in tubes. The *Sirex* larvae continued to live until the *Ibalia* emerged. These *Ibalia* subsequently completed their development. From this it would appear that the best time to collect *Ibalia* larvae for shipment would be during the early stages while they are inside the *Sirex* larvae.

Logs cut from large standing trees were frequently found to contain three generations of *Sirex* and a period of seven years elapses between the time when the first *Sirex* eggs are laid to the time when the last of the parasites emerge from the timber. Trees of this description gave rise to three generations of *Sirex*, three generations of *Ibalia* and five generations of *Rhyssa*. The contents of such a tree varies from year to year and an entirely different combination of insects in various stages of development is to be found according to the year in which the material is examined. Each of these large trees represents a separate *Sirex* colony and the composition of the population is often very complex owing to the different stages in which the various species are to be found at any given time. This rendered the task

TABLE IV.

Inter-relations of Sirex, Ibalia *and* Rhyssa *in a tree in which three successive generations of* Sirex *breed.*

Period	*Sirex*	*Ibalia*	*Rhyssa*
1st Summer ...	Oviposits 1st gen.	Parasitizes eggs or young larvae.	—
1st Winter ...	Larvae begin to burrow.	Eggs or 1st stage larvae inside *Sirex* larvae.	—
2nd Summer	Larvae 1st gen. about one-third grown ; oviposits 2nd generation.	Larvae feeding as internal parasites ; parasitizes 2nd gen.	Parasitizes *Sirex* larvae of 1st gen., some of which contain *Ibalia.*
2nd Winter ...	Larvae 1st gen. about half grown ; larvae 2nd gen. begin to burrow.	Larvae feeding as internal parasites in 1st and 2nd gen. *Sirex.*	Larvae 1st gen. lying full-fed in *Sirex* galleries (Plate III, fig. 1).
3rd Summer	Larvae 1st gen. about two-thirds grown ; larvae 2nd gen. about one-third grown ; oviposits 3rd gen.	Larvae 1st gen. emerge from host and devour remains; 2nd gen. internal parasites ; oviposits 3rd gen.	1st gen. pupate and emerge ; oviposits 2nd gen. on larvae of *Sirex* and *Ibalia* of 1st gen. also on larvae of *Sirex* 2nd gen., some of which may contain *Ibalia* larvae.
3rd Winter ...	Larvae 1st gen. full-grown (Plate I, fig. 2) ; larvae 2nd gen. about half grown (Plate I, fig. 1) ; larvae 3rd gen. begin to burrow.	Larvae 1st gen. full-grown lying in pupal chamber (Plate III, fig. 2) ; larvae 2nd and 3rd gen. internal parasites.	Log contains exit holes of 1st gen.; larvae of 2nd gen. which have fed on 1st gen. *Sirex* and *Ibalia* larvae are full-grown ; larvae of 2nd gen. which have fed on 2nd gen. *Sirex* larvae are full-grown.
4th Summer	1st gen. pupate and emerge ; 2nd gen. about two-thirds grown ; 3rd gen. about one-third grown.	1st gen. pupate and emerge ; 2nd gen. emerge from host larvae ; 3rd gen. internal parasites.	2nd gen. pupate and emerge. Oviposits 3rd gen. on *Sirex* and *Ibalia* pupae of 1st gen., also on *Sirex* and *Ibalia* larvae of 2nd gen. and *Sirex* larvae of 3rd gen.
4th Winter ...	Log contains exit holes of 1st gen. ; larvae 2nd gen. full-grown ; 3rd gen. about half grown.	Log contains exit holes of 1st gen. ; larvae 2nd gen. lying full-grown ; larvae 3rd gen. internal parasites.	Log contains exit holes of 1st and 2nd gens. ; larvae of 3rd gen. full-grown (Plate V, fig. 3).
5th Summer	2nd gen. pupate and emerge ; 3rd gen. about two-thirds grown.	2nd gen. pupate and emerge ; 3rd gen. emerge from host larvae.	3rd gen. pupate and emerge ; 4th gen. oviposits on pupae of *Sirex* and *Ibalia* 2nd gen. and larvae of *Sirex* and *Ibalia* 3rd gen.
5th Winter ...	Log contains exit holes of 1st and 2nd gens. ; larvae 3rd gen. full-grown.	Log contains exit holes of 1st and 2nd gens. ; larvae 3rd gen. full-grown.	Log contains exit holes of *Sirex* 1st, 2nd and 3rd gens. ; larvae 4th gen. full-grown.
6th Summer	3rd gen. pupate and emerge.	3rd gen. pupate and emerge.	4th gen. pupate and emerge ; oviposits 5th gen. on pupae of *Sirex* and *Ibalia* of 3rd gen.
6th Winter ...	Log contains exit holes of 1st, 2nd and 3rd gens.	Log contains exit holes of 1st, 2nd and 3rd gens.	Log contains exit holes of 1st, 2nd, 3rd and 4th gens. ; larvae fed on *Sirex* and *Ibalia* pupae full-grown.
7th Summer	—	—	5th gen. pupate and emerge.

of the solution of the general problem more difficult, but the examination of the contents of large numbers of trees and the careful comparison of contents of each tree with the types of exit holes found in the bark, enabled the writer to work out the inter-relationships of the species concerned.

Table IV shows what a tree of this description may be expected to contain at any period during the development of the colony.

With a view to ascertaining the approximate number of *Sirex* and parasites such a tree would produce, a silver fir showing *Sirex* holes of last summer and the previous summer was selected for examination. This tree was 50 ft. in length by 8½ inches qqt. under bark. A section 6 ft. in length from the middle of the tree showed 376 exit holes and contained 31 *Sirex* larvae of the 3rd generation ready to pupate, and 11 *Rhyssa* larvae. The exit holes were fairly evenly distributed over the whole surface of the tree, so that taking this 6 ft. section as a basis, it will be seen that a tree of 25 c. ft. had supported more than 3,000 *Sirex* and parasites. A 3 ft. section of this tree is seen on Plate V, fig. 2. It was, of course, quite impossible to undertake the task of determining the percentage of parasitism, as this would necessitate an examination of each pupal chamber and exit hole. This is the only way in which it is possible to determine with certainty whether an exit hole is that of *Sirex* or a parasite. Owing to the great variability in size of *Sirex* and *Rhyssa,* the external appearance of the exit hole gives no definite clue, except in the case of very large holes such as will accommodate the end of an ordinary lead pencil. These are obviously made by large female *Sirex,* as seen in Plate II, fig. 2. Holes a little smaller may be those of male *Sirex* or very large *Rhyssa* (Plate IV, fig. 2). Very small holes may be those of *Ibalia* or small *Rhyssa.* More than half the holes in the log were too small to be those of *Sirex.* The exit holes of *Sirex* may readily be distinguished from those of *Rhyssa* or *Ibalia* by examining a longitudinal section of the pupal chamber and exit hole. The pupal chamber of *Sirex* is entirely without lining and the diameter is approximately the same as that of the exit tunnel.

The pupal chamber of *Rhyssa* is lined with a thin cocoon. This can be seen in Plate V, fig. 1, and the diameter of the exit tunnel is considerably less than the diameter of the pupal chamber, which, of course, was made by the full-grown *Sirex* larva.

The exit tunnel of *Ibalia* is less in diameter than the pupal chamber but as there is no lining to the latter it can by this means be distinguished from that of *Rhyssa.*

Although the exit tunnel of *Ibalia* is, on the average, less in diameter than that of *Rhyssa,* it will readily be seen that owing to a large number of *Ibalia* larvae being parasitized by *Rhyssa,* the size of the exit hole cannot be taken as a criterion.

In discussing the inter-relations of *Ibalia* and *Rhyssa* in his paper on "Studies of the *Sirex* parasites" (pp. 55–57), Dr. Chrystal (1930) gives detailed particulars of the contents of a larch log, as reproduced below :—

Sirex, Ibalia *and* Rhyssa *obtained from a larch log (Brandon, Suffolk), 11–20th June, 1929.*

Ibalia			*Sirex*		*Rhyssa*	
Larvae Full-grown	Prepupae	Pupae	Larvae	Pupae	Pupae	Adults
140	5	39	152	68	3	7
Total : 184 = 44·4 per cent.			Total : 220 = 53·1 per cent.		Total : 10 = 2·4 per cent.	
Grand Total : 414.						

He states: " The above total, representing, as it does, the total population of a single tree, indicates that the abundance of *Ibalia* in the Brandon area can be correlated with the scarcity of *Rhyssa* in the same region. One further observation of interest was obtained from the Brandon log. The *Sirex* were practically all in the advanced larval or pupal stage ; the *Ibalia* were in the majority of cases about to pass into the pre-pupal state and would have emerged this year, while the *Rhyssa* were also in the pupal or adult stage. Last season had evidently witnessed the emergence of quite a number of wood-wasps and parasites (most of the latter, to judge by the tunnels, were also *Ibalia*) and this season will probably see the last of the wood-wasp-parasite population leave the tree. This uniformity of development was very striking and is comparable to similar cases which have been found in logs from Dorset."

The present writer considers that the above figures and remarks give an inaccurate interpretation of the biological complex which they are intended to explain. In the first place, it is to be noted that Dr. Chrystal regards the whole of the population of the larch tree as forming one generation of *Sirex* and its parasites, and assumes that the whole of this population would normally reach maturity and emerge from the tree during the current season. However, the log contents clearly indicate that two generations of *Sirex*, two generations of *Ibalia* and only part of one generation of *Rhyssa* are present. Dr. Chrystal states that " The *Ibalia* were in the majority of cases about to pass into the pre-pupal state and would have emerged this year," but his own published life-cycle of *Ibalia* (Table C., p. 52) reproduced below, does not agree with this hypothesis.

TABLE C.

Distribution of Stages in a Three Year Life-cycle of Ibalia

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1927 ...								E	E	E	E 1	E 1
1928 ...	E 1	E 1	E 1	E 1	E 1	E 1	E 1 2	E 1 2	1 2 3	1 2 3	1 2 3	1 2 3
1929 ...	2 3	2 3	2 3	3	3	3 4	3 4	3 4	3 4	4	4	4
1930 ...	4	4	4	4	4	P	P	A	A			

E. = Embryonic stage. P. = Pupa.
1, 2, 3, 4. = Larval Stages. A. = Adult.

During several seasons the present writer has bred *Ibalia* from parasitized *Sirex* larvae and in each case the results have corresponded with those of Dr. Chrystal as shown in the above table. Reference to the Table IV, showing the inter-relations of *Sirex* and its parasites, indicates that the contents of the Brandon larch log correspond exactly with what we might expect to find in a log during the 5th summer of infestation, and that it would be as follows :—

TABLE V.

Sirex	*Ibalia*	*Rhyssa*
Pupae of 2nd gen. due to emerge as adults during summer of 1929.	Pupae of 2nd gen. due to emerge as adults during summer of 1929.	Pupae and adults 3rd gen. due emerge during 1929.
Larvae of 3rd gen. two-thirds grown remain in log until summer of 1930.	Larvae of 3rd gen. emerge from host larvae and remain in log until summer of 1930.	—

Dr. Chrystal further assumes that no *Rhyssa* adults have emerged from the log during the current season, notwithstanding the fact that he has already stated on page 55, that *Rhyssa* oviposition was at its height in May and June, during that season. This clearly implies that a very large proportion of the *Rhyssa* adults had emerged during May and June, since there is no evidence that *Rhyssa* ever survives the winter in the adult stage after having emerged from the timber. On 15th April, 1932, the present writer found a number of young *Rhyssa* larvae feeding on *Sirex* larvae in a larch log in Verulam Woods, near St. Albans. This indicates that *Rhyssa* may emerge and commence to oviposit as early as the beginning of April. As already stated, during the whole of the operations mentioned above no larvae of *Rhyssa* were found feeding between the end of November and the end of March. It will be observed that the examination of the Brandon larch log began on 11th June, and was completed on 20th June, 1929. In these circumstances it is not unreasonable to suppose that a large proportion of the *Rhyssa* adults had emerged and were not included in the figures on which the percentage of parasitism has been based. This element of uncertainty makes the figures of little value so far as the relative percentage of parasitism is concerned, but even if the log had been examined at the beginning of May and all the *Rhyssa* of the 3rd generation had been collected, the figures would not have given the correct percentage of parasitism, for several reasons. In the first place the *Sirex* larvae of the 2nd generation had already produced one generation of *Rhyssa* which had emerged during 1928, and the pupae were still liable to be parasitized during the summer of 1929, producing a further generation of *Rhyssa* adults which would emerge in 1930. The 152 *Sirex* larvae of the 3rd generation and the 140 *Ibalia* larvae of the 3rd generation found in the log would be subject to parasitism by *Rhyssa* during the summer of 1929, producing part of the generation of *Rhyssa* which would emerge as adults in 1930. While the *Sirex* and *Ibalia* larvae which escaped parasitism in 1929 would still be liable to parasitism by *Rhyssa* during the summer of 1930 while in the pupal stage, thus giving rise to the last generation of *Rhyssa* which would emerge as adults in 1931. It will be seen, therefore, that the *Rhyssa* found in a log in any one year do not represent the total number produced by a single generation of *Sirex*, since each generation of *Sirex* may, and normally does, produce three generations of *Rhyssa*. On the other hand, the problem is still further complicated by the fact that two or even three generations of *Sirex* may be present in the log at the same time. In this case each of the generations of *Sirex* will be liable to be parasitized and together will give rise to one and the same generation of *Rhyssa*. To illustrate this, let us suppose that the above Brandon larch log had been examined a year earlier. This would have been during the summer of 1928. It would at that stage have corresponded with the 4th summer as shown in Table IV and would have been found to contain :—

TABLE VI.

Sirex	*Ibalia*	*Rhyssa*
1st gen. pupae.	1st gen. pupae.	2nd gen. fed on 1st gen. *Sirex.*
2nd gen. larvae two-thirds grown.	2nd gen. full-grown larvae.	3rd gen. fed on 2nd gen. *Sirex.*
3rd gen. larvae one-third grown.	3rd gen. internal parasites.	

The 1st generation *Sirex*, 1st generation *Ibalia* and 2nd generation *Rhyssa* would emerge from the log during the summer of 1928, leaving the 2nd and 3rd generations of *Sirex* and the 2nd and 3rd generations of *Ibalia* to develop along with the 3rd generation of *Rhyssa* to which they would give rise. During the summer of 1928, the 2nd generation of *Rhyssa* would have six possible types of hosts, consisting of the pupae of *Sirex* 1st generation, pupae of *Ibalia* 1st generation, larvae of *Sirex* 2nd generation which had escaped being parasitized by *Ibalia*, full-grown larvae of *Ibalia* of the 2nd generation from *Sirex* 2nd generation, *Sirex* larvae of the 3rd generation which contained *Ibalia* larvae of the 3rd generation as internal parasites, and unparasitized larvae of *Sirex* of the 3rd generation. These six types of host may, for convenience, be regarded as three groups, since the 1st generation of *Ibalia* corresponds with the 1st generation of *Sirex*, while the second generation of *Ibalia* corresponds with the 2nd generation of *Sirex*, and the 3rd generation of *Ibalia* corresponds with the 3rd generation of *Sirex*. It only remains to be remembered that the *Ibalia* larvae of the 3rd generation are internal parasites in the one-year-old 3rd generation *Sirex*, that the *Ibalia* larvae of the 2nd generation emerge from the host larvae in the spring and lie full-grown in the *Sirex* galleries, while the corresponding 2nd generation *Sirex* larvae are about two-thirds grown, and that the 1st generation of *Sirex* and *Ibalia* are both in the 3rd year of their development and are therefore in the pupal stage during the early part of the summer and emerge as adults later in the season.

The following diagram indicates from which generation of hosts each generation of *Rhyssa* arises, and also shows how each generation of *Sirex* may produce three generations of *Rhyssa*.

TABLE VII.

Period	*Sirex*	*Rhyssa*
1st Summer, 1925	Eggs, 1st gen.	—
2nd Summer, 1926	1st gen., 1 year old, one-third grown Eggs, 2nd gen.	—
3rd Summer, 1927	1st gen., 2 years old, two-thirds grown 2nd gen., 1 year old, one-third grown Eggs, 3rd gen.	1st generation.
4th Summer, 1928	1st gen., 3 years old pupate and emerge 2nd gen., 2 years old, two-thirds grown 3rd gen., 1 year old, one-third grown	2nd generation.
5th Summer, 1929	2nd gen., 3 years old pupate and emerge 3rd generation, 2 years old, two-thirds grown	3rd generation.
6th Summer, 1930	3rd gen., 3 years old pupate and emerge	4th generation.
7th Summer, 1931		5th generation.

It will be seen that the 1st generation of *Sirex* produces the 1st generation of *Rhyssa* and also contributes to the 2nd and 3rd generations. The 2nd generation of *Sirex* contributes to the 2nd, 3rd and 4th generations of *Rhyssa*, while the 3rd *Sirex* generation contributes to the 3rd and 4th generations and produces the 5th generation.

The above is intended to illustrate what normally takes place in a single tree in which three successive generations of *Sirex* are bred. It must not be supposed that the 1st generation of *Rhyssa* necessarily gives rise to the 2nd generation and the 2nd to the 3rd, and so on. Actually, in the forest all sorts of combinations are found to occur. Some logs contain only one generation of *Sirex*, others two or even three generations. *Rhyssa* adults of the 1st generation from one log may give rise to the 1st, 2nd, 3rd, 4th or 5th generation in another log, while *Rhyssa* adults of the 5th or any other generation may do the same, but this does not in any way alter the sequence of events.

Let us further examine the Brandon larch tree. As we have seen, the 1st generation of *Rhyssa* emerged in 1927. The 1st generation *Sirex*, 1st generation *Ibalia* and 2nd generation *Rhyssa*, emerged during the summer of 1928. In June 1929 the tree contained the 2nd generation of *Sirex*, and the 2nd generation *Ibalia*, both in the pupal stage and due to emerge during that season. It also contained the 3rd generation *Sirex* and the 3rd generation *Ibalia*. These would remain in the larval stage until the summer of 1930, when they would normally pupate and emerge as adults. In addition it contained pupae and adults of the 3rd generation of *Rhyssa* ; an indefinite number of this generation of *Rhyssa* had emerged during the months of May and June. These *Rhyssa* had been parasitic on the *Sirex* and *Ibalia* of the 2nd and 3rd generations. A proportion of the *Rhyssa* of the 2nd generation which emerged in 1928 had also been parasitic on the 2nd generation of *Sirex* during the season 1927–28, at which time the 2nd generation of *Ibalia* larvae would be internal parasites. It will be seen that, in order to arrive at the correct percentage of parasitism, it would be necessary to include these two numbers in the calculation. This would give a considerably higher percentage of *Rhyssa* and a lower percentage of *Ibalia* and unparasitized *Sirex*. The effect of the 4th and 5th generations of *Rhyssa* would be to increase still further the percentage of *Rhyssa* and lower the percentage of *Ibalia* and unparasitized *Sirex*.

The above analysis shows the futility of trying to arrive at an accurate estimate of the percentage of parasitism by *Rhyssa* by means of calculations based on the contents of a single log or on a single generation. In fact, it is very difficult, if not quite impossible, to arrive at an absolutely accurate estimate of the percentage of parasitism. In the case of *Rhyssa* the difficulty is due to the fact that one generation of the host may produce three generations of the parasites over a period of three years, and, as we have seen, when three generations of hosts are present in the log the second generation of *Rhyssa* is produced by two generations of hosts, the 3rd generation of *Rhyssa* is produced by three generations of hosts and the 4th generation of *Rhyssa* is produced by two generations of hosts ; while figures obtained by calculations based entirely on the young *Sirex* larval stages cannot be considered final, because the percentage is liable to be modified by one or even two subsequent generations of *Rhyssa*.

In the absence of *Rhyssa* it would be fairly easy to ascertain the percentage of parasitism by *Ibalia*, as in this case all that would be necessary would be to collect and dissect all the *Sirex* larvae found in the logs during the winter months, adding to the numbers of parasitized larvae the total number of full-grown *Ibalia* larvae found in the material. The addition of the number of full-grown *Ibalia* larvae is essential, because results based entirely on dissected *Sirex* larvae would show a percentage of parasitism below the actual figure, unless all the material examined happened to be in the early stages, *i.e.*, during the first or second winter of infestation. In this case only one generation of host and parasite would be present and no full-grown

Ibalia larvae would be found. Logs collected from localities where an infestation has been in progress for more than two years would almost certainly include some material over two years of age, in which case full-grown *Ibalia* larvae would be present. It is imperative that only material collected from logs during the winter and early spring be included in the figures, as material collected from June to October, inclusive, would vitiate the results, owing to the fact that the population is in a state of flux during the summer and autumn and there is no certainty that the contents of logs examined during that period will represent the actual population. Where *Rhyssa* is present the true percentage of parasitism by *Ibalia* cannot be ascertained by the dissection of *Sirex* larvae collected from a number of logs selected at random, as *Rhyssa* is intrinsically superior to *Ibalia*, and the effects of parasitism by *Rhyssa* are cumulative during each generation of *Sirex*.

In any case it would be necessary to ascertain how many adults of each species had already emerged from the logs in order to ascertain the percentage of parasitism by either species where the infestation has been in progress for more than two years. Unfortunately Dr. Chrystal's figures, given in Appendix II of his paper, showing the percentage of parasitism by *Ibalia*, are based entirely on the results of the dissection of *Sirex* larvae collected from logs selected at random during all seasons of the year.

5. Possible Factors of Control, other than Parasites.

The writer has paid considerable attention to the study of factors, other than parasites, which might be expected to operate in the control of *Sirex* wood-wasps. The results of his observations in this direction, although almost entirely negative, are given below.

(*a*) *Birds.*

It is reasonable to expect that birds would play an important part in the control of a forest insect which spends a considerable part of its time boring oviposition holes in the bark of standing trees and felled logs, but the writer failed to observe a single instance of either *Sirex* or *Rhyssa* adults being attacked by birds.

Robins, wrens and titmice were observed to extract *Sirex* larvae from the ends of logs which had been crosscut, but none of these birds appeared to take the slightest notice of *Sirex* and *Rhyssa* adults which were ovipositing within 2 or 3 ft. of them. On one occasion a spotted flycatcher was seen to use a stack of *Sirex*-infested logs as a jumping-off place for its characteristic short flights to capture insects, but it made no attempt to catch the *Sirex* and *Rhyssa* adults which were ovipositing in the logs, or flying around the stack of logs in considerable numbers.

Sirex gigas certainly bears some resemblance to a wasp or hornet, and when touched while on the surface of a log *Sirex cyaneus* erects the abdomen in much the same way as the Devil's coach-horse beetle, to which insect it bears some resemblance in colour. The bright metallic lustre and somewhat piebald appearance of *Rhyssa* may suggest that the insect is inedible. Whether either the colour or habits of these insects afford them some measure of protection from birds is a matter for conjecture.

Of the hundreds of *Sirex*-infested trees cut up during the collection of parasite larvae, not a single silver fir tree showed any sign of the attack of woodpeckers. Other trees which were in a somewhat advanced stage of decay were favourite feeding-places for woodpeckers, but on examination these trees were found to contain *Rhagium* larvae, pupae and adults, and although many of them were perforated with numerous *Sirex* and *Rhyssa* exit holes, these trees were obviously too decayed for further use by *Sirex*, and no *Sirex* larvae were found in them.

Woodpeckers were frequently observed enlarging *Sirex* exit holes in trees and on examination similar exit holes were found to contain woodlice, hibernating flies and in some cases hibernating Chalcids. Birds are frequently observed at work on larch trees from which *Tetropium gabrieli* adults have emerged, and the exit holes of this insect seem to be a favourite hunting place.

Both *Tetropium* and *Sirex* attack the bark of sickly larch as soon as the tree is in a suitable condition for their breeding purposes. *Tetropium* completes its life-cycle in one year and although this species may not attack the tree until the year following the attack of *Sirex*, the *Tetropium* adults will have emerged while *Sirex* is still in the larval stage. This has led to the belief, expressed by some writers on forest entomology, that *Sirex* is secondary to *Tetropium* in its attack on the tree, which is certainly not the present writer's experience.

It has already been mentioned that the larval tunnels and pupal chambers of *Sirex* are often of a very superficial character in larch timber. This is particularly the case when the *Sirex* larva has been parasitized by *Ibalia*. In the majority of cases the larvae of *Ibalia* lie within a quarter of an inch of the surface of the timber and are often lying in that position during the period when the grestest activity of birds on the bark of larch takes place, namely during the winter following the summer during which *Tetropium* adults have emerged from the bark. In these circumstances it is not unreasonable to suppose that the *Ibalia* larvae may often be extracted and eaten by the birds.

The pupal chambers of the male *Sirex* often occupy this superficial position, so they also are particularly liable to destruction by birds. The pupal chamber of female *Sirex* are generally formed at a greater distance from the surface, but as seen in Plate V, fig. 3, they sometimes lie quite close to the surface, and as in all cases the larvae or pupae which occupy this superficial position in the timber are exceptionally liable to parasitism by *Rhyssa*, it will be seen that birds probably destroy more *Ibalia* and *Rhyssa* larvae than *Sirex* larvae.

During the collection of parasite larvae, *Tetropium*-infested larch trees which had been heavily attacked by birds were found to contain few *Sirex* parasites, consequently preference was given to silver fir, spruce, pine, and larch trees which did not show much sign of bird activities. The fact that an insect does not appear to be attacked by birds, or at any rate is not particularly attractive to them, during periods when the insect is comparatively scarce as compared with other species of insects on which the birds are observed to be feeding, must not be taken as evidence that the insects will be ignored, or even remain unattractive, during periods when other insects are not particularly numerous, or in localities or environments where other insects are relatively scarce, or when that particular species is exceptionally numerous, as in the case of an outbreak.

It is well known that birds often congregate in large numbers when an outbreak of the Oak Leaf-roller moth occurs, to devour these insects. In such circumstances birds which are not normally insectivorous are to be found feeding on insects; in the case of the Large Larch Sawfly infestation during the year 1906-1912, Hewitt (1912) states that starlings, jackdaws and rooks fed on the larvae in company with other birds, and Annand (1910) records that jays were very useful in extracting the sawfly larvae from the cocoons.

Although the present writer (1937) in discussing birds in relation to bark-beetle control, states that birds cannot be regarded as important factors in the control of bark-beetles under normal conditions in Britain, this is certainly not the case where large bark-beetle infestations arise, as sometimes happens in Europe. Trägrådh and Butovitsch (1938) state that in Sweden during an extensive bark-beetle infestation, birds destroyed immense numbers of the insects during the swarming period.

In the case of *Sirex*, Clark (1927) states that in New Zealand birds destroy considerable numbers of the insects. Their beneficial effects will, however, be greatly nullified if they also destroy the parasites, which have been introduced and liberated to control the wood-wasps.

(b). Fungi.

No evidence has been found to show that entomophagous fungi play any part in the control of *Sirex,* but certain species of phytophagous fungi cause the death of coniferous trees and are of considerable importance as agents contributing to the provision of suitable breeding material. Under certain conditions, however, these same fungi cause the death of *Sirex* pupae and adult insects.

During the winter of 1928-29 the writer personally cut up and dissected upwards of 30 tons of timber which had been used for the purpose of forming breeding-places for the parasites of *Sirex* during the previous summer. The bulk of this timber consisted of silver fir from the plantations in North Devon referred to later. Some of the trees had been killed by *Fomes annosus (FT.)* Cooke = *Tranmetes radiciperda,* Hartig, and others by *Armillaria mellea,* Vahl. = *Agaricus melleus,* L. The methods of attack and the effects of the two fungi are quite different, trees severely attacked by the latter generally die quickly, often within one or two years, while large trees attacked by the former may live for a considerable number of years. In the case of *Fomes annosus* the fungus attacks and kills the roots and the mycelium of the fungus attacks the heartwood, causing the tree to become hollow for several feet at the base of the stem. Large trees which have only a few of the roots attacked may continue to nourish and put on wide annual rings of timber, although the fungus may be actively destroying the heartwood, but if many of the roots are killed the trees are liable to be blown or may die standing. In either case the timber not actually invaded by the mycelium of the fungus is sound and indistinguishable from that of trees which have not been attacked. Once the vigour of the tree is reduced to the point when the foliage begins to wilt, whether standing or blown, the timber is attacked by *Sirex,* but in no case were the *Sirex* larvae found burrowing into timber which had become permeated by the mycelium of this fungus.

Armillaria mellea attacks the tree roots and the base of the stem just below ground-level. The mycelium of the fungus invades the cambium layer and spreads rapidly upwards between the bark and the timber. When once the base of the stem has been completely encircled by the mycelium of the fungus, the foliage wilts and the whole tree at once becomes suitable for the attack of *Sirex.* This type of tree is undoubtedly one of the most attractive breeding-places.

When the mycelium of the fungus reaches the stranded rhizomorph stage between the bark and the timber, the bark becomes loose and that portion ceases to be attractive for oviposition. At this stage the sapwood has become permeated by the fungus. In the meantime the *Sirex* larvae which hatched from the eggs of the previous season have begun to burrow towards the heartwood, which is still quite sound. Here they continue to feed until the autumn preceding the summer when they are due to emerge as adults. They then turn outwards and burrow through the sapwood, which may by this time have become quite decayed. In no instance were *Sirex* larvae found feeding in this fungus-infested material, and even the fully developed larvae do not in all cases successfully pupate and emerge as adults. Some of the pupae are destroyed by the fungus, and adults not infrequently perish. It is to this material that Dr. Chrystal refers in " *Sirex* Wood-wasps and their Importance in Forestry " (p. 235) when he states " The pupae of S. *cyaneus* when lying too deep in the wood often perish in situ, either in the pupal stage or as adults. For example, while examining silver fir logs for S. *gigas* material recently, I was struck by the number of adults that were found dead in their tunnels, sometimes in the pupal chamber, sometimes on their way to the outside. These adults were nearly always covered with fungus, but whether this fungus was the cause of death or an after-growth I do not know ; but I imagine that the death of the pupae and likewise that of the adults is due to some organism whose attack is induced by change of moisture conditions in the wood."

The particular logs to which he refers had been lying for some time on the ground, and the conditions had, therefore, been favourable for the rapid development of the fungus. While the trees remain standing the fungus develops more slowly and fewer deaths occur.

Buchner (1928) described special organs in *Sirex* and *Xyphydria* that harbour a fungus and provide for its transmission to the offspring, and regards this as a case of symbiosis. This has given rise to much speculation during recent years. Professor J. W. Munro (1931) suggested that the fungus acts as a pre-digestive and that *Sirex* larvae can develop only in material that is in a condition suitable for the development of the fungus, which has been identified as a species of *Stereum*.

On the other hand, Mansour and Mansour-Bek (1934) have shown that the true wood-feeding insects do not depend on micro-organisms for the digestion of wood. They comprise those without cellulose-breaking enzymes, which derive the necessary carbohydrates from the soluble sugar and starch in the wood on which they feed, and those with such enzymes, which can utilise the cellulose of the wood through the activity of their own secretions, and can therefore live on wood relatively poor in the simpler carbohydrates.

As a biological study symbiosis is a subject of great interest, but for all practical purposes, so far as the control of *Sirex* is concerned, the symbiont may be regarded as the equivalent of part of the insect.

(*c*). *Climatic and Physical Conditions.*

The range in extremes of climatic conditions in Britain is not sufficiently great to have any apparent effect on the development of *Sirex*. Both *Sirex gigas* and *S. cyaneus* are present at all elevations or latitudes suitable for the growth of the host trees. In the neighbourhood of the Cairngorms in Scotland, temperatures of −5°F. are frequently registered in winter, but *Sirex* does not appear to be adversely affected by these severe conditions. The writer has often examined the contents of logs during periods of severe frost and has found both *Sirex* and *Rhyssa* larvae completely encased in a layer of ice within the pupal chamber, but on being thawed out the larvae did not manifest any signs of having suffered ill effects, and other larvae in the same logs subsequently completed their development.

A period of severe drought sometimes has the effect of causing logs to dry out and become unattractive for *Sirex* oviposition, and in the case of logs which are already infested by *Sirex*, the development of the larvae may be arrested somewhat, and adult *Sirex* which have developed in exceptionally dry logs are often very small.

On the other hand, periods of severe drought often benefit the *Sirex* population as a whole by causing a serious reduction of the water level in the subsoil resulting in the death, or partial destruction, of overmature trees, which then become available for breeding purposes, so that on the whole, the conditions produced by drought are perhaps more favourable for *Sirex* increase than otherwise.

During prolonged wet periods the sapwood of logs, which have been lying in the forest for several seasons, becomes thoroughly saturated with water, and in the case of logs lying in wet places many of the *Sirex* larvae and pupae are killed by excess of moisture. But as the parasite larvae suffer in the same way the ratio of host and parasite will not be altered, and the only effect will be a slight reduction in the general population.

Here again, the conditions which, on the one hand, cause destruction to part of the insect population, compensate by the addition of benefits which these same conditions produce for the population as a whole. Prolonged wet periods cause low-lying land to become water-logged, often resulting in an unhealthy condition, or even the death of groups of trees which are unable to withstand exceptionally wet conditions. These trees are thus rendered suitable for the breeding purposes of *Sirex*.

Gales and snowbreak also provide large quantities of suitable breeding material. In fact it seems probable that all abnormal conditions in the forest ultimately result in more favourable breeding facilities, and consequently the increase of the *Sirex* population, and that with the exception of parasites, *Sirex* has no known natural enemies of any importance.

6. The Economic Status of Sirex in Britain.

The attack of *Sirex* on the tree is entirely for breeding purposes, and its activities in this respect are confined to the timber. The nature of the damage is of a technical character affecting the quality of the timber.

In common with other insects which breed in the bark or timber of standing trees, *Sirex* will attack any part of the tree as soon as that part is in a condition suitable for its requirements. In a spruce wood near Dulverton, Somerset, the writer saw exit holes of *Sirex* in a large bare patch of timber on the side of a big spruce tree from which the bark had been worn by the friction caused by a wire rope during haulage operations. Owing to the extent of the damage to the bark, occlusion had not been complete, although the rest of the tree was in a very flourishing condition.

Sirex sometimes makes mistakes and attacks trees which are not in a suitable condition, and occasionally pays for the mistake with its life, owing to its ovipositor becoming firmly held by the tissues of the timber. The writer has, on more than one occasion, found the ovipositor with part of the insect attached, sticking in the bark of growing trees.

For successful oviposition, in the case of living trees, the limiting factors are transpiration and the activity of the cambium. In a tree with a large healthy crown and root system, transpiration is rapid, the sapwood consequently contains large quantities of water and the cambium is very active. Both these factors are inimical to the successful establishment of *Sirex* in the tree. Occlusion of the oviposition tunnel takes place rapidly and excess of water occurs; the necessary air supply is not available for the successful hatching of the *Sirex* eggs and the development of the young larvae. This probably explains why a large crowned, wind-blown tree whose roots are still attached to the soil may be unsuitable for breeding purposes, while a similar tree which has been cut off and trimmed of branches may at once be successfully attacked. It frequently happens that some of the roots of a blown tree remain attached to the soil on one side, and when enough roots remain so attached, the vigour of the tree may be maintained for a considerable period, not, of course, at its original level, but at a level sufficiently high to render the tree unsuitable for *Sirex* for a season.

When felling operations were in progress during the summer, the writer on one occasion observed *Sirex* begin to oviposit in a felled larch even before the men had finished trimming off the branches, notwithstanding the fact that a few minutes previously the tree was quite unattractive. In this case the insect was evidently attracted by the odour from the freshly cut surfaces. Over-mature trees are always liable to attack and frequently suffer considerably.

While on the one hand, trees in a normal, vigorous state of health are not suitable as hosts for *Sirex*, the other extreme limit to the range of suitable conditions is reached when the cells of the timber are invaded by the mycelium of a fungus, other than the symbiont directly associated with the insect, or the timber becomes water-logged or decayed. Between these two extremes there is a wide range of conditions under which timber is suitable for successful attack.

Perhaps the least attractive trees are those which have been killed by excessive shade, but in this case it presumably is not the condition of the timber but the lack of light which deters *Sirex*. In the absence of other material more attractively situated, *Sirex* will attack trees which are heavily shaded. It sometimes happens that individual coniferous trees, particularly silver fir, which have grown in woods of broad-leaved species on long rotation, having attained a great height or developed some peculiar characteristic which gives them a sentimental value to the owner, are left standing when the surrounding trees are felled, or when very heavy thinnings are made in the woods. Often within a few years, owing to the exposure of the soil to the effects of sun and weather, and the consequent disintegration of the humus, the water-level in the soil is reduced and the trees are unable to obtain enough moisture to maintain the health and vigour of the large crown produced under more favourable circumstances. When this stage is reached, the trees begin to die back and become what is termed " stag-headed." In carrying out the large-scale collection of *Sirex* parasites in 1930–31, this type of tree provided very productive material. Trees with double leaders often lose one of the tops in a gale ; these tops were also very prolific in *Sirex* material. Trees killed or damaged by lightning, fire, felling or haulage operations, are also attacked. As already mentioned, larch felled in summer are particularly attractive. A larch plantation of about 20 years' growth was being thinned in Devon in August 1928. On the second day of the operations the writer observed several *Sirex gigas* adults ovipositing in small larch thinnings which had been felled the previous day.

During the winter of 1920 a large number of very fine larch trees were felled and the best trees were selected for telegraph poles. These poles were peeled by means of draw-knives during the summer of 1921. While this work was in progress the poles were attacked by *Sirex gigas* in considerable numbers.

It will be seen from the above observations that while certain conditions render timber unsuitable for *Sirex*, no peculiar pathological conditions are required to make the timber suitable.

The suggestion, which has frequently been made by writers on forest entomology during recent years, that *Sirex* and *Tetropium* may to some extent be regarded as beneficial, on the grounds that they call the attention of the forester to the existence of unsatisfactory conditions in the stand, is without foundation, since the presence of the sickly, dying or dead trees would be far more likely to attract the attention of the forester, and as has been shown above, *Sirex* often breed in material other than trees which are in a pathological condition. There is, perhaps, some justification for regarding *Sirex* as being somewhat useful, in common with *Rhagium* and *Asemum*, because they help to hasten the destruction and disintegration of useless material lying in the forest, and thereby facilitate its incorporation with the forest soil.

Under normal forest conditions, *Sirex* has never been known to become a pest in Britain. During the summers of 1937 and 1938, the writer spent several months in the pine forests of N.E. Scotland, and saw large areas of Scots pine up to 65 years of age which had never been thinned. Even in these areas *Sirex* is not very numerous on account of the control exercised by parasites, owing to the fact that in small poles the *Sirex* larvae are unable to burrow out of reach of *Rhyssa*.

When abnormal conditions arise, as for example in large windfall areas, where removal of the large trees is neglected, these conditions are exceptionally favourable for the increase of *Sirex* and considerable damage to the timber may result, but this is entirely due to the delay in removing or converting the large logs.

Conditions suitable for the increase of *Sirex* also occur where areas of forest are allowed to become water-logged and large numbers of trees become sickly and die.

Where normal felling operations are in progress the timber is seldom allowed to lie on the ground long enough to become seriously infested by *Sirex*, but in country sawmill yards logs can often be found which have been left lying neglected and have become the focus of a *Sirex* population.

Although *Sirex* cannot, under existing conditions in Britain, be regarded as a menace to the health or welfare of young coniferous crops, this would certainly not be the case in the absence of parasites. The chief limiting factor to its increase would then be the supply of suitable breeding material. All badly suppressed poles in a pine stand would be liable to attack and they would rapidly be reduced to a state in which they would be suitable for the breeding purposes of bark-beetles and other insects. This would result in an excess of suitable breeding material for these insects, thus upsetting the balance and turning the scale in their favour. They in turn would devastate the standing crops and provide fresh breeding material for *Sirex*. The insect would rapidly increase in numbers and would become a menace to nearly all coniferous timber, whether lying in the forest, stacked in timber yards or forming part of structures, unless adequately treated with preservatives before use.

So numerous are the parasites in *Sirex*-infested material, that it is difficult to find logs in which they do not preponderate. In 1935 the writer received a letter from Dr. E. A. Parkin of the Forest Products Research Laboratory, Princes Risborough, requesting him to supply *Sirex*-infested logs containing fully grown larvae and pupae, and as free as possible from parasites. He stated that some material he had received from Norfolk was, unfortunately, almost spoilt for his purpose by a positively enormous emergence of both *Rhyssa* and *Ibalia*. Since the receipt of Dr. Parkin's letter the writer has from time to time examined *Sirex*-infested logs, both in the New Forest and in the pine forests of N.E. Scotland, with the object of providing the desired material. In all cases, the material examined was found to be heavily parasitized.

It will be seen from the above observations that the status of *Sirex* in Britain is that of an insect under complete economic control.

This does not mean that *Sirex* is incapable of becoming a pest. Like every other species of insect which is capable of doing any kind of damage, *Sirex* would certainly become a serious pest were it not for the existence of the factors which keep it under control. In the case of *Sirex*, the writer is convinced that the parasites, *Rhyssa* and *Ibalia*, are by far the most important factors of control.

This view is not shared by all economic entomologists. In discussing "The Biological Control of Forest Insects," Professor J. W. Munro (1931) states: "Many other factors apart from animal parasites affect the well-being of insects, and the extravagant claims made by some entomologists in favour of parasite control cannot be accepted.

"The method, like all other methods, has its limitations, and it so happens that we know more of its limitations in forest entomology that in agricultural entomology. An important and valuable illustration of the inapplicability of parasite control is afforded by certain of the wood-wasps of the family SIRICIDAE."

Professor Munro doubtless selected this case as exhibiting with special force the weakness of the method of biological control as applied to forest entomology. It is therefore necessary to consider his arguments very carefully in order to ascertain whether his statement is substantially correct.

Professor Munro sets out to discuss the question of the introduction of parasites into New Zealand with the object of controlling *Sirex*, but the whole argument circles round the question of the desirability or otherwise of introducing parasites into Tubney Arboretum, Oxford.

After producing hypothetical reports by two fictitious investigators, one a forester and the other an entomologist, he concludes by saying "Here then is an instance where control by parasites is not only impracticable but wrong-headed."

Professor Munro's argument is based on the assumption that the occurrence of *Sirex* is governed by the existence of conditions favourable for the growth of its symbiotic fungus, *Stereum*, the vital factor being a peculiar pathological condition produced in timber by death through water-logging of the soil, and the attack of the fungi, *Fomes annosus* and *Armillaria mellea*. Before producing the imaginary reports of the forester and the entomologist, he is careful to state " The fungi *Fomes annosus* and *Armillaria mellea* are found on many of the trees, but not both together."

Both the reports are based on the data thus provided. The forester mentions the presence of *Tetropium* as confirming the existence of the pathological conditions and incidentally rendering the occurrence of *Sirex* tertiary.

Before we can accept Professor Munro's explanation of the conditions governing the occurrence of *Sirex*, it will be necessary to verify certain rather important details. For example, the presence in the area of the two fungi, *Fomes annosus* and *Armillaria mellea*, is of vital importance if they are to play their important part in the production of the hypothetical pathological conditions which favour the growth of the symbiotic fungus *Stereum*.

When introducing his mythical entomologist, Professor Munro says " If he is good at his work he will begin with a study of the literature." If he himself had followed this excellent advice, he would have discovered the following statement in Dr. Chrystal's paper " The *Sirex* Wood-wasps and their Importance in Forestry " (1928) :—

Field Studies in Tubney Wood, Oxford.

" Through the kindness of Mr. W. R. Day, Mycologist to the Imperial Forestry Institute, I was able to make a survey of the wood in company with him to collect data on the following points :

(1) The general condition of the larch and its relation to soil conditions, silvicultural treatment, etc.

(2) The presence of root fungi as antecedent to, or contemporary with, the *Sirex* attack.

" Two root fungi were looked for, *Armillaria mellea*, the honey fungus, and *Fomes annosus*. On a previous preliminary survey it was thought that one or both these fungi might be prevalent, causing primary injury. After searching both in the field and in the Laboratory, however, no sign of the rhizomorphs of *A. mellea* or of the mycelium of *Fomes* could be traced.

" On the other hand extensive root rot was present, the tap-roots of many trees being completely destroyed. This was entirely due to the waterlogged condition of the soil."

It appears, therefore, that Professor Munro's theory is without foundation, since it was built up entirely on the assumption that the two fungi were present in the area.

It is true that Dr. Chrystal does, in one or two of his papers, refer to *Sirex*-infested silver fir which had been killed by these fungi. These records do not, however, refer to Tubney Aboretum, but to some plantations in North Devon which he visited with the present writer in 1928.

The fact that no one has ever suggested the introduction of parasites into Tubney Arboretum, or even hinted that *Sirex* was a pest in that area, is of little importance.

Dr. Chrystal has shown that both *Rhyssa* and *Ibalia* are fairly numerous at Tubney, and presumably in order not to deplete the *Sirex* population there, which he required for his own studies, on 23rd November, 1928, he addressed a letter to the present writer asking him to collect as many living *Sirex* larvae as possible in Devon, as he was anxious to get these to send to a colleague in the north who was going to undertake a cytological study of them.

In discussing biological control, Professor Munro states : " The principle of the method in its simplest form is, briefly, that excessive increase of insects is caused by lack of natural enemies, of which parasitic insects are the most important, and that the best method of restoring the balance and of reducing the noxious insects to numbers which are harmless is to introduce to the areas affected large numbers of the parasites.

" If the premises are right and the increase of a noxious pest is the result of the absence or paucity of insects parasitic on it, the logic of the method is unassailable, and it is noteworthy that where these conditions hold, the success of parasite control is assured."

These are precisely the conditions which exist in New Zealand.

7. The Present Status of Sirex in New Zealand.

The following account of the present status of *Sirex* in New Zealand is taken from a paper written by Dr. D. Miller (1935), Chief Entomologist at the Cawthron Institute, and Mr. A. F. Clark, Forest Entomologist, State Forest Service, and is reproduced here because it constitutes an authentic statement of the conditions which exist, written by the men who are actually in charge of the operations in connection with the biolgoical control of *Sirex* in New Zealand ; also because the statement forms the foundation on which the present writer bases his conclusions on the discussion which follows.

" Although on the whole our plantations of exotic conifers, now amounting to some 500,000 acres, have not yet suffered from widespread epidemics, there are certain exotic insects already well established in the country that must be considered as potentially dangerous. Attention is being given to the most important of these.

" One species, though not a serious pest of healthy trees, has attracted considerable attention owing to its widespread establishment throughout the Dominion. This is the steel-blue horntail-borer or wood-wasp, *Sirex noctilio*, of Europe, which in this country attacks *Pinus radiata*, *P. laricis*, *P. muricata*, *P. austriaca*, *P. pinaster* and *Larix europaea*, whilst on one occasion it was found attempting to oviposit in the native Miro (*Podocarpus ferrugineus*). Attacking suppressed, dying and dead trees for the most part, this insect is nevertheless an important factor detrimental to forest protection since it may hasten the death of trees that could be utilised, as well as creating conditions favourable to the breeding of the European bark-beetle (*Hylastes ater*, Payk.) now well established in many regions. In this respect it is of importance to note that some large commercial concerns which have extensive pine forests, apparently intend to attempt the management of these upon a sustained yield basis with an extremely short rotation by a system of clear felling at the age of 12 to 16 years and subsequent replanting. Exotic conifers, maturing very rapidly in New Zealand, present ample pabulum for the larvae of *Sirex* at the above mentioned ages, and the stumps of such trees attacked by that insect and infested with *Hylastes*, will, after clear felling, be centres from which *Hylastes* will spread and attack the fresh crop of seedlings, as has already been the case. Further, since exotic conifers have been planted somewhat indiscriminately all over the land, often without due consideration of site, some areas, having reached a fairly advanced state, appear to be weakening and becoming susceptible to *Sirex* attack. A further factor contributing to the development of *Sirex* is the lack of suitable plantation management. The basic difficulty is usually the fact that thinning, instead of yielding an intermediate return, such as might be expected under Old World conditions, is in such cases a definite additional capital charge, since small sizes of the timbers grown can only on rare occasions be profitably utilised. It is, therefore, not surprising that the average plantation owner avoids thinning, even when he realises that trees have to be farmed, as has any other crop, with the result that suppressed, broken, and dead trees comprising dense thickets are common.

" Although suppression, breakage, and poor site are the most frequent causes inducing *Sirex* attack, the influence of fire and fungi cannot be overlooked.

" Very few plantations, outside those owned by the State and large commercial concerns, are adequately protected from fire, and it is no uncommon sight to see a considerable area of valuable trees irreparably damaged by accidental fires ; this is particularly so when the plantations are situated along main highways or in the vicinity of settlements. Fire-killed trees, provided they are dried out, are not favourable for the breeding of *Sirex*, but in the case of light ground fires which cause the tree to wilt and die gradually, the insect finds an excellent breeding ground . . . . *Sirex noctilio* has been present in the Dominion for a considerable time ; as far back as 1900 the insect was found in the Waiarapa district of the North Island. For many years it was by no means a common species, but with the development and extension of areas under exotic conifers it has correspondingly increased and is now one of the commonest species met with amongst our insects of economic importance."

Although it is at least 38 years since *S. noctilio* first became established in New Zealand, the insect has not yet become distributed throughout the whole country. This is an important fact, as it indicates the urgent necessity for dealing effectively with the insect without delay so as to localise the sphere of operations and if possible to restrict its distribution. It must be remembered that although the spread of the insect would, in the early stages be very slow, every year must witness a great increase in the area of infestation, owing to the rapidly increasing population spreading out over a much wider radius each year. The full extent and nature of the damage which *Sirex* is capable of causing will not be realised until a point is reached when further distribution is impossible. Owing to the strong powers of flight and very active habits of the adult insect, the present process of distribution tends to keep down the density of the population in any particular locality.

The rate of spread during the last few years cannot be regarded as a standard of comparison for the distribution during a similar period in the future. In all probability during the next few years *Sirex* will have become established in all coniferous stands throughout the country.

Once the possible range of distribution has been reached there will be a spontaneous increase in the density of the population. If, for example, in say the year 1945 there is an average of 100 female *Sirex* per acre, the next generation arising from these insects could, in the absence of natural enemies, number 40,000 per acre, since the biotic potential is 400 per female. If this stage is ever reached *Sirex* will have become a menace to the existence of the entire coniferous forest. Unfortunately the rate of progress of the spread of the insect is not easily seen as, unlike leaf-eating insects, the larvae develop out of sight and the adult insects are mostly hidden away in the forest and are not very conspicuous when not in flight.

The apparent scarcity of adult insects in any particular year must not be taken as an indication that the infestation is on the decline, because as *Sirex* normally has a three year life-cycle, major flight years might occur at intervals of three years, but as the life-cycle may sometimes be completed in two years, and under certain conditions may be extended to four or more years, the progeny of these exceptional cases get out of step and appear during the years forming the intervals between the main flight years. Periodicity of the flight years is, however, not so marked in the case of *Sirex* as with such insects as cockchafers, because the development of the latter is largely influenced by climatic and physical conditions affecting the temperature and moisture of the soil, and by cultural methods and crop rotation. These factors exercise little influence on the rate of the development of *Sirex*, since the insect develops in an entirely different medium.

Dr. Miller and Mr. Clark have pointed out that the clearance of large areas of pines on a short rotation will have the effect of providing a continual succession of fresh breeding-places for *Hylastes ater*, from which these insects will spread and attack the fresh crops of young trees. It might also be mentioned that these beetles will also attack the roots of suppressed trees in the older stands for breeding purposes and bring about their death, thus providing additional breeding material for *Sirex*. *Hylastes* may even attack and kill trees which are not badly suppressed, as sometimes occurs in Britain. Indeed this is very likely to happen where the insect is very numerous. It will be seen, therefore, that although *Hylastes* and *Sirex* belong to entirely different orders, they form a definite biological association of a particularly dangerous type, and their combined activities may, in favourable circumstances, result in the formation of a vicious circle.

8. The Introduction and Establishment of Rhyssa in New Zealand.

A short account of the collection of 7,830 *Rhyssa* larvae for shipment to New Zealand has already been given. The following account of the importation and liberation of the insect is based on a paper by Dr. Miller and Mr. A. F. Clark (1935), who were in charge of the work in New Zealand.

" Owing to the abnormal abundance of *S. noctilio* in the plantations of exotic conifers, steps were taken in 1927 to locate and introduce a parasite for its control. Adverse opinions were expressed upon the venture, since it was assumed that any attempt to introduce and establish a parasite of a wood-boring insect would fail. Why this should be so in the case of wood-boring parasites more than in the case of other insects, we failed to see ; and as the results to date have shown, the assumption was unfounded and demonstrates that one cannot definitely foretell the success or failure of any project connected with the biological control of insects.

" The importation of *Rhyssa persuasoria* was carried out between December 1928 and April 1929, and again between March and August 1931 ; during these periods nineteen consignments, totalling 7,830 individuals were sent us from Farnham Royal.

" The insects were shipped in the larval stage under cool storage conditions, and packed in gelatin capsules or corked glass tubes, a single larva to each receptacle. In some cases larvae had pupated and in others adults developed during the voyage.

" Some 160 parasite larvae of the 1928–29 consignments were sent in glass tubes, but in all other shipments gelatin capsules were used. The glass tubes were not a success, owing to the accumulation of moisture and the development of mould upon the larvae. Many of these mould-affected larvae were saved by brushing with a very fine brush dipped in a saturated solution of boracic powder in cold water. This treatment was effective in removing the mould and allowing about 40 per cent. of the infected larvae to pupate, but the adults emerging from these were in poor condition. The capsules and tubes of the 1928–29 consignments were packed in cottonwool and those of 1931 in sawdust ; both methods gave equally satisfactory results, though the sawdust apparently ensured more suitable conditions of moisture and temperature. In some cases sawdust was placed in the capsule with the insect, but no marked difference resulted."

The data furnished by Dr. Miller in his description of the state of the parasites in the various shipments on arrival in New Zealand are reproduced below. The living individuals are marked (+) and dead or diseased (—).

The data reveal a high rate of mortality during transit, a very unsatisfactory state of affairs, particularly in the case of insects which are so extremely difficult to collect in large numbers. This high rate of mortality is a matter of great importance, and the cause should be ascertained if possible. The data must, therefore, be examined in detail.

The first two shipments containing 201 parasites were received on 8th December, 1928, and 7th January, 1929. They were all in the larval stage on arrival and the total mortality was only 2·98 per cent.

The third and fourth shipments received on 9th and 15th January contained 460 parasites. On arrival 13 pupae were found in these shipments, showing that

Particulars of Shipments received during 1928–29.

Consign-ments	Received	No.	Condition on arrival			
			Larvae	Pupae	Adults	Percentage Alive
1st	8.xii.28 ...	51	47 (+) 4 (–)	—	—	92·16
2nd	7.i.29 ...	150	148 (+) 2 (–)	—	—	98·66
3rd	9.i.29 ...	143	111 (+) 31 (–)	1 (+)	—	78·32
4th	15.i.29 ...	147	120 (+) 15 (–)	12 (+)	—	89·75
5th	12.ii.29 ...	100	45 (+) 42 (–)	9 (+)	4 (+)	58·00
6th	14.ii.29 ...	147	57 (+) 29 (–)	5 (–)	56 (–)	38·77
7th	20.ii.29 ...	228	78 (+) 23 (–)	16 (+)	52 (+) 59 (–)	64·03
8th	7.iii.29 ...	207	82 (+) 56 (–)	2 (+)	67 (–)	40·57
9th	13.iii.29 ...	184	89 (+) 26 (–)	5 (–)	13 (+) 51 (–)	55·43
10th	14.iv.29 ...	96	37 (+) 11 (–)	7 (–)	3 (+) 38 (–)	41·66

Particulars of Shipments received during March and April, 1931.

Consign-ments	Received	No.	Condition on arrival			
			Larvae	Pupae	Adults	Percentage Alive
11th	6.iii.31 ...	610	515 (+) 43 (–)	52 (+)	—	92·95
12th	19.iii.31 ...	690	568 (+) 36 (–)	86 (+)	—	94·87
13th	24.iii.31 ...	556	392 (+) 31 (–)	133 (+)	—	94·42
14th	8.iv.31 ...	248	135 (+) 45 (–)	68 (+)	—	81·85
15th	13.iv.31 ...	337	251 (+) 35 (–)	51 (+)	—	89·32
16th	21.iv.31 ...	1,200	966 (+) 39 (–)	195 (+)	—	96·75
17th	14.iv.31 ...	1,043	696 (+) 100 (–)	247 (+)	—	90·41
18th	16.iv.31 ...	1,242	813 (+) 200 (–)	229 (+)	—	83·09

Particulars of Shipment received during August, 1931.

Consign-ments	Received	No.	Condition on arrival			
			Larvae	Pupae	Adults	Percentage Alive
19th	6.viii.31 ...	451	233 (+) 112 (–)	105 (+)	1 (+)	75·12

development was rapidly taking place. The mortality was 15·86 per cent. In all the other shipments, totalling 962 parasites received between 12th February and 14th April, 1929, adult insects were found. The material in these shipments may, therefore, be regarded as being in much the same state of development. The total mortality for these six shipments was 49·38 per cent.

These figures show that the mortality increased in direct ratio to the advance in state of development of the parasites at the time of their arrival, and probably, therefore, their collection and shipment.

The rate of mortality for the various stages in which the parasites in the last batch of shipments arrived, confirms this view. The figures are as follows :—

Larvae =32·52 per cent. mortality.
Pupae =38·64 per cent. mortality.
Adults =79·01 per cent. mortality.

Mortality among the adults was probably due to starvation, but this would not have occurred if all the material had been shipped early enough to arrive in the larval stage. It is unfortunate that these data were not available before the 1931 collections and shipments were made, as the figures clearly indicate the desirability of making early collections so as to get the larvae delivered before metamorphosis takes place.

It will be seen that the whole of the 1931 shipments contained no adults on arrival, although they all contained pupae. In this respect they resemble the stage of development found in shipments 3 and 4 in the 1929 collections, and as in the case of those two shipments, there is no mortality among the pupae. The total mortality of the 1931 shipments 11 to 18 is only 8·93 per cent., but this is much higher than is desirable.

The absence of adults in the 1931 shipments, although they were received at dates corresponding to the last 3 shipments of 1929, is accounted for by the fact that the majority of the parasites in 1931 were collected at an altitude of 1,000 ft. in a very exposed area in Montgomeryshire, during a spell of very severe weather. On the other hand, the whole of the 1929 collections were made at fairly low elevations in rather sheltered situations in Devonshire. It will be seen, therefore, that the development of the 1931 parasites would be considerably retarded as compared with that of the parasites in 1929. In fact, during 1929 some pupae and adults were found in the logs examined in the forest during the time of collection.

The 19th shipment received on 6th August, 1931, shows a mortality of 24·83 per cent. This is accounted for by the fact that the collection had been kept in the refrigerator at Farnham Royal throughout the summer. The mortality in this shipment compares favourably with that of the last six shipments of 1929.

Considering the enormous expenditure of labour and patience involved in the collection of these relatively scarce parasites, the importance of reducing the mortality during transit to a minimum is of the utmost importance, and the above analysis of the data emphasises the necessity for closer co-operation between the persons in charge of importation and liberation, and those responsible for the collection and shipment of the material.

Unfortunately, mortality during transit was not the only source of loss. A matter of even greater concern is the fact that a large proportion of the surviving females emerged with deformed ovipositor. In discussing this matter Dr. Miller and Mr. Clark (1937) state " The main difficulty encountered in New Zealand in connection with the establishment of *R. persuasoria* was the malformation of the ovipositor of the females in the case of insects which had been shipped from England. The reason for this malformation was never clearly demonstrated ; the larvae appeared perfectly healthy, the resulting pupae were large in most cases and well formed, but in many instances the adult emerged with the ovipositor so deformed that egg-laying was impossible. While a certain amount of success was obtained by artificial adjustment immediately after the adult emerged, out of the total of nearly 8,000 insects imported only 179 females were liberated."

The above remarks indicate that the actual loss of material due to malformation of the ovipositor of the females was of even greater importance than the loss sustained through mortality during transit. Malformation of the ovipositor is not a common occurrence under normal conditions in the forest. In fact the writer has not observed such an occurrence except in the case of specimens reared in capsules, and as Dr. Miller has pointed out in discussing the rearing of *Rhyssa* in New Zealand, " In no case was other than a perfect insect produced." It may, therefore, be reasonably assumed that deformity of the ovipositor is either the result of removal of the larva from the normal pupal chamber and transfer to the artificial pupal chamber, or the result of injury sustained during transit.

Under normal conditions, when fully grown, the *Rhyssa* larva spins a thin silken cocoon which lines the pupal chamber. In the majority of cases this cocoon had already been spun before the *Rhyssa* larvae were collected. In such cases, when transferred to a gelatin capsule, the adult insect on completing its development is enclosed in a pupal chamber with perfectly smooth sides which afford no foothold, and in consequence the insect is caused to struggle violently before it succeeds in biting its way out. This may result in causing the ovipositor to become twisted out of shape before it is sufficiently hardened, or the delay in affecting an exit may result in the ovipositor becoming hardened before it has become straight and assumed the position it normally occupies when ready for use. On the other hand, the deformity may be a direct result of the jolting which takes place during transit. In either case the difficulty could probably be overcome by collecting the larvae before they have spun their cocoons, thus allowing them to spin the cocoon inside the gelatin capsule, in which case exit of the adult would be greatly facilitated. The cocoon would also to some extent absorb the shock of jolting in transit. Another important point in this connection is the paying of greater attention to selecting a capsule of suitable size for each larva, so as to reduce the space in which it is tossed about during the journey through the post to the laboratory and during reshipment.

This is a point to which insufficient attention was paid owing to the fact that no one had previous experience in shipping such a large wood-boring parasite.

It seems probable that by early collection of the larvae and greater attention to their individual requirements in packing for shipment, and during the pupal period, mortality during transit and malformation of the ovipositor may be almost entirely eliminated.

In describing the establishment of *Rhyssa* in New Zealand, Dr. Miller and Mr. Clark say " The liberations were made during the years 1929, 1931 and 1932, in seven districts in the South Island, and two districts in the North Island. The rearing of the parasite was first undertaken in the insectary in 1931 and carried on with success. To date four New Zealand generations have been reared, and small liberations have been possible at Rotorua and in other districts. However, the total number of females placed in the field did not reach 200.

" It is not surprising that, although favourable reports were received from many observers for several years, the writers were unable to check and record the definite establishment of *R. persuasoria*. The small number of insects liberated and the large area of forest, presented very severe handicaps to recovery. The success of insectary rearings, however, pointed to the probability that establishment had taken place. This season, however, the recovery of *R. persuasoria* has been made in two districts in the South Island. Pine logs brought into the insectary from the Moutere District, Nelson, yielded the parasite, and one tree felled at Hanmer Springs and kept under caged conditions yielded several males and females.

" The strong establishment of the parasite at Hanmer Springs is particularly pleasing, as this is a large plantation area and provides ample breeding material."

Although several hundred larvae of *Ibalia leucospoides* were collected no attempt has been made to establish this species in New Zealand. A shipment was made but the material did not arrive in a satisfactory condition and Dr. Miller decided to concentrate on *Rhyssa*, at any rate until the latter had been successfully established. It is felt that the difficulties in connection with the transportation of *Ibalia* can easily be overcome and that the insect can be delivered in sufficiently large numbers if required.

The establishment of *Ibalia* will be rather more difficult than in the case of *Rhyssa* owing to the fact that it will be necessary to synchronise the emergence of the *Ibalia* adults with the period of oviposition of *Sirex*. This, however, should present no serious obstacle since the oviposition of *Sirex* extends over a considerable period, and the last larval stage of *Ibalia* extends over a complete year. This will allow considerable latitude for either the acceleration or retarding of development.

The question of the desirability of introducing *Ibalia* is, however, one which will require careful consideration. It has been shown that both parasites are very efficient ; each can produce a high percentage of parasitism, and their combined attack results in a higher percentage of parasitism than when each parasite is separately concerned.

Rhyssa is intrinsically superior to *Ibalia* and super-parasitism of the latter by the former is of very frequent occurrence. This has the effect of inflating the figures showing the percentage of *Rhyssa* at the expense of *Ibalia*, as every case of super-parasitism or hyper-parasitism by *Rhyssa* represents a duplication of work which has already been accomplished by *Ibalia*. On the other hand every *Ibalia* adult that emerges represents the destruction of a *Sirex* larva which has escaped parasitism by *Rhyssa*, and as *Ibalia* is incapable of destroying *Rhyssa*, the evidence appears to be all in favour of the introduction of both species.

The problem is not, however, so simple as the above facts seem to indicate. *Rhyssa* is extremely variable in size, the largest specimens the writer has found in Britain were just over 3 inches in length. Of this, slightly more than half represents the ovipositor. These specimens were bred from *Sirex gigas* hosts, smaller hosts produce smaller *Rhyssa* adults. When *Ibalia*, or a *Sirex* larva parasitized by *Ibalia*, is the host, the resulting *Rhyssa* adult is extremely small and the ovipositor is correspondingly short (often less than ½ inch in length), is incapable of penetrating very far into the timber, and in consequence has a very limited range of usefulness. Owing to the superficial position in the timber occupied by *Ibalia* larvae and *Sirex* larvae parasitized by *Ibalia*, it seems probable that they will be more susceptible to parasitism by *Rhyssa* than *Sirex* larvae which have escaped parasitism by *Ibalia*, as the latter burrow deeper into the timber. It seems, therefore, that the more numerous cases of parasitism by *Ibalia* become, the greater will be the number of very small *Rhyssa* adults. In the case of a *Sirex* population which is under control at a low level, where control is facilitated by the small diameter of the available breeding material, the size of *Rhyssa* is obviously a matter of little importance, since the size is to some extent automatically maintained by the fact that small adult parasites can often reach large host larvae, thus giving rise to large offspring.

With a rapidly increasing *Sirex* population and an adequate supply of breeding material of larger diameter, as is the case in New Zealand, the position may be entirely different. In this case the size of the parasite and corresponding length of ovipositor is of great importance, because a large parasite with a long ovipositor is doubtless more efficient than a small parasite with a short ovipositor.

The problem is, therefore, whether the margin of effective parasitism attained by *Ibalia* would more than compensate for the reduction in the efficiency of *Rhyssa*.

There is a possibility that the efficiency of *Rhyssa* might deteriorate to such an extent that its status would be reduced to the equivalent of a hyper-parasite and consequently cause a corresponding reduction in the efficiency of *Ibalia.*

Another point which ought to be investigated before any attempt is made to introduce *Ibalia* is the question of whether the reduction in size of the *Rhyssa* adult, either directly as a result of feeding on a small host, or indirectly through super-parasitism or hyper-parasitism, has any effect on the reproductive capacity of *Rhyssa.*

On the other hand there does seem to be a possibility of utilising *Ibalia* to fill an ecological niche. There appears to be some evidence that *Ibalia* is more numerous in larch timber than in silver fir or spruce. This may be because of the flaky nature of larch bark, possibly because the flakes of larch bark tend to deflect the ovipositor of *Rhyssa.* If this is found to be the case, the same would probably apply to Corsican pine, in which case it might be worth while establishing *Ibalia* alone in pure stands of these species. It is, however, a matter for further investigation.

The net results of the investigation started in 1927 can be stated as follows :—

(1) It has been shown that the parasites of *Sirex* can be collected in large numbers at relatively low cost, notwithstanding the fact that both *Rhyssa* and *Ibalia* were both formerly regarded as being very rare insects. In fact practically nothing was known about the latter.

(2) The biology and post-embryonic development of *Ibalia* has been studied in great detail by Dr. R. N. Chrystal at Oxford, and the results of his researches have been published.

(3) Field studies on the ecology and economic status of *Sirex*, and the inter-relationship of the insect and its parasites have been carried out on a large scale by the present writer, and considerable experience has been gained in the technique of collecting and shipping the parasites.

(4) Dr. D. Miller and Mr. A. F. Clark have succeeded in definitely establishing *Rhyssa* in New Zealand, and specimens have been recovered in the forest several years after the liberations.

It will be seen, therefore, that the investigation has had positive results. However, even the most enthusiastic advocate of biological control would not suggest that the liberation of one female parasite for each 2,500 acres of *Sirex*-infested forest could have any appreciable control effect on the population of a host with a biotic potential of 400, and a standing of over thirty years establishment ; and no practical consequences can be expected until the population of *Rhyssa* has increased to a point where it is comparable with that of *Sirex*, which may take many years. It might however, be possible to accelerate the process if further large-scale importations of the parasites of *Sirex* were made, since they could then be widely established over the whole of the infested area.

9. Methods of Control.

The foregoing excellent description by Dr. Miller and Mr. Clark of the conditions existing in the forest in New Zealand conveys to the mind of anyone conversant with the various species of trees and insects concerned a mental picture forming a background against which the possible methods of control may be considered.

Apart from the encouragement of birds and any other useful predators which may be present, it is obvious that some method of controlling the increase and spread of *Sirex* will have to be adopted if the insect is to be prevented from becoming a serious pest. These control methods may be considered as follows—(*a*) Silvicultural and mechanical control ; (*b*) biological control.

(*a*) *Silvicultural and Mechanical Control.*

During recent years frequent references have been made to the application of silvicultural practice in regard to the control of forest insect pests. Many of the statements are of an extremely vague character and give not the slightest indication as to what is meant. If it can be shown that any particular silvicultural operation can be carried out in such a way as to benefit the crop directly, and at the same time indirectly by helping to control insects which are detrimental to the crop, it is clear that full advantage should be taken of such an opportunity.

The choice of silvicultural system and the formation of mixed or pure stands, correct selection of site and situation for the various species concerned, length of rotation, arrangement of working circles and felling series, are subjects thoroughly understood by all officers in charge of State forests, and should also be understood by the forest entomologist, so that, in consultation, working plans can be so arranged as to afford the greatest possible measure of protection against insect damage and facilitate the control of the insect population, special rules being formulated to deal with any particular operation and its effects concerning any given species of insect. There is, however, a limit to what can be done in the way of insect pest control by silvicultural means, even if the whole of the forests concerned are directly under the jurisdiction of the forestry department. But when considerable areas of privately owned forest exist, the efforts of the forestry department are liable to be vitiated by neglect on the part of adjoining owners. It is, therefore, of the utmost importance that every effort should be made to enlist the co-operation of private owners.

It is clear that little can be done in New Zealand to control *Sirex* by means of change in silvicultural system, and there is no evidence to indicate that *Sirex* is less numerous in mixed woods than in pure coniferous stands in Britain. In any case half a million acres of coniferous plantations have already been established in New Zealand, and it is in these areas that the control of *Sirex* must be undertaken.

It has sometimes been stated that the increase of wood-boring insects and bark-beetles is determined by the amount of the available food supply. If this statement were true, *Sirex* would be extremely abundant in many of the unthinned pine forests in N.E. Scotland and in many parts of Europe, but such is not the case, although in the absence of the existing parasite population it seems probable that such a state of affairs would exist.

The popular impression that *Sirex* could be controlled in New Zealand by thinning operations is a fallacy. Much can be done by destroying the insects in certain areas from time to time, but this would not result in the control of the species.

Normal thinnings are only carried out as and when necessary, and the correct time is determined by the silvicultural requirements of the crop. A proportion of the suppressed trees must always be left standing in order to preserve the required density of the stand and maintain an unbroken canopy. Some of these suppressed trees would become suitable for breeding purposes within a very short time, and would doubtless be used for that purpose.

The frequency of normal thinnings is determined by the density of the stand and the rate of growth of the trees. This may differ for each species of tree, and is influenced by differences in soil and situation. As Dr. Miller and Mr. Clark have pointed out, the rate of growth of pines in New Zealand is exceptionally rapid. This means that the silvicultural requirements of the crop will demand light and frequent thinnings. The more rapid the growth of the crop, the sooner do suppressed trees become suitable for the breeding purposes of *Sirex*, and in order for the thinning operations to have any effect on the *Sirex* population the thinnings would have to be carried out at very short intervals, probably every five years. This would mean a thinning programme of 100,000 acres each year, the cost of which would be chargeable to the maintenance of the crop. These extensive thinning operations would inevitably result in a huge surplus of unsaleable material, which would be most abundant in the more remote areas. Normal silvicultural requirements would not necessitate the removal or destruction of this unsaleable material and it could with advantage be left on the ground to rot, but as a control measure for *Sirex* it would be necessary to collect and destroy it. Even at an average cost of £1 per acre this additional expense would amount to £100,000 per annum and would represent the cost of *Sirex* control. This would be a recurring charge and there would be no guarantee that it would have the effect of controlling *Sirex*.

Little can be done by way of mechanical control, but the following method would produce some result. Fresh-felled poles stacked against trestles in open places in the forest attract *Sirex* for oviposition. These poles should be destroyed late in the season after the eggs of *Sirex* have been laid in them.

The collection of eggs and destruction of breeding material can only be regarded as palliatives, and in the opinion of the writer they largely constitute a waste of public funds, as the process would have to be continued indefinitely.

(*b*). *Biological Control.*

Critics of biological control seldom take the trouble to ascertain what really are the factors which exercise control over insects during normal periods. Their observations are often based on exceptional cases, where, for one reason or another, the balance has been upset and an outbreak has occurred. Under such conditions it is quite clear that control is not, for the time being, in operation, but it is equally clear that abnormal circumstances such as these should not be used as a criterion. The proper time to collect evidence of control is during the period when control is actually in operation.

In cases where control has temporarily broken down, from whatever cause, it is generally necessary to adopt some form of artificial control in order to reduce the insect population as speedily as possible, to prevent excessive damage to the crop. Such control measures are generally expensive and can, as a rule, be used only as expedients ; the extent of their use generally being determined by the value of the crop. When certain crops are being grown in conditions under which they are known to be prone to excessive insect damage, it is often possible to prevent such damage by the use of chemicals. When such circumstances exist the most enthusiastic exponent of biological control would not hesitate to prescribe chemical treatment. Similarly under certain other conditions he would advocate mechanical control, such as various forms of trapping. All economic entomologists recognise that each of the methods of control must have their proper place if a complete system of pest control is to be established. No sane person has ever suggested that parasites are the only factors of control under all circumstances, and as has already been pointed out in the preceding pages, although one set of factors may normally be responsible for the control of an insect, quite a different set of factors may come into operation when abnormal conditions arise ; for example, parasites, predators, and other factors, operating in a block of unthinned pine forest may so effectively check the increase of the bark-beetle population under normal conditions that the insects are unable to become sufficiently numerous to cause appreciable damage. While this stage continues the bark-beetles are under economic control and these conditions may continue over a long period of years, the duration of the period being largely determined by the rate of growth of the crop. But if extensive wind-falls occur, or heavy felling operations are carried out, facilities for the rapid increase of the bark-beetle population occur, the beetles are able to distribute their egg galleries over a much larger area of exceptionally suitable breeding material, and the resident population of parasites and predators is inadequate to deal with the sudden change in circumstances. Under these changed conditions it is necessary to undertake energetic mechanical control measures.

The above illustration may appear to support the statement that the increase of the beetle population is governed by the amount of the available food supply, but the important point is that under normal conditions the beetles are kept in check by the parasites and predators, and it is the sudden increase of exceptionally suitable breeding material in the form of thick-barked timber that turns the scale almost entirely in favour of the beetles and results in upsetting the balance. This does not detract from the importance of the parasites and predators as control factors under normal conditions.

Similarly in the case of *Sirex*, control by parasites in an unthinned pine stand of say 50 or 60 years may be sufficiently complete to prevent an increase of the host insect, but if a few logs of large diameter are left lying about, these logs will provide exceptionally suitable conditions under which a large proportion of the *Sirex* larvae may escape parasitism by *Rhyssa*, and an increase in the *Sirex* population will follow. If the additional favourable breeding material is sufficiently abundant it will inevitably result in an outbreak of *Sirex* and the status of the insect as a pest will be determined by the amount of timber which has been ruined. Here again it will be seen that the parasites are efficient factors of control under normal forest conditions ; the host only becomes a pest when exceptionally favourable conditions are provided for its increase. When, however, there are no parasites to keep its increase in check, *Sirex* will become a pest under normal forest conditions.

Dr. Miller and Mr. Clark have drawn attention to the fact that large areas of coniferous trees are being grown in New Zealand on exceptionally short rotation and that the thinnings, instead of yielding a return, are a definite additional capital charge, and that the average plantation owner avoids thinnings on account of the small material being unsaleable, with the result that suppressed, broken and dead trees comprising dense thickets are common. These conditions are mentioned as an illustration of the difficulty in carrying out mechanical control of the insect.

Fortunately these are exactly the conditions which provide the maximum facilities for the increase of *Rhyssa*. It is in material of this description that the highest percentage of parasitism is found in Britain.

Similarly the numerous stumps resulting from the felling of these young plantations are referred to as forming centres from which *Hylastes ater* will spread and attack the fresh crop of young trees. Here again, the conditions are ideal for the rapid increase of the various species of *Rhizophagus* and other predators. An attempt to establish the predators of *Hylastes ater* has been made on a very small scale. *Rhizophagus ferrugineus*, *R. dispar* and *R. depressus*, to the number of 3,711 were shipped from Farnham Royal to New Zealand. Dr. Miller and Mr. Clark (1935) record the liberation of 865 specimens. As this works out at less than 1 pair of predators for each 1,000 acres of coniferous plantation, the liberation can only be regarded as an experiment in attempting to establish the insects and not, at present, as a typical example of the method of biological control. It has been pointed out that *Hylastes* and *Sirex* form a biological association of a very dangerous type, and their uncontrolled activities are certain to have disastrous results in extensive coniferous plantations. Notwithstanding the fact that statements have been made to the contrary, both these species are normally controlled almost entirely by their natural enemies in Britain, and as both pests have become firmly established in New Zealand, the absence or scarcity of their natural enemies will undoubtedly result in tremendous damage to the coniferous crops unless adequate steps are taken to introduce their natural enemies in numbers sufficient to deal with the situation. This would mean the liberation of parasites and predators by the hundred thousand, and it could be accomplished at relatively little cost. The expenditure of the sum of one penny per acre of coniferous forest would be sufficient to cover the cost of carrying out a comprehensive scheme of biological control that would ultimately result in reducing both *Sirex* and *Hylastes* to be desired level of economic control which these insects normally occupy in Britain. As Mr. A. F. Clark (1936) has stated : " The introduction of parasites for the control of the wood-wasp was, and is, necessary, for the very good reason that the essential silvicultural measures are not possible in many cases for economic reasons."

10. Summary and Conclusions.

1. The ecological study of *Sirex* and its parasites was begun in 1927 and continued while making large-scale collections of the parasites for shipment to New Zealand with the ultimate object of the control of *Sirex noctilio,* a species of wood-wasp which has been established in the Dominion for many years.

2. A brief outline of the life-cycle of *Sirex* and the parasites is given. The difference in the method of attack by the parasites on the host is described, and some points of interest in connection with insect behaviour are discussed.

3. The methods of collection are described and particulars given about the number of parasites collected.

4. The inter-relationship of the host and parasites is discussed. It is shown that a single generation of *Sirex* can support three generations of *Rhyssa* and one generation of *Ibalia*, and that the effects of parasitism by *Rhyssa* are cumulative. The percentage of parasitism by *Rhyssa* cannot, therefore, be calculated on the results of any one year. *Rhyssa* is intrinsically superior to *Ibalia* and super-parasitism of *Ibalia* by *Rhyssa* is of very frequent occurrence. It is shown that the figures for parasitism by *Ibalia* obtained by the dissection of *Sirex* larvae collected from a number of logs, over a period including summer months, are liable to be very misleading.

Both parasites are very efficient and each may obtain a very high percentage of parasitism, but the combined effects of the two parasites result in a higher percentage of parasitism than when each parasite is working alone.

Parasitism by *Rhyssa* reached its highest when *Sirex* is breeding in material under 3 inches in diameter, as the *Sirex* larvae are then within reach of the ovipositor of *Rhyssa* throughout the whole three seasons of their development. Parasitism by *Rhyssa* is often very low in logs of large diameter because the *Sirex* larvae may be out of reach during the second summer.

Diameter of the material in which *Sirex* is breeding does not affect parasitism by *Ibalia,* but the period of effective activity of the parasite is limited to the egg and early larval stage of the host.

A table is given showing the development of the *Sirex* and parasite complex and indicates what a log may be expected to contain in either summer or winter over a period of four years when one generation of *Sirex* and its parasites is present.

A large tree may support a colony of *Sirex* over a long period of years, and a table is given showing the inter-relationship of *Sirex* and its parasites over a period of seven years, when three generations of *Sirex* are present in the same piece of timber. In such cases, three generations of *Ibalia* and five generations of *Rhyssa* may emerge. A single generation of *Rhyssa* may be the product of one, two, or three generations of *Sirex*. A table is given showing from which generation of *Sirex* each of the generations of *Rhyssa* may arise. A large tree may support a population of more than 3,000 *Sirex* and parasites during that period.

5. Possible factors of control other than parasites are discussed, including birds, fungi, and climatic conditions. It is considered that birds are of little importance under normal conditions. Fungi destroy *Sirex* pupae and adults under certain conditions, but these organisms cause the death of trees and help to increase the amount of suitable breeding material.

Climatic conditions have little effect on mortality and probably do not alter the numerical ratio of host and parasite. Abnormal conditions in the forest tend to result in more favourable breeding facilities for *Sirex.*

6. The economic status of *Sirex* is discussed. The nature of the damage is of a technical character affecting the quality of the timber. For successful oviposition in living trees the limiting factors are rapidity of transpiration and activity of the cambium.

Sirex prefers fresh-felled, perfectly sound timber, and is not dependent on any peculiar pathological condition. Although trees killed by *Fomes annosus* and *Armillaria mellea* are readily attacked by *Sirex* for breeding purposes, that part of the timber actually permeated with the mycelium of these fungi is unsuitable for the insect's development.

It is stated that although *Sirex* is normally of little economic importance in Britain, circumstances may arise when the insect does considerable damage, but this is invariably due to neglect on the part of the owners of the timber concerned. Under normal forest conditions *Sirex* may be considered to be under economic control in Britain, and the parasites *Rhyssa* and *Ibalia* are the chief factors of control. It is pointed out that this view is not shared by all economic entomologists, and an example of adverse criticism of biological control is examined.

7. Reference is made to the present status of *Sirex* in New Zealand, and the presence of *Hylastes ater* is mentioned as an additional factor likely to contribute to the rapid increase of *Sirex*. It is pointed out that although the insects belong to different orders, they form a definite biological association of a particularly dangerous type.

8. Reference is also made to the introduction and establishment of *Rhyssa* in New Zealand. Details of the method of shipment and data showing the condition of the parasites on arrival are reproduced. The reason for the high rate of mortality in some of the shipments is discussed and suggestions are made which it is thought will result in a reduction in mortality and eliminate much loss caused by malformation of the ovipositor, if further shipments are made in the future. The net results of the investigation are summarized.

9. Methods of control are discussed under the headings: (i) Silvicultural and mechanical control; (ii) biological control.

It is shown that although the first method would bring about the destruction of large numbers of insects, there is no reason to suppose that it would result in the control of *Sirex*. The necessary operations would incur an enormous annual expenditure and for economic reasons cannot be put into practice. On the other hand, it is stated that biological control may reasonably be expected to bring about the desired results if carried out on an adequate scale, and that a comprehensive scheme of biological control could be carried out at relatively little cost.

11. Acknowledgments.

The writer desires to thank the following landowners, His Grace the Duke of Bedford, the Marquess of Bath, the Earl Fortescue and Lord Clinton, also the Forestry Commissioners, for permission to collect the parasites on their estates and for their generosity in gratuitously providing the necessary material. He also wishes to express his indebtedness to their foresters for their kindness in facilitating the work; to his fellow members of the staff at Farnham House Laboratory for their co-operation in handling the material for shipment, and to Dr. W. R. Thompson, Superintendent of Farnham House Laboratory, Dr. R. Neil Chrystal of the Imperial Forestry Institute, Dr. D. Miller of the Cawthron Institute, New Zealand, Mr. A. F. Clark, Forest Entomologist, State Forest Service, New Zealand, and Dr. J. G. Myers, for the part each has played in contributing to the success of the investigation.

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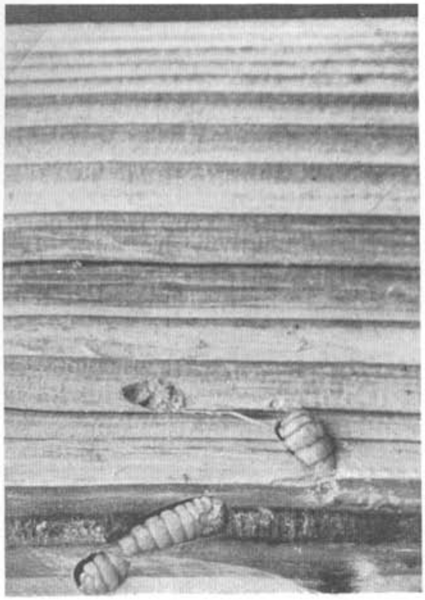
EXPLANATION OF PLATE 1.

Fig. 1.—*Sirex* larvae, which have escaped parasitism, burrowing in region of pith in winter. (Natural size.)

Fig. 2.—Full-grown *Sirex* larva in pupal chamber in winter. (Natural size.)

Fig. 3.—*Sirex* larval galleries, showing the region in which the larvae have burrowed during the summer while between the two stages shown above. (Natural size.)



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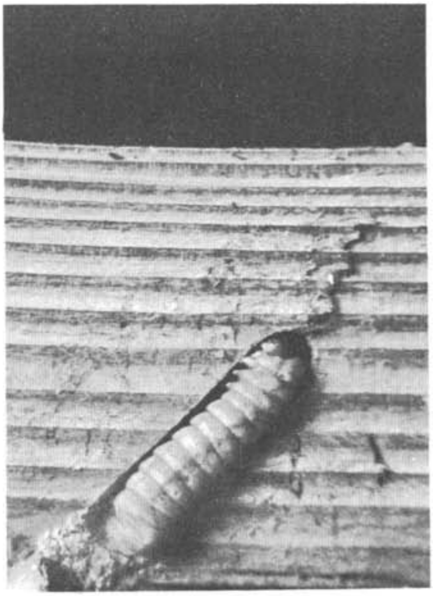

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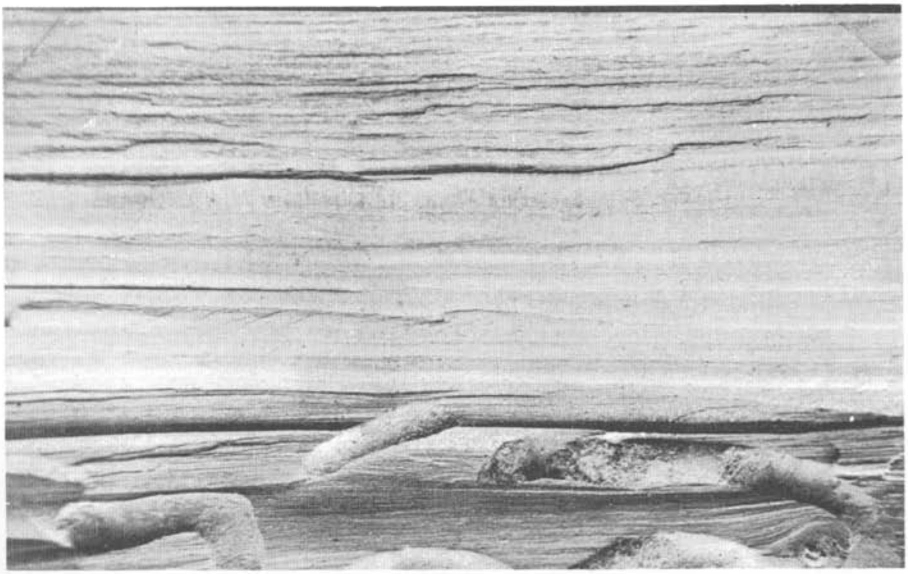

Fig. 3.

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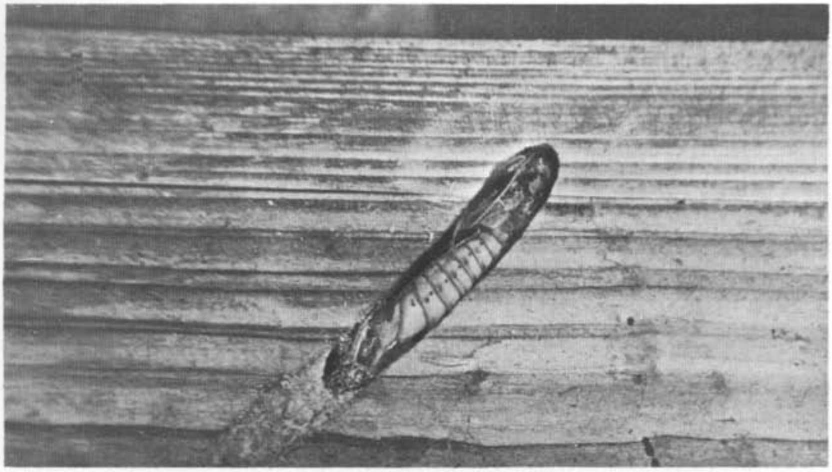
EXPLANATION OF PLATE II.

Fig. 1.—*Sirex cyaneus*, female pupa in pupal chamber.

Fig. 2.—*Sirex gigas*, female adult in pupal chamber ready to emerge.



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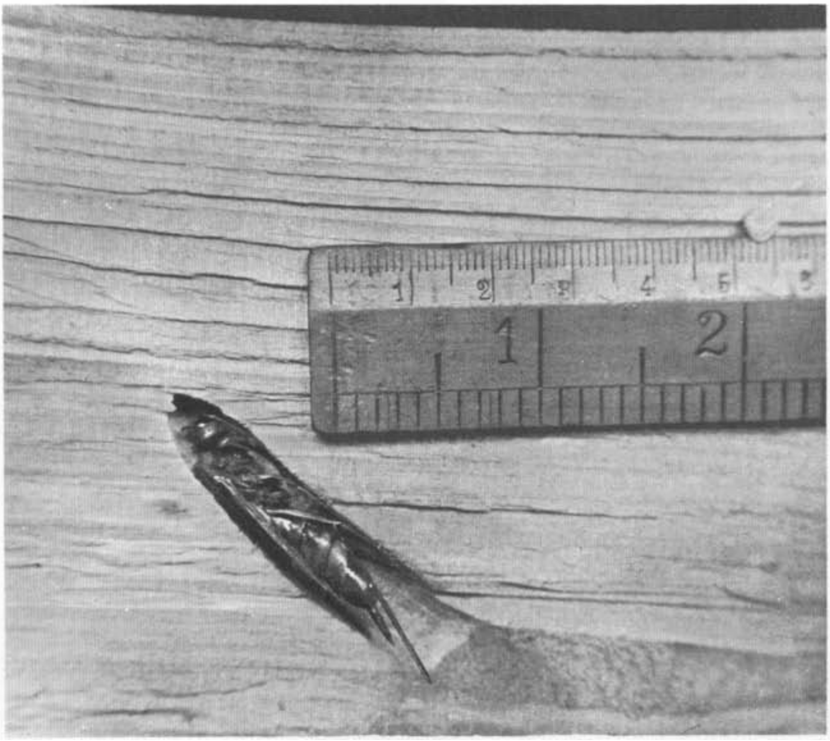

Fig. 2.

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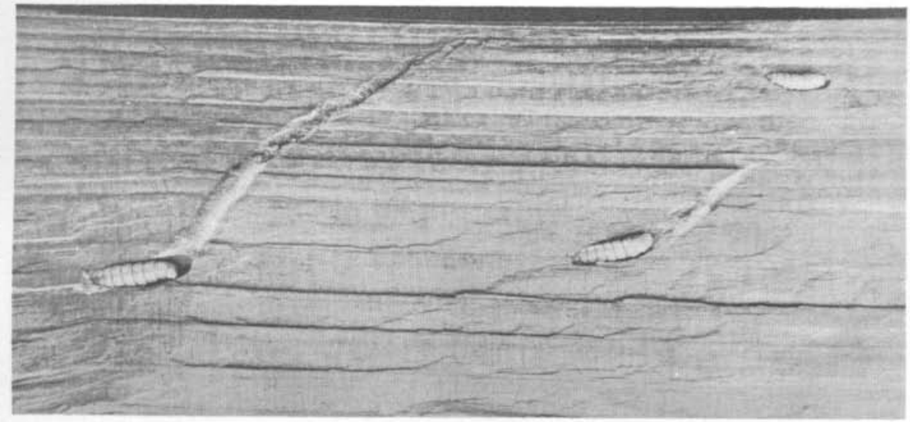
EXPLANATION OF PLATE III.

Fig. 1.—*Rhyssa* larvae, 1st generation ; two are in normal *Sirex* galleries, one is in a gallery characteristic of *Sirex* parasitized by *Ibalia* (super-parasitism). (Natural size.)

Fig. 2.—Full-grown *Ibalia* larvae in pupal chambers, also a *Rhyssa* larva (2nd generation) which has eaten one of the *Ibalia* larvae (hyper-parasitism). (Natural size.)

Fig. 3.—*Rhyssa* larva (2nd generation) in gallery of *Sirex* larva which was nearly full-grown. (Natural size.)



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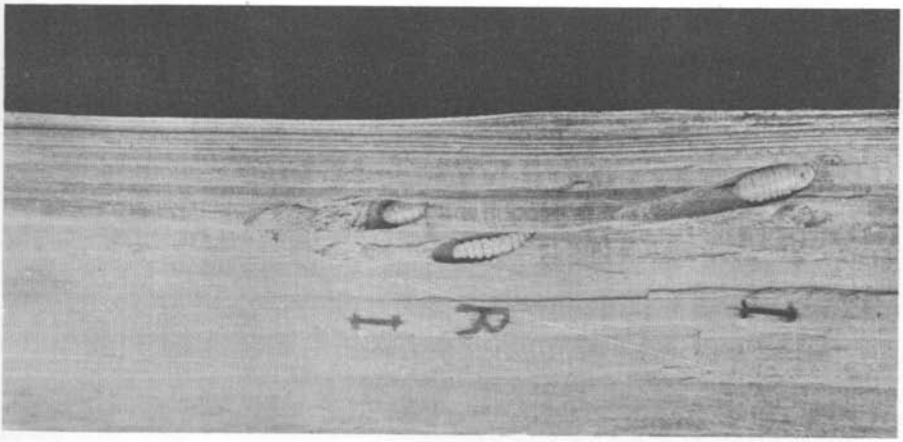

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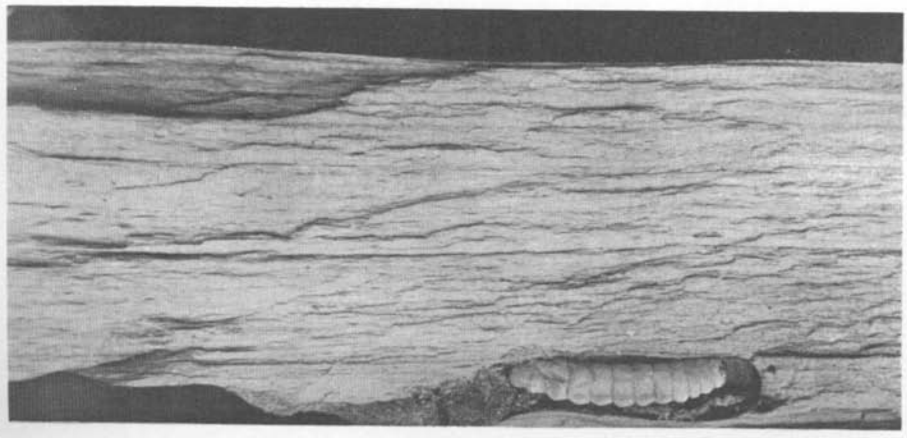

Fig. 3.

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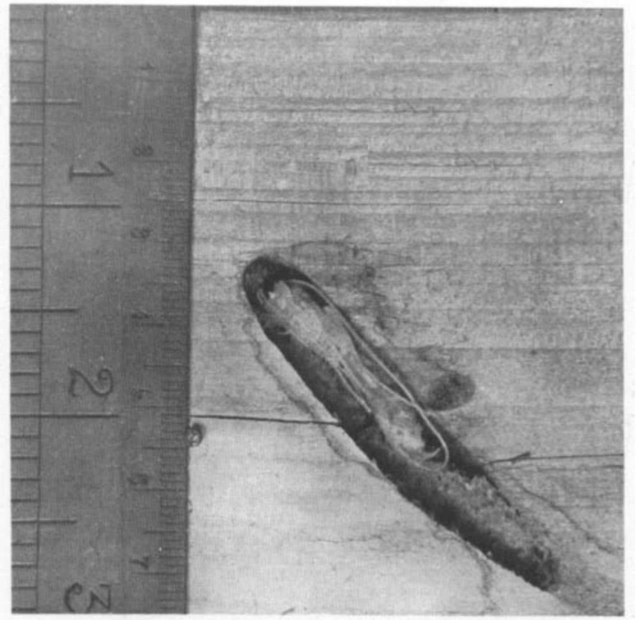
EXPLANATION OF PLATE IV.

Fig. 1.—*Rhyssa* pupa (3rd generation) in pupal chamber of *Sirex gigas*, with remains of full-grown *Sirex* larva.

Fig. 2.—Adult female *Rhyssa* tunnelling exit gallery from pupal chamber of *S. cyaneus*.



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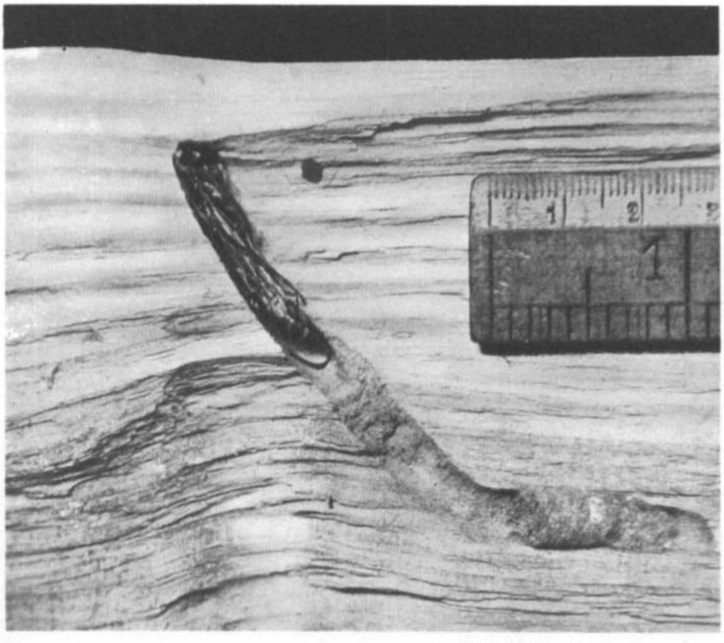

Fig. 2.

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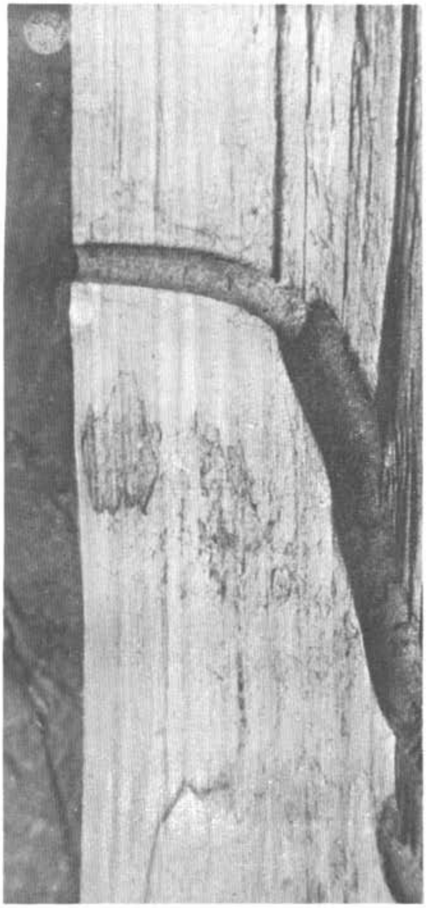
EXPLANATION OF PLATE V.

Fig. 1.—Pupal chamber and exit hole of *Rhyssa* (3rd generation); very large specimen. (Natural size.)

Fig. 2.—Sections of silver fir showing exit holes of *Sirex* and parasites.

Fig. 3.—Full-grown larva of *Rhyssa* in pupal chamber of *Sirex* with remains of an adult *Sirex cyaneus*.



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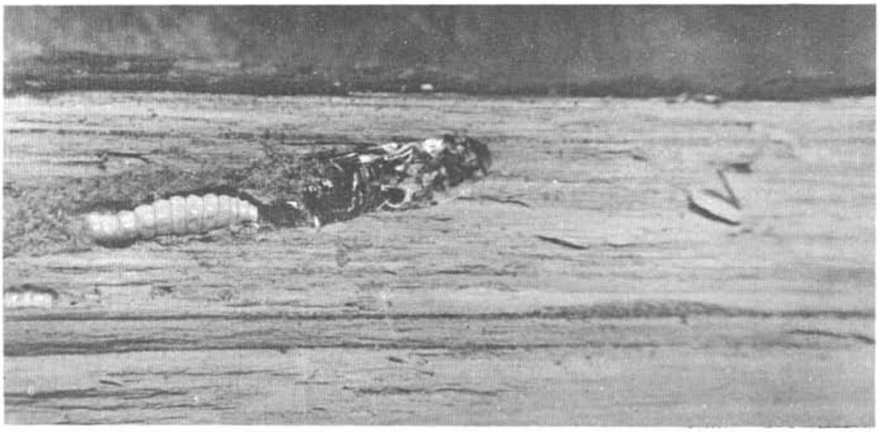

Fig. 3.

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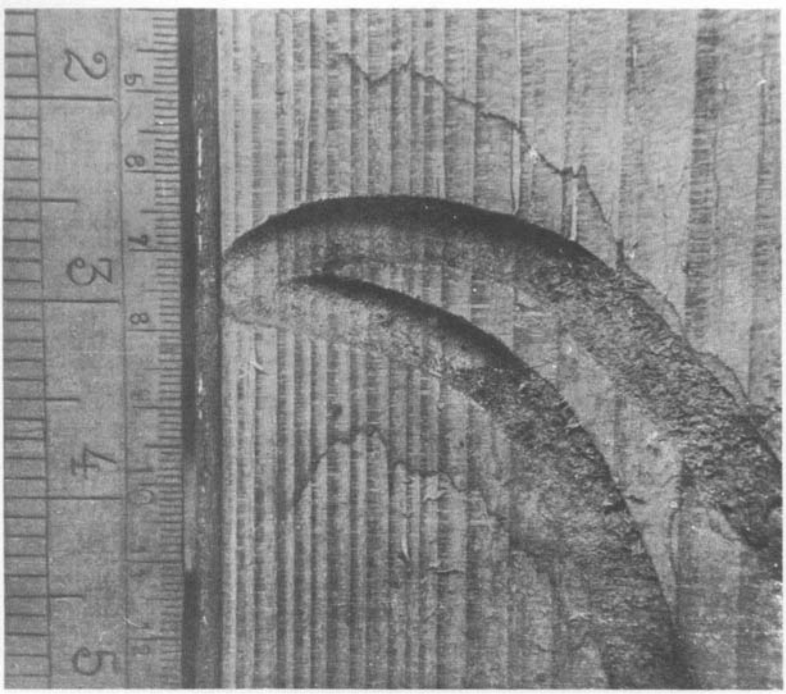
Explanation of Plate VI.

Fig. 1.—Two exit galleries of *Sirex gigas* converging to one exit hole.

Fig. 2.—Adult *Sirex cyaneus* female tunnelling exit gallery. (Natural size.)



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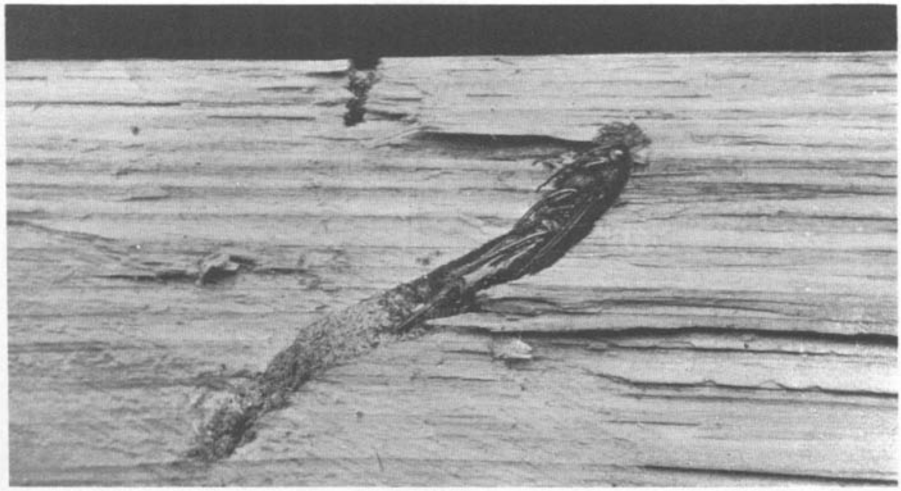

Fig. 2.

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