NATURAL ENEMIES OF *SIREX CYANEUS*, FABR., IN ENGLAND AND THEIR LIFE-HISTORY.

By R. N. CHRYSTAL,
Imperial Forestry Institute,
and
J. G. MYERS,
Imperial Bureau of Entomology.

(PLATE III.)

1. Introduction.

It has long been known that the wood-wasps of the genus *Sirex*, wherever they occur, are parasitised by large Pimpline ICHNEUMONIDAE belonging to *Rhyssa* and closely allied genera. There was also strong circumstantial evidence that the aberrant Cynipids of the subfamily IBALIINAE attack the same hosts. Unfortunately both these groups of parasites, especially in England, are considered by no means common, and *Ibalia* has been regarded as one of the rarest of all Hymenoptera. In these circumstances, the usual obscurity surrounding the biology of wood-boring insects was tremendously augmented, and the data recorded on the life-history have been extremely meagre. The investigations, on which the present paper forms a preliminary report, were undertaken by the Farnham House Laboratory of the Imperial Bureau of Entomology, in collaboration with the Imperial Forestry Institute, to fill some of the gaps in our knowledge and to discover means of introducing one or both of these parasites into New Zealand as a measure against the steel-blue wood-wasp, which has been accidently introduced into that country. Although the study was begun only in July last, sufficient data have been accumulated to indicate the main features of the life-history of *Rhyssa persuasoria*, L., and of *Ibalia leucospoides*, Hochenw., and it seems desirable to place on record the main facts. During the coming season it is hoped to elucidate further details with a view to publishing a comprehensive account of these parasites and of their host. All purely morphological considerations will be deferred till then.

We owe a debt of gratitude to the President and Fellows of Magdalen College, Oxford, for granting us every possible facility to carry out field work at Tubney Wood. In view of the rarity—apparent or real—of the parasites we wished to study, the first desideratum was a locality where these occurred in sufficient numbers to allow systematic observation. Tubney fulfilled these requirements in a remarkable manner.

We are indebted also to Dr. J. Waterston for deciding authoritatively the specific identity of both parasites and of their host. This was by no means a simple matter.

2. The Locality.

The part of Tubney Wood, where practically the whole of the field work was accomplished, consists of a stand of larches and pines, many of the former of which (*Larix europaea*, D.C.) are obviously growing in a situation far too damp for their general health. These manifestly unhealthy trees, many of which were in a dying state, brought about by adverse physiological conditions, were also considerably infested with the Longicorn beetle, *Tetropium gabrieli*, Weise, and supplied nearly all our material of *Sirex* and its parasites. *Sirex* oviposited in those still bearing much green foliage, *Ibalia* followed close on the heels of its host, while *Rhyssa* laid its eggs in trees containing nearly full-fed wood-wasp larvae. The abandoned tunnels were utilised by hosts of Crabronids and by a species of *Odynerus* (*O. gracilis*) for

storing their prey. These trees were thus the central organisms of a well defined and exceedingly interesting biocoenose which merits a study extending over a number of seasons.

3. **Rhyssa persuasoria**, L.

With a more detailed account in preparation it does not seem necessary to attempt here a complete bibliography. Perhaps the fullest of the older papers is that of Riley (1888), who showed that up to that time the notion was widely prevalent that the female *Rhyssa* or *Thalessa*, boring through bark and wood with its long ovipositor, inserted its eggs actually into the host larva. Riley gives evidence that this latter is not the case, and figures the young *Megarhyssa* (*Thalessa*) larva attached to the abdomen of a *Tremex* grub. Yet even in recent years it has been claimed that the older theory is correct and that *Rhyssa persuasoria* has an endophagous larva. Bordas (1917) describes an egg which he found in the general body cavity of a *Sirex* larva, just above the digestive tract. He attributes this egg to *Rhyssa* and even goes so far as to suggest that the liquid from the " glandes venimeuses," which he dissected, is injected into the victim at oviposition to produce anaesthesia and to prevent decay of the larval tissues. There was no evidence for this, and no indication that the egg found was that of *Rhyssa*.

One of the writers, enquiring into the subject on the continent in 1925, found the endophagous theory widely held in France (Barbey, 1925, p. 703; Hubault, *in litt.*). In Germany, however, Escherich and Eidmann were both sure that Riley's hypothesis was the correct one, and that *Rhyssa* laid its eggs in the burrow, on or near the host larva. Stebbing, also, subscribed to the same opinion in India, from his observations on *Rhyssa persuasoria* as a parasite of *Sirex imperialis*.

More recently Torka (1926) has published observations which he thinks indicate that *Rhyssa* uses the oviposition-bore of the *Sirex* in its own egg-laying. He disturbed a *Rhyssa* with its ovipositor sunk in a lightning-struck fir on which numerous *Sirex* females were ovipositing. The *Rhyssa* flew away, leaving its instrument stuck in the still green wood. Torka did not ascertain, as can be easily done, whether the ovipositor *had* entered a *Sirex* bore. He suggested that it had :—" In irgend einer Weise muss doch die Möglichkeit bestehen, dass der bis 65 mm. lange Böhrer der Schlupfwespe, der dabei so dunn und biegsam ist, gänzlich in das harte Holz versenkt werden kann." We shall see later that *Rhyssa*, however, has no difficulty in penetrating the soundest larch wood; but there is some evidence that when the tree, as in the above case, is still green, the ovipositor is hard to withdraw. This, coupled with sudden disturbance, probably accounts for most of the cases of ovipositors broken off in the wood; though Stebbing further suggests that old females, laying their last egg, may die naturally in this position, as he finds do also some Scolytid beetles.

Riley, and especially Miss Cheesman (1922) among others, believe that the *Rhyssa* larva wanders along the *Sirex* burrows devouring perhaps a number of grubs. It is true that the *Sirex* burrows sometimes, though rarely, cross one another; but there is not the slightest indication that the *Rhyssa* larva is any more capable of traversing these tunnels, closely packed with extremely hard, compacted frass, than of boring through the hardly more solid wood. Miss Cheesman has interpreted small *Rhyssa* larvae, found alone in burrows, as not yet full-fed. It is certain that this is incorrect, and that diminutive larvae are merely ones which have fed upon a small host grub, the size of the latter being due either to youth or to that general variation so frequent and so large in the dimensions of wood-feeding insects.

Oviposition.

The oviposition of *Rhyssa*, in correlation with the shorter ovipositor, is strikingly dissimilar to the process in *Megarhyssa* (*Thalessa*) as described by Riley and later

workers. It resembles distinctly that of *Ephialtes* figured and described by Dingler (*cf.* also Bischoff, 1927, fig. 158). The extraordinary bladder-like outgrowth of the membrane between abdominal segments vii and viii (Baumann, 1924), which functions so conspicuously to receive the basal portion of the stylets when *Megarhyssa* is boring, is scarcely represented in *Rhyssa* save by a certain stretching of the intersegmental membrane in question.

But to begin with the preliminary exploration ; the female *Rhyssa* crawls slowly over the bark, palpating the surface with antennae outstretched, fairly close together and curved downward. Apparently when the host larva is more nearly approached, the play of the antennae becomes more rapid, more circumscribed, and the ends of these organs are bent right over, downward and backward, so that even the dorsal surface of the tips may touch the wood.

When actual boring is to begin the ovipositor is brought downward and forward, by elevating to the utmost extent the abdomen, and standing almost on the head, the legs and antennae being meanwhile held rigid. The instrument seems to be held between the bases of the third coxae, and even to pass between the second (*cf.* also Johnson, 1919 ; Cheesman). By this means it is brought to a position at right angles with the surface and boring begins. As it proceeds, the ovipositor sheath is gradually disengaged, forming occasionally and for a time, a loop above the abdomen as in *Megarhyssa* though less conspicuously ; but finally taking up its usually caudal position in line with the long axis of the body. Johnson's belief that the sheath enters the wood with the terebra, is thus erroneous, and there is no doubt whatever that the egg passes down the channel between the stylets, extraordinarily small though this passage is. A single oviposition may take from 20 to 40 minutes.

There is also no longer any question as to the ability of *Rhyssa* to pierce, almost up to the hilt of the ovipositor, the soundest wood.* The resulting passage is much too narrow to admit a human hair, and is consequently very difficult to trace.

A very surprising feature is the large number of futile borings made by the females of *Rhyssa* in wood which contains no trace of *Sirex* or its burrows anywhere in the vicinity of the puncture. In some cases these borings penetrate only a few millimetres, but in others the instrument is buried to its usual depth. We unfortunately kept no figures of all the attempts observed ; but it is certain that at least 90 per cent. were apparently unsuccessful. In one case a *Rhyssa* was observed to make five punctures, all moderately deep and we afterwards proved that no *Sirex* was present in the log within several feet. The frequency of these so-called " errors of instinct " on the part of *Megarhyssa* led certain American observers to believe that the larva was entirely lignivorous and not parasitic after all ; and Riley, who quotes this opinion, was constrained to think that the ovipositing female does not seek the host larva, but merely any part of its burrow, along which the young larva wanders till it encounters a victim. We think the very tightly-packed frass would render such wandering impossible.

In any case the extent of this fallibility in *Rhyssa* must materially detract from its efficiency as a parasite of *Sirex*. In this respect, as we shall show, *Ibalia* is superior.

As to how the female *Rhyssa* finds the host larva, we are still almost completely in the dark, as also regarding the exact nature of the antennal sense-organs, which are manifestly the most important instruments in the later stages of the search. We found that after considerable experience we ourselves could select, with a remarkable degree of accuracy, larch trees containing *Sirex* eggs or larvae at a given

* Yet even as recently as 1908, Morley was able to write that it is still a moot point whether *Rhyssa* reaches larvae by intruding its long terebra along the victim's burrow or *in propria persona* bores through bark and solid wood to her prey !

stage of growth. This was accomplished, of course, by considering a number of minutiae of appearance. It seems probable that the female *Rhyssa* is guided, not alone by any hypertrophied single sense, such as olfaction, but by an *ensemble* of sensory cues, including, especially in the preliminary stages of the search, ones of a visual nature.

A large female *Rhyssa*, captured at Tubney on 7th September 1927, was liberated in an insectary of the Farnham Royal Laboratory the next day and well supplied with infested logs. She was without a male and was not observed to oviposit until the 16th, one day after a bred male had been liberated with her. This log was cut open on the 5th October and a *Sirex* burrow found, with a parasitised grub. The part of the tunnel immediately below the puncture was frass-filled, indicating that if the egg had been laid, as seems probable, near the host, the latter had bored further in the meantime. Unfortunately the minutest examination of the frass failed to show any sign of the *Rhyssa* egg-shell; so this point is still not incontrovertibly established. In the present case the nearest part of the burrow, in a more or less perpendicular direction from the oviposition puncture, was 27 mm., which represents the least distance through which the *Rhyssa* must have bored through solid and perfectly sound wood.

In another log in which the same female buried her ovipositor almost to the base (4th October) in two places, the passage was found to lead directly to old frass-filled burrows, abandoned by *Sirex*, of which the adults had emerged during the same season. Again there was no trace of an egg.

It appears indeed that the deposited egg has not yet been observed either of *Rhyssa* or *Megarhyssa*, although Bugnion (1905) describes the ripe eggs dissected from the abdomen of *R. persuasoria*. They are about 12 mm. long, of which 9 make up a narrow pedicel. Since writing this paper we have found eggs, in a number of cases, deposited on various parts of the body of the host larva or pupa. They agree with Bugnion's description but are even longer. As many as three may be laid on a single larva.

The Larva.

So far as our own and previous observations indicate, the larva of *Rhyssa* feeds ectoparasitically from the beginning. The larva which hatched in the insectary, as described above, was 7 mm. long when cut out on 5th October, or 19 days after laying. It was lying upon a full-grown *Sirex* larva, which already looked slightly flaccid. In the splitting of the log, this larva was inadvertently shaken off its host, but, after groping round actively for a few minutes, it regained its hold and continued feeding undisturbed. On 13th October, when the *Rhyssa* larva had attained a length of 9·5 mm., it was transferred with its host to a gelatin capsule. During this process the parasite lost hold a second time, but regained it. On the 17th, the *Rhyssa* was 13 mm. long and the host larva seemed a mere empty skin, though still white and fresh-looking. The former was no longer attached to its prey. On the 22nd, the larva was seen for the first time in three days, when it reached a length of 16 mm. and had finished feeding. It seemed restive. By the 10th November a diaphanous silken cocoon had been spun, just obscuring the transparency of the capsule walls and cutting off from the *Rhyssa* larva, at one end, the shrivelled remains of the *Sirex* grub.

The formation of a more or less complete cocoon, of almost colourless silk, is apparently a constant feature. In the natural burrow it is merely a lining of the walls, and as such may escape notice. One larva, isolated in an elder twig cell, closed with a plug of elder pith, gnawed off pieces of pith to a depth of a millimetre and incorporated the fragments in the fabric at one end.

The larva of *Rhyssa*, which has been described by Miss Cheesman and others, resembles closely that of *Megarhyssa* as figured by Riley (Pl. iii, fig. 1). Data on the number of instars are yet to be obtained.

There is a fairly copious black discharge at pupation.

The Pupa.

There is a fairly distinct pre-pupal stage in which the eyes show through the larval integument a faint purple or red. The pupa of *Rhyssa persuasoria* differs markedly from that of *Megarhyssa* in that the elements of the long ovipositor are curved directly backward over the dorsum and only just reach the occiput or in some cases apex of head, whereas in *Megarhyssa* (*Thalessa*) *lunator*, according to Riley's excellent figure, the pupal ovipositor extends caudally for nearly half the length of the body, then curves dorsally, passes round the head, right along the ventral surface, and ends nearly half the body-length behind the tip of the abdomen.

The pupa is at first pure white, the eyes being the first part to darken, and these are black long before any other parts show a trace of colour.

Rhyssa pupae are usually found in terminal burrows which do not appear to differ from those of unparasitised full-fed larvae of the host. They are often separated from the outer world by one centimetre of solid wood, exclusive of bark. The emerging adult excavates through this a passage of smaller calibre than the pupal chamber, with a very neat circular orifice, distinguishable from most of the *Sirex* exit-holes by its smaller size.

The Life-cycle.

The adult *Rhyssa* is most frequent in spring and early summer. It seems to confine its attentions to nearly or quite full-fed *Sirex* larvae or to pupae. Middle-aged grubs would in any case usually be too far in towards the heart of the tree, while younger instars would presumably be too small to nourish a *Rhyssa* larva. Whether the grubs attacked are always in their last summer, or penultimate, or either, is not yet clear. The actual feeding of the *Rhyssa*, assuming the egg laid in the insectary to have hatched within a few days, apparently takes about five weeks. Thereafter the autumn and winter are spent in the resting larval stage, within a cocoon which lines the burrow. Pupation takes place in early spring, and the whole cycle is thus annual. There is some evidence, however, that the larva may continue another year in the resting stage. Of a number (19) of full-fed larvae collected during 1927 and kept inside the laboratory under similar conditions, some have spun cocoons and pupated, and even emerged, while others still remain naked larvae (end March).

Adults and General Notes.

The variation in size is truly remarkable. Our smallest male is only 8·4 mm. long, our largest (S. Devon) 25.7 mm.

No hyperparasites or other natural enemies have been observed.

4. Ibalia leucospoides, Hochenw.

All previous data on the biology of the little-known insects of the subfamily IBALIINAE has been based upon the capture of isolated adults or the rearing of specimens from logs which contained various wood-boring insects. Taschenberg reared a species in large numbers from fir wood heavily infested with *Sirex juvencus*; Drewsen bred both parasite and the suggested hosts—*Sirex juvencus* and *S. noctilio*—from spruce; and Champlain (1922) saw *Ibalia ensiger*, Norton, in Pennsylvania, ovipositing in hemlock, whence he obtained pupae and adults from the cells of *Urocerus*

albicornis. Champlain believed also another American species, *I. maculipennis*, Hald., to be a parasite of *Tremex columba* in hickory. Ashmead (1903) gives most of the earlier American references, and Dalla Torre and Kieffer (1910) summarise the European literature. The most interesting contribution is undoubtedly that of Borries (1891). This observer, working in Denmark, found adults of *Ibalia drewseni*, Bor., still lying in the cells of *Sirex juvencus*. His data were thus hardly more extensive than those of his predecessors, but from a consideration of the habits of this supposed host he suggested a hypothetical life-history which is extraordinarily near the truth. *Ibalia* is active in August, when one finds normally one-year-old *Sirex* grubs fairly near the surface. Borries believed *Ibalia* must therefore oviposit in these, since the length of its ovipositor would not let it reach the older larvae, which at this season are deep in the wood. He thought it must therefore be endoparasitic, and must, from the appearance of the passages he traced, cause the parasitised *Sirex* grub to alter the normal course and to remain in the outer part of the log, finally excavating the pupal cell just under and parallel to the surface. All these suppositions of Borries, except that concerning the age of the host when parasitised, have proved correct.

It will be seen that before the present study the eggs and larval stages of any species of IBALIINAE were unknown.

Oviposition and Egg.

Both *Ibalia* and *Rhyssa* are exceptionally easy to observe while at work. A female *Ibalia* may even be transferred on the fingers from one tree trunk to another, upon which it will continue its search for *Sirex* oviposition-punctures as though no interruption had taken place.

According to our observations, which now number several hundreds, *Ibalia* always oviposits in the borings already made by *Sirex* in its own egg-laying. The extremely fine and hair-like terebra of the *Ibalia* ovipositor thus performs no actual boring—the way is left clear by the host itself. This is only one instance of extremely close co-ordination between the life-processes of *Ibalia* and those of its host.

The " exploration " preliminary to oviposition is extremely detailed. The antennae are bent from near the base at right angles to the long axis of the body, their extreme tips playing like a jet of water on the bark, leaving sometimes not half a square millimetre untouched. Occasionally the tips of the antennae are drawn over the surface with a kind of wiping motion. The wings are flicked slightly and the abdomen jerked up and down a little. Progression is slow. In walking, the long basitarsus of all three pairs of legs, but especially the third, is used like a tibia, only the succeeding tarsal segments ever lying flat on the substratum. Any tiny crack is usually examined with long and particular attention, and one or even both antennae may be inserted into the mouth of a *Sirex* egg-tunnel.

When oviposition is to take place, the abdomen is suddenly and momentarily bent forward and a broad, triangular knife-like structure swung forward from the base of the abdomen, like the blade of a clasp knife. The abdomen and the ovipositor sheath immediately resume their normal position, while from the apex of the " knife-blade " the thread-like ovipositor issues and " feels round," eventually entering the *Sirex* bore. During oviposition the antennae are usually held porrect and immobile. There is a complete absence of that obvious straining which accompanies the actual wood-boring of *Sirex* and *Rhyssa* when egg-laying. The process of oviposition may take upwards of an hour and ten minutes. *Sirex cyaneus* frequently makes egg-bores which are never used for eggs. These sometimes penetrate very slightly, while others are of normal depth. *Ibalia* will insert its ovipositor in these empty holes, and spend 4 to 5 minutes at each, sometimes returning and examining the same ones. Pin-pricks, made to simulate a *Sirex* bore, generally received scant attention ; but one

engaged an *Ibalia* for a minute and a half, during 35 seconds of which the ovipositor was actually inserted.

Ibalia will oviposit in dull weather, or even during light rain, and at times continue this actually till as late as 8.30 in the evening (" summer time " 1st September).

The egg is long and pedunculate, and thus of a general Cynipoid form, though similar also to that of *Rhyssa*. There is, however, this important difference, that in the former, as usual in Cynipids, the body of the egg enters first and the stalk may project from the body of the host, whereas in *Rhyssa*, according to Bugnion, the egg is laid pedicel first.

The egg of *Ibalia* is laid in the young larva just before hatching, or at times possibly in larvae just after hatching. It has been found in almost any part of the body cavity, and there may be two in the same host. *Sirex cyaneus*, more often than not, lays two or three eggs in the same boring, in a linear series, the spaces between and outside being filled with a gelatinous secretion, the source of which has not yet been traced. The female *Ibalia* will lay one egg after another in the same boring. This probably explains the lengthy nature of the process.

That the early development is extremely slow is shown by the occurrence of eggs in young larvae over four or five months after the last adult was seen in the field. It would thus seem that the late-deposited eggs pass the winter in that stage. Earlier eggs, however, seem to hatch in about a month (September).

The Larva.

The first stage larva of *Ibalia* is of an elongate shape, with gigantic sickle-shaped mandibles. As with the egg, there seems no definite localisation in the position of the parasite larva.

No definite information is yet available as to the number of stages. What appears to be a second instar is much longer, rounded anteriorly and tapering gradually caudally, with the sickle-shaped mandibles proportionately much smaller.

The full-fed larva, as usual in wood-boring insects and their parasites, varies considerably in size (Pl. iii, fig. 2). The average is from 12–15 mm. long. The segmentation is strongly marked, the head small and strongly retractile. The whole insect is sometimes so contracted as to appear nearly half as wide as long.

There is no evidence that *Ibalia* feeds ectoparasitically even in the latest stages. Apart from full-fed larvae, lying in empty cells, we have seen none outside the body of the host. Although, as we have seen, more than one egg may be laid in a single host larva, never more than one adult has been found to emerge. At what stage and in what manner one of the competitors is destroyed is not known. Two second (?) instar larvae, each about four-elevenths the length of the host, have been found in one *Sirex* grub.

In a number of cases it has been possible to trace the whole course of a parasitised *Sirex* grub, from the oviposition-bore of the parent to the pupal cell of the *Ibalia*. In every case Borries's observation that the burrowing of a parasitised larva is confined largely to the outer portions of the trunk seemed confirmed. There is also a very considerable shortening of the course, for the host larva is destroyed at a size, and presumably also at an age, much less than it would normally attain ; how much less it is not yet possible to state, since both size and boring activity may be affected by parasitisation.

The Pupa.

In the majority of cases the pupal cell lay just under and parallel to the surface, instead of, as normally, more or less at right angles. Sometimes, however, an *Ibalia* occurred at an angle with the surface, and once a healthy male *Sirex* was found in

a cell just beneath and parallel to the bark. Even when parallel, the *Ibalia* cell was sometimes as much as one centimetre beneath the surface, leaving this thickness of wood and bark to be bored by the emerging adult.

The pupal cell is extremely thinly lined with what appears to be a paste of triturated wood, the fibres of which, under magnification, are seen to be crossed in all directions.

There is a marked pre-pupal stage, as in *Rhyssa*.

The pupa is at first entirely white, the full coloration of the imago appearing during the last ten to twelve days before emergence.

The Life-cycle.

The 1927 season was exceptionally wet and cold, and its data are perhaps not applicable to other years. *Ibalia* was most plentiful in the field during the last week in August and most of September, *i.e.*, just after *Sirex cyaneus* is most active. Unhatched eggs were found as late as 12th December and second (?) instar larvae on 18th January. This, coupled with the finding of full-fed larvae in autumn (*e.g.* November), indicates that the life-cycle, contrary to that of *Rhyssa*, requires at least two years, and possibly longer.

The Adult.

The dead-black thorax, the wings held in vertical plane parallel with the body, and the strongly laterally compressed abdomen, make *Ibalia* very hard to discern on a tree-trunk. Even viewed laterally, the beautiful red sheen of the abdomen, like polished mahogany, is hidden by the smoky wings—save in the virgin female which holds the shining abdomen aloft, above the wings. The sexes are readily distinguished by the shape of the abdomen. In the female the ventral line of the abdomen is apically straight, or even slightly upcurved, and the tip of the ovipositor is just visible. In the male the tip of the abdomen is markedly downcurved.

Like *Rhyssa*, *Ibalia* seems remarkably free from natural enemies. No indications of hyperparasites were seen. Assisted by the length of the process of oviposition, spiders perhaps take a toll of egg-laying females. We thus observed *Amaurobius fenestralis*, Stroem (kindly determined by M. L. Berland) seize an ovipositing *Ibalia* and drag it to a silken tunnel in a crevice under the bark.

Probably in correlation with the fact that the host naturally does not display the greatest variation in size until the later stages *Ibalia* shows considerably less size variation than *Rhyssa*.

Ibalia is usually considered an aberrant Cynipid. Brues, however, believes that " it shows affinities with the SIRICIDAE, upon which it is parasitic."

5. Inter-relations of Rhyssa and Ibalia.

In the attempt to utilise natural enemies in the control of *Sirex*, one of the first questions to be decided is whether both species of parasites should be utilised or only one.

From this point of view, *Ibalia* would seem the more efficient parasite. It attacks the host at an earlier stage, decreasing the extent of its activity; and its method of using the oviposition bores of *Sirex* ensures extremely little ineffectual activity.

Rhyssa, on the other hand, though it kills the host much more rapidly, does so at a later stage, when its boring is nearly completed. Secondly, a great proportion of its time seems to be spent in boring into sites where *Sirex* is absent.

It would appear that *Rhyssa* does not oviposit in larvae young enough to contain *Ibalia* at any stage, so that the risk of superparasitism is probably absent. In these circumstances there can be no objection to utilising both parasites, and this it is proposed to do.

6. The Sirex Position in New Zealand.

The damage by *Sirex* in the pine plantations of New Zealand is due to one introduced steel-blue species which appears to be *Sirex juvencus*, a form now considered merely a variety of *S. noctilio* (Dr. Waterston). When this insect was imported and whence, it is not known, but it came originally probably from Europe. The greatest damage is done to *Pinus radiata*, Don., a native of Western North America. In New Zealand, therefore, both the tree and its pest are living under new conditions, to which Tillyard attributes the extent of the damage inflicted. *Sirex* is said to be attacking healthy trees (Tillyard), but whether this merely implies trees still green and not yet obviously attacked by other insects, though possibly affected by adverse edaphic conditions or fungi (as at Oxford), we have no means of knowing. *Pinus radiata* grows extremely rapidly in New Zealand, and is possibly more susceptible to attack there than in its native home. The position at Oxford is, however, not strikingly dissimilar, since the *Sirex* there is an introduced American species (*S. cyaneus*), and the tree affected (European larch), though indigenous, has been planted. The two parasites are both indigenous, and the fact that they attack *S. cyaneus* so extensively here augurs well for their success in New Zealand against *S. juvencus*.

It remains to state that there is already in New Zealand a large indigenous Rhyssine, *Rhyssa fractinervis*, Voll.,* which, curiously enough, is believed to parasitise the larvae of a large wood-boring weevil, *Rhynchodes ursus*, White (Hudson, Lindsay). *M. fractinervis* is very rare and has no known hyperparasites, and its host bores in dead southern beech trees (*Nothofagus* spp.); so that its occurrence is not likely to affect the present project.

Little seems to have been attempted anywhere in the biological control of forest insects. Yet methods of a more artificial nature are often impracticable. The establishment of the British Ichneumonid, *Mesoleius tenthredinis*, in Canada, as a measure against the larch sawfly, *Nematus erichsoni*, seems to have yielded good results in some localities; the gipsy-moth work in eastern U.S.A. is well-known; and the control of the Australian tree-fern weevil, *Syagrius fulvitarsis*, in Hawaii, by the imported Braconid, *Ischiogonus syagrii*, seems to be largely successful. Few other attempts to utilise the natural enemies of forest insects appear to have been made, though on the Continent, especially in Germany, the beneficial activities of birds and ants in this rôle have long been recognised and, where possible, encouraged.

7. Technique.

The difficulties attendant on the mass collection and rearing of wood-boring insects are so great that a few notes on the methods improvised in the present study may not be out of place.

The main points concern firstly the feeding of the adults—both hosts and parasites—and secondly the safe storage of the full-fed larvae through the very long resting period.

* Dr. Waterston has kindly examined this species and found it to be intermediate in structure between *Megarhyssa* (*Thalessa*) and *Rhyssa*, though it has the general facies of the former. In oviposition (Lindsay) a large bladder near the apex of the abdomen functions as in the former genus.

Large infested larch logs were stood on end on damp sand in a completely-gauzed insectary at Farnham Royal, and the adult insects allowed to fly at will under the vita-glass roof. Mating and oviposition of *Sirex*, *Rhyssa* and *Ibalia* occurred here with facility. One female *Rhyssa* captured on the 7th September lived here for five weeks. A male lived a similar period. In the present year (1928) we have kept one female for over 14 weeks. At the time of capture this female was probably unfertilised, for no attempts at oviposition were observed until the 16th September, one day after a bred male had been liberated in the insectary. Thereafter oviposition continued nearly every day at least until the 4th October. A number of other *Rhyssa*, of both sexes, lived under the same conditions for shorter periods. *Ibalia* adults, usually of unknown age, lived from one to over three and a half weeks. Most of these latter were kept in a large cage in the same insectary.

All parasites were supplied with honey-water and split raisins. *Sirex* was once observed drinking the honey water. *Ibalia* fed constantly at the split raisins, and the favourite food of *Rhyssa* (both sexes) was honey-dew from Aphids on several hawthorn-bushes standing in the same insectary. They also used the honey-water provided and the split raisins.

Full-fed larvae of both *Rhyssa* and *Ibalia* were placed in individual small gelatin capsules, which were lightly pricked at one end and packed in sawdust in metal boxes with close-fitting lids. A piece of blotting-paper projecting from beneath this lid was moistened about once a week in order to prevent dessication, though the atmosphere was never allowed to become sufficiently moist to soften the gelatin capsule or to allow the growth of moulds. *Rhyssa* was found to emerge in a very natural manner from these capsules, by biting a circular hole at one end. It is proposed to ship the parasites to New Zealand in the form of full-fed larvae packed in this manner, thus utilising the long resting stage.

8. Summary.

Rhyssa persuasoria and *Ibalia leucospoides*, both parasitic on *Sirex cyaneus*, have been studied at Oxford.

Rhyssa lays its eggs in the burrow of and near to the almost or quite full-fed host larva or the pupa, by piercing the solid wood with its ovipositor. Feeding is entirely ectoparasitic and takes only a few weeks, during which the host larva may burrow a little further. The winter is passed by *Rhyssa* as a resting larva. Pupation takes place in the spring, and the whole life-cycle normally occupies one year.

Ibalia oviposits in the young larva just before or more rarely just after hatching, utilising the oviposition-bores of the *Sirex* for this purpose. The first-stage larva is elongate, with sickle-shaped mandibles, and larval feeding seems wholly endoparasitic. *Sirex* larvae parasitised by *Ibalia* confine their boring largely to the outer portions of the trunk, and usually make their final cell just under and approximately parallel to the surface. The life-cycle of *Ibalia* requires at least two years.

Owing to the very different instars which they attack, there seems no risk of superparasitism of *Ibalia* by *Rhyssa* or *vice versa*, and it is therefore suggested that both species be introduced into New Zealand as a measure against *Sirex juvencus*, which is there very destructive to plantations of *Pinus radiata*.

Adults of both *Rhyssa* and *Ibalia* may be easily kept in captivity. The former feed readily on honey-dew or honey-water, and the latter on split raisins.

The resting larvae of both may be kept in gelatin capsules packed in sawdust which is not allowed to become entirely dry.

References.

ASHMEAD (W. H.). 1903. Classification of the Gall-wasps and the parasitic Cynipoids of the Superfamily Cynipoidea.—Psyche, Boston, Mass. x, pp. 7–13, 59–73, 140–155, 210–216.

BARBEY (A.) 1925. Traité d'Entomologie forestière. 2nd ed. Paris.

BAUMANN (C.). 1924. Uber den Bau des Abdomens und die Funktion des Legeapparates von *Thalessa leucographa*.—Zool. Anz., Leipzig, lviii, pp. 149–162.

BISCHOFF (H.). 1927. Biologie der Hymenopteren. Berlin.

BORDAS (M. L.). 1917. Du rôle de quelques Ichneumonides comme auxiliaires de l'Arboriculture forestière.—C. R. hebdom. Acad Sci. Fr., Paris, clxiv, pp. 923–925.

BORRIES (H.). 1891. Om Slaegten *Ibalia* Latr.—Ent. Medd., Copenhagen, iii, pp. 53–57.

BRUES (C. T.). 1927. Observations on wood-boring Insects, their Parasites and other associated Insects.—Psyche, Boston, xxxiv, pp. 73–90.

BUGNION (E.). 1905. Les oeufs pédiculés et la tarière de *Rhyssa persuasoria*.—Extr. C.R. 6e Cong. int. de Zool., Sess. de Berne 1904, Geneva, pp. 511–521, 1 pl., 2 figs.

CHAMPLAIN (A. B.). 1922. Records of Hymenopterous Parasites in Pennsylvania.—Psyche, Boston, xxix, pp. 95–100.

CHEESMAN (L. E.). 1922. *Rhyssa persuasoria*: Its Oviposition and Larval Habits.—Proc. S. London Ent. Soc., 1921–22, pp. 1–2.

DALLA TORRE (K. W.) & KIEFFER (J. J.). 1910. Cynipidae: *in* Das Tierreich, Berlin, xxiv, 891 pp.

HUDSON (G. V.). 1927. The Giant Ichneumon-fly, *Rhyssa fractinervis* Voll.—N.Z.Jl. Sci. & Techn., ix, p. 118.

JOHNSON (W. F.). 1919. *Rhyssa persuasoria* in the Counties of Down and Fermanagh.—Irish Naturalist, xxviii, pp. 115–118.

LINDSAY (S.). 1925. The Giant Ichneumon-fly *Rhyssa fractinervis* Voll.—N.Z. Jl. Sci. & Techn., viii, pp. 31–32.

RILEY (C. V.). 1888. The Habits of *Thalessa* and *Tremex*.—Insect Life, i, pp. 168–179, figs. 36–39, 1 pl.

TORKA (V.). 1926. Beobachtungen über die Eiablage von *Sirex spectrum* L. und den Schmarotzer *Rhyssa persuasoria* L. — Anz. Schädlingsk., Berlin, ii, p. 166.

TILLYARD (R. J.). 1927. The Giant Horntail. A Serious Menace to Pine Plantations.—Nelson Evening Mail, 9th Feb. 1927, p. 6.

Fig. 1. Larva of *Rhyssa persuasoria*, L., fully fed, lying in a tunnel on the remains of the *Sirex* host.

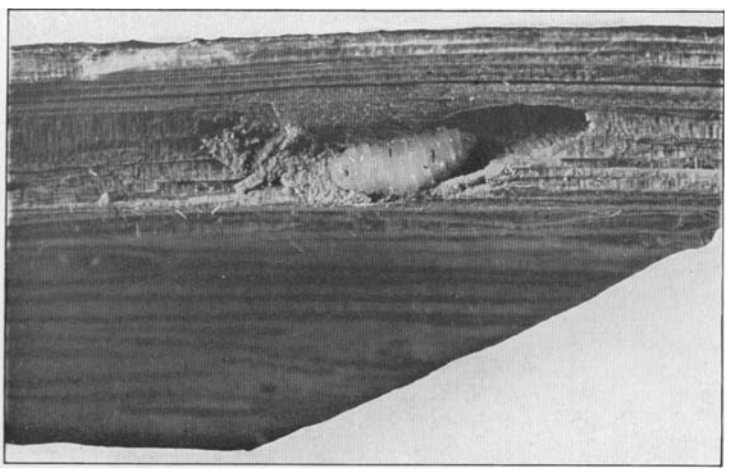

Fig. 2. Larva of *Ibalia leucospoides*, fully fed.