A NEMATODE INFECTION OF *SIREX NOCTILIO* (F.) IN NEW ZEALAND

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Summary

A nematode, parasitic on the woodwasp *Sirex noctilio* (Fabricius), was first recorded in 1962 from the North Island; it has not yet been found in the South Island. As high as 95% of a *Sirex* population has been parasitised by these nematodes.

The nematode, designated by Bedding as a *Deladenus* sp., family Neotylenchidae, is bisexual with two female forms, one non-infective and the other infective. The former can repeat its life cycle indefinitely in the wood of a killed tree as long as the symbiotic "sirex" fungus is present; the latter which invades the *S. noctilio* larvae or prepupae, produces progeny viviparously during the host's pupal stage. The juveniles infiltrate the host's gonads causing the testes to hypertrophy and the ovaries to atrophy, thus sterilising the hosts.

Sexual and oviposition behaviour of the host is not affected. An infected female *Sirex* is able to insert her eggs (which contain juvenile nematodes) and oidia of the symbiotic fungus essential for killing trees and/or the development of both the *Sirex* larvae and the nematodes, into the host trees, infecting the trees with the nematodes.

The life history, behaviour and pathology of the nematode within the tree and *vis a vis* its host and insect parasites are described.

The nematodes have not been found in other insects dwelling in bark of pines that have died after successful *Sirex* attack.

INTRODUCTION

Sirex noctilio (Fabricius), an introduced palaearctic woodwasp, is considered to be the most potentially harmful insect of New Zealand exotic pine forests. Between 1946 and 1951 the insect and its symbiotic fungus caused severe mortality in the extensive *Pinus radiata* plantations of the North Island. During the past 10 years the population of *Sirex* in forests in both islands has persisted at low to moderate levels with occasional local heavy mortality to trees. The low population level is considered to be caused by three factors, (a) climatic conditions favourable to tree growth and unfavourable to increase in *Sirex* numbers, (b) more intensive silvicultural management of pine forests and (c) the establishment of biological control agents, the most important of which appears to be a nematode discovered in 1962.

Infection of *Sirex noctilio* by this nematode was first discovered in adult females emerging in the FRI insectary from *Pinus patula* logs from Rotoehu State Forest. I found that the ovaries and eggs of these woodwasps were smaller than normal (Fig. 1), the eggs contained juvenile nematodes, and larger nematodes were in the body cavity.

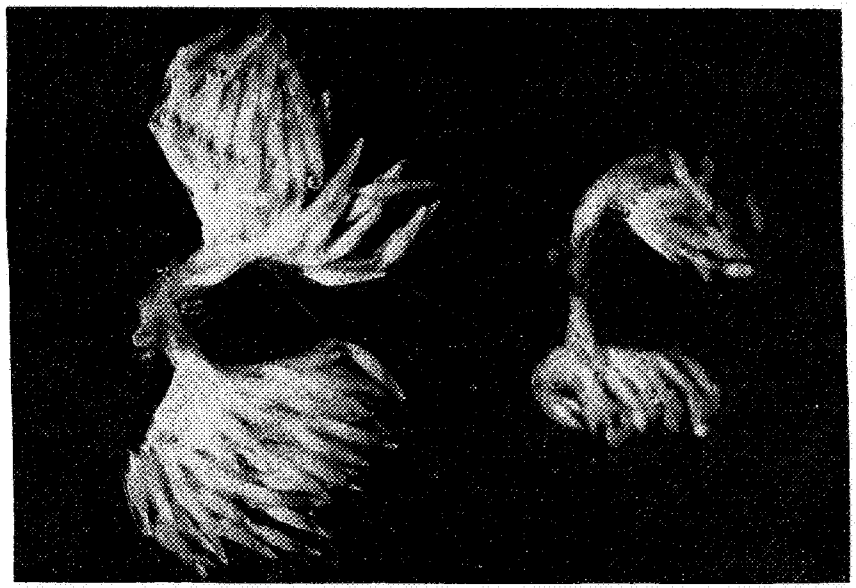

FIG. 1—Ovaries of adult female *Sirex noctilio*, adults of equal size. Left: Normally developed ovaries and eggs. Right: Infected by nematodes.

Subsequently, adult male *Sirex* from Rotoehu were dissected and were found to have large nematodes in the body cavity and hypertrophied testes (Figs 2 and 3) containing many thousands of juvenile nematodes. *Sirex* larvae and pupae also contained large nematodes.

To make sure that the infection had not originated in the insectaries where the logs had been stored prior to the emergence of the adult *Sirex*, more logs were collected from the same compartment of Rotoehu State Forest and the *Sirex* were examined immediately.

Infection level of emerging adults was 95·4%; of immature stages (both larvae and pupae) 63·3%. The latter figure, in the light of present knowledge, was probably the result of a lesser degree of infection in logs from which the larvae were obtained.

No nematodes were found at that time in *Sirex* adults that emerged from *P. radiata*, *P. ponderosa* or *P. nigra* from six other North Island and South Island forests.

Surveys subsequent to 1963 have shown that the nematodes are present in most North Island pine forests and in *Pinus* species additional to those mentioned above. They had not been found in the South Island before 1967, when deliberate introductions were made.

The nematode is considered to be a very useful biological control agent, since infection renders a large percentage of the *Sirex* population

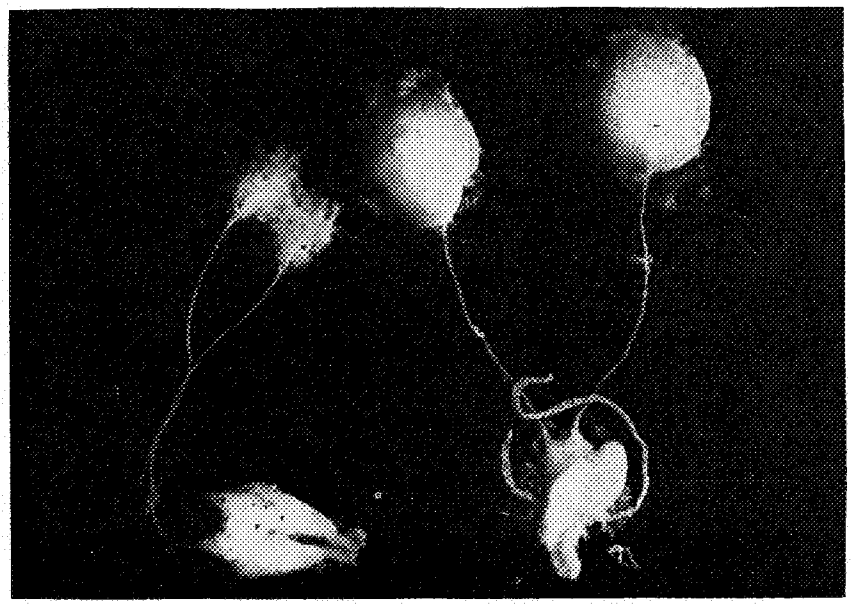

FIG. 2—Internal reproductive organs of male *Sirex noctilio*. Left: Testes not infected. Right: Infected hypertrophied testes. Note the infective adult nematode coiled round the seminal vesicles.

infertile. It may also be of particular interest to Australian authorities who have undertaken an intensive research programme on several aspects of *Sirex* ecology and control since 1962 when the woodwasp was found on Australia's mainland (Irvine, 1962). My investigations on this nematode have been confined to studies of its distribution, pathological effects on and importance to *Sirex*, some aspects of the nematode's life cycle, its effects on *Sirex* parasites, and to testing methods by which the nematode may be established in the field.

As I was not familiar with nematodes the co-operation of a nematologist was sought. Dr W. C. Clark, Massey University, Palmerston North, co-operated initially, and at the 1962 conference of the Entomological Society of New Zealand, advanced a tentative life history. Other commitments prevented him from continuing the investigation. In 1966 the FRI arranged for Dr C. L. Massey of Rocky Mountain Forest and Range Experiment Station, Albuquerque, New Mexico, to visit New Zealand for six weeks to work on some aspects of the nematode's taxonomy and life history. Meanwhile, in 1965, Dr R. A. Bedding had been appointed by CSIRO to work with the Australian Sirex Biological Control Unit, Silwood Park, England, as nematode infection had been found in Siricidae and their parasites in Europe. He advanced a life history

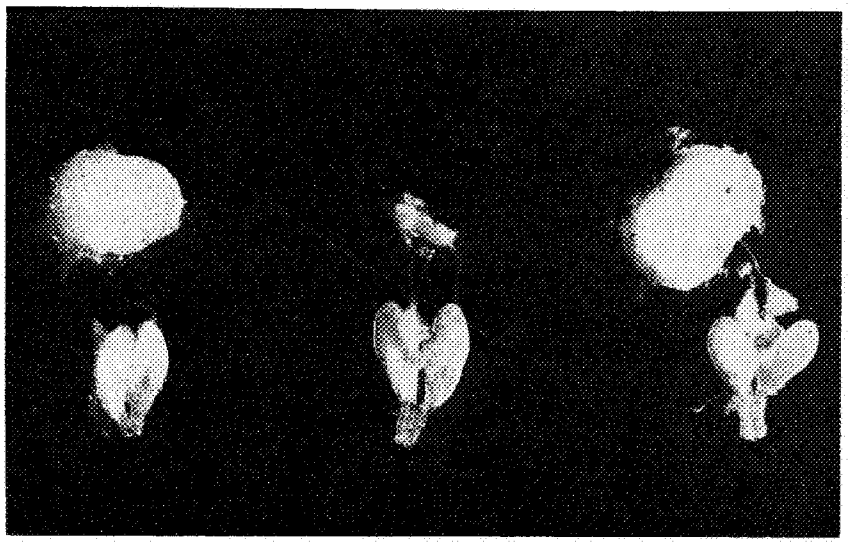

FIG. 3—Internal reproductive organs of male *Sirex noctilio*. Centre: Normal. Left and right: Infected hypertrophied testes.

(Bedding, 1967) and placed the nematode in the genus *Deladenus* Thorne of the family Neotylenchidae.

A major problem that still remains is the taxonomic status of the nematode. It is possible also that in New Zealand more than one species is involved.

LIFE HISTORY OF *Sirex noctilio* AND ITS FUNGAL SYMBIONT IN NEW ZEALAND

Essential details of the life history of *Sirex noctilio* are summarised here to clarify the relationship of the woodwasp and the nematode.

The larvae of Siricidae are woodborers and most of the species depend on specific symbiotic fungi to kill the tree, and render the wood suitable for their larvae to feed on (Francke-Grosmann, 1939, and many others). (See for literature review on bionomics Morgan, 1968.) Only the female larvae and adults have special organs which contain this symbiotic fungus. In larvae the fungus is carried in intersegmental pockets between the first and second abdominal segment and in the adult, in the hypopleural organs, situated internally near the base of the ovipositor components. The fungus is introduced into a tree with or without eggs, during drilling with the ovipositor components, as oidia.

The fungus is a basidiomycete which does not produce fruiting bodies in nature. That associated with *Sirex noctilio* is at present regarded as an

Amylostereum sp. (Talbot, 1964), probably *A. chailletii* (Fr.) Boidin. It is considered to be a weak pathogen, able to kill only those trees weakened by other factors of their environment.

The flight season of *Sirex* begins in late December, reaches a peak in February, and may continue until late April. On sunny days, adults congregate in the treetops where they mate. *Sirex* is facultatively parthenogenetic, fertilised eggs producing females, unfertilised eggs males. Adults do not feed but depend on their body fat for sustenance. Males live for 5–12 days; females, in the absence of oviposition sites, live 5–12 days, but given access to oviposition sites, live only 2–6 days.

During the initial stages of attack on trees, many holes are drilled in the trunks into which the fungus is deposited, but no eggs. The eggs are usually deposited with a clump of oidia 10–16 mm deep in the sapwood. The fungus ramifies in the wood under favourable conditions and development of *Sirex* larvae appears to depend on their having a sufficiency of the fungus as a food as well as its action in modifying the wood physically and chemically. Larval tunnels may extend eventually from close to the bark to the centre of the trunk.

Wilting of *P. radiata* trees which have been successfully attacked is rarely seen in February or March of the summer in which the attack occurred; discoloration of the foliage and obvious mortality are usually more apparent from the following September onwards. Larval growth through the winter is generally slow, only a few larvae being well-developed by October.

Larval growth is faster after October and may be associated with the fall in wood moisture content, but if the wood dries rapidly growth of the larvae may be arrested and some larvae die. There is a close relationship between wood moisture, fungus development and eventual adult size of the *Sirex*; moisture content controls the vitality of the symbiotic fungus in the wood.

Pupae can be found from early December onwards, and the pupal stage lasts 16–21 days. After ecdysis, the teneral adult remains in the pupal chamber for a few days before chewing its way out of the tree and flying off. Both sexes are reproductively mature at emergence and each female has oidia of the symbiotic fungus in the hypopleural organs.

Generally, *Sirex* develops in one year in *P. radiata*, *P. patula* and some economically minor pine species, but in *P. ponderosa* and *P. nigra*, a 2-year life cycle is usual. Adults may oviposit on trees which were killed in the previous year and the larvae may develop quickly when conditions are favourable. Such an oviposition may give the impression that *Sirex* has a 2-year life cycle in *P. radiata*, and a one-year cycle in *P. ponderosa* and *P. nigra*.

How and why *Sirex* select particular trees for preferential attack is not fully understood. There may be an olfactory attraction caused by the subnormal physiological condition of the tree. It has been observed that attack on one tree by a few individuals is often followed by mass attack by others. Attack on certain trees may be spread over several weeks. Nor are the mechanisms underlying the death of trees clearly understood, since some trees do not succumb even after heavy oviposition.

Mortality has been more often encountered in untended stands, but incorrectly timed and/or applied silvicultural treatments have resulted in unexpected mortality soon after the stands have been tended.

LIFE HISTORY OF THE NEMATODE

The life history of the *Deladenus* sp. infecting *Sirex* in New Zealand does not differ essentially from that of the European population (Bedding, 1967).

Both infected and uninfected *Sirex* deposit their eggs and the symbiotic fungus in the wood of the host trees. When the tree has been successfully attacked, the fungus invades the wood tissues. Larvae develop from the eggs deposited by the uninfected female; eggs from infected females are infertile and are closely packed with juvenile nematodes, which move into the wood, feeding on the *Amylostereum* hyphae.

The juvenile nematodes comprise both males and females; they grow, mature and mate. Each mated female lays 50–500 eggs. Males and two types of females develop from these eggs. One type of female is non-infective to *Sirex* and repeats its free-living cycle indefinitely while the fungal hyphae are present in the tree; the other type of female is the insect-infective form which invades *Sirex* larvae and prepupae, probably after it has mated. Several may invade a single host. Once inside the host, these females grow rapidly inside its body cavity. Large numbers of young are produced viviparously during the host's pupal stage. These juveniles congregate in the host's gonads; the ovaries and eggs atrophy and the testes hypertrophy, rendering the host completely sterile. When too many nematodes invade a *Sirex* larva the host may die.

The deposition of infected eggs and oidia by the infected *Sirex* and oviposition by healthy *Sirex* in fresh host trees starts the nematode life cycle again.

METHODS FOR DETERMINING *Deladenus* IN *Sirex* AND IN WOOD

In Sirex

No external differences or behavioural changes have been detected between healthy and infected *Sirex*. Dissection of the abdomen is the

only reliable way of determining nematode infection at any stage of the development of *Sirex*.

Infection in living females that have oviposited at least once, and in recently dead females can be demonstrated by placing the ovipositor in water; the juvenile nematodes in the ovipositor components disperse into the water. To detect infection in living larvae they are placed in water and the clear space on the dorsal side of the 8th abdominal segment where the body fat is separated is examined; the large female nematodes with their greenish tinge may often be seen.

Neither method is fully reliable; only dissection of the abdomen gives unequivocal evidence.

In adults the abdomen is cut off, placed on a glass slide, and some water is added. The abdomen is opened and the large nematodes are clearly visible under 10X magnification, while juveniles can be expressed from the gonads and appear in the water as a wriggling mass. Generally, infected ovaries and eggs are smaller and atrophied and testes are hypertrophied compared with normal organs.

Larvae or pupae are placed on a glass slide with water and dissected. The large female nematodes are most easily detected. More care is needed to discover those nematodes that have recently invaded the immature hosts and those that are still small. After the insect has been cut open under water, the fat bodies, the large nematodes and other debris are removed with a capillary tube attached to a suction pump. Even then the small stages can be easily overlooked.

It is safe to assume that the nematode females in pupae are fully grown.

In Wood

Nematodes may be extracted from wood billets from which infected *Sirex* have emerged, or in which infected immature stages of *Sirex* have been found.

Billets are reduced to small sizes by hand- or machine-planing or by splitting. Nematodes are extracted by a Baermann funnel technique (Goodey, 1963) which has been modified to suit the equipment available. To avoid mortality, extracted nematodes are left in water not longer than 24 hours. Split billets may still yield nematodes after even four extractions.

Extractions yield generally both the free-living and infective stages of *Deladenus* and also other nematodes. *Deladenus* has been extracted from wood which had neither *Sirex* larvae nor their tunnels, but which did have *Sirex* oviposition holes.

Deladenus are found in both sapwood and heartwood. Their position vis a vis *Sirex* oviposition sites suggests that they can move through all the wood components (tracheids, ray cells, resin canals, parenchyma).

The exact location of the nematodes in the wood components is difficult to determine. Wood sections are placed in water and examined under transmitted light. Nematodes betray their presence by movement. They are easily displaced by the cutting knife and move away from cut surfaces. For this reason the wood sections must not be too thin, but also not so thick as to prevent observation by transmitted light.

The moisture content of the wood in relation to *Amylostereum* and the needs of *Deladenus* requires more investigation. More nematodes can be extracted from moist wood than from dry wood.

RELATIONSHIPS BETWEEN *Sirex*, *Deladenus*, *Amylostereum* AND WOOD TISSUES

Adult Sirex

The number of large viviparous infective *Deladenus* females present in the haemocoel is an obvious feature of infection. Generally, 50–70 are present (range 1–489). The body length varies and appears to depend on the numbers present; it is usually 10–14 mm (range 5–22 mm) and attains the greatest size when fewest are present.

Infected females have atrophied ovaries and this, a striking anatomical feature, is considered to be the result of fewer and smaller eggs having developed.

Sirex eggs are normally fusiform (about 1·5 mm long by 0·3 mm wide), with a thick chorion. Eggs from infected *Sirex* are shorter and relatively stouter (0·5–0·6 mm long by 0·3 mm wide) and with a thinner chorion (Fig. 4). Infected eggs lack developmental tissue and each contains up to 200 juvenile nematodes. *Deladenus* juveniles have also been found (but rarely) in the hypopleural organs.

Infected male *Sirex* have hypertrophied testes which are usually loosely fused together. Spermatozoa are absent. Hypertrophy is apparently caused by the immense number (30,000–40,000) of juvenile *Deladenus* which are closely packed into this organ. The seminal vesicles and the vasa deferentia are usually free of nematodes. The number of juveniles has not been found to increase markedly with any increase in the number of infective females present.

The number of juveniles encountered in the haemocoel is very small indeed, indicating that infestation of the gonads appears soon after release by the viviparous females.

Infection by *Deladenus* sterilises both sexes of *Sirex*. The number of fat bodies is markedly reduced in both sexes of the infected adult hosts; this could affect their length of life. Flight and mating behaviour does

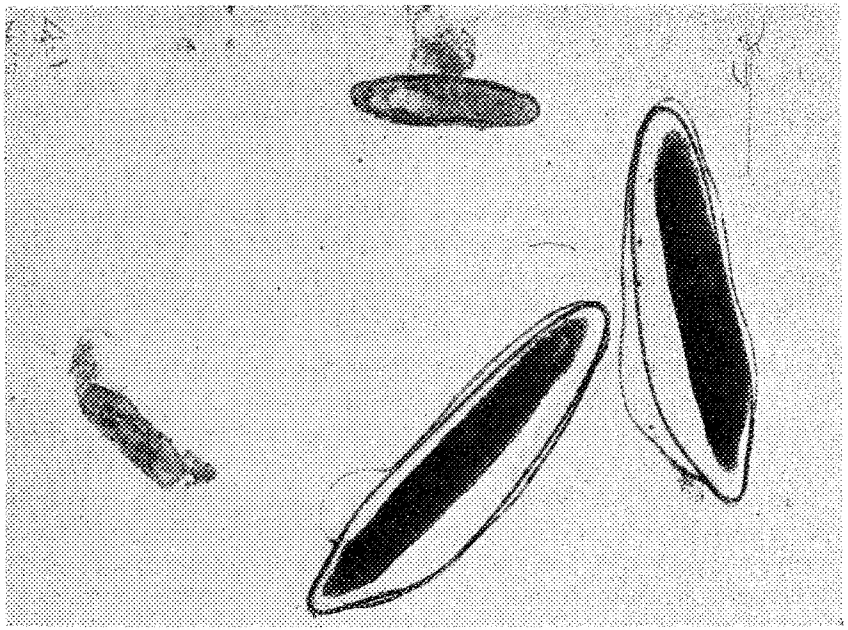

FIG. 4—Eggs of *Sirex noctilio*. Large eggs uninfected, small eggs infected.

not appear to be affected by infection. Urges to copulate and oviposit are undiminished.

Infected adult male *Sirex* do not have an important role in disseminating *Deladenus*. No transfer of juvenile nematodes was found in 54 matings between infected males and uninfected females. Any transfer during copulation appears to be unlikely, as nematodes are packed closely together in the testes and it is difficult to visualise their passage through the narrow vasa deferentia.

The possibility of such a transfer, however, cannot be entirely ruled out. In late autumn, 1966, three female *Sirex* (caught in the insectaries in which logs from infected and uninfected *Sirex* had been obtained) had ovaries and oviducts infected by juvenile nematodes; the *Sirex* eggs were fully developed but no large infective nematodes were found in the haemocoel.

Infected male *Sirex* are sterile so mating with a healthy female produces males. But *Sirex* females may mate more than once, and may later mate with a fertile male to produce both males and females.

Large infective *Deladenus* females without progeny have been observed, though rarely, in adult *Sirex*.

Sirex Larvae

Insect-infective *Deladenus* females, 1–2 mm long, invade the host larvae in which they grow rapidly, as usually large specimens are found. Their presence in the haemocoel is the obvious feature of nematode infection in the larvae. Small infective stage nematodes are generally not easily discovered when the large females are present; careful dissection and extraction techniques are needed to demonstrate them. No juvenile nematodes are produced by the infective females while the host remains in the larval stage.

I often found host larvae with a translucent, flabby body. Dissection showed that these larvae had a greatly reduced number of fat globules, sometimes none at all, and contained many large infective *Deladenus* females of which the cuticle appeared reticulated, smaller females with a normal cuticle, and other still smaller individuals. The last group was thought at first to be progeny of the larger specimens, but they are apparently females which have been arrested in their growth.

When such host larvae are found in the wood, dead and dying larvae also occur close by. Larvae are killed by a heavy invasion of nematodes. The number of nematodes needed to kill a larva varies; no general rule is apparent, since adult *Sirex* which emerge from the wood often carry an extremely high number of nematodes.

Death of larvae from infection has been observed more often in logs exposed to oviposition in the insectaries than those naturally exposed in the field. This is probably the cause of the low returns obtained from the breeding of *Ibalia* species in the insectaries. It was observed that in logs exposed to *Sirex*, including those infected by *Deladenus*, the mortality of the woodwasp immatures was high after nine months; remaining larvae that were still alive were found to be heavily infected, and had the translucent, flabby appearance described earlier. It is most likely that although under natural conditions the number of *Deladenus* present in *Ibalia*-parasitised woodwasps is generally low (see later), the mass infection could result in the deaths of parasites and *Sirex*.

Sirex Pupae

Large nematodes are the obvious feature of infection of the pupal stage.

Infection of gonads in pupae extracted from the wood varied greatly with maturity and gonad development. Intensity of gonad infection increased as the pupae approached maturity until, at the teneral adult stage, the gonads were completely infected.

Larvae were taken out of the wood and reared in test tubes by Rawlings' (1953) method to obtain pupae of known age. Although mortality was

heavy from parasitism by *Ibalia leucospoides* (Hochenwarth) or from fungal attack, enough pupae were obtained to arrive at an approximate time scale for infection of *Sirex* gonads by *Deladenus* juveniles. It is:

8th day; FEMALE PUPAE: A few juveniles, including some one-third to half the size of those found in adult host ovaries were present in the ovarioles but not yet in the developing eggs.

MALE PUPAE: Juveniles the same size as those which infect adult gonads, already infect the testes.

12th day; FEMALE PUPAE: Small numbers of juveniles are present, but most are the same size as are found in adult gonads. The developing eggs have become infected.

MALE PUPAE: A slight hypertrophy of the testes is apparent.

14th day; FEMALE PUPAE: More juveniles are present in the gonads.

17–18th days; MALE AND FEMALE PUPAE: All eggs present are infected; invasion of the testes has advanced.

In teneral adult hosts infective female nematodes are still producing their young, and infection of the gonads still occurs.

There appears to be much variation in the timing of the first infection of the gonads; developing gonads could be infected before the 8th day of the pupal stage. Three pupae showed infection of the gonads by the third day after ecdysis; in two others no infection of the gonads was found in 6-day-old pupae.

General

It is apparent that the early infiltration of the *Deladenus* juveniles prevents the host eggs from developing to normal size, so the reduction in number of eggs and size of the eggs results in the atrophy of the ovaries.

In the early stages of gonad infection the nematodes are extremely small (range 0·75–0·95 mm). Their presence coincides with the presence of identical small unborn juveniles in the early adult female nematode. Late adult females contain mostly larger (2 mm) unborn juveniles. It appears that the first nematodes born are small and that these make the first invasion of the host's gonads.

Stubby (3–4 mm long) female nematodes were frequently found in the testes of adult *Sirex* dissected. Close confinement had apparently arrested their growth. They were found more often in hosts which had been reared in test tubes or in logs artificially inoculated with *Deladenus* than in hosts emerging from, or cut out from logs which had been naturally infected in the field. Logs which were artificially inoculated were usually treated when larvae were in an advanced stage of development so that some of the hosts were infected at a later stage of growth than they would have been under natural conditions.

Some *Sirex* adults had large infective *Deladenus* females in the haemocoel. No infection by juveniles was found; these also were absent from the *Deladenus* female .

The most important deviation from the normal pattern of nematode infection is that the hosts can die when the immature hosts are heavily infected with *Deladenus*.

After the death of the *Sirex* adult, the nematode juveniles present in the gonads were found to be dead after 2–3 days when the *Sirex* were kept at room temperature. Decay of the host organs may be the cause, as dead hosts stored at 40–44°F, contained live juveniles 14 and even 21 days after host's death.

When the ovipositor components of an infected recently dead female *Sirex* are placed in water, some nematode juveniles can escape into the water. No nematodes escape from dead males.

The wood-inhabiting stages of *Deladenus* may be extracted from wood several months after the *Sirex* adults have finished emerging.

Information is too scant to form any conclusions on the rate of movement of *Deladenus* in wood.

NEMATODE INFECTION OF OTHER WOOD-INHABITING INSECTS OF *Pinus*

Other insects present in pine logs infested with *Deladenus* have been examined for infection with the nematode. Particular attention was paid to insect parasites of *Sirex* that are already established in New Zealand.

Parasites of Sirex noctilio

(i) *Ibalia leucospoides* (Hochenwarth) (Hymenoptera:Ibaliidae)

Ibalia deposits its eggs inside the *Sirex* eggs or in the larvae still present in the oviposition tunnel. Multiple parasitism is rare. The first two instars are endoparasitic, the third moves out of and consumes its host; the fourth instar is free-living in the wood from November onwards. The development from egg to adult usually takes a year.

When *Ibalia* larvae have been found in *Sirex* larvae infected by nematodes, the number of infective-stage females has usually been 2–3 (highest 11). Larvae infected with nematodes but free of *Ibalia* have contained the usual number (range 50–70) of nematodes. Why the number of nematodes should be so depressed in *Sirex* larvae parasitised by *Ibalia* is not known: it may be antagonism between the two parasitic species.

To determine whether *Ibalia* could survive on *Sirex* larvae that were infected by nematodes, a number of *Sirex* larvae were removed from the wood and reared in test tubes. The 20 *Ibalia* larvae which emerged from

infected *Sirex* larvae showed no sign of infection. Nine *Ibalia* larvae were reared to adults and were also not infected.

Between 1964 and 1966, over 100 *Ibalia* larvae (mostly 4th instar and free-living in the wood) and over 500 *Ibalia* adults reared from logs infected with *Deladenus* were dissected. No infection was found. In 1967, infection of *Ibalia* adults by *Deladenus* was found in 133 of 2,174 specimens (6·1%). Reproductive organs of *Ibalia* were not affected and all the *Deladenus* were dead.

Most of the *Ibalia* had only a few nematodes up to 8 mm long; some also had a few smaller juveniles about 1·5 mm long.

(ii) *Ibalia ensiger* Norton

Consignments of *Ibalia ensiger*, a North American parasite of Siricidae, were free of nematodes when imported. In 1967 a small number of the progeny of these importations, which were bred with a small percentage of *Sirex* infected with nematodes, were found to be infected without harm to their reproductive organs. Here again, the nematodes were dead. The returns from the breeding were low.

(iii) *Rhyssa persuasoria persuasoria* (Linnaeus) (Ichneumonidae)

Like other *Rhyssa* and *Megarhyssa* spp., this parasite deposits its eggs on *Sirex* larvae after stinging and paralysing them. The *Rhyssa* larva feeds externally on the host and changes to its final larval stage in 4–6 weeks, leaving only the shrivelled remains of the host. Most larvae of *Rhyssa* and *Megarhyssa* spp. remain in diapause until the next spring, but a small number, mostly males, may complete their development without diapause and emerge within 3–4 months.

No nematode infection was found in more than 100 *Rhyssa p. persuasoria* larvae found free-living in the wood or in over 500 adults which emerged from wood in which infected *Sirex* had been found. It was established experimentally that *Rhyssa* larvae could develop on infected *Sirex*. *P. ponderosa* logs that were known to contain *Sirex* infected with *Deladenus* were exposed for 4–6 weeks to gravid *R. p. persuasoria*. The logs were then split up and the *Rhyssa* and *Sirex* larvae were examined for nematodes. Of the 45 *Sirex* larvae, only one was not infected. None of the 22 *Rhyssa* larvae was infected; of these 22, 10 were still feeding on their infected host; only the shrivelled remains of the other *Sirex* hosts were found.

In Tasmania, adult *R. p. persuasoria* imported from Europe were infected with *Deladenus* sp. (Hocking, 1967), but the nematode may be a different species from that infecting *S. noctilio* in New Zealand. No specimens of *R. p. persuasoria* have been introduced into New Zealand lately.

(iv) *Rhyssa persuasoria himalayensis* Wilkinson

This species was introduced into New Zealand and Tasmania from India and Pakistan. Nematode infection was found in consignments from India in 1965. Of the 280 females and 10 males received in New Zealand, 26 females and 2 males were found to be infected. A few of the progeny of the 1964 consignments were also infected, although the specimens in the consignments were expected to be free of infection.

Infection in both subspecies of *R. persuasoria* has been described by Hocking (1967) and my findings agree in most respects with hers. In *R. p. himalayensis* the nematodes affect the reproductive organs and as many as 70 infective stage females can be present in a *Rhyssa* female, while the juvenile nematodes adversely affect ovaries and eggs. However, in several specimens I found that juveniles were present in the ovaries, but the eggs were fully developed.

In breeding *R. p. himalayensis* at FRI stress was laid on obtaining stock free of nematodes. To test insects, which did not show obvious external signs of infection, the ovipositors were placed in water after the insects had oviposited. From most of the infected specimens the juvenile nematodes were freed in the water. Although many infected specimens could be found in this way, as with *Sirex* the method was not diagnostically conclusive, all the adults were dissected after death for critical diagnosis.

Nematode-free stocks were obtained in 1966, but their progeny was kept in quarantine for a further season; field releases were made in 1967.

Nematodes from *R. p. himalayensis* differed from the *Deladenus* sp. affecting *S. noctilio* in New Zealand (W. C. Clark, P. S. Dale, pers. comm.).

(v) *Rhyssa lineolata* (Kirby)

R. lineolata is established in several forests in New Zealand, but no specimens have yet been available for examination.

(vi) *Megarhyssa nortoni nortoni* (Cresson)

Consignments of this parasite introduced from North America were free of nematodes when imported; nothing is known about nematode infection in North American Siricidae and their parasites. In 1967, a small number of the adults was found to be infected by *Deladenus* species, but without any deterioration of their gonads. The parasites were bred on logs containing *S. noctilio* infected by *Deladenus*. This parasite has been liberated in several forests.

(vii) *Guiglia schauinslandi* (Ashmead) (Orussidae)

Guiglia is an endemic wood-borer parasite, which has included *Sirex* in its host range. It is not so frequently encountered as *I. leucospoides* and

R. p. persuasoria. It is primarily ectoparasitic, but is infrequently found feeding inside the host. Of the 73 adults obtained from *Deladenus* infected logs only two males were infected. Infective stage females were found in the haemocoel. No further investigations have yet been made.

(viii) Other Introduced Parasites

Rhyssa amoena Gravenhorst, *Megarhyssa emarginatoria* Thunberg have been introduced from Europe and *Megarhyssa praecellens* Tosquinet from Japan. The numbers imported were small and the prospects of breeding not promising.

R. amoena and *M. praecellens* were already infected by a *Deladenus* sp. and in the breeding of these species more stress is laid on obtaining a nematode-free stock.

Wood Dwellers Other Than Sirex Parasites

The most common wood-dwellers in dead pine trees, successfully attacked by *Sirex* and its fungal symbiont, are *Hexatricha pulverulenta* (Westwood), *Stenopotes pallidus* Pascoe, two *Hybolasius* spp. (Coleoptera: Cerambycidae); two Anthribidae (Coleoptera) and species of Mycetophilidae (Diptera) under the bark. *Hylastes ater* (Paykull) and *Pachycotes peregrinus* (Chapuis) (Coleoptera:Scolytidae) were less frequently encountered. All, except *P. peregrinus*, largely feed in or just under the bark.

None of these carried the *Sirex* infective *Deladenus* sp.. *H. pulverulenta* and *S. pallidus* carried nematodes under the elytra, *P. peregrinus* and *H. ater* contained several external and internal nematode species. No nematodes were observed in the other above-mentioned species. Samples of the insects found to be infected by nematodes were forwarded to Mr P. S. Dale for further study.

RELEVANCE OF *Deladenus* TO BIOLOGICAL CONTROL OF *Sirex noctilio*

The infection of *S. noctilio* by *Deladenus* has now been found in several forests in the North Island, but not in any forests in the South Island. A high percentage of nematode infection in emerging adult *Sirex* has been encountered in several areas.

The nematode infection, which results in a complete sterilisation of the adult woodwasps of either sex and death of larvae after being heavily infected, shows the nematode to be a potentially important factor in the control of this woodwasp. Parasitism by nematodes has sometimes been found to be higher than those of the combined efforts of the insect parasites *I. leucospoides* and *R. p. persuasoria*. That both parasites can develop in and on nematode-infected *Sirex* larvae makes it extremely difficult to apportion *Sirex* mortality between nematode and insect parasites. Although some of the parasites have been found to be infected by the nematodes, the incidence can be regarded as of little importance to parasite survival.

So far it is not known whether more than one species of *Deladenus* is involved in the *S. noctilio*-parasite complex in New Zealand.

Ovipositing adult *Sirex* females are apparently the major means of disseminating the nematode under natural conditions. Because *Sirex* females tend to oviposit close together and at different times, the transmission of the nematodes to the next generation is facilitated. The degree of infection of *Sirex* by the nematode obviously depends on the number of infected and uninfected *Sirex* ovipositing on one tree, the ability of the nematodes to move through the timber, multiply, produce the insect-infecting stage, and survival of the symbiotic fungus and progeny of the uninfected *Sirex*. It is not surprising that the intensity of infection may vary from tree to tree in the forest and even at different heights on a single tree.

A number of methods of establishing the nematodes in the field by natural and artificial means can be suggested. Several of these have been tried successfully in the laboratory and in 1967 a field trial was carried out. These trials will be reported in a future paper.

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