THE LIFE CYCLE OF THE FUNGAL SYMBIONT OF SIREX NOCTILIO †

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SYNOPSIS

Since the 1946–51 epiphytotic, much work has been done at the Forest Research Institute on various aspects of the pine wood wasp Sirex noctilio *and its symbiotic fungus,* Amylostereum *sp. What has been discovered, both overseas and in New Zealand, about the symbiotic association of this fungus with the larval, pupal, and adult stages of the insect, and about its effect on the tree (particularly* Pinus radiata) *is briefly described here. Although there are considerable gaps in our knowledge, a workable hypothesis has been put forward on the life-cycle of this fungus which can be used as a basis for further study.*

INTRODUCTION

The fact that a symbiotic association exists between certain basidiomycete fungi and various siricids is now well established. Büchner (1928 and 1930) was the first to find and describe the fungal carrying bodies, a pair of small invaginated intersegmental sacs in the female adults of *Sirex,* and he suggested the symbiotic association. Since that time various aspects of this association have been investigated by Cartwright (1929, 1938), Clark (1933), Müller (1934), Gilbert and Miller (1952), Orman (1958), Stillwell (1960) and particularly by Parkin (1942), Francke-Grosman (1938, 1939, 1957), Rawlings (1948, 1951, 1953, 1959, 1961), as well as Zondag, Osborn and Gilmour (unpublished).

In this account it is proposed to describe briefly the main features of the life-cycle of the fungal symbiont of *Sirex noctilio,* which are so important in the life of the insect and in causing a lethal wilt disease in pines.

The evidence so far suggests that this disease occurs through mass inoculation of tree trunks with a weakly parasitic fungus which the adult female wood wasp injects into oviposition tunnels with her eggs.

Observations in the field suggest that a previous reduction in tree vigour, brought about mainly by suppression and abnormal drought conditions, predisposes the trees to successful attack by the fungus. These debilitating factors also favour rapid increase of the *Sirex* population.

Sirex noctilio, which was introduced at the turn of the century along with its symbiotic fungus, is considered very much a secondary parasite in Europe, its place of origin. However, it approached primary status in New Zealand when, in 1946–1951, it reached epiphytotic proportions in large areas of overstocked pine stands affected by

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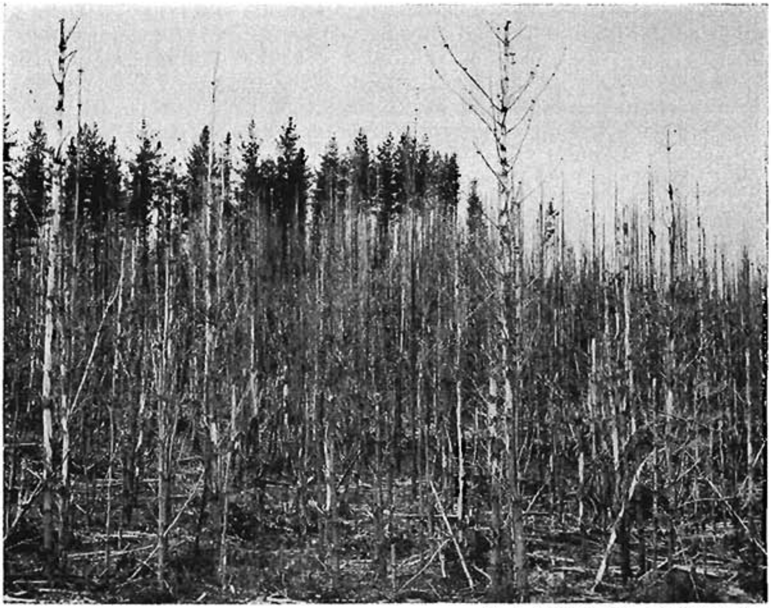

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Fig. 1: *Section of 23-year-old stand of* P. radiata *on site 1 showing in the foreground the dead trees left after logging (1953). The dead trees were killed by the* Sirex *fungus epiphytotic between 1946 and 1951, when the stocking was reduced from* ca. *600 to 130 trees per acre. Unlogged portion of stand in left background.*

the 1946 drought. It was estimated that, during this period, a quarter to one-third of the trees were killed throughout 300,000 acres of *Pinus radiata* in the central North Island. However, because mortality was mainly confined to malformed and suppressed trees, and because there was no immediate prospect of utilization, the sudden widespread mortality provided a beneficial thinning in these severely overstocked stands (Figs. 1 and 2).

With the return of normal wet summers, the incidence of this disease decreased, and at present, although some loss of valuable crop trees still occurs following thinning and pruning, the loss is not very great. This insect-fungal disease has been the most important, to date, in New Zealand forestry, and is still the greatest threat to the production of pine timber in New Zealand. It remains to be seen whether its parasites can keep the insect populations below a damaging level when conditions again become favourable for an epiphytotic outbreak.

IDENTITY OF THE FUNGUS

The fungus, which is a basidiomycete, may be classed as a weak facultative pathogen and wood rotter but, unlike most fungi, it is not known to produce a fruiting body in nature. Several attempts have been made in New Zealand and Australia to identify it from a few fruiting bodies artificially produced under laboratory conditions, but the lack of naturally produced fruiting bodies makes the taxonomist's task extremely difficult. Nevertheless, Talbot (1964), a fungal taxonomist at the Waite Agricultural Research Institute, and Boidin, a French taxonomist in this group of fungi, have tentatively identified it as a species of *Amylostereum* Boiden.

ADULT FEMALE — TREE STAGE

The only known means of dissemination of this fungus and infection of the host tree is inoculation by the wood wasp, and

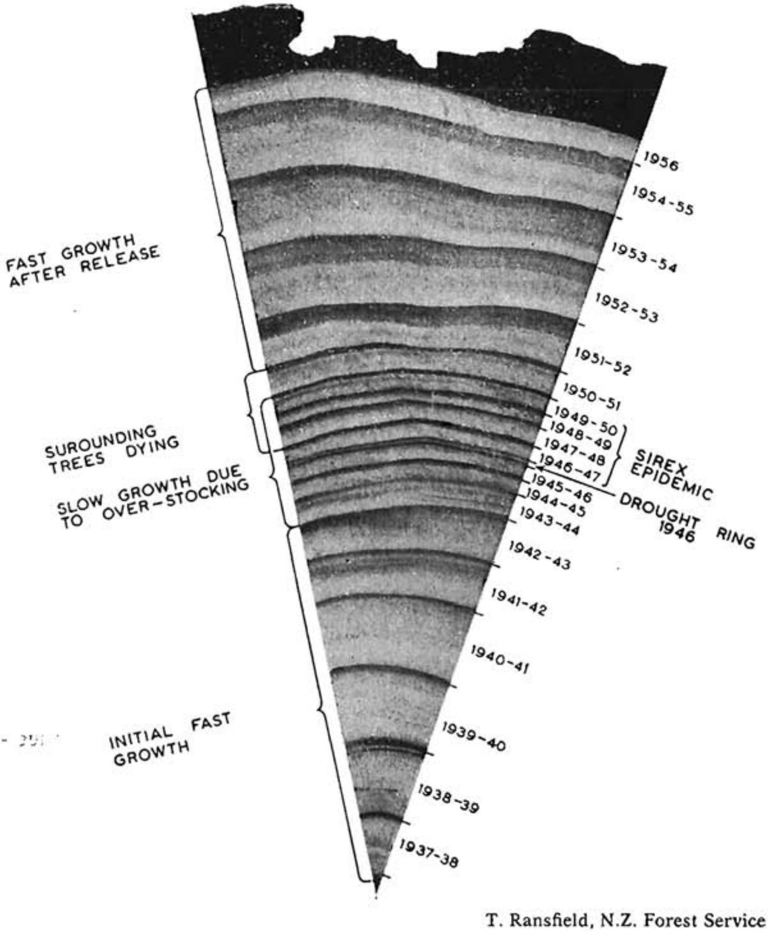

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Fig. 2: *Segment of a section at breast height of a dominant* P. radiata *(d.b.h. 17 in., age 23) showing response in diameter growth in stand thinned from* ca. *600 to 130 trees per acre by the* Sirex *fungus disease during the 1946–51 epiphytotic.*

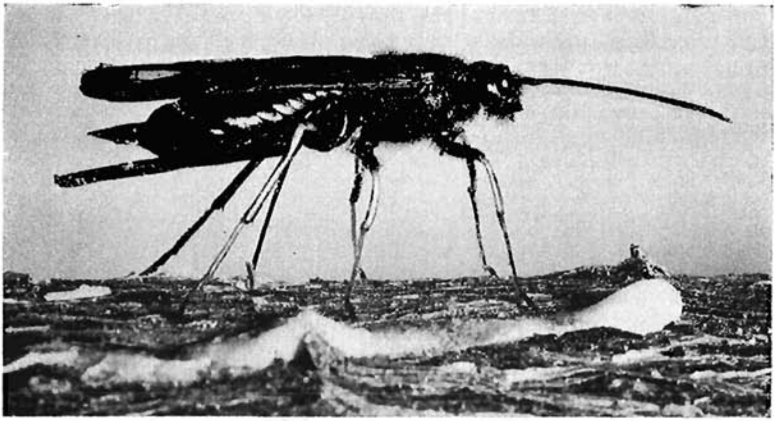

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Fig. 3: *Female* Sirex noctilio *in the act of boring an oviposition tunnel in a tree trunk. Her ovipositor is just forward of her hind pair of legs. In the foreground is shown a typical thin resin dribble from an oviposition puncture.* (× 2)

this takes place by design, not accident. At the base of the ovipositor of the adult female there are two internal sacs which contain small fragments of mycelium and oidia of the fungus (Fig. 6). Each sac is connected by a duct to the tube down which the egg passes during egg laying (Fig. 5). In this way each egg is inoculated with the fungus immediately before passing down the ovipositor into the tree. Before laying her eggs, the insect drills a hole about ⅓ to ¾ in. deep in a live tree trunk, and in the bottom of this she deposits her egg, together with a small amount of fungal inoculum (Figs. 3 and 4). Sometimes she deposits the fungus in the tree without the egg. Now, if the fungus can kill the tree or part of the tree, the development of the larval stage from the egg is assured, but if the tree resists the fungal attack, then the larva will not develop. Some trees appear to resist the attack of the fungus by secreting resins and other substances into and around the oviposition tunnel. The factors which govern this response of some trees to infection are still not very clear, but the response seems to be correlated with moisture conditions within the wood and with the number of infection points per unit area. The insect has been observed to carry out what appears to be a random test-boring operation of a number of trees in a stand until she finds a tree that, for reasons best known to herself, is more to her liking. On this tree she will stay and continue to oviposit. Resin exudes from many of these punctures and runs down the trunk in a characteristic thin dribble (Fig. 3). The "chosen" tree then suffers mass infection from this female and from others that appear to be attracted to it by some unknown factor.

If inoculation is heavy enough, and if sufficient adjacent small areas of wood and cambium have been killed and invaded by the fungus to girdle one section of the trunk, then the whole tree will die; otherwise only part of the trunk may be killed or only severe loss of growth may result. The fungus, having killed part or all of the tree, then proceeds to decay the wood, causing a firm white mottled rot; the wood shows little sign of physical change although mechanically it is very brittle (Fig. 4). It is in this decaying wood that the *Sirex* larvae develop. In a "resistant" tree a ring of traumatic tissue is formed which constitutes a line of weakness in the timber.

THE TREE — LARVAL STAGE

The larvae cannot feed on sound wood, but must feed on wood partly decayed by their "own" fungus. It is in this respect that the insect is dependent on the fungus. In the artificial breeding of *Sirex* larvae for parasite establishment, Rawlings (1953) found this to be the most critical factor — *i.e.*, to make sure that the females reared in test tubes carried the fungus so that the larvae developing from their eggs would have the correct diet in the breeding logs in the insectaries.

Not only the female adults, but also the female larvae, possess special fungus-carrying organs. The males, both larvae and adults, have none. In the female larvae these organs (called hypopleural organs in siricids) are situated externally, one on each side of the body, between the first and second abdominal segments; they consist of pockets formed from folds in the skin (Fig. 7). The pockets are filled with short mycelial threads, formed into coils with some protein-like substance, and surrounded by a protective coating of

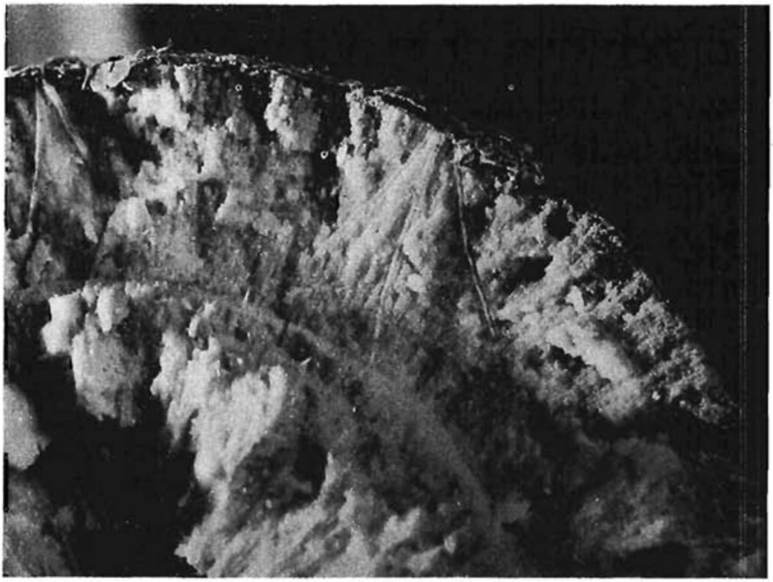

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Fig. 4: *Part of a broken section of a small stem of* P. radiata *showing two puncture sites with three oviposition tunnels (centre) and two oviposition tunnels (extreme left). Tunnels approximately ½ to ¾ in. deep.* (× 2)

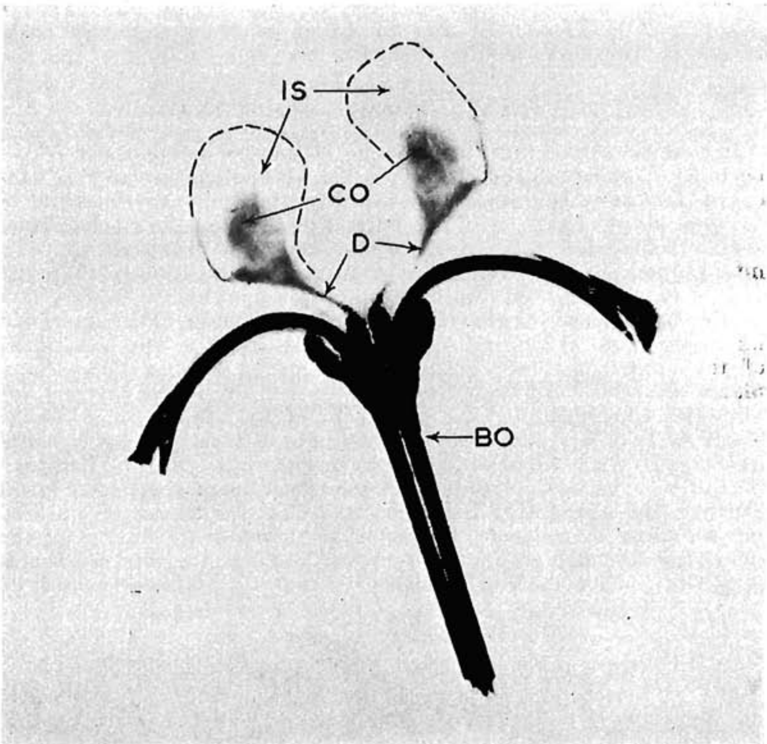

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Fig. 5: *Basal part of ovipositor dissected from* Sirex noctilio, *showing I S, intersegmental sacs (partly dotted in) in which the fungus is carried; C O, the colbin organ (secretory glands); D, connecting duct to genital opening down which the fungal filaments travel; and B O, basal part of the ovipositor, down the centre of which passes the egg together with the fungus.* (× *10*)

wax-like material (Fig. 8). The function of this hypopleural organ has not been definitely determined, but it would appear to be an organ of fungal conservation. The resistant waxy material covering the fungal coils within the pockets apparently ensures viability of the mycelium throughout the larval stages. This is important, for it would appear that it is by means of these hyphal coils that the intersegmental sacs in the adult female become inoculated, just before the insect emerges from the tree. Thus, even if the fungus dies in the wood on account of desiccation before pupation is complete, the fungus inoculum is not lost. Just how and when inoculation of the hypopleural organs in the larvae occurs is not known, although these organs are present in both early- and late-stage larvae. The organs grow with the larvae, probably by the pockets becoming larger and more numerous as the larvae develop. The number and size of the pockets is apparently characteristic for each species of siricid, and Parkin (1942) has suggested that this character, combined with the ratio of length to breadth of the entire organ in the late-stage larvae, may be useful for identification purposes. Also, of course, since the organ is absent from the male larvae its presence readily identifies the female of the species.

THE LARVAL — PUPAL — ADULT STAGE

It is very curious that, in the pupal stage, the hypopleural organ becomes evaginated and the pupae do not appear to possess any organ to carry the fungus. According to Francke-Grosmann, a German entomologist, it is not until after the pupal skin has been shed and the adult begins to bore her way out of the wood that the intersegmental sacs become inoculated. She postulates that the "wax plates" containing the fungus become loosened in the pockets of the hypopleural organ in the last larval stage. The shrivelled larval skin and the pupal skin remain attached to the ovipositor of the adult up to the time of emergence, so that these "wax plates" become completely freed and broken up by the involuntary pounding movements of the ovipositor of the adult female as she starts to bore her way out. It is thought that at this time some particles of the wax plates come in contact with the working ovipositor and, because of their sticky surface, become attached to it. Further, the alternating movements of the two halves of the ovipositor cause the adhering wax scales to travel up the outside of the ovipositor, through the genital opening, and into the intersegmental sacs. Once inside the sacs, which presumably contain a favourable

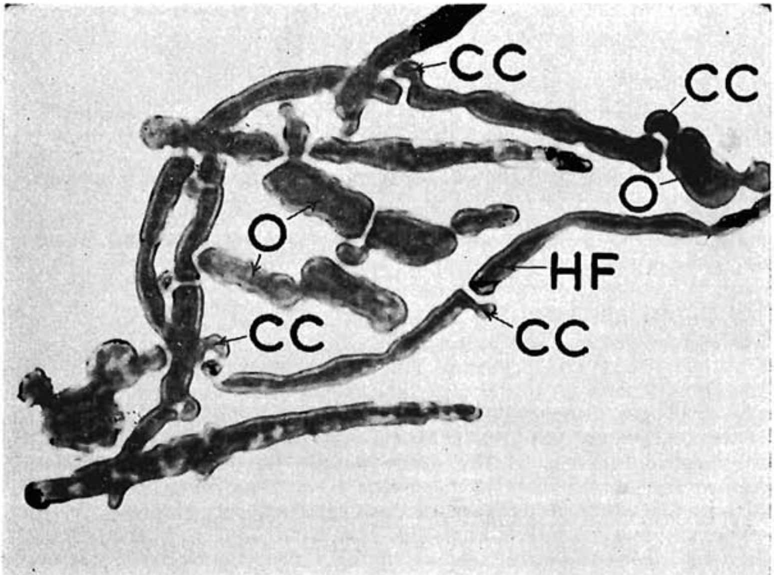

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Fig. 6: *High-power photomicrograph of germinating oidia (O) and hyphal filaments (H F) of the* Sirex *symbiotic fungus, taken from the intersegmental sacs of the adult female insect. Note the conspicuous clamped cross wall (C.C.). (× 1,000)*

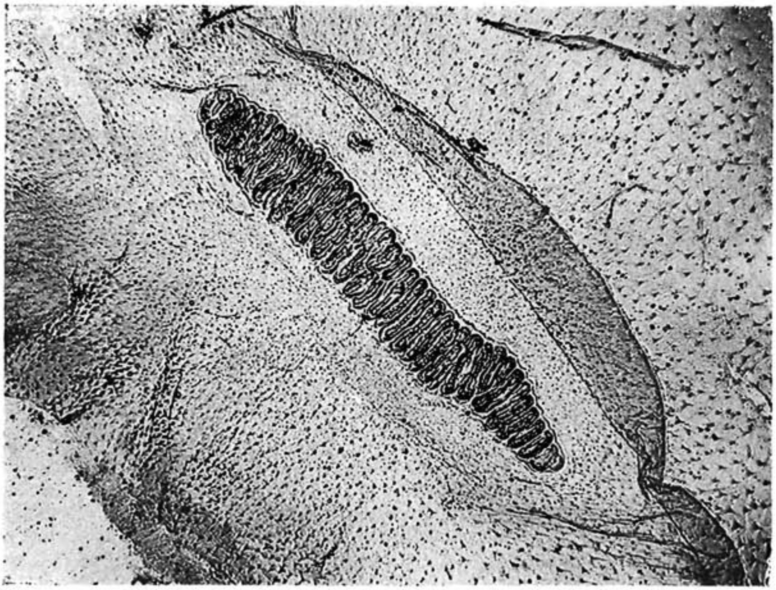

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Fig. 7: *Surface view of the hypopleural organ (still attached to the skin) of* Sirex noctilio, *showing large pockets extending full width of organ, each of which is occupied by a coil of fungal filaments coated with a protective wax-like substance.* (× *50*)

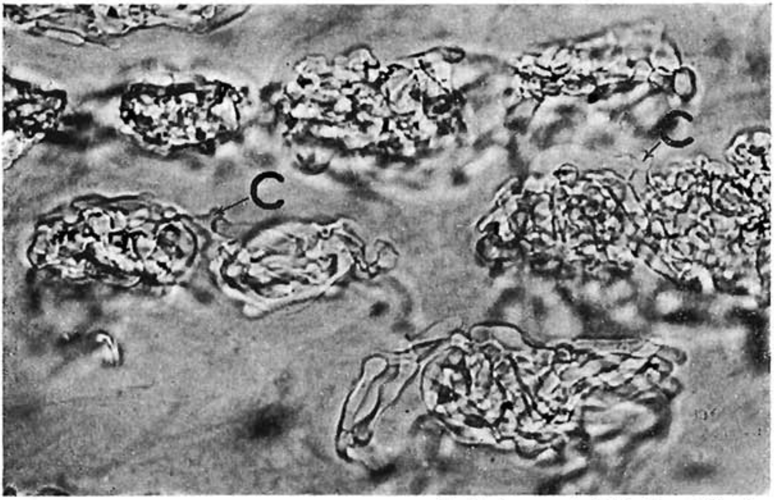

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Fig. 8: *High-power photomicrograph of the coils of hyphae within the pockets of the hypopleural organ of* ?Urocerus xanthus, *ex Pakistan, showing clamped cross walls (C).* (× *750*)

growing medium secreted by the insect, the fungus grows out from the broken wax plates and proliferates, forming a mass of short hyphal filaments and oidia. At emergence the sacs are fully packed with these oidia and hyphal filaments, ready to be injected into a living tree.

If the wood dries out to a stage at which fungal development in the wood is arrested, then larval development is also arrested. If this occurs at an early stage in the life of the larvae, the larvae will pupate and then small adults only will emerge. Nevertheless, even these premature adults will be inoculated with the fungus because of the viable inoculum that has been conserved in the hypopleural organs of the female larvae.

RECAPITULATION

The complicated life-cycle of the *Sirex* fungus starts with the oidia in the intersegmental sacs of the adult female, who injects them into live trees when she lays her eggs. If the tree is susceptible to infection, the fungus will attack and kill it. After the death of all or part of the tree, the fungus, acting as a saprophyte, proceeds to decay the wood to a limited extent. In this partly decayed wood, the larvae of the insect develop and at an early stage the female larvae become inoculated with the fungus, which they carry in special organs, called hypopleural organs, outside their bodies. At metamorphosis, the fungus is apparently transferred from the hypopleural organs into the intersegmental sacs within the body of the adult female, and by the time she emerges from the tree the fungus has proliferated in the intersegmental sacs and is again ready to be inoculated into a living tree. During its life-cycle the *Sirex* fungus has thrived on the diet of wood in the tree, and of insect "juices" both in the hypopleural organs of the larvae and in the intersegmental sacs of the female adult.

This, in broad outline, is the picture, but much painstaking work remains to be carried out, especially on the insect-fungus-tree relationships, before all the details can be authoritatively filled in.

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