A review of the genus *Amylostereum* and its association with woodwasps

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A fascinating symbiosis exists between the fungi, *Amylostereum chailletii, A. areolatum* and *A. laevigatum,* and various species of siricid woodwasps. These intrinsic symbioses and their importance to forestry have stimulated much research in the past. The fungi have, however, often been confused or misidentified. Similarly, the phylogenetic relationships of the *Amylostereum* species with each other, as well as with other Basidiomycetes, have long been unclear. Recent studies based on molecular data have given new insight into the taxonomy and phylogeny of the genus *Amylostereum*. Molecular sequence data show that *A. areolatum* is most distantly related to other *Amylostereum* species. Among the three other known *Amylostereum* species, *A. laevigatum* and *A. ferreum* are most closely related. Sequence data have also made it possible to develop PCR restriction fragment length polymorphism (RFLP) fingerprints to delineate *Amylostereum* species, which presents a solution to the difficulties that are generally experienced when identifying these fungi using traditional methods. Furthermore, sequence data suggest that there is an evolutionary relationship between divergent groups of hymenomycetes such as *Amylostereum* species and *Echinodontium* species, as well as with *Russula* species, *Heterobasidion* species and *Peniophora* species. Recent studies that investigated the population structure of *A. areolatum* and *A. chailletii* have also substantially increased our understanding of the ecology of these species that are associated with woodwasps. Clonal lineages have been shown to occur in both *A. areolatum* and *A. chailletii*. These genetic lines, that arise as a result of the association with woodwasps, are distributed over large distances and are preserved in time. This character of the populations now presents an opportunity to trace the geographical origin of these fungi and their associated wasps as they spread across the world. The occurrence of heterogenic sequences in the nuc-IGS-rDNA region of isolates of *A. areolatum* also gives insight into the structure and relationship among populations of this fungus that are isolated as a result of its association with different woodwasp species. We review these recent developments and opportunities for future research.

Introduction

Amylostereum represents a fascinating genus of Basidiomycetes, of which three species live in a symbiosis with siricid woodwasps. Internal glands that contained fungal oidia in some woodwasp species were first reported in the 1920s.[1–3] The presence of clamp connections suggested that these fungi belonged to the Basidiomycetes, but their identities were uncertain. Subsequently, these fungi were identified as *Stereum sanguinolentum, S. chailletii,* a species of *Stereum,* and a species of *Peniophora,* among others.[4] Eventually, it was conclusively shown that these fungi should reside in the genus *Amylostereum.*[5–7] Today *A. chailletii, A. areolatum* and *A. laevigatum* are known to be symbionts of a variety of woodwasp species.[7–9]

The relationship between *Amylostereum* species and woodwasps is highly evolved and has been shown to be obligatory species-specific.[7–10] The principal advantage of the relationship for the fungus is that it is spread and effectively inoculated into new wood, during wasp oviposition.[11,12] In turn the fungus rots and dries the wood, providing a suitable environment, nutrients and enzymes that are important for the survival and development of the insect larvae (Fig. 1).[13–17]

The burrowing activity of the siricid larvae and rotting of the wood by *Amylostereum* species makes this insect–fungus symbiosis potentially harmful to host trees, which include important commercial softwood species. In the northern hemisphere, where the Siricidae are native, the insect is of little economic importance.[18–20] Here a natural balance exists between the insect–fungus complex, its natural parasites and host trees. In contrast, *Sirex noctilio* and *A. areolatum,* that have been introduced into various countries of the southern hemisphere, have caused extensive mortality in exotic pine plantations (Fig. 2).[21–25] Biological controls that use parasitic nematodes and wasps have been in place for three decades.[21–26] Despite the costly efforts to monitor and control the wasp and fungus, the pest complex continues to kill significant numbers of trees and spread to previously unaffected areas in Australia, South Africa and South America.

The association between woodwasps and *Amylostereum* and their combined importance to forestry in the southern hemisphere has stimulated much research in this field. This work has been reviewed in the past[4,5,17,23,26–28] and details will not be repeated here. However, much of this research has concentrated on the woodwasps, and especially their control, in the southern hemisphere. Recent studies on the fungal symbionts of Siricidae have provided new insight into the taxonomy, phylogeny and ecology of these fungi. The aim of this review is, therefore, to provide a contemporary view of *Amylostereum* and its symbiosis with woodwasps. Together with the reviews mentioned above, this paper provides a more complete picture of the current knowledge of this pest complex, which is important for the continued efforts to control it. Questions of both practical and academic interest that have newly arisen or have remained unanswered are also discussed.

Taxonomy and phylogeny

Amylostereum species

The genus *Amylostereum* was established in 1958 by Boidin to accommodate species of *Stereum* that have, among other characteristics, smooth amyloid basidiospores, hyaline-encrusted cystidia, and resupinate to effuso-reflexed fruiting bodies.[29] The genus then included *A. chailletii* (Pers.:Fr.) Boid., the type species, *A. areolatum* (Fr.) Boid. and *A. laevigatum* (Fr.) Boid. Boidin and Lanquetin[30] added a fourth species, *A. ferreum* (Berk. & Curt.) Boid. & Lanq. (= *Stereum ferreum*), to the genus.

In a recent review, Thomsen[4] noted that many misidentifications of isolates of *Amylostereum,* especially the species associated with

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woodwasps, were made in the past. This can, in most cases, be ascribed to the rarity or absence of the sporocarps of these fungi and the fact that the sporocarps of *A. chailletii* and *A. areolatum* are very similar and thus confusing.[31] Careful examination, however, showed that spore size and the colour and texture of the sporocarps can be used to distinguish these species.[31] The symbionts of woodwasps often have to be studied entirely in culture or from the mycangia of the wasps, where *A. chailletii* and *A. areolatum* are morphologically similar. These species can nevertheless be distinguished because only *A. areolatum* forms arthrospores in culture.[7,30,31] *Amylostereum laevigatum* and *A. ferreum* cause less confusion. Unlike the other species, *A. laevigatum* has a monomytic hyphal system, whereas *A. ferreum* has been isolated only from *Podocarpus* in Brazil and is not associated with woodwasps.[30,32]

Although it is possible to distinguish the species of *Amylostereum* morphologically,[30,31] the many misidentifications in the past show that the small differences that delineate species such as *A. chailletii* and *A. areolatum* still present difficulties for inexperienced researchers. Another method that successfully distinguishes the species of *Amylostereum* is polymerase chain reaction restriction fragment length polymorphism (PCR-RFLP) fingerprinting of the nuc-IGS-rDNA region.[33] This method has the potential to serve as a quick, yet precise, identification tool to distinguish morphologically similar fungal species in culture, as has been shown for other Basidiomycetes fungi.[34]

Boidin and Lanquetin[30] used mating studies and the Buller phenomenon[35] to evaluate the phylogenetic relationships among the *Amylostereum* species. The results from this study showed an unusual triangular mating system. *Amylostereum chailletii* and *A. laevigatum* were completely incompatible, but both species were partially compatible with *A. ferreum. Amylostereum areolatum* was not compatible with any of these species.

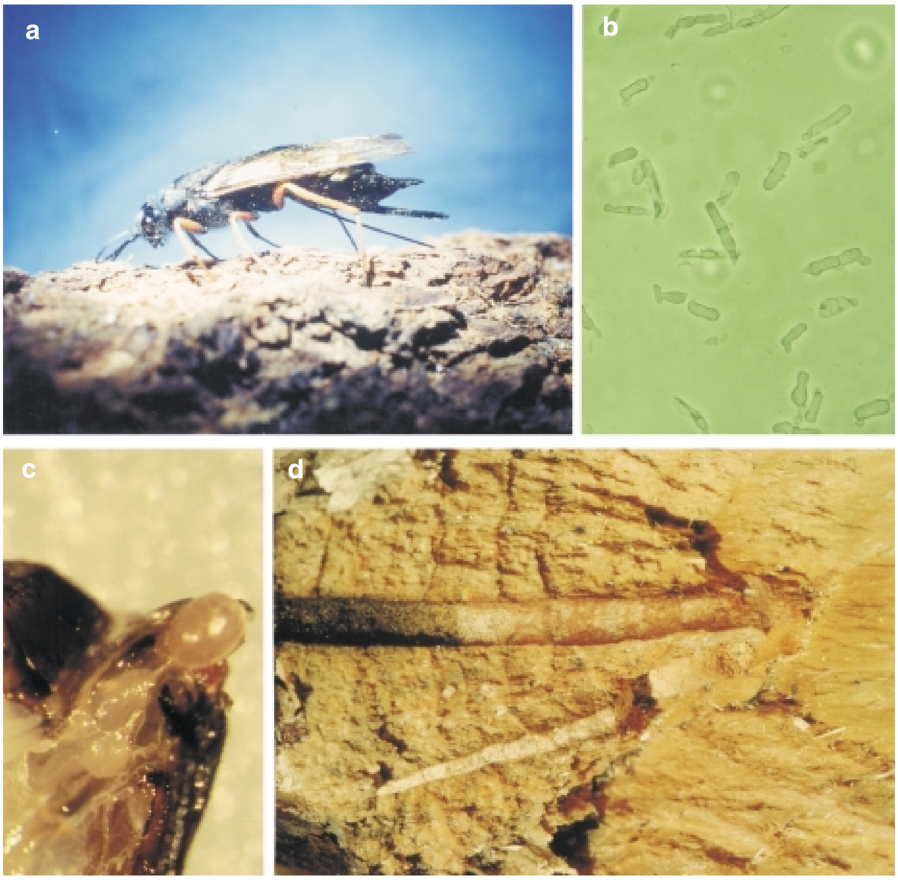

Fig. 1. The symbiosis of the woodwasp, *Sirex noctilio,* and Basidiomycete fungus, *Amylostereum areolatum.* The adult female wasp (**a**) carries the fungal arthospores (oidia) (**b**), which are asexually produced, in internal mycangia (**c**) near the base of the ovipositor. The longest part of the life cycle of the wasp is spent inside the host tree, where the larvae burrow through the wood, which is being decayed (white rot) by the symbiotic fungus, and pupates just under the bark (**d**).

Fig. 2. Signs and damage of *Sirex* attack in pine trees in South Africa. In spring and early summer, emerging female wasps lay hundreds of eggs, fungal spores and phytotoxic mucus in the phloem of suitable trees, producing resin flow from oviposition drills (**a**). The needles of heavily attacked trees will turn reddish brown within months of attack (**b**) and the tree might die soon afterwards. The wasps emerge after one to three years, leaving characteristic round exit holes of approximately 0.5–1 cm in diameter (**c**).

The conclusion was that *A. areolatum,* which is morphologically close to *A. chailletii,* must have diverged earlier. Furthermore, these results showed that the other three species were more closely related, although their specific relationships to each other were not clearly defined. Following these observations, Boidin and Lanquetin[30] concluded that a more complete study, including a wider range of isolates that were associated with gymnosperms, would provide a more lucid view of the speciation process in lignicolous fungi.

Sequence data from the nuc-ITS and nuc-IGS rDNA, mt-SSU-rDNA regions and partial manganese-dependent peroxidase gene support previous hypotheses regarding the phylogeny of *Amylostereum* species, but also give new insight into previously unclear relationships.[33,36–38] All these studies support the hypothesis[30] that *A. areolatum* is the most clearly defined species, which also has diverged earlier than the rest. The three remaining species form a sister group of *A. areolatum.* Of the species in this sister group, *A. laevigatum* and *A. ferreum* are the most closely related. In the light of these findings, it is interesting to recall that sexual mating was partially compatible more often (60%) between *A. ferreum* and *A. laevigatum* than between *A. chailletii* and *A. ferreum* (44%).[30]

For many years, only *A. chailletii* and *A. areolatum* were known to be involved in symbioses with woodwasps.[7,10] It is only recently that Tabata and Abe[8,9] showed that *A. laevigatum* is the symbiont of *Urocerus japonicus* and *U. antennatus* in Japan. Isolates of *A. laevigatum* from Japan and Europe, however, group in two distinct clades based on ITS-rDNA and Mn-dependent peroxidase gene sequence data.[38] Some isolates from Europe also fall into both groups. It has been proposed that isolates of *A. laevigatum* from *Juniperus* and *Taxus* in Europe might be distinct taxa (Eriksson and Ryvarden, 1973, cited in Vasiliauskas *et al.*,[36] and Tabata *et al.*[38]).

The wasp *S. areolatus* is believed to carry *A. chailletii.*[7] An isolate from the mycangia of *S. areolatus* has, however, been shown to be more closely related to the *A. laevigatum* and *A. ferreum* group than to *A. chailletii.*[33,37,38] The isolate is most closely related to *A. laevigatum* based on these data, but it is clearly distinct from it and might represent a new species or alternatively a sub-group of *A. laevigatum.* This finding is important, as *A. laevigatum* has never been implicated in symbioses with *Sirex* species in North America or Europe. There is clearly a need to study the relationships amongst different groups within *A. laevigatum* and its association with different wasp genera and species.

Amylostereum areolatum is carried by various wasp species.[7] The association with different wasps and predominance of asexual reproduction separates populations of this fungus genetically. The occurrence and combination of heterogenic sequences of the nuc-IGS-rDNA region in isolates of *A. areolatum* makes it possible to determine the relationship between such separated populations of the fungus.[33] At least four such heterogenic sequences of the nuc-IGS-rDNA region have been shown to occur in five different patterns (three combinations of two haplotypes each and two patterns containing only one haplotype) in isolates of *A. areolatum.*[33] A preliminary study using these data showed that isolates of *A. areolatum* associated with *S. noctilio* and *S. juvencus* did not, however, form two distinct genetic groups.[33] These populations shared rather some of the heterogenic sequences.

Relatedness to other Basidiomycetes

The relationship of *Amylostereum* to other Basidiomycetes has been uncertain when only morphological data were used for comparison. Before Boidin[29] described the genus *Amylostereum,* species resided in *Stereum,* as *S. chailletii, S. areolatum, S. juniperi* and *S. ferreum. Amylostereum laevigatum* was, however, better known as *Peniophora laevigata.* This classification and the general macro-morphological similarities between some *Amylostereum* species and species of *Stereum* (for example, *A. chailletii* and *S. sanguinolentum*), supported the view that *Amylostereum* belongs to the family Stereaceae.[39,40] Boidin and Lanquetin,[30] however, argue that, based on the presence of gloeocystidia that react positively in sulphuric-aldehyde, normal nuclear behaviour and a tetrapolar mating system in all four *Amylostereum* species, makes this genus more closely related to *Peniophora* than to the family Stereaceae. Parmasto,[41] using 86 morphological and physiological characters in a cladistic study of the genera of Corticoid fungi, found that *A. chailletii* forms a sister group of *Stereum* and *Xylobolus,* while this clade groups basal to *Peniophora.*

In a study including 89 Basidiomycetes species, Hibbett *et al.*[42] showed that morphological characters can be misleading and that molecular data might provide a more lucid view of the true phylogeny of these fungi. From this study it became clear, for example, that a major character, such as gills in a mushroom, might have evolved up to six times. Phylogenetic studies have, however, also produced conflicting views regarding *Amylostereum* species. In a study using mt-SSU-rDNA sequence data of a number of Basidiomycetes fungi, Hsiau[43] found that *A. chailletii* grouped more closely to *Stereum* than to *Peniophora.* By contrast, Hallenberg and Parmasto,[44] using a combination of LSU-rDNA and morphological characteristics, provided convincing evidence that *Amylostereum* forms a sister clade of *Peniophora* and not *Stereum.* However, when *Amylostereum* species were included in the extended databases of ITS and mt-SSU-rDNA sequence data sets, these species grouped with neither *Stereum* nor *Peniophora,* but strongly with the wood-decay fungus *Echinodontium tinctorium*[37,45] Tabata *et al.*[38] showed that members of the genus *Echinodontium* are paraphyletic, and that some species, for example, *E. tinctorium, E. tsugicola* and *E. japonicum,* are more closely related to *Amylostereum* than to *Stereum* species.

Various studies[37,42,43] support the view that there is a close relationship between *Amylostereum, Echinodontium, Russula* and *Heterobasidion.* Hsiau[43] showed that *R. compacta* and *Heterobasidion annosum* group together and close to *A. chailletii.* Hibbett *et al.*[42] grouped *Russula compacta* and *E. tinctorium* together and this clade more closely to *Peniophora* than to *Stereum.* Slippers *et al.*[37] grouped *R. compacta* and *Heterobasidion annosum* together and more closely to the *Amylostereum*/*Echinodontium* group than to *Stereum* and *Peniophora.* ITS-rDNA data, however, indicate that *Amylostereum* and the *Echinodontium* form a sister group of the family Gleocystidiellaceae, and show that it is also closely related to the Bondarzewiaceae (including *Heterobasidion*).[45] This latter study does not support the relationship of *Russula* and *Peniophora* to the other genera mentioned.

Boidin[45] erected a new monotypic family for *Amylostereum,* namely Amylostereaceae. Despite obvious macro-morphological differences between the *Amylostereum* species and *Echinodontium* species, all these species have amyloid basidiospores and thick-walled, heavily encrusted cystidia.[29,39,40,46,47] In these studies, including the initial description, these characters were considered important in distinguishing both groups. The consistent association between *Amylostereum* and *Echinodontium* based on sequence data from three gene regions[37,38,45] together with the micro-morphological evidence, strongly support the view that both genera should be accommodated in the family Echinodontiaceae as described by Donk[39,46] and Gross.[40]

Population structure and spread

Amylostereum species are heterothallic and have a tetrapolar nuclear state.[30] The heterokaryotic isolates that are thus derived from the pairing of primary mycelia arising from basidiospores, will give rise to genetically different entities. The *Amylostereum* species are, however, also spread by woodwasps in the form of asexually produced oidia (thus genetically identical) in a very strict symbiosis.[10]

In the northern hemisphere, it has been shown that, as a result of the spread of oidia of *A. areolatum* and *A. chailletii* by woodwasps, clonal lines of these fungi are conserved and are spread over large areas.[48–50] These studies also showed that the presence of clones was common among isolates of *A. areolatum,* but more rare among isolates of *A. chailletii.* It can be concluded from these studies that *A. areolatum* is predominantly spread by woodwasps with which it is associated, whereas *A. chailletii* is regularly spread both via basidiospores and by woodwasps. This is in accordance with the fact that the sporocarps of *A. areolatum* are much less common than those of *A. chailletii.*[31]

Amylostereum areolatum was introduced, together with *S. noctilio,* into various pine growing regions of the southern hemisphere during the twentieth century. It was reported in New Zealand around 1900, in Tasmania in the early 1950s, on mainland Australia in 1961, in South America in the 1980s and in South Africa in 1994.[21,23,51–53] Large vegetative compatibility groups (VCGs) have been shown to occur in isolates of *A. areolatum* associated with *S. noctilio* in the southern hemisphere.[54] Isolates from South Africa, Brazil and Uruguay represent the same VCG. Partial vegetative compatibility was also observed between isolates representing this VCG and isolates from New Zealand and Tasmania. This suggests that the spread of *Sirex* through the southern hemisphere during this century has taken place across the continents and countries of the southern hemisphere, rather than the result of introductions from the northern hemisphere. The clonal nature of populations of *A. areolatum* in the southern hemisphere further indicates that the fungus mainly spreads asexually, through its association with *S. noctilio* in this region. This is also confirmed by the fact that sporocarps of *A. areolatum* have never been found in the southern hemisphere.

Vegetative compatibility groups do not necessarily constitute clonality.[55] Vasiliauskas *et al.*[49] have, however, shown that VCGs of *A. areolatum* found in northern Europe represent clonal lines. Molecular markers, such as those that have been used in the northern hemisphere,[49] must be applied to studies of the population structure of *A. areolatum* from the southern hemisphere, in order to establish the true genetic structure of these isolates.

The nematode, *Deladenus siricidicola* (= *Beddingia siricidicola*), sterilizes female *S. noctilio* wasps during a parasitic phase of its life cycle.[26] This nematode is used extensively in biological control programmes in the southern hemisphere.[26] For this purpose the mycetophagous phase of the life cycle of the nematode, during which it feeds on *A. areolatum,* is used to mass-rear the nematode. Isolates of *A. areolatum* that are used to rear *D. siricidicola* have, however, been shown to be genetically distinct from other field isolates from South Africa, Brazil, New Zealand and Tasmania.[54] This nematode has been imported and released in both South Africa and Brazil as part of a biological control initiative against *S. noctilio.* A different genetic entity of the fungus has thus been introduced into these countries along with *D. siricidicola.* This introduction has the potential to influence the population structure of *A. areolatum* in these countries. The efficacy of *D. siricidicola* as a biocontrol agent might also be negatively influenced by a strain of the fungus in South Africa and Brazil, that is different from the one on which it was reared.[54] This might be a contributing factor to the lower than expected infection levels of wasps by the nematode during early parts of the biocontrol programmes.

The predominance of asexual reproduction and spread of *A. areolatum* in its symbiosis with woodwasps has led to the preservation of heterogenic sequences of the nuc-IGS-rDNA region in this fungus, as discussed earlier.[33] The distribution of such heterogenic sequences among isolates of the fungus can be useful in characterizing populations of the fungus. Isolates from the southern hemisphere, for example, share the same combination of these sequences.[33] This supports the hypothesis, based on VCG studies,[54] that the isolates from different regions in the southern hemisphere are genetically related.

Conclusions

Molecular techniques, particularly those based on DNA sequencing, have only recently been applied to questions pertaining to *Amylostereum.* These have clarified previous hypotheses that were based on morphological and mating studies, regarding the relationships among *Amylostereum* species. They have also raised new and challenging questions, for example the identity of the fungal isolates associated with woodwasps such as *S. areolatus.* Furthermore, these techniques can now be used to determine other phylogenetic relationships, such as the one between the two types of *A. laevigatum* thought to exist on different hosts in Europe and Japan.

PCR-RFLP fingerprinting successfully differentiates the various *Amylostereum* species. This technique provides a useful tool to overcome difficulties in identifying in culture the morphologically similar *Amylostereum* symbionts of woodwasps.

There is a phylogenetic relationship between *Amylostereum* species and *Echinodontium* species that was not recognized using traditional methods. These conclusions indicate that both genera belong to the family Echinodontiaceae. There are also indications of a phylogenetic relationship with other Basidiomycetes such as members of the family Gleocistideaceae, as well as *Russula, Heterobasidion, Peniophora* and *Stereum.* Further studies that include all the relevant taxa are needed to resolve the exact evolutionary relationships among these morphologically disparate fungi. These studies should include DNA sequence data from the different DNA regions that have thus far been used in isolation, as well as morphological, physiological and ecological information.

Extensive clonal lineages exist among isolates of *A. areolatum* and *A. chailletii* that are associated with siricid woodwasps. A study of the population structure of these fungi from many parts of the world, using both VCGs and molecular markers, will give insight into the geographical origin and spread of these fungi, as well as their associated siricid wasps. Such data have already identified patterns of spread amongst countries in the southern hemisphere and between local populations in northern Europe. The northern hemisphere origins of southern hemisphere populations of *Sirex* and *Amylostereum* are, however, not known. This information is potentially valuable for expanding biological control programmes. Knowledge of local populations of *Amylostereum* is important for the rearing and release of the biological control nematode, *D. siricidicola.*

Heterogenic sequences in the nuc-IGS-rDNA region of isolates of *A. areolatum* make it possible to compare and characterize populations of these fungi that are associated with different wasp species. The occurrence and specific combinations of these sequences provide insight into both the geographical distribution and evolutionary relationships of populations and species of *Amylostereum*. A combination of these IGS sequence data with those from more conserved DNA regions, such as mt- and nuc-SSU, in comparison with phylogenetic information on the wasp, will show how the symbiosis between the fungal and insect groups developed. The IGS sequence data, combined with other variable molecular markers, will increase understanding of recent changes in genetic structure and the importance of sexual versus asexual dispersal in the current fungal populations.

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