

= Amylostereum =

Amylostereum is the single genus in the fungal family Amylostereaceae . The genus currently comprises four saprotrophic and parasitic species , which live off living or dead wood . The Amylostereaceae cause white rot in the wood by disintegrating the tissue component lignin . They produce crust @-@ like , partially wavy fruit bodies on the surface of infested trees , which are similar to those produced by Stereum species .

There are four described species in the Amylostereaceae : *A. chailletii* ( the type ) , *A. areolatum* , *A. ferreum* and *A. laevigatum* . The species were initially considered part of Stereum until mycologist Jacques Boidin found atypical microscopic differences between them . Forty years after his extensive researches from 1958 , Boidin reclassified Amylostereum into its own family .

Three Amylostereum species are symbionts of wood wasps in the genera *Sirex* , *Urocerus* , and *Xoanon* , which infest conifers . The female wood wasps deposit their eggs together with fungal spores and mucus in trees , and the fungus is eaten by the wasp 's larva as food . The fungus propagates vegetatively through the formation of asexual spores in newly emerged females that are stored in special structures adapted for the transport of symbiotic fungi . The *A. areolatum* ? *Sirex* woodwasp ( *S. noctilio* ) symbiont complex has been studied extensively because of its potential to cause substantial economic losses in the forestry industry , particularly in non @-@ native regions .

= Taxonomy and history of research =

Amylostereaceae species were for a long time classified in the genus Stereum , based primary on the layered structure of the fruit body and the similar physiological activity . Mycologist Jacques Boidin separated Amylostereum from Stereum in 1958 , justifying this decision by explaining that microscopic differences such as amyloid spores and encrusted cystidia were sufficiently distinct to warrant recognition as a new genus . Although the type species of the genus ( today called *A. chailletii* ) was initially named *Trichocarpus ambiguus* , the name *Trichocarpus* had already been used for a genus in the flowering plant family Malvaceae . Boidin thus chose the genus name Amylostereum , referring to the amyloid spores .

Based on DNA analysis , Boidin in 1998 moved Amylostereum into a new , monotypic family , the Amylostereaceae , which he attributed to the Hericiales order . Later studies , however , supported the initial classification in the Russulales .

= = Classification = = =

The classification of the Amylostereaceae is not completely resolved . The next closest relatives might be ? depending on the research ? either *Echinodontium tinctorium* and most other species of the genus *Echinodontium* , or *Artomyces pyxidatus* . Most of the previous DNA analysis results suggest a narrow relation to *Echinodontium* , but several results of studies partially contradict this conclusion . Only the classification to the Russulales is regarded as correct . Some authors have suggested that Amylostereum should be placed in the family Echinodontiaceae .

The similarities between *A. chailletii* and *A. areolatum* have caused some confusion regarding their placement in the genus . As only the size of their fruit bodies differ from each other in appearance , researcher German Josef Krieglsteiner assumed that both are the same species in different age stages . Experiments with pure cultures of the fungi , however , showed that the mycelia of *A. chailletii* , *A. laevigatum* and *A. ferreum* were partially compatible to each other , but the mycelium of *A. areolatum* was incompatible to other species . Boidin believes that the common ancestor of all Amylostereum fungi used yellowwoods as a host . This genus of conifers was native in Europe until the Paleogene and Neogene Periods ( 66 million to 2 @.@ 6 million years ago ) , but became extinct there , so the Amylostereum fungi specialized on other conifers and differentiated into several species . Only *A. ferreum* specialized on yellowwoods in South America .

Compatibility tests as well as molecular analysis indicated that *A. areolatum* separated very early from other Amylostereum fungi . The other three species separated later from each other and are

thus partially compatible to each other . *A. ferreum* and *A. laevigatum* produced in 59 % of all cases a common mycelium , *A. ferreum* and *A. chailletii* only in 44 % . There is an undescribed species in *Amylostereum* ; according to DNA analysis , it stands between *A. laevigatum* and *A. ferreum* . This is remarkable , as these fungi originated from *Mycetangae* ( storing organs of *Platypodinae* ) of a North American wood wasp , while *A. laevigatum* has never been seen as symbiont of wood wasps , neither in North American nor in Europe . The fungus possibly represents a separated species or a subtaxon of *A. laevigatum* . As *A. areolatum* and *A. chailletii* mainly reproduce asexually through the symbiosis of wood wasps , the genetic variability within these species is relatively low .

#### = = Description = =

#### = = = Macroscopic = = =

The *Amylostereaceae* produce crust @-@ like , dry and leathery @-@ corky fruit bodies on the bark of infested trees . The fruit bodies are 0 @.@ 5 ? 1 @.@ 5 mm ( 0 @.@ 02 ? 0 @.@ 06 in ) thick , irregularly shaped and are able to cover a large surface on the bark or otherwise can appear as small spots . They lie directly on the bark . The ochrous , grey or brownish fruit body ( hymenium ) has a smooth to warty surface texture and is turned outwards . It is bordered by a highly bent and wavy ( effuso @-@ reflex ) edge on all species except *A. laevigatum* , which has a churlish surface ( a tomentum ) and is usually dirty @-@ brown coloured . In some species , the tomentum stands clearly above and forms a kind of roof above the fruit body ; if it completely surrounds this roof , there might appear cuplike shapes .

#### = = = Microscopic = = =

The *Amylostereaceae* possess a dimitic trama , meaning that there are in its mycelia two kinds of hyphae . The first type is brownish skeletal hyphae , which provide stability to the fruit body . These hyphae run parallel to the bark and often have hairpin @-@ like turns , so that the loops form thick @-@ walled , cystidium @-@ like structures , the so @-@ called pseudocystidia . The second type is generative hyphae . They are translucent ( hyaline ) and serve to promote the growth of the fungus . Genuine cystidia arise in the hymenium and the layer directly below , the subhymenium . Both pseudocystidia and cystidia are encrusted , meaning that they feature crystal @-@ like structures on the top .

With the exception of *A. laevigatum* , all species have a thin separating layer , the cortex , between the hymenium and the tomentum . A cortex is also present on many *Stereum* fungi ( on a broader front ) and serves to bend up the fruit body . As this cortex is missing on *A. laevigatum* , its fruit body lies flat on the bark .

The basidia are 15 ? 25 × 3 @.@ 5 ? 5 @.@ 5 µm and have a slim , club @-@ like shape . Each basidium features four sterigmata , each of which bear one spore . The spores ' shape is slimly ellipsoidal or cylindrical . Their surface is smooth and their walls are thin . Although they are colourless and hyaline , the spores are amyloid , meaning they will turn bluish or purple when stained with Melzer 's reagent . This characteristic differs from other very similar species , and this gave the genus its name .

#### = = Distribution = =

The range of the *Amylostereaceae* originally comprised only Holarctic regions , including North America and Eurasia , and the Neotropics , with Central and South America . The introduction of *A. areolatum* and its symbionts , the *Sirex* woodwasps , saw the spread of the genus to all continents except Antarctica .

*Amylostereum chailleti* is common in the temperate regions of North America and Eurasia . *A. laevigatum* can be also found in temperate Eurasia , but it is unclear how broadly this species is

distributed in North America . *A. areolatum* is originally native in North Africa and Eurasia ; it was however distributed through the 20th century in Australia , New Zealand , Southern Africa as well as in South and North America . Only *A. ferreum* is originally native in the tropics and is common in Brazil and the Caribbean .

#### = = Ecology = =

Amylostereaceae usually infest only dead or cut down conifer wood . Three species ? *A. areolatum* , *A. laevigatum* and *A. chaillatii* ? may also establish a symbiosis with wood wasps ( *Siricidae* ) , which beside freshly logged trees also infest living trees and infect them with fungi . Symbioses have been recorded with several species : *Sirex noctilio* , *S. juvencus* , *S. nitobei* , *S. cyaneus* , *S. edwardsii* , *S. nitidus* , and , in Japan , *Urocerus antennatus* and *Xoanon matsumurae* . Wasps of the genera *Sirex* and *Urocerus* store oidia ( the hypha of fungi split up to spores ) in special abdominal organs . The wood wasps infect trees by splashing a phytotoxic secretion below the bark and at the same time injecting fungal spores into the hole . The secretion weakens the tree and temporarily diminishes its immune system , whereby the fungus can spread along the xylem . The infection with Amylostereaceae fulfill two functions for the wasps : it provides the larvae food , because the white rot softens the wood ; at the same time , the mycelia of the fungi serves as food for the larvae . After the larvae pupate , it absorbs the mycelia of the Amylostereaceae into its body to oviposit together with its eggs . The fungus benefits from the symbiosis as it spreads faster and more effectively than through airborne spores and furthermore does not need to develop fruit bodies . *A. ferreum* is the only *Amylostereum* species that has not been associated with any woodwasps .

#### = = Host spectrum = =

The host spectrum of the Amylostereaceae comprises several , partially very different genera of Coniferae . *A. chaillatii* usually infests Pinaceae such as firs ( *Abies* ) and spruces ( *Picea* ) , but also cedars ( *Cedrus* ) and Douglas firs ( *Pseudotsuga* ) . *A. areolatum* has a similar host spectrum , which uses mainly firs , Japanese cedars ( *Cryptomeria* ) , larches ( *Larix* ) , spruces , pines ( *Pinus* ) and Douglas firs as hosts . While spruces dominate as hosts in the native habitat , this species is more common in pines on other locations . The host spectrum of *A. laevigatum* comprises Cupressaceae such as junipers ( *Juniperus* ) or cypresses ( *Cupressus* ) and the English yew ( *Taxus baccata* ) . *A. ferreum* is , however , only common on neotropical yellowwoods ( *Podocarpus* ) .

#### = = Symptoms of infestation = =

The Amylostereaceae are white rot pathogens . They disintegrate the lignin of the host wood , whereby the infested wood parts become less stable and take a fibrous structure . The wood bleaches as fungal enzymes break down and remove the brown @-@ pigmented lignin . The distribution in wood takes place mainly along the transport channels in the xylem . If the wood is crosscut , the red rot is vertically positioned , on which bleached , infested areas contrast with intact wood . Symptoms of infestation by the symbiotic partner ? wood wasps ? include circular exit holes in the crust and acute stress through dryness , common in hanging , falling or tanning needles .

#### = = Ecological and economical importance = =

In their native habitat , all *Amylostereum* species have a minor importance as forest pests . The infestation through wood wasps does not assume greater dimensions and is , compared with other pests , almost insignificant . The infection rates are even lower during sexual reproduction via fruit bodies , as the wasps do not play a part in the process . Furthermore , the *Amylostereum* fungi are alone often incapable of infesting healthy trees . They thus mostly act as saprobiontics . Pine monocultures in Australia , New Zealand , Africa and South America were shown to be susceptible to the *Sirex* woodwasp ( *Sirex noctilio* ) , which was introduced there and which is associated with *A.*

areolatum . The wasp 's phytotoxic secretion , its larvae and the fungus combine very effectively with each other and contribute to forest decline rates of up to 80 % . This is mainly owing to the poor water and nutrient supply of the trees , which can poorly reconcile the drought stress caused by infestation . *S. noctilio* was detected in North America in the 2000s ( decade ) ; in Canada alone , the total economic loss to the forestry industry caused by the Sirex ? *Amylostereum* symbiosis could be as high as \$ 254 million per year for the next 20 years .

As a countermeasure , cultures of the nematode *Deladenus siricidicola* have been used as biological control to protect trees since the 1980s . This parasite feeds on the mycelia of *A. areolatum* and is therefore a food competitor of wood wasp larvae . Where *S. noctilio* larvae are present , the parasite infects and sterilizes the eggs of female wasps , causing them to be infertile . These infertile females lay infected eggs into new trees and thus spread the nematode . This control method has proven to be relatively successful to combat the Sirex ? *Amylostereum* complex . In the Southern Hemisphere , where the technique has been widely employed , reductions of parasitism levels of 70 % ? 100 % have been achieved .