

Diversity and ecology of wood-inhabiting aphylloroid basidiomycetes on fallen woody debris in various forest types in Switzerland

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This study on the ecology of aphylloroid wood-inhabiting basidiomycetes in Switzerland showed a remarkably high species diversity of both saprophytes and mycorrhiza-forming species. *Phlebiella vaga*, a saprophytic species, and *Amphinema byssoides*, a mycorrhizal symbiont, were the two most abundant species. A total of 3339 samples of fungal fruitbodies in 86 plots distributed all over Switzerland belonged to 238 species. The five main biogeographical regions of Switzerland showed different pattern of fungal species richness: while the Plateau at lower altitudes was found to be rather rich, the Northern Alps and Central Alps, with the highest amount of forests cover, yielded less species. Although the Southern Alps exhibited the lowest species richness, this region harbours a specific species set. These findings encourage for further studies in Central Europe, where many species of aphylloroid wood-inhabiting basidiomycetes seem to be highly under-investigated.

Keywords: coarse wood debris (cwd), decomposition process, forestry, fine wood debris (fwd), habitat preferences, regional differences

Dead wood is one of the most important components of temperate forests, on which many different organisms like insects, birds, small mammals and fungi depend (e.g. HARMON et al. 1986; PRIMACK 2002). Aphylloroid wood-inhabiting fungi are among the major wood-decaying organisms involved in the wood decay process and they play an important role in the nutrient cycle in temperate forest ecosystems.

The great variability of dead wood, as twigs, branches or logs of different degrees of decomposition, volume and tree species, offers a wide range of niches for wood-inhabiting fungi. Moreover, wood undergoes several physical and chemical changes during the decay process (LEIBUNDGUT 1982). Logs are especially prone to harbour a high species richness as they do not decompose equally over the whole length and thus offer niches for early and late stage species at the same time (HEILMANN-CLAUSEN & CHRISTENSEN 2003).

Most studies on biodiversity on dead wood focus on coarse woody debris (CWD), i.e. wood debris with a minimum diameter of 10 cm (e.g. HARMON et al. 1986; SCHIEGG 2001). Fine (FWD) and very fine woody debris (VFWD) are rarely studied. However, significant quantities of dead wood for fun-

gal growth and fruiting are often found in a high proportion in the form of fine and very fine woody debris (KÜFFER & SENN-IRLET 2005). Furthermore, they showed that FWD and VFWD may be particularly species rich in wood-inhabiting basidiomycetes, especially where there is little other substrate available, such as in managed forests. However, even in natural forests FWD harbour a great number of wood-inhabiting fungal species. Especially ascomycetes highly depend on FWD for growth and fruiting, but also for basidiomycete diversity FWD is crucial (NORDÉN et al. 2004).

Virgin temperate forests contain more CWD, than most forests in Europe (KORPEL'S 1995; LEIBUNDGUT 1982) and therefore potentially more fungal species. Nevertheless, many species seem to be specialised on FWD for fruiting (NORDÉN et al. 2004). Thus, FWD serves not only as an alternative substrate, but is also itself a valuable substrate for wood inhabiting fungi.

In temperate forests tree species diversity is one of the determining factors increasing the diversity of wood-inhabiting fungi. Many aphylloroid basidiomycetes are host selective and grow only on one single host genus or even host species. Thermophilic tree species, e.g. lime or sweet chestnut, and shrub species, e.g. honeysuckle, may play an especially important role in the maintenance of fungal diversity on a regional level (KÜFFER & SENN-IRLET 2005).

With its different geographical regions – the Swiss plateau with extensive beech forest separating the hilly Jura mountains and the slopes of the Alps – Switzerland harbours a relatively high amount of macrofungi (SENN-IRLET et al. 2001).

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Tab. 1: Important geographical features of the five biogeographical regions of Switzerland.

regions of Switzerland	forest fraction on potentially forested area	forest at high altitudes (> 1000 m asl) [in 1000 ha]	forest at low altitudes (< 1000 m asl) [in 1000 ha]	main forest types
Jura mountains	43.8 %	62.9	137.8	beech forests
Plateau	26.4 %	5.5	221.4	beech forests
Northern Alps	37.9 %	129.2	91.1	fir-beech forests
Central Alps	47.6 %	347.6	67.4	spruce forests, larch-stone pine forests
Southern Alps	76.1 %	112.0	59.1	spruce-fir forests, chestnut plantations

Nonetheless, for the case of the aphylloroid wood-inhabiting fungi, data are scarce and an extensive survey on the basis of random sampling is lacking.

In this study, we focus on two groups of aphylloroid wood-inhabiting fungi: the corticioid and poroid basidiomycetes. Among them, we may find species representative for both major ecological groups of fungi: wood-decaying species and mycorrhiza-forming species.

Corticioid species are among the most important wood decomposing fungi (SWIFT 1982). Mycorrhiza forming species use dead wood primarily as substrate to develop their fruitbodies. They do not decompose dead wood in a significant way. However, their symbiotic activities are vital for tree growth and establishment (SMITH & READ 1997), especially in conifer forests, where corticioid mycorrhiza-forming species are wide-spread and abundant. Hitherto, primarily ectomycorrhizal symbionts with big, fleshy fruitbodies mainly of agaricoid species were investigated and only recently emphasis was placed on corticioid species (KÖLJALG et al. 2000; PETER, AYER & EGLI 2001).

Our study aims to answer the following questions: (1) How diverse are the wood-inhabiting fungi in Switzerland and how are they distributed in the different geographical regions? and (2) Is it possible to ecologically classify the different species of wood-inhabiting fungi in the wood-decomposition process and do they show preferences for substrate (volume, length, host)?

Material and methods

In the five main biogeographical regions of Switzerland, viz. the Jura mountains (16 plots), Swiss plateau (25 plots), Northern Alps (18 plots), Central Alps (14 plots) and Southern Alps (13 plots), (GONSETH et al. 2001), 86 rectangular plots of 50 m² were selected randomly (Fig. 1). The aim was to cover the predominant forest types. These ranged from stone pine forests in the Alps to spruce plantations on the Swiss Plateau, with an emphasis on beech forests, the potentially dominating forest type in the Swiss lowlands.

The plots reflect the influence of a wide range of factors with indirect ecological effects such as altitude (from 310 to 2000 m asl), inclination (from completely flat to 20°) and exposition (covering all expositions, with a bias towards northern-oriented slopes). They show similar ranges of variation in accordance with our aim to cover a major part of range of variation in forested areas in Switzerland. Tab. 1 summarises important forest features for the five regions of Switzerland (BRASSEL & BRÄNDLI 1999).

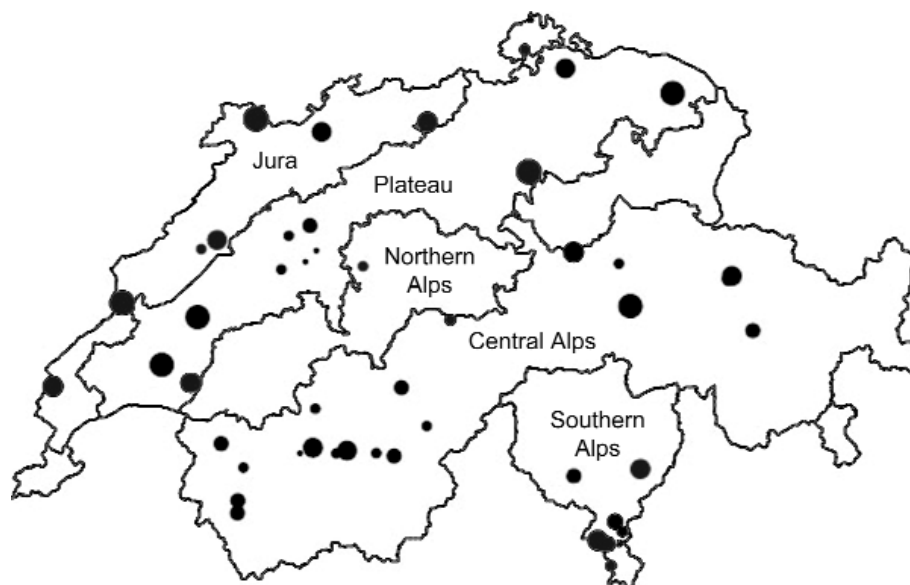
The main host tree species surveyed were beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*), followed by fir (*Abies alba*), Scots pine (*Pinus sylvestris*) and sweet chestnut (*Castanea sativa*). The fungi were collected during the main fruiting season in autumn, from 2000–2002, with a single visit at each site.

In every plot dead woody debris, i.e. twigs and branches, including both coarse and fine woody debris (KRUYSS & JONSSON 1999), as well as very fine woody debris (KÜFFER & SENN-IRLET 2005) was checked for fungal fruitbodies. Dead woody debris with visible fruitbodies of an aphylloroid basidiomycete (checked with a binocular lens) was removed for further identification.

This dead woody debris was characterised according to the following parameters: size (length and diameter), degree of decomposition and wood type (host tree species). The degree of decomposition of the wood was measured with a penetrometer PNR10 (Petrotest™). In this instrument a free-falling test body, mostly needle-shaped, penetrates the wood to be examined under its own mass and during a predetermined period. The depth the needle reaches in the wood gives a measure of the degree of decomposition. To enable statistical analyses with the woody debris collected, the different types of wood were multiplied with their relative densities. The values for these calculations were drawn from KUČERA & GFELLER (1994) and SELL (1997).

Statistical significance was tested, after checking for normal distribution of the data and, if necessary, fitting with a least-squares regression. Univariate analyses were used to check each fungal species for positive correlation with one of the above mentioned characters. The data of a single species

Fig. 1: The location of the 86 plots in Switzerland in the five geographical regions: Jura mountains, Swiss Plateau, Northern Alps, Central Alps and Southern Alps. Dot size indicates the species number in the plot (the larger the dot, the more species).



were compared with the overall mean of all collected fruitbodies, using Student's T-test statistics. Because of the statistical requirements, only species with more than 20 records (EDMAN & JANSSON 2001) were taken into consideration.

The collected fruitbodies were identified, following mostly ERIKSSON & RYVARDEN (1973, 1975, 1976), ERIKSSON, HJORTSTAM & RYVARDEN (1978, 1981, 1984), HJORTSTAM, LARSSON & RYVARDEN (1987, 1988), JÜLICH (1984) and BREITENBACH & KÄNZLIN (1986). In addition, for some groups special literature was consulted, among them KÖLJALG (1996) for the Tomentelloideae. The nomenclature is based on the checklist by HJORTSTAM (1997). Voucher specimens are deposited in the Herbarium ETH Zürich.

Results

Species richness and distribution

Among a total amount of 3339 samples of fruitbodies of wood-inhabiting basidiomycetes were found belonging to 238 species. A total of 3143 samples of woody debris were collected. Thus on 196 samples of woody debris more than one fungal species could be found. Out of the 238 species, 156 species (or 65.6 %) belonged to the Corticiaceae s.l., 32 (13.4 %) were polypores and 19 (7.9 %) were members of the thelephoraceous subfamily Tomentelloideae, which contains many important mycorrhiza-forming species. Heterobasidiomycetes were represented by 15 species (6.3 %).

Two main ecological groups within the wood-inhabiting basidiomycetes were found: 212 species belonging to the wood-decomposing mycoflora and 26 to the mycorrhizal symbionts (mainly of the genus *Tomentella*). These mycorrhiza-forming species were still important in terms of number of fruitbodies (465 fruitbodies of mycorrhizae-formers vs. 2874 of decomposers).

Species richness varied between 7 and 39 species per plot of 50 m², with most plots exhibiting between 10 and 15 species. The richest plots were all located at lower altitudes (cf. Fig. 1).

The 3339 samples of woody debris were almost equally distributed on coniferous and deciduous tree species: 1606 (48.1 %) from coniferous trees and 1733 (51.9 %) from deciduous trees. Species richness was higher on deciduous host species (175 fungal species) than on coniferous trees (134 species).

Most species could be found on beech (141 species), followed by spruce (101 species) and black alder with 52 fungal species. For further details on this issue, especially on the dependence of fungal species richness on high host tree diversity confer with KÜFFER & SENN-IRLET (2005).

Among the collected fruitbodies, fungal species were unevenly distributed, with a few species heavily dominating. Thus, species rank abundance follows a steep power function (Fig. 2), where only 36 (or 15.1 %) species could be found more than ten times and 6 (or 2.5 %) species could be found more than 100 times. This six species were: *Amphinema byssoides*, *Athelia epiphylla* s.l., *Hyphodontia sambuci*, indet I, *Phlebiella vaga* and *Vuilleminia comedens*, they sum up almost a third (32.1 %) of all samples of woody debris (Tab. 2).

Amphinema byssoides is a mycorrhiza-forming species with conifer trees in Switzerland. It has a main distribution in the subalpine conifer forests of the Northern Prealps, but can also be found in conifer plantations of the Swiss Plateau. Ninety-five % of all specimens could be found on coniferous wood. We think that this species does not decompose the wood in an ecologically significant way and uses the dead wood only as substrate for fructification.

Athelia epiphylla is treated here as an aggregate species as in ERIKSSON & RYVARDEN (1973), i.e. *A. epiphylla* s.str., *A. salicum* Pers., *A. tenuispora* Jülich and *A. ovata* Jülich were

Tab. 2: The 32 most abundant fungal species (found more than twenty times) with their substrate characteristics, p-values indicate differences from mean for all samples (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

Species	no of samples	length [cm]	diameter [cm]	degree of decomposition ¹	main host tree species	main region ²
<i>Amphinema byssoides</i> (Pers. ex Fr.) J.Erikss. M	280	63.1 +/- 24.1	1.89 ** +/- 0.51	strong ***	<i>Picea</i> 51.4 %, <i>Abies</i> 29.3 %	Northern Alps, Central Alps
<i>Athelia epiphylla</i> s.l. Pers.	102	45.2 *** +/- 12.4	1.21 *** +/- 0.41	sparse ***	<i>Picea</i> 48.0 %, <i>Larix</i> 23.5 %	Central Alps, Northern Alps
<i>Botryobasidium vagum</i> (Berk. & Curt.) Rogers	73	63.8 +/- 25.7	2.13 +/- 0.61	exhaustive ***	<i>Picea</i> 58.9 %, <i>Abies</i> 6.9 %	Plateau, Jura Mountains
<i>Coniophora arida</i> (Fr.) Karst.	26	32.2 *** +/- 11.0	1.96 +/- 0.33	medium	<i>Pinus sylvestris</i> 96.2 %	Central Alps
<i>Exidiopsis calcea</i> (Pers. ex St.Adams) Wells	92	75.8 * +/- 24.2	1.50 *** +/- 0.28	sparse ***	<i>Picea</i> 78.3 %, <i>Abies</i> 16.3 %	Northern Alps, Central Alps
<i>Exidiopsis effusa</i> (Bref. ex Sacc.) Pat.	63	67.9 +/- 19.1	1.44 *** +/- 0.34	weak **	<i>Fagus</i> 82.5 %, <i>Alnus</i> 6.4 %	Jura mountains Plateau
<i>Exidiopsis grisea</i> (Pers.) Bourd. & Maire	24	44.8 ** +/- 13.2	1.53 * +/- 0.52	sparse ***	<i>Picea</i> 83.5 %, <i>Fagus</i> 16.7 %	Northern Alps
<i>Hyphoderma praetermissum</i> (Karst.) J.Erikss. & Strid	94	64.1 +/- 37.3	2.38 +/- 0.80	strong	<i>Picea</i> 40.4 %, <i>Fagus</i> 35.1 %	Jura Mountains, Plateau
<i>Hyphodontia crustosa</i> (Pers. ex Fr.) J.Erikss.	52	50.3 +/- 20.4	2.02 +/- 0.75	medium	<i>Picea</i> 44.2 %, <i>Fagus</i> 26.9 %	Plateau, Northern Alps
<i>Hyphodontia nespori</i> (Bres.) J.Erikss. & Hjortst.	39	63.4 +/- 21.1	1.71 ** +/- 0.37	weak	<i>Picea</i> 79.5 %, <i>Corylus</i> 12.8 %	Central Alps, Plateau
<i>Hyphodontia sambuci</i> (Pers.) J.Erikss.	106	39.5 *** +/- 17.3	1.78 ** +/- 0.44	medium	<i>Picea</i> 30.2 %, <i>Fagus</i> 28.3 %	Plateau, Jura Mountains
indet I ³	307	47.2 *** +/- 17.1	1.68 *** +/- 0.49	weak *	<i>Fagus</i> 41.4 %, <i>Picea</i> 30.9 %	Northern Alps, Plateau
indet III ⁴	69	52.0 * +/- 19.5	1.57 *** +/- 0.35	weak	<i>Picea</i> 18.8 %, <i>Castanea</i> 13.0%, <i>Fagus</i> 13.0%	Northern Alps, Southern Alps
<i>Megalocystidium luridum</i> (Bres.) Jülich	40	74.4 +/- 29.9	2.71 +/- 1.55	medium	<i>Fagus</i> 32.5 %, <i>Alnus</i> 15 %	Plateau, Jura Mountains
<i>Merismodes fasciculata</i> (Schwein.) Earle	24	52.3 +/- 19.5	1.04 *** +/- 0.18	sparse ***	<i>Betula</i> 33.3 %, <i>Alnus</i> 29.2 %	Plateau
<i>Peniophora cinerea</i> (Pers. ex Fr.) Cooke	58	74.8 +/- 28.0	1.46 *** +/- 0.32	weak	<i>Fagus</i> 55.2 %, <i>Betula</i> 10.3 %	Plateau, Southern Alps
<i>Peniophora pithya</i> (Pers.) J.Erikss.	28	64.7 +/- 23.0	1.30 *** +/- 0.22	sparse ***	<i>Picea</i> 100 %	Northern Alps, Central Alps
<i>Phellinus ferruginosus</i> (Schrad. ex Fr.) Pat.	25	81.2 +/- 58.9	3.37 ** +/- 0.89	exhaustive ***	<i>Fagus</i> 64 %, <i>Alnus</i> 24 %	Jura Mountains, Plateau
<i>Phlebiella vaga</i> (Fr.) Karst.	168	57.8 +/- 21.6	2.36 *** +/- 0.75	strong **	<i>Fagus</i> 48.8 %, <i>Picea</i> 34.4 %	Jura Mountains, Northern Alps
<i>Radulomyces confluens</i> (Fr.) M.P. Christ.	61	70.8 +/- 23.4	2.06 +/- 0.78	weak	<i>Fagus</i> 49.2 %, <i>Picea</i> 34.4 %	Plateau, Jura Mountains
<i>Resinicium bicolor</i> (Alb. & Schwein. ex Fr.) Parm.	24	64.9 +/- 25.0	2.81 +/- 1.01	weak	<i>Picea</i> 87.5 %	Plateau, Northern Alps
<i>Schizopora paradoxa</i> (Schrad. ex Fr.) Donk	46	58.5 +/- 34.6	2.09 +/- 0.59	strong	<i>Fagus</i> 43.5 %, <i>Picea</i> 32.6 %	Plateau, Jura Mountains
<i>Scopuloides rimosa</i> (Cooke) Jülich	44	62.7 +/- 22.8	2.61 * +/- 0.72	exhaustive *	<i>Fagus</i> 68.2 %, <i>Abies</i> 15.9 %	Plateau, Jura Mountains
<i>Steccherinum fimbriatum</i> (Pers. ex Fr.) J.Erikss.	27	43.7 +/- 14.9	1.99 ** +/- 0.42	exhaustive **	<i>Fagus</i> 88.9 %	Northern Alps, Plateau
<i>Stereum hirsutum</i> (Willd. ex Fr.) S.F. Gray	77	69.8 +/- 27.2	1.44 *** +/- 0.42	weak ***	<i>Castanea</i> 71.4%, <i>Fagus</i> 15.6 %	Southern Alps, Plateau
<i>Tomentella stuposa</i> (Link) Stalpers M	30	61.3 +/- 28.6	2.98 +/- 1.76	weak	<i>Picea</i> 40.0 %, <i>Fagus</i> 33.3 %	Jura Mountains, Northern Alps

Tab. 2: Continued

Species	no of samples	length [cm]	diameter [cm]	degree of decomposition ¹	main host tree species	main region ²
<i>Tomentella subulacina</i> (Ellis. & Holw.) Wakef. M	26	59.9 +/- 22.7	2.44 +/- 0.63	strong	<i>Fagus</i> 50 %, <i>Picea</i> 15.4 %	Plateau, Central Alps
<i>Trechispora farinacea</i> (Pers. ex Fr.) Liberta	66	60.9 +/- 40.1	2.09 +/- 1.05	weak	<i>Picea</i> 63.6 %, <i>Fagus</i> 22.7 %	Northern Alps, Central Alps
<i>Trechispora</i> sp.	39	38.6 *** +/- 14.7	1.20 *** +/- 0.39	weak	<i>Fagus</i> 69.6 %	Northern Alps, Plateau
<i>Tubulicrinis subulatus</i> (Bourd. & Galz.) Donk	21	69.1 +/- 32.2	3.13 +/- 1.68	medium	<i>Pinus sylvestris</i> 42.9%, <i>Picea</i> 28.6 %	Central Alps, Northern Alps
<i>Vesiculomyces citrinus</i> (Pers.) Hagström	41	55.4 +/- 28.9	2.15 +/- 0.62	medium	<i>Picea</i> 51.2 %, <i>Pinus sylv</i> 9.8 %	Plateau, Central Alps
<i>Vuilleminia comedens</i> s.l. (Nees ex Fr.) Maire	108	74.5 * +/- 22.6	1.61 *** +/- 0.38	weak	<i>Castanea</i> 51.9%, <i>Fagus</i> 31.5 %	Southern Alps, Plateau

1 : for class definition cf. Table 2;

2: in order of decreasing importance;

3: indet I is a species of the *Trechispora-Phlebiella* group;

4: indet III basidiomycete species without specifying characters;

M: mycorrhizal species.

included in *A. epiphylla* s.l. This species grows preferably on rather thin conifer branches and twigs. It can be regarded as an early species in the decomposition process. The differentiation into six closely related species, of which the four mentioned above could be found in this study, is rather difficult and not every specimen can be determined undoubtedly. On the ecological differences between these species, too little is known.

Hyphodontia sambuci is a typical species for deciduous forests on the Swiss Plateau, where it grows on a wide range of various tree species and even on coniferous wood, when suitable substrate is lacking.

Indet I is an undetermined species out of the *Phlebiella-Trechispora* complex, with a dense hymenium and a typical incrustation on the hyphae. It grows on both on deciduous and coniferous wood, mostly in an early stage of the succession process.

Phlebiella vaga is a very widespread species in all regions of Switzerland. It prefers rather thick branches and can be found in the later stages of the decomposition process.

Vuilleminia comedens s.l. grows only on deciduous wood, preferably on beech. The recently described species *V. alni* Boidin et al. is not always clearly separable. This species grows underneath the bark and disrupt it when developing the fruitbodies. In Switzerland it is very often found in the Southern Alps on beech and sweet chestnut.

The analysis of the woody debris characteristics in the five regions, revealed several striking differences (Tab. 3): In none of the regions, length of the woody debris samples was significantly different from an overall mean.

Differences, however, could be found in the diameter and degree of decomposition. In the Jura mountains and the Sou-

thern Alps, woody debris samples were slightly thicker than the average and in the Jura mountains in a more advanced stage of decay. The Northern Alps and the Central Alps had a very low degree of woody debris decomposition and poorer species richness, both in fungal and host tree species. The Plateau is often neglected when dealing with biodiversity, because of its fragmented and managed forests, and its low degree of naturalness (e.g. DELARZE, GONSETH & GALLAND 1999). Here, population density is high, with many cities and towns and their connecting facilities. Nevertheless, it seems to be rather rich in the amount of woody debris, as well as species number per plot.

Overall species richness was highest in the Plateau with 120 species, followed by the Jura mountains harbouring 106 species. The Southern Alps were the poorest region: only 91 fungal species could be found there. Nearly, the same pattern could be found when analysing the mean number of species per plot instead of the overall species richness. An analysis of variance could, however, not detect any significant differences. For every region some typical species could be found, indicating a centre of distribution. For the Jura mountains *Scopuloides rimosa* and *Schizopora paradoxa*, for the Plateau *Hyphodontia crustosa*, *H. sambuci* and *Megalocystidium lucidum*. In the Northern Alps mainly the mycorrhizal species *Amphinema byssoides* and the heterobasidiomycete *Exidiopsis calcea*, in the Central Alps *Coniophora* spp. and *Tubulicrinis subulatus*, and in the Southern Alps *Phanerochaete martelliana*.

Species and the decomposition process

The most frequent species (> 20 specimens) were characterised with the factors measured for all samples of woody debris,

Tab. 3: The mean values of some host parameters (with standard errors), listed for the five biogeographical regions in Switzerland. Degree of decomposition-classes: < 2 mm = sparse, 2–3 mm = weak, 3–4 mm = medium, 4–5 mm = strong, > 5 mm = exhaustive, see text for explanation. Differences from mean for all samples indicated with ***: $p < 0.001$.

regions of Switzerland	no of plots	no of species per region	length of woody debris [cm]	mean diameter [cm]	degree of decomposition	woody debris per plot	mean species no per plot	mean tree species no per plot
Jura mountains	16	106	61.5 +/- 34.4	2.53 *** +/- 1.23	strong ***	38.5 *** +/- 1.8	17.12 +/- 2.11	1.99 ***
Plateau	25	120	61.5 +/- 33.4	2.08 +/- 0.95	medium	51.0 *** +/-16.8	19.42 *** +/- 4.87	3.25 ***
Northern Alps	18	102	68.0 +/-35.7	1.93 +/- 1.16	weak ***	47.2 +/- 6.8	14.69 *** +/- 1.16	1.93 ***
Central Alps	14	99	62.4 +/- 33.5	2.02 +/- 1.01	weak ***	49.1 *** +/- 9.5	15.97 *** +/- 2.12	2.16 ***
Southern Alps	13	91	66.0 +/- 28.0	1.87 *** +/- 0.53	medium	39.2 *** +/- 4.8	15.68 *** +/- 1.66	2.46
overall mean			63.6	2.09	medium	45.9	16.83	2.42

i.e. length, diameter and degree of decomposition (Tab. 2). There were not many significant values regarding the length of the woody debris. In contrast, the values for diameter and degree of decomposition show higher variability. *Amphinema byssoides* and *Peniophora* spp. prefer thin branches or twigs for fructification, while other species, such as *Phebiella vaga* or *Scopuloides rimosa*, need thicker woody debris.

In early stages of the decomposition process, specialised species, like *Athelia epiphylla* or *Exidiopsis* spp. can be found. Others prefer to grow on wood in a more advanced stage of decomposition, e.g. *Phellinus ferruginosus* or *Steccherinum fimbriatum*.

The two main host tree species, European beech and Norway spruce, show similar pattern regarding the fungal species richness during the decomposition process: the least and the most advanced stages of decay, i.e. recently dead branches and severely decomposed woody debris, harbour the highest number of different fungal species, whereas the intermediate stages seem to be rather species poor (Figure 3). The maximal species number, however, is in beech on the most advanced stage of decay (99 species or 70.2 % of all species found on beech), whereas on spruce the first decay stage is the most species rich one (85 species or 84.2 % of all species found on spruce).

Discussion

Species richness

Although literature focusing on wood-inhabiting basidiomycetes in Central Europe is rather scarce, the total number of species found in this study (238 species) is in accordance with the findings of previous studies. DÄMON (2001) found 294 species in an extensive survey in the Region of Salzburg (Austria). GROSSE-BRAUCKMANN (1994) listed 137 species

from an alluvial forest along the Rhine River (Germany) and again GROSSE-BRAUCKMANN (1999) investigated a woodruff beech forest, where she found 155 species, in one single forest type. Thus the literature available suggests our data are representative for Central Europe.

The uneven distribution of species, with a few dominating and a majority represented with less than five specimens, is typical for studies in fungal ecology (e.g. TOFTS & ORTON 1998).

The most important species in this study, *Amphinema byssoides*, is a frequent mycorrhiza-forming species, especially in conifer forests. This underlines the ecological importance of this group of fungi.

A great variability of different characteristics of the dead woody debris seems to be a major factor contributing to fungal biodiversity, by creating a wide range of niches. A broad diversity of host tree species, of various volumes and diameters, i.e. logs, branches or twigs, and degree of decomposition tend to favour rich fungal communities (KÜFFER & SENN-IRLET 2005). Several further site-specific factors related to logs were found to influence species richness in an autochthonous Danish beech forest (HEILMANN-CLAUSEN & CHRISTENSEN 2003): soil contact, a luxurious herb layer, and the variety in the structure of logs.

Regional differences

Although many forests are strongly managed and fragmented in this region, the highest species richness was found on the Plateau. The high diversity of host tree species in this region, especially of thermophilic species or in alluvial forests, may have a positive influence on fungal species richness. The variable disturbance regime (rather small-scaled forest management, traffic on even small forest roads, intense recreational tourism etc.) may also help to explain the unexpected species

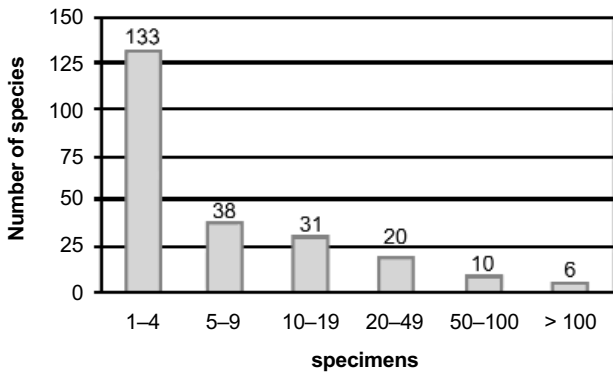


Fig. 2: The uneven distribution of the species is typical for macrofungi. The six most abundant species cover almost one third of all specimens ($n = 3339$).

richness of this region. On the other end of the scale, the poorest region was the Southern Alps. This is probably due to the often very young character of the forests in the southern part of Switzerland, consisting mainly of abandoned sweet-chestnut plantations (CONEDERA et al. 2000). Regular fire in the dryer summer months may impoverish fungal species richness too, by hampering fungal growth and fruiting as well as diminishing substrate supply.

Regarding the species composition, the Swiss Plateau and the Jura mountains are very similar, as well as the Central Alps and the Northern Alps. The most prominent differences probably arise from the different appearance of host trees. On the Plateau and in the Jura mountains, the main forest types are beech forests or mixed deciduous forests, whereas in the Central Alps and Northern Alps, coniferous forests prevail largely.

Even though the Southern Alps are the poorest regions, they harbour a much specialised species composition, which was not found in other regions. Similarly, not only wood-inhabiting fungi show such distribution patterns, but also agaricoid species (SENN-IRLET et al. 2003). Thus, also fungi seem to follow roughly the same biogeographical pattern as seen for higher plants (WOHLGEMUTH 1996).

Regarding the characteristics of woody debris in the different regions, the Jura mountains and the Southern Alps show significant differences for diameter measurements. These differences are best explained by the forest history. In the Southern Alps the thinner samples of woody debris seem to be a consequence of the young character of the forests (BRASSEL & BRÄNDLI 1999). This idea is also supported by the smaller amount of woody debris per plot.

In the Jura mountains the problem is ambiguous: the thicker mean diameter is probably due to reduced management practices, as well as the more advanced degree of decomposition.

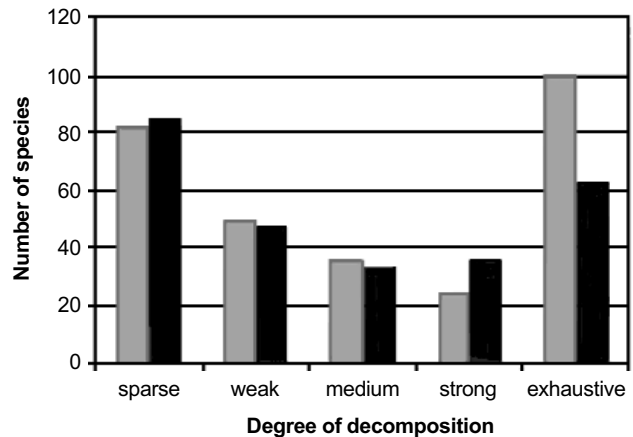


Fig. 3: The number of fungal species found per degree of decomposition. Grey bars for European beech ($n = 141$) and black bars for Norway spruce ($n = 101$).

The less advanced degree of decomposition in the Northern Alps and Central Alps, as well as the poorer species richness found, may be due to the rather unfavourable climate and thus shorter growing period in these regions resulting in a lower accrescence (BRASSEL & BRÄNDLI 1999) and also in a slower decomposition process. There is a trend to poorer species richness in higher altitudes, but not significant. Some forests in high altitudes harbour indeed a rather high species richness, which may partly be explained by the low management pressure in higher altitudes.

Red-list species

The preliminary Red List of Switzerland (SENN-IRLET et al. 1997) numbers three of the species found during this study, i.e. *Hymenochaete cruenta*, *Osteina obducta* and *Pulcherricium caeruleum*. When comparing with the Red Lists of Germany (DGFM & NABU 1992) and Austria (KRISAI-GREIL-HUBER 1999), fourteen and one species were found to be on the Red Lists. The rather low number of listed species in all three countries is probably due to the sparse studies so far (e.g. KÜFFER & SENN-IRELT 2005) on aphylophoroid wood-inhabiting basidiomycetes in Central Europe and to the sound elaboration of distinct threats. Further studies are needed to investigate the real status of this ecologically important group of fungi. Two of the Red List species mentioned above (*Pulcherricium caeruleum* and *Osteina obducta*) are considered to grow in the later stages during the wood decomposition process.

Species in the wood decomposition process

The values from Tab. 2 give some indications where to place the most abundant species during the wood decomposition process. It is assumed that by analysing spatially different stages of decay at a single moment, certain conclusions on the

succession in time can be drawn (e.g. RENVALL 1995). Two main groups can be distinguished: Pioneer species, preferring sparse to weak degree of decomposition and late stage species, with a preference for strong or exhaustive stage of decay. Primary decayers or pioneer species colonise wood quickly after its death and are usually fast growing, but weak competitors (BODY & RAYNER 1988), whereas typical late stage species grow slowly, but are strong competitors. This group of late stage species seems to be very species-rich (RENVALL 1995; NIEMELÄ, RENVALL & PENTTILÄ 1995), but threatened because of intensive forest management and habitat fragmentation (e.g. NUSS 1999; BADER, JANSSON & JANSSON 1995).

In the present study, only the fungal species growing on beech wood partly follow this pattern: the most species rich decomposition stage is the most advanced stage of decay, whereas on spruce it is different. The mostly very small samples of spruce woody debris (i.e. twigs and branches or VFWD in KÜFFER & SENN-IRLET (2005), decay only very slowly and have, in relation to their volume, a large surface area to enable colonisation by fungal spores or mycelium. Additionally, many spruce samples come from generally species poor spruce plantations.

Other wood-decomposing fungal groups, such as ascomycetes or agaricoid basidiomycetes, have different requirements for growth and fruiting: whereas ascomycetes rather grow on FWD and in the initial stages of the decomposition process, the agaricoid basidiomycetes prefer thicker CWD in the latter stage of decay (NORDÉN et al. 2004). The investigated aphylophoroid basidiomycetes may be placed in between.

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Appendix A. List of recorded species.

- Amphinema byssoides* (Pers. ex Fr.) J.Erikss.
Amylostereum chailletii (Pers. ex Fr.) Boidin
Antrodia malicola (Berk. & Curt.) Donk
Antrodia serialis (Fr.) Donk
Asterostroma cervicolor (Berk. & Curt.) Mass.
Athelia acrospora Jülich
Athelia arachnoidea (Berk.) Jülich
Athelia bombacina (Pers.) Jülich
Athelia decipiens (Höhn. & Litsch.) J.Erikss..
Athelia epiphylla Pers.
Athelia neuhoffii (Bres.) Donk
Athelia pyriformis (M.P.Christ.) Jülich
Athelopsis lacerata (Litsch.) J.Erikss. & Ryv.
Auricularia auricula-judae (Bull. ex St.-Am.) Wettst.
Basidiodendron caesiocinereum (Höhn. & Litsch.) Luck-Allen
Basidiodendron cinereum (Bres.) Luck-Allen
Bjerkandera adusta (Willd. ex Fr.) P.Karst.
Boidinia subasperispora (Litsch.) Jülich
Botryobasidium botryoideum (Overh.) Parmasto
Botryobasidium candicans J.Erikss.
Botryobasidium laeve (J.Erikss.) Parmasto
Botryobasidium medium J.Erikss
Botryobasidium obtusisporum J.Erikss.
Botryobasidium pruinaum (Bres.) J.Erikss.
Botryobasidium subcoronatum (Höhn. & Litsch.) Donk
Botryobasidium vagum (Berk. & Curt.) Rogers
Botryohypochnus isabellinus (Fr.) J.Erikss.
Brevicellium olivascens (Bres.) Larsson & Hjortstam
Bulbillomyces farinosus (Bres.) Jülich
Byssocorticium atrovirens (Fr.) Bond. & Singer
Byssocorticium pulchrum (Lundell) Christ.
Ceraceomyces tessulatus (Cooke) Jülich
Ceratobasidium cornigerum (Bourd.) Rogers
Ceriporia purpurea (Fr.) Donk
Ceriporia reticulata (Hoffm. ex Fr.) Domański
Ceriporiopsis mucida (Pers. ex Fr.) Gilb. & Ryv.
Christiansenia pallida Hauerslev
Climacocystis borealis (Fr.) Kotl. & Pouz.
Coniophora arida (Fr.) P.Karst.
Coniophora olivacea (Fr.) P.Karst.
Coniophora puteana (Schum.ex Fr.) P.Karst.
Cristinia gallica (Pilát) Jülich
Cristinia helvetica (Pers.) Parmasto
Cylindrobasidium laeve (Pers. ex Fr.) Chamuris
Dacrymyces stillatus Nees ex Fr.
Daedaleopsis confragosa (Bolt.ex Fr.) Schröter
Datronia mollis (Sommerf. ex Fr.) Donk
Datronia stereoides (Fr.) Ryv.
Dendrothele acerina (Pers. ex Fr.) P.A.Lemke
Exidia glandulosa Fr.
Exidiopsis calcea (Pers. ex St.-Am.) Wells
Exidiopsis effusa (Bref. ex Sacc.) Möller
Exidiopsis grisea (Pers.) Bourd. & Maire
Fomitopsis pinicola (Sw.ex Fr.) P.Karst.
Galzinia incrustans (Höhn. & Litsch.) Parmasto
Globulicium hiemale (Laurila) Hjortst.
Gloeocystidiellum lactescens (Berk.) Boid.
Gloeocystidiellum ochraceum (Fr.) Donk
Gloeocystidiellum porosum (Berk. & Curt.) Donk
Gloeophyllum odoratum (Wulf. ex Fr.) Imaz.
Gloeophyllum trabeum (Pers. ex Fr.) Murrill
Heterobasidium annosum (Fr.) Bref.
Hydrabasidium subviolaceum Peck
Hymenochaete cinnamomea (Pers.) Bres.
Hymenochaete cruenta (Pers.ex Fr.) Donk
Hymenochaete fuliginosa (Pers.) Bres.
Hymenochaete rubiginosa (Dicks.ex Fr.) Lév.
Hymenochaete subfuliginosa (Bourd. & Galz.) Hruby
Hyphoderma argillaceum (Bres.) Donk
Hyphoderma definitum (H.S.Jacks.) Donk
Hyphoderma mutatum (Peck) Donk
Hyphoderma nemorale K.-H.Larss.

- Hyphoderma orphanellum* (Bourd. & Galz.)
Donk
- Hyphoderma praetermissum* (P. Karst.)
J. Erikss. & A. Strid
- Hyphoderma puberum* (Fr.) Wallr.
- Hyphoderma setigerum* (Fr.) Donk
- Hyphoderma* sp.
- Hyphoderma subdefinitum* J. Erikss. & A. Strid
- Hyphodermella corrugata* (Fr.) J. Erikss. & Ryv.
- Hyphodontia alutacea* (Fr.) J. Erikss.
- Hyphodontia alutaria* (Burt.) J. Erikss.
- Hyphodontia arguta* (Fr.) J. Erikss.
- Hyphodontia aspera* (Fr.) J. Erikss.
- Hyphodontia barba-jovis* (Bull. ex Fr.) J. Erikss.
- Hyphodontia breviseta* (P. Karst.) J. Erikss.
- Hyphodontia cineracea* (Bourd. & Galz.)
J. Erikss. & Hjortst.
- Hyphodontia crustosa* (Pers. ex Fr.) J. Erikss.
- Hyphodontia hastata* (Litsch.) J. Erikss.
- Hyphodontia nespori* (Bres.) J. Erikss. & Hjortst.
- Hyphodontia pallidula* (Bres.) J. Erikss.
- Hyphodontia sambuci* (Pers.) J. Erikss.
- Hyphodontia subalutacea* (P. Karst.) J. Erikss.
- Hypochniciellum molle* (Fr.) Hjortst.
- Hypochnicium eichleri* (Bres.) J. Erikss. &
Ryvarden
- Hypochnicium geogenium* (Bres.) J. Erikss.
- Hypochnicium polonense* (Bres.) A. Strid
- Hypochnicium punctulatum* (Cooke) J. Erikss.
- Hypochnus fusisporus* Schröter
indet I
indet II
indet III
indet IV
indet Pfy2
indet V
indet VII
- Jaapia ochroleuca* (Bres.) Nannf. & J. Erikss.
- Laetiporus sulphureus* (Bull. ex Fr.) Murrill
- Leptosporomyces galzinii* (Bourd.) Jülich
- Leptosporomyces mutabilis* (Bres.)
L.G. Krieglst.
- Leucogyrophana mollusca* (Fr.) Pouzar
- Litschauerella clematidis* (Bourd. & Galz.) J. Erikss. & Ryvarden
- Lopharia spadicea* (Pers. ex Fr.) Boidin
- Macrotyphula fistulosa* (Fr.) Petersen
- Megalocystidium luridum* (Bres.) Jülich
- Membranomyces spurium* (Bourd.) Jülich
- Merismodes fasciculata* (Schwein.) Earle
- Merulicium fusisporum* (Romell) J. Erikss. &
Ryvarden
- Mycocacia aurea* (Fr.) J. Erikss. & Ryvarden
- Mycocacia uda* (Fr.) Donk
- Osteina obducta* (Berk.) Donk
- Paulliticium pearsonii* (Bourd. & Galz.)
J. Erikss.
- Peniophora cinerea* (Fr.) Cooke
- Peniophora incarnata* (Pers. ex Fr.) P. Karst.
- Peniophora laeta* (Fr.) Donk
- Peniophora lilacea* Bourd. & Galz.
- Peniophora limitata* (Chaill. ex Fr.) Cooke
- Peniophora lycii* (Pers.) Höhn. & Litsch.
- Peniophora nuda* (Fr.) Bres.
- Peniophora piceae* (Pers.) J. Erikss.
- Peniophora pithya* (Pers.) J. Erikss.
- Peniophora quercina* (Pers. ex Fr.) Cooke
- Peniophora violaceo-livida* (Sommerf.) Masee
- Phanerochaete affinis* (Burt) Parmasto
- Phanerochaete calotricha* (P. Karst.) J. Erikss.
& Ryv.
- Phanerochaete filamentosa* (Berk. & Curt.)
Burds.
- Phanerochaete jose-ferreirae* (D.A. Reid)
D.A. Reid
- Phanerochaete martelliana* (Bres.) J. Erikss. &
Ryvarden
- Phanerochaete sanguinea* (Fr.) Pouzar
- Phanerochaete sordida* (P. Karst.) J. Erikss. &
Ryvarden
- Phanerochaete* sp.
- Phanerochaete tuberculata* (P. Karst.)
Parmasto
- Phanerochaete velutina* (DC ex Fr.) P. Karst.
- Phellinus ferrugineofuscus* (P. Karst.) Bourd. &
Galz.
- Phellinus ferruginosus* (Schröd. ex Fr.) Pat.
- Phellinus vorax* (Harkness) Černý
- Phlebia deflectens* (P. Karst.) Ryvarden
- Phlebia lilascens* (Bourd.) J. Erikss. &
Ryvarden
- Phlebia livida* (Pers. ex Fr.) Bres.
- Phlebia radiata* Fr.
- Phlebia rufa* (Fr.) M.P. Christ.
- Phlebia* sp.
- Phlebiella allantospora* (Oberw.) Larss. &
Hjortst.
- Phlebiella christiansenii* (Parmasto) Larss. &
Hjortst.
- Phlebiella tulasnelloidea* (Höhn. & Litsch.)
Ginns & Lefebvre
- Phlebiella vaga* (Fr.) P. Karst.
- Phlebiopsis gigantea* (Fr.) Jülich
- Physisporinus sanguinolentus* (Alb. &
Schwein. ex Fr.) Pilát
- Piloderma byssinum* (P. Karst.) Jülich
- Piloderma croceum* J. Erikss. & Hjortst.
- Piptoporus betulinus* (Bull. ex Fr.) P. Karst.
- Plicatura crispa* (Pers. ex Fr.) Rea
- Polyporus badius* (Pers. ex S.F. Gray) Schw.
- Polyporus varius* (Pers.) Fr.
- Pseudotomentella tristis* (Karst.) M.J. Larsen
- Pseudotomentella mucidula* (Karst.) Svrček
- Pulcherricium caeruleum* (Schröd. ex Fr.)
Parmasto
- Pycnoporus cinnabarinus* (Jacq. ex Fr.)
P. Karst.
- Radulomyces confluens* (Fr.) M.P. Christ.
- Resinicium bicolor* (Alb. & Schw. ex Fr.) Parm.
- Resinicium furfuraceum* (Bres.) Parm.
- Saccoblastia farinacea* (Höhn.) Donk
- Schizopora paradoxa* (Schröd. ex Fr.) Donk
- Schizopora radula* (Pers. ex Fr.) Hallenb.
- Scopuloides rimosa* (Cooke) Jülich
- Scytinostroma portentosum* (Berk. & Curt.)
Donk
- Sebacina epigaea* (Berk. & Br.) Neuh.
- Sebacina incrustans* (Pers. ex Fr.) Tul.
- Sistotrema brinkmannii* (Bres.) J. Erikss.
- Sistotrema diademiferum* (Bourd. & Galz.)
Donk
- Sistotrema efibulatum* (J. Erikss.) Hjortst.
- Sistotrema octosporum* (Schröd. ex Höhn. &
Litsch.) Hallenb.
- Sistotremastrum niveocreum* (Höhn. &
Litsch.) J. Erikss.
- Skeletocutis nivea* (Jungh.) Keller
- Steccherinum fimbriatum* (Pers. ex Fr.) Erikss.
- Steccherinum ochraceum* (Pers. ex Fr.)
S.F. Gray
- Steccherinum oreophilum* Lindsey & Gilb.
- Stereum hirsutum* (Willd. ex Fr.) Gray
- Stereum ochraceoflavum* (Schwein.) Ellis
- Stereum rugosum* (Pers. ex Fr.) Fr.
- Stereum sanguinolentum* (Alb. & Schw. ex Fr.)
Fr.
- Subulicium rallum* (Jacks.) Jülich & Stalpers
- Subulicystidium longisporum* (Pat.) Parm.
- Tomentella asperula* (P. Karst.) Höhn. & Litsch.
- Tomentella badia* (Link) Stalpers
- Tomentella bryophila* (Pers.) M.J. Larsen
- Tomentella coerulea* (Bres.) Höhn. & Litsch.
- Tomentella crinalis* (Fr.) M.J. Larsen
- Tomentella ellisii* (Sacc.) Jülich & Stalpers
- Tomentella ferruginea* (Pers. ex Fr.) Pat.
- Tomentella fuscocinerea* (Pers. ex Fr.) Donk
- Tomentella lilacinogrisea* Wakef.
- Tomentella radiosa* (P. Karst.) Rick
- Tomentella* sp.
- Tomentella stuposa* (Link) Stalpers
- Tomentella sublilacina* (Ellis & Holw.) Wakef.
- Tomentella subtestacea* Bourd. & Galz.
- Tomentella terrestris* (Berk. & Broome)
M.J. Larsen
- Tomentella umbrinospora* M.J. Larsen
- Tomentella viridula* Bourd. & Galz.
- Tomentellopsis echinospora* (Ellis) Hjortst.
- Trametes gibbosa* (Pers. ex Fr.) Fr.
- Trametes hirsuta* (Wulf. ex Fr.) Pilát
- Trametes pubescens* (Schum. ex Fr.) Pilát
- Trametes versicolor* (L. ex Fr.) Pilát
- Trechispora cohaerens* (Schwein.) Jülich &
Stalpers
- Trechispora farinacea* (Pers. ex Fr.) Liberta
- Trechispora mollusca* (Pers. ex Fr.) Liberta
- Trechispora* sp.
- Trichaptum abietinum* (Pers. ex Fr.) Ryv.
- Trichaptum fuscoviolaceum* (Ehrenb. ex Fr.)
Ryv.
- Tubulicrinis accedens* (Bourd. & Galz.) Donk
- Tubulicrinis angustus* (Rogers & Weresub)
Donk
- Tubulicrinis globisporus* K.-H. Larss. & Hjortst.
- Tubulicrinis gracillimus* (Ellis & Everh. ex
Rogers & Jacks.) Cunn.
- Tubulicrinis medius* (Bourd. & Galz.) Oberw.
- Tubulicrinis regificus* (Jacks. & Dearden) Donk
- Tubulicrinis sororius* (Bourd. & Galz.) Oberw.
- Tubulicrinis subulatus* (Bourd. & Galz.) Donk
- Tulasnella calospora* (Boud.) Juel
- Tulasnella* sp.
- Tulasnella violea* (Quél.) Bourd. & Galz.
- Tylospora asterophora* (Bon.) Donk
- Tylospora fibrillosa* (Burt) Donk
- Tyromyces caesius* (Schröd. ex Fr.) Murrill
- Tyromyces subcaesius* David
- Vesiculomyces citrinus* (Pers.) Hagström
- Vuilleminia comedens* (Nees ex Fr.) Maire
- Xenasma pruinatum* (Pat.) Donk