

# Variation of morphological characters in the lichenicolous ascomycete genus *Abrothallus*

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The morphological variation of 65 samples of the exclusively lichenicolous ascomycete genus *Abrothallus* was studied by means of multivariate statistical approach (discriminant analysis). The samples were analysed in order to estimate the possible taxonomic implications of the characters frequently mentioned in literature. Colour of the epihymenium and hypothecium, shape of the ascomata, pruinosity of the ascomata, and Lugol reaction of the hyphae appeared to be the most distinguishing features for group recognition.

**Key words:** *Abrothallus*, Ascomycetes, host specificity, morphological variation, taxonomy

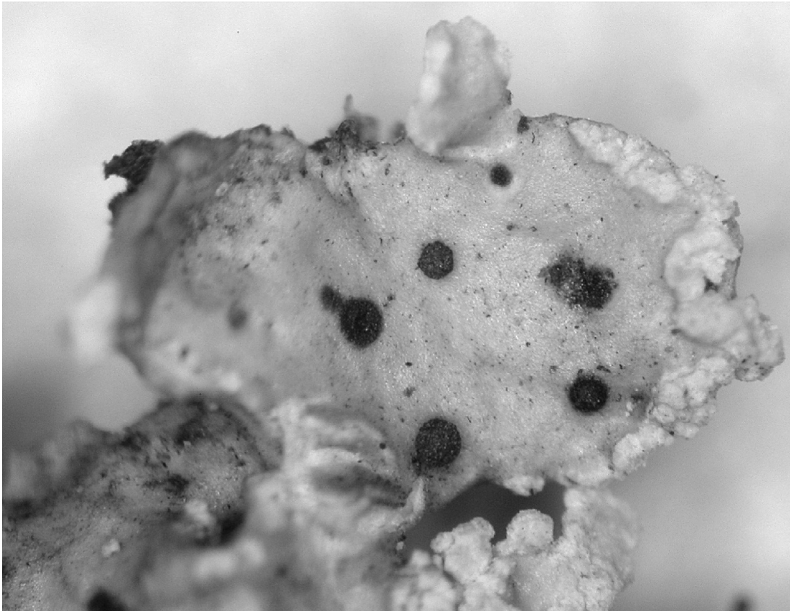
## Introduction

The ascomycete genus *Abrothallus* (Ascomycota, *incertae sedis*) was introduced by de Notaris (1845) to accommodate *A. bertianus*. However, the genus was originally described as a lichen because of the misinterpretation of the host thallus. A few years later it was confirmed to be a lichenicolous fungus (Montagne 1851). Still, even in subsequent studies, *Abrothallus* was included either in *lichenes athallii* (Tulasne 1852) or *microlichens* (Lindsay 1857, 1869).

The question about the systematic position of *Abrothallus* has remained unclear due to the fact that the genus has no clear similarities with any other genera. A relationship with the family Phacidiaceae (Saccardo 1889) or with the orders Arthoniales (Jatta 1911, Bellemere *et al.* 1986) and Patellariales (Keissler 1930, Nannfeldt 1932)

has been proposed. Still, in modern classification systems of Ascomycota (Kirk *et al.* 2001, and <http://www.umu.se/myconet/M10a.html>), the position of *Abrothallus* remains uncertain.

Various taxa have been introduced in the genus, many of which have later been transferred to other genera, such as *Arthonia*, *Clypeococcum*, *Dactylospora*, and *Phacopsis* (e.g. Zahlbruckner 1924, 1931, Hawksworth 1977, Hafellner 1979, Triebel & Rambold 1988). According to the current circumscription, the genus comprises ca. 20 species, known on a wide range of hosts, especially Parmeliaceae (e.g. *Melanohalea*, *Melanelixia*, *Parmelia*, *Platismatia*, *Usnea*, etc.), but also Lobariaceae (*Sticta*, *Nephroma*, *Pseudocyphellaria*), Ramalinaceae (*Ramalina*), Stereocaulaceae (*Stereocaulon*) and Cladoniaceae (*Cladonia*). The genus is cosmopolitan, known from the Arctic (Alstrup & Hawksworth 1990)



**Fig. 1.** Ascomata of *Abrothallus* specimen on thallus of *Vulpicida pinastri*. (Photo A. Saag).



**Fig. 2.** Cross-section of *Abrothallus* specimen on *Parmelia* spp. (Photo A. Suija).

as well as from tropical regions (Wedin 1994, Etayo 2002).

*Abrothallus* is a rather well-defined genus morphologically: (1) globose or almost globose immarginate ascomata, sometimes with golden or green pruina, (2) bitunicate asci with four to eight ascospores, (3) brown, 2- to 4-celled, warted asymmetric ascospores, (4) ramified-anastomosed paraphyses, and (5) the epihy-

menium layer with granulose pigments which often dissolve in potassium hydroxide (KOH) (Figs. 1 and 2). In many cases, pycnidia of the *Vouauxiomyces* type have been found mixed with ascomata. Already Tulasne (1852) proposed that the pycnidia represent an imperfect state of *Abrothallus*.

Despite the clear circumscription of the genus, the subgeneric division has been a subject of dispute (Lindsay 1857, Kotte 1909, Keissler 1930, Santesson 1960) and of different interpretations (Hawksworth 1983, Clauzade *et al.* 1989, Santesson 1993, Santesson *et al.* 2004) for a long time: both broad (e.g. Keissler 1930, Hawksworth 1983, Santesson 1993) and narrow definitions of species have been used (e.g. Kotte 1909, Clauzade *et al.* 1989, Santesson *et al.* 2004). The confusion is caused by different levels of significance attributed to the relevant characters by various authors. For example, Kotte (1909) emphasized the importance of the iodine reaction of the vegetative hyphae, dimensions of ascospores and conidia as well as preference to a certain host as diagnostic features for species delimitation. In contrast, Keissler (1930) denied the taxonomical meaning of the iodine reaction and host preference, using characters such as presence of greenish pruina over ascomata, colour of epihymenium and reaction of hymenium with

KOH (K) instead. In the most recent complex treatments of lichenicolous fungi (Clauzade *et al.* 1989, Nash *et al.* 2004), the authors favoured the narrow species concepts proposed by Kotte (1909), applying, however, some additional characters used by Keissler (1930), such as pruinosity of ascomata, hymenium reaction with K, etc.

This study is a first step towards an assessment of the status of some 2-celled taxa of *Abrothallus* regarding the generic characters and their relative importance. The aim is to elucidate the host specificity of the genus and the value of the characters frequently used in the literature.

## Material and methods

### Material

Dried herbarium specimens (C, H, S, TU, UPS, UGDA-L) were used for the analysis of morphological features. The quantity of the material from different hosts and the availability of healthy specimens were the main criteria for material selection. In the final analysis, 65 specimens from eight different hosts were exploited. The main criterion for group separation was host specificity: (1) specimens on *Hypogymnia physodes* (in the further text *Hyp*), (2) on *Melanohalea* spp. (*Mel*), (3) on *Parmelia* spp. (*Par*), (4) on *Platismatia* spp. (*Pla*), (5) on *Sticta* spp. (*Sti*), (6) on *Usnea* spp. (*Usn*), (7) on *Vulpicida* spp. (*Vul*), (8) on *Xanthoparmelia* spp. (*Xan*).

### Microscopy

Character examination was carried out with the stereomicroscope TECHNIVAL 2 (Carl Zeiss Jena) (magnification 50×) and with the light microscope Olympus CX41 (magnification 1200×). Routine methods of light microscopy were used: cross-sections were made with a razor blade, at first the sections were mounted in tap water and later in ca. 10% KOH (K) or Lugol's solution (I, Fluka 62650). The iodine reaction of the vegetative hyphae was examined without pre-treatment with K. The procedure was performed twice to avoid the amyloid reaction remaining unnoticed. All measurements

were made in the water medium. Microphotographs were taken with the digital camera Olympus Camedia Z4040.

### Characters

Morphological characters for analysis were selected according to two criteria: (1) they were proposed as diagnostic in earlier studies (Kotte 1909, Hawksworth 1983, Clauzade *et al.* 1989, Diederich 1989), and (2) they were relatively easy to observe. The number of characters was higher initially but some of them (e.g. hymenium height) were not used later. The reaction with K, which has been considered to be important in species delimitation, was excluded because of rather constant positive greenish reaction shown on most of the studied specimens. The only difference was observed in its intensity (*see also* Calatayud & Barreno 1995).

As the colour of the epihymenium ranges from brown to dark red, this character was divided in two clearly distinguishable, but not transitional, character states. The shape of the ascomata was visually appraised by the dominance of either a flattened or a globose type. The ascomata of almost half of the examined specimens were mixed with the pycnidia of the *Vouauxiomyces* type. In some cases only one or two pycnidia were found. In other cases, mainly in older herbarium specimens, the conidiomata were empty. Therefore, in only two groups, *Vul* and *Xan*, the conidiomata were sufficiently mature to make an adequate number of measurements of conidia.

The dimensions of ascomata, ascospores and conidia were measured at least in ten replications, the dimensions of asci in two to five replications. The width of each ascospore cell was measured and treated as two separate characters. The width of the ascus was measured from the broadest point. Altogether sixteen characters were finally selected, among them six characters were quantitative, eight characters were qualitative, and two were calculated ratios.

List of the characters used and their abbreviations:

ASCD = diameter of the ascoma (mm),

ASLEN = length of the ascospore ( $\mu\text{m}$ ),  
 ASWI1 = width of the broader cell of the ascospore ( $\mu\text{m}$ ),  
 ASWI2 = width of the narrower cell of the ascospore ( $\mu\text{m}$ ),  
 ASRA = ratio of ascospore length to the width of the broader cell,  
 ASCLEN = length of the ascus ( $\mu\text{m}$ ),  
 ASCWI = width of the ascus ( $\mu\text{m}$ ),  
 ASCRA = ratio of ascus length to ascus width,  
 HYMCO = colour of the epihymenium (0 = dark red, 1 = brown),  
 LUG = reaction of sterile hyphae with Lugol's solution (0 = negative reaction, 1 = positive reaction),  
 ASCP = pruinosity of the ascomata (0 – without green pruina, 1 – with green pruina),  
 HYPOL = colour of the hypothecium (0 = dark brown, 1 = brown, 2 = light brown),  
 ASCS = shape of the ascomata (0 = globose, 1 = flattened),  
 CONID = presence/absence of conidiomata (0 = absence, 1 = presence),  
 CONLEN = length of the conidium ( $\mu\text{m}$ ),  
 CONWI = width of the conidium ( $\mu\text{m}$ ).

## Statistical methods

In order to test the concordance of the conventional and predicted identifications of individu-

als, classificatory discriminant analysis (DA) was applied with Statistica 6.0 (Statsoft Inc. 2001). Data were analysed with standard methods of discriminant analysis. As characters 1 to 14 were observed in all studied specimens, they were selected for testing with this multivariate statistical method. Two separate discriminant analyses were performed. At first, the classification matrix was calculated where all specimens were grouped according to their host species. In the second classification matrix, two groups of specimens on *Parmelia* spp. were segregated according to the reaction of the hyphae with Lugol solution: *Par+* specimens with a positive blue reaction and *Par-* with a negative reaction.

Means, standard deviations, minimum and maximum values were calculated for each specimen and for each quantitative character. Mean values of quantitative characters (ASLEN, ASWI1, ASWI2, ASRA, ASCD, ASCLEN, ASCWI) were compared pairwise with Student's *t*-test. Comparison of the characters CONLEN and CONWI was applied only for the groups *Vul* and *Xan*.

## Results

Summary of the distribution of the qualitative characters is presented in Table 1 and the descriptive statistics of the quantitative characters in Table 2.

**Table 1.** Distribution of qualitative characters. For abbreviations of group names and characters, see Material and methods; pos. = positive, neg. = negative, d. brown = dark brown, l. brown = light brown, *n* = number of studied specimens.

Character		<i>Hyp</i> ( <i>n</i> = 4)	<i>Mel</i> ( <i>n</i> = 7)	<i>Par</i> ( <i>n</i> = 18)	<i>Pla</i> ( <i>n</i> = 10)	<i>Sti</i> ( <i>n</i> = 4)	<i>Usn</i> ( <i>n</i> = 6)	<i>Vul</i> ( <i>n</i> = 9)	<i>Xan</i> ( <i>n</i> = 7)
HYMCO	red	4	0	0	0	0	6	0	0
	brown	0	7	18	10	4	0	9	7
LUG	neg.	4	1	8	1	0	0	0	0
	pos.	0	6	10	9	4	6	9	7
CONID	absence	4	5	11	5	2	0	0	1
	presence	0	2	7	5	2	6	9	6
ASCP	without	4	5	14	3	0	6	9	7
	with	0	2	4	7	4	0	0	0
HYPOL	d. brown	2	1	6	0	1	3	7	7
	brown	0	1	5	4	2	0	0	0
	l. brown	2	5	7	6	1	3	2	0
ASCS	globose	2	7	2	0	0	6	1	2
	flattened	2	0	16	10	4	0	8	5

The results of the first classificatory discriminant analysis (DA) showed a classification accuracy of 88% (Table 3). According to DA, 8 of a total of 65 individuals were re-classified into another group. The lowest rate of classification accuracy was observed for *Vul* (67%), in which two misclassified specimens were mixed with *Xan* and the other one with *Par*. The distinction

of *Hyp*, *Mel*, *Usn*, *Pla* and *Sti* from the rest was obvious: the proportion of correctly classified specimens was 100%.

The proportion of correctly classified specimens in the second analysis was rather similar to that in the first analysis (86%), and nine specimens were re-grouped (Table 4). The observed classification was entirely in accordance with

**Table 2.** Mean values and standard deviations of qualitative characteristics of analyzed groups (mean  $\pm$  S.E.). For abbreviations of characters and groups, see Material and methods.

Character	<i>Hyp</i> (n = 4)	<i>Mel</i> (n = 7)	<i>Par</i> (n = 18)	<i>Pla</i> (n = 10)	<i>Sti</i> (n = 4)	<i>Usn</i> (n = 6)	<i>Vul</i> (n = 9)	<i>Xan</i> (n = 7)
ASCD (mm)	0.24 $\pm$ 0.07	0.24 $\pm$ 0.07	0.28 $\pm$ 0.09	0.28 $\pm$ 0.08	0.44 $\pm$ 0.13	0.26 $\pm$ 0.11	0.23 $\pm$ 0.06	0.24 $\pm$ 0.06
ASLEN ( $\mu$ m)	12.96 $\pm$ 1.14	12.32 $\pm$ 1.65	14.16 $\pm$ 1.49	13.55 $\pm$ 1.3	15.14 $\pm$ 1.44	10.93 $\pm$ 1.08	11.49 $\pm$ 1.19	13.7 $\pm$ 1.46
ASWI1 ( $\mu$ m)	5.28 $\pm$ 0.78	4.68 $\pm$ 0.58	5.39 $\pm$ 0.69	5.15 $\pm$ 0.56	6.19 $\pm$ 1.44	4.7 $\pm$ 0.5	4.68 $\pm$ 0.52	5.36 $\pm$ 0.63
ASWI2 ( $\mu$ m)	4.42 $\pm$ 0.66	3.94 $\pm$ 0.55	4.4 $\pm$ 0.68	4.16 $\pm$ 0.49	5.12 $\pm$ 0.54	3.87 $\pm$ 0.37	3.87 $\pm$ 0.55	4.46 $\pm$ 0.6
ASRA	2.5 $\pm$ 0.38	2.66 $\pm$ 0.38	2.67 $\pm$ 0.42	2.66 $\pm$ 0.34	2.46 $\pm$ 0.24	2.34 $\pm$ 0.27	2.48 $\pm$ 0.36	2.58 $\pm$ 0.38
ASCLEN ( $\mu$ m)	45.47 $\pm$ 5.47	42.07 $\pm$ 6.26	48.45 $\pm$ 6.96	45.53 $\pm$ 6.64	54.84 $\pm$ 7.63	45.03 $\pm$ 7.4	40.64 $\pm$ 5.11	41.85 $\pm$ 6.26
ASCWI ( $\mu$ m)	12.59 $\pm$ 1.92	11.48 $\pm$ 1.17	11.96 $\pm$ 1.68	11.42 $\pm$ 1.26	13.32 $\pm$ 1.62	10.08 $\pm$ 1.18	11.02 $\pm$ 1.77	12.15 $\pm$ 1.68
ASCRA	3.76 $\pm$ 0.88	3.7 $\pm$ 0.65	4.15 $\pm$ 0.91	4.05 $\pm$ 0.85	4.2 $\pm$ 0.75	4.56 $\pm$ 1.07	3.8 $\pm$ 0.85	3.5 $\pm$ 0.69
CONLEN ( $\mu$ m)							6.17 $\pm$ 0.84	10.51 $\pm$ 2.78
CONWI ( $\mu$ m)							4.2 $\pm$ 0.54	3.78 $\pm$ 0.79

**Table 3.** Classification matrix I. Rows: observed classifications. Columns: predicted classifications. The number in brackets after the group name corresponds to the number of specimens.

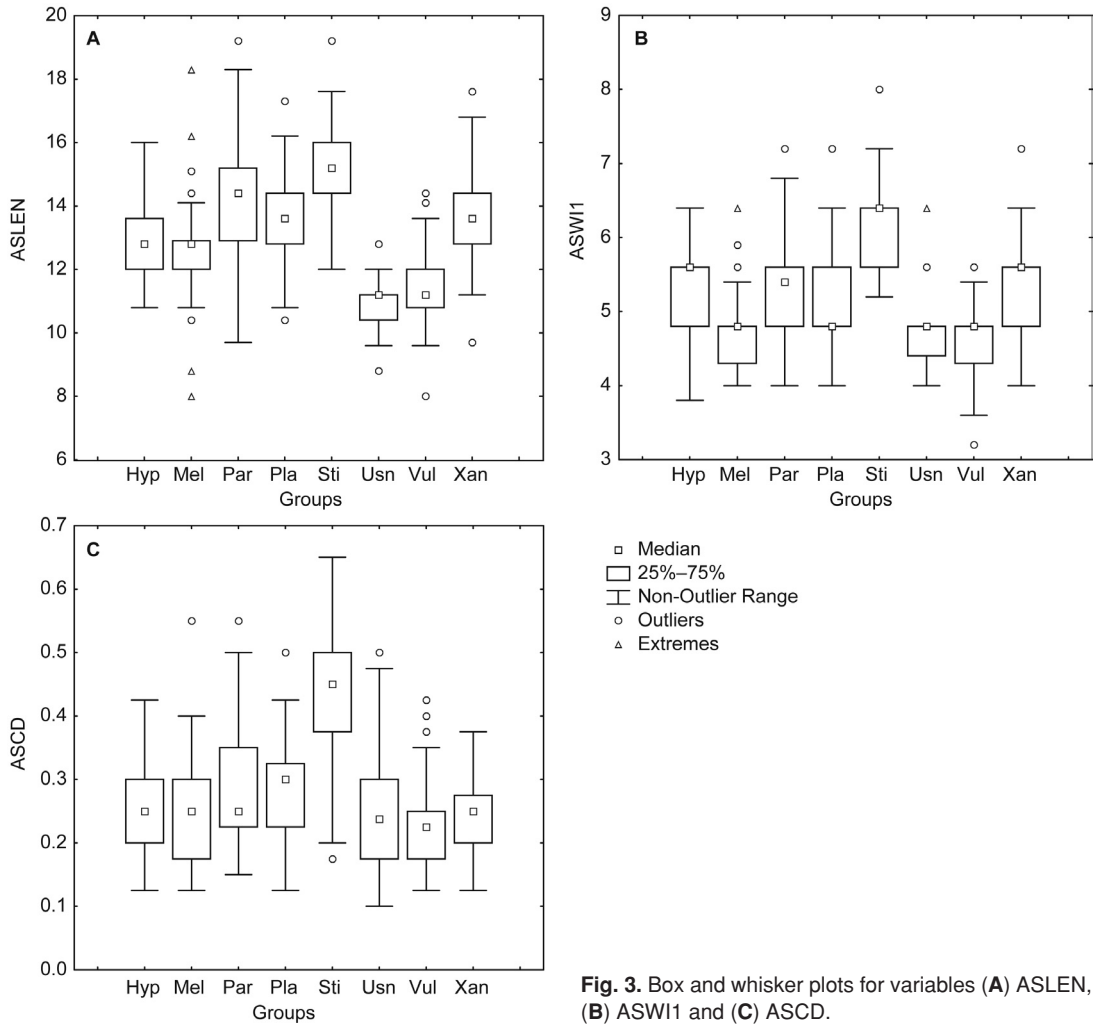
Group	% correct	<i>Hyp</i>	<i>Mel</i>	<i>Par</i>	<i>Pla</i>	<i>Sti</i>	<i>Usn</i>	<i>Vul</i>	<i>Xan</i>
<i>Hyp</i> (4)	100	4	0	0	0	0	0	0	0
<i>Mel</i> (7)	100	0	7	0	0	0	0	0	0
<i>Par</i> (18)	78	1	2	14	2	0	0	0	0
<i>Pla</i> (10)	100	0	0	0	10	0	0	0	0
<i>Sti</i> (4)	100	0	0	0	0	4	0	0	0
<i>Usn</i> (6)	100	0	0	0	0	0	6	0	0
<i>Vul</i> (9)	67	0	0	0	1	0	0	6	2
<i>Xan</i> (7)	86	0	0	0	0	0	0	1	6
Total	88	5	9	14	10	4	6	8	6

**Table 4.** Classification matrix II. Rows: observed classifications. Columns: predicted classifications. The number in brackets after the group name corresponds to the number of specimens.

Group	% correct	<i>Hyp</i>	<i>Mel</i>	<i>Par</i> -	<i>Par</i> +	<i>Pla</i>	<i>Sti</i>	<i>Usn</i>	<i>Vul</i>	<i>Xan</i>
<i>Hyp</i> (4)	100	4	0	0	0	0	0	0	0	0
<i>Mel</i> (7)	86	0	6	1	0	0	0	0	0	0
<i>Par</i> - (8)	100	0	0	8	0	0	0	0	0	0
<i>Par</i> + (10)	70	0	1	0	7	2	0	0	0	0
<i>Pla</i> (10)	80	0	0	1	1	8	0	0	0	0
<i>Sti</i> (4)	100	0	0	0	0	0	4	0	0	0
<i>Usn</i> (6)	100	0	0	0	0	0	0	6	0	0
<i>Vul</i> (9)	78	0	0	0	0	1	0	0	7	1
<i>Xan</i> (7)	86	0	0	0	0	0	0	0	1	6
Total	86	4	7	10	8	11	4	6	8	7







**Fig. 3.** Box and whisker plots for variables (A) ASLEN, (B) ASWI1 and (C) ASCD.

according to the presence or absence of this reaction. In this case, all *Par* specimens with a negative reaction (*Par*<sup>-</sup>) were correctly classified, contrary to the specimens with a positive blue reaction (*Par*<sup>+</sup>), which were mixed with *Mel* and *Pla* (Table 4).

Finally, a character with rather a high discriminative power was also the presence or absence of greenish pruina on ascomata (ASCP). Four groups (*Hyp*, *Usn*, *Vul* and *Xan*) out of the eight were characterized by absence and one group (*Sti*) by presence of this character (Table 1). The situation was more complicated with *Mel*, *Par* and *Pla*, in which pruinose ascomata were common but not constant. It is notable that greenish pruina was best developed on younger ascomata, but were not always observed on older ones.

According to DA, quantitative characters such as dimensions of ascomata, ascospores and asci were insignificant for group separation (Table 5). Still, for some groups the *t*-test showed a statistically significant ( $p < 0.05$ ) distinction (Table 6). The specimens of *Sti* differed from all others in the quantitative characters ASCD, ASLEN, ASWI1 and ASWI2: the mean values of both ascomata and ascospores were higher than the corresponding values of the rest of the taxa (Table 2 and Fig. 3A–C). There occurred also intrinsic distinction between *Usn* and *Vul* regarding the ascospore dimensions: the ascospores in these groups were on average shorter than those in the other groups (Table 2 and Fig. 3A) but there was no significant distinction between *Vul* and *Usn*.

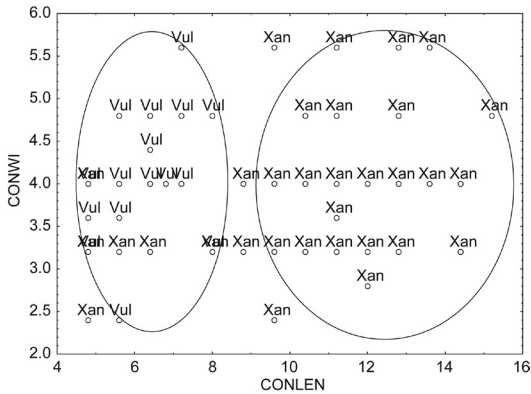


Fig. 4. Distribution of variables CONLEN and CONWI in groups *Vul* and *Xan*.

Although the size of conidia has been considered to be a distinctive character, at least for some taxa, in the studied material only *Vul* and *Xan* possessed enough mature conidiomata to test their discrepancy. According to the *t*-test, the distinction of the conidia between these two groups was statistically significant: the conidia of *Xan* were longer and more slender in comparison with those of *Vul*, which were shorter and thicker (Table 2 and Fig. 4).

## Discussion

*Abrothallus*, containing exclusively lichenicolous taxa, is a rather well known and widespread genus whose taxonomic relationships are unclear. Despite the distinctness of the genus, its subgeneric division is still a subject of interpretation. For this preliminary study, eight conventionally identified groups were tested to estimate host specificity and the value of the characters used in previous studies (Kotte 1909, Keissler 1930, Hawksworth 1983, Clauzade *et al.* 1989, Diederich 1989).

Discriminant analysis demonstrated that at least three groups (*Usn*, *Sti*, *Hyp*) can be well defined by the proposed morphological characters (Table 3). In addition, groups *Vul* and *Xan*, which are distinct from the other groups but not so distinct from each other by their ascomatal characters, were clearly distinguishable by their pycnidial characters (Table 2 and Fig. 4). However, the morphological boundaries of the groups

*Par*, *Mel* and *Pla* remained unclear and require further examination (Tables 3 and 4).

Two of the characters, presence of green pruina over ascomata and amyloid reaction of vegetative hyphae, which were considered in most studies (e.g. Kotte 1909, Keissler 1930, Hawksworth 1983, Clauzade *et al.* 1989, Diederich 2004), showed more variation than expected. The presence of greenish pruina, which has been considered to be one of the main diagnostic characteristics in *Abrothallus* (Keissler 1930, Hawksworth 1983, Clauzade *et al.* 1989), seems to be mainly applicable to younger ascomata (*see* the note in Hawksworth 1983). Moreover, in older herbarium specimens, the pruina might be swept off. Problems related to the pruina as a taxonomic character have also been pointed out in studies of lichenized fungi (Heidmarsson 1996). Hence, even if the character itself seems to be advantageous, one has to be careful when applying it in taxonomic studies.

Colour reactions with iodine solutions as diagnostic markers have been routinely used in the systematics of non-lichenized and lichenized fungi (reviews in Baral 1987, Common 1991). In *Abrothallus* systematics, the reaction of vegetative hyphae with Lugol reactive has been applied to subgeneric division since the publication by Kotte (1909). At the same time, exploitation of amyloid reaction in separation of *Abrothallus* species has been questioned in some earlier studies (Schaechtelin & Werner 1927, Keissler 1930), partly because of the difficulties with observation (Schaechtelin & Werner 1927).

Considering the studied material, the presence or absence of amyloid reaction seems to be a useful feature in taxon delimitation. There was one exception: the group *Par* included a more or less equal number of specimens with a positive reaction and specimens with a negative reaction (Table 1), which may indicate that more than one *Abrothallus* species can grow on the host genus *Parmelia*. Therefore, a second discriminant analysis, where the specimens of *Par* were further grouped according to the presence or absence of this reaction, was performed. Based on this analysis, all specimens of *Par* with a negative reaction (*Par*-) plus one specimen of *Mel* and one of *Pla* formed a distinct entity. Although the group *Par* with a positive reaction (*Par*+) showed low



resolution, a similar trend was observed: the misclassified specimens were grouped into *Mel* and *Pla*, and *vice versa* (Table 4).

The data on diaspore (ascospores, conidia) dimensions vary in literature because of the different species concepts used (e.g. Kotte 1909, Hawksworth 1983, Diederich 1989) or because of overly generalized data (Clauzade *et al.* 1989). Both make comparison of the variation rates of diaspores with corresponding literature data difficult or even impossible. Although, according to DA, the dimensions of ascospores and ascomata were insignificant for grouping, yet comparison of the mean values revealed some significant trends. Based on the presented data, the length, width and the length/width ratio of ascospores serve as useful distinguishing characters for the specimen groups *Sti*, *Usn* and *Vul* (Table 6).

It has been supposed that the conidiomata referred to as the anamorph genus *Vouauxiomyces* represent an asexual stage of *Abrothallus* (Tulasne 1852, Kotte 1909, Galløe 1950, Nordin 1964, Hawksworth 1981, Wedin 1994). However, this evidence is based on the frequent co-occurrence of ascomata and conidiomata and has not yet been proved by additional culture experiments. The anamorph may also appear regularly without the teleomorph (Hawksworth 1981, Kondratyuk 1996). Considering literature data (Kotte 1909, Hawksworth 1981, 1983, Clauzade *et al.* 1989) as well as the present data, the characters originating from the imperfect state of *Abrothallus* are also acceptable in delimitation of taxa. In the present study, the distinction between *Vul* and *Xan* was more evident by the size (and shape) of conidia than by the characters of ascomata.

## Conclusions

The analyses based on 65 samples from eight host genera showed a clear tendency towards host specificity in the exclusively lichenicolous genus *Abrothallus*. This finding, however, was not so clear for specimens growing on *Parmelia* (*Par*), *Melanohalea* (*Mel*) and *Platismatia* (*Pla*). Recent achievements in elucidating phylogenetic relationships within the lichen family Parmeliaceae (e.g. Crespo & Cubero 1998, Blanco *et*

*al.* 2004) indicate rather a high affinity between the above lichen genera. Theoretically, the phylogeny of host taxa may also elucidate the phylogeny of their parasites.

The usefulness of several anatomical-morphological characters (i.e. pruinosity of ascomata, amyloid reaction of hyphae, colour of the epihymenium) for taxon separation was supported by discriminant analysis. In addition, for recognition of *Abrothallus* on *Sticta* spp. (*Sti*), *Vulpicida* spp. (*Vul*) and *Usnea* spp. (*Usn*), dimensions of ascospores proved statistically significant. For distinguishing between *Abrothallus* on *Vulpicida* spp. (*Vul*) and *Abrothallus* on *Xanthoparmelia* spp. (*Xan*), the characters of the anamorph appeared to be better indicators than the characters of the teleomorph.

The obtained results are in good agreement with the contemporary standpoint about the high host-specificity of the lichenicolous fungi (Lawrey & Diederich 2003). However, further detailed research of the complicated taxonomy of *Abrothallus* requires more material from different host lichens and more specific characters (e.g. DNA sequences, anamorph characters) as well as aspects of pathogenity.

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## Appendix. Examined specimens

*Hyp*: *Hypogymnia physodes* with *Abrothallus* sp. **Estonia**: Pärnu county, Halinga forestry, on *Betula* sp. 1999 Jüriado (TU), Herb. MSC. no. 5715. *A. prodiens*, parasitic on *Hypogymnia physodes* on twig of *Salix aurita* at the border of the bog. **Sweden**: Småland, S of Ljungby, the raised bog Gölsjömossa alt. 140 m. 1970 Christiansen coll. no. 70.664a, det. Alstrup (C), Arnold, Lich. Monac. Exs. 452. *A. parmeliarum* auf *Imbricaria physodes* (= *Hypogymnia p.*) an dünnen Fichtenzweigen in einem Wäldchen bei Grosshesselohe, München. 1896 Schnabl (C), *A. parmeliarum* on *Parmelia physodes* (= *Hypogymnia p.*). 1892 Wegner (S-F30159).

*Mel*: *Abrothallus* sp. on *Parmelia olivacea* (= *Melanohalea o.*). **Russia**: Buryatia. Chamar-Daban mountains. On *Abies sibirica*. 1979 Trass (TU), *A. bertianus* on *Melanelia olivacea* (= *Melanohalea o.*). **Estonia**: Viljandi county, park in Polli, on *Betula verrucosa*. 1957 Siinmaa (TU), *A. bertianus* on *Melanelia olivacea* (= *Melanohalea o.*). Ida-Viru county, pine forest in Aa, on *Pinus sylvestris*. 1945 Parmasto (TU-3785), Hepp, Flechten Eur. 319. *A. Smithii* auf *Imbricaria olivacea* (= *Melanohalea o.*) on S öfan im Waldn bei Eichstätt. 1865 Arnold (C), Herbarium MSC no. 2305. *A. parmeliarum*, parasitic on *Parmelia olivacea* (= *Melanohalea o.*). **Norway**: Oppland, Vang, on birch (*Betula pubescens*) in the birch copse near northern shore of the lake Helin, alt. ab. 900 m a.s.l. 1982 Christiansen coll. no. 82.237 (C), From an incomplete set: Santesson, Fungi Lichenicoli Exs. 1. *A. bertianus* on *Parmelia olivacea* (= *Melanohalea o.*). **Sweden**: Väsmanland, Kila par., N of the lake Stävresjon. On a fallen *Betula* in a *Populus tremula-Corylus avellana* grove. 1965 Nordin coll. no. 2954 (C).

*Par*: *Parmelia saxatilis* with *Abrothallus* sp. **Russia**: Sakhalin, Ostrososhevka bay, on cliffs. 1990 Paal (TU), *Parmelia saxatilis* with *Abrothallus* sp. **Finland**: Sav. Kuopio, in saxis rudis. 1905 Lönnbohm (TU), *Parmelia saxatilis* f. *furfuracea* with *Abrothallus* sp. **Russia**: Kamchatka (TU), *Parmelia saxatilis* with *Abrothallus* sp. **Russia**: Buryatia, Chamar-Daban mountains, Misiha. On *Abies sibirica*. 1981 Pärn (TU), *A. parmeliarum* on *Parmelia sulcata*. **Estonia**: Lääne county, Vormsi island, Hullo. 1968 Kubo (TU-3782), *A. parmeliarum* parasitic on *Parmelia omphalodes*. **Faroe Islands**: Streymoy, Hoyvik. Alt. 15 m a.s.l. 1985 Alstrup coll. no. 851526 (C), *A. parmeliarum* parasitic on *Parmelia saxatilis*. **Greenland**: Narsaaq district, S slope of Narsaaq Fjeld. Alt. 120 m. 1978 Alstrup coll. no. 243927 (C), *A. parmeliarum* on *Parmelia saxatilis*. **Greenland**: Sukkertoppen distr., Kangerdluarssuk, Qivåge. Alt. 50 m a.s.l. 1977 Alstrup coll. no. 77996a (C), *A. parmeliarum* parasitic on *Parmelia saxatilis*. **Greenland**: Narsaaq district. Alt. 30 m. 1980 Alstrup coll. no. 80653 (C), *A. parmeliarum* parasitic on *Parmelia sulcata*. **Germany**: Schleswig-Holstein, Krs. Flensburg, an Eichen im Jerrishöer Holz. 1926 Erichsen coll. no. 5456 (C), *A. Smithii* on *Imbricaria saxatilis* (= *Parmelia s.*). **Sweden**: Nässjö. 1869 (C), *A. parmeliarum*. **Canada**: British Columbia, Sphats Falls Lower Oroboreal Subzone (Interior Cedar – Hemlock Zone). On *Parmelia*. 1994 Alstrup coll. no. C1404 (C), Herb. MSC no. 6400. *A. parmeliarum* parasitic on *Parmelia saxatilis*. **U.S.A.**: Idaho, Valley County. *Parmelia* on granitic rocks mixed open *Pinus ponderosa* and *Pseudotsuga* forest South Fork of the Salmon River 40 miles upstream from its confluence with the Main Salmon. 4050 ft. 1983 Rosentrater #3558 (C), Herb. MSC no. 7074. Lichenes Exsiccati prepared by G. K. Merrill. 204. *Buellia Parmeliarum* parasitic on *Parmelia sulcata*. **U.S.A.**: Rockland, Maine. 1910 Merrill (C), *A. parmeliarum* on *Parmelia fraudans*. **Norway**: Finmark, Kautekelno county, Avzzi, 7 km E of Kautokeino. W side of Lake Loav'skajav'ri. E-exposed, vertical greenstone rock. Alt. 300–350 m. 1983 Søchting coll. no. 4186, det. 1986 Alstrup (C), From an incomplete set: Santesson, Fungi Lichenicoli Exs. 2. *A. parmeliarum* on *Parmelia sulcata*. **Sweden**: Jämtland, Åre par., S of Stortävlan (WSW of Storlien). Alt. ca. 550 m. On trunks of birch in a birch-forest. 1948 Santesson coll. no. 48.320 (C), From an incomplete set: Santesson, Fungi Lichenicoli Exs. 126. *A. bertianus* on *Parmelia fraudans*. **Greenland**: West Greenland, head of the northern branch of Søndre Strømfjord (Kangerdlugssuaq), in the scree at the foot of Mt. Hassel. Alt. 50–100 m. Growing over mosses or on a thin layer of loess soil on the horizontal surface of boulders. 1946 Christiansen coll. no. 5455, det. Santesson (H), Herb. MSC. no. 5518. *Parmelia saxatilis*, ca. fung. *A. parmeliarum* + *Vouauxiomyces santessonii*. **Greenland**: South Greenland, Narssarsuaq, at the head of the Tunugdliarfik Fjord, on boulder in a copse of *Betula pubescens* in a valley, alt. 0–50 m. (Coll. WG – 232, b). Christiansen, det. 1989 Hawksworth & Alstrup (C), *A. parmeliarum*. **Sweden**: Hälsingland. Paroec. Ängersjö, Turegården fra ilen. 1902 Östman (S-F30111), *A. parmeliarum* + *Nesolechia oxyspora*. **U.S.A.**: Alaska, ca. 300 km NNW Fairbanks, ca. 400 m E Dalton highway at mile 180.2. Mixed coniferous/deciduous forest 50–300 m N Marion Creek. On *Betula* sp. Alt. ca. 370 m. 1989 Thor coll. no. 8882 (S-F30133), Santesson: Fungi Lichenicoli Exs. 227. *A. parmeliarum* on *Parmelia saxatilis*. **Spain**: Navarra, W of Pamplona, Sierra de Urbasa, Pto de Urbasa. On *Fagus*. 1991 Diederich coll. no. 9649 & Etayo (S-F30141).

*Pla*: Räsänen, Lich. Fenn. Exs. Fasc. XX (nr. 951–1000). 1000. *A. parmeliarum*. **Finland**: Karelia borealis, Rautavaara, Pappilanmäki prope templum. Super thallum *Cetrariae glaucae* (= *Platismatia glauca*) in piceeto. 1945 Mannerkorpi (TU), *A. parmeliarum* on *Cetraria glauca* (= *Platismatia g.*). **Finland**: Ks. Kuusamo. Maanselkä. Forest of *Hylocomium-Myrtillus*-type. On branches of spruce. 1964 Ulvinen (TU), *A. parmeliarum* on *Platismatia glauca*. **Norway**: N-Trøndelag, Overhalla ca 1 km W of Foss. Alt. 50–100 m. Old spruce forest. Boreal rain forest. 1993 Alstrup (C), From an incomplete set: Santesson, Fungi Lichenicoli Exs. 127. *A. parmeliarum* on *Platismatia glauca*. **Sweden**: Jämtland, Åre par., Storlinen ca. 1 km NE of Brudslöjan waterfall. Alt. ca. 500 m. On the trunk of a *Picea abies* in a *Picea* forest. 1948 Santesson coll. no. 48466 (C), *A. parmeliarum*. **Sweden**: Jämtland, Åre par., Enafors, Enaforsholm, Alt.: 600 m. On *Cetraria* (= *Platismatia*) upon *Picea*. 1978 Søchting (C), *A. cetrariae*. **Ukraine**: Gory Czywczynskie, Preluki, na *Platismatia glauca* na *Picea*. 1934 Sulma (UGDA-L), *A. parmeliarum* på *Cetraria glauca* (= *Platismatia g.*). **Sweden**: Jämtland, Åre s:n. 2 km SSO om Enafors. På gran i tät granskog. ca. 550 m ö.h. 1948 Santesson coll. no. 48.459a (S-F30116), Santesson: Fungi Lichenicoli Exs. 176. *A. parmeliarum* on *Platismatia*

*norvegica*. **Norway:** Nord-Trøndelag, Overhalla par., ca. 1 km W of Foss. Old spruce forest. Boreal rain forest. 1993 *Santesson* coll. no. 33565 (S-F30124), *A. cetrariae* auf *Cetraria glauca* (= *Platismatia* g.). **Italy:** Südtirol, Paneveggio. 1907 *Zopf* (S-F30179), *A. Smithii*. *Lojka* no. 1246 (S-30221).

*Sti:* *A. secendens*, parasite on *Sticta limbata*. **U.S.A.:** Lane County, Oregon. Dune wetland mosaic, often dense shrubs and broken *Pinus contorta*-*Pinus sitchensis* forest. BLM property, just inland from Heceta Beach, immediate coast. 2 km N of Florence, OR & 5 km inland from ocean. *Rosentrater* #9029, det. *Alstrup* (C), Leighton, Lich. Brit. Exs. 191. *A. welwitschii* parasitic on *Sticta fuliginosa*. **England:** New Cut, Meadfort, Torquay, Devon (H), *A. welwitschii*. **Madeira:** Vista Navios. 1.3 km SW of Poiso. Alt. 1400 m. On *Vaccinium maderense*. Host: *Sticta limbata*. 1969 *Tibell* coll. no. 3257, rev. 1980 *Santesson* (UPS-(L-118594) 223971), *Santesson*, Fungi Lichenicoli Exs. 201. *A. welwitschii* on *Sticta limbata*. **Canary Islands:** La Palma, Cumbre Nueva, 1 km N of Refugio Forestal. Alt. ca. 1450 m. In the outskirts of a *Pinus canariensis*-forest, on the trunk of a *Pinus canariensis*. 1991 *Hafellner* coll. no. 23524 (S-F30094).

*Usn:* Herb. MSC. no. 5930. *A. usneae* forming mycocecidia on *Usnea rigida* (fix 786–788) or hyperparasite on *Biatoropsis usnearum*. **France** (Cantal, Auvergne): Plomb du Cantal. Forêt du Lioren, on the trunk of old silver fir in a wood of silver fir mixed with beech, alt. ab. 1250 m. 1969 *Christiansen* coll. no. 69.051 (C), Herb. MSC no. 6120 *A. usneae* + *Biatoropsis usnearum*. **U.S.A.:** Oregon, Benton County, Kunley Wildlife Refuge 10 miles S of Corvallis, OR., *Quercus* woodland habitat, on *Quercus garyana*, alt. 300 ft. 1988 *Rosentrater et al.* coll. no. 4806 (C), Erik P. Vrang, Lichens Exs. *A. parmiliarum*. Königstuhl. 1880 (S-F30096), Arnold, Lich. Exs. 735. *A. usneae*. **Switzerland:** Parasitisch auf *Usnea barbata* im Sihlwalde bei Zürich. 1877 *Winter* (S-F30158), Rabenhorst, Lich. Europ. Exs. 551. *A. usneae* ad inter. Auf *Usnea florida* um Wallendorf in den Karpathen. *Kalchbrenner* (S-F30161), *A. usneae* auf *Usnea florida*. Sihlwald bei Zürich. 1877 *Winter* (S-F30165).

*Vul:* *Buellia smithii* on *Vulpicida pinastri*. **Estonia:** Järva county, mixed forest close to Varangu, on granite. 1946 *Parmasto* coll. no. 727/728. (TU), Norrlin, Herb. Lich. Fenn. Fasc. VII (1882). 331. *Lecidea parmiliarum* Sommerf. **Finland:** In Tavastia, Hersala (Hollola), supra *Platysma pinastri* (= *Vulpicida p.*). 1870 *Norrlin* (TU), *A. peyritchii* on *Vulpicida pinastri* on base of spruce. **U.S.A.:** Minnesota, Cook County, Canoe Area Wilderness, Muskeg Lake. Jack pine with small cliffs at the water's edge, mixed cedar, birch, fir, and spruce further from the water. 1996 *Cole*, coll. no. 4084, det. *Alstrup* (C), *A. peyritchii* on *Vulpicida pinastri*. **Estonia:** Harju county, close to Jägala factory, on *Juniperus communis*. 1937 *Aasamaa*, det. 2001 *Suija* (TU), *A. peyritchii* on *Vulpicida pinastri*. **Canada:** Ontario, Thunder Bay Dist., Slate Is., in lake Superior, Patterson I., McCreevy Har., on *Betula papyrifera* in rich forest on lake shore. 1958 *Ahti* coll. no. 3976 (H), *A. Smithii* auf *Cetraria pinastri* (= *Vulpicida p.*). **Germany:** Im Allgäu, ca. 3600 m. 1860 (S-F30170), *A. Parmiliarum* var. *Peyritchii* parasitisch auf *Platysma pinastri* (= *Vulpicida p.*) an Larixrinde am Hühnerspiel bei 1400 met. Oberhalb Gossensass in Tirol. 1878 *Stein* (S-F30219), *A. Smithii* auf *Cetraria pinastri* (= *Vulpicida p.*). Bei Obersdorf. *Rehm* (S-F30169).

*Xan:* *Xanthoparmelia somloensis* with *Abrothallus* sp. **Russia:** Evrejskaja avtonomnaja oblast. Oblutshje, on the foot of the mountain, on stones. 1961 *Pärn* (TU), *Santesson*: Fungi Lichenicoli Exs. 76. *A. bertianus* on *Parmelia taractica* (= *Xanthoparmelia somloensis*). **Sweden:** Uppland, Uppsala, between Norby and the stream Hågaån (not far from Norbylund). On open rocks in a meadow. 1946 *Santesson* (H), *A. parmiliarum* på *Parmelia stenophylla* (= *Xanthoparmelia somloensis*). **Sweden:** Bohuslän, Fjällbacken, Bräcke medre. 1945 (S-30255), *A. Vezda*: Lich. Sel. Exs. 1500. *A. bertianus*. **Czech Republic:** Moravia, distr. Brno: Veverská Bítýška, in valle fluminis prope arvesm Veveří, alt. m. s. n. Ad saxa silicea, in thallo *Parmeliae taracticae* (= *Xanthoparmelia somloensis*) vigens. 1974 *Vezda* (S-F30436), Krypt. Exs. 2761. *Abrothallus* sp. on *Parmelia taractica* (= *Xanthoparmelia somloensis*). **Norway:** Lyngør. Ad rupes maritimas. *Lynge* (S-F30435), Rabenhorst, Lich. Europ. Exs. 550. *A. Smithii* auf den Porfurblocken des "Breiten Berges", nordöflich von Wurzén (Sachsen) auf *Imbricaria* (Cfr. N. 90). gef. *Von Delitsch*. (S-F30153), *Santesson*: Fungi Lichenicoli Exs. 76. *A. bertianus* on *Parmelia taractica* auct. (= *Xanthoparmelia somloensis*). **Sweden:** Uppland, Uppsala, between Norby and the stream Hågaån (not far from Norbylund). On open rocks in a meadow. 1946 *Santesson* (S-F30257).