The Polyol Pattern, Chemotaxonomy, and Phylogeny of the Fungi *)

PFYFFER, Gaby E., PFYFFER, B. U. **) & RAST, Dora M.

Department of Plant Biology, University of Zürich,
CH-8008 Zürich, Switzerland, and

**) Department of Forestry, Canton of Lucerne, CH-6002 Lucerne, Switzerland

Abstract. – Acyclic polyols are widely distributed within the fungi and also represent the fungal metabolites studied most intensively. Therefore, the taxonomic evaluation of the alditol pattern of fungi suggests itself as a tool for a model testing of existing classifications at higher levels of hierarchy. To this aim, all data on the systematic distribution of polyols within the Eumycetes (nearly 600 records, representing some 400 species) have been processed with the database facility of the integrated software package Lotus® Symphony 1.1 installed on an IBM® PC XT. When delimiting groups on account of the polyol character (3 states: P_0, polyols absent; P_1, polyols, except mannitol, present; P_2, mannitol [and other polyols] present), the taxa thus formed coincide with the Oomycetes (P_0), the Zygo- and Hemiascomycetes (P_1), and the Chytridio-, Euasco-, Basidio-, and Deuteromycetes group (P_2), as defined by classical criteria. Not unexpectedly, the Blastomycetes are heterogeneous with respect to the polyol pattern. As judged from the very few apparent exceptions (5), the polyol character appears to be extremely conservative and, therefore, lends itself as a marker for the assignment of species of doubtful systematic position to conventional taxa, as well as for the unravelling of evolutionary relationships within the fungi. These patterns, together with other biochemical traits, are integrated into a phylogenetic scheme, using the classification system of AINSWORTH & al. (1971) as the reference.

Introduction

Traditionally, the taxonomy, systematics, and phylogeny of the fungi have been – and mostly still are – based on morphological traits, especially those displayed during reproductive behaviour (cf. [198]). In the continuous quest for an information retrieval system suitable for identification as well as for unravelling the evolution of the fungi, the use of such characters is not only firmly entrenched but also has been vigorously defended (cf. [179]). Nevertheless, this approach has its limitations, especially in cases where distinctive morphological features are scarce or lacking [83].

To compensate for these insufficiencies, various attempts have been made to determine molecular characteristics of fungi and, thence, to introduce chemical differential characters into fungal taxonomy [201, 9, 208, 216, 172, 173, 186, 187, 102, 171, 18, 19, 20,

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11]. However, many of these efforts have proved unsuccessful or, at the best, unsatisfactory, especially as systematics at higher levels of hierarchy is concerned. Thus, many characteristics studied have not displayed sufficient taxonomic 'resolving power', as e. g. the patterns of fatty acids [172, 173] and carotenoids [118, 11]. For others, the compounds concerned were found to be restricted to groupings of low taxonomic rank only, such as the confinement of psilocybin to *Psilocybe* and *Conocybe* species [207, 225], and of certain complex toxic cyclopeptides to *Amanita* [207, 225] and some *Galerina* [209] and *Lepiota* (cf. [34]) representatives. Occasionally, deductions have been made from studies encompassing merely a few species (e. g. the distribution of some non-protein amino acids in a few agarics [90]), or the chemical characteristics investigated could intrinsically not be expected to yield two-state criteria (e. g. the (G + C) percentage of DNA [187, 188], although a large number of species (ca. 500) was studied in this case).

The notable exceptions to this unsatisfactory situation concern differences in intermediates of the lysine biosynthetic pathway [216], in the sedimentation pattern of enzymes involved in tryptophan biogenesis [102], and in cell wall composition [9, 18, 19]. Thus, on the one hand, the Oomycetes are discrete by any of these three criteria and, on the other, the Zygomycetes by their unique combination of type of organization of the tryptophan pathway and of cell wall construction. The Chytridio-, Euasco-, Homobasidio-, and Deuteromycetes, finally, constitute one single group, inasmuch as their representatives display identical physico-chemical properties of the enzymes involved in tryptophan synthesis as well as a high degree of similarity in cell wall composition, with chitin as the major microfibrillar component. The coincidence of chemotaxonomic and conventional groupings – though data are based on a limited number of species (some 25, 20, and 90, respectively) – is indicative of the highly conservative nature of these traits and, thus, also of their highly predictive systematic value (cf. [93]).

To test further whether the employment of chemical data for the construction of general purpose as well as evolutionary classifications of the fungi, is, indeed, a feasible aim, a consideration of the distribution of the acyclic sugar alcohols (alditols: cf. [35]) suggests itself for a model investigation, because polyols in the free form are the fungal components studied most widely (see Results). The reasons for this are twofold: (1) as polyols crystallize easily from alcoholic solutions, their existence in fungi has been known for nearly two centuries [32, 111], and over this period a considerable amount of information on their distribution has been accumulated (see [231, 123, 156, 105]), particularly as – in contrast to earlier times – polyols are now assessed easily by gas-liquid chromatography [156], or by thin-layer chromatography using spray reagents which discriminate them from their corresponding monoses [87, 156, 224]; and (2) polyols have physiological functions, of which the storage of carbon and reducing power [123], involvement in the control of growth [61, 62] and of water potential [106], regulation of cytoplasmic pH value [105] and – where applicable – the maintenance of the proper chemical potential gradient for carbon movement in host-parasite associations [176] are presently the most favoured experimental hypotheses.

The aim of the present investigation was to compile all data on the identity and systematic distribution of acyclic sugar alcohols in the fungi and to delimit phenetic groups based on the polyol pattern of their component members, in order to possibly add another "objective criterion" (cf. [50, 16]) for classifying the fungi at higher taxonomic levels and to, thus, finally also gain further insight into their phylogeny.

Compilation, Systematic Evaluation, and Taxonomic Application of Data

This paper presents a comprehensive enumeration of the fungi that have been studied hitherto with respect to the occurrence of acyclic polyols. The species have been arranged either in alphabetical order (Tables 1–5), or according to the systematic scheme of Ainsworth & al. ([6]; Table 6). *Binomials are as stated by the authors themselves,* i. e. *any taxonomic or nomenclatural changes which might subsequently have occurred have been disregarded.* Hence, synonymy has not been accounted for. The lists do not include those studies of fungi not identified by their specific epithets, nor do they encompass works in which the presence of a particular sugar alcohol has not conclusively been established but simply been inferred from enzymic tests or from the similarity observed in the mobility of a compound with that of an authentic polyol using merely one single chromatographic method with limited sensitivity. Furthermore, reference is not made to papers stating the absence of a particular polyol in a given species if this has later been found to contain the compound in question. Finally, in view of a taxonomic evaluation of the data (see below), reports based on analyses of mixed fungus/plant or fungal/algal material have also been omitted, since the identity of the polyol-synthesizing partner of the associations remained uncertain. Reference to studies of this type that relate to phytopathogenic symbioses (sensu [46]) is made separately in Table 7. The possibility that fungal infection may elicit polyol formation in a green plant is not a far-fetched idea, because: (i) some vascular plants do contain polyols (mainly sorbitol or mannitol: see

[122]), and (ii) the green algal symbionts within lichens apparently synthesize a polyol but cease to do so upon removal of the fungus (see [46, 168]). On the other hand, works that explicitly state the absence of polyols even in phytopathogenic associations of fungi are included in Table 1. The computation was carried out on an IBM® model XT Personal Computer; the database was established with Lotus® Symphony 1.1 (Lotus Development Corp., Cambridge, MA, USA).

The present study comprises nearly 600 records relating to approximately 400 different species representing some 1.3% of the lower and 1.0% of the higher fungi, respectively (based on the estimated total number of species given in [6]). To date, the occurrence of at least one polyol has been reported in some 390 species (Table 2), whereas the absence of sugar alcohols has been established in 7 species (Table 1) – all Oomycetes (cf. Table 6). The other lower fungi are heterogeneous with regard to their polyol pattern: beside of glycerol, ribitol is present in Zygomycetes, and mannitol in Chytridiomycetes. Throughout the higher fungi – except the Hemiascomycetes – mannitol is being accumulated. The most versatile organisms with respect to polyol synthesis appear to be clustered within the Ascomycetes-Heterobasidiomycetes-Deuteromycetes group, inasmuch as glycerol, erythritol, threitol, ribitol, arabitol, xylitol, dulcitol, and sorbitol may be present, e. g. in *Claviceps purpurea, Puccinia graminis tritici,* and *Pyrenochaeta terrestris* (Table 6). The polyol pattern of the Homobasidiomycetes, finally, consists almost exclusively of mannitol, as other polyols have only occasionally been found.

Groups of species (A-E: Tables 1–5) have been made according to the following criteria: (i) absence of polyols, (ii) presence of polyols, (iii) presence of polyols, except mannitol, (iv) presence of mannitol (and other polyols), and (v) presence of uncommon polyols. As judged by classical criteria (see Introduction) group A consists entirely of representatives of the Oomycetes (see also above), whereas all species of group B belong to the Chytridio-, Asco-, Basidio-, or the Deuteromycetes. Group B is subdivided into the groups C and D by the criteria (iii) and (iv) as detailed in Tables 3 and 4. Group D encompasses only members of the higher fungi and Chytridiomycetes, group C Zygomycetes and, for the rest, mostly yeasts (Hemiascomycetes as well as Blastomycetes). The appearance, in group C, of a representative of the genus *Torula,* i. e. of a hyphomycete, is almost certainly due to a taxonomic mis-statement as to the fungus actually analyzed, which appears to have been *Candida utilis,* not *Torula utilis*, as judged from the description of the experimental organism by the authors themselves [71] as well as from the notions of Barnett & al. [19] and Ahearn [5] that *C. utilis* is often wrongly referred to as

Table 1: Chemotaxonomy of fungi: group of species containing no polyols in the water-soluble fraction (group A)

Achlya radiosa 156	*Phytophthora cinnamomi* 156
Albugo tragopogonis 126	*Phytophthora infestans* 30
Peronospora parasitica 202	*Plasmopara viticola* 30, 33
Phytophthora cactorum 27	

Torula yeast. Since all Homobasidiomycetes species analyzed and also the Hyphomycetes do synthesize mannitol (see Table 6), it can, furthermore, safely be assumed that the three *Penicillia* listed in group C have simply not been thoroughly searched for the presence of the hexitol and it, hence, appears justified to allocate them in the neighbourhood of group D. This may also hold for some Blastomycetes listed in group C. In comprising either Hemiascomycetes (most of which contain arabitol) or Zygomycetes (in which the occurrence of ribitol is common: see above), the remainder of group C consists of two well-defined entities. That the group of species synthesizing a rare polyol (group E: Table 5), *viz* threitol, ribitol, xylitol, dulcitol, sorbitol, volemitol, *meso-glycero-ido*-heptitol, or D-*glycero*-D-*ido*-heptitol, would, as a whole, be heterogeneous with respect to the position in conventional systematics of the organism concerned was to be expected, since these substances are in themselves structurally and, conceivably, also biosynthetically (see [105]) quite different, and since gain of the ability to elaborate a given rare secondary compound by singular members of phylogenetically even very distant lines is a fairly common phenomenon (see [66, 89, 206, 34]). Also, compounds which appear erratically are generally suitable for systematic purposes only at low taxonomic level (species, or below: cf. [91]) and not for the study of taxa of higher ranks as aimed at in the present investigation (see Introduction). Nevertheless, despite of its conceptionally artificial character, group E has been established and its members presented in Table 5 – for the sake of completeness of this compilation.

When now delimiting chemosystematic taxa on account of the characters P_0 (no polyols present), P_1 (a polyol, except mannitol, present), and P_2 (mannitol present), the three groups obtained coincide with (1) the Oomycetes, (2) the Zygo- and Hemiascomycetes, and (3) the Chytridio-, Euasco-, Basidio-, and Deuteromycetes group (except some Imperfect Yeasts), as shown by Table 6. Heterogeneity of the Blastomycetes as to the polyol pattern cannot be a surprise. These and the (apparent) exceptions, i. e. the absence of mannitol in *“T.” utilis* and some *Penicillia* (see also above), as well as the P_2-pattern of *Coccidioides immitis* and of *Byssochlamys* species (see Tables 4 and 6) are dealt with in the Discussion.

Table 2: Chemotaxonomy of fungi: group of species containing free polyol(s) (group B). * References are not given separately to the original publications antedating this review article.

Acanthocystis petaloides 72
Acetabula vulgaris 231*
Actinomucor elegans 156, 157
Agaricus arvensis 28
Agaricus bisporus 166, 60, 81, 59, 61, 182, 84, 155
Agaricus campester 72, 163
Agaricus campestris 134, 63
Agaricus eryngii 231*
Agaricus silvaticus 28
Agaricus silvicola 72
Agaricus xanthoderma 72
Allomyces arbuscula 156
Alternaria alternata 101
Alternaria tenuissima 156
Amanita aspera 231*
Amanita bulbosa 231*
Amanita caesarea 231*, 28
Amanita citrina 72, 28
Amanita muscaria 231*, 72, 28
Amanita pantherina 231*, 28
Amanita phalloides 72, 28
Amanita porphyria 28
Amanita rubescens 231*, 28
Amanita vaginata 231*
Amanitopsis vaginata 28
Armillaria caligata 103
Armillaria mellea 231*, 25, 155, 130, 79
Armillariella mellea 72
Ascobolus stercorarius 156
Aspergillus candidus 175, 190, 143
Aspergillus clavatus 98
Aspergillus elegans 23, 80
Aspergillus fischeri 162
Aspergillus glaucus 228
Aspergillus nidulans 23
Aspergillus niger 230, 15, 117, 2
Aspergillus oryzae 192, 99
Aspergillus terreus 184, 116
Aspergillus versicolor 85
Aspergillus wentii 24

Blastocladiella emersonii 156
Boletus aereus 28
Boletus appendiculatus 231*
Boletus aurantiacus 231*
Boletus badius 231*
Boletus bovinus 231*, 219, 103, 74
Boletus calopus 231*
Boletus chrysenteron 231*
Boletus cyanescens 231*
Boletus edulis 231*, 103, 28, 166
Boletus erythropus 231*, 155
Boletus luridus 231*, 28
Boletus luteus 231*, 103
Boletus pachypus 231*
Boletus pruinatus 231*
Boletus rufus 72, 28
Boletus satanas 28
Boletus scaber 231*, 28
Boletus subtomentosus 231*, 103
Boletus variegatus 231*
Botrytis cinerea 117, 154, 30
Bulgaria inquinans 231*, 72
Byssochlamys fulva 165
Byssochlamys nivea 156

Candida albicans 22, 158
Candida arborea 148
Candida diddensii 78
Candida guilliermondii 150, 196, 170, 68
Candida lipolytica 197
Candida parapsilosis 22
Candida pelliculosa 109
Candida polymorpha 146, 148, 151, 196
Candida pseudotropicalis 22
Candida tropicalis 146, 22, 78
Candida utilis 100, 154
Candida zeylanoides 86

Table 3: Chemosystematics of fungi: polyol-synthesizing organisms not reported to contain free mannitol (group C)

Actinomucor elegans 156, 157

Candida albicans 122, 158
Candida arborea 148
Candida diddensii 78
Candida guilliermondii 150, 196, 170, 68
Candida parapsilosis 22
Candida pelliculosa 109
Candida polymorpha 146, 148, 151, 196
Candida pseudotropicalis 22
Candida tropicalis 146, 22, 78
Circinella mucoroides 51
Circinella muscae 51
Circinella rigida 51
Circinella simplex 51
Circinella umbellata 51

Debaryomyces hansenii 150, 1
Debaryomyces sake 146, 195

Hansenula anomala 146
Hansenula suaveolens 196

Kluyveromyces fragilis 78

Mortierella ramanniana 156, 157
Mucor miehei 156, 157
Mucor mucedo 154
Mucor rouxii 156

Penicillium brevi-compactum 152
Penicillium cyclopium 152
Penicillium herquei 75
Phycomyces blakesleeanus 156
Pichia farinosa 146
Pichia guilliermondii 136
Pichia miso 146, 147, 195
Pichia quercibus 194, 196

Rhizopus oligosporus 154
Rhizopus stolonifer 156
Rhodosporidium toruloides 78
Rhodotorula graminis 55

Saccharomyces acidifaciens 196
Saccharomyces carlsbergensis 78
Saccharomyces cerevisiae 78
Saccharomyces diastaticus 78
Saccharomyces fragilis 146
Saccharomyces mellis 223
Saccharomyces monacensis 146
Saccharomyces paradoxus 146
Saccharomyces rouxii 146, 26, 104, 150, 196, 78
Saccharomyces sake 146, 78
Saccharomycopsis fibuligera 78
Schizosaccharomyces pombe 78
Syncephalastrum racemosum 51

Torula utilis 71
Torulopsis candida 78
Torulopsis famata 146, 196
Torulopsis halophila 196
Torulopsis magnoliae 82
Trichosporon melibiosaceum 78
Trigonopsis variabilis 151

Zygorhynchus moelleri 156, 157
Zygosaccharomyces acidifaciens 153
Zygosaccharomyces barkeri 153
Zygosaccharomyces fermentati 153
Zygosaccharomyces mandschuricus 153
Zygosaccharomyces mellis 153
Zygosaccharomyces nadsonii 153
Zygosaccharomyces nussbaumeri 153
Zygosaccharomyces priorianus 153
Zygosaccharomyces richteri 153
Zygosaccharomyces rugosus 153
Zygosaccharomyces wyocena 153

Table 4: Chemotaxonomy of fungi: group of species containing free mannitol (group D). * References are not given separately to the original publications antedating this review article.

Acanthocystis petaloides 72
Acetabula vulgaris 231 *
Agaricus arvensis 28
Agaricus bisporus 166, 60, 81, 59, 61, 182, 84, 155
Agaricus campester 72, 163
Agaricus campestris 134, 63
Agaricus eryngii 231 *
Agaricus silvaticus 28
Agaricus silvicola 72
Agaricus xanthoderma 72
Allomyces arbuscula 156
Alternaria alternata 101
Alternaria tenuissima 156
Amanita aspera 231 *
Amanita bulbosa 231 *
Amanita caesarea 231 *, 28
Amanita citrina 72, 28
Amanita muscaria 231 *, 72, 28
Amanita pantherina 231 *, 28
Amanita porphyria 28
Amanita rubescens 231 *, 28
Amanita phalloides 72, 28
Amanita vaginata 231 *
Amanitopsis vaginata 28
Armillaria caligata 103
Armillaria mellea 231 *, 155, 130, 79
Armillariella mellea 72
Ascobolus stercorarius 156
Aspergillus candidus 175, 190, 143
Aspergillus clavatus 98
Aspergillus elegans 23, 80
Aspergillus fischeri 162
Aspergillus glaucus 228
Aspergillus nidulans 23
Aspergillus niger 15, 117, 2
Aspergillus oryzae 192, 99
Aspergillus terreus 116
Aspergillus versicolor 85
Aspergillus wentii 24
Blastocladiella emersonii 156
Boletus aereus 28
Boletus appendiculatus 231 *
Boletus aurantiacus 231 *
Boletus badius 231 *
Boletus bovinus 231 *, 103
Boletus calopus 231 *
Boletus chrysenteron 231 *
Boletus cyanescens 231 *
Boletus edulis 231 *, 103, 28, 166
Boletus erythropus 231 *, 155
Boletus luridus 231 *, 28
Boletus luteus 231 *, 103
Boletus pachypus 231 *
Boletus pruinatus 231 *
Boletus rufus 72, 28
Boletus satanas 28
Boletus scaber 231 *, 28
Boletus subtomentosus 231 *, 103
Boletus variegatus 231 *
Botrytis cinerea 117, 154, 30
Bulgaria inquinans 231 *, 72
Byssochlamys fulva 165
Byssochlamys nivea 156
Candida lipolytica 197
Candida utilis 154
Candida zeylanoides 86
Cantharellus cibarius 231 *, 166
Cantharellus tubaeformis 231 *
Chaetomium elatum 156
Chaetomium globosum 3, 154
Clavaria aurea 72
Clavaria coralloides 231 *
Clavaria corniculata 96
Clavaria flava 231 *
Clavaria formosa 231 *, 103
Clavaria pistillaris 231 *, 28
Claviceps curreyana 47
Claviceps nigricans 47
Claviceps purpurea 231 *, 215, 47, 48
Clitocybe aurantiaca 28

Table 5: Chemosystematics of fungi: group of species containing free threitol, ribitol, xylitol, dulcitol, sorbitol, volemitol, *meso-glycero-ido*-heptitol, or D-*glycero*-D-*ido*-heptitol (group E)

Agaricus bisporus 59, 61
Armillaria mellea 25, 155, 130

Boletus bovinus 219
Boletus erythropus 155

Candida albicans 158
Candida diddensii 78
Candida guilliermondii 150, 170
Candida pelliculosa 109
Candida polymorpha 146, 148, 196
Candida tropicalis 146, 78
Candida utilis 100
Chaetomium elatum 156
Circinella mucoroides 51
Circinella muscae 51
Circinella rigida 51
Circinella simplex 51
Circinella umbellata 51
Claviceps purpurea 215, 48

Endothia parasitica 156

Geotrichum candidum 183

Hansenula anomala 146

Kluyveromyces fragilis 78

Lactarius volemus 31

Mucor miehei 156, 157
Mucor rouxii 156

Pichia farinosa 146
Pichia guilliermondii 136
Pichia miso 146, 147
Pichia quercibus 194
Pleurotus ostreatus 156
Poria vincta 130
Psalliota campestris 112
Puccinia graminis tritici 53, 131, 130, 133
Pyrenochaeta terrestris 226

Rhodosporidium toruloides 78
Rhodotorula graminis 55

Saccharomyces acidifaciens 196
Saccharomyces carlsbergensis 78
Saccharomyces cerevisiae 78
Saccharomyces diastaticus 78
Saccharomyces rouxii 146, 196, 78
Saccharomyces sake 78
Saccharomycopsis fibuligera 78
Schizophyllum commune 130
Schizosaccharomyces pombe 78
Sclerotinia sclerotiorum 221
Sporobolomyces roseus 130
Syncephalastrum racemosum 51

Torula utilis 71
Torulopsis candida 78
Torulopsis famata 146
Torulopsis versatilis 146
Trichosporon melibiosaceum 78

Zygorhynchus moelleri 156, 157

Discussion

Alditols in the free form have been found in autotrophs as well as heterotrophs, but especially occur in lower forms of life (see [88, 205, 159, 123, 204, 105]). In particular, most of the Eumycetes synthesize at least one polyol (mainly mannitol). Exceptions appear to be taxonomically restricted, or can otherwise be rationalized (see below). Thus, the Oomycetes lack polyols as a whole (Tables 1 and 6), and the Zygo- and Hemiascomycetes do seem not to elaborate mannitol (Tables 3 and 6). Therefore, the metabolism of soluble carbohydrates of the large majority of the fungi (i) displays likeness to that of the invertebrates, especially the arthropods (cf. [43]) – where mannitol is, however, replaced by sorbitol that, conversely, is rare among the fungi (Table 5) – (ii) resembles that of certain heterofermentative Lactobacillariaceae (cf. [57]), and (iii) sets off nicely against the corresponding features of the higher plants, although a few of them do synthesize mannitol, dulcitol or sorbitol (see below); but, then, there is co-occurrence with sucrose, and not with trehalose as in the Eumycetes, bacteria and invertebrates (cf. [65]).

Table 6: The distribution of polyols (G, E, T, R, A, X, M, D, S, V, H, I, 0) in the fungi. The major taxa are according to AINSWORTH & BISBY's Dictionary of the Fungi (1971); within these, species are listed in alphabetical order.

G	glycerol	X	xylitol	H	*meso-glycero-ido*-heptitol
E	erythritol	M	mannitol	I	D-*glycero*-D-*ido*-heptitol
T	threitol	D	dulcitol	0	no polyols
R	ribitol	S	sorbitol		
A	arabitol	V	volemitol		

MASTIGOMYCOTINA

	G	E	T	R	A	X	M	D	S	V	H	I	0
Oomycetes													
Achlya radiosa													0
Albugo tragopogonis													0
Peronospora parasitica													0
Phytophthora cactorum													0
Phytophthora cinnamomi													0
Phytophthora infestans													0
Plasmopara viticola													0
Chytridiomycetes													
Allomyces arbuscula	G						M						
Blastocladiella emersonii	G						M						

ZYGOMYCOTINA

	G	E	T	R	A	X	M	D	S	V	H	I	0
Zygomycetes													
Actinomucor elegans	G												
Circinella mucoroides				R									
Circinella muscae				R									
Circinella rigida				R									
Circinella simplex				R									
Circinella umbellata				R									
Coccidioides immitis							M						

Mortierella rammaniana	G								
Mucor miehei	G		R						
Mucor mucedo	G								
Mucor rouxii	G		R	A					
Phycomyces blakesleeanus	G								
Rhizopus oligosporus	G								
Rhizopus stolonifer	G								
Syncephalastrum racemosum			R						
Zygorhynchus moelleri	G		R						

ASCOMYCOTINA

Hemiascomycetes

Byssochlamys fulva						M			
Byssochlamys nivea	G	E				M			
Debaryomyces hansenii	G			A					
Debaryomyces sake				A					
Hansenula anomala	G			A			D		
Hansenula suaveolens				A					
Kluyveromyces fragilis					X				
Pichia farinosa				A			D		
Pichia guilliermondii			R	A					
Pichia miso	G	E		A	X		D	H	I
Pichia quercibus				A	X				
Saccharomyces acidifaciens	G			A	X				
Saccharomyces carlsbergensis					X				
Saccharomyces cerevisiae					X				
Saccharomyces diastaticus					X				
Saccharomyces fragilis	G			A					
Saccharomyces mellis				A					
Saccharomyces monacensis	G								
Saccharomyces paradoxus	G								
Saccharomyces rouxii	G			A	X		D		
Saccharomyces sake	G				X				
Saccharomycopsis fibuligera					X				
Schizosaccharomyces pombe					X				
Zygosaccharomyces acidifaciens	G			A					
Zygosaccharomyces barkeri	G			A					
Zygosaccharomyces fermentati				A					
Zygosaccharomyces mandschuricus				A					
Zygosaccharomyces mellis				A					
Zygosaccharomyces nadsonii	G			A					
Zygosaccharomyces nussbaumeri	G			A					
Zygosaccharomyces priorianus	G			A					
Zygosaccharomyces richteri	G			A					
Zygosaccharomyces rugosus	G			A					
Zygosaccharomyces wyocena	G			A					

Plectomycetes

Monascus ruber	G	E				M			

Pyrenomycetes

Chaetomium elatum			T		A		M		
Chaetomium globosum	G						M		
Claviceps curreyana					A		M		
Claviceps nigricans					A		M		
Claviceps purpurea	G	E	T		A	X	M	D	
Cochliobolus miyabeanus	G						M		
Endothia parasitica	G				A		M		S
Epichloe typhina							M		
Gelasinospora cerealis	G						M		
Gibberella fujikuroi	G				A		M		
Neurospora crassa							M		
Neurospora sitophila							M		
Xylaria polymorpha							M		

Discomycetes

Acetabula vulgaris							M		
Ascobolus stercorarius							M		
Bulgaria inquinans							M		
Coryne sarcoides	G				A		M		
Elaphomyces asperulus							M		
Elaphomyces echinatus							M		
Elaphomyces granulatus							M		
Elaphomyces leveillei							M		
Elaphomyces variegatus							M		
Galactinia olivacea							M		
Helvella esculenta							M		
Morchella conica							M		
Morchella esculenta							M		
Morchella semilibera							M		
Peziza badia							M		
Peziza nigra							M		
Peziza ochracea							M		
Peziza onotica							M		
Peziza venosa							M		
Sarcosphaera coronaria							M		
Sclerotinia curreyana					A		M		
Sclerotinia sclerotiorum	G			R	A	X	M	D	S
Sclerotinia tuberosa							M		
Tuber cibarium							M		

DEUTEROMYCOTINA

Blastomycetes

Candida albicans	G			R	A				
Candida arborea					A				
Candida diddensii						X			
Candida guilliermondii	G			R	A	X			
Candida lipolytica		E			A		M		
Candida parapsilosis					A				
Candida pelliculosa						X			
Candida polymorpha		E		R	A	X		D	

Candida pseudotropicalis				A				
Candida tropicalis	G			A	X		D	
Candida utilis	G			A	X	M	D	
Candida zeylanoides		E				M		
Cryptococcus neoformans	G					M		
Rhodotorula graminis	G			A				S
Sporobolomyces roseus		E		A	X	M		S
Torulopsis anomala	G					M		
Torulopsis candida					X			
Torulopsis famata		E		A			D	
Torulopsis halophila				A				
Torulopsis magnoliae	G							
Torulopsis mannitofaciens				A		M		
Torulopsis nodaensis	G			A		M		
Torulopsis versatilis	G			A		M	D	
Trichosporon melibiosaceum					X			
Trigonopsis variabilis		E						

Hyphomycetes

Alternaria alternata					M
Alternaria·tenuissima				A	M
Aspergillus candidus					M
Aspergillus clavatus	G	E	R	A	M
Aspergillus elegans					M
Aspergillus fischeri					M
Aspergillus glaucus					M
Aspergillus nidulans					M
Aspergillus niger	G	E		A	M
Aspergillus oryzae					M
Aspergillus terreus		E			M
Aspergillus versicolor					M
Aspergillus wentii	G				M
Botrytis cinerea	G			A	M
Dendryphiella salina	G			A	M
Fusarium solani					M
Geotrichum candidum	G	E	R	A	M
Helminthosporium geniculatum	G				M
Helminthosporium oryzae					M
Microsporum gypseum				A	M
Myrothecium verrucaria					M
Penicillium brefeldianum		E			M
Penicillium brevi-compactum		E			
Penicillium chrysogenum	G	E		A	M
Penicillium cyclopium		E			
Penicillium griseofulvum				A	M
Penicillium herquei		E			
Penicillium italicum	G	E		A	M
Penicillium notatum					M
Penicillium oxalicum	G	E		A	M
Phymatotrichum omnivorum					M
Pyricularia oryzae	G	E		A	M
Rhizoctonia repens					M
Rhizoctonia solani	G			A	M

Sterigmatocystis nigra							M		
Torula utilis								D	
Verticillium albo-atrum	G	E			A		M		
Verticillium dahliae	G	E			A		M		
Verticillium fungicola		E					M		
Verticillium intertextum	G				A		M		

Coelomycetes

Colletotrichum gloeosporioides					A		M		
Diplodia viticola					A		M		
Pyrenochaeta terrestris	G	E			A		M		S

BASIDIOMYCOTINA

Teliomycetes

Puccinia coronata							M		
Puccinia graminis tritici	G	E		R	A	X	M		S
Rhodosporidium toruloides						X			
Stereostratum corticoides							M		
Ustilago esculenta		E					M		
Ustilago maydis	G	E			A		M		
Ustilago nuda	G	E					M		

Hymenomycetes

Acanthocystis petaloides							M		
Agaricus arvensis							M		
Agaricus bisporus	G				A	X	M		
Agaricus campester							M		
Agaricus campestris							M		
Agaricus eryngii							M		
Agaricus silvaticus							M		
Agaricus silvicola							M		
Agaricus xanthoderma							M		
Amanita aspera							M		
Amanita bulbosa							M		
Amanita caesarea							M		
Amanita citrina							M		
Amanita muscaria							M		
Amanita pantherina							M		
Amanita phalloides							M		
Amanita porphyria							M		
Amanita rubescens							M		
Amanita vaginata							M		
Amanitopsis vaginata							M		
Armillaria caligata							M		
Armillaria mellea	G	E	T		A	X	M		S
Armillariella mellea							M		
Boletus aereus							M		
Boletus appendiculatus							M		
Boletus aurantiacus							M		

Boletus badius				M	
Boletus bovinus		A		M	S
Boletus calopus				M	
Boletus chrysenteron				M	
Boletus cyanescens				M	
Boletus edulis				M	
Boletus erythropus	G	A	X	M	
Boletus luridus				M	
Boletus luteus				M	
Boletus pachypus				M	
Boletus pruinatus				M	
Boletus rufus				M	
Boletus satanas				M	
Boletus scaber				M	
Boletus subtomentosus				M	
Boletus variegatus				M	
Cantharellus cibarius				M	
Cantharellus tubaeformis				M	
Clavaria aurea				M	
Clavaria coralloides				M	
Clavaria corniculata				M	
Clavaria flava				M	
Clavaria formosa				M	
Clavaria pistillaris				M	
Clitocybe aurantiaca				M	
Clitocybe cyanophaea				M	
Clitocybe geotropa				M	
Clitocybe infundibuliformis				M	
Clitocybe nebularis				M	
Clitocybe odora				M	
Clitocybe socialis				M	
Collybia butyracea				M	
Collybia confluens				M	
Collybia dryophila				M	
Collybia erythropus				M	
Collybia fusipes				M	
Collybia maculata				M	
Collybia platyphylla				M	
Coprinus atramentarius		A		M	
Coprinus comatus				M	
Coprinus friesii	G			M	
Coprinus micaceus				M	
Cordiceps capitata				M	
Coriolus versicolor				M	
Cortinarius alboviolaceus				M	
Cortinarius berkeleyi				M	
Cortinarius bivelus				M	
Cortinarius bolaris				M	
Cortinarius brunneus				M	
Cortinarius bulliardi				M	
Cortinarius collinitus				M	
Cortinarius elatior				M	
Cortinarius fulmineus				M	
Cortinarius infractus				M	
Cortinarius largus				M	

Cortinarius torvus		M
Cortinarius violaceus		M
Cortinellus shiitake		M
Craterellus cornucopioides		M
Crepidotus nidulans		M
Entoloma clypeatum		M
Entoloma lividum		M
Entoloma nidorosum		M
Entoloma sinuatum		M
Fistulina hepatica	A	M
Flammula spectabilis		M
Flammulina velutipes	A	M
Fomes ignarius		M
Gomphidius roseus		M
Gomphidius viscidus		M
Hydnum erinaceus		M
Hydnum ferrugineum		M
Hydnum hybridum		M
Hydnum imbricatum		M
Hydnum repandum		M
Hydnum squamosum		M
Hygrophoropsis aurantiaca		M
Hygrophorus agathosmus		M
Hygrophorus cossus		M
Hygrophorus hypotheius		M
Hygrophorus nemoreus		M
Hygrophorus olivaceo-albus		M
Hygrophorus virgineus		M
Hypholoma fasciculare		M
Hypholoma hydrophilum		M
Hypholoma sublateritium		M
Inocybe praetervisa		M
Ixocomus bovinus		M
Ixocomus luteus		M
Ixocomus piperatus		M
Ixocomus variegatus		M
Laccaria laccata		M
Lactarius blennius		M
Lactarius chrysorrheus		M
Lactarius controversus		M
Lactarius deliciosus		M
Lactarius musteus		M
Lactarius pallidus		M
Lactarius piperatus		M
Lactarius plumbeus		M
Lactarius pubescens		M
Lactarius pyrogalus		M
Lactarius quietus		M
Lactarius rufus		M
Lactarius subdulcis		M
Lactarius torminosus		M
Lactarius turpis		M
Lactarius uvidus		M
Lactarius vellereus		M
Lactarius vietus		M

Lactarius violascens					M		
Lactarius volemus					M		V
Lactarius zonarius					M		
Lentinus cochleatus					M		
Lentinus edodes			A		M		
Lenzites flaccida					M		
Lenzites saepiaria	G		A		M		
Lepidella vittadinii					M		
Lepiota clypeolaria					M		
Lepiota cristata					M		
Lepiota excoriata					M		
Lepiota friesii					M		
Lepiota procera					M		
Lepiota rhacodes					M		
Leucocoprinus rhacodes					M		
Marasmius hariolorum					M		
Melanopus squamosus					M		
Mycena galericulata	G		A		M		
Mycena pelianthina					M		
Nematoloma fasciculare					M		
Omphalia scyphoides					M		
Oudemansiella mucida	G		A		M		
Panus conchatus					M		
Panus stipticus					M		
Paxillus atrotomentosus					M		
Paxillus involutus					M		
Pholiota aurivella					M		
Pholiota lubrica		E	A		M		
Pholiota mutabilis					M		
Pholiota praecox					M		
Pholiota radicosa					M		
Pholiota togularis					M		
Pleurotus cornucopioides					M		
Pleurotus dryinus					M		
Pleurotus japonicus					M		
Pleurotus olearius					M		
Pleurotus ostreatus	G	E			M	S	
Pleurotus serinus					M		
Pluteus cervinus					M		
Pluteus pellitus					M		
Polyporus frondosus					M		
Polyporus intybaceus					M		
Polyporus officinalis					M		
Polyporus pomaceus					M		
Polyporus ptychogaster					M		
Polyporus robustus					M		
Polyporus umbellatus					M		
Poria vincta		E	A	X	M		
Psalliota arvensis					M		
Psalliota campestris				X	M		
Psalliota placomyces					M		
Psalliota silvicola					M		
Russula adusta					M		
Russula albonigra					M		
Russula coerulea					M		

Russula cyanoxantha							M		
Russula delica							M		
Russula drymeia							M		
Russula fellea							M		
Russula foetens							M		
Russula fragilis							M		
Russula integra							M		
Russula lepida							M		
Russula nigricans							M		
Russula ochroleuca		E					M		
Russula pseudoviolacea							M		
Russula queletii							M		
Russula sanguinea							M		
Russula sardonia							M		
Russula torulosa							M		
Russula virescens							M		
Sarcodon repandum							M		
Schizophyllum commune	G	E			A	X	M		S
Serpula lacrimans	G	E			A		M		
Spongipellis spumeus							M		
Tricholoma albo-brunneum							M		
Tricholoma album							M		
Tricholoma amarum							M		
Tricholoma columbetta							M		
Tricholoma equestre							M		
Tricholoma flavobrunneum							M		
Tricholoma nudum							M		
Tricholoma pessundatum							M		
Tricholoma resplendens							M		
Tricholoma russula							M		
Tricholoma sulfureum							M		
Tricholoma terreum							M		
Tricholoma ustale							M		
Tylopilus felleus							M		
Ungulina betulina							M		
Volvaria speciosa							M		
Volvaria volvacea							M		
Xerocomus badius	G						M		
Xerocomus chrysenteron							M		

Gasteromycetes

Geaster rufescens							M		
Lycoperdon pusillum							M		
Lycoperdon pyriforme							M		
Phallus impudicus							M		
Rhizopogon luteolus							M		
Scleroderma verrucosum							M		
Scleroderma vulgare							M		

Whereas in vascular plants some cases are quoted where the distribution of alditols seems to follow a systematic pattern (the presence of mannitol is characteristic of the Oleaceae and Apiaceae, dulcitol has been found in certain Celastrales and Scrophulariales, and sorbitol is synthesized by Rosaceae: for refs., see [177] and [122]), sugar alcohols have attracted hardly any attention in the taxonomy of fungi despite the fact that they represent the class of fungal compounds studied most widely (see Introduction).

Any consideration of polyols as taxonomic markers at higher levels of hierarchy requires their being not only widespread (what, indeed, holds: Tables 2 and 6) but also displaying constancy [54]. This appears to be the case: considering the factor most liable to influence the polyol composition of a fungus, i. e. the carbohydrate nutrient source, the polyol fraction expectedly varied quantitatively in response to changes in the medium composition inasmuch as mostly the synthesis of that alditol was favoured whose immediate sugar precursor served as the C-source (e. g. in *C. purpurea* [215], *P. terrestris* [226], and *S. sclerotiorum* [221]), whereas the general pattern of sugar alcohols remained constant under any of the conditions tested (studied extensively in *G. candidum* [42/1], *P. chrysogenum* [12], *S. sclerotiorum* [45], and *D. salina* [97], as well as in *A. bisporus, P. italicum,* and *Z. moelleri* [155]).

Using the criteria (i) absence of polyols (Table 1), (ii) presence of polyols, except mannitol (Table 3), and (iii) presence of mannitol (Table 4), three phenetic groups, displaying characters P_0, P_1, and P_2, were established. These perfectly coincide with taxa, or groups of taxa, as delimited in some widely accepted conventional classifications, i. e., the Oomycetes, the Zygo- and Hemiascomycetes, and the Chytridio-, Euasco-, Basidio-, and Deuteromycetes complex (for a discussion of the few apparent exceptions, see below). Thus, the P_0 group (Table 6) comprises only Oomycetes that also single out using three other biochemical markers, namely, the pathway of lysine biogenesis, the sedimentation pattern of enzymes of tryptophan biosynthesis, and the type of cell wall construction, with cellulose as the major microfibrillar component (characters L_1, T_1, and W_1, respectively: Fig. 1). The very special position of the Oomycetes with respect to all other classes of Eumycetes is, furthermore, underlined by additional chemical traits, i. e. the molecular weight of the 25 S ribosomal RNA components (Oomycetes, $1.4–1.43 \times 10^6$; all other fungi, $1.3–1.36 \times 10^6$: [127]), significant amounts of hydroxyprolin in cell wall protein [10], the presence of histones [164], and the occurrence of desmosterol, 24-methylene-cholesterol, and fucosterol – in the absence of ergosterol [135, 38, 164, 222]. Also, they do not accumulate polyphosphates, in contrast to representatives of all other groups of fungi [42/2]. When considering all these features, together with characters P_0, L_1, T_1 and W_1, it would be justified to ally the Oomycetes, or their respective ancestors, to green algae (see also [102, 164]), an opinion already brought forward on account of comparative morphology [76, 218, 40].

The P_1 group (Table 3) is homogeneous also with respect to the L character. It is subdivided into two taxa when considering the different states of characters T and W (T_2/T_3; W_2/W_3: chitosan/chitin *vs* mannan-glucan type as delimited by BARTNICKI-GARCIA [18, 19]; see Fig. 1) as well as the ability to synthesize trisporic acids [37, 210]. The phenetic groups thus obtained embody the Zygomycetes on the one hand, and the Hemiascomycetes on the other. In the former, accumulation of ribitol appears to prevail whereas arabitol is rare; for representatives of the Hemiascomycetes the reverse holds true (Table 6; see also [156]).

The component members of the Zygo- and Hemiascomycetes having polyol-synthesizing ability and state of character L in common with the Chytridio-, Euasco-, and Basidiomycetes indicates a monophyletic origin of all of these groups, with rhodophytean and/or phaeophytean types of organisms being discussed as precursors (cf. [164] and [142]). Because of their distinctive polyol pattern and other special chemical characteristics (see above and Fig. 1), the Zygomycetes did, however, probably separate early from the common ancestor pool originally shared with present-day higher fungi, as suggested already before [102, 19]. By the same token, the Hemiascomycetes would also represent a side-line from the main evolutionary trunk [102, 19]. When, additionally, considering characteristics of sexual reproductive behaviour, the Zygomycetes do, however, show a lower degree of phenetic and, hence, very likely also of cladistic relationship with the Euasco- and Basidiomycetes, although – *on account of the P, T and W characters only* – the diversity of the Zygomycetes from the latter two groups would be the same as that of the Hemiascomycetes. Supposing a closer kinship of the Ustilaginales with the Hemiascomycetes than with the other Basidiomycetes (cf. [76, 218]) and accounting for the fact that the *Ustilago* species studied are of the P_2-type (Table 6), one would have to conclude that the P_1-pattern of the Hemiascomycetes has arisen by a loss of the ability, or tendency, to synthesize mannitol. – For an interpretation of the fact that the P_1-group also contains (some) Blastomycetes, see below.

In contrast to all other groups of the lower fungi, the Chytridiomycetes posses the P_2 character ([156]; Table 6). An analogous situation exists with respect to the L, T and W characters (Fig. 1): in exhibiting the $L_2/T_4/W_5$ combination they are, thus, unique within the lower fungi and belong to the same phenetic group as the Euasco- and Basidiomycetes (as well as anamorphs assigned to them). Hence, chytridiomycetous fungi single out as the likely ancestors of these (Fig. 1), as proposed already on account of classical criteria (cf. [141]). For reasons detailed above, the Zygomycetes can, however, not represent a link between the Chytridiomycetes and the

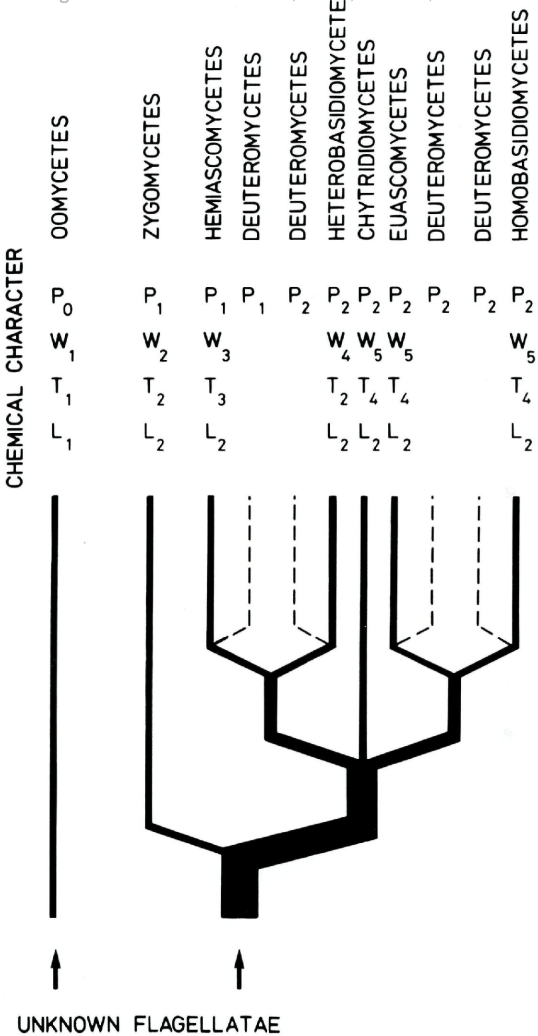

Fig. 1. Chemotaxonomy and macroevolutionary scheme of the Eumycetes, as based on classical criteria and chemical traits (polyol character: states P_0, P_1, and P_2 [this work]; cell wall composition: types W_1–W_5, partly according to BARTNICKI-GARCIA [18, 19]; organization of the tryptophan pathway: categories T_1–T_4 [102]; and lysine biosynthetic pathway: alternatives L_1 and L_2 [216]).

Euasco-, Basidio-, and Deuteromycetes group, an idea that has been strongly favoured by some classical mycologists [76, 110, 17], and rejected by others ([102, 19]; see also [141]).

Since the classification of fungi on account of their alditol composition affords groups that coincide almost completely with major taxa of a conventional, i. e. mainly morphologically-based classification (see caption to Fig. 1), and since the polyol pattern is retained even in dual organismic interactions (for refs. concerning phytopathogenic associations, see Table 7), the polyol character must be regarded as highly conservative and, therefore, entitles itself as a taxonomic marker (see also below). The correctness of this conclusion is underlined by the fact that the five situations not conforming to the general rule that Oomycetes are of the P_0-, Zygo- and Hemiascomycetes of the P_1-, and the other Eumycetes of the P_2-type, probably represent only apparent exceptions. The following reasons may account for these: (i) mis-quotation of the experimental organism (case *T. utilis* instead of *C. utilis* ([71]; see also above), or incomplete description of the material analyzed (case *Rhodosporidium toruloides,* a member of the Ustilaginales [14], where actually only the anamorph *Rhodotorula gracilis* has been studied [78], and which would, therefore, formally have to be included in the paragraph Blastomycetes of Table 6); (ii) incomplete analysis (*P. brevi-compactum* and *P. cyclopium* [152] as well as *P. herquei* [75] and possibly also *Rh. toruloides* anamorph [see also below] which should all be of the P_2-type); and (iii) doubtful position of species within the classification used here as the reference (cases *C. immitis* in the Zygomycetes, and *Byssochlamys* in the Hemiascomycetes, but both displaying the P_2- and not the P_1-character: see Table 6). The former has in the meantime been transferred to the Hyphomycetes [174]. Similarly, *Byssochlamys* is no longer held as belonging to the Hemiascomycetes, but to the Plectomycetes [185], where it is considered to be transitional between the Thermoascaceae and the Eurotiaceae [70].

The Blastomycetes is well known as the 'junk yard' of fungi growing in the yeast form that have a generally unknown teleomorph, or may not have any at all, and within which the "delimitation of a species is rather subjective", i. e. "largely depending on the insight and the ideas of the taxonomist studying the group" (cited from [124]). Heterogeneity even within a genus is, therefore, considered a common feature of the taxonomy of Imperfect Yeasts [124]. The *Candida-Torulopsis* group represents an extreme in this respect [213, 214]; in addition, the two are distinguished only by a "totally inadequate intergeneric criterion" [16]. – Hence, Blastomycetes is *eo ipso* an artificial taxon [124], its component members waiting for transfer into a systematically more established, natural (cf. [93])

Table 7: Polyol Synthesis in Phytopathogenic Associations

Fungus/Plant Association	Polyol pattern[a]	Reference
Claviceps purpurea/Secale sp.	A M	56
Claviceps purpurea/Triticum sp.	A M	56
Epichloe typhina/Agrocystis stolonifera	M	203
Erysiphe cichoracearum/ Cucumis sativus	G E A M	30
Erysiphe graminis hordei/Hordeum sp.	A M	64
Melampsora aecidioides/ Populus canescens	A M	169
Melampsora lini/Linum sp.	A M	140
Microsphaera alphitoides/Quercus robur	A M	92
Puccinia coronata avenae/Avena sativa	A M	138
Puccinia graminis tritici/ Triticum sativum	M	129
Puccinia graminis tritici/Triticum sp.	R A M S	131
Puccinia graminis tritici/ Triticum aestivum	A M	138
Puccinia malvacearum/Althaea rosea	A M	139
Puccinia pelargonii-zonalis/ Pelargonium inquinans	A M	139
Puccinia poarum/Tussilago farfara	A M	94, 95
Sclerotinia sclerotiorum/Daucus carota	M	45
Sclerotinia trifoliorum/Daucus carota	M	45
Uncinula necator/Vitis vinifera	A M	30, 33
Uromyces appendiculatus/ Vigna sesquipedalis	A M	180
Ustilago esculenta/Zizania caduciflora	E M	41

[a] For abbreviations, see caption to Table 6

group. Considering now the highly predictive value of the polyol pattern with respect to the position of a species within the major (other) higher taxa in a conventional classification system of the fungi (see Table 6 and above) and, therefore, also its high *a priori* weight (cf. [93]) for the assignment of a species of unknown systematic position to one of these, the application of the polyol character suggests itself as an "objective criterion" (see Introduction) for the taxonomy of Imperfect Yeasts. By this token, *C. lipolytica, C. utilis,* and *C. zeylanoides* (Tables 4 and 6) would have to be associated with Basidiomycetes and not with Hemiascomycetes. For some candidas the genus *Leucosporidium* has been established [69]. Also *C. albicans* has been regarded as a yeast of heterobasidiomycetous affinity [211]. However, this has never been confirmed by others, and based on our analyses, *C. albicans* appears to be of the P_1-type (and this irrespective of growth form [158]) – in contrast to *T. versatilis* (syn. *T. anomala* [214], after the transfer of *Torulopsis* to the genus *Candida* [229], now *C. versatilis*), *T. nodaensis* (nom. invalid. [214] =

C. nodaensis [229]), and *T. mannitofaciens* (nom. nud., see [16]). Similarly, *S. roseus* has since quite some time been considered to be of basidiomycetous nature ([124]; see also [13, 189]). For *C. neoformans,* finally, teleomorphs have been found that form basidiospores – though in a somewhat extravagant manner – and for which the genus *Filobasidiella* has been created [113–115]. The likelihood of a (hetero)basidiomycetous kinship of *C. neoformans* is further supported by its possessing the T_2-type (as do some *Tremella, Ustilago, Sporobolomyces,* and *Rhodotorula* species [102]), in addition to the P_2-character (Fig. 1), as well as its developing an intensely dark-red colour upon exposition to aqueous solutions of stabilized aromatic diazonium salts [212]). The other Blastomycetes species listed in Table 6 would have to be linked to Hemiascomycetes – if the analyses of their polyol composition are complete, a condition which, at least in some cases, does not seem to have yet been met (e. g. for some of the species studied by Salewski & al. [170], Miersch & al. [136], Bernard & al. [22], and Gong & al. [78]; for further refs., see Table 3).

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