

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

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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: P₀, polyols absent; P₁, polyols, except mannitol, present; P₂, mannitol [and other polyols] present), the taxa thus formed coincide with the Oomycetes (P₀), the Zygo- and Hemiascomycetes (P₁), and the Chytridio-, Euasco-, Basidio-, and Deuteromycetes group (P₂), 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,

*) Dedicated to Prof. Dr. Hans WANNER (Zürich, Switzerland) on the occasion of his 70th birthday.

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)

<i>Achlya radiosa</i> 156	<i>Phytophthora cinnamomi</i> 156
<i>Albugo tragopogonis</i> 126	<i>Phytophthora infestans</i> 30
<i>Peronospora parasitica</i> 202	<i>Plasmopara viticola</i> 30, 33
<i>Phytophthora cactorum</i> 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.

<i>Acanthocystis petaloides</i> 72	<i>Aspergillus versicolor</i> 85
<i>Acetabula vulgaris</i> 231 *	<i>Aspergillus wentii</i> 24
<i>Actinomucor elegans</i> 156, 157	
<i>Agaricus arvensis</i> 28	<i>Blastocladiella emersonii</i> 156
<i>Agaricus bisporus</i> 166, 60, 81, 59, 61, 182, 84, 155	<i>Boletus aereus</i> 28
<i>Agaricus campester</i> 72, 163	<i>Boletus appendiculatus</i> 231 *
<i>Agaricus campestris</i> 134, 63	<i>Boletus aurantiacus</i> 231 *
<i>Agaricus eryngii</i> 231 *	<i>Boletus badius</i> 231 *
<i>Agaricus silvaticus</i> 28	<i>Boletus bovinus</i> 231 *, 219, 103, 74
<i>Agaricus silvicola</i> 72	<i>Boletus calopus</i> 231 *
<i>Agaricus xanthoderma</i> 72	<i>Boletus chrysenteron</i> 231 *
<i>Allomyces arbuscula</i> 156	<i>Boletus cyanescens</i> 231 *
<i>Alternaria alternata</i> 101	<i>Boletus edulis</i> 231 *, 103, 28, 166
<i>Alternaria tenuissima</i> 156	<i>Boletus erythropus</i> 231 *, 155
<i>Amanita aspera</i> 231 *	<i>Boletus luridus</i> 231 *, 28
<i>Amanita bulbosa</i> 231 *	<i>Boletus luteus</i> 231 *, 103
<i>Amanita caesarea</i> 231 *, 28	<i>Boletus pachypus</i> 231 *
<i>Amanita citrina</i> 72, 28	<i>Boletus pruinatus</i> 231 *
<i>Amanita muscaria</i> 231 *, 72, 28	<i>Boletus rufus</i> 72, 28
<i>Amanita pantherina</i> 231 *, 28	<i>Boletus satanas</i> 28
<i>Amanita phalloides</i> 72, 28	<i>Boletus scaber</i> 231 *, 28
<i>Amanita porphyria</i> 28	<i>Boletus subtomentosus</i> 231 *, 103
<i>Amanita rubescens</i> 231 *, 28	<i>Boletus variegatus</i> 231 *
<i>Amanita vaginata</i> 231 *	<i>Botrytis cinerea</i> 117, 154, 30
<i>Amanitopsis vaginata</i> 28	<i>Bulgaria inquinans</i> 231 *, 72
<i>Armillaria caligata</i> 103	<i>Byssochlamys fulva</i> 165
<i>Armillaria mellea</i> 231 *, 25, 155, 130, 79	<i>Byssochlamys nivea</i> 156
<i>Armillariella mellea</i> 72	<i>Candida albicans</i> 22, 158
<i>Ascobolus stercorarius</i> 156	<i>Candida arborea</i> 148
<i>Aspergillus candidus</i> 175, 190, 143	<i>Candida diddensii</i> 78
<i>Aspergillus clavatus</i> 98	<i>Candida guilliermondii</i> 150, 196, 170, 68
<i>Aspergillus elegans</i> 23, 80	<i>Candida lipolytica</i> 197
<i>Aspergillus fischeri</i> 162	<i>Candida parapsilosis</i> 22
<i>Aspergillus glaucus</i> 228	<i>Candida pelliculosa</i> 109
<i>Aspergillus nidulans</i> 23	<i>Candida polymorpha</i> 146, 148, 151, 196
<i>Aspergillus niger</i> 230, 15, 117, 2	<i>Candida pseudotropicalis</i> 22
<i>Aspergillus oryzae</i> 192, 99	<i>Candida tropicalis</i> 146, 22, 78
<i>Aspergillus terreus</i> 184, 116	<i>Candida utilis</i> 100, 154
	<i>Candida zeylanoides</i> 86

- Cantharellus cibarius* 231 *, 166
Cantharellus tubaeformis 231 *
Chaetomium elatum 156
Chaetomium globosum 3, 154
Circinella mucoroides 51
Circinella muscae 51
Circinella rigida 51
Circinella simplex 51
Circinella umbellata 51
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
Clitocybe cyanophaea 103
Clitocybe geotropa 231 *
Clitocybe infundibuliformis 72
Clitocybe nebularis 231 *, 72
Clitocybe odora 28
Clitocybe socialis 231 *
Coccidioides immitis 125
Cochliobolus miyabeanus 156
Colletotrichum gloeosporioides 117
Collybia butyracea 231 *
Collybia confluens 231 *
Collybia dryophila 231 *
Collybia erythropus 72
Collybia fusipes 231 *, 72
Collybia maculata 231 *
Collybia platyphylla 28
Coprinus atramentarius 231 *, 28, 154
Coprinus comatus 72, 28
Coprinus friesii 156
Coprinus micaceus 72, 28
Cordiceps capitata 199
Coriolor versicolor 28
Cortinarius alboviolaceus 28
Cortinarius berkeleyi 72
Cortinarius bivelus 231 *
Cortinarius bolaris 28
Cortinarius brunneus 231 *
Cortinarius bulliardi 72
Cortinarius collinitus 231 *, 28
Cortinarius elatior 231 *
Cortinarius fulmineus 28
Cortinarius infractus 231 *
Cortinarius largus 28
Cortinarius torvus 28
Cortinarius violaceus 72, 28
Cortinellus shiitake 103
Coryne sarcoides 96
Craterellus cornucopioides 28
Crepidotus nidulans 72
Cryptococcus neoformans 149
Debaryomyces hansenii 150, 1
Debaryomyces sake 146, 195
Dendryphiella salina 8, 97, 128, 155, 107
Diplodia viticola 191
Elaphomyces asperulus 231 *
Elaphomyces echinatus 231 *
Elaphomyces granulatus 231 *
Elaphomyces leveillei 231 *
Elaphomyces variegatus 231 *
Endothia parasitica 156
Entoloma clypeatum 28
Entoloma lividum 28
Entoloma nidorosum 231 *
Entoloma sinuatum 231 *
Epichloe typhina 203
Fistulina hepatica 73, 28
Flammula spectabilis 72
Flammulina velutipes 108
Fomes ignarius 58
Fusarium solani 44
Galactinia olivacea 72
Geaster rufescens 231 *
Gelasinospora cerealis 154
Geotrichum candidum 42/1, 183, 52

- Gibberella fujikuroi* 156
Gomphidius roseus 28
Gomphidius viscidus 72

Hansenula anomala 146
Hansenula suaveolens 196
Helminthosporium geniculatum
 24
Helminthosporium oryzae 30
Helvella esculenta 231*
Hydnum erinaceus 72
Hydnum ferrugineum 231*, 28
Hydnum hybridum 231*
Hydnum imbricatum 154
Hydnum repandum 231*, 28, 166,
 154
Hydnum squamosum 231*
Hygrophoropsis aurantiaca 28
Hygrophorus agathosmus 231*
Hygrophorus cossus 231*
Hygrophorus hypotheius 231*
Hygrophorus nemoreus 72
Hygrophorus olivaceo-albus 231*
Hygrophorus virgineus 231*
Hypholoma fasciculare 231*, 28
Hypholoma hydrophilum 28
Hypholoma sublateritium 231*,
 103

Inocybe praetervisa 28
Ixocomus bovinus 28
Ixocomus luteus 28
Ixocomus piperatus 28
Ixocomus variegatus 28

Kluyveromyces fragilis 78

Laccaria laccata 28
Lactarius blennius 231*, 72, 28
Lactarius chrysorrheus 72, 28
Lactarius controversus 231*, 72
Lactarius deliciosus 231*, 72, 21,
 28, 166
Lactarius musteus 28
Lactarius pallidus 231*, 72

Lactarius piperatus 231*, 103, 72
Lactarius plumbeus 72, 28
Lactarius pubescens 72
Lactarius pyrogalus 231*, 72
Lactarius quietus 231*
Lactarius rufus 231*, 28
Lactarius subdulcis 231*
Lactarius torminosus 231*, 72
Lactarius turpis 231*
Lactarius uvidus 28
Lactarius vellereus 231*, 72, 28
Lactarius vietus 231*
Lactarius violascens 72
Lactarius volemus 31, 231*
Lactarius zonarius 231*, 72
Lentinus cochleatus 231*, 72
Lentinus edodes 137
Lenzites flaccida 28
Lenzites saepiaria 154
Lepidella vittadinii 72
Lepiota clypeolaria 72
Lepiota cristata 72
Lepiota excoriata 231*
Lepiota friesii 231*
Lepiota procera 231*
Lepiota rhacodes 231*
Leucocoprinus rhacodes 72
Lycoperdon pusillum 231*
Lycoperdon pyriforme 72

Marasmius hariolorum 72
Melanopus squamosus 72
Microsporium gypseum 119
Monascus ruber 156
Morchella conica 231*
Morchella esculenta 231*
Morchella semilibera 231*
Mortierella ramanniana 156, 157
Mucor miehei 156, 157
Mucor mucedo 154
Mucor rouxii 156
Mycena galericulata 96
Mycena pelianthina 231*
Myrothecium verrucaria 132

- Nematoloma fasciculare* 72
Neurospora crassa 193
Neurospora sitophila 220
Omphalia sciaphoides 231*
Oudemansiella mucida 217
Panus conchatus 231*
Panus stipticus 231*
Paxillus atrotomentosus 231*, 72
Paxillus involutus 231*, 72
Penicillium brefeldianum 156
Penicillium breviscompactum 152
Penicillium chrysogenum 24, 12, 2
Penicillium cyclopium 152
Penicillium griseofulvum 117
Penicillium herquei 75
Penicillium italicum 156
Penicillium notatum 29
Penicillium oxalicum 156
Peziza badia 231*
Peziza nigra 231*
Peziza ochracea 231*
Peziza onotica 231*
Peziza venosa 231*
Phallus impudicus 231*
Pholiota aurivella 72
Pholiota lubrica 155
Pholiota mutabilis 103, 28
Pholiota praecox 72
Pholiota radicata 231*
Pholiota togularis 231*
Phycomyces blakesleeanus 156
Phymatotrichum omnivorum 67
Pichia farinosa 146
Pichia guilliermondii 136
Pichia miso 146, 147, 195
Pichia quercibus 194, 196
Pleurotus cornucopioides 72
Pleurotus dryinus 231*
Pleurotus japonicus 103
Pleurotus serinus 103
Pluteus cervinus 72
Pluteus peltitus 72
Pleurotus olearius 72
Pleurotus ostreatus 103, 72, 154, 156
Polyporus frondosus 72
Polyporus intybaceus 103
Polyporus officinalis 231*
Polyporus pomaceus 28
Polyporusptychogaster 231*
Polyporus robustus 28
Polyporus umbellatus 72
Poria vincta 130
Psalliota arvensis 231*, 103
Psalliota campestris 231*, 103, 112
Psalliota placomyces 103
Psalliota silvicola 231*
Puccinia coronata 200
Puccinia graminis tritici 160, 161, 167, 227, 53, 39, 131, 130, 133
Pyrenochaeta terrestris 226
Pyricularia oryzae 154, 30
Rhizoctonia repens 178
Rhizoctonia solani 178, 156, 30
Rhizopogon luteolus 231*
Rhizopus oligosporus 154
Rhizopus stolonifer 156
Rhodosporeidium toruloides 78
Rhodotorula graminis 55
Russula adusta 231*
Russula albonigra 28
Russula coerulea 28
Russula cyanoxantha 231*, 28
Russula delicata 231*, 72
Russula drymeia 72
Russula fellea 231*, 28
Russula foetens 231*, 28
Russula fragilis 103, 28
Russula integra 231*
Russula lepida 231*, 28
Russula nigricans 231*, 72, 28
Russula ochroleuca 231*, 28, 96
Russula pseudoviolacea 28
Russula queletii 231*
Russula sanguinea 72
Russula sardonica 28
Russula torulosa 28
Russula virescens 231*

- 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
Sarcodon repandum 72
Sarcosphaera coronaria 72
Schizophyllum commune 144, 7, 181, 130
Schizosaccharomyces pombe 78
Scleroderma verrucosum 231*, 72
Scleroderma vulgare 231*, 72
Sclerotinia cureyana 47, 4
Sclerotinia sclerotiorum 120, 221
Sclerotinia tuberosa 231*
Serpula lacrimans 36
Spongipellis spumeus 72
Sporobolomyces roseus 130
Stereostратum corticoides 200
Sterigmatocystis nigra 145, 72
Syncephalastrum racemosum 51

Torula utilis 71
Torulopsis anomala 149
Torulopsis candida 78
Torulopsis famata 146, 196
Torulopsis halophila 196
Torulopsis magnoliae 82
Torulopsis mannitofaciens 151, 196
Torulopsis nodaensis 149, 196
Torulopsis versatilis 146, 149, 196
Tricholoma albo-brunneum 28
Tricholoma album 231*
Tricholoma amarum 28
Tricholoma columbetta 231*, 28
Tricholoma equestre 103, 28
Tricholoma flavobrunneum 231*

Tricholoma nudum 231*, 103
Tricholoma pessundatum 231*
Tricholoma resplendens 231*
Tricholoma russula 231*, 103
Tricholoma sulfureum 231*, 72
Tricholoma terreum 231*
Tricholoma ustale 231*, 103
Trichosporon melibiosaceum 78
Trigonopsis variabilis 151
Tuber cibarium 231*
Tylopilus felleus 72

Ungulina betulina 72
Ustilago esculenta 41
Ustilago maydis 232, 155
Ustilago nuda 77

Verticillium albo-atrum 121
Verticillium dahliae 121, 30
Verticillium fungicola 156
Verticillium intertextum 156
Volvaria speciosa 72
Volvaria volvacea 231*

Xerocomus badius 28, 154
Xerocomus chrysenteron 28
Xylaria polymorpha 231*

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

<i>Actinomucor elegans</i> 156, 157	<i>Rhodosporeidium toruloides</i> 78
	<i>Rhodotorula graminis</i> 55
<i>Candida albicans</i> 122, 158	
<i>Candida arborea</i> 148	<i>Saccharomyces acidifaciens</i> 196
<i>Candida diddensii</i> 78	<i>Saccharomyces carlsbergensis</i> 78
<i>Candida guilliermondii</i> 150, 196, 170, 68	<i>Saccharomyces cerevisiae</i> 78
<i>Candida parapsilosis</i> 22	<i>Saccharomyces diastaticus</i> 78
<i>Candida pelliculosa</i> 109	<i>Saccharomyces fragilis</i> 146
<i>Candida polymorpha</i> 146, 148, 151, 196	<i>Saccharomyces mellis</i> 223
<i>Candida pseudotropicalis</i> 22	<i>Saccharomyces monacensis</i> 146
<i>Candida tropicalis</i> 146, 22, 78	<i>Saccharomyces paradoxus</i> 146
<i>Circinella mucoroides</i> 51	<i>Saccharomyces rouxii</i> 146, 26, 104, 150, 196, 78
<i>Circinella muscae</i> 51	<i>Saccharomyces sake</i> 146, 78
<i>Circinella rigida</i> 51	<i>Saccharomycopsis fibuligera</i> 78
<i>Circinella simplex</i> 51	<i>Schizosaccharomyces pombe</i> 78
<i>Circinella umbellata</i> 51	<i>Syncephalastrum racemosum</i> 51
	<i>Torula utilis</i> 71
<i>Debaryomyces hansenii</i> 150, 1	<i>Torulopsis candida</i> 78
<i>Debaryomyces sake</i> 146, 195	<i>Torulopsis famata</i> 146, 196
	<i>Torulopsis halophila</i> 196
<i>Hansenula anomala</i> 146	<i>Torulopsis magnoliae</i> 82
<i>Hansenula suaveolens</i> 196	<i>Trichosporon melibiosaceum</i> 78
	<i>Trigonopsis variabilis</i> 151
<i>Kluyveromyces fragilis</i> 78	
<i>Mortierella ramanniana</i> 156, 157	<i>Zygorhynchus moelleri</i> 156, 157
<i>Mucor miehei</i> 156, 157	<i>Zygosaccharomyces acidifaciens</i> 153
<i>Mucor mucedo</i> 154	<i>Zygosaccharomyces barkeri</i> 153
<i>Mucor rouxii</i> 156	<i>Zygosaccharomyces fermentati</i> 153
	<i>Zygosaccharomyces mandschuricus</i> 153
<i>Penicillium brevi-compactum</i> 152	<i>Zygosaccharomyces mellis</i> 153
<i>Penicillium cyclopium</i> 152	<i>Zygosaccharomyces nadsonii</i> 153
<i>Penicillium herquei</i> 75	<i>Zygosaccharomyces nussbaumeri</i> 153
<i>Phycomyces blakesleeana</i> 156	<i>Zygosaccharomyces priorianus</i> 153
<i>Pichia farinosa</i> 146	<i>Zygosaccharomyces richteri</i> 153
<i>Pichia guilliermondii</i> 136	<i>Zygosaccharomyces rugosus</i> 153
<i>Pichia miso</i> 146, 147, 195	<i>Zygosaccharomyces wyocena</i> 153
<i>Pichia quercibus</i> 194, 196	
<i>Rhizopus oligosporus</i> 154	
<i>Rhizopus stolonifer</i> 156	

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.

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

- Clitocybe cyanophaea* 103
Clitocybe geotropa 231 *
Clitocybe infundibuliformis 72
Clitocybe nebularis 231 *, 72
Clitocybe odora 28
Clitocybe socialis 231 *
Coccidioides immitis 125
Cochliobolus miyabeanus 156
Colletotrichum gloeosporioides
 117
Collybia butyracea 231 *
Collybia confluens 231 *
Collybia dryophila 231 *
Collybia erythropus 72
Collybia fusipes 231 *, 72
Collybia maculata 231 *
Collybia platyphylla 28
Coprinus atramentarius 231 *, 28,
 154
Coprinus comatus 72, 28
Coprinus friesii 156
Coprinus micaceus 72, 28
Cordiceps capitata 199
Coriolus versicolor 28
Cortinarius alboviolaceus 28
Cortinarius berkeleyi 72
Cortinarius bivelus 231 *
Cortinarius bolaris 28
Cortinarius brunneus 231 *
Cortinarius bulliardi 72
Cortinarius collinitus 231 *, 28
Cortinarius elatior 231 *
Cortinarius fulmineus 28
Cortinarius infractus 231 *
Cortinarius largus 28
Cortinarius torvus 28
Cortinarius violaceus 72, 28
Cortinellus shiitake 103
Coryne sarcoides 96
Craterellus cornucopioides 28
Crepidotus nidulans 72
Cryptococcus neoformans 149
Dendryphiella salina 8, 97, 128,
 155, 107
Diplodia viticola 191
Elaphomyces asperulus 231 *
Elaphomyces echinatus 231 *
Elaphomyces granulatus 231 *
Elaphomyces leveillei 231 *
Elaphomyces variegatus 231 *
Endothia parasitica 156
Entoloma clypeatum 28
Entoloma lividum 28
Entoloma nidorosum 231 *
Entoloma sinuatum 231 *
Epichloe typhina 203
Fistulina hepatica 28
Flammula spectabilis 72
Flammulina velutipes 108
Fomes ignarius 58
Fusarium solani 44
Galactinia olivacea 72
Geaster rufescens 231 *
Gelasinospora cerealis 154
Geotrichum candidum 42/1, 183,
 52
Gibberella fujikuroi 156
Gomphidius roseus 28
Gomphidius viscidus 72
Helminthosporium geniculatum
 24
Helminthosporium oryzae 30
Helvella esculenta 231 *
Hydnum erinaceus 72
Hydnum ferrugineum 231 *, 28
Hydnum hybridum 231 *
Hydnum imbricatum 154
Hydnum repandum 231 *, 28, 166,
 154
Hydnum squamosum 231 *
Hygrophoropsis aurantiaca 28
Hygrophorus agathosmus 231 *
Hygrophorus cossus 231 *
Hygrophorus hypothecius 231 *
Hygrophorus nemoreus 72
Hygrophorus olivaceo-albus 231 *
Hygrophorus virgineus 231 *
Hypholoma fasciculare 231 *, 28
Hypholoma hydrophilum 28

- Hypoholoma sublateritium* 231 *, 103, 28
Inocybe praetervisa 28
Ixocomus bovinus 28
Ixocomus luteus 28
Ixocomus piperatus 28
Ixocomus variegatus 28
Laccaria laccata 28
Lactarius blennius 231 *, 72, 28
Lactarius chrysorrheus 72, 28
Lactarius controversus 231 *, 72
Lactarius deliciosus 231 *, 72, 21, 28, 166
Lactarius musteus 28
Lactarius pallidus 231 *, 72
Lactarius piperatus 231 *, 103, 72
Lactarius plumbeus 72, 28
Lactarius pubescens 72
Lactarius pyrogalus 231 *, 72
Lactarius quietus 231 *
Lactarius rufus 231 *, 28
Lactarius subdulcis 231 *
Lactarius torminosus 231 *, 72, 28
Lactarius turpis 231 *
Lactarius uvidus 28
Lactarius vellereus 231 *, 72, 28
Lactarius vietus 231 *
Lactarius violascens 72
Lactarius volemus 231 *
Lactarius zonarius 231 *, 72
Lentinus cochleatus 231 *, 72
Lentinus edodes 137
Lenzites flaccida 28
Lenzites seipariaria 154
Lepidella vittadinii 72
Lepiota clypeolaria 72
Lepiota cristata 72
Lepiota excoriata 231 *
Lepiota friesii 231 *
Lepiota procera 231 *
Lepiota rhacodes 231 *
Leucocoprinus rhacodes 72
Lycoperdon pusillum 231 *
Lycoperdon pyriforme 72
Marasmius hariolorum 72
Melanopus squamosus 72
Microsporium gypseum 119
Monascus ruber 156
Morchella conica 231 *
Morchella esculenta 231 *
Morchella semilibera 231 *
Mycena galericulata 96
Mycena pelianthina 231 *
Myrothecium verrucaria 132
Nematoloma fasciculare 72
Neurospora crassa 193
Neurospora sitophila 220
Omphalia scyphoides 231 *
Oudemansiella mucida 217
Panus conchatus 231 *
Panus stipticus 231 *
Paxillus atrotomentosus 231 *, 72
Paxillus involutus 231 *, 72
Penicillium brefeldianum 156
Penicillium chrysogenum 24, 12, 2
Penicillium griseofulvum 117
Penicillium italicum 156
Penicillium notatum 29
Penicillium oxalicum 156
Peziza badia 231 *
Peziza nigra 231 *
Peziza ochracea 231 *
Peziza onotica 231 *
Peziza venosa 231 *
Phallus impudicus 231 *
Pholiota aurivella 72
Pholiota lubrica 155
Pholiota mutabilis 103, 28
Pholiota praecox 72
Pholiota radicata 231 *
Pholiota togularis 231 *
Phymatotrichum omnivorum 67
Pleurotus cornucopioides 72
Pleurotus dryinus 231 *
Pleurotus japonicus 103
Pleurotus olearius 72
Pleurotus ostreatus 103, 72, 154, 156
Pleurotus serinus 103

- Pluteus cervinus* 72
Pluteus pellitus 72
Polyporus frondosus 72
Polyporus intybaceus 103
Polyporus officinalis 231 *
Polyporus pomaceus 28
Polyporus ptychogaster 231 *
Polyporus robustus 28
Polyporus umbellatus 72
Poria vincta 130
Psalliota arvensis 231 *, 103
Psalliota campestris 231 *, 103, 112
Psalliota placomyces 103
Psalliota silvicola 231 *
Puccinia coronata 200
Puccinia graminis tritici 161, 167, 227, 53, 39, 131, 130, 133
Pyrenochaeta terrestris 226
Pyricularia oryzae 155, 30

Rhizoctonia repens 178
Rhizoctonia solani 178, 156, 30
Rhizopogon luteolus 231 *
Russula adusta 231 *
Russula albonigra 28
Russula coerulea 28
Russula cyanoxantha 231 *, 28
Russula delica 231 *, 72
Russula drymeia 72
Russula fellea 231 *, 28
Russula foetens 231 *, 28
Russula fragilis 103, 28
Russula integra 231 *
Russula lepida 231 *, 28
Russula nigricans 231 *, 72, 28
Russula ochroleuca 231 *, 28, 96
Russula pseudoviolacea 28
Russula queletii 231 *
Russula sanguinea 72
Russula sardonica 28
Russula torulosa 28
Russula virescens 231 *
Sarcodon repandum 72
Sarcosphaera coronaria 72

Schizophyllum commune 144, 7, 181, 130
Scleroderma verrucosum 231 *, 72
Scleroderma vulgare 231 *, 72
Sclerotinia curreyana 47, 4
Sclerotinia sclerotiorum 120, 221
Sclerotinia tuberosa 231 *
Serpula lacrimans 36
Spongipellis spumeus 72
Sporobolomyces roseus 130
Stereostromatium corticoides 200
Sterigmatocystis nigra 145, 72
Torulopsis anomala 149
Torulopsis mannifaciens 151
Torulopsis nodaensis 149
Torulopsis versatilis 149
Tricholoma albo-brunneum 28
Tricholoma album 231 *
Tricholoma amarum 28
Tricholoma columbetta 231 *, 28
Tricholoma equestre 103, 28
Tricholoma flavobrunneum 231 *
Tricholoma nudum 231 *, 103
Tricholoma pessundatum 231 *
Tricholoma resplendens 231 *
Tricholoma russula 231 *, 103
Tricholoma sulfureum 231 *, 72
Tricholoma terreum 231 *
Tricholoma ustale 231 *, 103
Tuber cibarium 231 *
Tylopilus felleus 72

Ungulina betulina 72
Ustilago esculenta 41
Ustilago maydis 232, 155
Ustilago nuda 77
Verticillium albo-atrum 121
Verticillium dahliae 121, 30
Verticillium fungicola 156
Verticillium intertextum 156
Volvaria speciosa 72
Volvaria volvacea 231 *

Xerocomus badius 28, 154
Xerocomus chrysenteron 28
Xylaria polymorpha 231 *

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)

<i>Agaricus bisporus</i> 59, 61	<i>Pichia farinosa</i> 146
<i>Armillaria mellea</i> 25, 155, 130	<i>Pichia guilliermondii</i> 136
	<i>Pichia miso</i> 146, 147
<i>Boletus bovinus</i> 219	<i>Pichia quercibus</i> 194
<i>Boletus erythropus</i> 155	<i>Pleurotus ostreatus</i> 156
	<i>Poria vincta</i> 130
<i>Candida albicans</i> 158	<i>Psalliotia campestris</i> 112
<i>Candida diddensii</i> 78	<i>Puccinia graminis tritici</i> 53, 131, 130, 133
<i>Candida guilliermondii</i> 150, 170	<i>Pyrenochaeta terrestris</i> 226
<i>Candida pelliculosa</i> 109	
<i>Candida polymorpha</i> 146, 148, 196	<i>Rhodosporeidium toruloides</i> 78
<i>Candida tropicalis</i> 146, 78	<i>Rhodotorula graminis</i> 55
<i>Candida utilis</i> 100	
<i>Chaetomium elatum</i> 156	<i>Saccharomyces acidifaciens</i> 196
<i>Circinella mucoroides</i> 51	<i>Saccharomyces carlsbergensis</i> 78
<i>Circinella muscae</i> 51	<i>Saccharomyces cerevisiae</i> 78
<i>Circinella rigida</i> 51	<i>Saccharomyces diastaticus</i> 78
<i>Circinella simplex</i> 51	<i>Saccharomyces rouxii</i> 146, 196, 78
<i>Circinella umbellata</i> 51	<i>Saccharomyces sake</i> 78
<i>Claviceps purpurea</i> 215, 48	<i>Saccharomycopsis fibuligera</i> 78
	<i>Schizophyllum commune</i> 130
<i>Endothia parasitica</i> 156	<i>Schizosaccharomyces pombe</i> 78
	<i>Sclerotinia sclerotiorum</i> 221
<i>Geotrichum candidum</i> 183	<i>Sporobolomyces roseus</i> 130
	<i>Syncephalastrum racemosum</i> 51
<i>Hansenula anomala</i> 146	
	<i>Torula utilis</i> 71
<i>Kluyveromyces fragilis</i> 78	<i>Torulopsis candida</i> 78
	<i>Torulopsis famata</i> 146
<i>Lactarius volemus</i> 31	<i>Torulopsis versatilis</i> 146
	<i>Trichosporon melibiosaceum</i> 78
<i>Mucor miehei</i> 156, 157	
<i>Mucor rouxii</i> 156	<i>Zygorhynchus moelleri</i> 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 <i>meso-glycero-ido-heptitol</i>
E erythritol	M mannitol	I <i>D-glycero-D-ido-heptitol</i>
T threitol	D dulcitol	0 no polyols
R ribitol	S sorbitol	
A arabitol	V volemitol	

MASTIGOMYCOTINA

Oomycetes

<i>Achlya radiosa</i>	0
<i>Albugo tragopogonis</i>	0
<i>Peronospora parasitica</i>	0
<i>Phytophthora cactorum</i>	0
<i>Phytophthora cinnamomi</i>	0
<i>Phytophthora infestans</i>	0
<i>Plasmopara viticola</i>	0

Chytridiomycetes

Allomyces arbuscula	G	M
Blastocladiella emersonii	G	M

ZYGOMYCOTINA

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 hanseni	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
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
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
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Pyrenomyces

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

Blastomyces

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

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

Hyphomycetes

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

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

Coelomycetes

<i>Colletotrichum gloeosporioides</i>			A		M
<i>Diplodia viticola</i>			A		M
<i>Pyrenochaeta terrestris</i>	G	E	A		M S

BASIDIOMYCOTINA

Teliomycetes

<i>Puccinia coronata</i>					M
<i>Puccinia graminis tritici</i>	G	E	R	A	X M S
<i>Rhodosporidium toruloides</i>					X
<i>Stereostратum corticoides</i>					M
<i>Ustilago esculenta</i>		E			M
<i>Ustilago maydis</i>	G	E	A		M
<i>Ustilago nuda</i>	G	E			M

Hymenomycetes

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

<i>Cortinarius torvus</i>		M
<i>Cortinarius violaceus</i>		M
<i>Cortinellus shiitake</i>		M
<i>Craterellus cornucopioides</i>		M
<i>Crepidotus nidulans</i>		M
<i>Entoloma clypeatum</i>		M
<i>Entoloma lividum</i>		M
<i>Entoloma nidorosum</i>		M
<i>Entoloma sinuatum</i>		M
<i>Fistulina hepatica</i>	A	M
<i>Flammula spectabilis</i>		M
<i>Flammulina velutipes</i>	A	M
<i>Fomes ignarius</i>		M
<i>Gomphidius roseus</i>		M
<i>Gomphidius viscidus</i>		M
<i>Hydnum erinaceus</i>		M
<i>Hydnum ferrugineum</i>		M
<i>Hydnum hybridum</i>		M
<i>Hydnum imbricatum</i>		M
<i>Hydnum repandum</i>		M
<i>Hydnum squamosum</i>		M
<i>Hygrophoropsis aurantiaca</i>		M
<i>Hygrophorus agathosmus</i>		M
<i>Hygrophorus cossus</i>		M
<i>Hygrophorus hypotheius</i>		M
<i>Hygrophorus nemoreus</i>		M
<i>Hygrophorus olivaceo-albus</i>		M
<i>Hygrophorus virgineus</i>		M
<i>Hypholoma fasciculare</i>		M
<i>Hypholoma hydrophilum</i>		M
<i>Hypholoma sublateralitium</i>		M
<i>Inocybe praetervisa</i>		M
<i>Ixocomus bovinus</i>		M
<i>Ixocomus luteus</i>		M
<i>Ixocomus piperatus</i>		M
<i>Ixocomus variegatus</i>		M
<i>Laccaria laccata</i>		M
<i>Lactarius blennius</i>		M
<i>Lactarius chrysorrheus</i>		M
<i>Lactarius controversus</i>		M
<i>Lactarius deliciosus</i>		M
<i>Lactarius musteus</i>		M
<i>Lactarius pallidus</i>		M
<i>Lactarius piperatus</i>		M
<i>Lactarius plumbeus</i>		M
<i>Lactarius pubescens</i>		M
<i>Lactarius pyrogalus</i>		M
<i>Lactarius quietus</i>		M
<i>Lactarius rufus</i>		M
<i>Lactarius subdulcis</i>		M
<i>Lactarius torminosus</i>		M
<i>Lactarius turpis</i>		M
<i>Lactarius uvidus</i>		M
<i>Lactarius vellereus</i>		M
<i>Lactarius vietus</i>		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 radicata				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 vineta	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 pseudoviolvea					M
Russula queletii					M
Russula sanguinea					M
Russula sardonica					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 biosynthesis, 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 arabinol 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-, Eusco-, and Basidiomycetes indicates a monophyletic origin of all of these groups, with rhodophycean and/or phaeophycean 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 Eusco- 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 possess 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 Eusco- 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

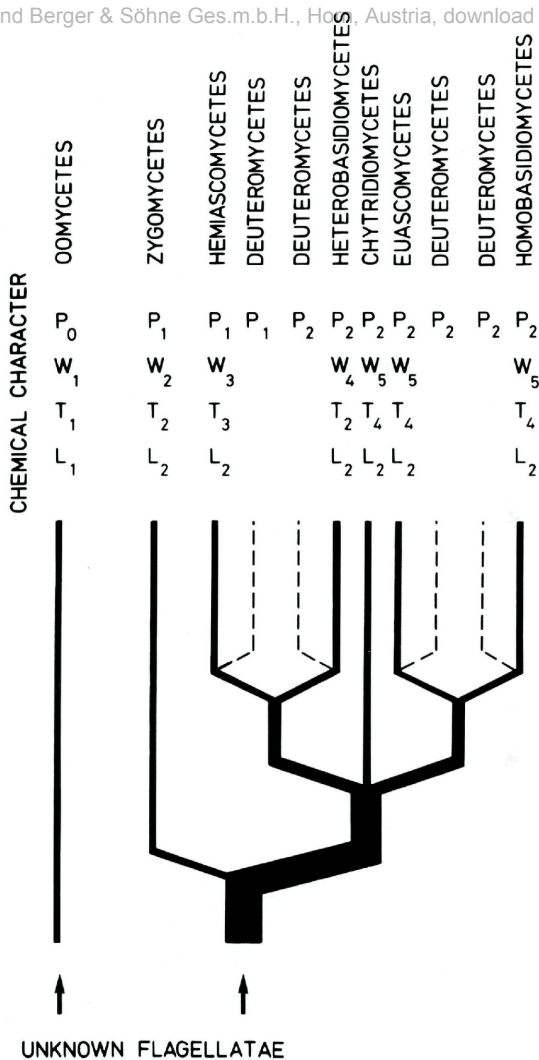


Fig. 1. Chemotaxonomy and macroevolutionary scheme of the Eumycetes, as based on classical criteria and chemical traits (polyol character: states P_0 , P_1 , and P_2 [this work]; cell wall composition: types W_1 – W_6 , partly according to BARTNICKI-GARCIA [18, 19]; organization of the tryptophan pathway: categories T_1 – T_4 [102]; and lysine biosynthetic pathway: alternatives L_1 and L_2 [216]).

Eusco-, 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 *Rhodosporeidium 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 P₁-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 T₂-type (as do some *Tremella*, *Ustilago*, *Sporobolomyces*, and *Rhodotorula* species [102]), in addition to the P₂-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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