Ontogeny and phylogeny of gasteroid members of Agaricaceae (Basidiomycetes)

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Contents

Introduction

Gasteromycetes are a morphologically defined group of the class Basidiomycetes, characterised by spore formation within enclosed basidiomata (cleisto- or angiocarpy) and statismosporic basidia, leading to passive spore release (Reijnders 2000). These fungi and their fruitbodies are collectively referred to as gasterothecia here to avoid confusion with the nomenclatural use of the suffix “-mycetes”. Gasteromycetation, the evolutionary process facilitating production of gasterothecia instead of hymenothecia with exposed hymenium and active spore discharge, occurred many times independently within Agaricomycetidae (Heim 1971, Singer 1986, Matheny et al. 2006). Often, gasterothecia do not at all resemble their hymenothecial relatives. Others, the secotioid fungi, still possess such features, and have thus been treated sometimes as Hymenomycetes (Gäumann 1926, Rauschert 1956). Their existence did initiate an intensive debate on the evolution of these fungi. Some authors did consider Gasteromycetes as derived from gilled fungi, others did propose the opposite (e. g. Heim 1971, Smith 1971, Thiers 1984, Singer 1986). This was complicated by the fact that the relationships among gasteroid taxa were equally unknown, although most authors did assume independent “lineages” (Kreisel 1969, Malencon 1955), progressing between simple ancestral features towards derived complex ones. The evolutionary process has been proposed to be unidirectional (Hibbett 2004).

Gasteromycetes were usually treated as a taxonomic unit to avoid conflicts with existing taxonomy as long as concise relationships were not resolved (e. g. Jülich 1984, Sarasini 2005). Some anatomical and chemical links between secotioid and gilled fungi were known (e. g. Heim 1971, Smith 1971). However, they revealed no insight into the direction of evolution. Comparison of ontogenetic features was not widely considered, although some work was present (e. g. Rehsteiner 1892, Conard 1915, Lohwag 1924, Swartz 1933, 1935, Maublanc & Malencon 1930, Townsend 1954). The issue remained unresolved until the advance of molecular systematics, initially confirming assumed and revealing new relationships between gasteroid and nongasteroid groups (Hopple & Vilgalys 1994, Hibbett et al. 1997). These results were followed successively by detection of gasteromycetation events among russuloid (Miller et al. 2001), cortinarioid (Peintner et al. 2001), boletoid (Binder & Bresinsky 2002) and agaricoid Basidiomycetes (Moncalvo et al. 2002). However, the specific evolutionary and phylogenetic relationships remained widely unresolved.

Agaricaceae are a major family of Basidiomycetes. They are defined by their free lamellae, the presence of velar structures, often dextrinoid spores that are metachromatic in cresyl blue, and common presence of cheilocystidia (Singer 1986, Vellinga 2004). Members of the family were classified in the tribes of Agariceae, Lepioteae, Leucocoprineae and Cystodermateae (Singer 1986), the latter being excluded on behalf of their adnate lamellae (Bas 1988). Inclusive of Cystodermateae and Nidulariaceae, Agaricaceae include 1340 accepted species (Kirk et al. 2009). Members of the family were among the first Basidiomycetes to be analysed in ontogenetic studies, as *Agaricus campestris* L.: Fr. by Hoffmann (1856); and were the focus of the "école americaine" of Atkinson (Reijnders 1963). Similar fruitbody development led Reijnders (1975) to propose a general pattern of ontogeny for Agaricaceae.

However, some secotioid species, such as *Endoptychum agaricoides* Czern. (Conard 1915, Fig. 1a), *Endoptychum depressum* Singer & Smith (Singer & Smith 1958, Fig. 1b), or *Podaxis pistillaris* (Pers.) Fr. (Lohwag 1924, Fig. 1c) were long assumed to be connected to agaricacean gilled fungi. Yet, these results were only rarely considered systematically important (Gäumann 1926), and sometimes altogether questioned (Cunningham 1944). In discussions on the direction of evolution between gilled and gasteroid fungi, agaricacean secotioids played a minor role (Heim 1971, Smith 1971, Kreisel 1973, Thiers 1984, Singer 1986). The advance of molecular phylogeny did show some secotioid fungi to be sister groups to or even members of agaricacean genera (Johnson & Vilgalys 1998, Moncalvo et al. 2002, Geml 2004, Vellinga 2004, Lebel et al. 2004). However, the gasteroid Lycoperdaceae and Tulostomataceae (Krüger et al. 2001, Moncalvo et al. 2002) as well as ink caps of *Coprinus* sect. *Coprinus* and the genus *Montagnea* (Hopple & Vilgalys 1994, Redhead et al. 2001) were also included. Some of these results got support from by anatomical analyses (Agerer 2002). All these groups have to be re-visited to allow for phylogenetic resolution of gasteromycetation events.

The family of Lycoperdaceae or true puffballs is a well defined group, characterised by gasteroid appearance with drying glebal structures (Fig. 1d). Their spores are pigmented; often ornamented and branched capillitium is present. Relationships within Lycoperdaceae were analysed by Larsson and Jeppson (2008). On base of the ontogeny, relationships with *Hymenogaster* (Rehsteiner 1892) and corticioid fungi (Lohwag 1925) were discussed. However, *Hymenogaster* is now classified as Cortinariaceae (Peintner et al. 2001), and corticoid fungi are present in various major taxa of Agaricomycetidae (Binder et al. 2005), but not in Agaricaceae. Also, Geastraceae, which are related to the gomphoid/phalloid fungi (Hibbett et al. 1997, Hosaka et al. 2006), were sometimes considered within Lycoperdaceae

(Fischer 1900, Cunningham 1944, Sarasini 2005). Brefeld (1877), and Underwood (1889) depicted relationships with certain hymenothecial groups without discussing them in detail.

The family Tulostomataceae is a gasteroid group with powdery gleba at maturity, and with true stipes (White 1901), that do not protrude into or through the gleba (Fig. 1e). However, *Podaxis* (Fig. 1c) with a stipe protruding through the gleba was often considered within this family (Fischer 1900, Cunningham 1944), mainly on account of the presence of persistent clusters of basidia. Their relationships remained unclear so far, despite some ontogenetic work (Schröter 1877, Greis 1937, Malençon 1930, Maublanc & Malençon 1935a, b). Even more so, detailed connections to gilled basidiomycetes remained elusive.

Relationships between the ink caps of *Coprinus*, especially the section *Coprinus* (Fig. 1f), and the genus *Montagnea*, were early noticed (de Bary 1966) on account of their spore, velar and stipe characteristics. Thus, *Montagnea* was repeatedly not considered gasteroid (see Rauschert 1964), despite its angiocarpic development. Since ontogenetic analyses are present only for *Coprinus comatus* (O. F. Müll.: Fr.) Pers. (Brefeld 1877, Atkinson 1916), no comparative treatment exists. Molecular phylogeny indicated *Coprinus* sect. *Coprinus* and *Montagnea* to form a clade related to Agaricaceae, distinct from the majority of *Coprinus* (Hopple & Vilgalys 1994, Redhead et al. 2001). Veil anatomy and the type of spore pigmentation support this result (van de Bogart 1976, Redhead et al. 2001).

Although molecular phylogeny has been applied to these groups, the phylogenetic relationships among and within them were not convincingly resolved, and further analyses were suggested (Vellinga 2004). Still, Lycoperdaceae, Tulostomataceae, Phelloriniaceae and Podaxaceae were synonymised with Agaricaceae (Vellinga 2004, Kirk et al. 2009). This approach resulted in a family with highly divergent anatomical characters, which is impossible to define by morphological characteristics. However, the presence of gasteroid and hymenothecial taxa in a relatively close related group was proven. Therefore, Agaricaceae can be used as an ideal model for studying the evolutionary process of gasteromycetation. To facilitate communication, the group is referred to as Agaricaceae s. l. when all gasteroid taxa are included. This allows use of the familiar Tulostomataceae, Lycoperdaceae and Coprinaceae.

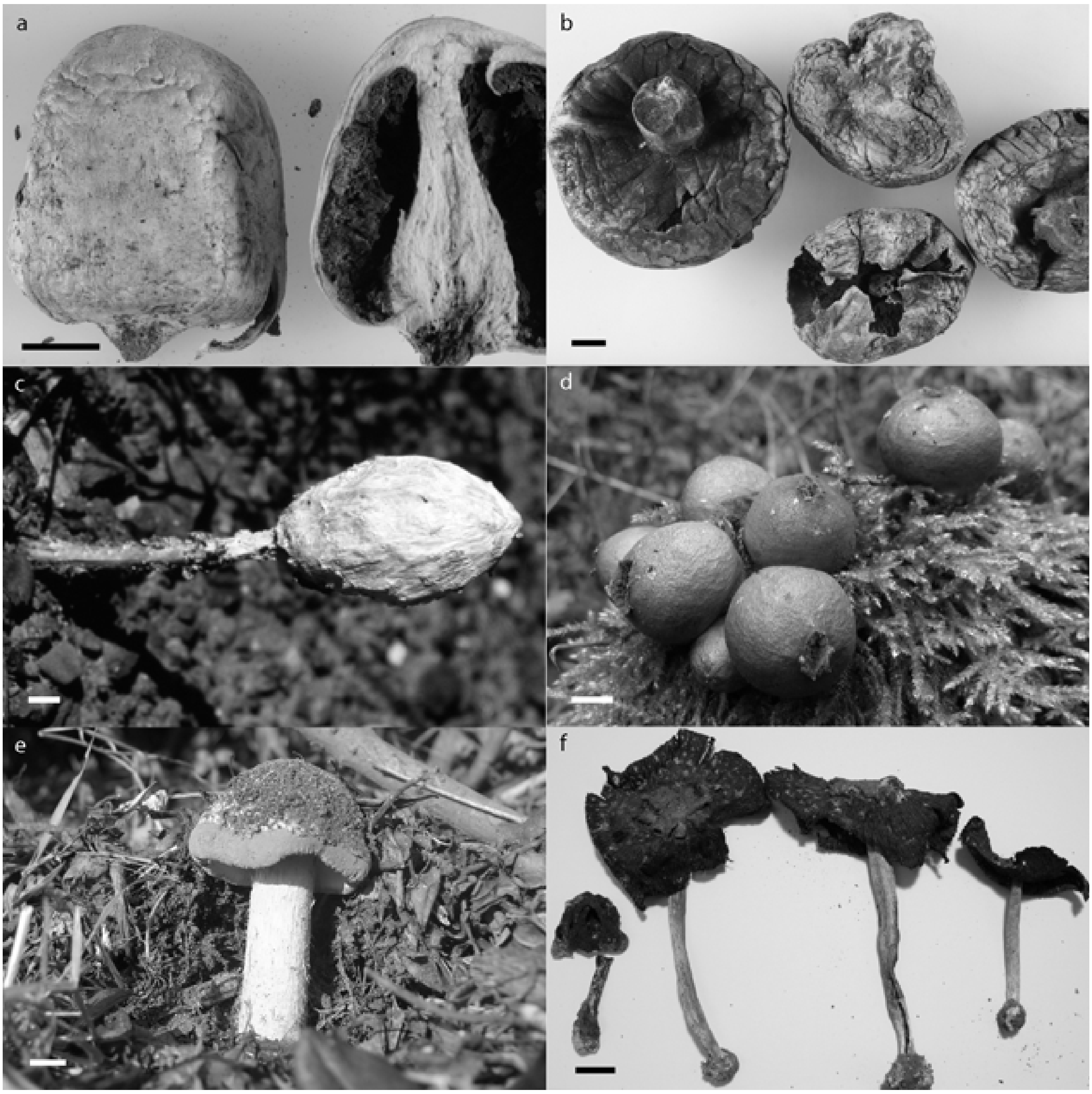

FIG. 1: Fruitbodies of gasteroid (a–e) and coprinoid (f) relatives of Agaricaceae. Scale bars refer to 1 cm. a: *Endoptychum agaricoides* MICH 08116; b: *Endoptychum depressum* MICH 08171; c: *Podaxis pistillaris*, U.S.A., Hawaii, Kawaihae; d: *Lycoperdon pyriforme*, Germany, Thuringia, Themar; e: *Battarraea phalloides*, Germany, Saxony-Anhalt, Teutschenthal; f: *Coprinus sterquilinus*, JE Gröger 14.V.1989. Photos: H. Dörfelt (a, b, e), M. Gube (c, d, f).

Analysis of gasteromycetation requires profound knowledge of the systematic relationships of taxa within the group studied. The available work is far from being sufficient in this respect. Therefore, molecular phylogenetic analyses were undertaken, incorporating DNA sequences of nrDNA (ITS region and LSU) and partial sequences of the largest subunit of RNA polymerase II (RPB1) to resolve phylogenetic relationships. The sequences used have been shown to contain sufficient information for large or small scale phylogenetic analyses (e. g. Matheny et al. 2002, Moncalvo et al. 2002, Larsson & Jeppson 2008). Combined analyses of several genetic marker loci can overcome weaknesses inherent to single loci (Matheny et al.

2006). Using a large taxon set limits the danger of long branch attraction. Therefore DNA of about 650 taxa was extracted and analysed by Maximum Likelyhood approaches and Bayesian Inference (Chapter 1).

As this study is focused on the evolution of distinctive morphological structures, anatomical, especially ontogenetic analyses are mandatory. Ontogenetic studies are a basal requirement for homologisation of otherwise incomparable features and can therefore lead to a better understanding of morphological character evolution (Hibbett 2007). Although ontogenetic studies are available for some members of the analysed group, recent work is scarce. Unfortunately, many fungi, among them the Lycoperdaceae and Tulostomataceae, have resisted cultivation so far, and studies have to rely on fruitbody primordia collected in the field. Any survey on the ontogeny of these groups therefore can only focus on details, gradually leading to a more complete view. As the genus *Langermannia* of the Lycoperdaceae was not previously analysed, its ontogeny was compared with that of other Lycoperdaceae and with that of *Agaricus* within these studies (Chapter 2).

A basal requirement for any systematic or ecological study is knowledge of the distribution of the considered group, facilitating adequate taxon sampling. In many areas, especially in developing countries, such studies are scarce or completely lacking, and yet these countries are often centres of fungal diversity. For saprobic gasterothecia with air-borne spore dispersal (anemochory), the natural open land biomes are of special interest. Such habitats exist in Central Asia, therefore the secotioid fungi of Mongolia have been investigated (Chapter 3).

The densely forested and extremely moist habitats of the tropical rainforests provide a completely different setting. Yet, they accommodate a considerable number of gasteroid fungi (Dennis 1970). Thus, a floristic study of the Gasteromycetes of Panama is included here (Chapter 4). Comparison of gasterothecia from differing habitats allows differentiating between convergent adaptation in response to similar evolutionary constraints from features inherently associated with the gasteromycetation process. This facilitates the perception of homologues. Features generally evolve from existing characters, with results that may, in extreme cases, not at all resemble the ancestral shape, but often still possess some hidden homologies. Consideration of the ecological circumstances in comparison with anatomical and ontogenetic features can ease homologisation by tracing features back to ecological constraints and pointing out other features as evolutionary heritage. Such studies are especially needed when anatomical features are as highly dissimilar as in Agaricaceae s. l., allowing for interpretation of morphological changes during this evolutionary process (Chapter 5).

The main objective of this work is the phylogenetic, ontogenetic, anatomical and ecological study of gasteromycetation events within Agaricaceae s. l. Molecular phylogeny allows to review the number, extent and direction of such events, and to verify the existing phylogenetic concepts. The ontogenetic, morphological and ecological features of gasterothecia are comparatively analysed and interpreted. As a result, the presence of certain anatomical features can be traced back to ancestral heritage or to ecological constraints. Thus, insights into the evolution of gasterothecia and its circumstances are gained. Agaricaceae s. l. are used as a model for investigation of gasteromycetation, which will enable revision of gasteromycetation events in other fungal lineages following the same concept.

Manuscript overview

M. GUBE, M. THIENES, L. NÁGY, E. KOTHE 2009: Ten times angiocarpy – gasteromycetation events within Agaricaceae s. l. (Agaricales, Basidiomycetes) (in preparation for Molecular Phylogenetics and Evolution)

An extended molecular phylogeny of Agaricaceae is presented, with special emphasis on gasteroid taxa. Five major clades are resolved, which incorporate ten gasteromycetation events. Several systematic relationships are newly revealed.

Contributions of the authors:
M. Gube: Acquisition of material, laboratory work, evaluation of data, manuscript preparation.
M. Thienes: Methods for extraction of ancient DNA, provision of lab facilities for testing of several DNA extraction methods.
L. Nágy: Provision of extensive material for analysis, cooperation in field excursions in Southern Hungary.
E. Kothe: Supervision of the project.

M. GUBE 2007: The gleba development of Langermannia gigantea (Batsch: Pers.) Rostk. (Basidiomycetes) compared to other Lycoperdaceae, and some systematic implications. Mycologia, **99** (3): 396–405.

The fruitbody and hymenial development of Lycoperdaceae is shown to deviate from previous interpretations. While the hymenium of Langermannia gigantea develops in a novel flabelloid manner, hymenial ontogeny of the remaining Lycoperdaceae is referred to as coralloud-lacunar.

H. DÖRFELT, M. GUBE 2007: Secotioid Agaricales (Basidiomycetes) from Mongolia. Feddes Repertorium, **118** (3–4): 103–112.
All records of secotioid fungi in Mongolia are reviewed. An overview of distribution and systematic relationships is given. Two species are newly recorded for the country.

Contributions of the authors:
H. Dörfelt: Acquisition of material, evaluation of data.
M. Gube: Laboratory work, evaluation of data, manuscript preparation.

M. GUBE, M. PIEPENBRING 2009: Preliminary annotated checklist of Gasteromycetes in Panama (in revision for Nova Hedwigia, submission confirmation 06.02.2009, accepted for publication after revision 25.02.2009)

All findings of gasteroid fungi in Panama are reviewed and compiled to a preliminary checklist. These are discussed in respect of their distribution, nomenclature and systematic relationships. Nine species are new records for the country, and one species is presumably new to science.

Contributions of the authors:
M. Gube: Laboratory work, evaluation of data, manuscript preparation.
M. Piepenbring: Acquisition of material, evaluation of data.

M. GUBE, H. DÖRFELT 2009: Anatomy and ecology of the gasteromycetation process in Agaricaceae s. l. (in preparation for Feddes Repertorium)

The morphological features of gasteroid Agaricaceae s.l. are discussed under consideration of their systematic and ecological background. The main dispersal strategies are outlined. All gasteromycetation events within the family are proposed to have occurred in semiarid openland habitats.

Contributions of the authors:
M. Gube: Acquisition of material, laboratory work, evaluation of data, manuscript preparation.
H. Dörfelt: Acquisition of material, evaluation of data.

Ten times angiocarpy – gasteromycetation events within Agaricaceae s. l. (Agaricales, Basidiomycetes)

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Abstract

This study provides an extended phylogenetic treatment of Agaricaceae s. l. with special emphasis on the gasteroid taxa. DNA sequence data of nrDNA and RPB1 was used for phylogenetic reconstruction in partitioned data sets with independent rate optimisation. Detailed independent analyses with enhanced taxon sampling were performed for clades that either not exclusively include gasteroid species, or were underrepresented so far. Results are compared with morphological, especially ontogenetic studies to facilitate the understanding of character evolution during the process of gasteromycetation. The entire group is confirmed to be monophyletic, with five major subclades being resolved. These correspond widely to the traditionally accepted families of Tulostomataceae, Coprinaceae s. str., Lepiotaceae, Lycoperdaceae, and Agaricaceae s. str. Four of these clades are either completely gasteroid (Tulostomataceae, Lycoperdaceae) or include gasterothecia (Coprinaceae s. str., Agaricaceae s. str.). From phylogenetic analysis, ten gasteromycetation events could be inferred. Existing phylogenetic knowledge is improved furthermore by detection of polyphyly of the *Macrolepiota* sect. *Laevistipedes*/*Chlorophyllum*/*Endoptychum* group, and in assigning *Podaxis* to *Macrolepiota* s. str. Additionally, *Montagnea* is indicated to have evolved within *Coprinus* s. str., and *Endoptychum arizonicum* (Shear & Griffiths) Singer & Smith is proposed as an independent lineage related to *E. agaricoides* Czern. and *Chlorophyllum*. Despite anatomic similarities, which led to their classification as gasteromycetes, many features are unique to the independent gasteroid taxa. In secotioid taxa, they correspond to the hymenothecial relatives.

Introduction

Gasteromycetation characterises the evolution of Basidiomycete fruitbodies with exposed hymenia (hymenothecia) towards such with enclosed spore forming structures (gasterothecia) (Reijnders 2000). This process is found in various ecological settings and occurred independently several times within Agaricomycetidae (Hopple & Vilgalys 1994, Hibbett et al. 1997, Krüger et al. 2001, Peintner et al. 2001, Moncalvo et al. 2002, Binder & Bresinsky

2002, Lebel et al. 2004, Geml et al. 2004, Vellinga 2004, Matheny et al. 2006). The most prominent morphological changes include spore ripening in enclosed basidiomata, loss of ballistospore discharge, and partly loss of stipe and a change of hymenial and basidial organisation (Thiers 1984, Reijnders 2000). The underlying genetics are widely unknown, though paedomorphosis probably plays a role (Fritsche & von Sengbusch 1968, Thiers 1984, Reijnders 2000). Considering the morphological and anatomical differences between the extremes of this process, it is not surprising that, in traditional mycology, gasterothecia were placed within an own class, Gasteromycetes, being distinct from the Hymenomycetes (Fries 1821–32). However, some gasteroid species show clear morphological evidence of hymenothecial relationship. These are referred to as secotioid fungi. *Montagnea*, one of these, was repeatedly either treated as hymenomycete, gasteromycete, or member of an independent intermediate group (Rauschert 1964). The systematic position of secotioid species was debated until Singer (1986), who discussed Gasteromycetes as a basal taxon and assumed gilled fungi to be derived from secotioids. Although there was morphological and chemical evidence (e.g. Conard 1915, Gäumann 1926, Demoulin 1967, Reijnders 2000), the advance of molecular systematics triggered wide acceptance of gasteromycetes as a morphologically defined group without nomenclatural or phylogenetic implication.

Agaricaceae were traditionally one of the best defined families of the Basidiomycetes, characterised by free lamellae, presence of universal or partial veil, often dextrinoid spores that are metachromatic in cresyl blue, and common presence of cheilocystidia (Singer 1986, Vellinga 2004). However, recent molecular systematic studies revealed a number of gasteroid and secotioid species showing clear relationships to members of the Agaricaceae (Hibbett et al. 1997, Moncalvo et al. 2002, Lebel et al. 2004, Geml et al. 2004, Vellinga 2004, Matheny et al. 2006). Additionally, some species of the genus *Coprinus,* including the type species, and the secotioid genus *Montagnea* were proposed to be Agaricaceae (Hopple & Vilgalys 1994, Redhead et al. 2001). Thus, this family of Basidiomycetes especially well suited to investigate the morphological and systematic diversity of gasterothecia. Previous studies provided a partial coverage of the family, or included few taxa. This limited sampling impeded a complete view, so far. Some studies led to nomenclatural recombinations of secotioid species (Vellinga 2002, Vellinga et al. 2003, Geml et al. 2004), which, however are not followed here, since some nomenclatural issues remain unresolved (Dörfelt & Gube 2007).

The most complete study on Agaricaceae so far (Vellinga 2004) could not finally clarify relationships between major subclades, and suggested inclusion of more gasteroid taxa. Therefore, the relationships between and among the hymenothecial and the secotioid or gasteroid groups within Agaricaceae s. l. were re-investigated in this study including a broader taxon sampling. A multilocus molecular systematic treatment of the Agaricaceae with special emphasis on the gasteroid and secotioid taxa is presented. Using DNA sequence data of ITS, LSU, and RPB1, a comprehensive view on the phylogenetic implications of independent gasteromycetation events within Agaricaceae is gained. Furthermore, the phylogenetic relationships among the major clades of Agaricaceae are reviewed with respect to morphological and ontogenetic features.

Material and methods

About 150 exsiccated specimens of Agaricaceae s. l. were analysed, which were collected in the field or obtained on loan from public and private herbaria (NY, BPI, CANB, OSC, JE, GLM, WU, MICH, Herbarium H. Dörfelt). Each collection was revised and determined. Furthermore, two cultures from the DSMZ Braunschweig were used.

DNA extraction was performed with Omega bio-tek E.Z.N.A. Plant DNA Mini Kit (Norcross, Georgia, U.S.A.), Quiagen Plasmid Mini Kit (Hilden, Germany) and Analytik Jena innuPREP Plant DNA Kit (Jena, Germany). For very old collections, or such with extremely scarce material, N-Phenylthiazoliumbromide was added to the lysis buffer of the Analytik Jena innuPREP Plant DNA Kit to a concentration of 2.5 mM to improve yield (Erickson et al. 2005, Telle & Thienes 2009). DNA of some lycoperdoid taxa was kindly provided by E. Larsson and M. Jeppson (Göteborg, Sweden). PCR was performed with Bioline Mango Taq, and for difficult templates, Bovine Serum Albumine (Roth, Karlsruhe, Germany) was added in concentrations between 0.5 and 0.8 µg/µl to the PCR reagents (Kreader 1996). For ITS amplification, primers ITS 1, ITS4 (White et al. 1990), or ITS1F and ITS4B (Gardes & Bruns 1993) were used, with annealing temperatures of 54 °C or 56 °C, yielding fragment lengths of about 650 bp or 800 bp, respectively. Primers LR0R and LR6 were used for LSU amplification (Vilgalys & Hester 1990) at an annealing temperature of 52 °C yielding fragments of about 1050 bp. For amplification of partial RPB1 sequences including the first intron, the primers RPB1-PL4 (CCCCACCATCCCAATTTTC) and RPB1-PR3 (CGAATYTTGTCCGCGAAATT) were newly designed from available GeneBank sequences. This primer set is specific for Agaricaceae and Strophariaceae, but *Battarraea* is excluded from amplification. PCR was performed at an annealing temperature of 58 °C yielding fragments lenghts of about 450 bp. A touchdown PCR approach was performed for difficult amplifications for all loci (Hecker & Roux 1996). PCR products were purified enzymatically (Werle et al. 1994) with Exonuclease A and Shrimp Alkaline Phosphatase (both Fermentas, St. Leon-Rot, Germany). Sequencing was performed by Macrogen Inc., (Seoul, Korea).

Additionally, public sequence databases were screened for DNA sequences of Agaricaceae, and sequences of 88 specimens or cultures were included in the study. If available, several markers were used, when they were perceptibly obtained from the same specimen. Accession numbers are given in the corresponding figures.

Misidentification of species is common within fungi, and nomenclature may change with time, resulting possibly in uncertainties of species recognition. This applies equally to herbarium specimens, cultures, or especially GeneBank entries. Therefore, the specimen list contains the original determination along with the results of revision (Suppl. Tab. 1). GeneBank entries are presented as stated in the database, since the specimens could not be revised.

Sequences of the ITS region and RPB1 were aligned independently with the Q-INS-i option of MAFFT v6 (Katoh & Toh 2008), which considers secondary structure, for ITS, and the E-INS-i option for RPB1, which assumes multiple conserved domains and long gaps. For alignment of LSU, MUSCLE 3.6 (Edgar 2004) was used with the default options. For truncation of the sequences to equal lenghts, avoidance of overlap between ITS and LSU, and for manual adjustment, BIOEDIT (Hall 1999) was used. Separate analyses of the markers minimised the inclusion of paralogs (data not shown). Four data sets were formed, with three sets focusing on certain clades and one overall set with reduced taxon sampling for these clades.

Alignment over all taxa led to highly erroneous results with both MUSCLE and MAFFT. Thus, for the overview data set, four independent alignments of greater subclades, were created using the above described procedure. These were used as constraints for a set of ingroup taxa both within and outside the clades, and of outgroup taxa, using the iterative FFT-NS-i option of MAFFT 6.

Phylogenetic reconstruction was performed using TREEFINDER v10.2008 (Jobb 2008) and MrBayes v3.2-cvs (Ronquist et al 2008). Data was prepared as a five-partition dataset, corresponding to ITS1, 5.8S, ITS2, LSU, and RPB1. As all loci are completely or predominantly non-coding sequences, codon positions were not considered in partitioning. For Maximum Likelyhood (ML) analysis, partition-specific substitution models were proposed by TREEFINDER, which was also used for the ML analysis under optimisation of partition rates, and 1000 replicates of LR-ELW branch support. For Bayesian analysis, GTR+G was assumed as substitution model for all partitions, with optimisation of partition rates. State frequencies, shape parameters and substitution rates were unlinked among partitions. For all datasets, two runs with each 1000000 generations in four chains were performed, sampling every 100 generations, and with a burn-in of 20 percent. Results were evaluated with TRACER (Rambaut & Drummond 2007), all analyses had log likelyhood ESS values above 100. For visualisation of phylogenetic trees, NJPlot (Perrière & Gouy 1996) and FigTree v1.0 (Rambaut 2006) were used.

Results and discussion

Overview of gasteromycetation within Agaricaceae

Agaricaceae s. l. constitute a monophyletic grouping, and five major clades can be distinguished (Fig. 1). These include two exclusively gasteroid groups, Lycoperdaceae and Tulostomataceae; the exclusively hymenothecial *Cystolepiota/ Lepiota* group; and two clades with secotioid and hymenothecial species: *Coprinus* s. str. with the secotioid *Montagnea*; and a clade including *Agaricus*, *Leucocoprinus*, *Macrolepiota*, *Chlorophyllum* and several secotioid species. These clades are considered separate families (see below).

These subclades include the families of Tulostomataceae, Lycoperdacaeae, Lepiotaceae, Coprinaceae and Agaricaceae s. str. The most basal clade is constituted by Tulostomataceae (see Moncalvo et al. 2002, Vellinga 2004). On the first view, the basal position of this exclusively gasteroid group could propose a gasteroid origin of the Agaricaceae s. l., as implicitly stated by Vellinga (2004). However, this would necessitate a reinvention of the active spore discharge mechanism, which has been disputed (Reijnders 2000, Hibbett 2004). It seems more probable that a basal gasteromycetation event occured in the remote past of that clade, and that the ancestral hymenothecial relative is either extinct or evolved to the remaining Agaricaceae s. l.

Coprinaceae are the second clade to emerge, and include a single gasteromycetation event with the secotioid *Montagnea*, and the emergence of autolysis of lamellae in *Coprinus*.

Lepiotaceae constitute the next clade, including *Lepiota* s. str., *Cystolepiota*, *Melanophyllum*, *Lepiota* sect. *Echinoderma*, and *Chamaemyces fracidus* (Fr.) Donk. The latter was proposed to be a taxon basal to all Agaricaceae s. l. (Vellinga 2003, 2004), which is not confirmed here. Monophyly of Lepiotaceae is moderately supported, and contrasts to the results of previous studies (Johnson & Vilgalys 1998, Johnson 1999, Vellinga 2003). Contrary to other studies (Johnson & Vilgalys 1998, Vellinga 2004), *Coprinus comatus* (O. F. Müll.: Fr.) Pers. is not included in this clade. Among-clade relationships cannot be analysed due to our taxon sampling being focused on gasterothecia. Remarkable is the well supported *Cystolepiota/ Echinoderma/ Melanophyllum* -clade, that was only weakly or not supported in previous analyses (Johnson & Vilgalys 1998, Vellinga 2003). The clade contains no known gasteromycetation event, and is thus not discussed in detail.

The sister clades of Lycoperdaceae and Agaricaceae s. str. constitute the last major split of Agaricaceae. Loss of clamp connections occurred three times in this group, clamps are lacking in *Agaricus*, the *Leucoagaricus/ Leucocoprinus* clade, and in Lycoperdaceae with the exception of *Mycenastrum*. Most species of the other clades of Agaricaceae s. l. possess clamps (Velinga 2004). Like in Tulostomatatceae, a close hymenothecial relative of Lycoperdaceae is not present. Despite inclusion of *Mycenastrum*, the clade contains a single basal gasteromycetation event, in contrast to results of Krüger et al. (2001) and Bates (2004), and corresponding to Larsson and Jeppson (2008).

Agaricaceae s. str. include the monophyletic subclades *Macrolepiota* s. str. with *Podaxis* and *Leucocoprinus*/*Leucoagaricus* with several attine symbionts (see also Johnson & Vilgalys 1998). Another subclade within Agaricaceae s. str. is represented by the paraphyletic *Chlorophyllum/ Endoptychum/ Macrolepiota* sect. *Laevistipedes* group, with the monophyletic *Agaricus* emerging from it, including its secotioid relatives.

With the seven independent gasteromytation events of this subclade, the total number of such events sums up to ten. *Secotium gueinzii* Kunze, which has not been analysed within this study, could constitute another event of gasteromycetation within Agaricaceae s. l. (Heim 1951).

Summarising, a more comprehensive view of the Agaricaceae s. l. is possible. An anatomical definition of Agaricaceae is not possible when Lycoperdaceae and Tulostomataceae are included (Kirk et al. 2009). Despite links like rhizomorph structures (Agerer 2002) or chemical features (Demoulin 1967), no truly uniting characteristics can be found. Thus, the family was defined for its gilled members only (Vellinga 2004). To overcome this problem, a definition based solely on molecular characters might be considered. However, this seems not useful when well supported subclades with apomorphic anatomical features are present. Therefore, these subclades are described here as families, including molecular and anatomical features.

Tulostomataceae

The exclusively gasteroid Tulostomataceae constitute the first emerging clade, with three subclades that are referred to as tribes here. Phellorinieae constitute the basal taxon, with Battarraeae and Tulostomateae as sister clades (Fig. 2). *Queletia mirabilis* is placed in Tulostomateae, but only with medium support.

As all Tulostomataceae are gasteroid, it is parsimonous to assume a single gasteromycetation event in the past of the clade. All its taxa show morphological similarities, as the general shape with a “true stipe” (Reijnders 2000), the rounded, often ornamented spores, and the presence of veil structures. They are furthermore united by the similar ontogeny of basidiomata. However, the pleurosporous plectobasidia (Fischer 1900) in Tulostomatae (Schröter 1877, Dumee & Maire 1913, Maublanc & Malençon 1930, Malençon 1935a, b) are clealy distinct from the hymenial cavities in Phellorinieae and Battaraeae. After White (1901) and Fischer (1933), no extensive treatment of this group is available. Recent work only exists on two of the subclades (Wright 1987, Martín et al. 2000). Few taxa were included in molecular phylogenies so far (Martin & Johannesson 2000, Martín et al. 2000, Moncalvo et al. 2002, Jeffries & McLain 2004, Vellinga 2004). Therefore, knowledge on relationships, and division of Tulostomataceae to tribes were based on morphological data only and remained widely unclear so far.

The subclade Phellorinieae contains desert species with persistent groups of basidia in the mature gleba, primitive capillitial elements and without complex peristomes (Malençon 1935a, b, Long & Plunkett 1940, Long & Stouffer 1946). Molecular phylogeny based on ITS sequence data proposed monophyly of the group (Martín et al. 2000), but included only few specimens. With our more extensive sample set, their results can be confirmed here widely. The two monotypic genera showing macroscopically distinct peridium and stipe, *Dictyocephalos* with irregular dehiscence and *Chlamydopus* with an irregular peristome, are shown to be monophyletic. Irregular peridium dehiscence and a peridium continuous with the stipe are the main characters of the genus *Phellorinia* (Malençon 1935a, Kreisel 1961). The species, and probably generic concept of the genus was subject to debate (Kreisel 1961, Dring & Rayss 1963, Martín et al. 2001), based on differences in the structure of the exoperidium.

Our data propose the genus to be paraphyletic, in contrast to Martín et al. (2000), who included only two specimens from Spain in their study. To establish a reliable taxonomic concept in this group, further studies with widely extended taxon sampling are necessary.

The tribe of Battarraeae is characterised by a cushion-like endoperidium, which opens by circumscission (*Battarraea*) or by multiple irregular pores (*Battaraeoides*). Distinctive are furthermore the presence of elaters, capillitial elements with impressive spiral wall thickenings; and the voluminous volva (Maublanc & Malençon 1930, Rea 1942). The species concept within *Battarraea* has been subject to intensive debate in the past (White 1901, Maublanc & Malençon 1930, Rea 1942, Long 1943, Dörfelt & Gerlach 1989). Our analyses indicate a separate placement of the multiostiolate *Battarraeoides diguetii* (Pat. & Har.) Heim & Herrera, while a revision of the species concept is proposed within *Battarraea* (see also Martin & Johannesson 2000, Jeffries & McLain 2004).

Species with morphologically separate stipes that are inserted into the rounded endoperidium; and with pleurosporous plectobasidia (Schröter 1877, Dumee & Maire 1913) are referred to as Tulostomateae. The genus *Tulostoma* represents the majority of species of this group, and the entire family; with 139 species being recognised in the monography on the genus (Wright 1987). The related genera *Schizostoma* and *Queletia* are comparatively small, each with two described species. Both are characterised by irregular dehiscence of the peridium, whereas *Tulostoma* has a more or less defined peristome. In respect to the overwhelming number of *Tulostoma* species, only the most common European, some Central Asian, and few North American species were included here. Supported clades include *T. brumale* Pers.: Pers. with *T.* cf. *cineraceum* Long, *T. melanocyclum* Bres., *T. squamosum* Gmel.: Pers., *T. polymorphum* Long, a group around *Tulostoma kotlabae* Pouzar, *T. pulchellum* Sacc., *T. fimbriatum* Fr., *T. simulans* Lloyd, and *T.* cf. *evanescens* Long & Ahmad. Relationships among these are not well supported. However, noticeable are the rather distinct relationship of *T. brumale* and *T. melanocyclum*, which resemble each other closely morphologically. Apart from these, *Queletia turkestanica* Petrov and the genus *Schizostoma* ermerge in a distinct clade within *Tulostoma*, together with *T. cretaceum* Long and *T. macrocephalum* Long. They share the features of relatively dark pigmented, weakly or not ornamented spores, cyanophilous capillitium and an indefinite peristome or irregular rupturing of the peridium in *Schizostoma* and *Queletia turkestanica*. Such species have already been subsummarised under *Tulostoma* by Léveillé (1846) and Fischer (1933). Additionally, both *Schizostoma* and *Queletia* are seen paraphyletic in our results, indicating the feature of peridium rupture to be overemphasised.

The placement of *Queletia mirabilis* Fr. basal to Tulostomeae has only medium branch support. The species shows remarkable differences to *Tulostoma*, such as the lignicolous habit and the very thick stipe. On the other hand, *Queletia* possesses pleurosporous plectobasidia like *Tulostoma* (Dumee & Maire 1913), which is a unique feature in Agaricales.

Coprinaceae

Coprinus s. str. (sect. *Coprinus*) and *Montagnea* are the second emerging monophylum within Agaricaceae. *Coprinus xerophilus* Bogart is the most basal species, followed by the *Montagnea* clade, *C. sterquilinus* (Fr.: Fr.) Fr. and finally *C. spadiceisporus* Bogart and the *C. comatus* group (Fig. 3). Within *C. comatus*, two main lineages are present. They are not distinct morphologically or differ in their distribution, but are clearly separated in our analyses. The latter was proposed by Ko et al. (2001), and cannot be followed here with increased taxon sampling. As an addition to the outgroup, GeneBank entries of *C. fissolanatus* Kemp, *C. bellulus* Uljé, *C. silvaticus* Peck, an undetermined *Coprinus* sequence, and a sequence misidentified as *C. comatus* were included in this study. They were classified as Agaricaceae in GeneBank. The *Coprinus* clade contains a single event of gasteromycetation, leading to the monophyletic secotioid taxon *Montagnea*.

Relationships between *Coprinus* sect. *Coprinus* and *Montagnea* have been proposed before (Underwood 1899, Hopple & Vilgalys 1994, Hopple & Vilgalys 1999, Redhead et al. 2001), but taxon sampling was not sufficient to clarify the systematic position of *Montagnea*. The genus shows many morphological similarities to the related *Coprinus* species. These led to a remarkable number of misidentifications in the herbarium collections (suppl. Tab. 1). Such features are the hollow stipes filled with a central yarn-like strand, the ellipsoidal, pigmented spores with conspicuous germ pores, lack of cystidia and the presence of a fibrillose universal veil without sphaerocysts (van de Bogart 1976, Redhead et al. 2001) Unique to *Montagnea* are the expanding lamellae or “gussets” (Miller & Miller 1988), which tear the thin pileus trama apart and do not perform autolysis like in *Coprinus*. Additionally, they lack active spore discharge. Developmental analyses have been performed for *C. comatus* (Brefeld 1877, Atkinson 1916), which should be extended to other *Coprinus* species and *Montagnea*. It can be hypothesised that evolution of the gills proceeded from non deliquefying lamella (like in *C. xerophilus*) towards either deliquescence (*C. comatus* group) or secotioid habit (*Montagnea*). Specimens determined as *Montagnea haussknechtii* Rabenh. form a well supported clade of their own, however situated within *Montagnea arenaria* (De Cand.) Zeller.

M. haussknechtii is currently considered an independent taxon (Reid & Eicker 1991). Chen (1999) proposed *Montagnea* to be monotypic, but the study suffered from the lack of an outgroup and included probably only a single sample of *M. haussknechtii*. It seems probable, that the speciation process is very recent, and that the ancestral population of *M. haussknechtii* can be placed within the variation range of *M. arenaria*. Mating analyses including *M. haussknechtii* could solve the matter, but cultures of this species could not be obtained.

Lycoperdaceae

Lycoperdaceae, including *Mycenastrum* and *Arachnion* are presented as a well supported monophyletic clade in our analysis (Fig. 1). They are characterised by their completely gasteroid appearance; chambered gleba lined with euhymenium (Clemencon 2004) that gets powdery upon maturation; usually rounded and ornamented spores and abundant, highly differentiated capillitium and paracapillitium. Lycoperdaceae share rhizomorph (Townsend 1956, Agerer 2002, Gube 2007) and biochemical (Demoulin 1967) features with Agaricaceae. Hibbett et al. (1997) proposed relationships to agaricoid genera based on ribosomal DNA. Molecular studies (Krüger et al. 2001, Krüger & Kreisel 2003, Bates 2004, Larsson & Jeppson 2008, Krüger & Gargas 2008) were restricted to a certain taxonomic group or geographical area, and only Larsson & Jeppson (2008) analysed enough taxa to distinguish main clades and subclades of Lycoperdaceae. Their results are widely confirmed here. However, we restrain from reviewing Lycoperdaceae in all detail for now, including only some representatives in our analysis. Further detailed work on this group is in process.

Mycenastrum is characterised morphologically by pitted spores, clamp connections in the peridium, and spiny, short branched capillitium (Hansen 1962, Bronchard & Demoulin 1973). This led to its placement in a separate family, Mycenastraceae (Zeller 1949). Its basal position was established by Larsson & Jeppson (2008), contrasting to earlier results (Krüger et al. 2001, Bates 2004). Other basal clades of Lycoperdaceae include the semihypogeous genera *Abstoma* with reticulate spores, scanty, often spiralled capillitium and irregular peridial dehiscence; and *Disciseda* with verrucose, shortly pedicellate spores, spiralled capillitium and spore dispersal at the former mycelium attachment site (Underwood 1899, Kreisel 1962, Kers 1975, Wright & Suarez 1990). The clade of *Calvatia* and *Langermannia* is monophyletic (Larsson & Jeppson 2008), which is supported here. The genera are characterised by irregular peridium dehiscence, septated capillitium of the *Calvatia*-type (Kreisel 1992, Krüger et al. 2001) and their peculiar flabelloid gleba ontogeny that has been proven for *L. gigantea* (Gube

2007), but is also present in *C. craniiformis* (Schwein.) Fr. (Swartz 1935). *Arachnion* is defined by smooth spores, and by a membrane enclosing the glebal cavities at maturity, thus forming peridioles (Demoulin 1980). An ontogenetic study (Lander 1934) proposed these gleba membranes to be formed from remains of basidia and tramal tissue, and discussed close relationships with Lycoperdaceae. Bates (2004) did show *Arachnion* to be included to Lycoperdaceae. Still, the family of Arachniaceae Coker and Couch was continued and is often considered valid (e.g. Kasuya 1996). *Lycoperdon pyriforme* Schaeff.: Pers. was discussed to belong to *Morganella* (Krüger & Kreisel 2003), now subgenus of *Lycoperdon* (Lasrsson & Jeppson 2008), mainly on account of its lignicolous habit and deviating subgleba. The analyses of Bates (2004) and Larsson and Jeppson (2008) suggested this species to be rather distantly related to *Lycoperdon*, which is confirmed here. The genus *Bovista* includes relatively small Lycoperdaceae with lacking or compact subgleba, and smooth or furfuraceous exoperidium (Kreisel 1962). In our analysis, only the subgenus *Bovista* is included, whose relationships to the subgenus *Globaria* have been shown to be somewhat ambiguous (Larsson & Jeppson 2008). *Lycoperdon* itself, exclusive of *L. pyriforme* and inclusive of *Morganella* and *Vascellum,* is shown to be well supported, also corresponding to previous analyses (Larsson & Jeppson 2008). It includes species with primarily cellular subgleba, which is sometimes reduced; sphaerocysts in the exoperidium; verrucose spores; and capillitium of the *Lycoperdon*-type that may be replaced by paracapillitium (Kreisel 1962, Kreisel & Dring 1967).

Secotioid taxa of Agaricaceae s. str.

The secotioid species of Agaricaceae s. str. are related to *Macrolepiota* s. str., the *Chlorophyllum*/*Macrolepiota* sect. *Laevistipedes* group, or to *Agaricus* (Fig. 4). No gasteromycetation was observed in the *Leucoagaricus*/*Leucocoprinus* clade (Fig. 1).

The species related to *Macrolepiota* have been shown to be systematically very heterogeneous (Vellinga et al. 2003, Vellinga 2004), and this also applies to their gasteroid relatives. *Podaxis*, resembling morphologically a cleistocarpic *Coprinus* species, is associated to *Macrolepiota* s. str. Contrasting to other secotioid genera, *Podaxis* did obviously not evolve very recently from hymenothecial taxa, as already noted by Vellinga (2004). It constitutes apparently the most ancient secotioid group within Agaricaceae. *Podaxis* and *Macrolepiota* s. str. share elongated, mostly smooth spores with germ pores of similar organisation (Meléndez-Howell 1967, de Villiers et al. 1988) and stipe organisation with a large bulb

(Morse 1933). Furthermore, in both *Macrolepiota* and *Podaxis*, the pileipellis/exoperidium is covered with trichodermal hyphae (de Villiers et al. 1988, Vellinga et al. 2003). Peculiar to *Podaxis* is the pigmentation of the spores, and its gasteroid morphology. *Podaxis* was proposed to be related with *Coprinus comatus* and *Montagnea* by morphological (Underwood 1899, Miller & Miller 1988) and molecular characters (Hopple & Vilgalys 1994, Hopple & Vilgalys 1999, Redhead et al. 2001). Additionally, relationships with *Phellorinia* (Fischer 1934) and with *Agaricus* and *Endoptychum* (Brasfield 1937) were proposed, based on comparative ontogeny. However, the development of *Macrolepiota* s. str. has never been analysed. *Podaxis* houses a number of described species, but species concepts differ widely among authors (e.g. Morse 1933, de Villiers 1988). In our analysis, only *Podaxis pistillaris* (Pers.) Fr. was analysed, but close relationship with the other species can be assumed from their morphology. Therefore, a single gasteromycetation event is proposed for this group, which clearly clusters within Agaricaceae s. str.

In *Endoptychum*, the most extreme case of polyphyly is realised; all three analysed species constitute clades of their own and evolved independently. The similar sublamellar, regular hymenophoral trama, globose spores without germ pores, and the total lack of cystidia (Singer & Smith 1956) thus have to be considered as parallelisms. This is supported by the presence of these features in several genera of Agaricaceae; among them *Agaricus*, *Chlorophyllum* and *Macrolepiota* sect. *Laevistipedes*. Indeed, *Endoptychum agaricoides*, the type species, was shown to be related with the latter *Macrolepiota* sect. *Laevistipedes*, and *E. depressum* Singer & Smith has been included into *Agaricus* as *A. inapertus* Vellinga (Vellinga et al. 2003). *E. agaricoides*, *Chlorophyllum molybdites* (G. Meyer: Fr.) Mass., and the related *Macrolepiota* species have been compiled under the genus name *Chlorophyllum* (Vellinga 2002, Vellinga & de Kok 2002). This nomenclaturally problematic approach (Dörfelt & Gube 2007) was furthermore hardly supported by molecular phylogeny (Johnson & Vilgalys 1998, Vellinga et al. 2003, Vellinga 2004). Our data reveal *Chlorophyllum* ss. Vellinga (2002) as a paraphyletic clade basal to *Agaricus*, a state already indicated, but not discussed by Johnson and Vilgalys (1998) and in one of the analyses in Vellinga et al. (2003). This arrangement counterindicates the generic recognition of *Chlorophyllum* in the sense of Vellinga (2002).

Among the clades related to *Chlorophyllum* are two independent secotioid lineages, *E. agaricoides* and *E. arizonicum*, interspersed with a clade of *C. molybdites*, *M. globosa* Mossebo, and *M. neomastoidea* (Hongo) Hongo. The relatives of *M. rachodes* (Vittad.) Singer and of *C. hortense* (Murrill) Vellinga are more basal clades. Each of these groupings is well supported, but their interrelationships are weakly resolved. *E. agaricoides* is morphologically characterised by olive spores, reddening of stipe plecenchyma like *M. rachodes* and a stipe protruding the whole basidiocarp (Singer & Smith 1956, Dörfelt & Gube 2007). *E. arizonicum* has extremely thick-walled, white to pale yellow spores, a stipe not reaching the apex of the peridium, and no colour reaction when exposed to the air (Shear 1902, Singer & Smith 1956). Their hymenothecial relatives may, or may not, show a colour reaction upon bruising, and have either unpigmented or, in *C. molybdites*, lightly greenish spores. Following ontogenetic analyses, relationships of *E. agaricoides* with *Agaricus* (Conard 1915), *Podaxis* (Brasfield1937) and *Phallaceae* (Lohwag 1924) were discussed. Indeed development of the species fits into the general mode of agaricoid ontogeny, including *M. rachodes* (Reijnders 1975).

Unfortunately, *Endoptychum melanosporum* (Berk.) Singer & Smith could not be analysed molecularly, while morphology (Singer & Smith 1956) does not clearly hint to relationships with Agaricaceae s. l.

Agaricus is one of the hymenothecial genera of the group easy to characterise, and yet species determination is often a major task (Geml et al. 2004). Nonetheless, monographic treatments on the genus are present (Galli 2004), and so are molecular phylogenetic studies, which revealed close relationship with four gasteroid species (Vellinga et al. 2003, Geml 2004, Geml et al. 2004, Lebel et al. 2004, Vellinga 2004). These correspond to four independent events of gasteromycetetion within the genus. Revealed relationships of hymenothecial taxa confirm previous results (Geml 2004, Geml et al. 2004)

Of the gasteroid species related with *Agaricus*, only *Barcheria willisiana* Lebel shows no morphological similarity (Lebel et al. 2004). Development of this Australian species has not been observed, however, the orange-red discoloration of bruised or cut fruitbodies points towards Agaricaceae. Judging from the original description, *B. willisiana* resembles primordia of Agaricaceae. It is therefore probable that this fungus evolved as a result of extreme paedomorphosis, judging from the lack of hymenial organisation. Its placement in the section *Xanthodermei* (Lebel et al. 2004) is confirmed, but weakly supported. This is due to the lack of genetic data other than LSU in public sequence databases and the unavailability of specimens for loan.

Endoptychum depressum was also suggested to be closely related with *Agaricus* sect. *Arvenses* by morphological (Singer & Smith 1956) and molecular features (Vellinga et al. 2003, Geml 2004, Geml et al. 2004). The species has rounded, dark pigmented spores, and corresponds macroscopically to short stiped species of *Agaricus*, yet with a persistent annulus that keeps the lamellar cavity closed. However, its discoloration and cumarinous odor (Singer

& Smith 1956) give strong evidence for relationships to the section *Arvenses*, where it is placed in our analyses as. A revision of the type specimens is still pending.

Gyrophragmium and *Longula* are two other gasteroid genera that show close morphological resemblance to *Agaricus*. Their veil structures, odor, yellow bruising, regular lamellar trama, and smooth, dark pigmented, subglobose spores, resemble *Agaricus* (Kreisel 1973). Volatile compounds are actually similar; additionally, fresh basidiocarps react strongly with the Schaeffer-reagents (Rapior et al. 2000, Geml 2004). Close relationship of *L. texensis* Zeller to *Agaricus* was also indicated in an ontogenetic study (Barnett 1943), and *G. dunalii* (Fr.) Zeller was shown to enrich certain heavy metals as seen with *Agaricus* species, especially Cadmium (Stijve et al. 2001). Both *Longula* and *Gyrophragmium* possess anastomosed lamellar gleba, with an almost irpecoid appearance in mature stages. Relationships and validity of the two genera were controversely discussed, *Gyrophragmium* is distinguished from *Longula* by a rooting stipe base and the presence of a volva (Zeller 1943, Kreisel 1973). Both *L. texensis* and *G. dunallii* were renamed as *A. texensis* Geml, Geiser & Royse and *A. aridicola* Geml, Geiser & Royse, due to molecular evidence (Geml et al. 2004). In our analysis, the majority of specimens, originally mostly determined as various *Gyrophragmiun* species, cluster together with the Genebank entry for *L. texensis* basal to the *Agaricus* sections *Minores* and *Arvenses*. In contrast, *G. dunallii* is shown to have evolved within *Minores*. This placement confirms previous results (Vellinga et al. 2003, Geml et al. 2004). While is the samples of *L. texensis* originate exclusively from the south western United States, *G. dunallii* includes only non-American collections, and a GeneBank entry without locality. Altogether, Agaricaceae contain seven of the ten gasteromycetation events of all five major clades, most being secotioid.

Conclusions

Gasteromycetation, the process resulting in angio- or cleistocarpic basidiomycete fruitbodies with statismospores, caused a high diversity of gasterothecial forms within Agaricaceae s. l. This includes taxa lacking obvious morphological similarities with hymenothecia, and species closely resembling their hymenothecial relatives. In previous studies, monophyly of this group, and lack of internal branch resolution led to inclusion of all related taxa in Agaricaceae (Vellinga 2004). Using nrDNA and partial RPB1 sequences in a partitioned data set with independent rate optimisation, we could confirm monophyly of the clade. However, our study furthermore reveals five distinct subclades, which correspond widely to traditionally acknowledged families, and can be defined by morphological features. Four of these contain at least ten independent events of gasteromycetation. This includes exclusively gasteroid groups like Tulostomataceae and Lycoperdaceae, traditionally representing families and lacking close hymenothecial relatives; and secotioid relatives of genera like *Agaricus*, *Coprinus*, or *Macrolepiota* and *Chlorophyllum*. The latter were so far acknowledged as genera of their own, and only recently and partly included in hymenothecial genera (Vellinga 2002, Vellinga et al. 2003, Geml et al. 2004), despite many morphological similarities. Main results include furthermore detection of the paraphyly of *Chlorophyllum* ss. Vellinga (2002) caused by *Agaricus*, and close relationship of *Podaxis* and *Macrolepiota* s. str. Furthermore, *Coprinus* s. str. is shown to be monophyletic only when the secotioid genus *Montagnea* is included, and the rare secotioid *Endoptychum arizonicum* is established as an independent gasteroid clade close to *Chlorophyllum* and *Endoptychum agaricoides*. Apart from molecular data, morphological features support our results. This is especially true for ontogenetic features (e. g. Conard 1915, Gube 2007), which could, in combination with extended knowledge of the genetic background and consideration of their phylogenetic relationships, facilitate establishment of evolutionary developmental studies of gasteromycetation.

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References

AGERER, R. 2002: Rhizomorph structures confirm the relationship between Lycoperdales and Agaricacae (Hymenomycetes, Basidiomycota). Nova Hedwigia **75** (3–4): 367–385.

ATKINSON, G. F. 1916: Origin and development of the lamellae in *Coprinus*. Bot. Gaz. **61** (2): 89–130.

BARNETT, H. L. 1943: The Development and Structure of *Longia texensis*. Mycologia **35** (4): 399–408.

BATES, S. T. 2004: Arizona members of the Geastraceae and Lycoperdaceae (Basidiomycota, Fungi). Master thesis Arizona State University, Tempe, Arizona.

BINDER, M., BRESINSKY, A. 2002: Derivation of a polymorphic lineage of Gasteromycetes from boletoid ancestors. Mycologia **94** (1): 85–98.

BRASFIELD, T. W. 1937: The morphology of *Podaxis pistillaris*. University of Iowa Studies in Natural History **17** (5): 199–211.

BREFELD, O. 1877: Botanische Untersuchungen über Schimmelpilze. III: Heft: Basidiomyceten I. Leipzig.

BRONCHARD, R., DEMOULIN, V. 1973: Ultrastructure de la paroi sporale des gasteromycètes *Mycenastrum corium* et *Abstoma reticulatum* en rapport avec leur position systématique. Bull. Soc. R. Bot. Belg. **106**: 267–272.

CHEN, C. 1999: Genetical and molecular systematic study on the genus *Montagnea* Fr. Master thesis Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

CLÉMENÇON, H. 2004: Cytology and Plectology of the Hymenomycetes. Bibl. Myc **199**. Berlin, Stuttgart.

CONARD, H. S. 1915: The Structure and Development of *Secotium agaricoides*. Mycologia **7** (2): 94–104.

DE VILLIERS, J. J. R., EICKER, A., VAN DER WESTHUIZEN, G. C. A. 1988: A new section and two new species of *Podaxis* (Gasteromycetes) from South Africa. S. Afr. J. Bot. **55** (2): 159–164.

DEMOULIN, V. 1967: Intérêt des certaines substances a fonctions basiques en chimiotaxinomie des Gastéromycètes. Bull. Soc. Mycol. France **83**: 342–353.

DEMOULIN, V. 1980: Observations sur le genre *Arachnion* Schw. (Gasteromycetes). Can. J. Bot. **58**: 641–655.

DÖRFELT, H., GERLACH, H. 1989: Zur Identität von *Battaraea phalloides* und *B. stevenii* (Basidiomycetes/ Tulostomatales). Wiss. Z. Univ. Halle. **39**:90–100.

DÖRFELT, H., GUBE, M. 2007: Secotioid Agaricales (Basidiomycetes) from Mongolia**.** Feddes Repert. **118** (3–4): 103–112.

DRING, D. M., RAYSS, T. 1963: The gasteromycete fungi of Israel. Israel J. Bot. **12**: 147–178.

DUMÉE, P., MAIRE, R. 1913: Note sur la *Queletia mirabilis* Fr. et sa découverte aux environs de Paris. Bull. Soc. Mycol. France **29**: 495–502.

EDGAR, R. C. 2004: MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. **32:**1792–97.

ERICKSON, D. L., SMITH, B. D., CLARKE, A. C., SANDWEISS, D. H., TUROSS, N. 2005: An Asian origin for a 10,000 year-old domesticated plant in the Americas. Proc. Natl. Acad. Sci. USA **102** (51): 18315–18320.

FISCHER, E. 1900: Hymenogastrineae, Lycoperdineae, Nidulariineae, Plectobasidiineae in: ENGLER, A., PRANTL, K. (Hrsg.): Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigen Arten insbesondere den Nutzpflanzen. I. Teil, Abt. 1**. Leipzig. 296–346.

FISCHER, E. 1933: Gastromyceteae. in ENGLER, A., PRANTL, K. (Hrsg.): Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigen Arten insbesondere den Nutzpflanzen. 2. Aufl. Band 7a. Leipzig. S. 1–72.

FISCHER, E. 1934: Zur Kenntnis der Fruchtkörperentwicklung von *Podaxis*. Ber. schweiz. botan. Ges. **43**: 11–18

FRIES, E. M. 1821–1832: Systema mycologicum. Vol I-IV. Gryphiswaldiae.

FRITSCHE, G., VON SENGBUSCH, R. 1968: Beispiel der spontanen Entwicklung neuer Fruchtkörperformen beim Kulturchampignon. Der Züchter **33** (7): 270–274.

GALLI, R. 2004: Gli *Agaricus*. Milano.

GARDES M., BRUNS, T.D. 1993: ITS primers with enhanced specifity for Basidiomycetes: application to identification of mycorrhizae and rusts. Mol. Ecol. **2**:113–118.

GÄUMANN, E. 1926: Vergleichende Morphologie der Pilze. Jena.

GEML, J. 2004: Evolution in Action: molecular evidence for recent emergence of secotioid genera *Entoptychum*, *Gyrophragmium* and *Longula* from *Agaricus* ancestors. Acta Microbiol. Immunologica Hungarica **51**(1–3): 97–108.

GEML, J. GEISER, D. M., ROYSE, D.J. 2004: Molecular evolution of *Agaricus* species based on ITS and LSU rDNA sequences. Mycol. Progress **3**(2): 157–176.

GUBE, M. 2007: The gleba development of *Langermannia gigantea* (Batsch: Pers.) Rostk. (Basidiomycetes) compared to other Lycoperdaceae, and some systematic implications. Mycologia **99** (3): 396–405.

HANSEN L. 1962: A Danish find of *Mycenastrum corium* with notes on its anatomy. Bot Tidsskr **58**: 204–212.

HECKER, K. H, ROUX, K. H. 1996: High and Low Annealing Temperatures Increase Both Specificity and Yield in Touchdown and Stepdown PCR. BioTechniques **20**: 478–485.

HEIM, R. 1951: Notes sur la flore mycologique des Terres du Pazifique Sud. III. Sur les *Secotium* de Nouvelle-Zélande et la phylogénie de ce genre. Rev. Mycol. (Paris) **16**: 129–153.

HIBBETT, D. S. 2004: Trends in Morphological Evolution in Homobasidiomycetes Inferred Using Maximum Likelihood: A Comparison of Binary and Multistate Approaches. Syst. Biol. **53** (6): 889–903.

HIBBETT, D. S.; PINE E. M.; LANGER, E.; LANGER, G., DONOGHUE, M. J. 1997: Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. Proc. Nat. Acad. Sci. USA **94**: 12002–12006.

HOPPLE, J. S., VILGALYS, R. 1994: Phylogenetic relationships among coprinoid taxa and allies based on data from restriction site mapping of nuclear rDNA. Mycologia **86**(1): 96–107.

HOPPLE, J. S., VILGALYS, R. 1999: Phylogenetic Relationships in the Mushroom Genus *Coprinus* and Dark-Spored Allies Based on Sequence Data from the Nuclear Gene Coding for the Large Ribosomal Subunit RNA: Divergent Domains,Outgroups, and Monophyly. Mol. Phylog. Evol. **13**(1): 1–19.

JEFFRIES, P., MCLAIN, L. 2004: Synonymy between *Battarrea phalloides* and *B. stevenii*. English Nature Research Reports **625**, Peterborough.

JOBB, G. 2008: TREEFINDER version of October 2008. Distributed by the author at www.treefinder.de.

JOHNSON, J. 1999: Phylogenetic relationships within *Lepiota* sensu lato based on morphological and molecular data. Mycologia **91** (3): 443–458.

JOHNSON, J., VILGALYS, R. 1998: Phylogenetic systematics of *Lepiota* sensu lato based on nuclear large subunit rDNA evidence. Mycologia **90** (6): 971–979.

KASUYA, T., ORIHAYA, T., FUKIHARU, T., YOSHIMI, S. 1996: A lycoperdaceous fungus, *Arachnion album* (Agaricales, Arachniaceae), newly found in Japan. Mycoscience **47**: 385–387

KATOH, K., TOH, H. 2008: Recent developments in the MAFFT multiple sequence alignment program. Briefings in Bioinformatics 9 (4): 286–298.

KERS, L. E. 1975: The genus *Disciseda* (Gasteromycetes) in Sweden. Svensk Bot. Tids. **69**: 405–438.

KIRK, M. P., CANNON, P. F., MINTER, D. W., STALPERS, J. A. 2009: Ainsworth & Bisby's dictionary of the fungi. 10th ed. Wallingford.

KO, K. S., LIM, Y. W., KIM, Y. H., JUNG, H. S. 2001: Phylogeographic divergences of nuclear ITS sequences in *Coprinus* species sensu lato. Mycol. Res. **105**: 1519–1526.

KREADER, C. A. 1996: Relief of Amplification Inhibition in PCR with Bovine Serum Albumin or T4 Gene 32 Protein. Appl. Env. Microbiol. **62** (3): 1102–1106.

KREISEL, H. 1961: Über *Phellorinia herculeana* (Pers.) Kreisel comb. nov. und ihr Vorkommen in Europa. Česka Myk. **15** (4): 195–200.

KREISEL, H. 1962: Die Lycoperdaceae der Deutschen Demokratischen Republik. Feddes Repert. **64**: 89–201.

KREISEL, H. 1973: Die Gattung *Gyrophragmium* Mont. und ihre Stellung im System der Basidiomycetes. Feddes Repert. **83**: 577–583.

KREISEL, H. 1992: An emendation and preliminary survey of the genus *Calvatia* (Gastromycetidae). Persoonia **14** (4), S. 431–439.

KREISEL, H., DRING, D. M. 1967: An emendation of the genus *Morganella* Zeller (Lycoperdaceae). Feddes Repert. **74**: 109–122.

KRÜGER, D.; BINDER, M.; FISCHER, M., KREISEL, H. 2001: The Lycoperdales. A molecular approach to the systematics of some gasteroid mushrooms. Mycologia **93** (5): 947–957.

KRÜGER, D., KREISEL, H. 2003: Proposing *Morganella* subgen. *Apioperdon* subgen. nov. for the puffball *Lycoperdon pyriforme*. Mycotaxon **86**:169–177.

KRÜGER, D., GARGAS, A. 2008: Secondary structure of ITS2 rRNA provides taxonomic characters for systematic studies d a case in Lycoperdaceae (Basidiomycota). Mycol. Res. **112**: 313–330.

LANDER, C. A. 1934: The development of the fruiting body of *Arachnion album*. J. Elisha Mitchell Soc. Sci. **50**: 275–282.

LARSSON, E., JEPPSON, M. 2008: Phylogenetic relationships among species and genera of Lycoperdaceae based on ITS and LSU sequence data from North European taxa. Mycol. Res. **112**: 4–22.

LEBEL, T.; THOMPSON, D. K., UDOVICIC, F. 2004: Description and affinities of a new sequestrate fungus *Barcheria willisiana* gen. et spec. nov. (Agaricales) from Australia. Mycol. Res. **108** (2): 206–213.

LÉVEILLÉ, J.-H. 1846: Descriptions des champignons de l'herbier du muséum de Paris. Ann. Sci. Nat. **5**: 111–167.

LLOYD, C. G. 1902: The genera of gastromycetes. Cincinnati.

LOHWAG, H. 1924: Entwicklungsgeschichte und systematische Stellung von *Secotium agaricoides* (Czern.) Holl. Öst. Bot. Zeit. **73** (7–9): 161–174.

LONG, W. H. 1943: Studies in the Gasteromycetes: VIII. *Battarraea laciniata*. Mycologia **35** (5): 546–556.

LONG, W. H., PLUNKETT, O. A. 1940: Studies in the Gasteromycetes. I. The Genus *Dictyocephalos*. Mycologia **32** (6): 696–709.

LONG, W. H., STOUFFER, D. J. 1946: Studies in the Gasteromycetes. XIV. the Genus *Chlamydopus*. Mycologia **38** (6): 819–829.

MALENÇON, G. 1935a: Etudes sur les Phellorinés. I. La *Phellorinia delastrei* (Dur. et Mtgn.) Ed. Fischer. Ann. Cryptog. Exot. **8**: 5–48.

MALENÇON G.1935b: Etudes sur les Phellorinés. II. Le *Dictyocephalus curvatus* Underwood. Ann. Cryptog. Exot. **8**: 102–132.

MARTÍN, M. P., HIDALGO, E., ALTÉS, A., MORENO, G. 2000: Phylogenetic relationships in Phelloriniaceae (Basidiomycotina) based on ITS rDNA sequence analysis. Cryptogamie Mycol. **21** (1): 3–12.

MARTÍN, M. P., JOHANNESSON, H. 2000: *Battarrea phalloides* and *B. stevenii*, insight into a long-standing taxonomic puzzle. Mycotaxon **74**: 67–75.

MAUBLANC, A., MALENÇON, G.. 1930: Recherches sur la *Battarraea Guicciardiniana* Ces. Bull. Soc. Myc. France **46**: 43–73.

MATHENY, P. B., CURTIS, J. M., HOFSTETTER, V., AIME, M. C., MONCALVO, J. M., GE, Z. W., YANG, Z. L., SLOT, J. C., AMMIRATI, J. F., BARONI, T. J., BOUGHER, N. L., HUGHES, K. W., LODGE, D. J., KERRIGAN, R. W., SEIDL, M. T., AANEN, D. K., DENITIS, M., DANIELE, G. M., DESJARDIN, D. E., KROPP, B. K., NORVELL, L. L., PARKER, A., VELLINGA, E. C., VILGALYS, R., HIBBETT, D. S. 2006. Major clades of Agaricales: a multi-locus phylogenetic overview. Mycologia **98** (6): 982–995.

MELÉNDEZ-HOWELL, L. M. 1967: Recherches sur le pore germinatif des basidiospores. Ann. Sci. Nat. Bot. Sér. **12** (8): 487–638.

MILLER, O. K., MILLER, H. H. 1988: Gasteromycetes. Morphological and development features with keys to orders, families and genera. Eureka.

MONCALVO, J.-M., VILGALYS, R., REDHEAD, S. A., JOHNSON, J. E., JAMES, T. Y., AIME, M. C., HOFSTETTER, V., VERDUIN, S. J. W., LARSSON, E., BARONI, T. J., THORN, R. G., JACOBSSON, S., CLÉMENCON, H., MILLER, O. K. 2002: One hundred and seventeen clades of euagarics. Mol. Phylog. Evol. **23**: 357–400.

MORSE, E. E. 1933: A study of the genus *Podaxis*. Mycologia **25** (1): 1–32.

PEINTNER, U., BOUGHER, N. L., CASTELLANO, M. A., MONCALVO, J.-M., MOSER, M. M., TRAPPE, J. M., VILGALYS, R. 2001: Multiple origins of sequestrate fungi related to *Cortinarius* (Cortinariaceae). Am. J. Bot. **88**: 2168–2179.

PERRIÈRE, G., GOUY, M. 1996: WWW-Query: An on-line retrieval system for biological sequence banks. Biochimie **78**: 364–369.

RAMBAUT, A. 2006: FigTree v1.0. Tree Figure Drawing Tool. Published by the author at tree.bio.ed.ac.uk/software/figtree.

RAMBAUT, A., DRUMMOND, A. J. 2007: Tracer v1.4. Published by the authors at beast.bio.ed.ac.uk/software/tracer.

RAPIOR, S., MAURUC, M.-J., GUINBERTEAU, J., MASSON, C.-L., BESSIÈRE, J.-M. 2000: Volatile composition of *Gyrophragmium dunallii*. Mycologia **92** (6): 1043–1046.

RAUSCHERT, S. 1964: *Montagnea arenaria* (DC . ex Fries) Zeller, ein für Deutschland neuer Steppenpilz. Westf. Pilzbr. **5** (1): 1–13.

REA, P. M. 1942: Fungi of Southern California. I. Mycologia **34** (5): 563–574.

REDHEAD, S. A., VILGALYS, R., MONCALVO, J.-M., JOHNSON, J., HOPPLE, J. S. 2001: *Coprinus* Pers. and the disposition of *Coprinus* species sensu lato. Taxon **50**: 203–241.

REID, D., EICKER, A. 1991: A taxonomic survey of the genus *Montagnea* (Gasteromycetes) with special reference to South Africa. S. Afr. J. Bot. **57** (3): 161–170.

REIJNDERS, A. F. M. 1975: The development of three species of Agaricaceae and the ontogenetic pattern of this family as a whole. Persoonia **8** (3): 307–319.

REIJNDERS, A. F. M. 2000: A morphogenetic analysis of the basic characters of the gasteromycetes and their relation to other hymenomycetes. Mycol. Res. **104** (8): 900–910.

RONQUIST, F, HUELSENBECK, J. P., VAN DER MARK, P. 2008: MrBayes v3.2-cvs (Bayesian Analysis of Phylogeny). Published by the authors at people.sc.fsu.edu/~ronquist/MrBayes

SCHRÖTER, J. 1877: Ueber die Entwickelung und die systematische Stellung von *Tulostoma* Pers. Cohn Beitr. Biol. Pfl. **2** (1): 65–72.

SHEAR, C. L. 1902: Mycological Notes and New Species. Bull. Torrey Bot. Club **29** (7): 449–457.

SINGER, R. (ed.) 1986: The Agaricales in modern taxonomy. Koenigstein.

SINGER, R., SMITH, A. H. 1958: Studies on secotiaceous fungi – II. *Endoptychum depressum*. Brittonia **10**: 216–221.

STIJVE, T., ANDREY, D., GOESSLER, W., GUINBERTEAU, J., DUPUY, G. 2001: Étude comparative des métaux lourds et d'autres éléments traces dans *Gyrophragmium dunalii* et dans les agarics jaunissants de la section *Arvenses*. Bull. Soc. Mycol. France **117**: 133–144.

SWARTZ, D. 1935: The development of *Calvatia craniiformis*. *Mycologia* **27**, S. 439–448.

TELLE, S., THIENES, M. 2008: Amplification of *cox2* (~620 bp) from 2 mg of up to 129 years old herbarium specimens, comparing 19 extraction methods and 15 polymerases. PLoS ONE 3 (10): e3584. doi:10.1371/journal.pone.0003584.

TOWNSEND, B. B. 1954: Morphology and development of fungal rhizomorphs. Trans. Br. Mycol. Soc. **37**: 222–233.

THIERS, H. D. 1984. The secotioid syndrome. Mycologia **76** (1):1–8.

UNDERWOOD, L. M. 1899: Moulds Mildews and Mushrooms. A guide to the systematic study of the fungi and mycetozoa and their literature. New York.

VAN DE BOGART, F. 1976: The genus *Coprinus* in Western North America, Part I: Section *Coprinus*. Mycotaxon **4** (1): 233–275.

VELLINGA, E. C. 2002: New combinations in *Chlorophyllum*. Mycotaxon **83**: 415–417.

VELLINGA, E. C. 2003: Phylogeny of *Lepiota* (Agaricaceae) – Evidence from nrITS and nrLSU sequences. Mycol. Progress **2** (4): 305–322.

VELLINGA, E. C. 2004: Genera in the family Agaricaceae: evidence from nrITS and nrLSU sequences. Mycol. Res. **108** (4): 354–377.

VELLINGA, E. C., DE KOK, R. P. J. 2002: Proposal to conserve the name *Chlorophyllum* Massee against *Endoptychum* Czern. (Agaricaceae). Taxon **51**: 563–564.

VELLINGA, E. C., DE KOK, R. P. J., BRUNS, T. D. 2003: Phylogeny and taxonomy of *Macrolepiota* (Agaricaceae). Mycologia **95** (3): 442–456.

VILGALYS, R., HESTER, M. 1990: Rapid Genetic Identification and mapping of Enzymatically Amplified Ribosomal DNA from Several *Cryptococcus* Species. J. Bacteriol. 172 (8): 4238–4246.

WERLE, E, SCHNEIDER, C., RENNER, M., VÖLKER, M., FIEHN, W. 1994: Convenient single-step, one tube purification of PCR products for direct sequencing. Nucleic Acids Res. **22** (20): 4354–4355.

WHITE T. J., BRUNS T. D., LEE S., TAYLOR J. 1990: Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J. (eds.): PCR protocols, a guide to methods and applications. San Diego, California: 315–322.

WHITE, V. S. 1901: The Tylostomaceae of North America. Bull. Torrey Bot. Club. **28** (8): 421–444.

WRIGHT, J. E. 1987: The Genus *Tulostoma* (Gasteromycetes) – A World Monograph. Bibl. Myc. **113** Berlin, Stuttgart.

WRIGHT, J. E., SUAREZ, V. L. 1990: South American Gasteromycetes IV. The genus *Abstoma*. Crypt Bot. **1**: 372–383.

ZELLER, S. M. 1943: North American species of *Galeropsis*, *Gyrophragmium*, *Longia*, and *Montagnea*. Mycologia **35**: 409–421.

ZELLER, S. M. 1948: Notes on certain Gasteromycetes, including two new orders. Mycologia **40** (6): 639–668.

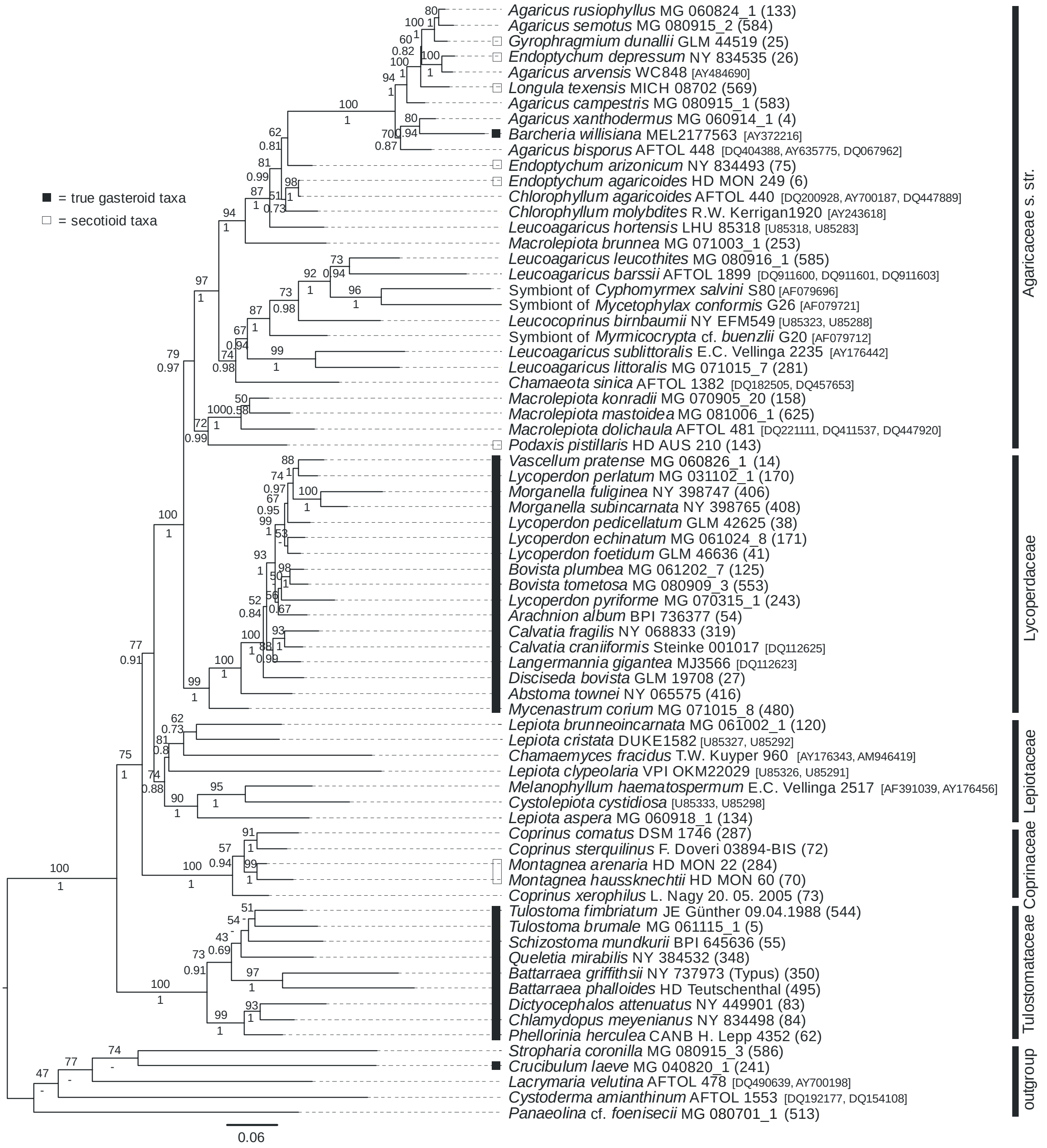

FIG. 1: ML phylogram of gasteromycetation events within Agaricaceae s. l.. LR-ELW support values are indicated above corresponding branches, Bayesian posterior probability values are indicated below. Lack of support is indicated by a horizontal stroke. Culture collection or herbarium reference is given after the species binomial. GeneBank entries are indicated by their accession numbers in edged brackets, availability of several loci is indicated by their corresponding accession numbers in the order ITS, LSU, RPB1. Reference numbers corresponding to Tab. 1 (see supplemental material) are indicated in rounded brackets.

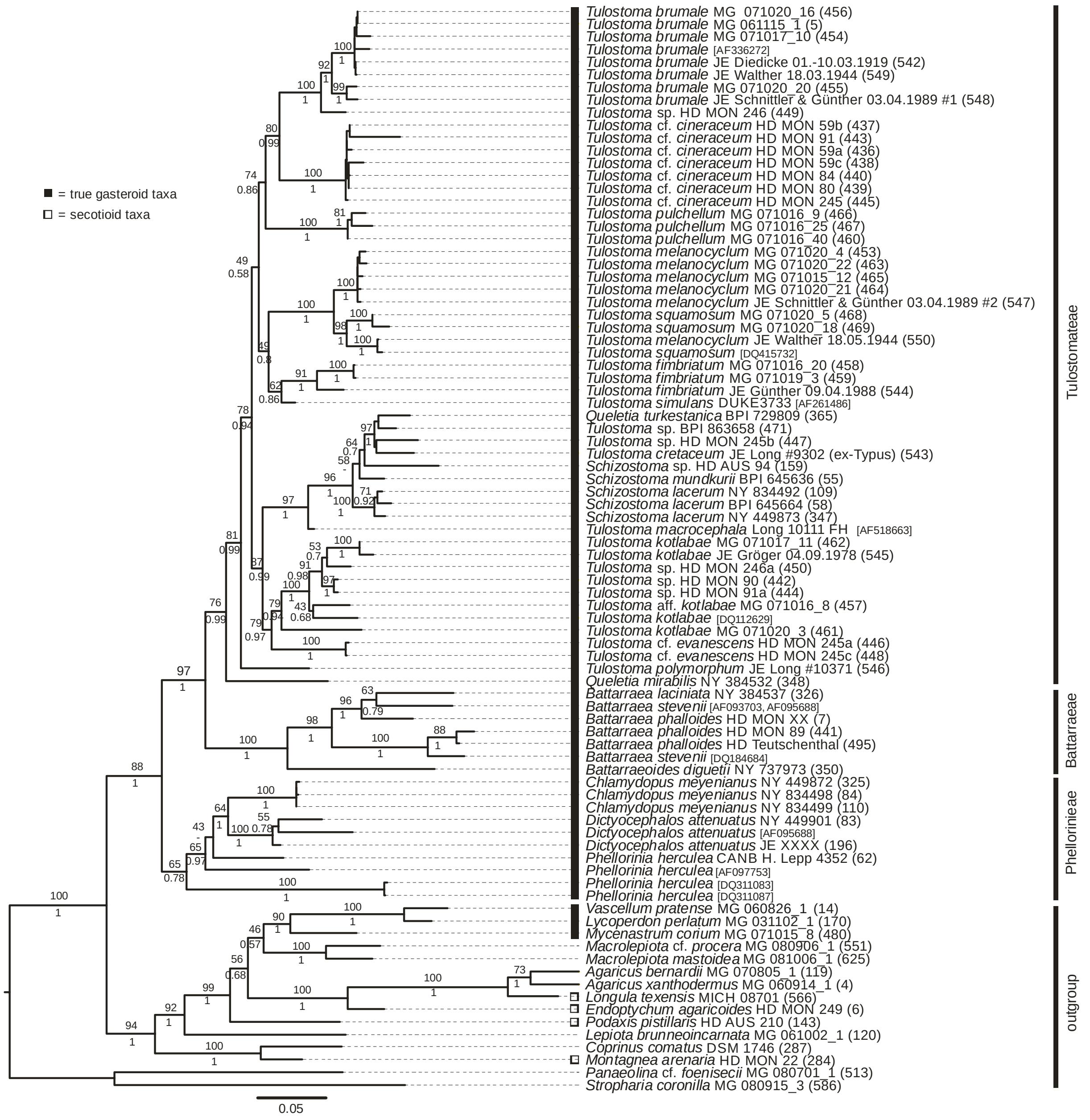

FIG. 2: ML phylogram of Tulostomataceae. LR-ELW support values are indicated above corresponding branches, Bayesian posterior probability values are indicated below. Lack of support is indicated by a horizontal stroke. Culture collection or herbarium reference is given after the species binomial. GeneBank entries are indicated by their accession numbers in edged brackets, availability of several loci is indicated by their corresponding accession numbers in the order ITS, LSU, RPB1. Reference numbers corresponding to Tab. 1 (see supplemental material) are indicated in rounded brackets.

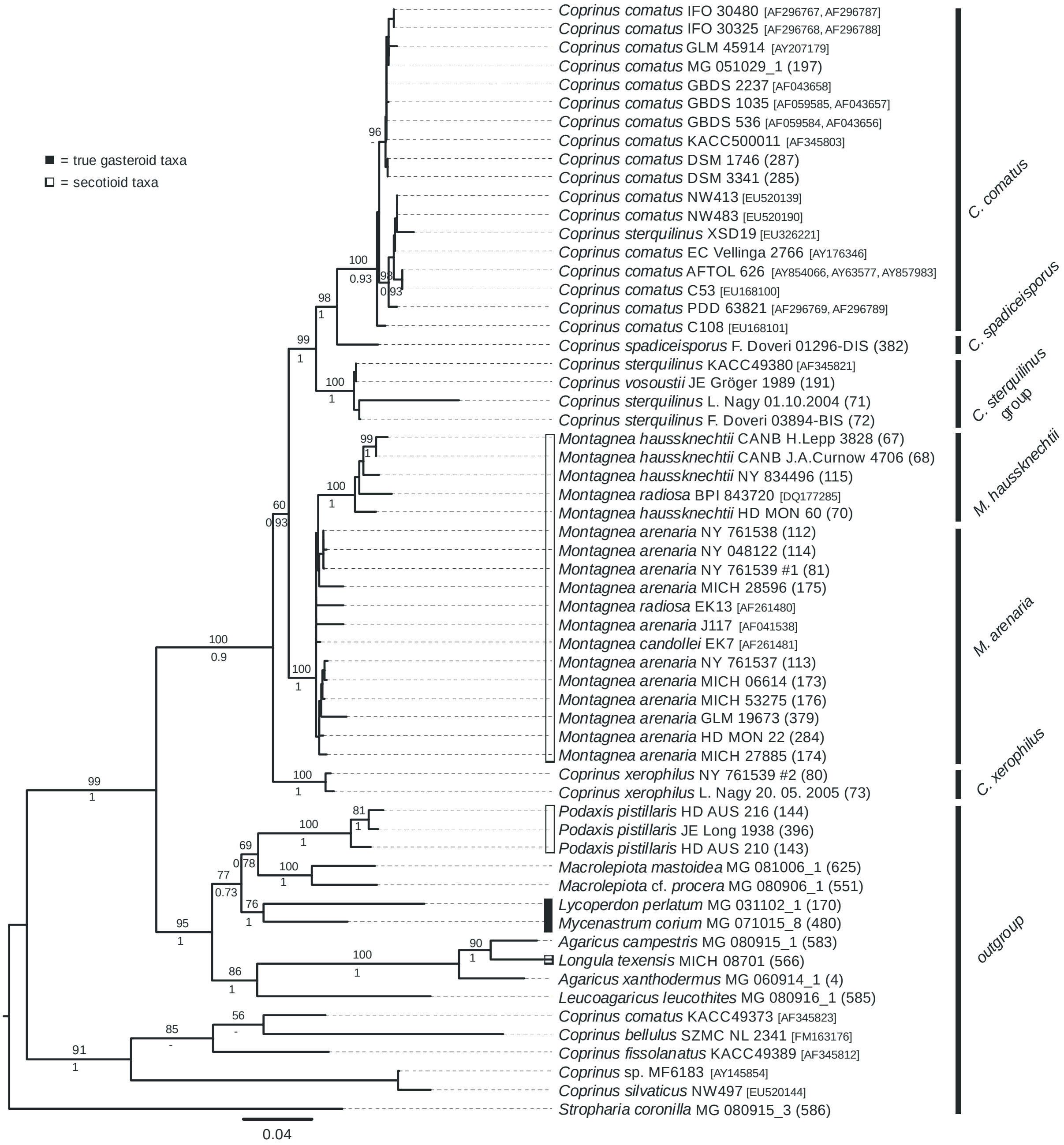

FIG. 3: ML phylogram of Coprinaceae. LR-ELW support values are indicated above corresponding branches, Bayesian posterior probability values are indicated below. Lack of support is indicated by a horizontal stroke. Culture collection or herbarium reference is given after the species binomial. GeneBank entries are indicated by their accession numbers in edged brackets, availability of several loci is indicated by their corresponding accession numbers in the order ITS, LSU, RPB1. Reference numbers corresponding to Tab. 1 (supplemental material) are indicated in rounded brackets.

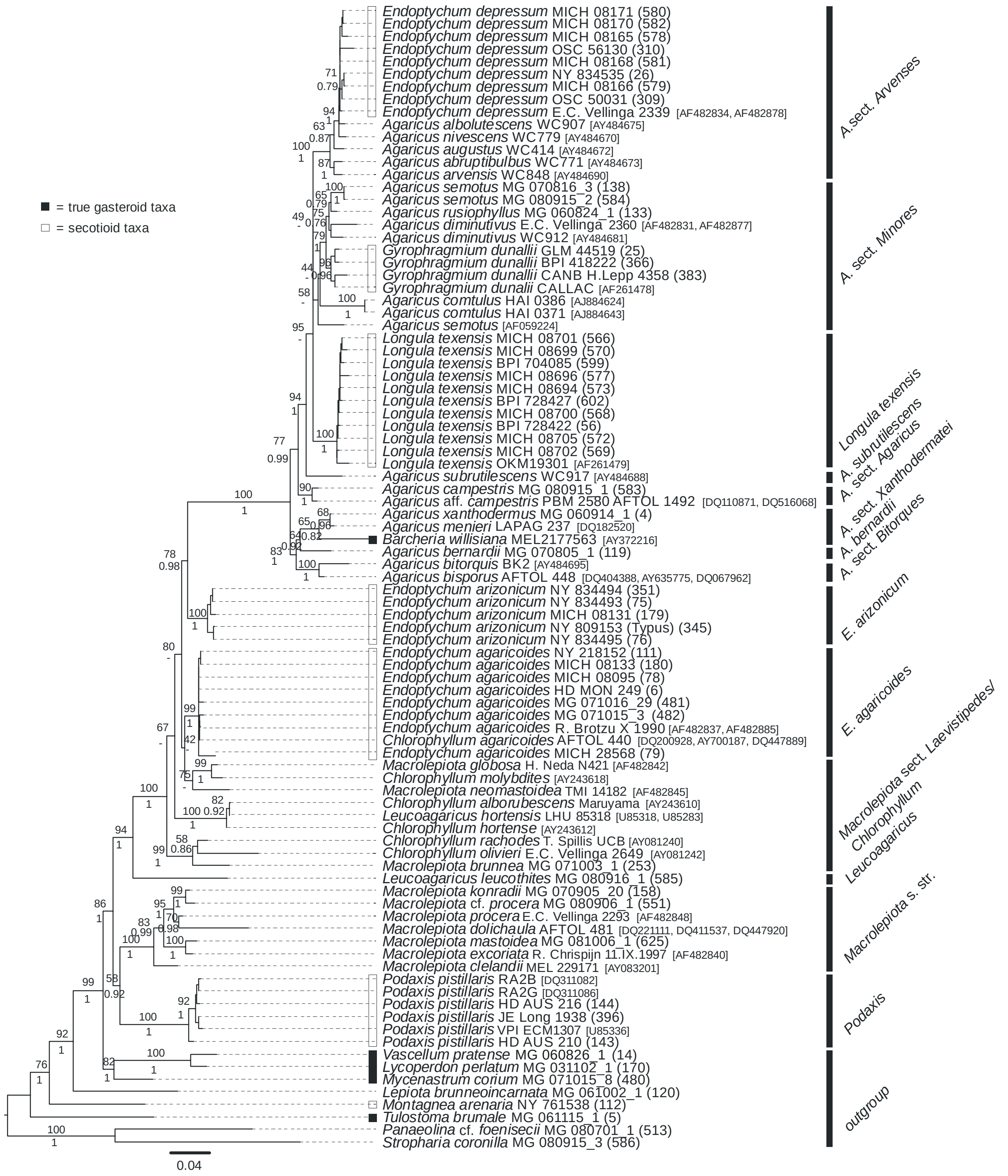

FIG. 4: ML phylogram of Agaricaceae s. str. LR-ELW support values are indicated above corresponding branches, Bayesian posterior probability values are indicated below. Lack of support is indicated by a horizontal stroke. Culture collection or herbarium reference is given after the species binomial. GeneBank entries are indicated by their accession numbers in edged brackets, availability of several loci is indicated by their corresponding accession numbers in the order ITS, LSU, RPB1. Reference numbers corresponding to Tab. 1 (see supplemental material) are indicated in rounded brackets.

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The gleba development of *Langermannia gigantea* (Batsch: Pers.) Rostk. (Basidiomycetes) compared to other Lycoperdaceae, and some systematic implications

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Abstract: The fruit body and in particular the gleba development of several species of Lycoperdaceae has been examined by light microscopic analysis of microtome sections of fruit body primordia in different ontogenetic stages. The gleba of *Langermannia gigantea* develops in a unique and previously unknown manner: the hymenium-forming palisade structures are borne on fan-like branches of hyphae. Hence the term of flabelloid glebal development is introduced. The other genera of Lycoperdaceae, including the genus *Calvatia*, are characterized by both lacunar and coralloid development of the gleba. Because these features cannot be distinguished clearly, this type of glebal development is referred to as coralloid-lacunar. Due to the peculiar ontogeny I suggest keeping the genus *Langermannia* separate from *Calvatia*.

Key words: fruit body development, gleba development, *Langermannia gigantea*, Lycoperdaceae

INTRODUCTION

In spite of several detailed examinations of the Lycoperdaceae (e.g. Fischer 1933, Kreisel 1962, 1967, Demoulin 1971), the developmental characters of their basidiocarps and in particular their glebal characters have been examined only rarely. The work on the ontogeny of this family published several decades ago (Rehsteiner 1892, Rabinowitsch 1894, Cunningham 1926, Lander 1933, Swartz 1933, 1935, 1936a, b, Brandza and Solacolu 1937, Swoboda 1937, 1938, Ritchie 1948, Ahmad 1950, Marchant 1969) did not include the genus *Langermannia* Rostk., only the peridial features were analyzed once (Swoboda 1940). Considering the systematic relationships with the relatively well studied genus *Calvatia* Fr. (Swartz 1933, 1935, Brandza and Solacolu 1937), a similar type of fruit body development had been assumed.

Langermannia consists of three species (Kirk et al 2001), of which only *L. gigantea* (Batsch : Pers.) Rostk., the type species, is common in the temperate zone (Kreisel 1994). This species is commonly known as giant puffball. It forms one of the world's largest basidiocarps from single primordia, a development known as monocentric (Clémençon 1997). Like all members of the Lycoperdaceae, it is a saprobiotic organism. Its fruit bodies are common on fertile meadows or in open woodland.

The exoperidium of the genus consists of only one layer; it lacks the pseudoparenchymatous endostratum typical of all other Lycoperdaceae. The dehiscence of the peridium is irregular; there is no defined ostiolum. The capillitium of the Lycoperdon-type is septated. *Langermannia* shares the last two features with *Calvatia*.

The genus *Langermannia* was erected by Rostkovius (1844) for species with irregular dehiscence of the peridia, allowing the mature glebal mass with its strongly developed capillitium to tumble away with the wind. He included five species into the genus, *L. candida* (= *Calvatia candida*), *L. aculeata, L. flavescens* and *L. punctata* (all = *Calvatia excipuliformis*) and the type species *L. gigantea*. When *Calvatia* was erected by Fries (1849) he included only the type species, *Calvatia craniiformis* (Schwein.)Fr. He transferred *Langermannia* into *Lycoperdon*. With the emendation of Morgan (1890) all species of Lycoperdaceae with an irregular dehiscence of the peridium, including *Langermannia*, were incorporated into *Calvatia*. Many authors followed this generic concept (Hollós 1904, Lloyd 1905, Fischer 1933, Šmarda 1958, Zeller and Smith 1964). Kreisel (1962) accepted *Langermannia* due to the anatomy of its peridium but discussed its close relationship to *Calvatia*. In later publications he included it into *Calvatia* because of the type of peridial dehiscence and the features of the capillitium (Kreisel 1992, 1994). Many authors follow his notion (Pegler et al 1995, Winterhoff 2000) while others accept *Langermannia* as a genus (Calonge and Martín 1990, Lange 1993, Calonge 1998, Kirk et al 2001).The genus *Calvatia* is a nomen conservandum against *Langermannia* (Greuter et al 1999).

The systematic relationships of *Langermannia* and *Calvatia* are discussed controversially (Kreisel 1992, 1994, Calonge and Martín 1990, Lange 1993, Calonge

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1998). Recent molecular systematic studies (Krüger et al 2001, Moncalvo et al 2002, Krüger and Kreisel 2003, Bates 2004, Lebel et al 2004, Vellinga 2004) could not clarify this matter but revealed close relationships of the Lycoperdaceae and the Agaricaceae. The present study contributes a novel argument for the separation of *Langermannia* from *Calvatia* by means of comparative anatomical investigation of the ontogenetic stages of several species of Lycoperdaceae.

MATERIALS AND METHODS

Methods.—Primordial basidiocarps were collected in central and eastern Germany in 2003–2005. Species were determined with mature fruit bodies growing next to the primordia. After the studies these will be transferred to GLM (Herbarium Naturkundemuseum Görlitz), together with the preparates. The primordia were fixed for at least 7 d in Pfeiffer's solution containing methanol (absolute), formalin (40%) and acetic acid (10%) in equal proportions. Dehydration was performed with a Pfeiffer's solution in methanol dilution series. The objects were embedded in Technovit 7100 (Kulzer Mikrotechnik). Deviating from the manufacturer's instructions, the time of pre-infiltration was increased (1–2 d instead of 2 h), as well as the quantity of hardener (8.3% instead of 6.7%). Primordia were sectioned with a rotation microtome Mikrom HM 355; sections were adjusted to 8–10 μm thick. Sections were attached on glass slides with n-Propanol (Clémençon 1990) and stained with toluidine blue O (0.1% w/v in H_2O) and safranine O (0.5% w/v in H_2O). Cover slips were attached with Merckoglas (Merck). The slides were examined with a Jenalumar microscope; microphotographs were taken with a Olympus Camedia digital camera (C3040ZOOM) and evaluated with software analySIS (version 3.2).

Materials.—*Bovista plumbea* Pers. : Pers. : Jena (Thuringia): on a meadow near Möbis, 1.5 km south of Münchenroda, 9 Sep 2004, leg./det.: M. Gube; *Bovista aestivalis* (Bonord.) Demoulin: Jena (Thuringia): on foliage litter of *Quercus petraea* at Tännicht, 0.5 km southeast of Jenaprießnitz, 1 Oct 2004, leg./det.: M. Gube; *Calvatia excipuliformis* (Pers.) Perdeck: Marienberg (Saxony): on needle litter of *Picea abies* and between *Avenella flexuosa* at the edge of a path between Ansprung and Rübenau, 3 km south of Rübenau, 3 Sep 2005, leg./det.: M. Gube; *Langermannia gigantea* (Batsch : Pers.) Rostk.: Jena (Thuringia): beneath *Quercus robur* at the edge of a meadow near Möbis, 1.5 km south of Münchenroda, 9 Sep 2004, leg./det.: M. Gube; *Lycoperdon foetidum* Bonord.: Zittau (Saxony): on needle litter of *Picea abies* on the northern slope of the Lindeberg, 2.5 km northwest of Hainewalde, 3 Jul 2004, leg./det.: M. Gube; *Lycoperdon lambinonii* Demoulin: Lobenstein (Thuringia): on needle litter of *Picea abies* at the Tännig, 2 km southeast of Lobenstein, 25 Sep 2004, leg./det.: M. Gube; *Lycoperdon perlatum* Pers. : Pers. : Zittau (Saxony): On litter of *Picea abies* and *Sorbus aucuparia* at the northern slope of the Buchberg, 1 km southwest of Jonsdorf, 2 Nov 2003, leg./det.: M. Gube ; Jena (Thuringia): on foliage litter of *Quercus petraea* and *Fagus sylvatica* at the northern slope of the Hirschberg, 1 km southeast of Jenaprießnitz, 1 Oct 2004, leg./det.: M. Gube; *Lycoperdon pyriforme* Schaeff. : Pers. : Jena (Thuringia): on a decayed stump of *Fagus sylvatica* inside the Langer Grund, 3.5 km west of Jena, 18 Nov 2003 and 30 Sep 2004, leg./det.: M. Gube; *Vascellum pratense* (Pers. : Pers.) Kreisel: Ellrich (Thuringia): on a meadow, 1 km west of Sülzhayn, 18 Oct 2003, leg./det.: M. Gube

RESULTS AND EVALUATION

Gleba development typical for the genus Lycoperdon.—Developing basidiomata of many stages, from 1 mm diam to 45 × 25 mm, were examined. The glebal development of all examined species of *Lycoperdon* occurs in a similar manner; therefore the species of that genus are treated as a whole.

The differentiation process of the primordial plectenchyme starts in primordia of 1 mm diam. Radially oriented, frequently septated hyphae appear on the surface of the primordium to form the exoperidium (FIG. 1). The first internal differentiation occurs in primordia of 2 mm diam, where an area of gaps emerges in the central primordium, later forming the glebal cavities. Such a formation of gleba is lacunar because the gaps emerge independently inside the previously undifferentiated primordial plectenchyma, according to Fischer (1933). They arise from separation and splitting, as well as from autolysis of some hyphae. This has been discussed controversially by other authors (Rehsteiner 1892, Cunningham 1926, Fischer 1933, Lander 1933, Swartz 1933, Marchant 1969). Cavity formation extends centrifugally. In primordia of 5 × 4 mm, the gleba differentiates further as hyphae originating from the surrounding plectenchyma grow into the cavities to form a palisade layer of hyphal tips (FIGS. 2–3), shown also by Swartz (1933) and Ritchie (1948). Because this occurs centrifugally as well the central part of some cavities can be covered with palisades while the peripheral part remains undifferentiated (FIGS. 2–4). Lohwag (1925) described such a glebal formation as coralloid because this outwardly progressing differentiation leads to coral-like branches of the trama while the cavities between them usually are connected.

Subglebal cavities differentiate similarly but often emerge at distance from each other. In young primordia of 2 mm up to around 8 × 5 mm, these cavities usually are rounded and unlobed (FIG. 5). They show a gradual transition into their glebal counterparts. Therefore they can be kept apart only by their position in young stages, as already mentioned by Rehsteiner (1892).

In primordia of 9 × 5 mm and larger the centrifugally progressing differentiation reaches the

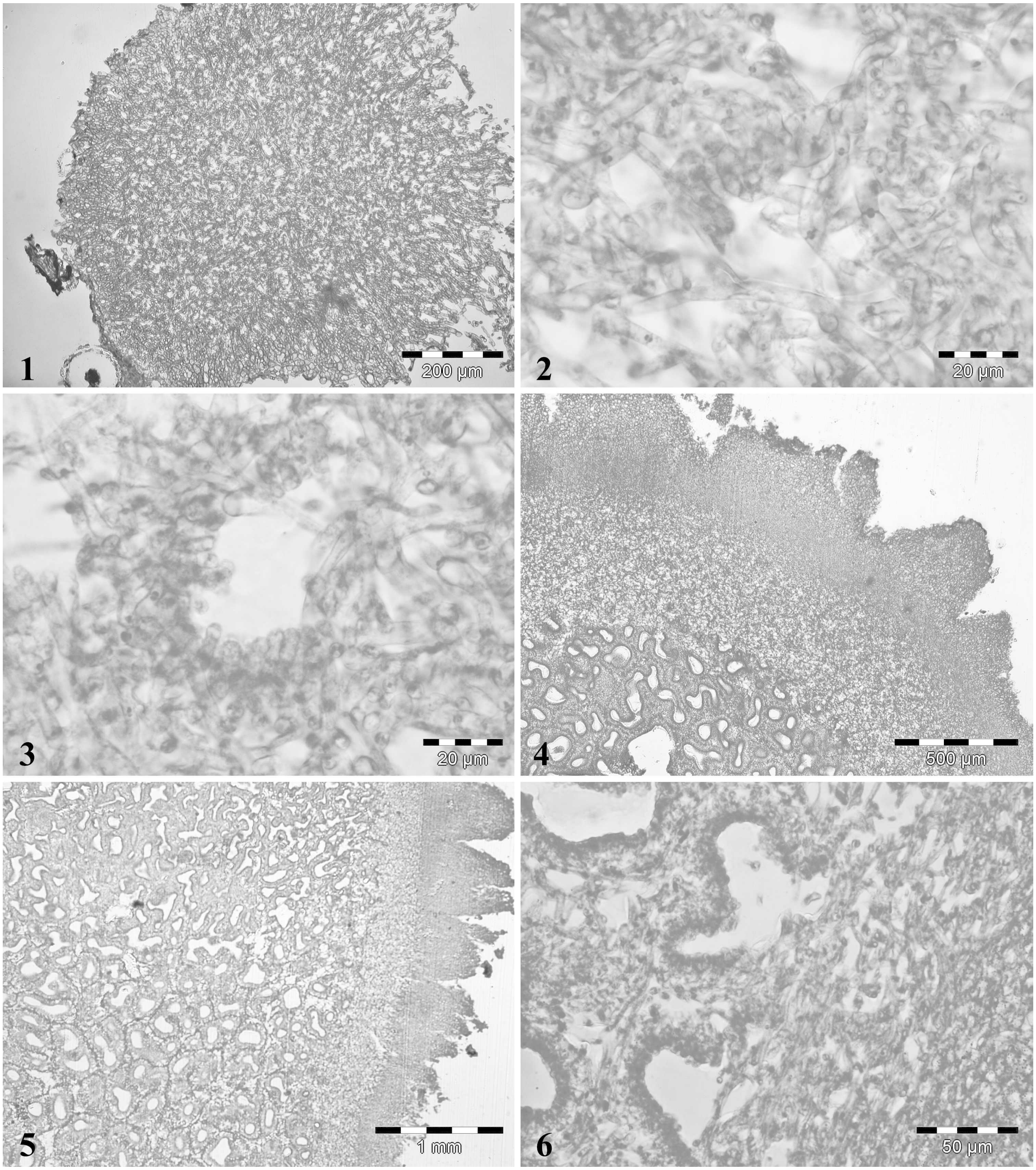

FIG. 1. Young primordium of *Lycoperdon perlatum*. 1.5 mm diam, 125×. The radially oriented hyphae of the exoperidium surround the undifferentiated plectenchyme in the center. FIG. 2. Developing gleba chamber of *Lycoperdon foetidum*, initial stage, 5 × 4 mm, 1000×. Irregular clusters of hyphae appear at the inner part of the cavity. FIG. 3. Developing gleba chamber of *Lycoperdon foetidum*, more advanced stage, 5 × 4 mm, 1000×. The peripheral half of the cavity is still undifferentiated, while the inner parts are covered by an already even palisade layer. FIG. 4. Primordium of *Lycoperdon pyriforme*, 5 × 3 mm, 63×. The exoperidium formation is finished, the gleba still differentiates centrifugally and the endoperidium is not yet present. FIG. 5. Primordium of *Lycoperdon foetidum*, 8 × 5 mm, 32×. The glebal and peridial features are developed; subgleba and gleba are distinguishable but merge gradually into each other. FIG. 6. Glebal cavities and endoperidium of *Lycoperdon lambinonii*, 25 ×

endoperidial layer, which has differentiated in the meantime. The periclinally arranged hyphae of the endoperidium do not differentiate further. Therefore the peripheral part of the cavities in this region is bordered by endoperidial hyphae without palisades (FIG. 6).

The palisade layer surrounding the glebal cavities consists of clavate hyphal tips with deep staining plasmatic content (FIG. 7). These probasidia pass basally into a subhymenium, while their tips form an even surface. Therefore it is obvious that this layer forms a true hymenium later on. Yet it is referred to as palisade layer or prehymenium because no ripe basidia with spores were observed. In more mature primordia only the apical part of the palisades stains deeply due to vacuole formation while the plasma retreats toward the apical region (FIG. 8). This is typical for the senescence of hymenial palisades (Marchant 1969). The subhymenial plectenchyme remains thin-walled and equally frequent septated during differentiation (FIGS. 7–8). In the subgleba it is weakly developed and is compressed due to growth of the cavities (FIG. 9). Further inside the trama branches hyphae are arranged in parallel bundles (FIGS. 7–9). Their cell walls are thicker, they stain metachromatic and usually are septated sparsely. In the gleba some of these hyphae form the latter capillitium while they develop into the walls of the persistent chambers in the subgleba. The hyphae of the endoperidium are differentiated similarly; there are even transitions where trama branches meet it (FIGS. 6).

Like the palisades, subhymenial and tramal hyphae show initially no defined border between gleba and subgleba in young primordia (FIG. 5). In mature primordia however the subgleba differs from the gleba; because the palisade layer shows other signs of senescence they are lacking plasmatic content then and become thick-walled (FIG. 9). In addition the cavities stretch along the boundary region of gleba and subgleba in later stages.

Features of the glebal development of Bovista, Calvatia*, and* Vascellum *deviating from* Lycoperdon.—Species of *Bovista, Calvatia* and *Vascellum* have similar glebal ontogeny compared to *Lycoperdon.* Species of *Bovista* differ somewhat in the features of the palisades; they are larger and more capitate than those of *Lycoperdon, Vascellum* or *Calvatia* (FIG. 10). Primordia of *Calvatia excipuliformis* develop distinctly slower than those of other Lycoperdaceae. With primordia at 4 mm diam, when the palisades usually emerge, only the first signs of cavities are noticeable. Fully developed palisades may not be found in fruit bodies smaller than 25 × 12 mm.

Peculiar features are the distinct diaphragm in mature basidiomata of *Vascellum* and the pseudodiaphragm in some species of *Calvatia*, both separating gleba and subgleba (Kreisel 1962). These structures could not be observed in the examined specimens. However the cavities of more mature basidiomata of *V. pratense* (7 × 6 mm) and *C. excipuliformis* (25 × 12 mm) are stretched along the border of the already distinguishable glebal and subglebal plectenchyme (FIGS. 11–12). Diaphragm and pseudodiaphragm arise from stretched glebal and subglebal cavities. This was observed by Rabinowitsch (1894), whereas Cunningham (1926) supposed these structures to be formed from subglebal cavities only.

Gleba development of Langermannia gigantea.—*L. gigantea* shows a gleba formation quite different from that of the other Lycoperdaceae. In the earliest examined stages (at 7 mm diam) the palisade layer does not cover the surface of cavities but was found to be carried on fan-like branched hyphae (FIG. 13). For them the term of flabelloid structures is introduced here. They form a nearly continuous, irregularly lobed zone with the palisade layer growing outward into the undifferentiated plectenchyme (FIGS. 14) and sideways, thus forming secondary cavities at later stages (FIGS. 15–16). In primordia (at 11 mm diam) more palisade layers emerge inside while the primordium grows. The palisade layers replace only undifferentiated plectenchyme. Hyphae transmitting the palisade structures often are observed (FIG. 17). These are probably remains of the replaced plectenchyma because they are more common in the periphery, where palisades are newly formed. While the basidiocarp grows the outer zone of palisades extends and the most exterior parts of the undifferentiated plectenchyme are stretched to form the peridia. The differentiation into exo- and endoperidium was not yet detectable. Also the definition of boundaries between glebal and peridial plectenchyma could not be observed at the stages examined.

Features of the palisades differ only little from those of the other examined Lycoperdaceae. The

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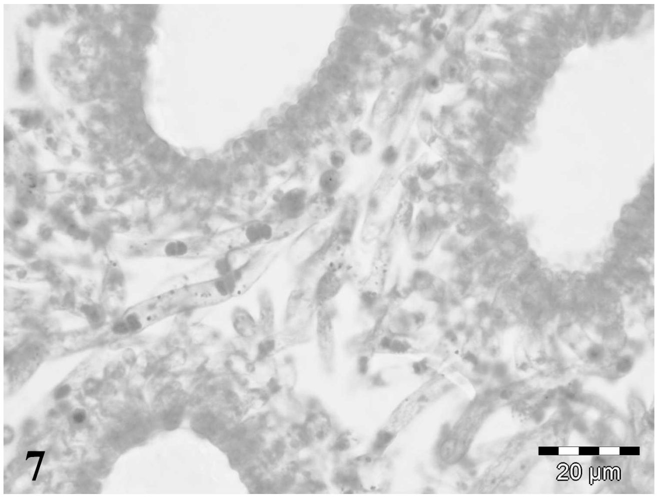
15 mm, 500×. Cavities are lined with endoperidium hyphae in their peripheral parts; endoperidium hyphae merge with central trama hyphae.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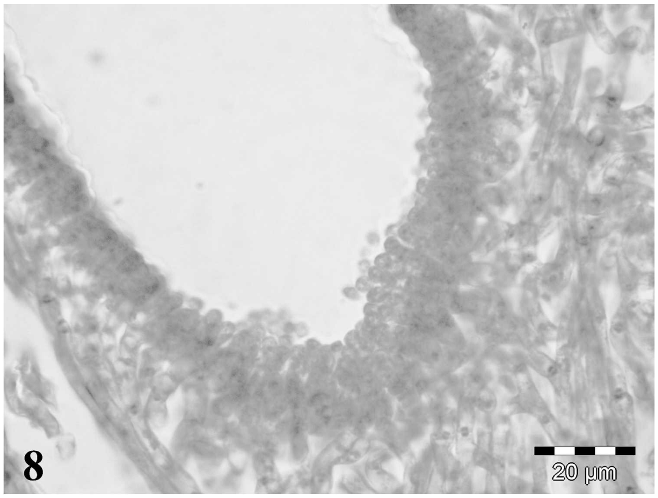
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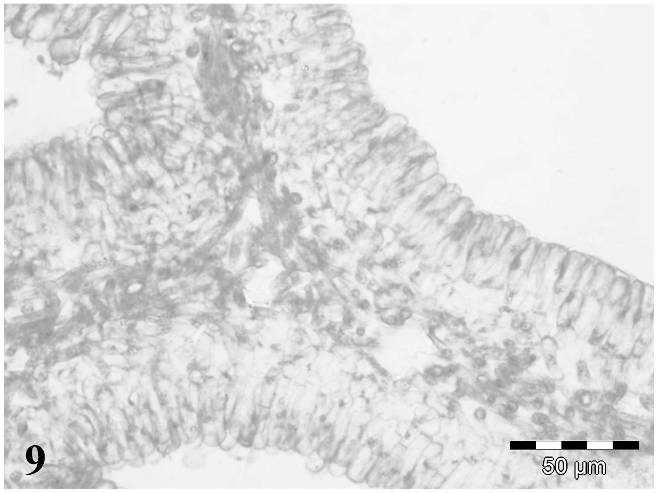
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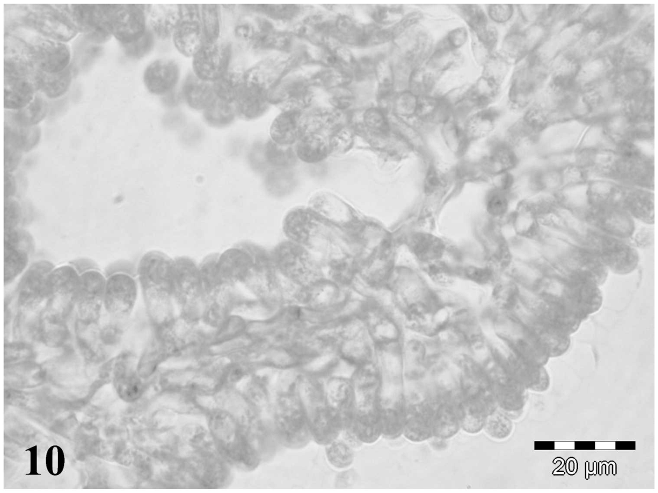
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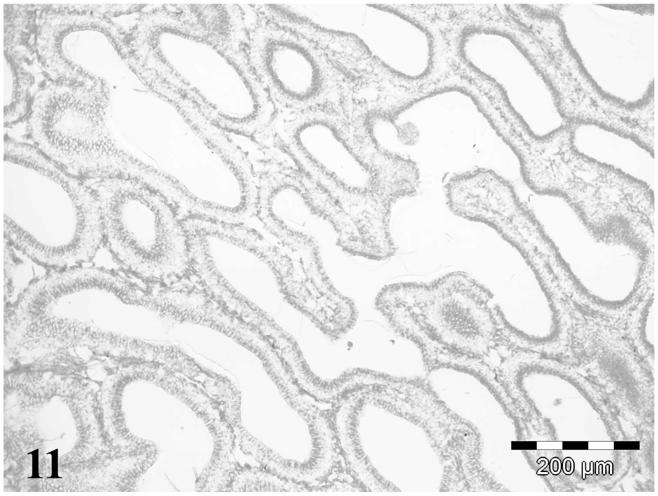
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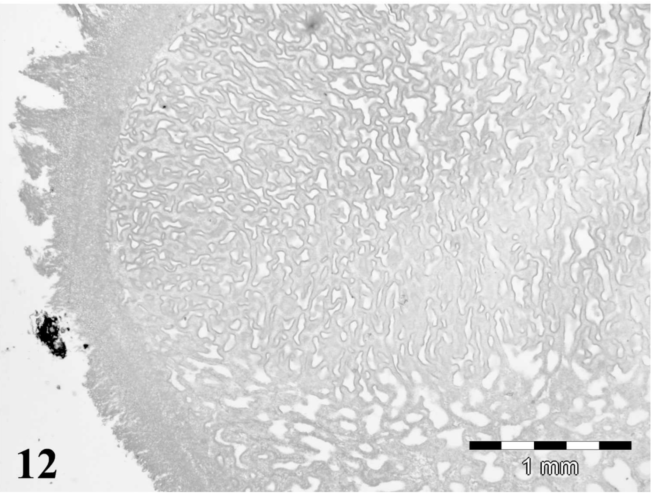
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FIG. 7. Glebal palisades of *Lycoperdon lambinonii*, 25 × 15 mm, 1000×. Clavate hyphal tips form the palisades, borne by subhymenial hyphae originating from metachromatic trama hyphae; dolipore complexes are visible at septa. FIG. 8. Glebal palisades of *Lycoperdon perlatum*, 45 × 25 mm, 1000×. Due to senescence the palisades stain darker apically. FIG. 9. Subglebal palisades of *Lycoperdon perlatum*, 45 × 25 mm, 500×. Palisades are lacking plasmatic content and are thick-walled; central trama hyphae are strongly developed; in contrast to subhymenial plectenchyme. FIG. 10. Palisades of *Bovista plumbea*. The palisades consist of more capitate hyphal tips on a short subhymenium rising from central trama hyphae. FIG. 11. Glebal and subglebal cavities of *Calvatia excipuliformis*, 25 × 12 mm, 125×. Subglebal (lower left) and glebal palisades (upper right) differ only slightly and transmit into each other. FIG. 12. Primordium of *Vascellum pratense*, 7 × 6 mm, 32×.

layer of palisades has an even surface and is composed of parallel, clavate hyphal tips that stain deeply (FIG. 17). Several of these originate from one multibranched hypha, which is itself a branch of higher order (FIG. 13). Therefore a whole fan may be traced back to a few or even a single subhymenial hypha. Therefore great areas of the glebal trama show a low density of hyphae (FIGS. 15–16). Only in the surrounding of the secondary cavities do hyphae exist resembling the central trama hyphae of other Lycoperdaceae (FIG. 15). They are relatively thin-walled but stain metachromatic and are more sparsely septated, in contrast to the subhymenial hyphae. The compact subgleba, which is weakly developed even in mature fruit bodies, cannot be observed in the primordia.

Visibility of dolipore septa.—At the septa of subhymenial and central tramal plectenchyme of most Lycoperdaceae, as well as in the undifferentiated plectenchyme of *Langermannia gigantea*, large dolipore complexes up to 2 µm diam are visible (FIGS. 7–8, 17). This also can be observed in primordia of *Agaricus bisporus* (Lge.) Sing., indicating that this staining method is not unique for Lycoperdaceae (FIG. 18). The high visual quality of the dolipore structures surpasses that of most other staining methods. The exceptional size and stainability of the dolipore complexes might have been caused by the aldehyde fixation, which can induce swelling of dolipore complexes (Hoch and Howard 1981).

DISCUSSION

Both types of gleba development discussed here do not correspond to the traditional distinction of the coralloid (Lohwag 1925) or lacunar type (Fischer 1933). This system of classifying gleba development of gasteromycetes has been criticized because of numerous intermediates between the extremes (Reijnders 1976, 2000). However it still is widely accepted (Kreisel 1969, Dring 1973, Jülich 1981, Miller and Miller 1988). Coralloid gleba development is considered to be a typical character for the Lycoperdaceae (Kreisel 1962).

Gleba development of the genera *Lycoperdon, Bovista, Vascellum* and also *Calvatia* however does show elements of both the coralloid and the lacunar type. On the one hand many cavities arise without connection to other already existing cavities, particularly in the beginning of gleba formation and in the subgleba, implying lacunar development. On the other hand the differentiation processing outward and the connections between several cavities point toward coralloid development. In addition the examined species show neither a continuous, coral-like branched glebal cavity, as illustrated by Fischer (1933) for coralloid development, nor completely isolated chambers, as described by Lohwag (1925) for the lacunar type.

These features have been described in most publications on the development of Lycoperdaceae (Rehsteiner 1892, Rabinowitsch 1894, Cunningham 1926, Lander 1933, Swartz 1933, 1935, 1936a, b, Brandza and Solacolu 1937, Swoboda 1938, Ritchie 1948, Ahmad 1950, Marchant 1969, Reijnders 1976). Gleba development was interpreted in many different ways, ranging from a generally coralloid (Kreisel 1962, Fischer 1936) to predominantly lacunar (Ahmad 1950) and everything in between (e.g. Fischer 1933). Neither coralloid nor lacunar correctly describe this development, where features of both types obviously merge. Therefore the coralloid-lacunar type of gleba development is introduced here for the Lycoperdaceae.

The gleba formation of *Langermannia gigantea* deviates from hitherto known types. There are no primary glebal cavities, but the palisades themselves equal those of other Lycoperdaceae. The flabelloid structures bearing the palisades may form secondary cavities or remain as palisade zones among undifferentiated plectenchyme. Such a zone is formed in the region of the gleba facing the later peridia. This type of gleba development is referred to as flabelloid.

Yet another type of gleba development has been proposed for *Calvatia bicolor* (Lév.) Kreisel (Swoboda 1937). In this species the gleba is described as being composed of coralloid, thin branches of hyphal bundles bearing basidia directly attached to them and thus not forming a true hymenium. Since then *C. bicolor* has not been analyzed to verify Swoboda's observations. In addition no other examined species of Lycoperdaceae show similar features, so the record remains doubtful.

In addition to the type of gleba development several other features are unique to *Langermannia.* It is the only genus of the Lycoperdaceae with only two-layered rhizomorphs, lacking cortex hyphae. They strikingly resemble those of *Agaricus* (Agerer 2002, Gube 2005) instead of the three- to four-layered

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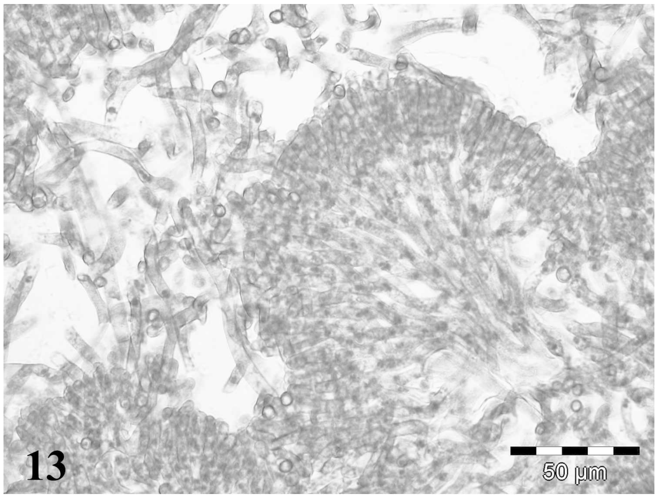
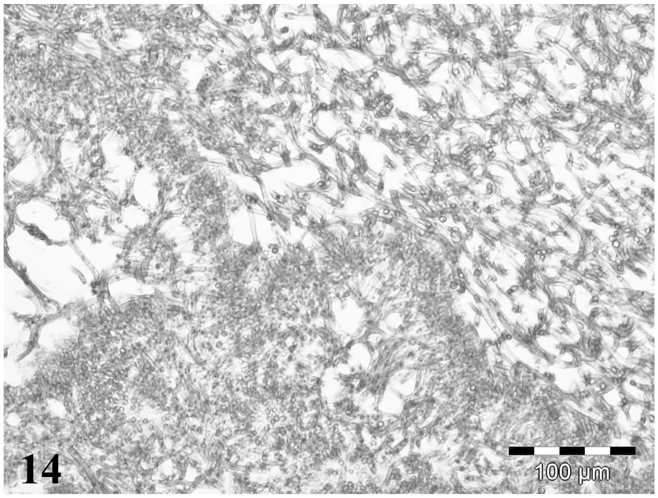
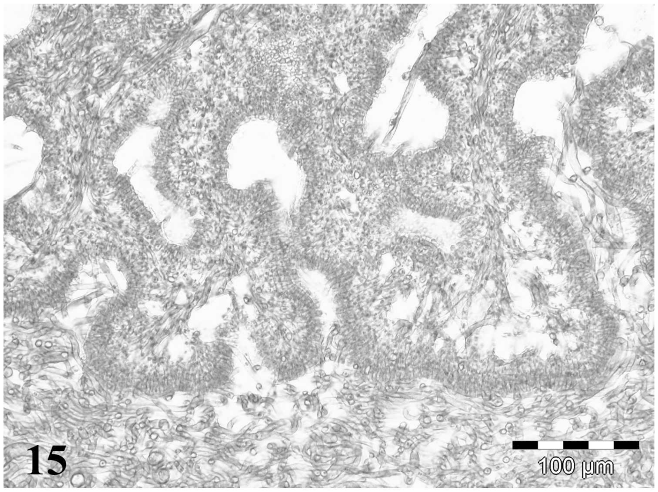
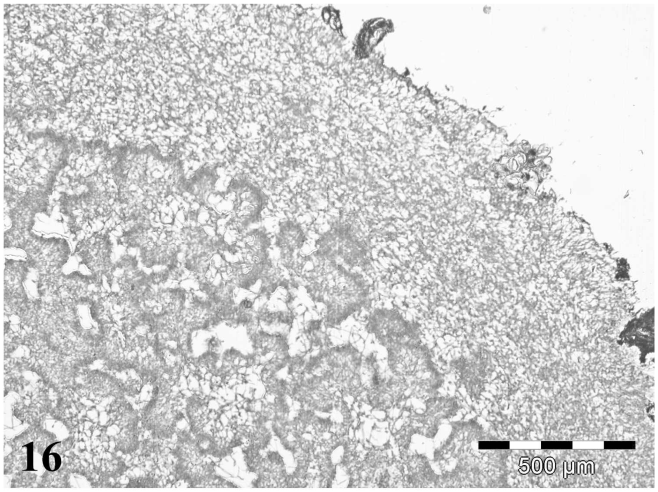
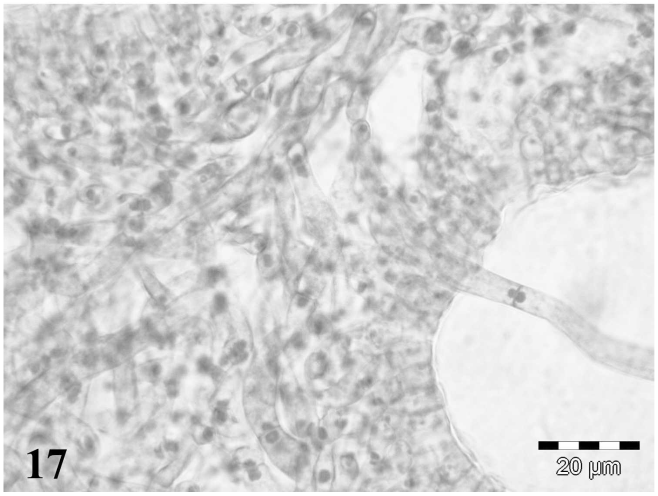
Between glebal and subglebal chambers a distinct border exists, where cavities are longitudinally stretched; a diaphragm is lacking.











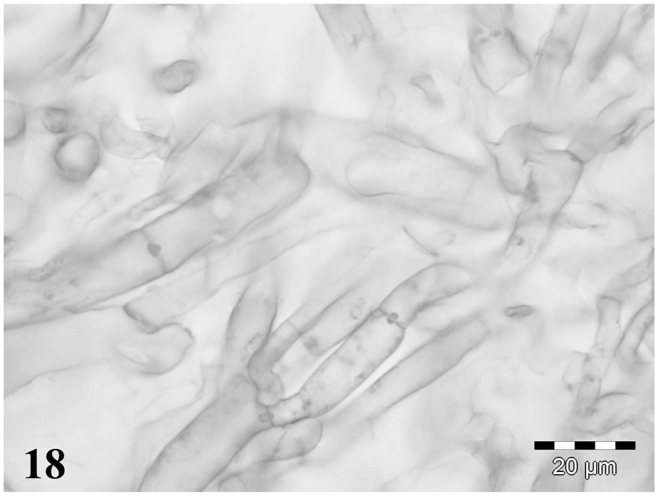


FIG. 13. Palisade structures of *Langermannia gigantea*, 7 mm diam, 500×. Fan-like branched hyphae bear the palisades. FIG. 14. Developing palisade structures of *Langermannia gigantea*, 7 mm diam, 250×. Palisades are oriented outward, facing and replacing the undifferentiated primordial plectenchyme. FIG. 15. Secondary cavities of *Langermannia gigantea*, 11 mm diam, 250×. Cavities are formed by anastomosing and joining palisade zones. FIG. 16. Primordium of *Langermannia gigantea*, 11 mm diam, 63×. Palisades are visible on flabelloid structures and in secondary cavities. FIG. 17. Palisades of *Langermannia gigantea*, 11 mm diam, 1000×. Subcylindrical hyphal tips form the palisades, born by subhymenial hyphae, hyphae transmit the palisades, dolipore complexes are visible at septa. FIG. 18. Undifferentiated primordial plectenchyme of *Agaricus bitorquis*, 22 × 15 mm, 1000×. Dolipore complexes are visible at septa.

rhizomorphs typical for Lycoperdaceae (Townsend 1954, Cairney et al 1988, Agerer 2002, Gube 2005). The one-layered exoperidium lacking pseudoparenchyma is unique within this family. It is present however in the Mycenastraceae (Hansen 1962, Kreisel 1962), which are supposed to be closely related (Bates 2004). Finally, even in primordia at 11 mm diam, exo- and endoperidia are indistinguishable while they are clearly differentiated in primordia of other Lycoperdaceae when reaching that size.

The features that are common to *Langermannia* and *Calvatia* are shared by other members of the family. The typical dehiscence of the peridia is also common in *Vascellum pratense*, although not as distinctive.

The septated capillitium of the *Lycoperdon*-type (Kreisel 1962) can be observed in both *Langermannia* and some species of *Calvatia*. Species of *Calvatia* with unseptated capillitium and slit-like pits in the capillitial threads have been separated by Kreisel (1989, 1992) forming the genus *Handkea*. Many authors do not accept this genus (Calonge and Martín 1990, Lange 1993, Calonge 1998, Kirk et al 2001); the slit-like pores are products of rupturing along the true, fine pores in the thin-walled capillitium, according to Lange (1993). In addition true septa occur in both genera as well as in the capillitium of species of *Lycoperdon* and *Disciseda*, although there they are found only scarcely (Kreisel 1962).

Recent work on the molecular systematics of Lycoperdaceae supports a clade of *Langermannia gigantea, Calvatia pachydermica* (Speg.) Kreisel and *C. bicolor* (Bates 2004). These species share several morphological features that differ from *Calvatia s. str.* (Kreisel 1992, 1994). However the fruit body development described for *C. bicolor* (Swoboda 1937) differs from both *L. gigantea* and other species of *Calvatia*. Other molecular systematic studies could not reveal the position of *Langermannia* within the Lycoperdaceae (Hibbett et al 1997, Krüger et al 2001, Moncalvo et al 2002, Krüger and Kreisel 2003, Lebel et al 2004, Vellinga 2004) because no or only few members of *Calvatia* or *Langermannia* were examined. Considering the available data *Langermannia* clearly differs in many important features from *Calvatia* and therefore should be referred to as a separate genus.

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LITERATURE CITED

Agerer R. 2002. Rhizomorph structures confirm the relationship between Lycoperdales and Agaricacae (Hymenomycetes, Basidiomycota). Nov Hedwig 75(3–4): 367–385.

Ahmad S. 1950. Morphology of *Disciseda cervina*. Mycologia 42:148–160.

Bates ST. 2004. Arizona members of the Geastraceae and Lycoperdaceae (Basidiomycota, Fungi) (Master's thesis). Tempe: Arizona State University. 445 p.

Brandza M, Solacolu T. 1937. Sur le développement et la maturation de quelques Gastéromycètes. Botaniste 28: 203–227.

Cairney JWG, Jennings DH, Veltkamp CJ. 1988. A scanning electron microscope study of the internal structure of mature linear mycelial organs of four basidiomycete species. Can J Bot 67:2266–2271.

Calonge FD. 1998. *Gasteromycetes,* I. *Lycoperdales, Nidulariales, Phallales, Sclerodermatales, Tulostomatales.* Madrid, Berlin: Real Jardín Botánico Madrid, Gebr. Bornträger: Flora Mycol Iber 3. 271 p.

———, Martín MP. 1990. Notes on the taxonomical delimitation in the genera *Calvatia, Gastropila* and *Langermannia* (Gasteromycetes). Bol Soc Micol Madrid 14:181–190.

Clémençon H. 1990. Fixierung, Einbettung und Schnittfärbungen für die plectologische Untersuchung von Hymenomyceten mit dem Lichtmikroskop. Mycol Helv 3(4):451–466.

———. 1997. Anatomie der Hymenomyceten. Lausanne: Université de Lausanne. 996 p.

Cunningham GH. 1926. Development of *Lycoperdon depressum* (Fungi). NZ J Sci Technol 8:228–232.

Demoulin V. 1971. Le genre Lycoperdon en Europe et en Amérique du Nord. Étude taxonomique et phytogéographique [Doctoral dissertation]. Liège: Université de Liège. 284 p.

Dring DM. 1973. Gasteromycetes. 24. In: Ainsworth GC, Sparrow FK, Sussman AS, eds. The Fungi. An advanced treatise. IVB. A Taxonomic Review with Keys: Basidiomycetes and Lower Fungi. New York, London: Academic Press. p 451–478.

Fischer E. 1933. Gastromyceteae. In: Engler A, Prantl K, eds. Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigen Arten insbesondere den Nutzpflanzen. 2nd. ed. Bd. 7a. Leipzig: Wilhelm Engelmann. p 1–72.

———. 1936. Neue Beiträge zur Kenntnis der Verwandtschaftsverhältnisse der Gastromyceten. Eine kritische Untersuchung. Ber schweiz botan Ges 45:231–247.

Fries EM. 1849. Summa vegetabilium scandinaviae, seu enumeratio systematica et critica plantarum quum cotyledonearum, tum nemearum inter mare occidentale et album, inter eidoram et nordkap, hactenus lectoram, indicata simul distributione geographica.

Sectio posterior. Holmiae, Lipsiae: A. Bonnier. p 259–572.

Greuter W, McNeill J, Barrie FR, Bardet HM, Demoulin V, Filgueiras TS, Nicolson DH, Silva DH, Skog JE, Trehane P, Turland NJ, Hawksworth DL, eds. 2000. International Code of Botanical Nomenclature (Saint Louis Code) adopted by the 16th International Botanical Congress, St Louis, Missouri, Jul–Aug 1999. Koeltz: Koenigstein. 474 p.

Gube M. 2005. Morphologisch-anatomische Studien an Fruchtkörperprimordien der Lycoperdaceae (Basidiomycetes) und ihre Bedeutung für die Systematik (Diploma thesis). FSU Jena. 72 p.

Hansen L. 1962. A Danish find of *Mycenastrum corium* with notes on its anatomy. Bot Tidsskr 58:204–212.

Hibbett DS, Pine EM, Langer E, Langer G, Donoghue MJ. 1997. Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. Proc Nat Acad Sci USA 94:12002–12006.

Hoch HC, Howard RJ. 1981. Conventional chemical fixations induce artifactual swelling of dolipore septa. Exp Mycol 5:167–172.

Hollós L. 1904. Die Gasteromyceten Ungarns. Leipzig: D. Weigel. 278 p.

Jülich W. 1981. Higher taxa of basidiomycetes. Bibliothec Mycol 85:1–485.

———. 1984. Die Nichtblätterpilze, Gallertpilze und Bauchpilze. Aphyllophorales, Heterobasidiomycetes, Gastromycetes. Jena: Gustav Fischer, Gams Kleine Kyptogamenflora IIb/1. Basidiomyceten. 1. Teil. 626 p.

Kirk PM, Cannon PF, David JC, Stalpers JA, eds. 2001. Ainsworth and Bisby's Dictionary of the Fungi. 9th ed. Wallingford: CABI Publishing. 655 p.

Kreisel H. 1962. Die Lycoperdaceae der Deutschen Demokratischen Republik. Feddes Rep 64:89–201.

———. 1967. Taxonomisch-Pflanzengeographische Monographie der Gattung Bovista. Beih Nov Hedwig 25:1–304.

———. 1969. Grundzüge eines natürlichen Systems der Pilze. Jena: Gustav Fischer. 245 p.

———. 1989. Studies in the Calvatia complex (Basidiomycetes). Nov Hedwig 48:281–296.

———. 1992. An emendation and preliminary survey of the genus *Calvatia* (Gasteromycetidae). Persoonia 14(4): 431–439.

———. 1994. Studies in the *Calvatia* complex (Basidiomycetes) 2. Feddes Rep 105:369–376.

Krüger D, Binder M, Fischer M, Kreisel H. 2001. The Lycoperdales. A molecular approach to the systematics of some gasteroid mushrooms. Mycologia 93(5):947–957.

———, Kreisel H. 2003. Proposing *Morganella* subgen. *Apioperdon* subgen. nov. for the puffball *Lycoperdon pyriforme*. Mycotaxon 86:169–177.

Lander CA. 1933. The morphology of the developing fruiting body of *Lycoperdon gemmatum*. Am J Bot 20: 204–215.

Lange M. 1993. Classifications in the *Calvatia* group. Blyttia 51(3–4):141–144.

Lebel T, Thompson DK, Udovicic F. 2004. Description and affinities of a new sequestrate fungus, *Barcheria willisiana* gen. et sp. nov. (Agaricales), from Australia. Mycol Res 108(2):206–213.

Lloyd CG. 1905. The Lycoperdaceae of Australia, New Zealand and neighboring islands. Cincinnati: The Lloyd Library. 42 p.

Lohwag H. 1925. Zur Entwicklungsgeschichte und Morphologie der Gastromyceten. Ein Beitrag zur Systematik der Basidiomyceten. Beih Bot Centralbl Abt II 42:177–334.

Marchant R. 1969. The fine structure and development of the fructifications of *Lycoperdon perlatum*. Trans Brit Mycol Soc 53(1):63–68.

Miller OK, Miller HH. 1988. Gasteromycetes. Morphological and development features with keys to orders, families and genera. Eureka: Mad River Press. 157 p.

Moncalvo J.-M, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC, Hofstetter V, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsson S, Clémençon H, Miller OK. 2002. One hundred seventeen clades of euagarics. Mol Phylogenet Evol 23:357–400.

Morgan AP. 1890. North American fungi. The Gasteromycetes. J Cincinnati Soc Nat Hist 12.

Pegler DN, Laessøe T, Spooner BM. 1995. British puffballs, earthstars and stinkhorns. An account of the British gasteroid fungi. Kew: Royal Botanic Gardens. 245 p.

Rabinowitsch L. 1894. Beiträge zur Entwickelungsgeschichte der Fruchtkörper einiger Gastromyceten. Flora, Erg Bd 78:385–418.

Reijnders AFM. 1976. Sur le développement de trois espèces de Gastéromycètes et l'origin coralloide ou lacunaire de la gleba. Bull Soc Mycol France 92(2):169–188.

———. 2000. A morphogenetic analysis of the basic characters of the gasteromycetes and their relation to other hymenomycetes. Mycol Res 104(8):900–910.

Rehsteiner H. 1892. Beiträge zur Entwicklungsgeschichte der Fruchtkörper einiger Gastromyceten. Bot Zeit 50: 761–878.

Ritchie D. 1948. The development of Lycoperdon oblongisporum. Am J Bot 35:215–219.

Rostkovius FWT. 1844. Die Pilze Deutschlands. In: Sturm J, ed. Deutschlands Flora in Abbildungen nach der Natur mit Beschreibungen. Part III, Vol 5. Nürnberg: published by the editor. 132 p.

Šmarda F. 1958. Lycoperdaceae. In: Pilát A, ed. Gasteromycetes. Flora ČSR. Ser. B, Vol. 1. Praha: Československé Akademie Věd. p 257–377.

Swartz D. 1933. Some developmental characters of species of Lycoperdaceae. Am J Bot 20:440–465.

———. 1935. The development of *Calvatia craniiformis*. Mycologia 27:439–448.

———. 1936a. The development of *Lycoperdon acuminatum*. Mycologia 28:278–283.

———. 1936b. The development of *Lycoperdon pedicellatum* Pk. (*Bovistella pedicellata* (Pk.) Lloyd. Am J Bot 23:4–7.

Swoboda F. 1937. Über den Fruchtkörperbau und die systematische Stellung von *Lanopila* Fries. Ann Mycol 35(1):1–14.

———. 1938. Zur Anatomie der Lycoperdaceen. I. *Lycoperdon marginatum* Vitt. Ann Mycol 36(2–3):95–118.

———. 1940. Zur Anatomie der Lycoperdaceen. II. *Calvatia pachyderma* (Peck) Morgan. Ann Mycol 38(1):1–13.

Townsend BB. 1954. Morphology and development of fungal rhizomorphs. Trans Brit Mycol Soc 37:222–233.

Vellinga EC. 2004. Genera in the family Agaricaceae: evidence from nrITS and nrLSU sequences. Mycol Res 108(4):354–377.

Winterhoff W. 2000. Epigäische Gasteromycetanae. In: Krieglsteiner GJ, ed. Die Großpilze Baden-Württembergs. Band 2. Stuttgart: Eugen Ulmer. p 103–183.

Zeller SM, Smith AH. 1964. The Genus *Calvatia* in North America. Lloydia 27(3):148–186.

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Secotioid Agaricales (Basidiomycetes) from Mongolia

With 2 Plates

Summary

A recapitulation of all findings of Mongolian secotioid Agaricales is given. Four species are known: *Montagnea arenaria*, *Montagnea haussknechtii*, *Endoptychum agaricoides* and *Gyrophragmium dunalii*. Two out of them, *M. haussknechtii* and *E. agaricoides*, are reported for the first time in Mongolia. An overview of distribution and systematic relationships of the taxa is given.

Zusammenfassung

Secotioide Agaricales (Basidiomycetes) aus der Mongolei

Es werden alle Funde secotioider Agaricales aus der Mongolei rekapituliert. Vier Arten sind bekannt: *Montagnea arenaria*, *Montagnea haussknechtii*, *Endoptychum agaricoides* und *Gyrophragmium dunalii*. Zwei von ihnen, *M. haussknechtii* und *E. agaricoides,* werden erstmals für die Mongolei erwähnt. Es wird ein Überblick über die Verbreitung und die systematischen Beziehungen der Taxa gegeben.

Introduction

Although Basidiomycetes with angio- or cleistocarpous Basidiomata (Gasteromycetes) are among the best known fungi of Mongolia (PILÁT 1972; KREISEL 1975; SCIRGIEŁŁO 1980; DÖRFELT & BUMŽAA 1986), several new findings show that this morphologically defined group of Agaricomycetidae (Homobasidiomycetidae) is still insufficiently known. During a mycological expedition in summer 2005 to Western Mongolia, particularly to Chovd ajmag and Bajan-Ölgij ajmag; several higher fungi were found. Amongst them were four secotioid species of Gasteromycetes, which was the motivation for this recapitulation of all Mongolian records.

The secotioid species of Agaricomycetidae are of crucial importance to get further insight into the evolutionary connections between gymno- and hemiangiocarpous (Hymenomycetes) and angio- or cleistocarpous Basidiomycetes (Gasteromycetes). The secotioid stage of organisation is without doubt a phase in the process of gasteromycetation, which occurred and still continues in the arid regions of the earth. The main vegetation types of Mongolia are continental, winter-cold steppe, semi-desert and desert regions. These are, especially in the northern and western mountainous areas, bordered by boreal coniferous forest, whose existence is bound on ectotropic mycorrhiza and saprobic destruents. Such regions have to be interpreted as the ecological matrix of gasteromycetation. They are also currently the preferred habitat of gasteromycetes including the secotioids. So it was to be expected that, apart from the two known species, further species could be found.

In the following, we compile all records of secotioid basidiomata in Mongolia and discuss them from both ecogeographic and systematic points of view.

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Material and methods

Date, locality, habitat and important features are given for the new findings. Already published findings are included with references. If possible, the existing material was revised. Photographs and micrographs were taken with a Canon 300D and an Olympus Camedia Digital Camera C3040ZOOM and were reproduced without graphical processing. Specimens were analysed and determined by light microscopy using Jenaval and Jenalab microscopes with planachromatic object lenses. Specimens of the new findings will be deposited at Naturkundemuseum Görlitz (GLZ). All coordinates reported for localities were obtained using a personal navigator, etrix Summit, Fa. Garmin (Nansas U.S.A.), geographical data were taken from the new Mongolian map system 1:500 000.

Results

Findings of secotioid fungi in Mongolia

***Montagnea arenaria* (DC.) ZELLER**

New finding:

04. VIII. 2005: Chovd ajmag, approx. 45 km northwest of Chovd and 26 km southwest of Erdeneburen [N 48°19′05″; E 91°17′59″], approximately 1.580 m NN; on grazed steppe with *Krascheninnikovia ceratoides* (L.) GUELDENST., leg. P. KARASCH.

Specimen: single specimen without base of stipe.

Stipe approximately 60 mm in length and 12 mm wide, curved, flattened, hollow inside, yellowish, nearly white at apex; gleba largely decomposed, remains of lamella up to 30 mm long and 9 mm wide.

Spores ellipsoid, ovoid, rarely edged or vaguely heart-shaped, smooth with large germ pore, 13–20/6.5–9 μm, often with significant hilar appendix of 1 μm in length, proportion of length to breadth (1.6–)1.9(–2.2):1, several spores with two germpores but a single hilar appendage originating from two-spored basidia.

Surface of dry lamella with collapsed basidia appearing cellular; irregularly rounded, edged or rarely irregularly square-shaped, more than 10 μm in diameter, often with four or seldom two rudiments of sterigmata (see Plate I, Fig. 3), sometimes small spores of 2–3 μm in diameter still attached.

References of recorded localities:

KREISEL (1975): Dornogov' ajmag, *Caragana* sand desert, leg. K. KLOSS (1973).

DÖRFELT (1978): Dundgov'ajmag, short grass steppe with *Allium polyrhizum* TURCZ. ex REGEL s.l. and *Stipa barbata* DESF. s.l., leg. K. HELMECKE (1977).

DÖRFELT & BUMŽAA (1983): Ömnögov'ajmag, desert vegetation, next to *Peganum nigellastrum* BUNGE, leg. D. BUMŽAA, H. DÖRFELT (1983).

DÖRFELT & TÄGLICH (1990): Ömnögov'ajmag, several findings, desert vegetation, partly next to *Haloxylon ammodendron* (C.A.MEY.) BUNGE; leg. H. DÖRFELT et al. (1988).

***Montagnea haussknechtii* RABENH.**

First finding in Mongolia:

09. VIII. 2005: Bajan-Ölgij ajmag, approximately 7 km southwest of Cengel on river Chovd gol [N 48°54′32″; E 90°05′35″], approximately 200 m NN; grazed, dry sand dune in wider flood plain area dominated by *Achnatherum splendens* (TRIN.) NEVSKI, leg. H. DÖRFELT, H. HEKLAU.

Specimens: one complete specimen collected and dried before being fully mature, several pilei with or without stipes.

Single complete stipe 49 mm long, all stipes around 2 mm in diameter, apically fibrous, outside compact plectenchymatic, with microscopic crystals; inwards fibrous, hollow; single preserved volva 7 mm long and 4 mm broad; pileus up to 30 mm in diameter, remains of pileus skin even in mature specimens, structured like the outer side of the volva.

Spores irregularly ellipsoid to nearly rhomboid, rarely drop-shaped, pear-shaped or heart-shaped; usually 5.5–7.5/(3.2) 3.5–5 μm, sometimes flattened and probably collapsed, then 6–7/3–5–4.5/2.5–3 μm; smooth, with germ pores, hilar appendage lacking; proportion (1.1–)1.3 (–1.6) : 1 of length to breadth.

Surface of dry lamella with collapsed basidia appearing cellular; usually irregularly square-shaped, around 5–6.5 μm in diameter, often with four remains of sterigmata (see Plate I, Fig. 6).

***Endoptychum agaricoides* CZERN.**

First finding in Mongolia:

25. VIII. 2005: Chovd ajmag; mountain ridge Chzargalant chajrchan above flood plain of river Uliastaun gol; approximately 25 km west of Cadman' [N 47°38′19″; E 92°27′39″], 1.837 m NN; deserted, terraced, formerly watered field with occurrence of several steppe plants, leg. J. CRISTAN, H. DÖRFELT.

Specimens: Six specimens were selected for collection of the numerous fresh specimens in all stages of development including almost fully mature ones.

Basidiomata subconical with a characteristic curved tip, half burrowed in soil, basally attached with a pseudorhiza originating from the stipe, cleistocarpous (lacking preformed opening mechanism), at their broadest part 30–60 mm in diameter, height including pseudorhiza around 50–75 mm, irregular dehiscence from the tip at maturity, premature specimens remind of young *Agaricus* basidiomata, mature ones of withered *Scleroderma* species.

Stipe (columella) at the apex 7–10 mm, at the base 25–40 mm in diameter, basally merging into the pseudorhiza of 20–30 mm in length, trama when cut white, reddening, maggot burrows dark brown.

Pileus whitish to hazel, getting scaly, particularly in the middle part, trama (peridium) apically 5 mm, in the periphery 2 mm thick, white when fresh, withering to brownish when ripe.

Hymenophor (gleba) consisting of radially oriented cavities, lamellar structure not distinctly visible, white when young, later getting olive to dark brown, consisting of spores and fine fibrous hyphal remains after autolysis.

Spores brown, globose to subglobose, around 5.8–6.5 µm, rarely ellipsoid, then 6.5–6/4–6 µm, with a single, often central oil body of 1.5–2 µm in diameter; without or with indistinct germpore, basally often with short, blunt, conical hilar appendage up to 1 µm in length and 1.3 µm in breadth, significantly longer rudiments of sterigmata are sometimes attached to them.

***Gyrophragmium dunalii* (FR.) ZELLER**

New finding:

24. VIII. 2005: border region of Zavchan ajmag and Gov'-Altaj ajmag, next to southeastern shore of lake Dörgön nuur; edge of desert area Mongol els [some km northeast of N 47°40′19″; E 93°36′55″], approximately 1.450 m NN; desert dunes, leg. H. DÖRFELT, H. HEKLAU.

Specimens: two basidiomata, growing 20 cm from each other, already dry when collected.

With volva broken off and recovered from soil, without annulus; stipe curved, around 70 mm long, in the middle part 5–6 mm broad, dark brown, basally slightly lighter, volva remains 20 mm long and 15 mm broad, whitish, outwards encrusted with sand, pileus almost conical, 20 mm broad and 17 mm high, skin dry, fragile, brownish black, lamellae black, fragile, partly over 3 mm broad.

Stipe curved, 35 mm long, around 2 mm broad, with volva and annulus, dark brown, volva stretched, little more than 20 mm long and 7 mm broad, apically lobed, annulus around 10 mm long lower part, surrounding stipe distantly, collar-like with a hem of 6 mm in diameter, blackish brown like pileus skin, pileus 17 mm in diameter, flat, skin dry, fragile, blackish brown, lamellae black, fragile, up to 2 mm broad.

Spores globose or subglobose with (4–) 5(5.8) µm in diameter, rarely oval, then 5–6/5–5.5 µm, without germ pores, often with hilar appendage of 0.7 mm length, usually with oil body of 1.5–2 µm in diameter.

References of recorded localities:

DÖRFELT (1980): Bajanchongor ajmag, desert vegetation, dry river valley with *Tamarix ramosissima* LEDEB., *Calligonum mongolicum* TURCZ., *Haloxylon ammodendron* (C.A.MEY.) BUNGE; leg. K. HELMECKE (1979).

Discussion

Systematics of the covered species

Secotioid fungi emerged in adaptation to arid climates from various groups of Agaricales, Boletales or Russulales and may be classified systematically to the families of these orders. All four species described above belong to Agaricaceae. The genus *Montagnea* was classified to Coprinaceae, which wore proven to be heterogenous. Alongside with the type of *Coprinus* [*C. comatus* (MÜLL.: FR.) PERS.], *Montagnea* is now considered to belong to Agaricaceae (KIRK et al. 2001; REDHEAD et al. 2001). This is supported by molecular systematic studies (HOPPLE & VILGALYS 1994, 1999; MONCALVO et al. 2002; LEBEL et al. 2004; VELLINGA 2004).

The type species, *Montagnea arenaria*, is a common fungus with worldwide distribution and varying fruitbody characters. This lead to many parallel descriptions of largely not acknowledged species, but also to a treatment as monotypic genus with very variable morphological and microscopic characters (HOLLÓS 1904; PILÁT 1958; JÜLICH 1984). Few authors accepted two species (LIU 1984). A critical revision of the genus by REID & EICKER (1991) lead to a convincing grouping into two well distinguishable species. The authors divided the specimens with constantly small spores and a differing pileus structure correctly from *M. arenaria*, forming *M. haussknechtii*. Although RABENHORST (1870) did mention the lack of a volva when introducing the latter species. This grouping is currently accepted by most gasteromycete specialists (e.g. KREISEL 2001). Recent doubts (CHEN 1999) are probably caused by missing specimens of *M. haussknechtii*.

According to REID & EICKER (1991), another critical, not carefully described species is "*Montagnites*" *schuppii* RICK. The concise description of that species by RICK (1939, 1961) fits *Gyrophragmium dunalii* in all details. The determining characters of germ pores and stipe morphology are not dealt with. Further characters differentiating between *Montagnea* and *Gyrophragmium* like the attachment and anastomoses of the lamellae or discoloration of the trama (DRING & RAYSS 1963; KREISEL 1973; JÜLICH 1984; LEBEL et al. 2004) are not easily detected in ripened, dry fruit bodies. Our collection from Mongolia includes one specimen without remains of the partial veil, and was initially supposed to be a *Montagnea* species. The characters of this basidiome fit to the description of *M. schuppii*, but its identity could be proven by comparison with better preserved specimens of *Gyrophragmium dunalii*. The name *Montagnites schuppii* should therefore be considered synonymous to *Gyrophragmium dunalii*.

The close systematic relationship between *Gyrophragmium* and *Agaricus* has already been discussed by KREISEL (1973). Recently it was confirmed by molecular systematic analyses (MONCALVO et al. 2002; VELLINGA 2004; GEML 2004; GEML et al. 2004). It was subsequently included into *Agaricus* and renamed as *Agaricus aridicola* GEML, GEISER & ROYSE in GEML et al. (2004: 172). Currently we cannot accept this new epitheton because of the missing proof of the synonyms, e.g. *Gyrophragmium delilei* MONTAGNE.

The genus *Endoptychum* is also classified into Agaricaceae (KIRK et al. 2001). According to molecular systematic analyses the genus is not monophyletic in its current state. The type species, *E. agaricoides* shows strong relationships to the genera *Chlorophyllum* and *Macrolepiota* (VELLINGA et al. 2003; VELLINGA 2004), whereas *Endoptychum depressum* is considered an agaricoid *Agaricus* species (VELLINGA et al. 2003; GEML 2004; GEML et al. 2004). This was already supposed by SINGER & SMITH (1958).

Chlorophyllum has been conserved against *Endoptychum*, since the name *Endoptychum* CZERN. 1845 is older than *Chlorophyllum* MASSEE 1898 (VELLINGA & DE KOK 2002; ICBN 2006). Also, the type species *E. agaricoides* was included into *Chlorophyllum* (VELLINGA 2002). This approach is nomenclaturally problematic, since the type of *Endoptychum* was included into the emended genus *Chlorophyllum* at the time of the combination. The existing combination *Chlorophyllum agaricoides* (CZERN.) VELLINGA was protected afterwards against *Endoptychum*, although this is not sanctioned by ICBN.

However, the placement of *E. agaricoides* into *Chlorophyllum* can currently not be accepted from systematic reasons. The molecular data sets used by VELLINGA et al. (2003) and VELLINGA (2004) do hardly or not at all support placement of *E. agaricoides*, *Chlorophyllum molybdites* and several *Macrolepiota* species into a monophyletic clade. This applies also to the morphology, although there is morphological indication of relationship between the *Macrolepiota* species and *C. molybdites*, which is not given for *E. agaricoides*. The spore colour of *C. molybdites* is just slightly greenish, whereas *E. agaricoides* has brown spores with a weak olive hue. Other characters, like the squamose surface are widely distributed in Agaricaceae and should not be taken into account. Even though these species may be closely related, their emendation into a single taxon is highly doubtful considering the present state of knowledge.

Distribution of the covered species

Montagnea arenaria and M. haussknechtii

Both species are widely distributed, mainly in steppe and desert areas. *M. arenaria* is described to be found in Africa including the Canary Islands, Europe, Asia, North and South America and Australia. The species has been found also in temperate regions, as in dry pastures in Middle Germany. *M. arenaria* is known from the Central Asian countries bordering Mongolia (SOROKIN 1884; VASIL'KOV 1954; PISARJEVA 1964; SOSIN 1973; LIU 1984).

M. haussknechtii is constricted closer to arid regions than *M. arenaria*. According to REID & EICKER (1991), KREISEL (2001) and KREISEL & AL-FATIMI (2004), the species occurs in Africa including the Canary Islands and in continental Asia. REID & EICKER (1991) also noted specimens from Argentina and Australia probably belonging to *M. haussknechtii*. The only record from central Asia is given by LIU (1984, ut *Montagnea tenuis*) from China. BASEIA & MILANEZ (2004) describe this species from Brazil. Their report about the occurrence of *M. haussknechtii* in North America is doubtful, as they correspond to ZELLER (1943), whose description clearly depicts *M. arenaria*, as already noted by REID & EICKER (1991). The report about its occurrence in Cuba (BASEIA & MILANEZ 2004) bases on a description by KREISEL (1971), who also cleary refers to *M. arenaria*. However, KREISEL & AL-FATIMI (2004), note to have collected *M. haussknechtii* from Cuba without giving localities.

The new finding of *M. arenaria* from Mongolia confirms the general distribution of that species in the steppe and desert areas of Central Asia. The finding of *M. haussknechtii* in the Mongolian Altay is the northernmost finding worldwide. It confirms the occurrence of this species in arid regions of the temperate zone. *M. haussknechtii* is therefore not restricted to the dry tropics, where the main distribution lies.

Endoptychum agaricoides

In a popular publication on Mongolian fungi by URANCIMEG (2004), *E. agaricoides* is included and imaged without giving details of localities. This publication is quite erroneous, since it reports about species that are not occurring in Mongolia. The images are mainly plagiates, which were not designed after Mongolian material. Images of *Boletus edulis* BULL.: FR. and *Boletus satanas* LENZ for instance, were obviously taken from MICHAEL et al. (1983), the latter species is not even occurring in Mongolia (see DÖRFELT & BRESINSKY 2003: 196/197).

E. agaricoides is like *M. arenaria* widely distributed in steppe and semidesert areas. The species is repeatedly recorded from areas around Mongolia (SOROKIN 1884, ut *Secotium acuminatum*; VASIL'KOV 1954; PISARJEVA 1964; SOSIN 1973; LIU 1984; GE & YANG 2006 ut *Chlorophyllum agaricoides*).

Gyrophragmium dunalii

KREISEL (1973) characterises *G. dunalii* as amphizonal, its area of occurrence ranging on the Northern Hemisphere from the meridional to the boreo-subtropical zone and on the Southern Hemisphere from the austro-subtropical to the austral zone. *G. dunalii* is the only species reported from Asia, but the taxonomic problems of the genus *Gyrophragmium* remain mainly unsolved, so some findings may belong to other species. The species is repeatedly recorded from areas around Mongolia (SOROKIN 1884, ut *G. delilei*; VASIL'KOV 1954; PISARJEVA 1964; SOSIN 1973, ut *G. delilei*; LIU 1984, ut *G. delilei*).

References

BASEIA, I. G. & MILANEZ, A. I. 2002: *Montagnea hausknechtii* Rab. (Podaxales) a rare agaricoid Fungus: first record from Brazil. – Acta Bot. Bras. **16**(3): 311–316.

Chen, C. 1999: Genetical and molecular systematic study on the genus *Montagnea* Fr. – Virginia Polytechnic Institute and State University, Blackburg, Virginia.

Dörfelt, H. 1978: Mykogeographisch interessante Gasteromyceten-Funde. – Boletus **2**: 9–17.

Dörfelt, H. 1980: Mykogeographisch interessante Gasteromyceten-Funde (II). – Boletus **4**: 35–38.

Dörfelt, H. & Bresinsky, A. 2003: Die Verbreitung und Ökologie ausgewählter Makromyceten Deutschlands. – Z. Mykologie **69**: 177–286.

Dörfelt, H. & Bumzaa, D. 1986: Die Gasteromyceten (Bauchpilze) der Mongolischen Volksrepublik. – Nova Hedwigia **43**: 87–111.

Dörfelt, H. & Täglich, U. 1990: Pilzfloristische Arbeitsergebnisse aus der Mongolischen Volksrepublik. – Boletus **14**: 1–27.

Dring, D. M. & Rayss, T. 1963: The Gasteromycete fungi of Israel. – Israel J. Bot. **12**: 147–178.

Geml, J. 2004: Evolution in Action: molecular evidence for recent emergence of secotioid genera *Entoptychum*, *Gyrophragmium* and *Longula* from *Agaricus* ancestors. – Acta Microbiol. Immunologica Hungarica **51**(1–3): 97–108.

Geml, J.; Geiser, D. M. & Royse, D. J. 2004: Molecular evolution of *Agaricus* species based on ITS and LSU rDNA sequences. – Mycolog. Progress **3**(2): 157–176.

Ge, Z. W. & Yang, Z. L. 2006: The genus *Chlorophyllum* (Basidiomycetes) in China. – Mycotaxon **96**: 181–191.

Hollós, L. 1904: Die Gasteromyceten Ungarns. – Leipzig.

Hopple, J. S. & Vilgalys, R. 1994: Phylogenetic relationships among coprinoid taxa and allies based on data from restriction site mapping of nuclear rDNA. – Mycologia **86**(1): 96–107.

Hopple, J. S. & Vilgalys, R. 1999: Phylogenetic Relationships in the Mushroom Genus *Coprinus* and Dark-Spored Allies Based on Sequence Data from the Nuclear Gene Coding for the Large Ribosomal Subunit RNA: Divergent Domains, Outgroups, and Monophyly. – Mol. Phylog. Evol. **13**(1): 1–19.

ICBN 2006: International Code of Botanical Nomenclature (Vienna Code). – Koenigstein.

Jülich, W. 1984: Die Nichtblätterpilze, Gallertpilze und Bauchpilze/Aphyllophorales, Heterobasidiomycetes, Gastromycetes. – In: H. Gams (Begr.), Kleine Kryptogamenflora, Band IIb/1, Basidiomyceten, 1. Teil. – Jena.

Kirk, P. M.; Cannon, P. F.; David, J. C. & Stalpers, J. A. 2001: Ainsworth & Bisby's Dictionary of the fungi. – Wellingford, UK.

Kreisel, H. 1971: Charakteristika der Pilzflora Kubas. – Biol. Rdsch. **9**: 65–73.

Kreisel, H. 1973: Die Gattung *Gyrophragmium* Mont. und ihre Stellung im System der Basidiomycetes. – Feddes Repert. **83**: 577–583.

Kreisel, H. 1975: Gasteromyzeten aus der Mongolischen Volksrepublik. – Feddes Rep. **86**: 321–328.

Kreisel, H. 2001: Checklist of the gasteral and secotioid Basidiomycetes of Europe, Africa and Middle East. – Österr. Z. Pilzkd. **10**: 213–313.

Kreisel, H. & Al-Fatimi, M. 2004: Basidiomycetes and larger Ascomycetes from Yemen. – Feddes Repert. **115**: 547–561.

Lebel, T.; Thompson, D. K. & Udovicic, F. 2004: Description and affinities of a new sequestrate fungus *Barcheria willisiana* gen. et spec. nov. (Agaricales) from Australia. – Mycol. Res. **108** (2): 206–213.

Liu, B. 1984: The Gasteromycetes of China. – Nova Hedwigia, Beih. **76**.

Michael, E.; Hennig, B. & Kreisel, H. 1983: Handbuch für Pilzfreunde. Bd. 1, ed. 5. – Jena.

Moncalvo, J.-M.; Vilgalys, R.; Redhead, S. A.; Johnson, J. E.; James, T. Y.; Aime, M. C.; Hofstetter, V.; Verduin, S. J. W.; Larsson; E.; Baroni, T. J.; Thorn, R. G.; Jacobsson, S.; Clémençon, H. & Miller Jr., O. K. (2002): One hundred and seventeen clades of euagarics. – Mol. Phylogenet. Evol. **23**: 357–400.

Pilát, A. (ed.) 1958: Gasteromycetes, Houby Brichatky. – In: Flora ČSR, 1. – Praha.

Pilát, A. 1972: Contribution a l'étude des Basidiomycètes Mongolie. – Bull. Soc. Myc. France **88**: 333–358.

Pisarjeva, N. F. 1964: K flore Gribov Aktjubinskoj oblasti. – Trudy Inst. Bot. Akad. Nauk Kazachskoj SSR **16**: 182–216.

Redhead, S. A.; Vilgalys, R.; Moncalvo, J.-M.; Johnson, J. & Hopple, J. S. 2001: *Coprinus* Pers. and the disposition of *Coprinus* species senso lato. – Taxon **50**: 203–241.

Rabenhorst; L. 1870: Übersicht der vom Herrn Professor Dr. Haussknecht im Orient gesammelten Kryptogamen. – Sitzungsber. Naturwiss. Ges. Isis Dresden **1870**: 225–236.

Reid, D. & Eicker, A. 1991: A taxonomic survey of the genus *Montagnea* (Gasteromycetes) with special reference to South Africa. – S. Afr. J. Bot. **57** (3): 161–170.

Rick, J. 1928: Resumo mycologico. – Egatea **13**: 432–439

Rick, J. 1939: Agarici Riograndensis IV. – Lilloa **4**: 75–104.

Rick, J. 1961: Basidiomycetes Eubasidii in Rio Grande do sul – Brasilia, 5. Agaricaceae. – Iheringia, Ser. Bot. **8**: 296–460.

Singer, R. & Smith, A. H. 1958: Studies on secotiaceous fungi – II. *Endoptychum depressum*. Brittonia **10**: 216–221.

SKIERGIEŁŁO, A. 1980: Two Gasteromycetes from the Mongolian People's Republic. – Kew Bull. **31**(3): 703–704

SOROKIN, N. V. 1884: Materialy dlja flory Sredny Asia. – Bull. Soc. Imp. Nat. Moscou **59**: 183–230.

SOSIN, P. E. 1973: Opredelitel' gasteromicetow SSSR. – Leningrad.

URANCIMEG, G. 2004: Mongol ornj chunsnij möög. – Ulaanbaatar.

VASIL'KOV, V. N. 1954: O nekotorych interesnych i novych vida Gasteromicetov v SSSR. – Trudy Bot. Inst. im. V. L. Komarova Akad. Nauk SSSR, Ser. II. **9**: 447–464.

VELLINGA, E. C. 2002: New combinations in *Chlorophyllum*. – Mycotaxon **83**: 415–417.

VELLINGA, E. C. 2004: Genera in the family Agaricaceae: evidence from nrITS and nrLSU sequences. – Mycol. Res. **108**: 354–377.

VELLINGA, E. C. & DE KOK, R. P. 2002: Proposal to conserve the name *Chlorophyllum* Massee against *Endoptychum* Czern. (Agaricaceae). – Taxon **51**: 563–564.

VELLINGA, E. C.; DE KOK, R. P. J. & BRUNS, T. D. 2003: Phylogeny and taxonomy of *Macrolepiota* (Agaricaceae). – Mycologia **95**(3): 442–456.

ZELLER, S. M. 1943: North American species of *Galeropsis*, *Gyrophragmium*, *Longia*, and *Montagnea*. – Mycologia **35**: 409–421.

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Explanations to Plate I and II

PLATE I

Figs. 1–3: *Montagnea arenaria*

Fig. 1: Normal spore with germ pore and a basidium with two deformed spores

Fig. 2: Spores, normally with one germpore, rarely adnated with two germpores or very large (right); scale bar 10 µm

Fig. 3: Side view of a gill with characteristically deformed rudiments of basidia; scale bar 10 µm

Figs. 4–6: *Montagnea haussknechtii*

Fig. 4: A fruit body, scale 1 mm

Fig. 5: Spores (normal, aggregated and deformed), scale bar 10 µm

Fig. 6: Side view of a gill with characteristically deformed rudiments of basidia, scale bar 10 µm

PLATE II

Figs. 7–10

Endoptychum agaricoides

Fig. 7: Fruit bodies at the finding place in Mongolia; scale bar 1 cm

Fig. 8: Section of a young basidioma (basally erubescent) and parts of mature basidiomata with the olive-brown gleba; scale bar 1 cm

Fig. 9: Spores from the same specimen, rarely with hilar appendages (Fig. top left); scale bar 10 µm

Fig. 10: Spores and hyphal remains of hymenial structures, scale bar 10 µm

Figs. 11, 12: *Gyrophragmium dunalii*

Fig. 11: Specimen from the new finding place (Mongol els), scale 1 mm

Fig. 12: Spores, normal and (top right) abnormal and with hilar appendices; scale bar 10 µm.

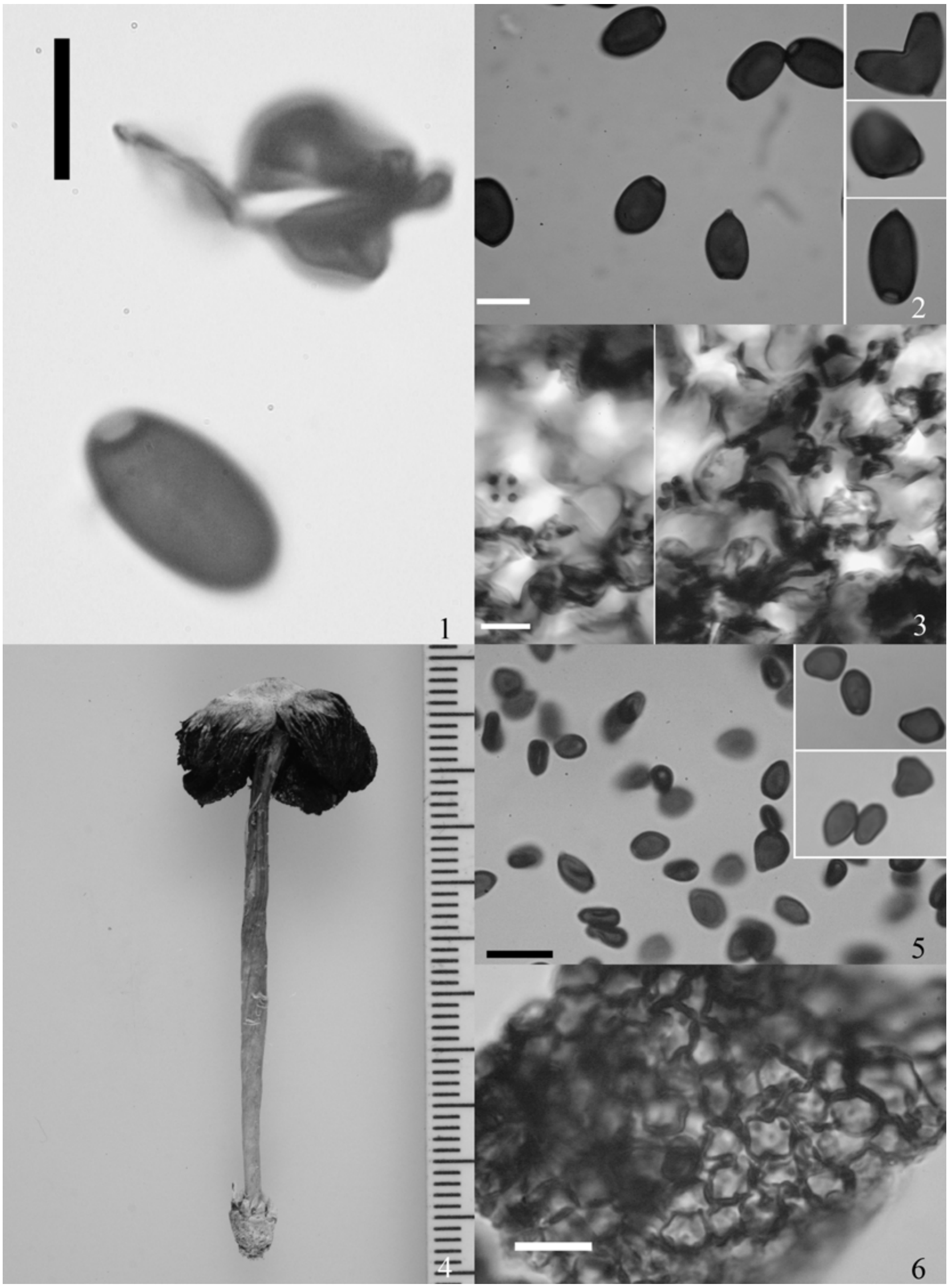

PLATE I

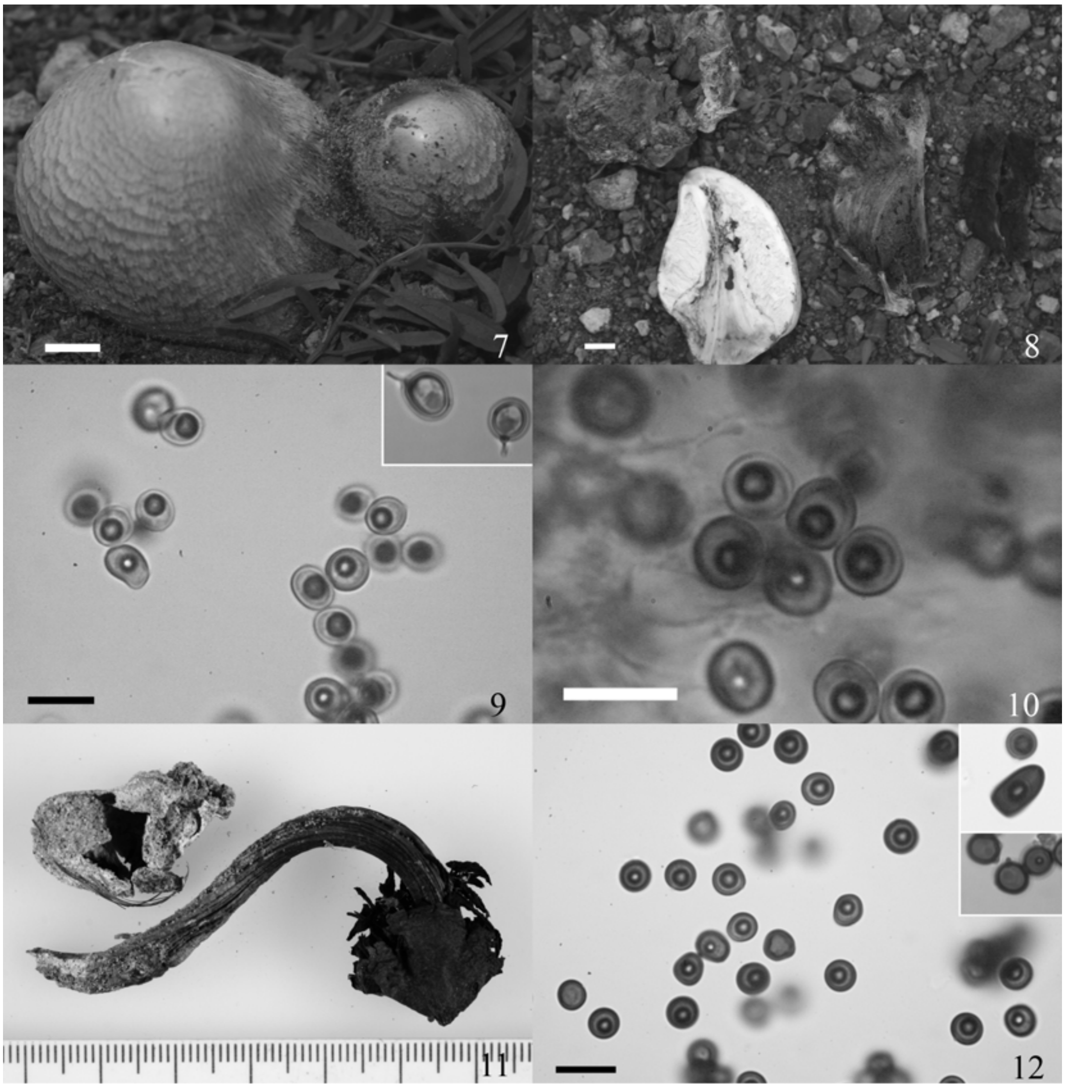

PLATE II

Preliminary annotated checklist of Gasteromycetes in Panama

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Abstract

Based on 18 recently collected specimens, 12 herbarium specimens and extensive literature research, a preliminary checklist of the Gasteromycetes of Panama is presented. Nine species are reported for the first time for Panama: *Bovista oblongispora*, *Calostoma cinnabarinum*, *Calvatia rosacea*, *Crucibulum laeve*, *Cyathus limbatus*, *Morganella velutina*, *Mutinus argentinus*, *Radiigera taylorii* and *Sphaerobolus stellatus*. In addition, an unknown species related to *Radiigera* is recorded. Known locations and descriptions of 33 species currently known for Panama are given, together with taxonomical and nomenclatural discussions, where necessary.

Key words: tropical mycology, *Basidiomycota*

Introduction

Despite of their abundance, often striking appearance and important ecological roles of tropical fungi, the knowledge of their diversity and distribution is far from being complete. This is especially true for Gasteromycetes, since their often problematic taxonomy and nomenclature, as well as scarce general works on the topic, make this group harder to approach than many other groups of *Basidiomycota.*

For Panama, the present knowledge on fungi including Gasteromycetes has been listed by Piepenbring (2006). Garner (1956) presented the only work dealing exclusively with Panamanian and Costa Rican Gasteromycetes so far. However, detailed descriptions and localities were not presented there. Further records of Panamanian Gasteromycetes are included in fungus-floristic studies of other countries (e.g. Dennis 1970), or monographs of certain genera (e.g. Kreisel & Dring 1967, Guzmán 1970).

Materials and methods

The present treatment is based mainly on collections made by M. Piepenbring and coworkers during field work in Western Panama and mycological courses held at the Universidad Autónoma de Chiriquí, Panama. Specimens of local importance are deposited at the Herbario Nacional de Panamá (PMA), critical ones in PMA and the Botanische Staatssammlung München (M). Further specimens were obtained by loan from the herbaria of the National Fungus Collection of the U.S. Department of Agriculture (BPI), New York Botanical Garden (NY) and Oregon State University (OSC). Specimens were analysed macroscopically and microscopically using a Carl Zeiss Stemi 2000 and a Jenalab microscope. Microscopical preparates were mounted in 3% KOH or lactic acid. Spore measurements are given excluding ornamentation. Microphotographs were taken with a Sony 3 CCD-hig camara. SEM images were made at the Institute for Systematic Zoology and Evolution at FSU Jena. Species without analysed specimens are described according to literature and specimens from other areas, where available. Specimen data is given as recorded in literature, or as indicated by the Virtual Herbarium of the New York Botanical Garden.

To allow geomycological conclusions, locations in Panama and distribution data within Central America and the Caribbean (excluding Mexico, Florida and South America south of Colombia and Venezuela) are given as exactly as possible. However, only self-revised or paper-published records were taken into account. In several cases, data are problematic due to taxonomical or nomenclatural uncertainty. In these cases, a discussion of these issues follows the description.

Results

Lycoperdaceae (Agaricaceae p. p.)

Bovista longispora Kreisel

Specimen visum: **Chiriquí**: Parque Nacional Volcán Barú, Sendero de los Quetzales, alt. approx. 2500 m, 02.X.2007, M. Piepenbring with licenciatura students 4073.

Macroscopical features: Fruitbodies (Fig. 1a) globose, 1.5–2.3 cm diam. Exoperidium middle to dark brown, granulose, lapsing at maturity, then yellowish endoperidium visible. Gleba olivaceous brown to umber. Subgleba almost absent, greyish, finely cellular, cavities less than 0.5 mm diam. White, branched rhizomorphs at base. On soil.

Microscopical features: Spores (Fig. 2a) ellipsoid to pear shaped, 4.5–6 x 2.8–3.5 µm, very weakly verruculose, as seen by light microscopy almost smooth, with short pedicel. Capillitium transition-type, up to 5.5 µm diam., without septa, with minute pores only in the upper part of the gleba.

The species is restricted to Central America and the Caribbean, it is a new record for Panama, being known to the present only from Costa Rica, Cuba, the Dominican Republic, Guadelupe and Puerto Rico (Kreisel 1967, Stevenson 1975, Minter et al. 2006, Calonge et al. 2005).

Bovista pusilla Batsch : Pers. agg

Syn.: *Lycoperdon ericetorum* Pers.

Specimina non visa: **Canal Zone**: Barro Colorado Island, G.W. Martin and A.L. Welden 7368, 7460, 8659, as *L. ericetorum* in Garner (1956).

Description based on other specimens of *B. pusilla* ss Kreisel 1967 and on literature (Kreisel 1967, Jülich 1984).

Macroscopical features: Fruitbodies globose, 0.5–1.5 cm diam. Peridium yellowish buff to light brown, smooth. Gleba brownish buff to brown. Subgleba absent. On soil in open areas.

Microscopical features: Spores 3–4 µm diam., globose, pale brown, finely warty to punctate, with short pedicel. Capillitium pale brown, transition-type, densely branched, up to 3.5 µm wide, abundantly pitted.

This species is cosmopolitan, apart from Panama (Garner 1956 as *L. ericetorum*) it is known from Colombia, Puerto Rico, Tobago and Venezuela (Kreisel 1967, Dennis 1970 (includes *Bovista polymorpha* (Vittad.) Kreisel), Stevenson 1975, Reid 1977, Minter et al. 2001). This record is given as aggregate species, incorporating *Bovista dermoxantha* (Vittad.) De Toni and *Bovista furfuracea* Pers. The scarce description does not allow for an exact determination; and the systematic relationships of the highly problematic group of *Bovista* subgen. *Globaria* are still to be revised. However, as most records in the area are determined as *B. pusilla*, the name is used here to avoid confusion. Revision of the specimen is needed to obtain an exact determination.

Calvatia cyathiformis (Bosc) Morg.

Specimina non visa: **Canal Zone**: Balboa, G.W. Martin 4167, 4217 (NY 068960).

Description based on other specimens and on literature (Jülich 1980, Kreisel 1994).

Macroscopical features: Fruitbodies globose to turbinate, up to 10 cm diam. Exoperidial surface smooth when young, cracking irregularly during ripening process. Gleba dark purple to purplish brown when ripe. Subgleba cup-shaped to flat, cellular, cream colored to purplish grey, lighter than gleba, gleba and subgleba are often separated by a diaphragm. Growing on ground, usually in grassland.

Microscopical features: Spores purplish, globose, 4–6.5 µm diam., coarsely verrucose. Capillitium violaceous brown, fragile, branched, *Lycoperdon*-type, 2.5–6 µm diam., with minute rounded pits.

The species has a worldwide distribution (Kreisel 1994) including Southern Europe (Demoulin pers. comm.). Records for Panama are published by Garner (1956) and Dennis (1970). In the vicinity of Panama, it has been recorded from Costa Rica, Colombia, Cuba, Jamaica, Puerto Rico, Trinidad and Venezuela (Dennis 1953, Dennis 1970, Kreisel 1971, Nieves-Rivera & Lodge 1998, Minter et al. 2001, Calonge et al. 2005, Calonge & Mata 2006). It is possible that this species is conspecific with *Calvatia fragilis* (Vittad.) Morgan, which is distinguished by a compact subgleba. (Kreisel 1994). Garner (1956) did obviously not discriminate between the two taxa. The numerous collections in the surrounding area make *C. cyathiformis* more probable, if both are considered as different species.

Calvatia rosacea Kreisel

Specimen visum: **Canal Zone**: Ft. Sherman area, 31.VII.1945, G.W. Martin 6137, as *Calvatia candida* (Rostk.) Hollós var *fusca* G. Cunn. (OSC 28213).

Specimen non visum: **Canal Zone**: Ft. Sherman area, G.W. Martin 6181, as *C. candida*.

Macroscopical features: One single cut fruitbody in collection, approximately 3.7 cm in height, 4 cm in width. Exoperidium finely granulose, almost smooth, yellowish to reddish brown, withered at glebal part, remains of peridium wrinkled in lower subglebal part. Gleba yellowish brown. Subgleba somewhat darker, cellular, obscured by insect damage, subglebal cavities (Fig. 2b) are crossed by hyphae. The collection is probably immature and was made from soil.

Microscopical features: Spores yellowish hyaline, globose to ellipsoidal, 2.8–4.5 x 2.8–3.7 µm, verrucose; capillitium light brown, fragile, *Lycoperdon*-type, sparsely septated by true and false septa, branched, no pits.

This is the second record of that species worldwide, the type being from the vicinity of Macas in Ecuador at the eastern base of the Andes in the tropical rainforest zone (Kreisel 1989). The fresh color of the fruitbody in Panama is not noted by the finder, it should have been rosaceous. The specimen has been recorded by Garner (1956), Dennis (1970) and Piepenbring (2006), in every case as *C. candida*. However, *C. candida* has a compact subgleba and is a temperate species from heaths and open land (Kreisel 1994). The related *Calvatia ochrogleba* Zeller from western USA (Oregon) has larger fruitbodies and echinulate spores; and *Calvatia rugosa* (Berk. & M.A. Curtis) D.A. Reid with pitted capillitium and compact subgleba, is a temperate to tropical species (Zeller 1947, Zeller & Smith 1964, Kreisel 1994) which has also been recorded for Cuba (Kreisel 1992) and Costa Rica (Calonge et al. 2005). The other specimen cited by Garner (1956) as *C. candida* (G.W. Martin 6181) was not analysed, it is therefore not sure whether it corresponds to *C. rosacea*.

Lycoperdon atropurpureum Vittad.
Syn.: *Lycoperdon mauryanum* Pat. ex Demoulin

Specimina non visa: **Chiriquí**: Casita Alta, G.W. Martin and A.L. Welden 8048; trail between Finca Lerida and Casita Alta, G.W. Martin and A.L. Welden 8216; Valley of Rio Chiriquí Viejo, G.W. Martin 2583, all alt. 1600–2200 m, as *L. molle* Pers. : Pers. in Garner (1956).

Description based on other specimens and on literature (Jülich 1984).
Macroscopical features: Fruitbodies capitate to almost cylindrical, 2–5.5 x 2–3 cm; exoperidium spiny, spines breaking away easily, yellowish brown to blackish, endoperidium in old specimens visible between spines, yellowish, shiny. Gleba purple brown when ripe. Subgleba yellowish to brown, chambered, cavities around 0.8 mm wide. On soil in open woods.
Microscopical features: Spores purplish, globose, 4–6 µm diam., coarsely verrucose, often mixed with sterigmal remains. Capillitium *Lycoperdon*-type, 4–8 µm diam., reddish brown, septated, with scarce small pores.
This species is distributed in warm temperate regions of the Northern hemisphere, but has apart from the Panamanian records as *L. molle* (Garner 1956, Dennis 1970) also been recorded from Costa Rica (Calonge et al. 2005, Calonge & Mata 2006) and Guatemala (Demoulin 1972, as *L. mauryanum*). *L. atropurpureum* was considered conspecific with *L. molle* when Garner (1956) wrote his article. According to his description, the gleba is dark purple and the spores are coarsely warted, therefore the records probably belong to *L. atropurpureum*. The gleba of *L. molle* is brown, sometimes with a slight purplish touch; and the spores are finely warted. Apparently, *L. molle* is restricted to temperate regions. The specimens have to be revised in order to resolve these taxonomic problems. The exclusively American species *L. mauryanum* is considered conspecific with *L. atropurpureum* here, it has slightly smaller spores and more scarce pores in the capillitium (Demoulin 1972).

Lycoperdon perlatum Pers.

Specimina non visa: **Chiriquí**: Trail between Finca Lerida and Casita Alta, alt. 2000–2200 m, G.W. Martin 8199; Cerro Respingo, approx. 6 km NW of town of Cerro Punta, 02.VII.1975, Dumont-PA 1634 (NY 871658).

Description based on other specimens and on literature (Jülich 1984).
Macroscopical features: Fruitbodies capitate, 2–8 x 1.5–5 cm. Exoperidium white, becoming cream to brown when ripe, spiny, spines 1–2 mm long, conical, easily falling away, leaving an areolate pattern on the endoperidium, which is cream and not shiny when ripe. Gleba olive brown to grey brown. Subgleba greyish brown, lighter than gleba, chambers up to 1.2 mm diam. On soil in woods, sometimes on very decayed wood.
Microscopical features: Spores light brown, 3–4.5 µm diam., coarsely warted, often mixed with sterigmal remains. Capillitium *Lycoperdon*-type, 4–8 µm diam., yellowish brown, scarcely septate, pores of irregular size, paracapillitium abundant.
This fungus has been recorded for Panama by Garner (1965) and Dennis (1970). The cosmopolitan species has been recorded in the Central American region from Costa Rica, Cuba, the Dominican Republic, Haiti, Jamaica, Venezuela (Dennis 1953, Benjamin and Slot 1969, Dennis 1970, Rodríguez Gallart 1997, Minter et al. 2001, Calonge et al. 2005). It seems to be quite common in the region at higher altitudes.

Lycoperdon lividum Pers.
Syn.: *Lycoperdon spadiceum* Pers.

Specimina non visa: **Canal Zone**: Barro Colorado Island, G.W. Martin and A.L. Welden 8492, 8577, all as *L. spadiceum*.

Description based on other specimens and on literature (Jülich 1984).
Macroscopical features: Fruitbodies capitate, 1–4.5 x 1–3 µm. Exoperidium whitish, brownish when ripe, granular, without spines; endoperidium greyish cream, shiny. Gleba olive to umber. Subgleba brownish, chambers up to 0.5 mm diam. On soil in open, dry places.
Microscopical features: Spores 3.3–5 µm diam., finely warted, with pedicel 0.5–5 µm long, without sterigmal remains. Capillitium *Lycoperdon*-type, 4–8 µm diam., yellowish brown, seldom septate, pores small, irregular.

Apart from the Panamanian records as *L. spadiceum* (Garner 1956, Dennis 1970), this species is known only from the temperate zone, usually from dry areas. Garner (1956) gave no description of the specimens; therefore they need to be revised.

Morganella fuliginea (Berk. & M.A. Curtis) Kreisel & Dring
Syn.: *Morganella mexicana* Zeller

Specimina visa: **Chiriquí**: Bocas del Toro, El Valle, Celestine, alt. approx. 600 m, 28.IX.2005, M. Piepenbring and participants of the Mycological Workshop 3598; **Coclé**: Base of Cerro Pilon, approx. 5 km NE of El Valle, alt. approx. 670 m, 13.VI.1975, Dumont-PA 164 (NY 398742); Dumont-PA 182 (NY 398741) and Dumont-PA 190 (NY 398743); **Panamá**: 2–3 km N of Pan American Highway on El Llano-Carti road, alt. approx. 180–245 m, 29.VI.1975, Dumont-PA 1363 (NY 398738); **San Blas**: Trail from Puerto Obaldia to Darien, alt. approx. 0–90 m, 22.VI.1975, Dumont-PA 968 (NY 398740); **Veraguas**: Lower slopes of Cerro Tuté, approx. 8 km NE of Santa Fe on property of Agricultural school Alto de Piedra, alt. approx. 610 m, 19.VI.1975, Dumont-PA 763 (NY 398745) and Dumont-PA 788 (NY 398744).

Specimina non visa: **Coclé**: El Valle de Anton, alt. 600–700 m, G.W. Martin 2933, 2973, as *M. mexicana*; **Panamá**: Rio Tucuman valley, 10 km E of Juan Diaz, G.W. Martin 3180, as *M. mexicana*; **Canal Zone**: Barro Colorado Island, G.W. Martin and A.L. Welden 7329, 7923, as. *Lycoperdon subincarnatum*; Ft. Sherman area, G.W. Martin 6183, 6201, as *M. mexicana*; **Veraguas**: Along road from St. Fe to Calovebora, Atlantic slope, vicinity Rio Caleborita, approx. 16 km from St. Fe, 18.VI.1975, Dumont-PA 551 (NY 398737).

Macroscopical features: Fruitbodies (Fig. 1b) globose, 1–2 cm diam. Exoperidium brown to blackish brown, rough, no distinct spines. Gleba light brown. Sterile base compact, very scarce or absent, yellowish. Branched white rhizomorphs on base. On more or less decayed wood in rain forest and degraded rain forest.

Microscopical features: Peridium (Fig. 2c) composed of chains of irregular cells, no setae visible. Spores (Fig. 2d) globose, 3.2–4 µm diam., yellowish hyaline, spinulose, Spines up to 0.5 µm long. Capillitium absent, paracapillitium (Fig. 2d) abundant, hyaline, septate and branched, up to 5.5 µm diam., threads joined and interwoven by glebal membranes.

Records of this species from Panama are given by Garner (1956, as *M. mexicana*), Dennis (1970), Stevenson (1975) and Piepenbring (2006). It has a Central and South American distribution. In the vicinity of Panama, it has been collected in Colombia, Costa Rica, Cuba, Dominica, the Dominican Republic, Grenada, Guadeloupe, Puerto Rico, Trinidad and Tobago and Venezuela (Baker and Dale

1951, Dennis 1953, 1970, Garner 1956, Kreisel & Dring 1967, Kreisel 1971, Ponce de León 1971, Morales et al. 1974, Stevenson 1975, Suárez & Wright 1996, Minter et al. 2001, Calonge et al. 2005). As quoted by Ponce de León (1971), *M. mexicana* has been included into this species, therefore the collections referred to this species are cited here. Some of the specimens listed in Garner (1956) as *M. subincarnata* (G.W. Martin 7329 and 7923) were included into *M. fuliginea* by Ponce de León (1979). Since the latter did not mention the other collections of this species collected by G.W. Martin, these are referred to as *M. subincarnata* here (see below). However, none of these problematic collections could be analysed within the scope of this project.

Morganella cf. *subincarnata* (Peck) Kreisel & Dring
Syn.: *Lycoperdon subincarnatum* Peck

Specimina non visa: **Canal Zone**: Barro Colorado Island, G.W. Martin 3157, G.W. Martin and A.L. Welden 7692, 7788, 7790, 7873, 8490, 8521, 8624; E of Arraijin, G.W. Martin and A.L. Welden 8377a; Rio Sardinella, G.W. Martin and A.L. Welden 7542; **Panamá**: 10–12 km N of Pan American highway on El Llano-Carti-Road, 28.VI.1975, Dumont-PA 1293 (NY 888670), 2–3 km N of Pan American highway on El Llano-Carti-Road, 29.VI.1975, Dumont-PA 1421 (NY 888671).

Description based on other specimens and on literature (Kreisel & Dring 1967, Ponce de León 1971).

Macroscopical features: Fruitbodies globose to short pyriform, 2–4 cm diam. Exoperidium reddish brown, spiny, spines often connivent, breaking away at maturity, endoperidium then becoming visible, yellowish brown, relatively stout, pitted like a thimble or a golf-ball. Gleba olive when mature. Subgleba cellular, cream to brownish, occupying one quarter to one third of the fruitbody. White, branched rhizomorphs at base. Lignicolous.

Microscopical features: Exoperidium composed of chains of irregular rounded cells, without setae. Spores 4–5 µm diam., yellowish hyaline, verrucose, sometimes with short pedicel. Capillitium absent, paracapillitium abundant, hyaline, septate and branched, up to 6.5 µm diam., threads joined and interwoven by glebal membranes.

This species has a predominantly North American distribution and is also known from some localities in Southern Europe according to Kreisel & Dring (1967) and Ponce de León (1971). For Panama, the species is recorded in Garner (1956) as *L. subincarnatum*. Only the cited records, one collection cited in Garner (1956) from Costa Rica (G.W. Martin and A.L. Welden 8277), and a further record from Costa Rica (Calonge & Mata 2006) are known from Central America, collections from Florida (Ponce de León 1971) turned out to be *Morganella velutina* (Berk. :

Massee) Kreisel & Dring (Morales and Kimbrough 1981). Concerning other species of *Morganella* with pitted endoperidium, *Morganella costaricensis* M.I. Morales with smooth spores (Morales et al. 1974, Suárez & Wright 1996) and *Morganella compacta* (G. Cunn.) Kreisel & Dring with large peridial spines (Kreisel & Dring 1967) are recorded for Costa Rica (Morales et al. 1974, Calonge et al. 2005, Calonge & Mata 2006) and might be found in Panama. Ponce de León (1971) determined some of the collections by G.W. Martin as *M. fuliginea*. These specimens could not be examined, and are filed under *M. fuliginea*. The other collections are treated under *M. subincarnata*. All these records need to be revised to prove the existence of this species in Central America.

Morganella velutina (Berk. ex Massee) Kreisel & Dring

Specimina visa: **Chiriquí**: Cerro Respingo, approx. 6 km NW of Town of Cerro Punta, alt. approx. 2300 m, 02.VII.1975, Dumont-PA 1667 (NY 398739) as *M. fuliginea*; Parque Internacional de la Amistad, Sendero de la Cascada, alt. approx. 2350 m, 02.IX.2007, M. Piepenbring with licenciatura students 3970.

Macroscopical features: Fruitbodies (Fig. 1c) 1–2 (–3) cm diam., globose. Exoperidium brown to violet when fresh, brown when dry, densely velutinous, velvety to the touch at least when dry. Gleba light brown. Subgleba scarce or lacking, compact. Lignicolous, often on thin branches.

Microscopical features: Exoperidium (Fig. 2e) composed of thick walled clavate setae up to 130 µm in length, visible even under hand lens. Spores (Fig. 2f) globose, 3.5–4 µm diam., yellowish hyaline, echinulate, spines up to 1 µm long. Capillitium absent, paracapillitium abundant, hyaline, septate, branched, joined and interwoven by glebal membranes.

This species has a Central and South American distribution like *M. fuliginea*, but seems to be more rare. It is often found at higher altitudes. This is the first record for Panama. In the vicinity it is known from Costa Rica and Venezuela (Kreisel & Dring 1967, Dennis 1970, Ponce de León 1971, Morales et al. 1974, Suárez & Wright 1996, Calonge et al. 2005).

Vascellum pratense (Pers. : Pers.) Kreisel
Syn.: *Lycoperdon pratense* Pers. : Pers.
Lycoperdon depressum Bonord.
Lycoperdon curtisii Berk.
Vascellum curtisii (Berk.) Kreisel
Vascellum subpratense (Lloyd) Ponce de León

Specimina non visa: **Chiriquí**: Llanos de Volcán, alt. 1250–1300 m, G.W. Martin 2051, as *L. curtisii*; **Coclé**: Valle de Anton, alt. 600–700 m, G.W. Martin 2927, as *L. curtisii*.

Description based on other specimens and on literature (Jülich 1984, Kreisel 1993).
Macroscopical features: Fruitbodies globose to turbinate, 2.5–6 cm diam. Exoperidium consists of 1 mm long, often connivent spines on upper part and irregular granules below, whitish to cream, brown when old, endoperidium grey brown, fragile. Gleba olive brown. Subgleba bowl-like, dark brown when ripe, then darker as gleba, chambers up to 1.5 mm diam., a parchment-like diaphram separates gleba and subgleba. On meadows and open land.
Microscopical features: Spores globose, 3–4.5 µm diam., finely verrucose to almost smooth. Capillitium scarce, only close to the diaphragm, red brown, up to 5 µm diam., without pores, paracapillitium abundant, hyaline, 3–8 µm diam., scarcely branched, septate.
This species has been recorded repeatedly from Panama as *L. curtisii* (Garner 1956, Dennis 1970). The common cosmopolitan fungus has also been recorded from Costa Rica, Cuba, Puerto Rico, Trinidad and Venezuela (Dennis 1953, 1970, Garner 1956, Minter et al. 2001, Calonge et al. 2005). Small American specimens with little subgleba and persistent white spines have been recorded usually as *V. curtisii* (Ponce de León 1970, Kreisel 1993). However, there is little reason to do so, since collections of *V. pratense* show, depending on the conditions of growth, extreme variability including the range of features of *V. curtisii* (M. Gube, unpubl.). The genus *Vascellum* should be included into *Lycoperdon* based on morphological (Reid 1977, M. Gube, unpubl.) and molecular systematic data (Jeppson & Larsson 2008, M. Gube, unpubl.).

Sclerodermataceae

Calostoma cinnabarinum Desv.

Specimen visum: **Chiriquí**: Parque Internacional de La Amistad, Cerro Picacho, alt. approx. 2600 m, 25.IX.2007, M. Piepenbring, T. Hofmann, E. Moreno 4013.

Description of mature features taken from literature (Massee 1888, Liu 1984)
Macroscopical features: Single immature fruitbody in collection 2.8 cm in height, head globose, 1.3 cm diam., pseudostipe 20 x 10 mm. Mature fruitbodies up to 4 cm in height. Pseudostipe and outer peridium gelatinous, hyaline, inner peridium bright red; peristome with 4–7 lobes. Gleba white to pale ochraceous. Growing on soil, probably mycorrhizal (Watling 2006).
Microscopical features: Immature spores (Fig. 2g) hyaline to yellowish, broad oval, 9–12 x 6.7–8

µm, mature spores pale ochraceous, 12–20 x 6,3–10 µm moderately to strongly pitted depending on degree of maturity.

The species is pantropically distributed, it is known from Costa Rica and Guatemala (Sharp 1948, Calonge et al. 2005) as well. This is the first record of this species for Panama.

Scleroderma cepa Pers.

Specimen non visum: **Chiriquí**: Casita Alta, alt. 2000–2200 m, G.W. Martin and A.L. Welden 8207.

Description based on other specimens and on literature (Guzmán 1970, Jülich 1984).

Macroscopical features: Fruitbody globose, 3–4 cm diam. Peridium thick, stout, yellowish to brown, smooth or irregulary cracked. Gleba dark greyish black. On soil, mycorrhizal.

Microscopical features: Spores globose, 9–15 µm diam., spiny, spines 1–1.5 µm long, not connected at base. Peridium thick, peridial hyphae rarely with clamps.

This fungus is distributed predominantly in the Northern hemisphere, but apart from the Panamanian records (Garner 1956, Dennis 1970), collections in the region are also known from Costa Rica and Cuba (Guzmán 1970, Calonge et al. 2005). Since the cited specimen is immature (Garner 1956), the record is not absolutely certain.

Scleroderma sinnamariense Mont.

Syn.: *Scleroderma chrysastrum* G.W. Martin

Specimina non visa: **Canal Zone**: Barro Colorado Island, G.W. Martin and A.L. Welden 7367 (type of *S. chrysastrum)*, 7472, 7696 (paratypes of *S. chrysastrum*); Miller trail, Ovrebo 3602, in Herb. SCZ (Smithsonian Tropical Research Institute, Balboa, Panama).

Description based on other specimens and literature (Guzmán 1970, Guzmán & Ovrebo 2000).

Macroscopical features: Fruitbodies globose, substipitate, up to 4.5 (–9) cm diam.; Peridium bright yellow when young, outside turning yellowish brown to brownish black in maturity; base, peridial interior and rhizomorphs always yellowish, smooth to warty due to cracking. Gleba dark grey to almost black. On soil, mycorrhizal.

Microscopical features: Spores globose, 5–8.5 µm diam., spiny, spines 0.5–1.5 µm long, reticulate at base, sometimes inconspicious.

This fungus is known from Central and South America and Australasia. It has been recorded for Panama by Martin (1954, as *S. chrysastrum*), Garner (1956, as *S. chrysastrum*), Dennis (1970 as *S.*

chrysastrum), Guzmán (1970), Guzmán & Ovrebo (2000) and Guzmán et al. (2004a). In the region it is also recorded for Costa Rica (Guzmán & Ovrebo 2000).

Scleroderma stellatum Berk.
Syn.: *Scleroderma echinatum* (Petri) Guzmán
Caloderma petrianum E. Fisch.

Specimina non visa: **Canal Zone**: Barro Colorado Island, Dodge (in Herb BPI); Barro Colorado Island, Miller Trail, Ovrebo 3603, 3638, in Herb SCZ and XAL (Instituto de Ecologia, Xalapa, Mexico); Barro Colorado Island, Latham trail, Ovrebo 4049, in Herb SCZ; Cerro San Bastarda, G.W. Martin and A.L. Welden 7508; Ft. Sherman, G.W. Martin and A.L. Welden 8708; **Colón**: E of Colón, G.W. Martin 6009; **San Blas**: Port Obaldia, Vitter 5717, in Herb. BPI.

Description based on literature (Guzmán 1970, Guzmán et al. 2004).
Macroscopical features: Fruitbodies globose or subglobose, sessile or short stipitate, up to 4,5 cm diam. Peridium reddish brown to dark brown, yellow near the base, with pyramidal scales up to 1,5 mm high, smaller near the base. Gleba dark purple to brownish violet when ripe. On soil, mycorrhizal.
Microscopical features: Spores 4–6 µm diam., spiny, spines up to 1.5 µm long, partly (when ripe) connected at base. Peridium 500 µm thick, clamps rare.
Records for Panama are given by Garner (1956, as *C. petrianum*), Dennis (1970, as *C. petrianum* and *S. stellatum*) and Guzmán et al. (2004a). The pantropical fungus is in the region also known from Barbados, Cuba, Puerto Rico and Venezuela (Dennis 1970, Guzmán 1970, Kreisel 1971, Minter et al. 2001, Guzmán et al. 2004a). The synonymisation of *S. stellatum* and *S. echinatum* (Guzmán et al. 2004) is
followed here, but has been doubted by some (Demoulin pers comm.).

Veligaster nitidum (Berk.) Guzmán & Tapia
Syn.: *Scleroderma verrucosum* (Bull.) Pers. p.p.
Scleroderma tenerum Berk. & M.A. Curtis

Specimina visa: **Chiriquí**: Rio Serena, carretera a Piedra Candela, alt. approx. 1400 m, 08.X.2005, M. Piepenbring 3633; Cerro Punta, Finca Alto los Reyes, alt. approx. 2500 m, 25.VIII.2007, leg: R. Rios, A. Gracia, in Herb. M. Piepenbring 3951.
Specimina non visa: **Canal Zone**:Barro Colorado Island, G.W. Martin and A.L. Welden 8594;

Chiriquí: Casita Alta, alt. 2000–2200 m, G.W. Martin and A.L. Welden 8113, 8167; Trail from Casita Alta to Finca Lerida, altitude 1600–2000 m, G.W. Martin and A.L. Welden 8206, 8208; Upper valley of the Rio Chiriquí Viejo, altitude 1600–1800 m, G.W. Martin 2080, 2081, 2089, 2183, 2206, 2207, 2208, 2209, 2210, 2222, 2327, 2412, 2492, 2503, 2528, 2549, 2665, 2674, 2709.

Macroscopical features: Fruitbodies 4–8 cm in height (Fig. 1d), capitate, with pseudostipe 2.5–6 x 0.5–1.5 cm and globose "head" with 1.5–3.5 cm diam. Peridium verrucose, verrucae dark brown, irregular, 0,5–1 mm diam. on top, getting gradually smaller below, peridium in between light brown to beige. Gleba grey to dark grey. On soil, mycorrhizal.

Microscopical features: Spores (Fig. 2h) globose, 6.5–9.5 µm diam., densely spiny, spines up to 2.5 µm long, not connected at base. Peridium thin, hyphae without clamps.

This common pantropical fungus is recorded for Panama by Garner (1956, as *S. verrucosum*), Dennis (1970, as *S. tenerum* and *S. verrucosum*) Guzmán (1970, as *S. verrucosum*) and Guzmán & Ovrebo (2000). In the region it is also known from Costa Rica, Cuba, Jamaica, Venezuela and the Virgin Islands (Dennis 1953, Dennis 1970, Kreisel 1971, Calonge et al. 2005, Guzmán & Ovrebo 2000, Minter et al. 2001, Guzmán et al. 2004). The species causes a lot of taxonomic uncertainty, since it has been listed as *S. verrucosum* (Garner 1956, Dennis 1970, Guzmán 1970, Calonge et al. 2005), as *S. tenerum* (Dennis 1953, Dennis 1970, Kreisel 1971) and as *V. nitidum* (Guzmán & Tapia 1995, Guzmán & Ovrebo 2000, Guzmán et al. 2004a). According to Guzmán & Tapia (1995), *V. nitidum* differs from *Scleroderma verrucosum* in having a long pseudostipe, subgelatinous patches at the upper pseudostipe, and smaller spores. However, the revised collections and some descriptions in literature (e.g. Guzmán & Ovrebo 2000), show not all of these features. Several features can be found in other species clearly situated within *Scleroderma* (Demoulin & Dring 1975). Judging from molecular phylogenetics, at least *Veligaster columnaris* (Berk. & Broome) Guzmán is to be transferred into *Scleroderma* (Binder and Bresinsky 2002). Yet, a recombination would require thorough analysis of the complete material, and so could not be included in this study. *Scleroderma areolatum* Ehrenb. (Syn.: *Scleroderma lycoperdoides* Schwein.) is rather similar, but differs by considerably larger spores (12–20 µm diam.), a shorter stipe (up to 2 cm) and regular, dark brown peridial verrucae (Guzmán 1970, Jülich 1984).

Nidulariaceae

Crucibulum laeve (Huds.) Kambly

Specimina visa: **Chiriquí**: Parque Internacional de La Amistad, Cerro Picacho, alt. approx. 2350 m, 23.II.2004, M. Piepenbring, R. Rincon et al. 3385; Parque Internacional de la Amistad, sendero de La Cascada, alt. approx. 2300–2500 m , 04.III.2003, M. Piepenbring, R. Kirschner et al. 3205; Parque Internacional de la Amistad, Sendero de la Cascada, Mirador, alt. approx. 2450 m, 02.IX.2007, M. Piepenbring with licenciatura students 3966.

Macroscopical features: Fruitbodies (Fig. 1e) inverse conical to urn shaped, 4–13 x 3–7 mm, reddish brown, hairy, not plicate. Peridioles whitish brown, with funiculus. On soil or rotten woody debris.

Microscopical features: Spores (Fig. 2i) elliptical, 6.5–12.3 x 4–5.3 µm, smooth, hyaline, thickwalled. Peridium one-layered, hairs spiny, reddish brown.

This is the first record of this cosmopolitan fungus in Panama. It has also been recorded in Costa Rica, the Dominican Republic and Venezuela (Dennis 1970, Minter et al. 2001, Calonge & Mata 2006, Calonge et al. 2005).

Cyathus limbatus Tul.

Specimen visum: **Chiriquí**: Parque Nacional Volcán Barú, Sendero de los Quetzales, alt. approx. 1920–2450 m, 21.VIII.2003, M. Piepenbring, H. Lezcano, D. Rodríguez 3325.

Macroscopical features: Fruitbodies inverse conical, 6–10 x 3–8 mm, dark brown, hairy externally, externally and internally plicate, ridges 0.75–1 mm apart. Peridioles silvery blackish, with funiculus. On soil.

Microscopical features: Spores (Fig. 2j) elliptical, (15–)20–25 x 9.2–15, hyaline, thickwalled. Peridium three-layered.

A pantropical fungus, recorded also from Costa Rica, Cuba, Trinidad and Tobago and Venezuela (Baker and Dale 1951, Dennis 1970, Reid 1977, Minter et al. 2001, Calonge et al. 2005). This is the first record for Panama.

Cyathus poeppigii Tul. & C. Tul.

Specimen visum: **Chiriquí**: Distr. Dolega, Corr. Dolega, Potrerillos Arriba, Brazo de Cochea, Camino a la Finca los Limones de R. Espinosa, alt. approx. 1100 m, 01.XI.2007, M. Piepenbring and R. Espinosa 4088.

Specimina non visa: **Canal Zone**: Barro Colorado Island, G.W. Martin and A.L. Welden 7158, 7262, 7296, 7430, 7441, 7484, 7580, 7622, 7856; Summit, G.W. Martin 2871, 2875; **Chiriquí**:

valley of the upper Rio Chiriquí Viejo, alt. approx. 1600–1800 m, G.W. Martin 2114, 2500; **Coclé**: Valle Chiquita, 7 km S of El Valle de Anton, alt. approx. 500–600 m, G.W. Martin 3001.

Spore size from literature (Brodie 1975).

Macroscopical features: Fruitbodies (Fig. 1f) 6–8 x 4–6 mm, dark reddish brown, black in age, inverse conical, deeply plicate outside and inside, ridges 0.5 mm apart. Peridioles black, shiny, with funiculus. On soil, plant debris, rotten wood.

Microscopical features: Spores elliptical, 30–42 x 20–28 µm, hyaline, thickwalled. Peridium formed by three layers.

Records of this fungus from Panama can be found in Garner (1956) and Dennis (1970). This common pantropical species has also been recorded in Colombia, Cuba, Puerto Rico, Trinidad and Tobago and Venezuela (Baker and Dale 1951, Dennis 1970, Brodie 1975, Stevenson 1975). Specimen 4088 had no spores in its peridioles; but as the other features fit it is placed here. However, it cannot be excluded that it is an abnormal collection of *C. limbatus*.

Cyathus stercoreus (Schwein.) De Toni

Specimen non visum: **Canal Zone**: Summit, G.W. Martin and A.L. Welden 8257.

Description from other specimens and literature (Brodie 1975).

Macroscopical features: Fruitbodies 5–15 x 4–8 mm, funnel shaped, not plicate, outside yellowish to blackish brown, tomentose when young, inside blue-grey; peridioles black, lenticulate, with funiculus; coprophilous or on manured soil.

Microscopical features: Spores subglobose to ovoid, 25–40 x 20–25 µm, hyaline, thickwalled; Peridium tree-layered.

The fungus is worldwide distributed. For Panama it has been recorded by Garner (1956), Dennis (1970) and Piepenbring (2006). In the region it is also known from Colombia, Costa Rica, Cuba, the Dominican Republic, Puerto Rico and Venezuela (Garner 1956, Dennis 1970, Stevenson 1975, Arnold 1985, Minter et al. 2001, Calonge et al. 2005).

Mycocalia reticulata (Petch) J.T. Palmer
Syn.: *Nidularia reticulata* Petch

Specimen non visum: **Canal Zone**: Balboa, G.W. Martin 3985, as *N. reticulata*.

Description from literature (Martin 1939a, Cejp & Palmer 1963).

Macroscopical features: Fruitbodies globose, up to 2 mm diam., first white, then brownish; Peridium thin, gelatinous, withering quickly; Peridioles solitary to several, lens-shaped, reticulate, yellowish brown, without funiculus; on plant debris.

Microscopical features: Peridiole cortex hyphae branched, tapering, main hyphae up to 20 µm in diam., spores hyaline, thickwalled, cylindrical, 8.5–9.5 x 4.5–5.5 µm; peridioles 450–550 x 200 µm; peridial wall consists of branched, apiculate, thickwalled hyphae, main axis up to 20 µm diam.

This cosmopolitan tropical species is in Central America only known from Panama so far. It has been recorded by Martin (1939a, as *N. reticulata*), Cejp & Palmer (1963), Dennis (1970, as *N. reticulata*), and Brodie (1975).

Sphaerobolaceae

Sphaerobolus stellatus Tode

Specimen visum: **Chiriquí**: Dolega, Los Algarrobos, below Casa de la Alemana, alt. approx. 145m, 14.VIII.2005, M. Piepenbring 3488.

Macroscopical features: Fruitbodies (Fig. 3a) globose, up to 2.5 mm diam. Peridium with whitish exterior, splitting open stellately with 8–10 teeth, exposing the yellow interior layer and the greenish-brown peridiole, inner peridial layers evert to eject the peridiole. On dung (usually cattle) or rarely plant debris.

Microscopical features: Spores elliptical, smooth, 8.7–9 x 4.7–5.5 µm.

A cosmopolitan species, apparently more common in temperate regions (Geml et al. 2005). Known also from the Dominican Republic, Puerto Rico, Trinidad and Tobago and Venezuela (Baker and Dale 1951, Dennis 1953, 1970, Stevenson 1975). This is the first record of this species from Panama.

Phallaceae

Mutinus argentinus Speg.

Specimen visum: **Chiriquí**: Dolega, Los Algarrobos, way to Las Gonzales, alt. approx. 140 m, 05.X.2005, M. Piepenbring and students of the UNACHI 3615.

Macroscopical features: Fruitbodies up to 9 x 0.8–0.9 cm, growing out of yellowish white egg measuring 15–20 x 13–15 mm which forms a gelatinous volva after stretching of the cellular receptaculum. Fertile portion of receptaculum up to one quarter of total length, bright red, covered with olivaceous, pungent spore mass; infertile part pale pink, lighter in the lower part. With white rhizomorphs. On soil, often under species of *Bambusoideae*.

Microscopical features: Spores (Fig. 2k) cylindrical, greenish hyaline, 3.5–5 x 0.8–1.5 µm, smooth.

A pantropical fungus frequently collected in Central America, in Costa Rica, Cuba, the Dominican Republic, Puerto Rico, Trinidad and Tobago (Baker and Dale 1951, Dennis 1953, 1970, Kreisel 1971, Reid 1977, Sáenz & Nassar 1980, Lodge 1984, Arnold 1985, Calonge et al. 2005). This is a new record for Panama.

Mutinus bambusinus (Zoll.) E. Fisch. might eventually be regarded as synonym of *M. argentinus*, and most of the records cited above are referring to *M. bambusinus*. The distinguishing features of *M. bambusinus* are a longer fertile portion, sterile tip of the fruitbody, and receptacular chambers opening to the exterior (Dring & Rose 1977, Reid 1977).

Phallus indusiatus Vent. : Pers.

Syn.: *Dictyophora indusiata* (Vent. : Pers.) Desv.

Specimen visum: **Chiriquí**: Dolega, Las Algarrobos, way to Las Gonzales, alt. approx. 140 m, 13.IX.2005, M. Piepenbring and participants of Mycological Workshop 3543.

Macroscopical features: Fruitbodies up to 25 x 2.5 cm, growing out of white egg forming a gelatinous volva after stretching of the cellular receptaculum. Fertile portion of receptaculum up to 3.5–5 cm, covered with blackish green, pungent smelling spore mass; absolute top sterile, basal receptaculum white to pinkish, chambered, hollow, well developed indusium hanging from fertile part, sometimes to the ground. With white rhizomorphs. On soil.

Microscopical features: Spores (Fig. 2l) greenish hyaline, elliptical, 2.5–3 x 1–2 µm, smooth.

The species has a worldwide distribution in tropical to warm temperate regions. Panamanian records can be found in Standley (1933, as *Dictyophora duplicata* (Bosc) E.Fisch.), Weston (1933, as *D. duplicata*), Dennis (1970, as *D. indusiata*) and Piepenbring (2006, as *Phallus duplicatus* Bosc). It is known also from Colombia, Costa Rica, Cuba, the Dominican Republic, Puerto Rico, Trinidad and Tobago and Venezuela (Baker and Dale 1951, Dennis 1953, 1970, Kreisel 1971, Stevenson 1975, Sáenz & Nassar 1980, Lodge 1984, Minter et al. 2001, Calonge et al. 2005, Vasco-Palacios et al. 2005). The temperate American species *P. duplicatus* has a much smaller indusium. The collections of Weston and Standley refer doubtless to the tropical *P. indusiatus*.

Staheliomyces cinctus E. Fisch.

Specimen non visum: **Canal Zone**: Barro Colorado Island, Fairchild trail, alt. approx. 26–145 m, 11.VIII.1997, PMA 1860.

Description based on literature (Sáenz & Nassar 1982, Leite et al. 2007).
Macroscopical features: receptacle up to 20 cm in height, growing from “egg”, fertile portion in upper half, constricted, covered with yellowish brown, smelling, mucilaginose spore mass, sterile part below and above fertile portion white, chambered.
Microscopical features: spores long ellipsoidal, 2.5–3 × 1.2 × 1.5 µm, smooth, hyaline
This species is recorded for Panama by Stevens (1930), Dennis (1970), Piepenbring (2006) and Leite et al. (2007). The fungus is restricted to tropical Central and South America, in the region it is also known from Costa Rica (Dennis 1970, Sáenz & Nassar 1980, Calonge et al. 2005, Leite et al. 2007).

Geastraceae

Geastrum javanicum (Lév.) Ponce de León
Syn.: *Geastrum velutinum* Morg.

Specimina non visa: **Canal Zone**: Barro Colorado Island, G.W. Martin and A.L. Welden 7156, 7643, 7651, all as *G. velutinum.*

Description from literature (Ponce de León 1968, Herrera et al. 2005).
Macroscopical features: Fruitbodies developing from a mycelial subiculum, 2–5 cm diam. when open. Exoperidium light brown outwards, dark brown inwards, with two usually separating fibrous layers, splitting in 6–8 rays, outer layer often getting attached firmly to the substrate, inner layer always free; endoperidium sessile, dark brown; peristome fimbriate, concolorous or brighter. Gleba dark brown. On soil or wood.
Microscopical features: Spores globose, brown, 2.5–4 µm, spiny. Capillitium 4–5 µm diam., branched at the ends.
Panamanian records of the fungus are given by Garner (1956) and Dennis (1953, 1970), all as *G. velutinum*. It is a tropical species with worldwide distribution, known from Costa Rica, Cuba, the Dominican Republic, Guadeloupe, Puerto Rico, Trinidad and Tobago, and Venezuela (Dennis 1953,

1970, Stevenson 1975, Reid 1977, Minter et al. 2001, Calonge et al. 2005). It may easily be taken for *G. schweinitzii*, which has an unbranched capillitium and non-separating layers of the endoperidium, and *G. saccatum*, which has no subiculum and non-separating endoperidial layers (Ponce de León 1968, Reid 1977, Calonge et al. 2005, Herrera et al. 2005). The identity of *G. velutinum* and *G. javanicum* is doubtful (Demoulin pers. comm.), but an emendation of this group would be needed to reject it.

Geastrum cf. *rufescens* Pers.
Syn.: *Geastrum schaefferi* Vittad.
Geastrum vulgatum Vittad.

Specimen non visum: **Canal Zone**: E of Arraiján, G.W. Martin and A.L. Welden 8381.

Description from other specimens and literature (Dörfelt 1985, Sunhede 1989).
Macroscopical features: Fruitbodies (2–) 5–16 cm diam. when open. Exoperidium outwards whitisch brown with rose tints, inwards flesh brown, reddening when bruised, splitting in 4–10 flat rays, endoperidium 1–4 cm diam., grey brown, sessile or subsessile; peristome fimbriate, concolorous. Gleba dark brown. On soil.
Microscopical features: Spores globose, 4.5–6 µm diam., verrucose, brown. Capillitium brown, straight, up to 9 µm diam.
The species is common in temperate regions, it is known from Panama (Garner 1956, Dennis 1970), and has also been recorded in Costa Rica (Calonge et al. 2005). Garner (1956) and Dennis (1970) cite the record as *G. rufescens*, but assume conspecifity with *G. fimbriatum* Fr. Both species are known from the region, *G. fimbriatum* has been recorded from Cuba (Ponce de León 1946). More recent studies (Pouzar 1971, Dörfelt & Müller-Uri 1984) clarify the matter, both species are to be considered independent. Here the name *G. rufescens* is used for the collection, since the description in Dennis (1970) points towards this species in the present opinion. However, the specimen should be revised to clarify the identification.

Geastrum saccatum Fr.

Specimen visum: **Chiriquí**: Volcán, Humedales Lagunas de Volcán, 20.IX.2005, M. Piepenbring and participants of Mycogical Workshop 3574.
Specimina non visa: **Canal Zone**: Barro Colorado Island, G.W. Martin and A.L. Welden 7096, 7172, 7705, 7884.

Macroscopical features: Fruitbodies 2–5 cm diam when open. Exoperidium light brown inwards and outwards, splitting with 5–8 recurved rays, endoperidium sessile, grayish brown, 0.5–2.5 cm diam.; peristome (Fig. 3b) fimbriate, distinct bright "court". Gleba dark brown. On soil.

Microscopical features: Spores globose, 3.2–4 µm, spinulose, spines up to 0.5 µm long. Capillitium straight, brown, up to 6 µm diam., unbranched, narrow lumen, incrusted.

This subcosmopolitan species is reported for Panama by Garner (1956). It is quite common in the region it has been recorded for Colombia, Costa Rica, Cuba, the Dominican Republic, Jamaica, Puerto Rico, Trinidad and Tobago (Ponce de León 1946, Dennis 1953, 1970, Stevenson 1975, Reid 1977, Lodge 1984, Guzmán et al. 2004b, Calonge et al. 2005, Vasco-Palacios 2005). Minter et al. (2001) synonymize *G. fimbriatum* with *G. saccatum*, therefore the records there cannot be taken for certain.

Geastrum schweinitzii (Berk. & Curt.) Zeller

Syn.: *Geaster mirabile* Mont.

Specimina non visa: **Canal Zone**: Balboa, G.W. Martin 2891; Barro Colorado Island, G.W. Martin and A.L. Welden 7184.

Description from other specimens and literature (Ponce de León 1968).

Macroscopical features: Fruitbodies developing from a mycelial subiculum, 2–5 cm diam. when open. Exoperidium brown outwards, tomentose, lighter brown inwards, splitting in 6–7 rays, endoperidium light grey-brown, 1–1.5 cm diam. peristome fimbriate. Gleba dark brown. On wood and woody debris.

Microscopical features: spores brown, globose, 3–3.5 µm diam., echinulate, spines up to 0.5 µm high. Capillitium brown, up to 6 µm diam., unbranched.

This is a relatively common pantropical species, which has been recorded for Panama by Standley (1933, as *G. mirabile*), Weston (1933, as *G. mirabile*), Garner (1956), Ponce de León (1968, incl var. *stipitatum* (Solms) P. Ponce) and Dennis (1970). It is also known from Costa Rica, Cuba, the Dominican Republic, Jamaica, Puerto Rico, Trinidad and Venezuela (Ponce de León 1946, 1968, Dennis 1953, 1970, Stevenson 1975, Lodge 1984, Minter et al. 2001, Calonge et al. 2005, Calonge & Mata 2006).

Geastrum triplex Jungh.

Syn. *Geastrum indicum* (Klotzsch) Rauschert

Specimina non visa: **Canal Zone**: Barro Colorado Island, G.W. Martin and A.L. Welden 7471, 8686.

Description from other specimens and literature (Dörfelt 1985, Sunhede 1989).
Macroscopical features: Fruitbodies 5–20 cm diam. when open. Exoperidium with irregular light and dark brown patches on the outer surface, radially cracking, lighter brown inwards, but getting much darker when withering, splitting into 4–8 recurved rays, the inner portion of the pseudoparenchymatic layer often separates from the fibrillose layer, often forming a collar around the endoperidium; endoperidium 1.5–4 cm diam., light brown; peristome fimbriate, with bright or dark "court". Gleba dark brown. Growing on soil.
Microscopical features: Spores globose, brown, 4.5–5.5 µm diam., echinulate, spines up to 1 µm long. Capillitium brown, up to 7 µm diam.
The fungus has been recorded for Panama by Garner (1956) and Piepenbring (2006). This cosmopolitan species has also been recorded from Costa Rica, Cuba, the Dominican Republic, Puerto Rico, Trinidad and Tobago, and Venezuela (Dennis 1970, Reid 1977, Minter et al. 2001, Calonge et al. 2005). Specimens without collar may easily be taken for *G. saccatum*, which is usually much smaller and also has smaller spores.

Radiigera cf. *taylorii* (Lloyd) Zeller

Specimen visum: **Chiriquí**: Cerro Punta, Finca Alto los Reyes, alt. approx. 2500 m, 25.VIII.2007, R. Rios and A. Gracia in Herb. M. Piepenbring 3955.

Features of ripe fruitbody were taken from literature (Domínguez de Toledo and Castellano 1996).
Macroscopical features: Fruitbodies (Fig. 3c) (1.5–) 3–4 cm diam., globose to subglobose, yellowish brown, Peridium 3–4 layered, outwards smooth to velutinous. Gleba white when young, darkening to grayish brown while ripening, distinct columella. On soil.
Microscopical features: immature specimen M. Piepenbring 3955: spores globose, 2–3 µm diam, finely verrucose, capillitium hyaline, 6–8 mm diam, lumen narrow; ripe spores globose, finely verrucose, brown; ripe Capillitium pale brown, 4 µm diam., not septate.
This species is known from Mexico and the USA (Dominquez de Toledo and Castellano 1996), this is the first record for Panama. Since the specimen is immature, the identification is not absolutely certain. Judging from spore size and the smooth peridium without debris, *R. taylorii* seems the only possibility.

Radiigera sp.

Specimen visum: **Canal Zone**: Jardin Botanico Summit, alt. approx. 70 m, 13.II.2003, M. Piepenbring and R. Kirschner 3136.

Macroscopical features: Fruitbodies (Figs. 3d, 3e) globose, 15–18 mm diam. Peridium white when fresh, brownish when dry, outwards slightly rough,.with beak-like structure on top (3.5 x 2 mm); thick peridium composed of four layers, inner layer easily separating. Gleba dark brown, no columella. Lignicolous (found on frond axils of *Elaeis oleifera*).

Microscopical features: Spores globose (Figs. 2m, 2n), 3.7–4.2 µm, verrucose, brown. Capillitium (Fig. 2n) hyphae up to 7 µm diam, brown, thickwalled, unbranched, growing radially outwards.

A probably new species with close relationships to *Radiigera* and *Geastrum*. It might even be an unopened *Geastrum*, but the growth on woody substrate excludes most species, the smoothness of the outer peridium as well. Also, no peristome was distinguishable despite the beak-like structure atop. The heterogeneous genus *Radiigera* should be revised molecularly and anatomically. It probably will have to be included in *Geastrum*.

Incertae sedis

Lycogalopsis solmsii E. Fisch.

Specimina visa: **Chiriquí**: Corr. Dolega, Los Algarrobos, cerca de la Casa de la Alemana, alt. approx. 150 m, 22.VII.2007, M. Piepenbring 3934; **Canal Zone**: Balboa, Missouri Botanical Garden Tropical Station, 20.VII.1935, G.W. Martin 2896 (BPI 736359); Barro Colorado Island, 24.VIII.1952, G.W. Martin and A.L. Welden 8694 (BPI 736358); Ft. Sherman area, 22.VII.1945, G.W. Martin 6104 (BPI 736360).

Specimina non visa: **Canal Zone**: Barro Colorado Island, G.W. Martin and A.L. Welden 7053, 7083, 7136, 7356, 7398, 7459; Ft. Sherman area, G.W. Martin 6026, 6095, 6104.

Macroscopical features: Fruitbodies (Fig. 3f) 3–15 mm diam., on a more or less developed white mycelial subiculum. Peridium whitish, fragile, no defined opening. Gleba white to yellowish white. lignicolous in moist forests.

Microscopical features: Spores (Fig. 2o) irregularly globose, 1.8–3 µm diam., verrucose, yellowish hyaline. Basidia more or less persistent, spindle- to club-shaped, bearing up to 6 spores each.

Capillitial threads (Fig. 2o) hyaline, in bundles, septate, with clamps, unbranched, lumen lacking or scarcely visible, 1–1.5 µm diam., often incrusted with debris.

Records for Panama are included in Martin (1939b), Dennis (1953, 1970), Stevenson (1975), Reid (1977) and Piepenbring (2006). This pantropical species is relatively common in the Central American region, it is known from Colombia, Costa Rica, Cuba, Honduras, Martinique, Puerto Rico, Trinidad and Tobago and Venezuela (Martin 1939b, Dennis 1953, 1970, Kreisel 1971, Stevenson 1975, Reid 1977, Lodge 1984, Guzmán et al. 2004b, Calonge et al. 2005, specimens BPI 736356, 736357). Its systematic position is unknown. Because of its glebal anatomy, however, it is probably to be placed next to the Geastraceae.

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Literature cited

ARNOLD, G.R.W. (1985): Beiträge zur Kenntnis der Pilze Kubas II. - Boletus **9** (2): 49-56.

BAKER, R.E.D. & W.T. DALE (1951): Fungi of Trinidad & Tobago. - Mycol. Papers **33**: 1-123.

BENJAMIN, C.R. & A. SLOT (1969): Fungi of Haiti. - Sydowia **23**: 125-163.

BINDER, M. & A. BRESINSKY (2002): Derivation of a polymorphic lineage of Gasteromycetes from boletoid ancestors. - Mycologia **94** (1): 85-98.

BRODIE, H.J. (1967): New records of Nidulariaceae from the West Indies. - Trans. Brit. Mycol. Soc. **50** (3): 473-478.

BRODIE, H.J. (1975): The bird's nest fungi. - University of Toronto Press, Toronto, Buffalo.

CALONGE, F.D. & M. MATA (2005): *Crucibulum leave* var. *magnum* var. nov. y *Arcangeliella scissilis*, encontrados en Costa Rica. - Bol. Soc. Micol. Madrid **29**: 43-48.

CALONGE, F.D., M. MATA & J. CARRANZA (2005): Contribución al catálogo de los Gasteromycetos (Basidiomycotina, Fungi) de Costa Rica. - An. Jard. Bot. Madrid **62** (1). 23–45.

CALONGE, F.D. & M. MATA (2006): Adiciones y correciones al catálogo de gasteromycetes de Costa Rica. - Bol. Soc. Micol. Madrid **30**: 111-119.

CEJP, K. & J.T. PALMER (1963): Rody *Nidularia* Fr. a *Mycocalia* J. T. Palmer v Československu a *Mycocalia sphagneti* J. T. Palmer sp. Nov. Z Anglie. - Česka Mycologie **17** (3): 113-126.

DEMOULIN, V. (1972): Espèces nouvelles ou méconnues du genre *Lycoperdon* (Gastéromycètes). - Lejeunea nouv. sér. **62**: 1-28.

DEMOULIN, V. & D.M. DRING (1975): Gasteromycetes of Kivu (Zaïre), Rwanda and Burundi. - Bull. Jard. Bot. Nat. Belg. **45**: 339-372.

DENNIS, R.W.G. (1953): Some West Indian Gasteromycetes. - Kew Bull. **8**: 307-328.

DENNIS, R.W.G. (1970): Fungus flora of Venezuela and adjacent countries. - Kew Bull. Add. Ser. **III**: 1-531.

DOMÍNGUEZ DE TOLEDO, L. S. & M. A. CASTELLANO (1996): A revision of the genera *Radiigera* and *Pyrenogaster*. Mycologia **88** (5): 863-884.

DÖRFELT, H. & C. MÜLLER-URI (1984): Studien zur Systematik der Geastrales. - Feddes Rep. **95** (9-10): 701-711.

DÖRFELT, H. (1985): Die Erdsterne. - Neue Brehm Bücherei **573**: 1-108.

DRING, D.M. & A.C. ROSE (1977): Additions to West African Phalloid Fungi. - Kew Bull. **31** (3): 741-751.

GARNER, J.H.B. (1956): Gasteromycetes from Panama and Costa Rica. - Mycologia **48** (5): 757-764.

GEML, J., D.D. DAVIS & D.M. GEISER (2005): Systematics of the genus *Sphaerobolus* based on molecular and morphological data, with the description of *Sphaerobolus ingoldii* sp. nov. - Mycologia **97** (3): 680-694.

GUZMÁN, G. (1969): *Veligaster*, a new genus of the Sclerodermataceae. - Mycologia **61**: 1117-1123.

GUZMÁN, G. (1970): Monografia del género *Scleroderma* Pers. emend. Fr. (Fungi, Basidiomycetes). - Darwiniana **16**: 233-407.

GUZMÁN, G. & F. TAPIA (1995): New species, new combinations and new records of *Veligaster*, (Sclerodermataceae). - Doc. Mycol. **25**: 185-195.

GUZMÁN, G. & C.L. OVREBO (2000): New observations on sclerodermataceous fungi. - Mycologia **92** (1): 174-179.

GUZMÁN, G., O.K. MILLER, D.J. LODGE & T.J. BARONI (2004a): *Scleroderma stellatum* versus *Scleroderma bermudense*: the status of *Scleroderma echinatum* and the first record of *Veligaster nitidum* from the Virgin Islands. - Mycologia **96** (6): 1370-1379.

GUZMÁN, G., M.G. TORRES, F. RAMÍREZ-GUILLÉN, A. RÍOS-HURTADO (2004b): Introducción al conocimiento de los macromicetos de Chocó, Colombia. - Rev. Mex. Mic. **19**: 33-43.

HERRERA, T., E. PÉREZ-SILVA, M. ESQUEDA & V.H. VALENZUELA (2005): Algunos Gasteromicetos de Calakmul, Campeche, México. - Rev. Mex. Mic. **21**: 23-27.

JÜLICH, W. (1984): Die Nichtblätterpilze, Gallertpilze und Bauchpilze. Aphyllophorales, Heterobasidiomycetes, Gastromycetes. Kleine Kryptogamenflora Bd. IIb/1 Basidiomyceten 1. Teil. - Gustav Fischer Verlag, Jena.

KREISEL, H. (1967): Taxonomisch-pflanzengeographische Monographie der Gattung *Bovista*. - Beih. Nova Hedwigia **25**: 1-244.

KREISEL, H. (1971); Clave para la identificación de los macromicetos de Cuba. - Ciencias Serie 4, Ciencias Biológicas, Universidad de la Habana **16**: 1-101.

KREISEL, H. (1989): Studies in the *Calvatia* complex (Basidiomycetes). - Nova Hedwigia **48** (3-4): 281-291.

KREISEL, H. (1992): An emendation and preliminary survey of the genus *Calvatia* (Gasteromycetidae). - Persoonia Suppl. **14** (4): 431-439.

KREISEL, H. (1993): A key to *Vascellum* (Gasteromycetidae) with some floristic notes. - Blyttia **3-4**: 125-129.

KREISEL, H. (1994): Studies in the *Calvatia* complex (Basidiomycetes) 2. - Feddes Rep. **105** (5-6): 369-376.

KREISEL, H. (2001): Checklist of the gasteral and secotioid Basidiomycetes of Europe, Africa, and the Middle East. - Österr. Z. Pilzk. **10**: 213-313.

KREISEL, H. & D.M. DRING (1967): An emendation of the genus *Morganella* Zeller (*Lycoperdaceae*). - Feddes Rep. **74** (1-2): 109-122.

LARSSON, E. & M. JEPPSON (2008): Phylogenetic relationships among species and genera of Lycoperdaceae based on ITS and LSU sequence data from North European taxa. - Mycol. Res. **112** (1): 4-22.

LEITE, A.G., B.D.B. SILVA, R.S. ARAÚJO & I.G. BASEIA (2007): Espécies raras de Phallales (Agaricomycetidae, Basidiomycetes) no Nordeste do Brasil. - Acta Bot. Bras. **21** (1): 119-124.

LIU, B. (1984): The Gasteromycetes of China. - Beih. Nova Hedwigia **76**: 1-235.

LODGE, D.J. (1984): Microorganisms. - In: REAGAN, D. P. & R.B. WAIDE (eds.): The Food Web of a Tropical Rain Forest: 53-108. - University of Chicago Press, Chicago.

MARTIN, G.W. (1939a): New or noteworthy fungi from Panama and Colombia. IV. - Mycologia **31** (5): 507-518.

MARTIN, G.W. (1939b): The genus «*Lycogalopsis*». - Lilloa **4**: 69-73.

MASSEE, G. (1888): A monograph of the genus *Calostoma*, Desv. (*Mitremyces*, Nees). - Ann. Bot. **2** (5): 25-45.

MINTER, D.W., M. RODRÍGUEZ HERNÁNDEZ & J. MENA PORTALES (2001): Fungi of the Caribbean. An annotated checklist. - PDMS Publishing, Isleworth.

MORALES, M.I., M. NASSAR & J.A. SAÉNZ (1974): Lycoperdaceae of Costa Rica. I. The genus *Morganella*. - Rev. Biol. Trop. **21** (2): 221-227.

MORALES, M.I. & J.W. KIMBROUGH (1981): The Lycoperdaceae of North Central Florida. II. The genera *Bovistella*, *Langermannia* and *Morganella*. - Rev. Biol. Trop. **29** (1): 95-104.

NIEVES-RIVERA, A.M. & D.J. LODGE (1998) Contributions to the study of Gasteromycetes of Puerto Rico. - McIlvainea **13** (2): 50-58.

PIEPENBRING, M. (2006): Checklist of fungi in Panama. - Puente Biológico **1**: 1-190.

PONCE DE LEÓN, P. (1946): Contribución al estudio de los Gasteromicetos Cubanos I. El género *Geastrum* en Cuba. - Rev. Soc. Cubana Bot. **1946**: 63-70.

PONCE DE LEÓN, P. (1968): A revision of the family Geastraceae. - Fieldiana Bot. **31** (11): 303-349.

PONCE DE LEÓN, P. (1970): Revision of the Genus *Vascellum* (Lycoperdaceae). - Fieldiana Bot. **32** (9): 109-125.

PONCE DE LEÓN, P. (1971): Revision of the Genus *Morganella* (Lycoperdaceae). - Fieldiana Bot. **34** (3): 27-44.

POUZAR, Z. (1971): *Geastrum sessile* (Sow.) Pouz., the Correct Name for *Geastrum fimbriatum* Fr. (*Gasteromycetes*). - Folia Geobot. Phytotax. **6**: 93-97.

REID, D.A. (1977): Some Gasteromycetes from Trinidad and Tobago. - Kew Bull. **31** (3): 657-690.

RODRÍGUEZ GALLART, C.A. (1997): Estudios en los macromicetos de la República Dominicana III. - Moscosoa **9**: 145-153.

SÁENZ, J.A. & M. NASSAR (1982): Hongos de Costa Rica: Familias Phallaceae y Clathraceae. - Rev. Biol. Trop. **30** (1): 41-52.

SHARP, A.J. (1948): Some fungi common to the highlands of Mexico and Guatemala and eastern United States. - Mycologia **40** (4): 499-502.

STANDLEY, P.C. (1927): The flora of Barro Colorado Island, Panama. - Smithsonian Misc. Coll. **78** (8): 1-32.

STEVENS, F.L. (1930): Parasitic fungi from Panama. - Ann. Mycol. **28**: 281-286.

STEVENSON, J.A. (1975): Fungi of Puerto Rico and the American Virgin Islands. - Contr. Reed. Herb. **23**: 1-743.

SUÁREZ, V.L. & J.E. WRIGHT (1996): South American Gasteromycetes V: The genus *Morganella*. - Mycologia **88** (4): 655-661.

SUNHEDE, S. (1989): Geastraceae (Basidiomycotina). Morphology, ecology, and systematics with special emphasis on the north european species. - Synopsis Fungorum **1**: 1-534.

VASCO-PALACIOS, A.M., A.E. FRANCO-MOLANO, C.A. LÓPEZ-QUINTERO & T. BOEKHOUT (2005): Macromicetes (ascomycota, basidiomycota) de la región del medio Caquetá, departamentos de Caquetá y Amazonas, Colombia. - Biota Colomb. **6** (1): 127-140.

WATLING, R. (2006): The sclerodermatoid fungi. - Mycoscience **47**: 18-24.

ZELLER, S.M. (1947): More notes on Gasteromycetes. - Mycologia **39**: 282-312.

ZELLER, S.M. & A.H. SMITH (1964): The Genus *Calvatia* in North America. - Lloydia **27** (3): 148-186.

PLATE 1: 1a *Calvatia rosacea* OSC 28213, exsiccated specimen; 1b *Morganella fuliginea* M. Piepenbring 3598, fresh specimen; 1c *Morganella velutina* M. Piepenbring 3970, fresh specimen; 1d *Veligaster nitidum* M. Piepenbring 3633, exsiccated specimen; 1e *Crucibulum laeve* fresh specimen M. Piepenbring 3205; 1f *Cyathus poeppigii* M. Piepenbring 4088, fresh specimen.

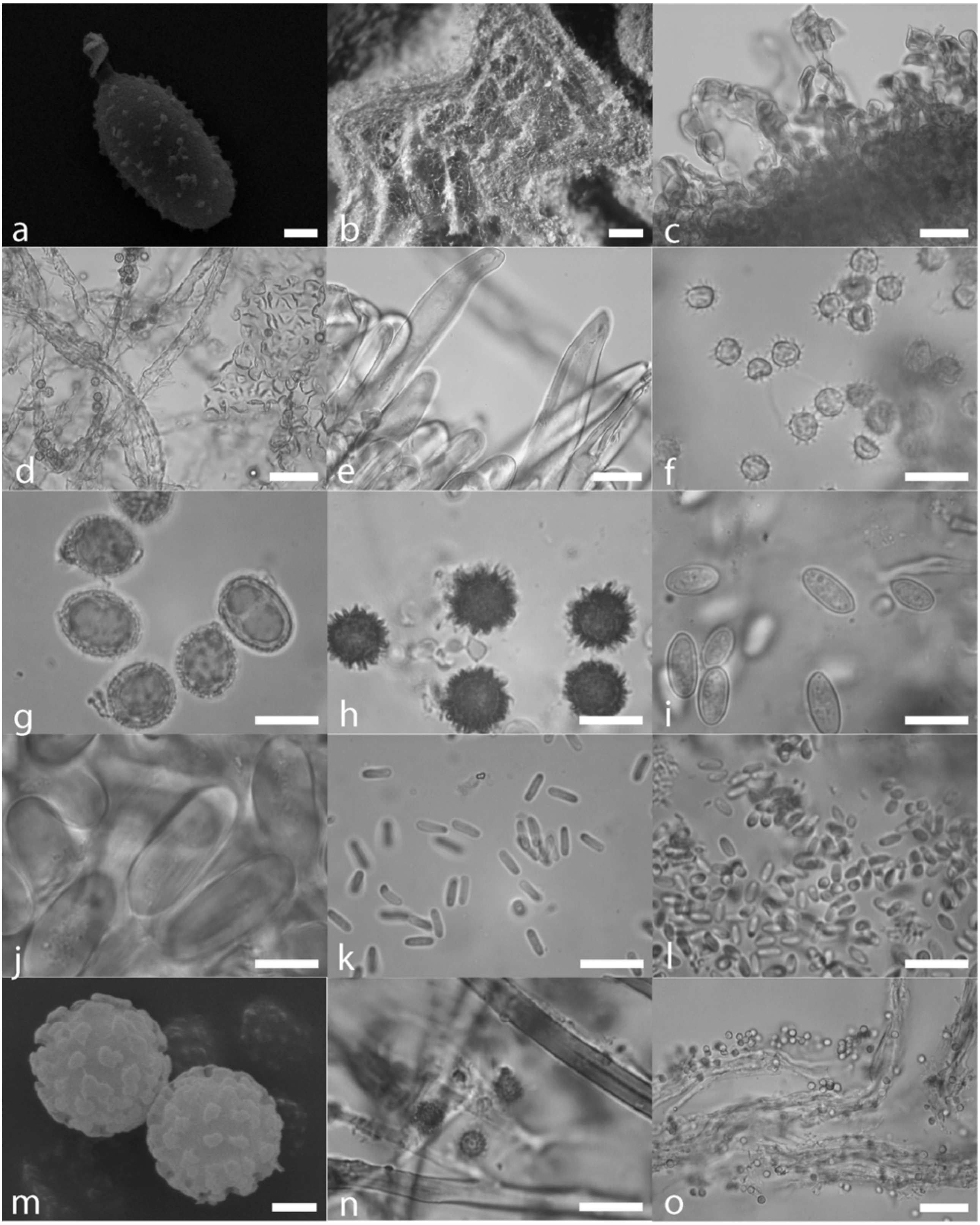

PLATE 2: 2a *Bovista longispora* M. Piepenbring 4073, SEM image of spore, scale 1 µm; 2b *Calvatia rosacea* OSC 28213, subgleba, cavities with crossing hyphae, scale 250 µm; 2c *Morganella fuliginea* NY 398740, exoperidial isodiametric elements, scale 20 µm; 2d *Morganella fuliginea* M. Piepenbring 3598, spores and paracapillitium with glebal membranes, scale 20 µm; 2e *Morganella velutina* NY 398739, exoperidial thickwalled setae, scale 20 µm; 2f *Morganella velutina* NY 398739, spinulose spores, scale 10 µm; 2g *Calostoma cinnabarinum* M. Piepenbring 4013, spores, scale 10 µm; 2h *Veligaster nitidum* M. Piepenbring 3633, spores, scale 10 µm; 2i, *Crucibulum laeve* M. Piepenbring 3966, spores, scale 10 µm; 2j *Cyathus limbatus* M. Piepenbring 3325, spores, scale 10 µm; 2k *Mutinus argentinus* M. Piepenbring 3615, spores, scale 10 µm; 2l *Phallus indusiatus* M. Piepenbring 3543, spores, scale 10 µm; 2m *Radiigera* sp. M. Piepenbring 3136, SEM image of spores, scale 1 µm; 2n *Radiigera* sp. M. Piepenbring 3136, spores and capillitium, scale 10 µm; 2o *Lycogalopsis solmsii* M. Piepenbring 3934, spores and capillitium, scale 20 µm.

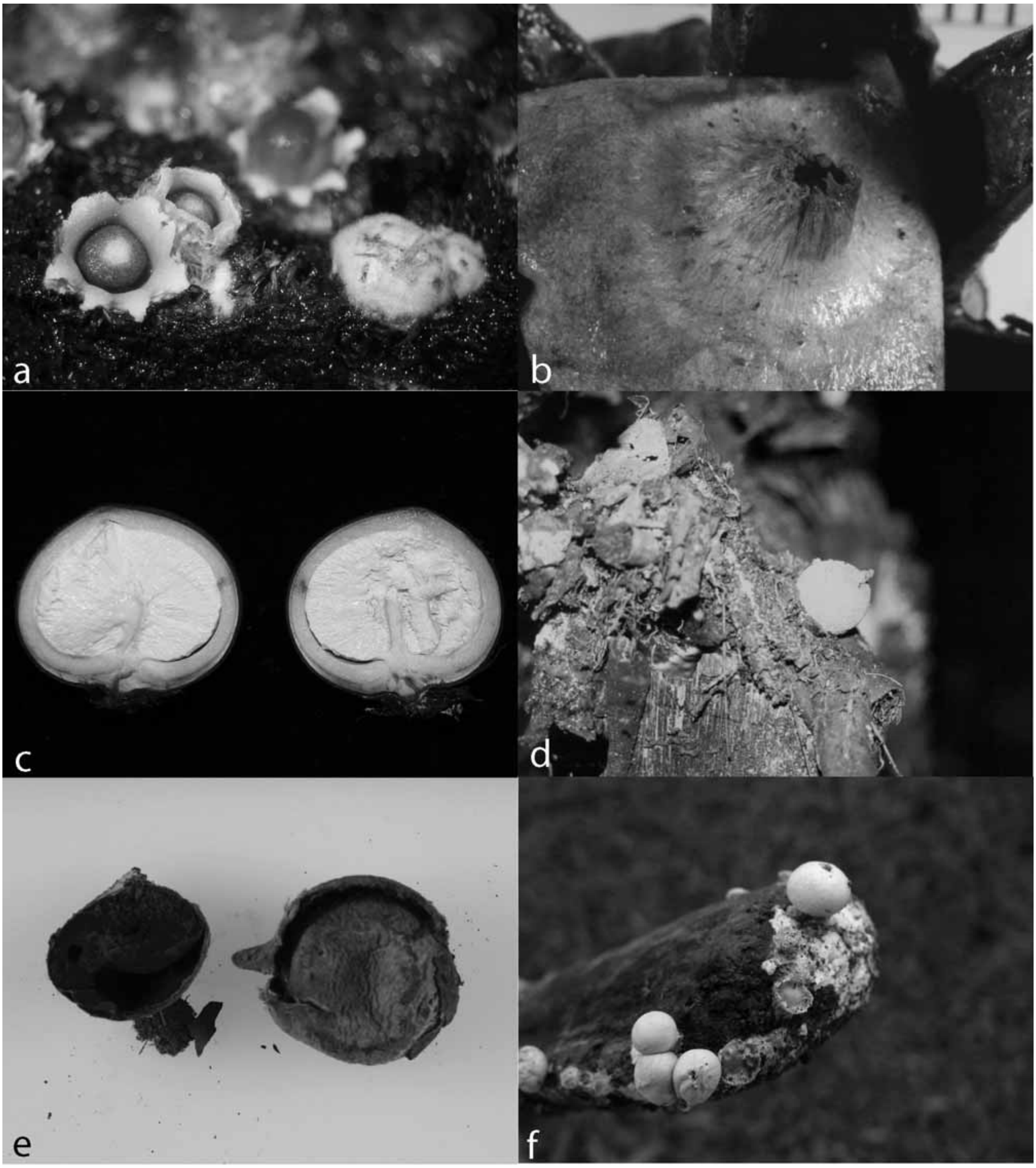

PLATE 3: 3a *Sphaerobolus stellatus* M. Piepenbring 3488, fresh specimen; 3b *Geastrum saccatum* M. Piepenbring 3547, endoperidium with fimbriate mouth and distinct "court"; 3c *Radiigera taylorii* fresh specimen M. Piepenbring 3955; 3d *Radiigera* sp. M. Piepenbring 3136, fresh specimen, 3e *Radiigera* sp. M. Piepenbring 3136, exsiccated specimen; 3f *Lycogalopsis solmsii* M. Piepenbring 3934, fresh specimen.

Anatomy and ecology of the gasteromycetation process in Agaricaceae s. l.

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Abstract

In this study, a review of the morphological features of gasteroid members of Agaricaceae is provided. Consideration of their ecological background and phylogenetic relationships allows for interpretation of the underlying process of gasteromycetation. The main dispersal strategies of gasterothecia are outlined. With Lycoperdaceae, Tulostomataceae and the secotioid species, three functional groups of agaricoid gasterothecia are defined. Whereas the first two are phylogenetic units as well, the latter are united exclusively by their close systematic and anatomical relationships to hymenothecia and their habitat. Semiarid openland habitats are proposed as origin of gasteromycetation for this group, as they incorporate the highest diversity of morphological adaptations and are inhabited by members of all analysed gasteroid taxa.

Introduction

E. M. Fries (1821–1832) defined Gasteromycetes as a systematic category, a class that included all fungi with angiocarp internal spore development. They were distinguished from Hymenomycetes, where the spore-producing cells are arranged in a hymenium at the surface of fruitbodies, and Hyphomycetes without fruitbodies. Fries' Gasteromycetes included groups that today are Ascomycetes, Myxomycetes, or Basidiomycetes. Within the late 19th century, when the fundamental differences between Asco- and Basidiomycetes were revealed, the class was restricted to Basidiomycetes with angiocarpic fruitbodies (e. g. Cooke 1871, Lloyd 1902). Until the second half of the 20th century, gasteromycetes were usually treated as taxon, on order (Esser 1986), subclass (Kreisel 1969) or class level (Webster 1983, Weber 1993). However, most of these authors state gasteromycetes to be a polyphyletic assemblage, whose members belong phylogenetically to various groups of Basidiomycetes. Brefeld (1877) and Underwood (1899) proposed first tree-like schemes of supposed interrelationships, the latter did even infer secotioid species and Lycoperdaceae from *Agaricus* and *Coprinus*. Detailed relationships between Gasteromycetes and Agaricales were discussed by de Bary (1866) concerning *Montagnites* (= *Montagnea*), Conard (1915) concerning *Endoptychum agaricoides* Czern., and by Lohwag (1925) concerning *Podaxis*. Polyphyly of Gasteromycetes in general was assumed by Gäumann (1926), who even placed Secotiaceae and Podaxaceae among the Agaricales, but this view was already revised as 'too conservative' in the english translation (Gäumann & Dodge 1928) and was later on named the 'crowning folly'of his work (Cunningham 1944). Von Arx (1967) used no uniting systematic rank for angiocarpic Basidiomycetes, Malençon (1955) separated between Exo- and Endogastrinae with and without true hymenium, and Gäumann (1964) distinguished Agaricogastrales, with obvious connections to Agaricales or Boletales, from Gastrales without such evidence. In the second half of the 20st century the polyphyly of Gasteromycetes was still debated (Smith 1971, Thiers 1984, Singer 1986), although anatomical (Conard 1915, Lohwag 1925, Townsend 1954, Heim 1971, Smith 1973, Reijnders 1977, Reijnders 2000, Agerer 2002) and chemotaxonomical (Demoulin 1967) evidence was present.

Angiocarpy of basidiomata as basal systematic criterion was finally falsified by molecular systematic work during the last decades (Hopple & Vilgalys 1994, Hibbett et al. 1997, Krüger et al. 2001, Peintner et al. 2001, Moncalvo et al. 2002, Binder & Bresinsky 2002, Lebel et al. 2004, Geml et al. 2004, Vellinga 2004b, Matheny et al. 2006). Gastromycetes remain a morphologically defined, polyphyletic group of Basidiomycetes. They share features such as spore production within enclosed fruitbodies (angio- or cleistocarpy), and loss of active basidiospore discharge (Reijnders 2000). The irreversibility of the latter is proposed to cause irreversibility of the whole process of gasteromycetation (Hibbett 2004). Although gasteromycete spores may develop either on hymenia or irregularly, no hymenium is visible in mature fruitbodies, or it is extensively changed, as in *Gyrophragmium* and *Montagnea*. Thus these fruitbodies are referred to as gasteroid basidiomata or gasterothecia. Since hymenia remain nearly unchanged in hemiangio- and gymnocarpous basidiomata at spore ripening, these are Hymenothecia. This classification allows using the traditional terms (de Bary 1966) without implying a general systematic value.

Knowing that the analysed taxa form a monophyletic clade with and among hymenothecial Agaricaceae, we still refer them to their traditionally used taxa to facilitate communication. Therefore, the families of Lycoperdaceae and Tulostomataceae including Phelloriniaceae and Battarraeaceae are not used as synonyms of Agaricaceae here, as was suggested by Moncalvo et al. (2002) and Vellinga (2004b).

Agaricomycetidae include a variety of gasteroid species, concentrated in the Gomphoid/Phalloid group, Russulales, Boletales, and Agaricales (Hibbett 2006). Within the latter, gasterothecia may be found in Cortinariaceae (*Thaxterogaster*), Bolbitiaceae (*Galeropsis*), Entolomataceae (*Richoniella*, *Rhodogaster*), and Amanitaceae (*Torrendia*), to give some examples (Moncalvo et al 2002). Families like Nidulariaceae are exclusively gasteroid. However, the highest diversity of gasterothecia is present in the Agaricaceae with the secotioid species of *Podaxis*, *Endoptychum*, *Gyrophragmium, Longula* and *Montagnea*; and the closely related Lycoperdacaeae and Tulostomataceae (Vellinga 2004b). The Australian gasteroid species *Barcheria willisiana* Lebel is extremely derived morphologically from the related *Agaricus* sect. *Xanthodermei* (Lebel et al. 2004). Many of these taxa possess structural and functional comparable features that yet did evolve independently, and are classified as families, genera, or single gasteroid species among hymenothecial lineages. Morphological, especially ontogenetical studies and molecular systematics are crucial for every attempt of homologisation of features, and for insights into the multiple pathways of gasteromycetation. However, this necessitates deeper knowledge of its ecological circumstances. These are being evaluated here within gasteroid Agaricaceae and related families to allow for interpretation of the morphological changes during this process.

Materials and methods

This study is based on about 800 specimens of agaricacean gasterothecia obtained on loan from the herbaria BPI, CANB, F, GLM, HAL, JE, MICH, NY, OSC and W, or from the private herbaria of the authors and of M. Piepenbring, Frankfurt a. M. Specimens were determined anew, photographed, and analysed by light microscopy. Cotton blue (0.04% w/v in lactophenol), toluidine blue O (0.1% w/v in H_2O), and indigotin (Wusitta, Sitzendorf, Germany) were used as stains. Microtome sections of primordia were performed as described in Gube (2007). SEM images of spores were taken at the IPHT (Jena, Germany).

Further information was gained by literature research. Main sources include: Agerer (2002), Barnett (1943), Bates (2004), Bottomley (1948), Brasfield (1937), Bronchard and Demoulin (1973), Butler and Day (1998), Calonge (1998), Clemençon (1997, 2004), Coker and Couch (1928), Conard (1915), Cunningham (1944), Demoulin (1980), de Villiers et al. (1988), Dörfelt and Gube (2007), Dring and Rayss (1963), Dumée and Maire (1913), Fischer (1900, 1933, 1934, 1936), Galli (2004), Gäumann (1926), Greis (1937), Gube (2005, 2007), Jacobson et al. (1999), Jülich (1984), Kreisel (1961, 1962, 1973, 1998, 2001), Kreisel and Al-Fatimi (2008), Kreisel and Dring (1967), Lange (1990), Lebel et al. (2004), Liu (1984), Lloyd (1902), Lohwag (1925, 1941), Long (1943, 1944), Long and Ahmad (1947), Long and Plunkett (1940), Long and Stouffer (1943, 1946), Malençon (1930, 1935a, b), Martin and Johannesson (2000), Maublanc and Malençon (1930), Meléndez-Howell (1967), Miller (1995), Miller and Miller (1988), Morse (1933), Rauschert (1964), Rea (1942), Redhead et al. (2001), Rehsteiner (1892), Reid and Eicker (1991), Reijnders (1975, 1977), Sarasini (2005), Schröter (1877), Swartz (1933); Townsend (1954), Vellinga (2004a, b), van de Bogart (1976), White (1901), Wright (1987), Wright and Suarez (1990), Zeller (1943). They are only cited in the descriptive part when the information is outstanding or controversial.

Results – Structural analysis

Primordial ontogeny

All species related to Agaricaceae develop in nodulocarpous fashion (Brasfield 1937, Reijnders 1975, Clémençon 1994, 1997, 2004, Gube 2005), within a bulb or nodulus of undifferentiated plectenchyma (Fig. 2a). In most cases, formation of the primordial nodulus occurs hypogeous, exceptions are present where this is hindered by the substrate. For many gasterothecia, a greater part of ontogeny takes place under the soil surface. This is especially true for *Montagnea*, the Tulostomataceae, and some Lycoperdaceae like *Abstoma*, *Arachnion* and *Disciseda* (Maublanc & Malençon 1930, Long & Ahmad 1947, Demoulin 1980, Miller & Miller 1988). These remain submerged until spore formation has taken place, and only then get exposed to the air by rapid stipe elongation. This explains why ontogenetic studies of these species are rare.

Hymenium

Presence or absence of hymenial structures was considered a major feature for classification in the beginning of the 20th century, as seen in the distinction of Gasteromycetes s. str and the so called Plectobasidiales (Fischer 1899). Although this feature was soon considered flawed

(Lloyd 1902, Fischer 1933), and represents parallelism (Patterson 2008), hymenial structures remain crucial for classification (Reijnders 2000, Gube 2007). In many gasterothecia, these structures are accessible only in early ontogenetic stages. Therefore, the associated features are less extensively analysed. A general distinction can be made between taxa with hymenial cavities and those without them.

Whereas the cavities of the secotioid species show clear evidence of lamella formation (Conard 1915, Fischer 1934, Brasfield 1937, Long & Plunkett 1940, Barnett 1943), and are homologous to the torus shaped hymenial cavities of Agaricaceae (Fig. 2b), true cavitated gleba is present in Lycoperdaeae, *Barcheria*, *Battarraea*, *Phellorinia* and *Dictyocephalus* (e.g. Rehsteiner 1892, Maublanc & Malençon 1930, Malençon 1935a, Malençon 1935b, Lebel et al. 2004, Gube 2007).

Lycoperdaceae have two different types of cavitation, that both cannot be tracked back to lamellar structures (Fig. 2g, Gube 2007). Some species of *Lycoperdon* and *Calvatia* possess a sterile, more or less chambered subgleba, which develops initially similar to the gleba. Later on, however, the subglebal cavities remain largely sterile, and their tramal hyphae get sclerified to a large extent. In contrast, the compact subgleba of *Langermannia* arises from the endoperidium and shows no sign of cavitation. In some species, the tramal plates between the cavities are persistent at maturity and form glebal membranes, in *Lycoperdon* sect. *Morganella* they connect paracapillitial threads; in *Arachnion* they surround glebal locules (Kreisel & Dring 1967, Demoulin 1980). The gleba of *Barcheria* is reported to be loculate (Lebel et al. 2004), but no concise description exists.

Gasterothecia of *Tulostoma*, *Queletia* and probably *Schizostoma* develop no cavitated gleba and lack hymenial structures (Fig. 2h), their basidia develop irregularly distributed in the gleba. Contrasting to all other Agaricales, *Tulostoma* basidia are pleurosporous, their spores develop laterally (Schröter 1877, Dumée & Maire 1913, Greis 1937). Only here, plectobasidia free from any trace of hymenial structure have been found so far.

Contradictory claims of presence (Malençon 1930, Maublanc & Malençon 1930) or absence (Jacobson et al. 1999) of hymenial structures have been made for *Battarraea*. However, judging from the descriptions, Jacobson et al. (1999) did examine specimens too mature. *Phellorinia* and *Dictycephalos* have minute glebal chambers comparable to those of Lycoperdaceae (Malençon 1935a, b). For *Chlamydopus* and *Mycenastrum*, hymenial development has not been studied, and the nature of their gleba remains unknown, but presence of chambers can be assumed, considering their systematic relationships.

If present, the anatomy of gasteroid hymenia differs usually not much from those of hymenothecia (Reijnders 2000), they can be referred to as euhymenium (Clémençon 1997, 2004). Basidia, intermixed with sterile hyphal ends, are borne on a densely packed subhymenium with candelaber-like basal ramifications. The hymenial trama tends to be less ordered and more loosely arranged, compared with Hymenothecia. Here again, secotioid species come closer to their hymenothecial relatives than other gasterothecia.

In *Phellorinia*, *Dictyocephalos*, *Chlamydopus*, *Battarraea*, and *Podaxis* (Fig. 2c), mature basidia can coagulate and persist in the developing or even mature gasterothecium (Morse 1933, Malençon 1935a, b, Long & Plunkett 1940, Jacobsen et al. 1999). Such fasciculate basidia are no reason to assume plectobasidia. Euhymenium has been demonstrated for these taxa, although it is not an even layer in the phellorinioid group (Malençon 1935 a, b), and hence to be called tilaiohymenium there (Clémençon 1997, 2004). In *Podaxis*, the fasciculate basidia form from dried out edges of lamellar gleba plates (Brasfield 1937), whereas candelabra-like bundles of basidia attached to a single hypha agglutinate at maturity in *Phellorinia* and *Dictycephalos* (Malençon 1935a, b).

Spores

Spore characteristics are among the best researched features of gasteroid Agaricaceae, since they are, like in other groups, crucial for determination. To the present knowledge all of them, even the secotioid species, have statismospores (Reijnders 2000). As the hilar appendage lacks, no active spore discharge can take place. However, in other groups like the Russulales, secotioid species with partly functional hilar appendage do exist (in *Elasmomyces* and *Arcangeliella*, see Reijnders 2000). Loss of ballistospore discharge facilitates the appearance of orthotropic spores, and of irregular basidia, both are common among gasteroid Agaricaceae. However, *Secotium gueinzii* Kunze, which possibly has affinities with Agaricaceae (Johnson & Vilgalys 1998), has heterotropic spores (Heim 1951).

Some groups possess spherical or slightly ovoid spores, like most Lycoperdaceae, Tulostomataceae, and some secotioids. These are, at least in Lycoperdaceae, often borne on exceptionally long sterigmata. Without the discharge mechanism, these sterigmata can break close to the basidium, resulting in pedicellate spores (Fig. 1a). Such spores are present in the genera *Bovista*, *Lycoperdon* und *Disciseda*, but spores with attached sterigmal remains are common also in other groups. Contrastingly, spores are often sessile on basidia of *Podaxis* (Brasfield 1937). There, in most secotioids, and in some Lycoperdaceae, spores are elongated. In many cases, exo- or episporium produce a verrucose to spiny (most Tulostomataceae, many

Lycoperdaceae, Fig. 1a, 1b) or reticulate surface (*Mycenastrum*, *Abstoma,* few *Tulostoma* species, Fig. 1c). In other cases, ripe spores are completely smooth (all secotioids, some Lycoperdaceae, few *Tulostoma* species, Fig. 1d). All gasteroid taxa in the revised group, except *Barcheria willisiana* and *Endoptychum arizonicum* (Shear & Griffiths) Singer & Smith, possess pigmented spores, which are often thick-walled.

Capillitium

Some central hyphae of the hymenial gleba of Lycoperdaceae and of *Podaxis* appear extraordinarily thick-walled and sparsely septate. Likewise scleletal hyphae can be found in the gleba of Tulostomataceae. They usually incorporate pigments during maturation, and resist the subsequent process of autolysis, becoming capillitial threads. These often cyanophilic hyphae are important for determination, and their occurence and features are consequently well documented. Capillitial threads may vary in their general shape septation, wall diameter, and wall features like pores, slits or spiral thickenings. Capillitium has evolved several times independently, probably from central hyphae of hymenial trama, and therefore is a good example for parallelism (Patterson 1988).

The capillitium of Lycoperdaceae consists generally of relatively long, smooth hyphae, that are frequently branched and unfrequently septated. It may be of the *Bovista*- type with relatively compact, free hyphal flocks with distinct main stems (Fig. 2d), or of the *Lycoperdon*-type with loose, more sparsely branched hyphae that are attached to the endoperidium and subgleba. The transition-type includes capillitium of both types (Kreisel 1962). Many Lycoperdaceae possess a second type of persistent hyphae, which remain unpigmented, normally septated, are not getting sclerified and are not cyanophilic. This paracapillitium is especially abundant in the *Lycoperdon*-sections *Morganella* and *Vascellum* and constitutes a defining character there. *Mycenastrum* shows very short capillitial hyphae, whose ramifications are short and pointed causing a spiny appearance (Fig. 2e). *Podaxis* has long, smooth, acyanophilic capillitium with sparse septa (Fig. 2c). It is initially attached to stipe and endoperidium (Morse 1933), and looses connection to the endoperidium in maturity. In *Tulostoma*, capillitial threads are acyanophilic, long and often richly septated, the septa are sometimes strongly swollen, whereas *Queletia* and *Schizostoma* have generally aseptate, cyanophilic threads. *Chlamydopus* possesses relatively short, unseptated and unbranched capillitium, the same is true for of *Dictyocephalus* (Malençon 1935b, Long & Plunkett 1940), in *Phellorinia* capillitium is sometimes stated as absent (Miller & Miller1988), but indeed hyaline, thick-walled hyphae are present (Malençon 1935a). Capillitial hyphae in *Battarraea* are of two types, either sparse, unseptated, vertically oriented paracapillitial threads, or hyphae even shorter than in *Chlamydopus* with spiral wall thickenings (Fig. 2f). Because of the latter feature these are referred to as elaters (Kirk et al. 2009), although their functionality has never been analysed. They arise probably from longer elements that break at constricted areas (Rea 1942). Capillitial hyphae are absent in *Barcheria* and the secotioid groups except *Podaxis*.

Peridia

Peridia, the structures surrounding the glebal structures of gasterothecia, are well analysed for their external appearance, mainly in behalf of their value for determination. However, their internal structure and especially ontogeny are far more informative concerning their relationships, and yet less well known.

In the Lycoperdaceae, two to four layers of peridium can be distinguished (Fig. 2g). These have been categorized as veil layer, exoperidium with exo- and endostratum, and endoperidium (Lohwag 1925, Kreisel 1962). The veil layer consists generally of more or less periclinally oriented hyphae, which can be undifferentiated or slightly swollen. The exoperidial endostratum is composed of pseudoparenchymatic hyphae with slightly anticlinal orientation that gradually change to the sphaerocysts of the exostratum. The endoperidial hyphae are periclinal at maturity, and are getting sclerified like the capillitium. Lycoperdaceae have no true peristome, but often a more or less defined apical or basal (in *Disciseda*) opening, in some species (*Lycoperdon excipuliforme* (Scop.) Pers., *L. utriforme* Bull., *L.* subgen. *Vascellum*, *Bovista* sect. *Bovista*, *Calvatia*, *Langermannia*, *Mycenastrum*) the peridium tends to irregular dehiscence (Rehsteiner 1892, Swartz 1933, Kreisel 1962, Gube 2005).

The peridium of *Tulostoma* consists of two layers. According to Wright (1987), the exoperidium can be membranous, with densely interwoven hyphae (Fig. 2h), or hyphal with rather loose hyphae. Both types frequently encrust with soil particles. Generally, these hyphae are undifferentiated, only the verrucose exoperidium of few tropical *Tulostoma* species is made up of short, thick-walled elements (Wright 1987). The endoperidium consists of tangential, densely interwoven hyphae, most of which are differentiated like the capillitium, others are generative; and short, extremely thick-walled mycosclereids may occur in some species (Wright 1987). The peristome of *Tulostoma* species is often predefined, and may be tubular, fimbriate, or indefinite. The latter type is gradually interchanging into a complete rupturing of the peridium, as in *Schizostoma* and *Queletia* (Wright 1987). In all three genera, the exoperidium forms a collar-like structure on the lower peridium, surrounding the insertion of the stipe (Fig. 2j). This structure corresponds to the volva and, in some species, to the scales on the stipe.

In *Battarraea*, the peridium is also devided into two layers, the exoperidium forming a distinctive volva, and rarely thin, sand-encrusted patches on the upper endoperidium (Long 1943, Jacobson et al. 1999). The endoperidium surrounds the gleba, the lower part being stronger developed. Dehiscence occurs by a circumscission, separating the upper and lower halves of the endoperidium or, in *Battarraeoides diguetii* (Pat. & Har.) Heim & Herrera, by irregular dehiscence of the upper part (Rea 1942, Jacobson et al. 1999). In the Phellorinoids, dehiscence is performed either by an indefinite peristome (*Chlamydopus*), or by withering of the peridium (*Phellorinia*, *Dictyocephalus*). The exoperidium is more extended, and often covered with warts, scales or spines, whereas the endoperidium is again made up of sclerified hyphae. In *Chlamydopus*, the greatest part of the thick, soft exoperidium of thin walled, generative hyphae flakes away early (Long 1946, Miller 1995). Later on, the structure of the peridium resembles the Tulostomataceae, with thin, sand-encrusted remains of exoperidium and an endoperidium of mostly sclerified hyphae.

The peridial structure of the secotioid genera including *Podaxis* can be traced back easily to pileus trama, pileipellis, and veil structures of their agaricoid relatives. The same is proposed for *Barcheria*. However, differences include a generally higher plectenchymatic density and stability, and a less extended pileus trama. The pileodermal scales of undifferentiated hyphae in *Podaxis*, *Endoptychum agaricoides*, and *Longula texensis* Zeller (Conard 1915, Morse 1933, Barnett 1943) are remnants of the veil; the lower part of the peridium of *Endoptychum depressum* Singer & Smith, and immature *Gyrophragmium dunallii* (Fr.) Zeller and *Longula texensis* (Barnett 1943) consists of veil structures remaining fully or partly connected to pileus and stipe. In all cases, the peridium ruptures irregularly to expose the spores. In *Montagnea*, pileus plectenchyma is getting highly reduced during maturity, allowing the drying lamellae to separate, ripping apart all pileus remnants with the exception of a small central disc. Still, a minor portion of velum and pileus plectenchyma remains on the upper part of the lamellae (Fig. 2i).

Many species have veil structures that form a volva around the stipe base (Tulostomataceae, *Gyrophramium*, *Longula*, *Montagnea*). In these species, the universal veil gets ruptured by the expanding stipe, and remnants of this veil may also form an exoperidium, which is often best preserved on the lower part of the endoperidium (Fig. 2j). Also, remains of the universal veil can be present on the surface of the stipe. In *Podaxis*, and many species with a volva, the lower portion of the stipe is expanded foot-like. The volva of *Battarraea* is often described as very complex with three layers, the middle layer being gelatinised or not (Maublanc & Malençon 1930, Rea 1942, Long 1943). This structure can be interpreted as gelatinisation initial present in the exoperidium, which is only effective in favourable moisture conditions. This view is supported by the frequent findings of the gelatinised forms in more humid; and of the non-gelatinized forms in more dry areas (Maublanc & Malençon 1930, Rea 1942), and by phylogeny of *Battarraea* not corresponding to the presence of a gelatinised layer (Martin & Johannesson 2000, Jeffries & McLain 2004).

Homology of gasterothecial peridia with velar structures of hymenothecia was assumed by Lohwag (1925), who did also homologise aeciospore chains of Uredinales with the exoperidial sphaerocysts of Lycoperdaceae, however. Homology of gasteroid peridia was not questioned historically as long as Gasteromycetes were considered a systematic group. Reijnders (2000) sees no real evidence for homology between gasteroid and hymenothecial veils and peridia, as long as younger primordia are not analysed.

Stipe

Since gasterothecia may show stipe like structures with varying anatomical background, one has to distinguish between true stipes and stipe analogues. True stipes are made up of a greater percentage of parallel hyphae, and grow by elongation of hyphae over their full length or from their base, and are homologous to the stipes of hymenothecia (Reijnders 2000). Such a structure is present in all secotioids (Fig. 2k) and Tulostomataceae (Fig. 2j), and lacks in Lycoperdaceae and *Barcheria*. Stipes can be hollow (*Montagnea*, *Battarraea,* many *Tulostoma* sp.), cottony stuffed (*Podaxis*), or massive; they can be fully (some *Tulostoma* sp.) or partly (*Battarraea*, *Gyrophragmium*, *Longula*, many *Tulostoma* sp.) submerged in the soil.

In all *Endoptychum* species, stipe elongation is partly reduced. The stipe protrudes the gleba and is attached to the peridium in most secotioids, only in *Endoptychum arizonicum* (Fig. 2k), and sometimes in *Podaxis* (Morse 1933), it does not reach through the gleba. In *Tulostoma* and *Battarraea*, the stipe is inserted into the endoperidium; whereas a more gradual interchange between both structures is observed in Phellorinioids.

Rhizomorphs

The abundance and in part anatomy of rhizomophs is dependant on the stand conditions, and thus can differ greatly between collections of a single species. Still, many features remain constant. As far as it they are known (Swartz 1933, Townsend 1954, Agerer 2002, Gube 2005), rhizomorphs of all species in the group possess at least two layers, the inner core composed of highly differentiated vessel hyphae intermingled with undifferentiated generative hyphae, which also form a sheath around the inner part. In Lycoperdaceae, this type of rhizomorphs is present in *Langermannia* (Gube 2005), but other genera possess an additional layer of sclerified hyphae (Swartz 1933, Townsend 1954, Agerer 2002, Gube 2005) inbetween the mantle layer of generative hyphae. These hyphae are always unseptated, and stain permanently with indigotin, a feature not found in any other rhizomorphs of the group (Fig. 1l). Nodulus formation of Lycoperdaceae seems to depend on rhizomorphs, which often remain attached to mature gasterothecia (Swartz 1933). Exceptions are species of *Disciseda* and *Bovista* sect. *Bovista*, which separate from their rhizomorphs in maturity. Rhizomorphs of *Montagnea*, *Battarraea*, *Barcheria* and Phellorinioids have not been found so far, but might well be present.

Rhizomorph structures have proven to contain valuable phylogenetic information, although some characters are apomorphic (Agerer 2002). Therefore, homology of the group specific features can only be assumed so far.

Discussion – Connections with ecology

One can distinguish between two main types of gasterothecia, concerning their ecology. There are taxa with fleshy or moist glebal structures, mostly adapted to endozoochory, and often present in humid zonobioms. These gasterothecia often belong to mycorrhizal groups (e.g. Peintner et al. 2001), and a model of the gasteromycetation process within such taxa was proposed by Thiers (1984). On the other hand, there are those with dry gleba at maturity, mostly adapted to some kind of anemochory, and present in all zonobioms, but with a higher diversity (not necessarily abundance!) in dry areas, like steppe, savannah, or deserts. All taxa reviewed here belong to the second group, and show inherent adaptations to their habitat.

Some species are found in true desert environments, with annual precipitation below 100 mm, and infrequent, short, but often heavy periods of rainfall. Among the gasterothecia of such habitats are the *Montagnea*, *Gyrophragmium*, *Longula*, and many Tulostomataceae (Long 1944, Long & Ahmad 1947, Kreisel 2001, Dörfelt & Gube 2007, Kreisel & Al-Fatimi 2008). Development is always hypogeous until the spores are mature. Afterwards, very a rapid stipe elongation occurs, and spores are quickly exposed. All species with enclosing peridium show no defined peristome, but an irregular opening (*Tulostoma*, *Chlamydopus*), or a peridial dehiscence by preformed (*Battarraea*) or undetermined (*Phellorinia, Dictyocephalus, Schizostoma, Queletia*) rupturing. If capillitial threads are present, they are usually very reduced and probably dysfunctional. The elaters of *Battarraea* might have a function in exposing the spores, but this has not been analysed so far. Spores are often smooth or weakly ornamented, with the exception of the strongly verrucose spores of *Queletia mirabilis* Fr.. This species is no true desert species, but grows only at extremely dry and hot habitats of warm temperate areas (White 1901, Dumée & Maire 1913). Although almost all gasteroid Agaricaceae possess pigmented spores, those of desert species are often comparatively stronger pigmented, a good example are the Tulostomataceae (Wright 1987). However, the darker appearance often reflects just thicker walls. This gives, apart from protection against ultra-violet radiation, additional adaptive advantage in arid regions. High rates of evaporation can endanger the integrity of spores, as seen in the large gas bubbles common within spores in dry atmosphere. They disappear with higher humidity, and reflect the high gas pressure differences inside and outside the spore (Gregory & Henden 1976). A more stable wall can better withstand this pressure. Another main function of presence, or lack, of ornamentation is the facilitation of anemochory. Ornamented spores are stirred with the slightest air movement, but are doubtlessly slower than smooth ones in linear jets of air. This is reflected in the generally less ornamented spores of openland, and especially of desert species, where strong winds are common. Capillitial and peridial features fit well to this euanemochorous strategy (Kreisel 1962), complex dispersal structures as in geanemochorous or even more in boleohydrochorous species (see below) are not established. Also, desert species have to take every chance of germination, explaining their smooth or weakly ornamented spores that get easily moistened (Kreisel & Al-Fatimi 2008). On the other hand, these spores can keep the ability to germinate for decades (Chen 1999).

In areas with regular annual rainfall above 100 mm, like dry steppe, savannah, or semideserts, the species mentioned above may also be present, but other gasterothecia appear as well. This includes *Mycenastrum, Disciseda, Langermannia, Podaxis, Endoptychum, Gyrophragmium*, *Barcheria*, species of *Tulostoma, Calvatia, Bovista*, and *Lycoperdon* subgen. *Vascellum* (summarised in Kreisel 2001). Here, several strategies are present in adaptation to the ecological circumstances. Steppe *Tulostoma* species possess regular, stable stomata. Their development is hypogeous like in the desert species, however, they have functional capillitium and a peridium that gets elastic in moist conditions. These features allow for spore dispersal by drops of rain or dew, which deform the peridium reversibly, causing the ornamented spores to be discharged through the peristome. These boleohydrochorous species (Kreisel 1962) have almost always strongly ornamented spores. The air movement caused by a raindrop on the peridium is probably very faint, therefore strong ornamentation is advantageous. Besides, spore ornamentation acts as a water-repellent preventing clumping of the spores (Kreisel & Al-Fatimi 2008) and slows also water uptake, allowing germination only in most favourable conditions. This dispersal strategy is much more common in humid areas (see below); the hypogeous development constitutes the main advantage of *Tulostoma* for such habitats.

Other species show no peristome at all, a spherical shape, and no or weakly developed subgleba. Either a light but tough peridium, and a loose mycelial connection are present (*Bovista* sect. *Bovista*, *Disciseda*), or an almost complete dehiscence of the peridial structures occurs (*Langermannia*). The capillitium is very stable and elastic, and without connection to the peridium; the spores are usually smooth or weakly ornamented. These species are geanemochorous tumblers (Kreisel 1962), where the whole fruitbody is blown before the wind, dispersing the spores. This explains the advantage of smooth spores here, they do not agglutinate, and can easily fall through capillitial threads and, subsequently, vegetation.

The most common dispersal strategy in steppe is that of euanemochorous species with irregular dehiscence of peridial stuctures, but an anchor of columella or stipe (*Endoptychum*, *Gyrophragmium*, *Longula*, *Podaxis*), subgleba (some *Calvatia* species, *Vascellum*), thickened peridium structures (*Mycenastrum*, some *Calvatia* species) or the soil itself (the hypogeous genera *Abstoma* and *Arachnion*). Like the desert species, these may possess smooth (with columella) or weakly ornamented (with subgleba or thick peridium), often thick-walled spores. Presence of reticulate or ridged ornamentation, as in *Abstoma*, *Mycenastrum* and some *Tulostoma* species (Bronchard & Demoulin 1973, Wright 1987), serves the same goal of draught protection and is less material-intensive. Many species have a no or a dysfunctional capillitium. An exception is *Podaxis*, where the strongly developed capillitium remains attached to the stipe in maturity and keeps spores exposed after dehiscence of the peridium. The differences in spore ornamentation indicate relationships besides adaptation here; the secotioid smooth spored species are all closely related to equally smooth spored hymenothecial species.

In more humid areas with annual rainfall above 300mm, from more humid savannah and steppe well into the area of temperate and boreal forests, the majority of species have defined peristomes, strongly ornamented spores, and develop mostly epigeous or subhypogeous. They include the majority of species of *Lycoperdon* and *Bovista* subgen. *Globaria*. Like the *Tulostoma* species of steppe areas, they are boleohydrochorous, and as such highly dependant on rainfall. Desert species occur only rarely, and only in extreme habitats or under unusual weather conditions. Species primarily adapted to steppe are present only in openland habitats, which are, with higher precipitation, increasingly of anthropogenous origin. The worldwide distribution of species like *Lycoperdon pratense* Pers.: Pers., *Bovista plumbea* Pers.: Pers., and *Langermannia gigantea* (Batsch: Pers.) Rostk., which are additionally nitrophilous, is clearly synanthropous.

Alpine meadows and arctic tundra, with often high rainfall, but short vegetation periods are inhabited mainly by species with dehiscing peridium (*Lycoperdon*, *Calvatia*), or geanemochorous species (*Bovista*, *Disciseda*) (Lange 1976, Lange 1990, Kreisel 1998). These habitats share the absence of trees and shrubs with steppe, but lack the high evaporation rates, therefore *Tulostoma* species would have no adaptive advantage, and are not present here.

Some gasterothecia are present in tropical rainforests, these belong mainly to *Lycoperdon* subgen. *Morganella*. Most are lignicolous, have ornamented spores and show an undetermined opening. All these features point towards an adaptation to the rapid nutrient cycling in tropical rainforests. Gasterothecia develop very fast in this zonobiom, and show signs of paedomorphosis like the generally small size and the presence of paracapillitium and glebal membranes replacing true capillitial elements. Spores are usually relatively thin-walled and weakly pigmented, but mostly ornamented. Their white rot ability gives them an advantage over fast growing molds, which is not given for degradation of other organic litter here. Some species possess mycosclereids, these may be a protecting feature against fungivores and aggressive molds and bacteria.

Overall, it is striking that the highest anatomical and systematic diversity of agaricoid gasterothecia is present in openland, especially in steppe. There, the youngest, the secotioid taxa all are present. As all Agaricaceae s.l. are saprobic (Vellinga 2004a), which gives adaptive advantage in openland habitats without competition from mycorrhizal fungi, many are openland species. Among them are the closest relatives of all secotiods, although they inhabit mostly more humid areas. Variance of anatomical features confirms this assumption.

All gasterothecial taxa have pigmented spores, those of the secotioids are equally or stronger pigmented when compared with related hymenothecia. Melanin delays enzymatic lysis of the spore wall and protects against UV radiation (Butler & Day 1998), allowing for a prolonged dormancy of the spores (Vellinga 2004a), especially when exposed to the sun. Furthermore, the euanemochorous dispersal strategy is the one with the least number of required anatomical changes, no complex mechanisms are necessary. This strategy is present in all analysed groups of gasterothecia, and all other ways of spore dispersal can be derived from it. Therefore, it can be concluded that the origin of these species is very probably to be found on openland and steppe habitats. Gasteromycetation gave a strong adaptive advantage there, and its success led, in the older groups, to colonisation of other biomes and evolution of adequate anatomical features.

Conclusions

Gasterothecia are a common sight in any zonobiom of our planet. It is obvious, however, that the main types of habitats, each with its specifical ecological circumstances, are inhabited by species with differing anatomical features. The often harsh ecological circumstances of these habitats are the causatives for the evolutionary success of gasterothecia, and an explanation for their anatomical and systematic diversity.

Fixation of anatomical changes may often be explained by ecological constraints where they give adaptive advantage. On the other hand, many features can be traced back to their phylogenetic heritage. Since both processes do interfere on the same features, the influence of each cannot be considered alone. Gasteromycetation is a process where the presence of comparable ecological constraints led to analogous anatomical changes, often concealing phylogenetic relationships to hymenothecial taxa. However, the process of evolution procedes continuously and several gasteromycetation events of differing evolutionary age are present among the revised group, facilitating study of this process. One can distinguish between three groups of gasterothecia related to Agaricaceae, the monophyletic Lycoperdaceae and Tulostomataceae, which are exclusively gasteroid and probably relatively old, and the various secotioid taxa of clearly polyphyletic origin, that are much younger.

Lycoperdacae are mainly found in steppe and temperate areas, but also in tundra und tropical rainforest. They do not occur in deserts. In steppe and tundra, two kinds of adaptation in spore dispersal mechanisms are present, geanemochory and irregular peridium laceration, both with innate morphological changes in spore, capillitium, and peridium anatomy. Tumblers are restricted to the genus *Langermannia* (= *Calvatia* sect *Gigantea*) and *Bovista* sect. *Bovista*. Species with irregular dehiscence of the peridium can be found in *Calvatia*, *Lycoperdon*, and *Mycenastrum*. Temperate and boreal Lycoperdaceae show generally boleohydrochory with defined peristomes and elastic capillitium and peridia. Most of these belong to the genus *Lycoperdon*, or to *Bovista* sect. *Globaria*. However, some steppe species are present synanthropically in grasslands and agricultural areas of these zonobioms. In tropical rainforest, gasterothecia show fast growth, connected with paedomorphosis, they belong mostly to *Lycoperdon* subgen. *Morganella*. Lycoperdaceae are anatomically most derived, it is currently impossible to homologise most features with hymenothecia. They possess no true stipe or obvious veil structure, and a different hymenial organisation.

Tulostomataceae are found predominantly in deserts and steppe, only few other openland habitats are suitable. Their main adaptive advantage is their hypogeous ontogeny. The desert species of the Tulostomataceae have mostly smooth or weakly ornamented spores, irregular peridial openings and tend to stronger pigmentation of spores. Their capillitium is often dysfunctional or at least somehow reduced, compared with the steppe species of *Tulostoma*. These are characterised by a defined peristome, and peridium and capillitium suitable for ombrohydrochory. This group shows more homologisable features, as the true stipe and probably homologous veils, however, hymenial organisation is at least as derived as that of Lycoperdaceae.

The secotioid species are mainly present in steppe and desert. The species of *Podaxis*, *Endoptychum*, *Gyrophragmium*, *Longula* and *Montagnea* vary greatly in their anatomy due to heterogenous relationships with hymenothecial species. Many of their features still reflect their evolutionary heritage, as the smooth, sometimes heterotropic spores with pigmentation resembling their hymenothecial relatives, the lamellar gleba and their velar structures. Others, like the presence of capillitium or the prolonged hypogeous ontogeny, are newly acquired under the ecological constraints of their habitat. *Barcheria willisiana* is as closely related to *Agaricus* as *Gyrophragmium* or *Longula* are, but contrastingly posesses extremely derived basidiomes. Anatomical, especially ontogenetic analysis of this rare fungus would be highly desirable.

Analysis of the range of anatomical features within and among the groups, and consideration of the accompanying ecological circumstances places gasteromycetation events within the analysed group to semiarid openland habitats. This coincides with the presence of the young secotioid groups, and with the highest amplitude of anatomical diversity there.

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References

AGERER, R. 2002: Rhizomorph structures confirm the relationship between Lycoperdales and Agaricacae (Hymenomycetes, Basidiomycota). – Nova Hedwigia **75** (3–4): 367-385.

BARNETT, H. L. 1943: The Development and Structure of *Longia texensis*. – Mycologia **35**(4): 399-408.

BATES, S. T. 2004: Arizona members of the Geastraceae and Lycoperdaceae (Basidiomycota, Fungi) (Master thesis). Tempe: Arizona State University.

BINDER, M. & A. BRESINSKY 2002: Derivation of a polymorphic lineage of Gasteromycetes from boletoid ancestors. – Mycologia **94** (1): 85-98.

BOTTOMLEY, A. M. 1948: Gasteromycetes of South Africa. – Bothalia **4** (3): 473-810.

BRASFIELD, T. W. 1937: The morphology of *Podaxis pistillaris*. – University of Iowa Studies in Natural History **17** (5): 199-211.

BRONCHARD, R. & V. DEMOULIN 1973: Ultrastructure de la paroi sporale des gasteromycètes *Mycenastrum corium* et *Abstoma reticulatum* en rapport avec leur position systématique. – Bull. Soc. R. Bot. Belg. **106**: 267-272.

BUTLER, M. J. & A. W. DAY (1998): Fungal melanins: a review. – Canad. J. Microbiol. **44**: 1115-1136.

CALONGE, F. D. 1998: Gasteromycetes, I. Lycoperdales, Nidulariales, Phallales, Sclerodermatales, Tulostomatales. Madrid, Berlin: Real Jardín Botánico Madrid, Gebr. Bornträger: Flora Mycol. Iber. **3**.

CHEN, C. 1999: Genetical and molecular systematic study on the genus *Montagnea* Fr. (Master thesis) Blacksburg: Virginia Polytechnic Institute and State University.

CLÉMENÇON, H. 1994: Der Nodulus und die Organogenese während der frühen Fruchtkörperentwicklung von *Psilocybe cyanescens*. – Z. Mycol. **60**: 49-68.

CLÉMENÇON, H. 1997: Anatomie der Hymenomyceten. Lausanne: Université de Lausanne.

CLÉMENÇON, H. 2004: Cytology and Plectology of the Hymenomycetes. Bibl. Myc **199**. Berlin, Stuttgart: Cramer, 488 p.

COKER, W. C. & J. N. COUCH 1928: The Gasteromycetes of the Eastern United States and Canada. Reprint 1974. New York.

CONARD, H. S. 1915: The Structure and Development of *Secotium agaricoides* – Mycologia **7** (2): 94-104.

COOKE, M. C. 1871: Handbook of British Fungi, With full Descriptions of all the Species, and Illustrations of the Genera. London, New York.

CUNNINGHAM, G. H. 1944: Gasteromycetes of Australia and New Zealand. Dunedin.

DE BARY, A. (1866): Vergleichende Morphologie der Pilze. Leipzig.

DEMOULIN, V. 1967: Intérêt des certaines substances a fonctions basiques en chimiotaxinomie des Gastéromycètes. – Bull. Soc. Mycol. France **83**: 342-353.

DEMOULIN, V. 1980: Observations sur le genre *Arachnion* Schw. (Gasteromycetes). – Can. J. Bot. **58**: 641-655.

DE VILLIERS, J. J. R., EICKER, A. & G. C. A. VAN DER WESTHUIZEN 1988: A new section and two new species of *Podaxis* (Gasteromycetes) from South Africa. – S. Afr. J. Bot. **55** (2): 159-164.

DÖRFELT, H. & M. GUBE 2007: Secotioid Agaricales (Basidiomycetes) from Mongolia**. -** Feddes Repertorium **118 (**3–4): 103-112.

DRING, D. M., & T. RAYSS 1963: The gasteromycete fungi of Israel. – Israel J. Bot. **12**: 147-178.

DUMÉE, P. & R. MAIRE 1913: Note sur la *Queletia mirabilis* Fr. et sa découverte aux environs de Paris. – Bull. Soc. Mycol. France **29**: 495-502.

ESSER, K. 1986: Kryptogamen; Cyanobakterien, Algen, Pilze, Flechten. Praktikum- und Lehrbuch. 2nd, newly revised ed. Berlin.

FISCHER, E. 1900: Hymenogastrineae, Lycoperdineae, Nidulariineae, Plectobasidiineae in: ENGLER, A., PRANTL, K. (Hrsg.): Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigen Arten insbesondere den Nutzpflanzen. I. Teil, Abt. 1**. Leipzig. 296-346.

FISCHER, E. 1933: Gastromyceteae. in ENGLER, A., PRANTL, K. (Hrsg.): Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigen Arten insbesondere den Nutzpflanzen. 2. Aufl. Band 7a. Leipzig. S. 1-72.

FISCHER, E. 1934: Zur Kenntnis der Fruchtkörperentwicklung von *Podaxis*. – Ber. schweiz. botan. Ges. **43**: 11-18

FISCHER, E. 1936: Neue Beiträge zur Kenntnis der Verwandtschaftsverhältnisse der Gastromyceten. Eine kritische Untersuchung. – Ber. schweiz. botan. Ges. **45**: 231-247.

FRIES, E. M. 1821-1832: Systema mycologicum. Vol I-IV. Gryphiswaldiae.

GALLI, R. 2004: Gli *Agaricus*. Milano.

GÄUMANN, E. 1926: Vergleichende Morphologie der Pilze. Jena.

GÄUMANN, E. 1964: E. Gäumann. Die Pilze. Gründzuge ihrer Entwicklungsgeschichte und Morphologie. Basel.

GÄUMANN, E. A. & C. W. DODGE 1928: Comparative morphology of fungi. Translated and revised by C. W. DODGE. New York, London.

GEML, J. 2004: Evolution in Action: molecular evidence for recent emergence of secotioid genera *Entoptychum*, *Gyrophragmium* and *Longula* from *Agaricus* ancestors. – Acta Microbiol. Immunologica Hungarica **51** (1–3): 97-108.

GREGORY, P. H. & D. R. HENDEN 1976: Terminal velocity of basidiospores of the giant puffball (*Lycoperdon giganteum*). – Trans. Br. Mycol. Soc. **67** (3): 399-407

GREIS, H. 1937: Fruchtkörperbildung und Basidienentwickelung von *Tulostoma mammosum* Fries. – Cohn Jahrb. Wiss. Bot. **84**: 517-552.

GUBE, M. 2005: Morphologisch-anatomische Studien an Fruchtkörperprimordien der Lycoperdaceae (Basidiomycetes) und ihre Bedeutung für die Systematik. Diploma thesis FSU Jena.

GUBE, M. 2007: The gleba development of *Langermannia gigantea* (Batsch: Pers.) Rostk. (Basidiomycetes) compared to other Lycoperdaceae, and some systematic implications. – Mycologia **99** (3): 396-405.

HEIM, R. 1951: Notes sur la flore mycologique des Terres du Pazifique Sud. III. Sur les *Secotium* de Nouvelle-

Zélande et la phylogénie de ce genre. – Rev. Mycol. (Paris) **16**: 129-153.

HEIM, R. 1971: The interrelationships between the Agaricales and Gasteromycetes. In: PETERSEN, R. H. (ed.): Evolution of the higher Basidiomycetes. University of Tennessee press, Knoxville: 505-534.

HIBBETT, D. S. 2004: Trends in morphological evolution in Homobasidiomycetes inferred using Maximum Likelihood: A comparison of binary and multistate approaches. – Syst. Biol. **53** (6): 889-903.

HIBBETT, D. S. 2006: A phylogenetic overview of the Agaricomycotina. – Mycologia **98**(6): 917-925.

HIBBETT, D. S.; PINE E. M.; LANGER, E.; LANGER, G. & M. J. DONOGHUE 1997: Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. – Proc. Nat. Acad. Sci. USA **94**: 12002–12006.

HOPPLE, J. S. & R. VILGALYS 1994: Phylogenetic relationships among coprinoid taxa and allies based on data from restriction site mapping of nuclear rDNA. – Mycologia **86** (1): 96–107.

HOPPLE, J. S. & R. VILGALYS 1999: Phylogenetic Relationships in the Mushroom Genus *Coprinus* and Dark-Spored Allies Based on Sequence Data from the Nuclear Gene Coding for the Large Ribosomal Subunit RNA: Divergent Domains,Outgroups, and Monophyly. – Mol. Phylog. Evol. **13** (1): 1–19.

JACOBSON, K. M., JACOBSON, P. J. & O. K. MILLER 1999: The autecology of *Battarrea stevenii* in ephemeral rivers of southwestern Africa. Mycol. Res. **103** (1): 9-17.

JEFFRIES, P. & L. MCLAIN 2004: Synonymy between *Battarrea phalloides* and *B. stevenii*. English Nature Research Reports **625**, Peterborough.

JÜLICH, W. 1984: Die Nichtblätterpilze, Gallertpilze und Bauchpilze. Aphyllophorales, Heterobasidiomycetes, Gastromycetes. Gams Kleine Kyptogamenflora IIb/1. Basidiomyceten. 1. Teil. Jena.

KIRK, M. P., CANNON, P. F., MINTER, D. W., STALPERS, J. A. 2009: Ainsworth & Bisby's dictionary of the fungi. 10th ed. Wallingford.

KREISEL, H. 1961: Über *Phellorinia herculeana* (Pers.) Kreisel comb. nov. und ihr Vorkommen in Europa. – Česka Mycologie **15** (4): 195-200.

KREISEL, H. 1962: Die Lycoperdaceae der Deutschen Demokratischen Republik. – Feddes Repert. **64**: 89-201.

KREISEL, H. 1969: Grundzüge eines natürlichen Systems der Pilze. Jena.

KREISEL, H. 1973: Die Gattung *Gyrophragmium* Mont. und ihre Stellung im System der Basidiomycetes. – Feddes Repert. **83**: 577-583.

KREISEL, H. 1998: Die Gattungen *Calvatia* und *Handkea* in Europa und der Arktis. – Österr. Z. Pilzk. **7**: 215-225.

KREISEL, H. 2001: Checklist of the gasteral and secotioid Basidiomycetes of Europe, Africa, and the Middle East. – Österr. Z. Pilzk. **10**: 213-313.

KREISEL, H., & M. AL-FATIMI 2008: Further Basidiomycetes from Yemen. – Feddes Repert. **119**(5-6): 463-483.

KREISEL, H. & D.M. DRING 1967: An emendation of the genus *Morganella* Zeller (Lycoperdaceae). – Feddes Repert. **74**: 109-122.

KRÜGER, D.; BINDER, M.; FISCHER, M. & H. KREISEL 2001: The Lycoperdales. A molecular approach to the systematics of some gasteroid mushrooms. – Mycologia **93** (5): 947-957.

LANGE, M. 1976: Some Gasteromycetes from North East Greenland. – Kew Bull. **31** (3): 635-638.

LANGE, M. 1990: Arctic Gasteromycetes II. Calvatia in Greenland, Svalbard and Iceland. – Nord. J. Bot. **9** (5): 525-546.

LEBEL, T.; THOMPSON, D. K. & F. UDOVICIC 2004: Description and affinities of a new sequestrate fungus *Barcheria willisiana* gen. et spec. nov. (Agaricales) from Australia. – Mycol. Res. **108** (2): 206–213.

LIU, B. 1984: The Gasteromycetes of China. Beih. Nova Hedwigia **76**.

LLOYD, C. G. 1902: The genera of gastromycetes. Cincinnati.

LOHWAG, H. 1925: Zur Entwicklungsgeschichte und Morphologie der Gastromyceten. Ein Beitrag zur Systematik der Basidiomyceten. – Beih. Bot. Centralbl. Abt. II **42**: 177-334.

LOHWAG, H. (1941): Anatomie der Asco- und Basidiomyceten. Handbuch der Pflanzenanatomie. Bd. VI, Abt. 2, Teilbd. 3,c. Berlin.

LONG, W. H. 1943: Studies in the Gasteromycetes: VIII. *Battarraea laciniata*. – Mycologia **35** (5): 546-556.

LONG, W. H. 1944: Studies in the Gasteromycetes X. Seven New Species of *Tylostoma*. – Mycologia **36** (4): 318-339.

LONG, W. H. & AHMAD, S. 1947: The genus *Tylostoma* in India. – Farlowia **3** (2): 225-267.

LONG, W. H. & PLUNKETT, O. A. 1940: Studies in the Gasteromycetes. I. The Genus *Dictyocephalos*. – Mycologia **32** (6): 696-709.

LONG, W. H. & STOUFFER, D. J. 1943: Studies in the Gasteromycetes. VII. The Genus *Schizostoma*. – Mycologia **35** (1): 21-32.

LONG, W. H. & STOUFFER, D. J. 1946: Studies in the Gasteromycetes. XIV. The Genus *Chlamydopus*. – Mycologia **38** (6): 819-829.

MALENÇON, G. 1930: Recherches complémentaires sur les basides de *Battarraea Guicciardiniana* Ces. – Ann. Crypt. Exot. **3**:194-199.

MALENÇON, G. 1935a: Etudes sur les Phellorinés. I. La *Phellorinia delastrei* (Dur. et Mtgn.) Ed. Fischer. – Ann. Cryptog. Exot. **8**: 5-48.

MALENÇON G.1935b: Etudes sur les Phellorinés. II. Le *Dictyocephalus curvatus* Underwood. – Ann. Cryptog. Exot. **8**: 102-132.

MALENÇON, G. 1955: Le développement du *Torrendia pulchella* Bres. et son importance morphogénétique. – Rev. Mycol. (Paris) **20**: 81-130.

MARTÍN, M. P. & H. JOHANNESSON 2000: *Battarrea phalloides* and *B. stevenii*, insight into a long-standing taxonomic puzzle. – Mycotaxon **74**: 67-75.

MATHENY, P. B.; CURTIS, J. M.; HOFSTETTER, V.; AIME, M. C.; MONCALVO, J. M.; GE, Z. W.; YANG, Z. L.; SLOT, J. C.; AMMIRATI, J. F.; BARONI, T. J.; BOUGHER, N. L.; HUGHES, K. W.; LODGE, D. J.; KERRIGAN, R. W.; SEIDL, M. T.; AANEN, D. K.; DENITIS, M.; DANIELE, G. M.; DESJARDIN, D. E.; KROPP, B. K.; NORVELL, L. L.; PARKER, A.; VELLINGA, E. C.; VILGALYS, R. & D.S. HIBBETT 2006. Major clades of Agaricales: a multi-locus phylogenetic overview. – Mycologia **98** (6): 982-995.

MAUBLANC, A. & G. MALENÇON 1930: Recherches sur la *Battarraea Guicciardiniana* Ces. – Bull. Soc. Mycol. France **46**: 43-73.

MELÉNDEZ-HOWELL, L. M. 1967: Recherches sur le pore germinatif des basidiospores. – Ann. Sci. Nat. Bot. Sér. 12 **8**: 487-638.

MILLER, O. K. 1995: Observations on unusual Gasteromycetes from North America. – Doc. Mycol. **25**: 259-267

MILLER, O. K., MILLER, H. H. 1988: Gasteromycetes. Morphological and development features with keys to orders, families and genera. Eureka.

MONCALVO, J.-M.; VILGALYS, R.; REDHEAD, S. A.; JOHNSON, J. E.; JAMES, T. Y.; AIME, M. C.; HOFSTETTER, V.; VERDUIN, S. J. W.; LARSSON, E.; BARONI, T. J.; THORN, R. G.; JACOBSSON, S.; CLÉMENCON, H. & O. K. MILLER 2002: One hundred and seventeen clades of euagarics. – Mol. Phylog. Evol. **23**: 357-400.

MORSE, E. E. 1933: A study of the genus *Podaxis*. – Mycologia **25** (1): 1-32.

PATTERSON, C. 1988: Homology in Classical and Molecular Biology. – Mol. Biol. Evol. **5** (6): 603-625.

PEINTNER, U., BOUGHER N.L., CASTELLANO M.A., MONCALVO J.-M., MOSER M.M., TRAPPE, J.M. & R. VILGALYS 2001: Multiple origins of sequestrate fungi related to *Cortinarius* (Cortinariaceae). – Am. J. Bot. **88**: 2168–2179.

RAUSCHERT, S. 1964: *Montagnea arenaria* (DC . ex Fries) Zeller, ein für Deutschland neuer Steppenpilz. – Westf. Pilzbr. **5** (1): 1-13.

REA, P. M. 1942: Fungi of Southern California. I. – Mycologia **34** (5): 563-574.

REDHEAD, S. A., VILGALYS, R., MONCALVO, J.-M., JOHNSON, J. & J. S. HOPPLE 2001: *Coprinus* Pers. and the disposition of *Coprinus* species sensu lato. – Taxon **50**: 203-241.

REHSTEINER, H. 1892. Beiträge zur Entwicklungsgeschichte der Fruchtkörper einiger Gastromyceten. – Bot. Zeit. **50**: 761-878.

REID, D., EICKER, A. 1991: A taxonomic survey of the genus *Montagnea* (Gasteromycetes) with special reference to South Africa. – S. Afr. J. Bot. **57** (3): 161-170.

REIJNDERS, A. F. M. 1975: The development of three species of Agaricaceae and the ontogenetic pattern of this family as a whole. – Persoonia **8** (3): 307-319.

REIJNDERS, A. F. M. 1977: The histogenesis of bulb and trama tissue of the higher Basidiomycetes and its phylogenetic implications. – Persoonia **9** (3): 329-362.

REIJNDERS, A. F. M. 2000: A morphogenetic analysis of the basic characters of the gasteromycetes and their relation to other hymenomycetes. – Mycol. Res. **104** (8): 900-910.

SARASINI, M. 2005: Gasteromiceti epigei. Milano.

SCHRÖTER, J. 1877: Ueber die Entwickelung und die systematische Stellung von *Tulostoma* Pers. – Cohn Beitr. Biol. Pfl. **2** (1): 65-72.

SINGER, R. (ed.) 1986: The Agaricales in modern taxonomy. Koenigstein.

SINGER, R. & SMITH, A. H. 1958: Studies on secotiaceous fungi – II. *Endoptychum depressum*. – Brittonia **10**: 216–221.

SMITH, A. H. 1971: The origin and evolution of the Agaricales. In: PETERSEN, R. H. (ed.): Evolution of the higher Basidiomycetes. Knoxville: 481-504.

SMITH, A. H. 1973: Chapter 23. Agaricales and Related Secotioid Gasteromycetes. In: AINSWORTH, G. C., SPARROW, F. K., SUSSMAN, A. S. (Hrsg.): The Fungi. An Advanced Treatise. Volume IVB. A Taxonomic Review with Keys: Basidiomycetes and Lower Fungi. New York, London: 419-450.

SWARTZ, D. 1933: Some developmental characters of species of Lycoperdaceae. – Am. J. Bot. **20**: 440-465.

THIERS, H. D. 1984. The secotioid syndrome. – Mycologia **76** (1):1–8.

TOWNSEND, B. B. 1954: Morphology and development of fungal rhizomorphs. – Trans. Br. Mycol. Soc. **37**: 222-233.

VAN DE BOGART, F. 1976: The genus *Coprinus* in Western North America, Part I: Section *Coprinus*. – Mycotaxon **4** (1): 233-275.

VELLINGA, E. C. 2004a: Ecology and Distribution of Lepiotaceous Fungi (Agaricaceae) – A Review. – Nova Hedwigia **78** (3-4): 273-299.

VELLINGA, E. C. 2004b: Genera in the family Agaricaceae: evidence from nrITS and nrLSU sequences. – Mycol. Res. **108** (4): 354–377.

VON ARX, J. A. 1967: Pilzkunde: ein kurzer Abriss der Mykologie unter besonderer Berücks. der Pilze in Reinkultur. Berlin, Stuttgart.

WEBER, H. 1993: Allgemeine Mykologie. Jena, Stuttgart.

WEBSTER, J. 1983: Pilze, eine Einführung. Berlin, Heidelberg, New York: Springer.

WHITE, V. S. 1901: The Tylostomaceae of North America. – Bull. Torrey Bot. Club. **28** (8): 421-444.

WRIGHT, J.E. 1987: The Genus *Tulostoma* (Gasteromycetes) – A World Monograph. – Bibl. Myc. **113** Berlin, Stuttgart.

WRIGHT, J. E. & V. L. SUAREZ 1990: South American Gasteromycetes IV. The genus *Abstoma*. – Crypt Bot. **1**: 372-383.

ZELLER, S. M. 1943: North American species of *Galeropsis*, *Gyrophragmium*, *Longia*, and *Montagnea*. – Mycologia **35**: 409-421.

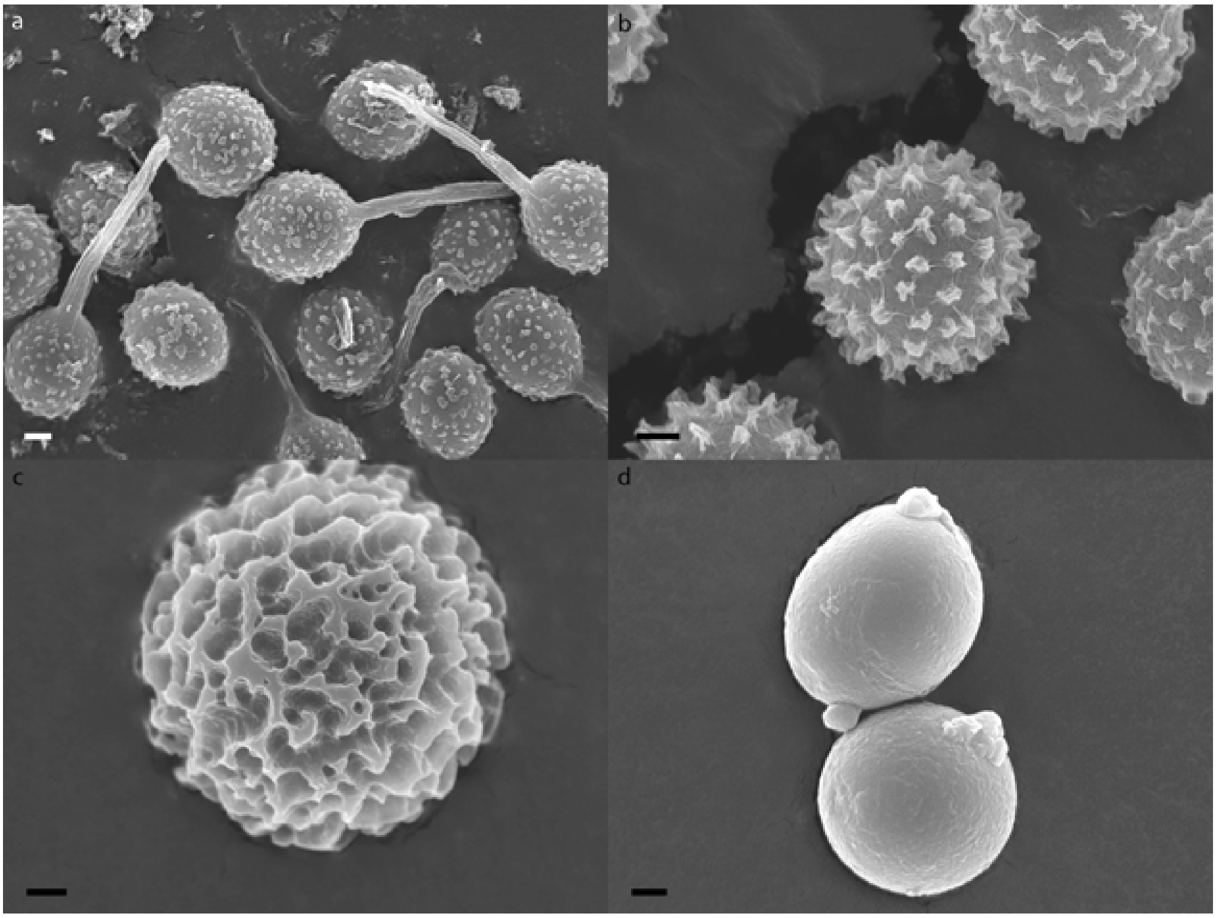

FIG. 1: SEM images of spores, scale 1 µm. a: *Bovista plumbea* MG 061202_7, verrucose spores with long pedicels, b: *Lycoperdon echinatum* MG 061024_8, spinulose spores, c: *Mycenastrum corium* HD MON 142, reticulate-pitted spore, d: *Endoptychum agaricoides* HD MON 249, smooth spores with short sterigmal remains. Photos: U. Neugebauer.

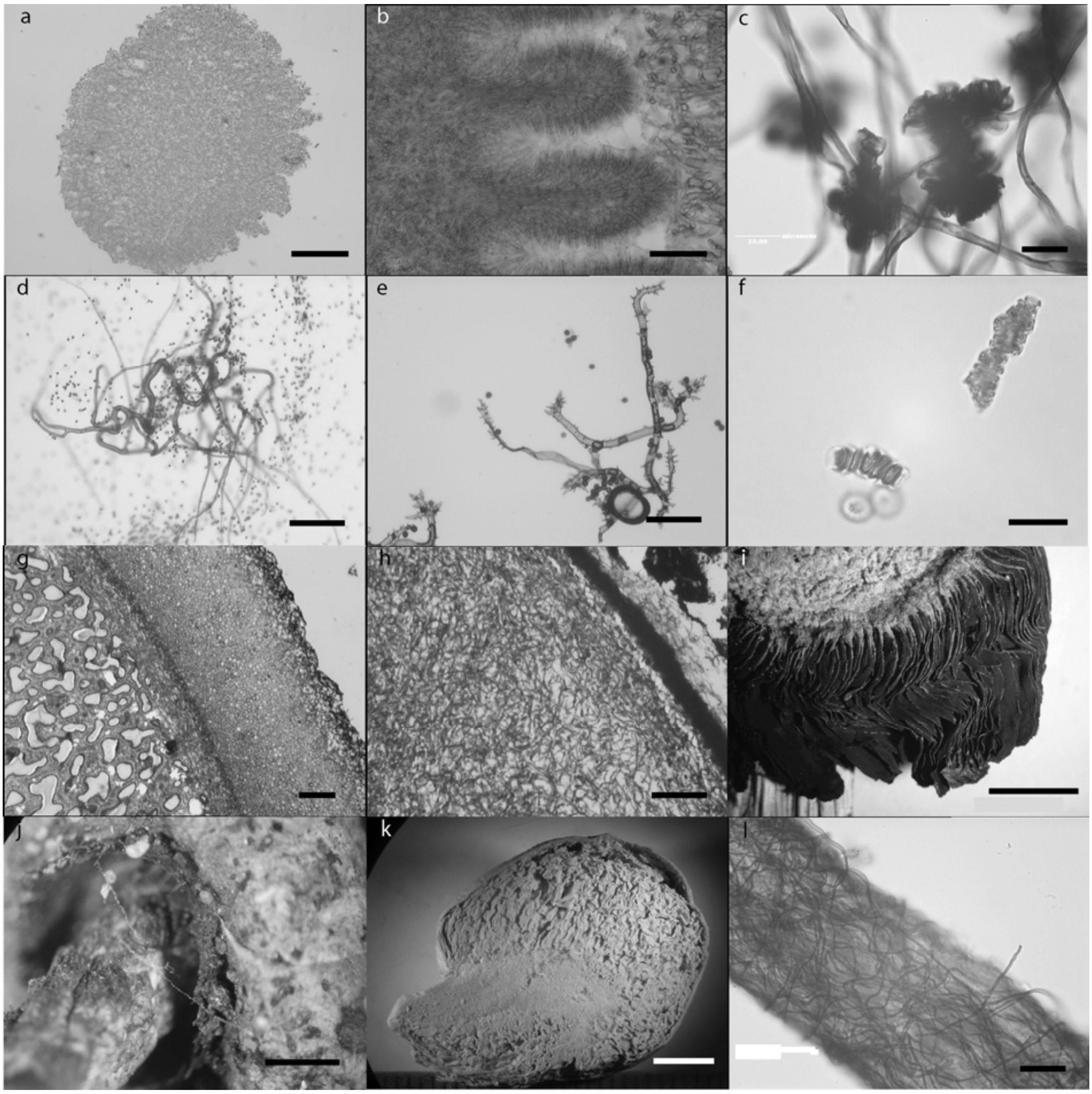

FIG. 2: Anatomical features of gasteroid Agaricaceae s. l. a: *Lycoperdon perlatum* MG 041001_1 , microtome section of young primordium, scale 50 µm, b: *Agaricus bisporus* HD Dederstedt, microtome section of developing lamellae, scale 50 µm, c: *Podaxis pistillaris* HD AUS 216, fasciculate basidia and capillitium, scale 20 µm, d: *Bovista tomentosa* GLM 40948, capillitium, scale 100 µm, e: *Mycenastrum corium* HD MON142, spinulose capillitium, scale 100 µm, f: *Battarraea phalloides* HD MON89, elaters, scale 10 µm, g: *Bovista plumbea* MG 040909_1, microtome section of peridium and hymenial cavities, scale 200 µm, h: *Tulostoma brumale* MG 061015_1, microtome section of peridium and developing gleba, scale 100 µm, i: *Montagnea arenaria* GLM 19673, lamellae tear pileus trama apart, scale 5 mm, j: *Tulostoma squamosum* MG 071020_18, stipe inserted into peridium, surrounded by exoperidial remains, scale 1 mm, k: *Endoptychum arizonicum* MICH 081031, stipe not protruding through gleba, scale 5 mm, l: *Bovista furfuracea* MG 071020_7, Rhizomorph with sclerified hyphae stained with indigotin, scale 20 µm. Photos: M. Gube

Discussion and future prospects

Gasteromycetation is an evolutionary process causing considerable changes in fruitbody formation and mature anatomy, especially spore formation. The complexity of this process is visible in the differences observed between various gasteroid groups that have been assigned to the family of Agaricaceae. These groups were traditionally treated as independent taxa, but molecular phylogenetic work has shown them to be closely related (Lebel et al. 2004, Geml 2004, Vellinga 2004b). Anatomical features helping to interpret this process have not been fully considered or were not available so far. This is especially true for the study of ontogeny. Developmental analyses in evolutionary context have faced a revival in the last decades (Theißen 2006). They were mainly focused genes involved in regulation of development in plants and metazoa (Wagner 2000, Theißen 2006), although work on fungi is present (Kothe 1997, 2008, Kües & Liu 2000, Hennicke et al. 2009, and references therein). Prerequisite of such work is knowledge on the features during ontogeny through mature anatomy, which can help to point out homologies and convergences. The findings can then be compared to phylogenetic relationships, which need to be resolved as well as possible.

Connections between Agaricaceae and gasterothecia were considered early (de Bary 1866, Underwood 1899, Conard 1915, Gäumann 1926) without general support (Gäumann & Dodge 1928, Cunningham 1944). After some kind of relationship of at least the secotioid taxa was accepted, hypotheses on the direction of evolution led to controversial disputes (Heim 1971, Smith 1971, Thiers 1984, Singer 1986). It was finally shown by molecular phylogenetic studies that many gasteroid groups originate among Agaricaceae s. l., even true gasteroid groups without known anatomical connections (Hopple & Vilgalys 1994, Hibbett et al. 1997, Krüger et al. 2001, Moncalvo et al. 2002, Lebel et al. 2004, Geml 2004, Vellinga 2004). However, the phylogenetic resolution of these studies did not allow for definition of gasteromyctation events, and further studies incorporating more gasteroid taxa were suggested (Vellinga 2004). To face this task, DNA of about 650 specimens from public and private collections was extracted, focusing on gasteroid groups. Since multi-gene analyses can improve the resolution of phylogenetic reconstruction (Matheny et al. 2006), three genetic markers were selected. Amplified loci include the complete nuclear ITS region, the 3’-region of 28S nrDNA, and the first intron of RPB1. For the Agaricaceae s. l., nrDNA has been proven to be informative (Moncalvo et al. 2002, Lebel et al 2004, Vellinga 2004, Larsson & Jeppson 2008), and RPB1 was suggested as informative marker for Basidiomycetes (Matheny et al. 2002). Concatenated, partitioned datasets were analysed by Maximum Likelyhood and by Bayesian Inference.

Agaricaceae s. l. were proven to be monophyletic within Basidiomycetes. Using the markers introduced above, five major clades were resolved. This contrasts to previous studies, where monophyly of Agaricaceae s. l. and relationships of its clades were widely unsupported (Johnson 1999, Moncalvo et al. 2001, Vellinga 2004). Four of these groups contain at least ten independent events of gasteromycetation, and are referred to as separate families. The most basal clade are the exclusively gasteroid Tulostomataceae, with a single ancient gasteromycetation event, corresponding to some of the analyses of Vellinga (2004). Among this clade, the relationships of Tulostomae, Phelloriniae and Battarraeae are resolved. The Coprinaceae clade includes *Coprinus* sect. *Coprinus* with a single gasteromycetation event, the secotioid genus *Montagnea*. This emphasises the view presented in some previous studies (Hopple & Vilgalys 1994, Hopple & Vilgalys 1999, Redhead et al. 2001). The family Lepiotaceae including the *Cystolepiota* group contains no known gasteromycetation events. However, they were not considered before as a monophyletic clade (Johnson & Vilgalys 1998, Johnson 1999, Vellinga 2003). Lycoperdaceae are the sister group to Agaricaceae s. str., and are descendants of a single gasteromycetation event. This conflicts with results of Bates (2004) and Krüger et al. (2001), and corresponds to results of Larsson and Jeppson (2008). Inclusion of *Mycenastrum* is proven for the first time with all other agaricacean clades present. A separate dataset incorporating 245 lycoperdacean taxa was analysed (Fig. 1), supplementing the analyses described above. Additionally, some conclusions can be drawn, partly supporting the results of Larsson and Jeppson (2008). For the first time, species of *Abstoma* have been analysed by molecular phylogeny, and the genus is shown to be paraphyletic, with *A. townei* and *A. reticulatum* constituting the second clade of Lycoperdaceae, and *A. verrucisporum* clustering with *Calvatia fumosa*. Spore and capillitium characteristics support this arrangement (Wright & Suarez 1990). Problematic is *Disciseda* in clustering in two distinct, but morphologically completely unsupported groups. This genus therefore needs to be checked for presence of paralogs. *Calvatia* is restricted to the sections *Gigantea* (= *Langermannia*), *Hippoperdon* and *Calvatia*, all species considered within the segregate genus *Handkea* (Kreisel 1992) cluster within *Lycoperdon*. Monophyly of *Bovista*, composed of the two strongly divergent subgenera *Bovista* and *Globaria*, is only weakly supported. Some specimens determined within *Bovista* subgen. *Globaria* apparently belong to *Lycoperdon*, as already noted for *Bovista dermoxantha* by Larsson and Jeppson (2008). *Lycoperdon pyriforme* and the genus *Arachnion* constitute a clade previously not separated

(Bates 2004). *L. pyriforme*, in addition, can be clearly differentiated from *Lycoperdon* subgen. *Morganella*, which was proposed by Krüger and Kreisel (2003). A clade of specimens determined as *Bovista pusilla* is the sister clade of the genus *Lycoperdon*. Without any morphological distinctive features, it also has to be checked for paralogs. *Lycoperdon* itself is well supported, but relationships of the subgeneric clades are only weakly supported. The distinctive clade including *L. pedicellatum*, *L. perlatum*, *Morganella* and *Vascellum* has already been indicated by Larsson and Jeppson (2008). Several species so far considered as *Calvatia*, *Handkea*, *Bovistella*, or *Calbovista* are included within *Lycoperdon*, improving the generic concept proposed recently (Larsson & Jeppson 2008).

Agaricaceae s. str. are represented by three subclades. *Macrolepiota* s. str. and *Podaxis* have not been considered related before, but share spore and veil characteristics (Meléndez-Howell 1967, de Villiers et al. 1988), in addition to the support in molecular phylogeny. Placement of the *Leucoagaricus*/*Leucocoprinus* group with several fungi symbiotic with attine ants corresponds to previous analyses (Johnson & Vilgalys 1998). *Chlorophyllum* in the sense of Vellinga (2004) was shown to be a paraphyletic assemblage, with *Agaricus* emerging from this group. Related to *Chlorophyllum* are *Endoptychum arizonicum* and *Endoptychum agaricoides*, constituting two independent gasteromycetation events. *Agaricus* was shown to accommodate several gasteroid taxa (Geml 2004, Lebel et al. 2004, Vellinga 2004), which has been confirmed here. Three secotioid taxa are related to sections *Arvenses* and *Minores*, while *Barcheria* belongs to the section *Xanthodermei*. No trace of evolution from gasteroid towards hymenothecial taxa was observed in any of the gasteroid taxa, supporting unidirectionality of gasteromycetation (Hibbett 2004).

Although ontogenetic features contain valuable phylogenetic information and may link taxa with deviating mature morphology by common early stages, no overall system of fungal development exists. This is partly caused by the plectenchymatic nature of fungal structures, which may gradually interchange and can always be traced back to two-dimensional hyphal growth. On the other hand, many fungi, among them most gasteroid taxa considered here, are not forming fruitbodies in culture so far. Ontogenetic analyses therefore have to rely on taxa and stages found in the field, which inevitably leads to incomplete desciptions of ontogeny. Relationships of the *Calvatia*/*Handkea*/*Langermannia* group of Lycoperdaceae were discussed controversially (Calonge & Martín 1990, Kreisel 1992, 1994, Lange 1993, Calonge 1998). Therefore the ontogeny of some species of that group was analysed by light microscopy of microtome sections. The results shown here provide information sustaining systematic relationships as deduced from molecular phylogeny.

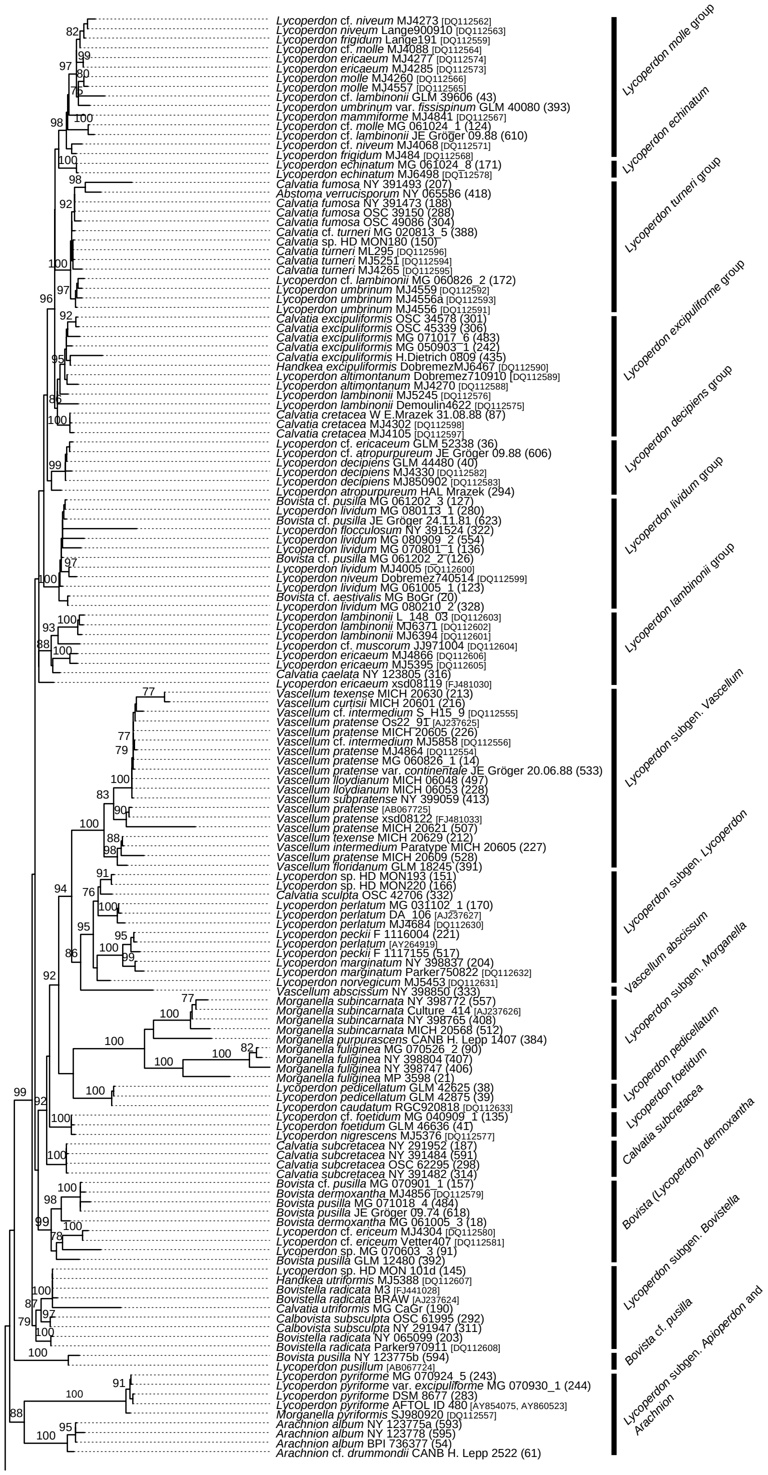

FIG. 1: ML phylogram of Lycoperdaceae. LR-ELW support values above 75 are indicated above corresponding branches. Culture collection or herbarium reference is given after the species binomial. Clades corresponding to Larsson and Jeppson (2008) are given as defined there; other clades are indicated by typical genera or species. GeneBank entries are indicated by their accession numbers in edged brackets, availability of several loci is indicated by their corresponding accession numbers in the order ITS, LSU, RPB1. Figure continued on next page.

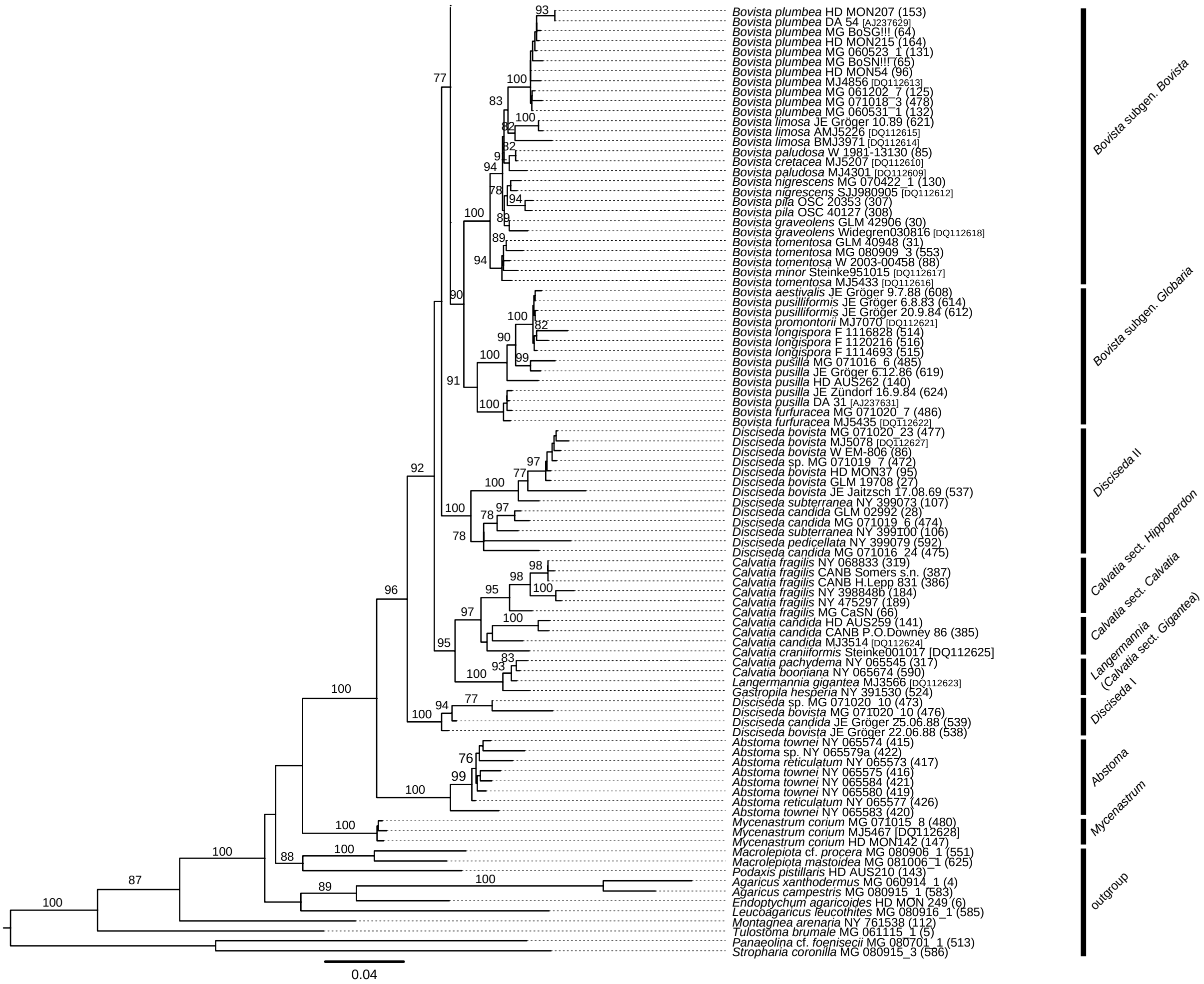

FIG. 1: Figure continued from previous page.

The hymenium of *Langermannia gigantea* was shown to develop in a unique flabelloid manner, which was previously unknown. The hymenium-forming palisade layers are borne on fan-like branches of hyphae, probably corresponding to tilaiohymenia as described by Clémençon (1997, 2004). The same mode is probably present in *Calvatia* sect. *Calvatia* and sect. *Gigantea*, as indicated by a figure of *Calvatia craniiformis* in Swartz (1935, Fig. 2a). Rhizomorph structures further distinguish *Langermannia* from other Lycoperdaceae, they resemble more closely those of *Agaricus bitorquis*. It was proposed to refer to *Langermannia* as separate from *Calvatia*, since only species now considered within *Lycoperdon* were analysed in this study. Hymenial development of the remaining Lycoperdaceae does also not agree with previous classifications, where lacunar and coralloid types were distinguished (Lohwag 1925, Fischer 1933, Miller & Miller 1988). However, elements of both are present here, visible in the descriptions of Lycoperdaceae to develop in an either lacunar (Ahmad 1950) or coralloid way (Fischer 1936, Kreisel 1962). Thus the coralloid-lacunar type of gleba development is introduced for the Lycoperdaceae (Fig. 2b).

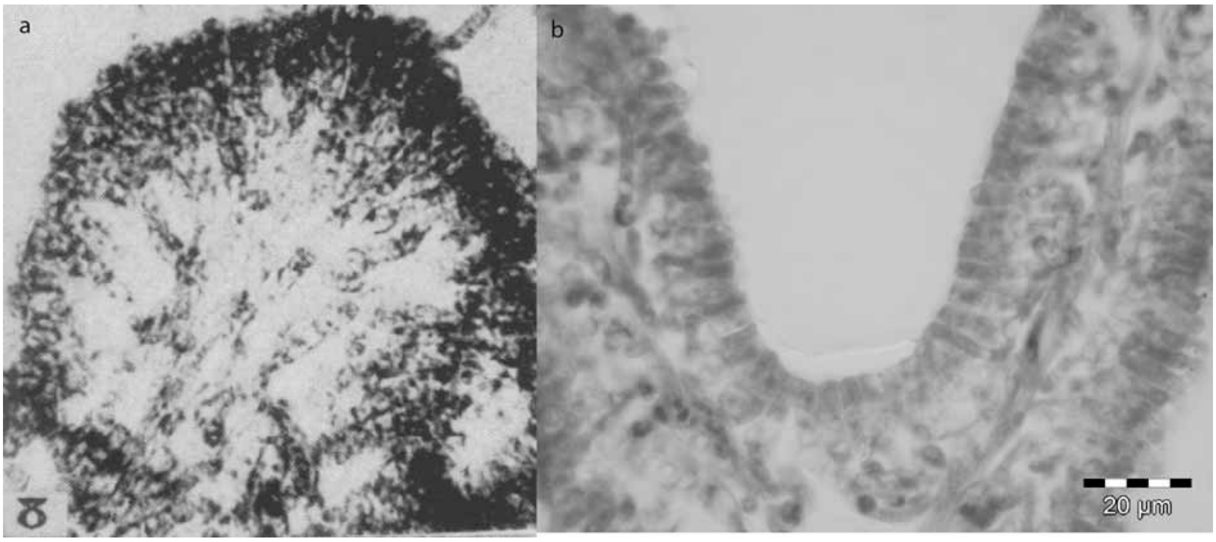

FIG. 2: Hymenial ontogeny of Lycoperdaceae. a: flabelloid hymenial development in *Calvatia craniiformis*; b: coralloid-lacunar gleba chamber in *Lycoperdon foetidum*. Photos: reproduced after D. Swartz 1935 (a), M. Gube (b).

Floristic studies provide the basis for any systematic and biogeographical studies.They provide information on distribution and facilitate appropriate taxon sampling for further analyses. Anemochorous gasterothecia are especially diverse in natural open land habitats such as the Central Asian steppe region. Others inhabit tropical rainforest, while still keeping anaemochorous dispersal strategies. Therefore, the secotioid fungi of Mongolia and the Gasteromycetes of Panama were revised, based on field and herbarium collections and literature research.

For Mongolia, two secotioids were newly reported, *Montagnea haussknechtii* and *Endoptychum agaricoides*. The general distribution, ecology and systematic relationships of all four secotioids known from Mongolia are discussed. Especially *M. haussknechtii* proved a very valuable record in indicating a worldwide distribution of that species, and in providing material of this rare species for further analysis. *Montagnites schuppi* Rick is proposed to be synonymous with *Gyrophragmium dunalii*. Furthermore, the inappropriate of synonymisation of *Endoptychum* to *Chlorophyllum* is shown.

For Panama, the known records of Gasteromycetes are revised and improved by nine new records and a putative new species of *Radiigera* (Geastraceae). For all 33 records, concise descriptions and details on local and worldwide distribution are given, together with some taxonomic and nomenclatural comments. Most valuable are the second record of *Calvatia rosacea* Kreisel apart from the locality of the type, and *Radiigera* cf. *taylorii*, which was so far known only from temperate and subtropical North America (Dominguez de Toledo &

Castellano 1996). Lycoperdacean specimens from Panama were incorporated into further analyses.

Since both ecological constraints and phylogenetic heritage may be causes for the presence of morphological features, analyses should consider the ecological circumstances of their evolution in addition to their phylogenetic relationships. Such studies can facilitate homologisation of features when phylogenetic heritage is concealed by adaptation to ecological constraints. This is especially true for Agaricaceae s. l., where morphological features differ in such apparent manner, and are rich in convergent characters. By extensive morphological studies of herbarium material, and under consideration of the literature, gasteroid fungi related to Agaricaceae s. l. are compared, and their dispersal strategies are discussed.

Three main groups are proposed relying on comparable basal features. This includes the exclusively gasteroid Lycoperdaceae and Tulostomataceae, and all secotioid species. All these species share nodulocarpous fruitbody initiation. Lycoperdacae are present in steppe and temperate areas, but also in tundra und tropical rainforest while they are absent from deserts. Two types of adaptation are present in spore dispersal mechanisms of steppe and tundra, geanemochorous tumblers like *Bovista* and species with irregular peridium laceration like many species of *Calvatia*. In temperate and boreal biomes, Lycoperdaceae are usually ombrohydrochorous, as most members of the genus *Lycoperdon*. Steppe species are present synanthropically in grasslands and agricultural areas of these zonobiomes. Fast growing, paedomorphic Lycoperdaceae are present in tropical rainforest and mostly belong to *Lycoperdon* subgen. *Morganella*. The family is anatomically extremely derived, hindering homologisation with hymenothecia. Tulostomataceae are predominantly present in deserts and steppe, and few other open land habitats. Desert Tulostomataceae are euanamochorous, in contrast to the ombrohydrochorous steppe species. Their main adaptive advantage is their hypogeous ontogeny. This group shows more homologisable features like the true stipe and probably homologous veils. However, hymenial organisation is as derived as that of Lycoperdaceae, and in the most extreme cases, no hymenium is formed at all. The secotioid species, equally, mainly are present in steppe and desert. The species of *Podaxis*, *Endoptychum*, *Gyrophragmium*, *Longula* and *Montagnea* vary greatly in their anatomy due to their differing hymenothecial relationships. They are generally euanemochorous. Many of their features still reflect their evolutionary heritage, as the smooth, sometimes heterotropic spores with pigmentation resembling their hymenothecial relatives, the lamellar gleba and their velar structures. Others, like the presence of capillitium or the prolonged hypogeous ontogeny, are newly acquired under the ecological constraints of their habitat. *Barcheria willisiana* is as closely related to *Agaricus* as *Gyrophragmium* or *Longula*, but in contrast to the latter possesses extremely derived basidiomes.

Gasteromycetation within Agaricaceae s. l. can generally be placed in semiarid open land biomes, such as steppe or savannah. This coincides with the presence of descendants of all gasteromycetation events in such habitats, the lack of competition from ectomycorrhizal species, and the acquirement of thick-walled or pigmented spores, even if the nearest hymenothecial relatives have neither. Furthermore, the dispersal strategy of euanemochory, which requires the least anatomical changes, is present in all analysed groups of gasterothecia, and all other ways of spore dispersal can be derived from it, allowing for colonisation of other biomes.

With the number of the gasteromycetation events known, and the phylogenetic relationships widely resolved, the time of emergence of the gasteroid clades still remains unknown. Since no Agaricacean fossils are available, any attempt of dating would have to rely on remotely related fossils (Hibbett et al. 1995, Hibbett et al. 2003). Determining absolute divergence times would necessitate assumption of comparable evolutionary rates, which would render results highly speculative. However, approaches revealing relative divergence times have recently been undertaken for Ecuadorian hoplocerine lizards (Torres-Carvajal & de Queiroz 2009). Comparison of relative divergence times of the gasteroid clades could prove the assumption of certain groups such as Lycoperdaceae and Tulostomataceae being much older than most secotioids, and precisely compare anatomical deviation over time.

Results of such studies would facilitate analyses of the connections between speciation and distribution of the gasteroid groups. Fungi are among the few organisms where sympatric speciation may be assumed, this is especially true for gasterothecia with their extreme adaptation to anemochory. A model for the study of this process could be *Montagnea*, with both known species worldwide distributed in appropriate habitats, of which one constitutes probably the ancestral population of the other. Furthermore, species such as *Longula texensis* and *Endoptychum depressum* or *E. arizonicum* are restricted to south-western North America, whereas *Montagnea*, *Podaxis*, or *Endoptychum agaricoides* are distributed worldwide. It would have to be checked if this corresponds to the relative age of the gasteromycetation event.

Evolution from gasterothecia towards hymenothecia has most likely never occurred in Agaricaceae s. l. The whole process has been credibly proposed as unidirectional (Reijnders 2000, Hibbett 2004), caused by the loss of the complex ballistospore mechanism. However, the existence of gasterothecia without reproductional barriers against their still existing ancestors has been proven for *Lentodium squamosum* (Hibbett et al. 1994) and assumed for *Gastrosuillus laricinus* (Baura et al. 1992). Thus it is reasonable to assume that ballistospore formation can be re-acquired, but only as long as mating is possible. Furthermore whole gasteroid lineages gave rise to other, morphologically highly divergent, but still gasteroid forms (Hosaka et al. 2006). The development of single gasteroid fruitbodies can be found also as environmentally controlled process. This is opposed to the genetically heritable gasteromycetation process. Changes in light regime (Watling 1971) or mechanical disturbances (Magnus 1906) have been described to cause fundamental changes in hymenial anatomy, including gasteroid forms. Additionally, mycelium of an initially gasteroid mutant of *Agaricus bisporus* reverted to production of normal, gilled fruitbodies after some time (Fritsche 1968). It thus seems that gasteromycetation is not generally linked with reproductive barriers, and can even be induced environmentally.

It can therefore be concluded that gasterothecia do not constitute a final point or summit of evolution, as sometimes assumed (Underwood 1899, Heim 1971, Singer 1986, Albee-Scott 2007), and are subject to selective constrains like any other living organism. Gasteromycetation can lead to reproductional isolation and subsequent speciation of survivors, if some adaptive advantage in appropriate habitats is given. Only then the process is truly irreversible. Ancestral state reconstruction analyses could further strenghten this view.

Generally, the occurrence of gasterothecia, both comparable and incomparable to hymenothecia, raises the question of the age of the corresponding clades being sufficient to explain this situation by assuming a gradual change. On the phenotypic level, one has to distinguish between adaptation to an environment by small gradual changes, visible in the varying dispersal strategies of Lycoperdaceae and Tulostomataceae; and fundamental changes in anatomy, which must have occurred in the ancestral populations of these two groups and, to a lesser extent, in the secotioid taxa. A so called “secotioid inertia” has been assumed (Albee-Scott 2007), leading gradually to gasterothecia and to extinction of hymenothecial relatives, thus causing the lack of missing links. This orthogenetic (Levit et al. 2008) approach is fundamentally flawed, as this implies the presence of nonselective constraints in evolution. Furthermore, it assumes an optimal final shape of the process, without considering groups other than Russulaceae. A more plausible alternative is based on the assumption of paedomorphosis. This process is characterised by sexual maturity in morphologically otherwise immature organisms, and is relatively common in plants and animals (Laurent et al. 1998, Wiens et al. 2005). It has been proposed that paedomorphosis plays a major role in gasteromycetation (Thiers 1984, Bruns et al. 1989), and it seems especially probable in agaricoid fungi, where the hymenial structures generally emerge enclosed within a nodulocarpous primordium (Reijnders 1977, Clémençon 2004). It is obvious that paedomorphosis requires disturbance of the successional expression of developmental genes. Such changes, especially in the early stages of developmental processes, can result in highly divergent mature anatomy, which might prove as “hopeful monsters” (Goldschmidt 1933, Gould 1977, Theißen 2006).

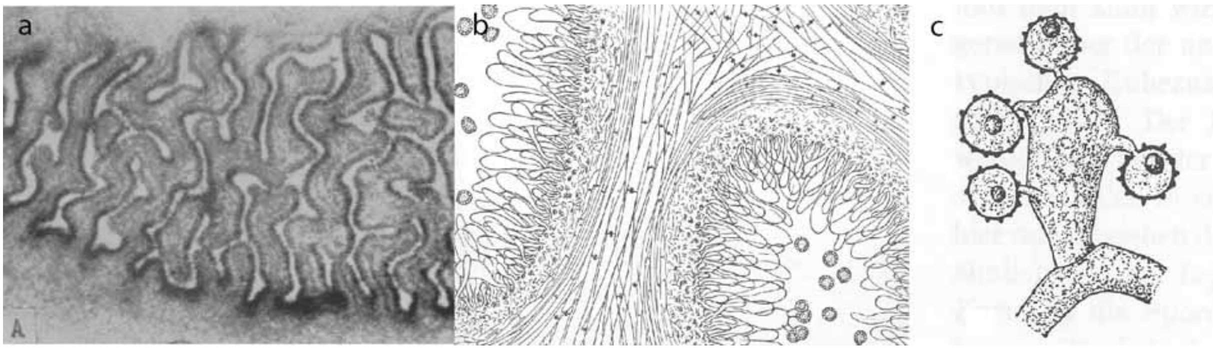

FIG. 3: Hymenial structures of gasteroid Agaricaceae s. l. a: Anastomosing lamellar plates of *Longula texensis*; b: Glebal chambers of *Battarraea phalloides*; c: Pleurosporous plectobasidium of *Tulostoma brumale*. Images reproduced after Barnett 1943 (a), Maublanc and Malençon 1930 (b), Greis 1937 (c).

An example may be the sterigmatal and hilar complex, which develops late in hymenial ontogeny to full functionality (Yoon & McLoughlin 1984, 1986). The development of basidiomata of cdc-42-mutants of the derived cyphelloid basidiomycete *Schizophyllum commune* is disturbed, insofar as later ontogenetical stages are lacking. However, dysfunctional spores are produced, borne on divergent sterigmata, which are thick-walled and longer than in the wildtype, and very probably not capable of active spore discharge (N. Knabe & F. Hennicke pers. comm.). In gasterothecia, sterigmata are also often highly divergent, as seen in the exceptionally long, sclerified pedicels of some Lycoperdaceae, the often sessile spores of *Podaxis*, or the pleurocarpous basidia of *Tulostoma* (Fig. 3c). Their incapabability of active spore discharge is part of the definition of gasterothecia. Furthermore, gasteroid fungi generally possess modified hymenial trama, which may consist of anastomosing lamellar plates in the secotioids (Fig. 3a), irregular chambers in most true gasteroids (Fig. 3b), or plectobasidia in *Tulostoma* (Fig. 3c). These features could be result of independent disturbances in the order of gene expression, leading to the common effect of loss of ballistospory. Summarising, if spores ripen before full functionality of the ballistosporic hymenium is gained, and environmental constraints allow for reproduction of the concerned fungus, a new gasterothecium is born. Analysis of the underlying genetical mechanisms is so far still hindered by insufficient knowledge of developmental genes. However, the studies incorporated here could contribute background information for such analyses.

Considering the available data, two major complexes of gasteroid appearance are realised in Basidiomycetes. Gasterothecia of mycorrhizal origin are often adapted to endozoochory, with moist, nutritious trama, and a tendency to subterranean growth with release of volatile compounds at maturity to prevent being consumed prematurely. This strategy has been revised by Thiers (1984) and Bruns et al. (1989). Saprobic gasterothecia, on the other hand, are not restricted to forested areas, and evolved in more or less arid open land habitats. Draught protection and the ability for prolonged spore dormancy is therefore generally realised (Thiers 1984, Vellinga 2004a) by protection of the developing spores within peridial structures or by prolonged subterranean ontogeny. Often, certain adaptations of the spores, such as melanin incorporation and thick spore walls, are present. These features are most distinctly realised in desert species (Kreisel & Al-Fatimi 2008). Anemochorous spore dispersal is initially more likely to be successful in open land, where stronger and more directed jets of air occur, and complicated changes in spore anatomy are not selectively enforced. More derived gasteromycete groups like Tulostomataceae and Lycoperdaceae gained adaptations to more sophisticated variants of anemochory, like capillitial threads, ornamented spores and functional peristomes, allowing for colonisation of forested biomes, where saprobic gasterothecia would otherwise be evolutionary counter-selected. This strategy is probably also realised in saprobic gasterothecia of differing phylogenetic heritage. Yet, these delineations remain hypothetical so far. Apart from the generalising nature of every model, lack of data is a main cause of this situation. Studies of anatomy, especially ontogeny, are widely outdated, and floristic or ecological studies are scarce, especially outside the industrial countries. The studies included in this thesis are a contribution to overcome these problems, and may serve as basis for further work on these topics.

Summary

The focus of this work are the gasteromycetation events of fungi related to the Basidiomycete family of Agaricaceae. These fungi occur in a high diversity of shapes, and yet they are all adapted to angio- or cleistocarpic, passive spore dispersal. Traditionally, these fungi were covered in the families of Lycoperdaceae and Tulostomataceae, or in various secotioid genera of uncertain assignment. Molecular phylogeny of the last years resulted in placement of all these groups into the Agaricaceae.

By molecular phylogeny, ten independent events of gasteromycetation were revealed within Agaricaceae s. l., and their relationships to hymenothecial taxa were shown. Five major clades were revealed, which are referred to as Tulostomataceae, Coprinaceae, Lepiotaceae, Lycoperdaceae and Agaricaceae s. str. The families of Tulostomataceae and Lycoperdaceae are exclusively gasteroid, the first constitutes the basal clade of Agaricaceae s. l., and the latter the sister group of Agaricaceae s. str. Gasterothecia are furthermore present in Coprinaceae with the genus *Montagnea* emerging within *Coprinus* sect. *Coprinus*.

The majority of gasteromycetation events is shown for Agaricaceae s. str., with the secotioid *Podaxis pistillaris* related to *Macrolepiota* s. str., and the independent lineages of *Endoptychum agaricoides* and *E. arizonicum* related to *Macrolepiota* sect. *Laevistipedes*. *Chlorophyllum*. *Longula texensis*, *Gyrophragmium dunallii*, *Endoptychum depressum* and *Barcheria willisiana* are emerging from *Agaricus*. Gasteromycetation events are not present in Lepiotaceae. Also, no sign of evolution from gasterothecia to hymenothecia was noticed. Existing phylogenetic knowledge was improved in the detection of polyphyly of the *Chlorophyllum*/*Endoptychum*/*Macrolepiota* sect. *Laevistipedes* group, and in assigning *Podaxis* to *Macrolepiota* s. str.

For *Langermannia gigantea*, the new flabelloid type of hymenial development is shown, with considerable differences to the remaining groups of Lycoperdaceae. Hymenial development of Lycoperdaceae generaly deviates from the results of previous analyses. *Langermannia* was therefore referred to as a genus independent from *Calvatia*. This result is supported by results of molecular phylogeny, with a greater part of *Calvatia*, among them the ontogenetically analysed species, belonging to *Lycoperdon*. However, some other species of *Calvatia* constitute a separate clade, together with *Langermannia*. The flabelloid type of ontogeny seems to be present in this clade. This demonstrates that morphological features within gasteroid clades are homologisable, enabling comparative analyses.

New data on distribution of gasteroid fungi was gained by fungus-floristic analyses of the secotioid fungi of Mongolia, and the gasteroid fungi of Panama. Two new records for Mongolia, and ten new findings for Panama are given. The presence of all other known species is discussed on account of nomenclatural, taxonomic and systematic points of view. All Mongolian, and a great part of the Panamanian findings enlarged the taxon sampling of the phylogenetic and morphological analyses.

In a review of the morphological features of gasteroid Agaricaceae s. l. under consideration of ecological background and phylogenetic relationships, three main functional groups are defined with Lycoperdaceae, Tulostomataceae, and the secotioid species. Gasteromycetation is explained as evolutionary process where the presence of comparable ecological constraints led to analogous anatomical changes, often concealing phylogenetic heritage. Many morphological and ontogenetic features of Lycoperdaceae und Tulostomataceae deviate strongly from hymenothecial relatives, hindering their homologisation. On the other hand, the secotioid groups possess many features linking them with hymenothecia.

The evolutionary age fails to fully explain the morphological differences between gasteroid groups. The secotioid genus *Podaxis* is phylogenetically quite old, but shares many features with the related hymenothecial genus *Macrolepiota*. Contrastingly, *Barcheria* deviates strongly from *Agaricus*, despite close relationship. Paedomorphosis, understood as disturbance of the succession of developmental regulation, is assumed as triggering process of gasteromycetation.

All ten gasteromycetation events within Agaricaceae s. l. occurred in semiarid openland habitats. The primary dispersal strategy of gasteroid Agaricaceae is euanemochory, which is established predominantly in steppe and desert habitats. From there, colonisation of other biomes by Lycoperdaceae and Tulostomataceae followed under evolution of ombrohydochory and geanemochory with adequate anatomical features. This is supported by the distribution of the different types of gasterothecia.

Zusammenfassung

Schwerpunkt dieser Untersuchung sind die Gasteromycetationsereignisse von Vertretern der Agaricaceae. Bauchpilze, die zu dieser Familie der Basidiomyceten gehören, sind durch eine hohe Formenvielfalt sowie passive und angio- oder cleistocarpe Sporenverbreitung gekennzeichnet. Traditionell wurden diese Pilze den Familien der Lycoperdaceae und Tulostomataceae oder aber secotioiden Gattungen zugeordnet. Als Resultat molekular-phylogenetischer Analysen der letzten Jahre wurden all diese Gruppen in die Agaricaceae integriert.

Mittels eigener molekular-phylogenetischer Analysen wurden zehn unabhängige Gasteromycetationsereignisse innerhalb der Agaricaceae s. l. nachgewiesen und Beziehungen zu hymenothecialen Taxa aufgedeckt. Fünf größere Claden wurden nachgewiesen, die den Tulostomataceae, Coprinaceae, Lepiotaceae, Lycoperdaceae und Agaricaceae s. str zugerechnet werden. Die Familien der Tulostomataceae und Lycoperdaceae sind ausschließlich gasteroid, erstere stellt die basale Gruppierung der Agaricaceae s. l. dar, letztere ist die Schwestergruppe der Agaricaceae s. str. Weitere Gasterothecien wurden in den Coprinaceae nachgewiesen. Die secotioide Gattung *Montagnea* entstand innerhalb von *Coprinus* sect. *Coprinus*.

Die Mehrzahl der Gasteromycetationsereignisse fand in den Agaricaceae s. str. statt. Hierzu gehören *Podaxis pistillaris* in der Verwandtschaft von *Macrolepiota* s. str. sowie *Endoptychum agaricoides* und *E. arizonicum,* die unabhängig voneinander nahe mit *Macrolepiota* sect. *Laevistipedes* und *Chlorophyllum* verwandt sind. Innerhalb der Gattung Agaricus entstanden *Longula texensis*, *Gyrophragmium dunallii*, *Endoptychum depressum* und *Barcheria willisiana*. In den Lepiotaceae lässt sich keine Gasteromycetation nachweisen. Es gibt keine Anzeichen einer Evolution von Gasterothecien zu Hymenothecien. Die Polyphylie der *Chlorophyllum*/*Endoptychum*/*Macrolepiota* sect. *Laevistipedes*-Gruppe und die engen Verwandtschaftsverhältnisse von *Podaxis* und *Macrolepiota* s. str. wird erstmals beschrieben.

Für *Langermannia gigantea* wird der neue flabelloide Typ der Hymenialentwicklung nachgewiesen, was die Art deutlich von anderen Lycoperdaceae unterscheidet. Generell weicht die Hymenialentwicklung der Lycoperdaceae von den Ergebnissen früherer Analysen ab. *Langermannia* wurde infolgedessen zunächst als unabhängig von der Gattung *Calvatia* angesehen. Dieses Ergebnis wird durch molekulare Phylogenie unterstützt, wonach ein

beträchtlicher Teil von *Calvatia*, darunter die ontogenetisch untersuchten Arten, zu *Lycoperdon* gehört. Allerdings stellen wenige andere *Calvatia*-Arten und *Langermannia* ein separates Taxon dar. Sie weisen vermutlich alle den flabelloiden Typ der Hymenialentwicklung auf. Damit wird gezeigt, dass morphologische Merkmale innerhalb gasteroider Gruppen homologisierbar sind, wodurch vergleichende Analysen ermöglicht werden.

Durch pilzfloristische Analysen werden neue Erkenntnisse zur Verbreitung der secotioiden Pilze der Mongolei und der Gasteromyceten von Panama gewonnen. Zwei Neunachweise für die Mongolei und zehn neue Funde für Panama werden beschrieben. Das Vorkommen aller anderen gasteroiden Arten wird unter nomenklatorischen, taxonomischen und systematischen Gesichtpunkten diskutiert. Alle mongolischen und ein großer Teil der Funde aus Panama werden ergänzend in die phylogenetischen und morphologischen Analysen einbezogen.

In einer Zusammenstellung der morphologischen Merkmale gasteroider Agaricaceae s. l. unter Berücksichtigung des ökologischen Hintergrunds und der Verwandtschaftsbeziehungen werden mit den Lycoperdaceae, Tulostomataceae und den secotioiden Vertretern drei funktionelle Gruppen unterschieden. Gasteromycetation wird als evolutiver Prozess definiert, in dem ökologische Zwänge zur Etablierung konvergenter morphologischer Merkmale führen. Dadurch wird der phylogenetische Hintergrund dieser Merkmale oft verdeckt. Viele morphologische und ontogenetische Merkmale der Lycoperdaceae und Tulostomataceae unterscheiden sich so stark von verwandten hymenothecialen Arten, dass nachvollziehbare Homologisierungen nicht möglich sind. Andererseits zeigen die secotioiden Taxa noch viele ursprüngliche Merkmale ihrer hymenothecialen Verwandten.

Die morphologischen Unterschiede der gasteroiden Gruppen können nicht allein auf ihr evolutionäres Alter zurückgeführt werden. Die secotioide Gattung *Podaxis* ist phylogenetisch relativ alt, teilt aber dennoch viele Merkmale mit der nächstverwandten hymenothecialen Gattung *Macrolepiota*. Andererseits unterscheidet sich *Barcheria* trotz enger Verwandtschaft sehr stark von *Agaricus*. Als Auslöser der Gasteromycetation wird Paedomorphose, also eine Störung des Ablaufs der ontogenetischen Regulation, angenommen.

Alle zehn Gasteromycetationsereignissen fanden in semiariden Offenlandhabitaten statt. Die primäre Verbreitungsstrategie der gasteroiden Agaricaceae ist Euanemochorie, welche vorrangig in Steppen und Wüsten auftritt. Von dort aus erfolgte die Kolonisierung anderer Lebensräume durch Lycoperdaceae und Tulostomataceae unter Evolution von Ombrohydrochorie und Geanemochorie mit entsprechenden anatomischen Merkmalen. Dies wird durch die Verbreitung der verschiedenen Typen von Gasterothecien gestützt.

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References

AGERER, R. 2002: Rhizomorph structures confirm the relationship between Lycoperdales and Agaricacae (Hymenomycetes, Basidiomycota). Nova Hedwigia **75** (3–4): 367–385.

AHMAD, S. 1950: Morphology of *Disciseda cervina*. Mycologia **42**: 148–160.

ALBEE-SCOTT, S. R. 2007: Does secotioid inertia drive the evolution of false-truffles? Mycol. Res. **111**: 1030–1039.

ARNOLD, G. R. W. 1985: Beiträge zur Kenntnis der Pilze Kubas II. Boletus **9** (2): 49–56.

ATKINSON, G. F. 1916: Origin and development of the lamellae in *Coprinus*. Bot. Gaz. **61** (2): 89–130.

BAKER, R. E. D., DALE, W. T. 1951: Fungi of Trinidad & Tobago. Mycol. Papers **33**: 1–123.

BARNETT, H. L. 1943: The Development and Structure of *Longia texensis*. Mycologia **35** (4): 399–408.

BAS, C. 1988: Orders and families in agarics and boleti. In BAS, C., KUYPER, T. W., NOORDELOOS, M. E., VELLINGA, E. C. (eds.): Flora Agaricina Neerlandica 1. Rotterdam: 40–49.

BASEIA, I., G., MILANEZ, A. I. 2002: *Montagnea hausknechtii* Rab. (Podaxales) a rare agaricoid Fungus: first record from Brazil. Acta Bot. Bras. **16** (3): 311–316.

BATES, S. T. 2004: Arizona members of the Geastraceae and Lycoperdaceae (Basidiomycota, Fungi). Master thesis Arizona State University. Tempe.

BAURA, G., SZARO, T. M., BRUNS, T. D. 1992: *Gastrosuillus laricinus* is a recent derivative of *Suillus grevillei*: Molecular Evidence. Mycologia 84 (4): 592–597.

BENJAMIN, C. R., SLOT, A. 1969: Fungi of Haiti. Sydowia **23**: 125–163.

BINDER, M., BRESINSKY, A. 2002: Derivation of a polymorphic lineage of Gasteromycetes from boletoid ancestors. Mycologia **94** (1): 85–98.

BINDER, M., HIBBETT, D. S., LARSSON, K.-H., LARSSON, E., LANGER, E., LANGER G. 2005: The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). Systematics and Biodiversity **3** (2): 113–157.

BOTTOMLEY, A. M. 1948: Gasteromycetes of South Africa. Bothalia **4** (3): 473–810.

BRANDZA, M., SOLACOLU, T. 1937: Sur le développement et la maturation de quelques Gastéromycètes. Le Botaniste **28**: 203–227.

BRASFIELD, T. W. 1937: The morphology of *Podaxis pistillaris*. University of Iowa Studies in Natural History **17** (5): 199–211.

BREFELD, O. 1877: Botanische Untersuchungen über Schimmelpilze. III: Heft: Basidiomyceten I. Leipzig.

BRODIE, H. J. 1967: New records of Nidulariaceae from the West Indies. Trans. Brit. Mycol. Soc. **50** (3): 473–478.

BRODIE, H. J. 1975: The bird's nest fungi. Toronto, Buffalo.

BRONCHARD, R., DEMOULIN, V. 1973: Ultrastructure de la paroi sporale des gasteromycètes *Mycenastrum corium* et *Abstoma reticulatum* en rapport avec leur position systématique. Bull. Soc. R. Bot. Belg. **106**: 267–272.

BRUNS, T. D., FOGEL, R., WHITE, T. J., PALMER, J. D. 1989: Accelerated evolution of a false-truffle from a mushroom ancestor. Nature **339**: 140–142.

BUTLER, M. J., DAY, A. W. 1998: Fungal melanins: a review. Canad. J. Microbiol. **44**: 1115–1136.

CAIRNEY, J. W.G., MARTÍN, M. P. 1990: Notes on the taxonomical delimitation in the genera *Calvatia*, *Gastropila* and *Langermannia* (Gasteromycetes). Bol. Soc. Micol. Madrid 14: 181–190.

CAIRNEY, J. W. G., JENNINGS, D. H., VELTKAMP, C. J. 1988: A scanning electron microscope study of the internal structure of mature linear mycelial organs of four basidiomycete species. Can. J. Bot. **67**: 2266–2271.

CALONGE, F. D. 1998: Gasteromycetes, I. Lycoperdales, Nidulariales, Phallales, Sclerodermatales, Tulostomatales. Flora Mycologica Iberica **3.** Madrid, Berlin.

CALONGE, F. D., MATA, M. 2005: *Crucibulum leave* var. *magnum* var. nov. y *Arcangeliella scissilis*, encontrados en Costa Rica. Bol. Soc. Micol. Madrid **29**: 43–48.

CALONGE, F. D., MATA, M. 2006: Adiciones y correciones al catálogo de gasteromycetes de Costa Rica. Bol. Soc. Micol. Madrid **30**: 111–119.

CALONGE, F. D., MATA, M., CARRANZA, J. 2005: Contribución al catálogo de los Gasteromycetos (Basidiomycotina, Fungi) de Costa Rica. An. Jard. Bot. Madrid **62** (1): 23–45.

CEJP, K., PALMER, J. T. 1963: Rody *Nidularia* Fr. a *Mycocalia* J. T. Palmer v Československu a *Mycocalia sphagneti* J. T. Palmer sp. Nov. Z Anglie. Česka Mycologie **17** (3): 113–126.

CHEN, C. 1999: Genetical and molecular systematic study on the genus *Montagnea* Fr. Master thesis Virginia Polytechnic Institute and State University. Blacksburg.

CLÉMENÇON, H. 1990: Fixierung, Einbettung und Schnittfärbungen für die plectologische Untersuchung von Hymenomyceten mit dem Lichtmikroskop. Mycol. Helv. **3** (4): 451–466.

CLÉMENÇON, H. 1994: Der Nodulus und die Organogenese während der frühen Fruchtkörperentwicklung von *Psilocybe cyanescens*. Z. Mycol. **60**: 49–68.

CLÉMENÇON, H. 1997: Anatomie der Hymenomyceten. Lausanne.

CLÉMENÇON, H. 2004: Cytology and Plectology of the Hymenomycetes. Bibl. Myc **199**. Berlin, Stuttgart.

COKER, W. C., COUCH, J. N. 1928: The Gasteromycetes of the Eastern United States and Canada. Reprint 1974. New York.

CONARD, H. S. 1915: The Structure and Development of *Secotium agaricoides*. Mycologia **7** (2): 94–104.

COOKE, M. C. 1871: Handbook of British Fungi, With full Descriptions of all the Species, and Illustrations of the Genera. London, New York.

CUNNINGHAM, G. H. 1926: Development of *Lycoperdon depressum* (Fungi). New Zealand J. Sci. Technol. **8**: 228–232.

CUNNINGHAM, G. H. 1944: Gasteromycetes of Australia and New Zealand. Dunedin.

DE BARY, A. 1866: Vergleichende Morphologie der Pilze. Leipzig.

DE VILLIERS, J. J. R., EICKER, A., VAN DER WESTHUIZEN, G. C. A. 1988: A new section and two new species of *Podaxis* (Gasteromycetes) from South Africa. S. Afr. J. Bot. **55** (2): 159–164.

DEMOULIN, V. 1967: Intérêt des certaines substances a fonctions basiques en chimiotaxinomie des Gastéromycètes. Bull. Soc. Mycol. France **83**: 342–353.

DEMOULIN, V. 1971: Le genre *Lycoperdon* en Europe et en Amérique du Nord. Étude taxonomique et phytogéographique. Doctoral dissertation Université de Liège. Liège.

DEMOULIN, V. 1972: Espèces nouvelles ou méconnues du genre *Lycoperdon* (Gastéromycètes). Lejeunea nouv. sér. **62**: 1–28.

DEMOULIN, V. 1980: Observations sur le genre *Arachnion* Schw. (Gasteromycetes). Can. J. Bot. **58**: 641–655.

DEMOULIN, V., DRING, D. M. 1975: Gasteromycetes of Kivu (Zaïre), Rwanda and Burundi. Bull. Jard. Bot. Nat. Belg. **45**: 339–372.

DENNIS, R. W. G. 1953: Some West Indian Gasteromycetes. Kew Bull. **8**: 307–328.

DENNIS, R. W. G. 1970: Fungus flora of Venezuela and adjacent countries. Kew Bull. Add. Ser. **III**: 1–531.

DOMÍNGUEZ DE TOLEDO, L. S., CASTELLANO, M. A. 1996: A revision of the genera *Radiigera* and *Pyrenogaster*. Mycologia **88** (5): 863–884.

DÖRFELT, H. 1978: Mykogeographisch interessante Gasteromyceten-Funde. Boletus **2**: 9–17.

DÖRFELT, H. 1980: Mykogeographisch interessante Gasteromyceten-Funde (II). Boletus **4**: 35–38.

DÖRFELT, H. 1985: Die Erdsterne. Neue Brehm Bücherei **573**: 1–108.

DÖRFELT, H., BRESINSKY, A. 2003: Die Verbreitung und Ökologie ausgewählter Makromyceten Deutschlands. Zeitschrift für Mykologie **69**: 177–286

DÖRFELT, H., BUMZAA, D. 1986: Die Gasteromyceten (Bauchpilze) der Mongolischen Volksrepublik. Nova Hedwigia **43**: 87–111.

DÖRFELT, H., GERLACH, H. 1989: Zur Identität von *Battaraea phalloides* und *B. stevenii* (Basidiomycetes/ Tulostomatales). Wiss. Z. Univ. Halle. **39**: 90–100.

DÖRFELT, H., GUBE, M. 2007: Secotioid Agaricales (Basidiomycetes) from Mongolia**.** Feddes Repert. **118** (3–4): 103–112.

DÖRFELT, H., MÜLLER-URI, C. 1984: Studien zur Systematik der Geastrales. Feddes Repert. **95** (9–10): 701–711.

DÖRFELT, H., TÄGLICH, U. 1990: Pilzfloristische Arbeitsergebnisse aus der Mongolischen Volksrepublik. Boletus **14**: 1–27.

DRING, D. M. 1973: Chapter 24. Gasteromycetes. In AINSWORTH, G. C., SPARROW, F. K., SUSSMAN, A. S. (eds.): The Fungi. An Advanced Treatise. Volume IVB. A Taxonomic Review with Keys: Basidiomycetes and Lower Fungi. New York, London: 451–478.

DRING, D. M., RAYSS, T. 1963: The gasteromycete fungi of Israel. Israel Journal of Botany **12**: 147–178.

DRING, D. M., ROSE, A. C. 1977: Additions to West African Phalloid Fungi. Kew Bull. **31** (3): 741–751.

DUMÉE, P., MAIRE, R. 1913: Note sur la *Queletia mirabilis* Fr. et sa découverte aux environs de Paris. Bull. Soc. Mycol. France **29**: 495–502.

EDGAR, R. C. 2004: MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. **32:** 1792–97.

ERICKSON, D. L., SMITH, B. D., CLARKE, A. C., SANDWEISS, D. H., TUROSS, N. 2005: An Asian Origin for a 10,000 year-old domesticated plant in the Americas. Proc. Natl. Acad. Sci. USA **102** (51): 18315–18320.

ESSER, K. 1986: Kryptogamen, Cyanobakterien, Algen, Pilze, Flechten. Praktikum- und Lehrbuch. 2nd, newly revised ed. Berlin.

FISCHER, E. 1900: Hymenogastrineae, Lycoperdineae, Nidulariineae, Plectobasidiineae. In ENGLER, A., PRANTL, K. (Hrsg.): Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigen Arten insbesondere den Nutzpflanzen. I. Teil, Abt. 1**. Leipzig: 296–346.

FISCHER, E. 1933: Gastromyceteae. In ENGLER, A., PRANTL, K. (Hrsg.): Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigen Arten insbesondere den Nutzpflanzen. 2. Aufl. Bd. 7a. Leipzig: 1–72.

FISCHER, E. 1934: Zur Kenntnis der Fruchtkörperentwicklung von *Podaxis*. Ber. schweiz. botan. Ges. **43**: 11–18.

FISCHER, E. 1936: Neue Beiträge zur Kenntnis der Verwandtschaftsverhältnisse der Gastromyceten. Eine kritische Untersuchung. Ber. schweiz. botan. Ges. **45**, 231–247.

FRIES, E. M. 1821–1832: Systema mycologicum. Vol I–IV. Gryphiswaldiae.

FRIES, E. M. 1849: Summa vegetabilium scandinaviae, seuenumeratio systematica et critica plantarum quum cotyledonearum, tum nemearum inter mare occidentale et album, inter eidoram et nordkap, hactenus lectoram, indicata simul distributione geographica. Sectio posterior. Holmiae, Lipsiae: 259–572.

FRITSCHE, G. 1968: Züchterische Arbeiten an „59 c“, einem Champignonstamm mit neuer Fruchtkörperform. I. Steigerung des Ertrages. Theor. Appl. Gen. **38**: 28–37.

FRITSCHE, G., VON SENGBUSCH, R. 1968: Beispiel der spontanen Entwicklung neuer Fruchtkörperformen beim Kulturchampignon. Der Züchter **33** (7): 270–274.

GALLI, R. 2004: Gli *Agaricus*. Milano.

GARDES, M., BRUNS, T. D. 1993: ITS primers with enhanced specificity for Basidiomycetes: application to identification of mycorrhizae and rusts. Mol. Ecol. **2**: 113–118.

GARNER, J. H. B. 1956: Gasteromycetes from Panama and Costa Rica. Mycologia **48** (5): 757–764.

GÄUMANN, E. 1926: Vergleichende Morphologie der Pilze. Jena.

GÄUMANN, E. 1964: E. Gäumann. Die Pilze. Gründzuge ihrer Entwicklungsgeschichte und Morphologie. Basel.

GÄUMANN, E. A., DODGE, C. W. 1928: Comparative morphology of fungi. Translated and revised by C. W. DODGE. New York, London.

GE, Z. W., YANG, Z. L. 2006: The genus *Chlorophyllum* (Basidiomycetes) in China. Mycotaxon **96**: 181–191.

GEML, J. 2004: Evolution in Action: molecular evidence for recent emergence of secotioid genera *Entoptychum*, *Gyrophragmium* and *Longula* from *Agaricus* ancestors. Acta Microbiologica et Immunologica Hungarica **51** (1–3): 97–108.

GEML, J., DAVIS, D. D., GEISER, D. M. 2005: Systematics of the genus *Sphaerobolus* based on molecular and morphological data, with the description of *Sphaerobolus ingoldii* sp. nov. Mycologia **97** (3): 680–694.

GEML, J., GEISER, D. M., ROYSE, D. J. 2004: Molecular evolution of *Agaricus* species based on ITS and LSU rDNA sequences. Mycol. Progress **3** (2): 157–176.

GOLDSCHMIDT, R. 1933: Some aspects of evolution. Science **78**: 539–547.

GOULD, S. J. 1977: The return of hopeful monsters. Nat. Hist. **86** (6): 24–30.

GREGORY, P. H., HENDEN, D. R. 1976: Terminal velocity of basidiospores of the giant puffball (*Lycoperdon giganteum*). Trans. Br. Mycol. Soc. **67** (3): 399–407.

GREIS, H. 1937: Fruchtkörperbildung und Basidienentwickelung von *Tulostoma mammosum* Fries. Cohn Jahrb. Wiss. Bot. **84**: 517–552.

GREUTER, W., MCNEILL, J., BARRIE, F. R., BARDET, H. M., DEMOULIN, V., FILGUEIRAS, T. S., NICOLSON, D. H., SILVA, D. H., SKOG, J. E., TREHANE, P., TURLAND, N. J., HAWKSWORTH, D. L. (eds.) 2000. International Code of Botanical Nomenclature (Saint Louis Code) adopted by the 16th International Botanical Congress, St Louis, Missouri, Jul–Aug 1999. Koenigstein.

GUBE, M. 2005: Morphologisch-anatomische Studien an Fruchtkörperprimordien der Lycoperdaceae (Basidiomycetes) und ihre Bedeutung für die Systematik. Diploma thesis FSU Jena. Jena.

GUBE, M. 2007: The gleba development of *Langermannia gigantea* (Batsch: Pers.) Rostk. (Basidiomycetes) compared to other Lycoperdaceae, and some systematic implications. Mycologia **99** (3): 396–405.

GUZMÁN, G. 1969: *Veligaster*, a new genus of the Sclerodermataceae. Mycologia **61**: 1117–1123.

GUZMÁN, G. 1970: Monografia del género *Scleroderma* Pers. emend. Fr. (Fungi, Basidiomycetes). Darwiniana **16**: 233–407.

GUZMÁN, G., OVREBO, C. L. 2000: New observations on sclerodermataceous fungi. Mycologia **92** (1): 174–179.

GUZMÁN, G., MILLER, O. K., LODGE, D. J., BARONI, T. J. 2004a: *Scleroderma stellatum* versus *Scleroderma bermudense*: the status of *Scleroderma echinatum* and the first record of *Veligaster nitidum* from the Virgin Islands. Mycologia **96** (6): 1370–1379.

GUZMÁN, G., TAPIA, F. 1995: New species, new combinations and new records of *Veligaster*, (Sclerodermataceae). Doc. Mycol. **25**: 185–195.

GUZMÁN, G., TORRES, M. G., RAMÌREZ-GUILLÉN, F., RÌOS-HURTADO, A. 2004b: Introducción al conocimiento de los macromicetos de Chocó, Colombia. Rev. Mex. Mic. **19**: 33–43.

HANSEN L. 1962: A Danish find of *Mycenastrum corium* with notes on its anatomy. Bot. Tidsskr. **58**: 204–212.

HECKER, K. H., ROUX, K. H. 1996: High and Low Annealing Temperatures Increase Both Specificity and Yield in Touchdown and Stepdown PCR. BioTechniques **20**: 478–485.

HEIM, R. 1951: Notes sur la flore mycologique des Terres du Pazifique Sud. III. Sur les *Secotium* de Nouvelle-Zélande et la phylogénie de ce genre. Rev. Mycol. (Paris) **16**: 129–153.

HEIM, R. 1971: The interrelationships between the Agaricales and Gasteromycetes. In PETERSEN, R. H. (ed.): Evolution of the higher Basidiomycetes. Knoxville: 505–534.

HENNICKE, F., GUBE, M., KOTHE, E. 2009: *Schizophyllum* revisited: A new type of fruit body development. Manuscript in preparation.

HERRERA, T., PÉREZ-SILVA, E., ESQUEDA, M., VALENZUELA, V. H. 2005: Algunos Gasteromicetos de Calakmul, Campeche, México. Rev. Mex. Mic. **21**: 23–27.

HIBBETT, D. S. 2004: Trends in Morphological Evolution in Homobasidiomycetes Inferred Using Maximum Likelihood: A Comparison of Binary and Multistate Approaches. Syst. Biol. **53** (6): 889–903.

HIBBETT, D. S. 2006: A phylogenetic overview of the Agaricomycotina. Mycologia **98** (6): 917–925.

HIBBETT, D. S. 2007: After the gold rush, or before the flood? Evolutionary morphology of mushroom-forming fungi (Agaricomycetes) in the early 21st century. Mycol. Res. **111**: 1001–1018.

HIBBETT, D. S., BINDER, M., WANG, Z., GOLDMAN, Y. 2003: Another fossil agaric from Dominican amber. Mycologia 95 (4): 685–687.

HIBBETT, D. S., GRIMALDI, D., DONOGHUE, M. J. 1995: Cretaceous mushrooms in amber. Nature 377: 487.

HIBBETT, D. S., PINE, E. M., LANGER, E., LANGER, G., DONOGHUE, M. J. 1997: Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. Proc. Nat. Acad. Sci. USA **94**: 12002–12006.

HIBBETT, D. S., TSUNEDA, A., MURAKAMI, S. 1994: The secotioid from of *Lentinus tigrinus*: genetics and development of a fungal morphological innovation. Amer. J. Bot. **81** (4): 466–478.

HOCH, H. C., HOWARD, R. J. 1981: Conventional chemical fixations induce artifactual swelling of dolipore septa. Exp. Mycol. **5**, 167–172.

HOFFMANN, H. 1856: Die Pollinarien und Spermatien bei *Agaricus*. Bot. Zeit. **14**: 137–148, 153–163.

HOLLÓS, L. 1904: Die Gasteromyceten Ungarns. Leipzig.

HOPPLE, J. S., VILGALYS, R. 1994: Phylogenetic relationships among coprinoid taxa and allies based on data from restriction site mapping of nuclear rDNA. Mycologia **86** (1): 96–107.

HOPPLE, J. S., VILGALYS, R. 1999: Phylogenetic Relationships in the Mushroom Genus *Coprinus* and Dark-Spored Allies Based on Sequence Data from the Nuclear Gene Coding for the Large Ribosomal Subunit RNA: Divergent Domains,Outgroups, and Monophyly. Mol. Phylog. Evol. **13** (1): 1–19.

HOSAKA, K., BATES, S. T., BEEVER, R. E., CASTELLANO, M. A., COLGAN III, W., DOMINGUEZ, L. S., NOUHRA, E. R., GEML, J., GIACHINI, A. J., KENNEY, S. R., SIMPSON, N. B., SPATAFORA, J. W., TRAPPE, J. M. 2006: Molecular phylogenetics of the gomphoid-phalloid fungi with an establishment of the new subclass Phallomycetidae and two new orders. Mycologia **98** (6): 949–959.

JACOBSON, K. M., JACOBSON, P. J., MILLER, O. K. 1999: The autecology of *Battarrea stevenii* in ephemeral rivers of southwestern Africa. Mycol. Res. **103** (1): 9–17.

JEFFRIES, P., MCLAIN, L. 2004: Synonymy between *Battarrea phalloides* and *B. stevenii*. English Nature Research Reports **625**. Peterborough.

JOBB, G. 2008: TREEFINDER version of October 2008. Distributed by the author at www.treefinder.de.

JOHNSON, J. 1999: Phylogenetic relationships within *Lepiota* sensu lato based on morphological and molecular data. Mycologia **91** (3): 443–458.

JOHNSON, J., VILGALYS, R. 1998: Phylogenetic systematics of *Lepiota* sensu lato based on nuclear large subunit rDNA evidence. Mycologia **90** (6): 971–979.

JÜLICH, W. 1981: Higher Taxa of Basidiomycetes. Bibl. Myc. **85**. Berlin, Stuttgart.

JÜLICH, W. 1984: Die Nichtblätterpilze, Gallertpilze und Bauchpilze. Aphyllophorales, Heterobasidiomycetes, Gastromycetes. Gams: Kleine Kyptogamenflora Bd. IIb/1. Basidiomyceten. 1. Teil. Jena.

KASUYA, T., ORIHAYA, T., FUKIHARU, T., YOSHIMI, S. 1996: A lycoperdaceous fungus, *Arachnion album* (Agaricales, Arachniaceae), newly found in Japan. Mycoscience **47**: 385–387.

KATOH, K., TOH, H. 2008: Recent developments in the MAFFT multiple sequence alignment program. Briefings in Bioinformatics **9** (4): 286–298.

KERS, L. E. 1975: The genus *Disciseda* (Gasteromycetes) in Sweden. Svensk Bot. Tids. **69**: 405–438.

KIRK, P. M., CANNON, P. F., DAVID, J. C., STALPERS, J. A. 2001: Ainsworth and Bisby's Dictionary of the Fungi. 9th ed. Wallingford.

KIRK, M. P., CANNON, P. F., MINTER, D. W., STALPERS, J. A. 2009: Ainsworth & Bisby's dictionary of the fungi. 10th ed. Wallingford.

KO, K. S., LIM, Y. W., KIM, Y. H., JUNG, H. S. 2001: Phylogeographic divergences of nuclear ITS sequences in *Coprinus* species sensu lato. Mycol. Res. **105**: 1519–1526.

KOTHE, E. 1997: Solving a puzzle piece by piece: sexual development in the basidiomycetous fungus *Schizophyllum commune*. Bot. Acta **110**: 208–213.

KOTHE, E. 2008: Sexual attraction: On the role of fungal pheromone/receptor systems. Acta Microbiologica et Immunologica Hungarica 55 (2): 125–143.

KREADER, C. A. 1996: Relief of Amplification Inhibition in PCR with Bovine Serum Albumin or T4 Gene 32 Protein. Appl. Env. Microbiol. **62** (3): 1102–1106.

KREISEL, H. 1961: Über *Phellorinia herculeana* (Pers.) Kreisel comb. nov. und ihr Vorkommen in Europa. Česka Mycologie **15** (4): 195–200.

KREISEL, H. 1962: Die Lycoperdaceae der Deutschen Demokratischen Republik. Feddes Repert. **64**: 89–201.

KREISEL, H. 1967: Taxonomisch-pflanzengeographische Monographie der Gattung *Bovista*. Beih. Nova Hedwigia **25**: 1–244.

KREISEL, H. 1969: Grundzüge eines natürlichen Systems der Pilze. Jena: Gustav Fischer.

KREISEL, H. 1971a: Charakteristika der Pilzflora Kubas. Biologische Rundschau **9**: 65–73.

Kreisel, H. 1971b: Clave para la identificación de los macromicetos de Cuba. Ciencias Serie 4, Ciencias Biológicas, Universidad de la Habana **16**: 1–101.

Kreisel, H. 1973: Die Gattung *Gyrophragmium* Mont. und ihre Stellung im System der Basidiomycetes. Feddes Repert. **83**: 577–583.

Kreisel, H. 1975: Gasteromyzeten aus der Mongolischen Volksrepublik. Feddes Repert. **86**: 321–327.

Kreisel, H. 1989: Studies in the *Calvatia* complex (Basidiomycetes). Nova Hedwigia **48**, 281–296.

Kreisel, H. 1992: An emendation and preliminary survey of the genus *Calvatia* (Gastromycetidae). Persoonia Suppl. **14** (4): 431–439.

Kreisel, H. 1993: A key to *Vascellum* (Gasteromycetidae) with some floristic notes. Blyttia **3–4**: 125–129.

Kreisel, H. 1994: Studies in the *Calvatia* complex (Basidiomycetes) 2. Feddes Repert. **105** (5–6): 369–376.

Kreisel, H. 1998: Die Gattungen *Calvatia* und *Handkea* in Europa und der Arktis. Österr. Z. Pilzk. **7**: 215–225.

Kreisel, H. 2001: Checklist of the gasteral and secotioid Basidiomycetes of Europe, Africa, and the Middle East. Österr. Z. Pilzk. **10**: 213–313.

Kreisel, H., Al-Fatimi, M. 2004: Basidiomycetes and larger Ascomycetes from Yemen. Feddes Repert. **115**: 547–561.

Kreisel, H., Al-Fatimi, M. 2008: Further Basidiomycetes from Yemen. Feddes Repert. **119** (5–6): 463–483.

Kreisel, H., Dring, D. M. 1967: An emendation of the genus *Morganella* Zeller (Lycoperdaceae). Feddes Repert. **74**: 109–122.

Krüger, D., Binder, M., Fischer, M., Kreisel, H. 2001: The Lycoperdales. A molecular approach to the systematics of some gasteroid mushrooms. Mycologia **93** (5): 947–957.

Krüger, D., Gargas, A. 2008: Secondary structure of ITS2 rRNA provides taxonomic characters for systematic studies d a case in Lycoperdaceae (Basidiomycota). Mycol. Res. **112**: 313–330.

Krüger, D., Kreisel, H. 2003: Proposing *Morganella* subgen. *Apioperdon* subgen. nov. for the puffball *Lycoperdon pyriforme*. Mycotaxon **86**: 169–177.

Krüger, D., Binder, M., Fischer, M., Kreisel, H. 2001: The Lycoperdales. A molecular approach to the systematics of some gasteroid mushrooms. Mycologia **93** (5): 947–957.

Kües, U., Liu, Y. 2000: Fruiting body production in Basidiomycetes. Appl. Microbiol. Biotechnol. **54**: 141–152.

Lander, C. A. 1933: The morphology of the developing fruiting body of *Lycoperdon gemmatum*. Amer. J. Bot. **20**: 204–215.

Lander, C. A. 1934: The development of the fruiting body of *Arachnion album*. J. Elisha Mitchell Soc. Sci. **50**: 275–282.

Lange, M. 1976: Some Gasteromycetes from North East Greenland. Kew Bull. **31** (3): 635–638.

Lange, M. 1990: Arctic Gasteromycetes II. Calvatia in Greenland, Svalbard and Iceland. Nord. J. Bot. **9** (5): 525–546.

Lange, M. 1993: Classifications in the *Calvatia* group. Blyttia **51** (3–4): 141–144.

Larsson, E., Jeppson, M. 2008: Phylogenetic relationships among species and genera of Lycoperdaceae based on ITS and LSU sequence data from North European taxa. Mycol. Res. **112**: 4–22.

Laurent, N., Bremer, B., Bremer, K. 1999: Phylogeny and generic interrelationships of the Stylidiaceae (Asterales), with a possible extreme case of floral paedomorphosis. Syst. Bot. 23: 289–304.

Lebel, T., Thompson, D. K., Udovicic, F. 2004: Description and affinities of a new sequestrate fungus *Barcheria willisiana* gen. et spec. nov. (Agaricales) from Australia. Mycol. Res. **108** (2): 206–213.

LEITE, A. G., SILVA, B. D. B., ARAÙJO, R. S., BASEIA, I. G. 2007: Espécies raras de Phallales (Agaricomycetidae, Basidiomycetes) no Nordeste do Brasil. Acta Bot. Bras. **21** (1): 119–124.

LÉVEILLÉ, J.-H. 1846: Descriptions des champignons de l'herbier du muséum de Paris. Ann. Sci. Nat. **5**: 111–167.

LEVIT, G. S., MEISTER, K., HOßFELD, U. 2008: Alternative evolutionary theories: A historical survey. J. Bioecon. **10**: 71–96.

LIU, B. 1984: The Gasteromycetes of China. Beih. Nova Hedwigia **76**: 1–235.

LLOYD, C. G. 1902: The genera of gastromycetes. Cincinnati.

LLOYD, C. G. 1905: The Lycoperdaceae of Australia, New Zealand and Neighboring Islands. Cincinnati.

LODGE, D. J. 1984: Microorganisms. In REAGAN, D. P., WAIDE, R. B. (eds.): The Food Web of a Tropical Rain Forest. Chicago: 53–108.

LOHWAG, H. 1924: Entwicklungsgeschichte und systematische Stellung von *Secotium agaricoides* (Czern.) Holl. Öst. Bot. Zeit. **73** (7–9): 161–174.

LOHWAG, H. 1925: Zur Entwicklungsgeschichte und Morphologie der Gastromyceten. Ein Beitrag zur Systematik der Basidiomyceten. Beih. Bot. Centralbl. Abt. II **42**: 177–334.

LOHWAG, H. 1941: Anatomie der Asco- und Basidiomyceten. Handbuch der Pflanzenanatomie. Bd. VI, Abt. 2, Teilbd. 3,c. Berlin.

LONG, W. H. 1943: Studies in the Gasteromycetes: VIII. *Battarraea laciniata*. Mycologia **35** (5): 546–556.

LONG, W. H. 1944: Studies in the Gasteromycetes X. Seven New Species of *Tylostoma*. Mycologia **36** (4): 318–339.

LONG, W. H., AHMAD, S. 1947: The genus *Tylostoma* in India. Farlowia **3** (2): 225–267.

LONG, W. H., PLUNKETT, O. A. 1940: Studies in the Gasteromycetes. I. The Genus *Dictyocephalos*. Mycologia **32** (6): 696–709.

LONG, W. H., STOUFFER, D. J. 1943: Studies in the Gasteromycetes. VII. The Genus *Schizostoma*. Mycologia **35** (1): 21–32.

LONG, W. H., STOUFFER, D. J. 1946: Studies in the Gasteromycetes. XIV. The Genus *Chlamydopus*. Mycologia **38** (6): 819–829.

MAGNUS, W. 1906: Über die Formgebung der Hutpilze. Arch. f. Biontologie **1** (1): 85–161.

MALENÇON, G. 1930: Recherches complémentaires sur les basides de *Battarraea Guicciardiniana* Ces. Ann. Crypt. Exot. **3**: 194–199.

MALENÇON, G. 1935a: Etudes sur les Phellorinés. I. La *Phellorinia delastrei* (Dur. et Mtgn.) Ed. Fischer. Ann. Cryptog. Exot. **8**: 5–48.

MALENÇON G. 1935b: Etudes sur les Phellorinés. II. Le *Dictyocephalus curvatus* Underwood. Ann. Cryptog. Exot. **8**: 102–132.

MALENÇON, G. 1955: Le développement du *Torrendia pulchella* Bres. et son importance morphogénétique. Rev. Mycol. (Paris) **20**: 81–130.

MARCHANT, R. 1969: The fine structure and development of the fructifications of *Lycoperdon perlatum*. Trans. Brit. Mycol. Soc. **53** (1): 63–68.

MARTIN, G. W. 1939a: New or noteworthy fungi from Panama and Colombia. IV. Mycologia **31** (5): 507–518.

MARTIN, G. W. 1939b: The genus "*Lycogalopsis*". Lilloa **4**: 69–73.

MARTÍN, M. P., HIDALGO, E., ALTÉS, A. MORENO, G. 2000: Phylogenetic relationships in Phelloriniaceae (Basidiomycotina) based on ITS rDNA sequence analysis. Cryptogamie Mycol. **21** (1): 3–12.

MARTÍN, M. P., JOHANNESSON, H. 2000: *Battarrea phalloides* and *B. stevenii*, insight into a long-standing taxonomic puzzle. Mycotaxon **74**: 67–75.

MASSEE, G. 1888: A monograph of the genus *Calostoma*, Desv. (*Mitremyces*, Nees). Ann. Bot. **2** (5): 25–45.

MATHENY, P. B., CURTIS, J. M., HOFSTETTER, V., AIME, M. C., MONCALVO, J. M., GE, Z. W., YANG, Z. L., SLOT, J. C., AMMIRATI, J. F., BARONI, T. J., BOUGHER, N. L., HUGHES, K. W., LODGE, D. J., KERRIGAN, R. W., SEIDL, M. T., AANEN, D. K., DENITIS, M., DANIELE, G. M., DESJARDIN, D. E., KROPP, B. K., NORVELL, L. L., PARKER, A., VELLINGA, E. C., VILGALYS, R., HIBBETT, D. S. 2006. Major clades of Agaricales: a multi-locus phylogenetic overview. Mycologia **98** (6): 982–995.

MATHENY, P. B., LIU, Y. J., AMMIRATI, J. F., HALL, B. D. 2002: Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). Amer. J. Bot. **89** (4): 688–698.

MAUBLANC, A., MALENÇON, G. 1930: Recherches sur la *Battarraea Guicciardiniana* Ces. Bull. Soc. Myc. France **46**: 43–73.

MCNEILL, J., BARRIE, F. R. BURDET, H. M., DEMOULIN, V., HAWKSWORTH, D. L., MARHOLD, K., NICOLSON, D. H., PRADO, J., SILVA, P. C., SKOG, J. E., WIERSEMA, J. H., TURLAND, N. J. 2006: International Code of Botanical Nomenclature (Vienna Code). Koenigstein.

MELÉNDEZ-HOWELL, L. M. 1967: Recherches sur le pore germinatif des basidiospores. Ann. Sci. Nat. Bot. Sér. 12 **8**: 487–638.

MICHAEL, E., HENNIG. B., KREISEL, H.: Handbuch für Pilzfreunde. Bd. 1. Jena.

MILLER, S. J., MCCLEAN, T. M., WALKER, J. F., BUYCK, B. 2001: A molecular phylogeny of the Russulales including agaricoid, gasteroid and pleurotoid taxa. Mycologia **93** (2): 344–354.

MILLER, O. K. 1995: Observations on unusual Gasteromycetes from North America. Doc. Mycol. **25**: 259–267.

MILLER, O. K., MILLER, H. H. 1988: Gasteromycetes. Morphological and development features with keys to orders, families and genera. Eureka.

MINTER, D. W., RODRÍGUEZ HERNÁNDEZ, M., MENA PORTALES, J. 2001: Fungi of the Caribbean. An annotated checklist. Isleworth.

MONCALVO, J.-M., VILGALYS, R., REDHEAD, S. A., JOHNSON, J. E., JAMES, T. Y., AIME, M. C., HOFSTETTER, V., VERDUIN, S. J. W., LARSSON, E., BARONI, T. J., THORN, R. G., JACOBSSON, S., CLÉMENCON, H., MILLER, O. K. 2002: One hundred and seventeen clades of euagarics. Mol. Phylog. Evol. **23**: 357–400.

MORALES, M. I., KIMBROUGH, J. W. 1981: The Lycoperdaceae of North Central Florida. II. The genera *Bovistella*, *Langermannia* and *Morganella*. Rev. Biol. Trop. **29** (1): 95–104.

MORALES, M. I., NASSAR, M., SAÈNZ, J. A. 1974: Lycoperdaceae of Costa Rica. I. The genus *Morganella*. Rev. Biol. Trop. **21** (2): 221–227.

MORGAN, A. P. 1890: North American fungi. The Gasteromycetes. Journ. Cincinnati Soc. Nat. Hist. 12.

MORSE, E. E. 1933: A study of the genus *Podaxis*. Mycologia **25** (1): 1–32.

NIEVES-RIVERA, A. M., LODGE, D. J. 1998: Contributions to the study of Gasteromycetes of Puerto Rico. McIlvainea **13** (2): 50–58.

PATTERSON, C. 1988: Homology in Classical and Molecular Biology. Mol. Biol. Evol. **5** (6): 603–625.

PEGLER, D. N., LAESSØE, T., SPOONER, B. M. 1995: British Puffballs, Earthstars and Stinkhorns. An account of the British gasteroid fungi. Kew.

PEINTNER, U., BOUGHER, N. L., CASTELLANO, M. A., MONCALVO, J.-M., MOSER, M. M., TRAPPE, J. M., VILGALYS, R. 2001: Multiple origins of sequestrate fungi related to *Cortinarius* (Cortinariaceae). Amer. J. Bot. **88**: 2168–2179.

PERRIÈRE, G., GOUY, M. 1996: WWW-Query: An on-line retrieval system for biological sequence banks. Biochimie **78**: 364–369.

PIEPENBRING, M. 2006: Checklist of fungi in Panama. Puente Biológico **1**: 1–190.

PILÁT, A. 1958 (ed.): Gasteromycetes, Houby Brichatky. In Flora ČSR, 1. Praha.

PILÁT, A. 1972: Contribution a l'étude des Basidiomycètes Mongolie. Bull. Soc. Myc. France **88**: 333–358.

PISARJEVA, N. F. 1964: K flore Gribov Aktjubinskoj oblasti. Trudy Instituta Botaniki Akademii nauk Kazachskoj SSR **16**: 182–216.

PONCE DE LEÓN, P. 1946: Contribución al estudio de los Gasteromicetos Cubanos I. El género *Geastrum* en Cuba. Rev. Soc. Cubana Bot. **1946**: 63–70.

PONCE DE LEÓN, P. 1968: A revision of the family Geastraceae. Fieldiana Bot. **31** (11): 303–349.

PONCE DE LEÓN, P. 1970: Revision of the Genus *Vascellum* (Lycoperdaceae). Fieldiana Bot. **32** (9): 109–125.

PONCE DE LEÓN, P. 1971: Revision of the Genus *Morganella* (Lycoperdaceae). Fieldiana Bot. **34** (3): 27–44.

POUZAR, Z. 1971: *Geastrum sessile* (Sow.) Pouz., the Correct Name for *Geastrum fimbriatum* Fr. (*Gasteromycetes*). Folia Geobot. Phytotax. **6**: 93–97.

RABENHORST, L. 1870: Übersicht der vom Herrn Professor Dr. HAUSSKNECHT im Orient gesammelten Kryptogamen. Sitzungsberichte der Naturwissenschaftlichen Gesellschaft Isis zu Dresden **1870**: 225–236.

RABINOWITSCH, L. 1894: Beiträge zur Entwickelungsgeschichte der Fruchtkörper einiger Gastromyceten. Flora, Erg. Bd. **78**: 385–418

RAMBAUT, A. 2006: FigTree v1.0. Tree Figure Drawing Tool. Published by the author at tree.bio.ed.ac.uk/software/figtree.

RAMBAUT, A., DRUMMOND, A. J. 2007: Tracer v1.4. Published by the authors at beast.bio.ed.ac.uk/software/tracer.

RAPIOR, S., MAURUC, M.-J., GUINBERTEAU, J., MASSON, C.-L., BESSIÈRE, J.-M. 2000: Volatile composition of *Gyrophragmium dunallii*. Mycologia **92** (6): 1043–1046.

RAUSCHERT, S. 1964: *Montagnea arenaria* (DC. ex Fries) Zeller, ein für Deutschland neuer Steppenpilz. Westf. Pilzbr. **5** (1): 1–13.

REA, P. M. 1942: Fungi of Southern California. I. Mycologia **34** (5): 563–574.

REDHEAD, S. A., VILGALYS, R., MONCALVO, J.-M., JOHNSON, J., HOPPLE, J. S. 2001: *Coprinus* PERS. and the disposition of *Coprinus* species senso lato. Taxon **50**: 203–241.

REHSTEINER, H. 1892. Beiträge zur Entwicklungsgeschichte der Fruchtkörper einiger Gastromyceten. Bot. Zeit. **50**: 761–878.

REID, D. A. 1977: Some Gasteromycetes from Trinidad and Tobago. Kew Bull. **31** (3): 657–690.

REID, D. A., EICKER, A. 1991: A taxonomic survey of the genus *Montagnea* (Gasteromycetes) with special reference to South Africa. S. Afr. J. Bot. **57** (3): 161–170.

REIJNDERS, A. F. M. 1963: Les Problèmes du Développement des Carpophores des Agaricales et de quelques Groupes voisins. Den Haag.

REIJNDERS, A. F. M. 1975: The development of three species of Agaricaceae and the ontogenetic pattern of this family as a whole. Persoonia **8** (3): 307–319.

REIJNDERS, A. F. M. 1976: Sur le développement de trois espèces de Gastéromycètes et l'origin coralloide ou lacunaire de la gleba. Bull. Soc. Mycol. France **92** (2): 169–188.

REIJNDERS, A. F. M. 1977: The histogenesis of bulb and trama tissue of the higher Basidiomycetes and its phylogenetic implications. Persoonia **9** (3): 329–362.

REIJNDERS, A. F. M. 2000: A morphogenetic analysis of the basic characters of the gasteromycetes and their relation to other hymenomycetes. Mycol. Res. **104** (8): 900–910.

RICK, J. 1928: Resumo mycologico. Egetea **13**: 432–439.

RICK, J. 1939: Agarici Riograndensis IV. Lilloa **4**: 75–104.

RICK, J. 1961: Basidiomycetes Eubasidii in Rio Grande do sul – Brasilia, 5. Agaricaceae. Iheringia, Serie Botanica **8**: 296–460.

RITCHIE, D. 1948: The development of *Lycoperdon oblongisporum*. Amer. J. Bot. **35**: 215–219.

RODRÍGUEZ GALLART, C. A. 1997: Estudios en los macromicetos de la República Dominicana III. Moscosoa **9**: 145–153.

RONQUIST, F., HUELSENBECK, J. P., VAN DER MARK, P. 2008: MrBayes v3.2-cvs (Bayesian Analysis of Phylogeny). Published by the authors at people.sc.fsu.edu/~ronquist/MrBayes

ROSTKOVIUS, F. W. T. 1844: Die Pilze Deutschlands. In STURM, J. (ed.): Deutschlands Flora in Abbildungen nach der Natur mit Beschreibungen. Abth. III, Bdch. 5. Nürnberg.

SÁENZ, J. A., NASSAR, M. 1982: Hongos de Costa Rica: Familias Phallaceae y Clathraceae. Rev. Biol. Trop. **30** (1): 41–52.

SARASINI, M. 2005: Gasteromiceti epigei. AMB: Milano.

SCHRÖTER, J. 1877: Ueber die Entwickelung und die systematische Stellung von *Tulostoma* Pers. Cohn Beitr. Biol. Pfl. **2** (1): 65–72.

SHARP, A. J. 1948: Some fungi common to the highlands of Mexico and Guatemala and eastern United States. Mycologia **40** (4): 499–502.

SHEAR, C. L. 1902: Mycological Notes and New Species. Bull. Torrey Bot. Club **29** (7): 449–457.

SINGER, R. (ed.) 1986: The Agaricales in modern taxonomy. Koenigstein.

SINGER, R., SMITH, A. H. 1958: Studies on secotiaceous fungi – II. *Endoptychum depressum*. Brittonia **10**: 216–221.

SKIERGIELLO, A. 1908: Two Gasteromycetes from the Mongolian People's Republic. Kew Bulletin **31** (3): 703–704.

ŠMARDA, F. 1958: Lycoperdaceae. In PILÁT, A. (ed.): Gasteromycetes. Flora ČSR, Ser. B, Vol. 1. Praha: 257–377.

SMITH, A. H. 1971: The origin and evolution of the Agaricales. In PETERSEN, R. H. (ed.): Evolution of the higher Basidiomycetes. Knoxville: 481–504.

SMITH, A. H. 1973: Chapter 23. Agaricales and Related Secotioid Gasteromycetes. In AINSWORTH, G. C., SPARROW, F. K., SUSSMANN, A. S. (eds.): The Fungi. An Advanced Treatise. Volume IVB. A Taxonomic Review with Keys: Basidiomycetes and Lower Fungi. New York, London: 419–450.

SOROKIN, N. V. 1884: Materialy dlja flory Sredny Asia. Bull. Soc. Imp. Nat. Moscou **59**: 183–230.

SOSIN, P. E. 1973: Opredelitel' gasteromicetow SSSR. Leningrad.

STANDLEY, P. C. 1927: The flora of Barro Colorado Island, Panama. Smithsonian Misc. Coll. **78** (8): 1–32.

STEVENS, F. L. 1930: Parasitic fungi from Panama. Ann. Mycol. **28**: 281–286.

STEVENSON, J. A. 1975: Fungi of Puerto Rico and the American Virgin Islands. Contr. Reed. Herb. **23**: 1–743.

STIJVE, T., ANDREY, D., GOESSLER, W., GUINBERTEAU, J., DUPUY, G. 2001: Étude comparative des métaux lourds et d'autres éléments traces dans *Gyrophragmium dunalii* et dans les agarics jaunissants de la section *Arvenses*. Bull. Soc. Mycol. France **117**: 133–144.

SUÁREZ, V. L., WRIGHT, J. E. 1996: South American Gasteromycetes V: The genus *Morganella*. Mycologia **88** (4): 655–661.

SUNHEDE, S. 1989: Geastraceae (Basidiomycotina). Morphology, ecology, and systematics with special emphasis on the north european species. Synopsis Fungorum **1**: 1–534.

SWARTZ, D. 1933: Some developmental characters of species of Lycoperdaceae. Amer. J. Bot. **20**: 440–465.

SWARTZ, D. 1935: The development of *Calvatia craniiformis*. Mycologia **27**: 439–448.

SWARTZ, D. 1936a: The development of *Lycoperdon acuminatum*. Mycologia **28**: 278–283.

SWARTZ, D. 1936b: The development of *Lycoperdon pedicellatum* Pk. (*Bovistella pedicellata* (Pk.) Lloyd). Amer. J. Bot. **23**: 4–7.

SWOBODA, F. 1937: Über den Fruchtkörperbau und die systematische Stellung von *Lanopila* Fries. Ann. Mycol. **35** (1): 1–14.

SWOBODA, F. 1938: Zur Anatomie der Lycoperdaceen. I. *Lycoperdon marginatum* Vitt. Ann. Mycol. **36** (2–3): 95–118.

SWOBODA, F. 1940: Zur Anatomie der Lycoperdaceen. II. *Calvatia pachyderma* (Peck) Morgan. Ann. Mycol. **38** (1): 1–13.

TELLE, S., THIENES, M. 2008: Amplification of *cox2* (~620 bp) from 2 mg of up to 129 years old herbarium specimens, comparing 19 extraction methods and 15 polymerases. PLoS ONE 3 (10): e3584. doi:10.1371/journal.pone.0003584.

THEIßEN, G. 2006: The proper place of hopeful monsters in evolutionary biology. Theory Biosci. **124**: 349–369.

THIERS, H. D. 1984. The secotioid syndrome. Mycologia **76** (1): 1–8.

TORRES-CARVAJAL, O., DE QUEIROZ, K. 2009: Phylogeny of hoplocercine lizards (Squamata: Iguania) with estimates of relative divergence times. Mol. Phyl. Evol. 50: 31–43.

TOWNSEND, B. B. 1954: Morphology and development of fungal rhizomorphs. Trans. Br. Mycol. Soc. **37**: 222–233.

UNDERWOOD, L. M. 1899: Moulds Mildews and Mushrooms. A guide to the systematic study of the fungi and mycetozoa and their literature. New York.

URANCIMEG, G. 2004: Mongol ornj chunsnij möög. Ulaanbaatar.

VAN DE BOGART, F. 1976: The genus *Coprinus* in Western North America, Part I: Section *Coprinus*. Mycotaxon **4** (1): 233–275.

VASCO-PALACIOS, A. M., A. E. FRANCO-MOLANO, C. A. LÓPEZ-QUINTERO, BOEKHOUT, T. 2005: Macromicetes (ascomycota, basidiomycota) de la región del medio Caquetá, departamentos de Caquetá y Amazonas, Colombia. Biota Colomb. **6** (1): 127–140.

VELLINGA, E. C. 2002: New combinations in *Chlorophyllum*. Mycotaxon **83**: 415–417.

VELLINGA, E. C. 2003: Phylogeny of *Lepiota* (Agaricaceae) – Evidence from nrITS and nrLSU sequences. Mycol. Progress **2** (4): 305–322.

VELLINGA, E. C. 2004a: Ecology and Distribution of Lepiotaceous Fungi (Agaricaceae) – A Review. Nova Hedwigia **78** (3–4): 273–299.

VELLINGA, E. C. 2004b: Genera in the family Agaricaceae: evidence from nrITS and nrLSU sequences. Mycol. Res. **108** (4): 354–377.

VELLINGA, E. C., DE KOK, R. P. 2002: Proposal to conserve the name *Chlorophyllum* Massee against *Endoptychum* Czern. (Agaricaceae). Taxon **51**: 563–564.

VELLINGA, E. C., DE KOK, R. P. J., BRUNS, T. D. 2003: Phylogeny and taxonomy of *Macrolepiota* (Agaricaceae). Mycologia **95** (3): 442–456.

VILGALYS, R., HESTER, M. 1990: Rapid Genetic Identification and mapping of Enzymatically Amplified Ribosomal DNA from Several *Cryptococcus* Species. J. Bacteriol. **172** (8): 4238–4246.

VON ARX, J. A. 1967: Pilzkunde: ein kurzer Abriss der Mykologie unter besonderer Berücksichtigung der Pilze in Reinkultur. Berlin, Stuttgart.

WAGNER, G. P. 2000: What Is the Promise of Developmental Evolution? Part I: Why Is Developmental Biology Necessary to Explain Evolutionary Innovations? J. Exp. Zool. **288**: 95–98.

WATLING, R. 1971: Polymorphism in *Psilocybe merdaria*. New Phytol. **70**: 307–326.

WATLING, R. 2006: The sclerodermatoid fungi. Mycoscience **47**: 18–24.

WEBER, H. 1993: Allgemeine Mykologie. Jena, Stuttgart.

WEBSTER, J. 1983: Pilze, eine Einführung. Berlin, Heidelberg, New York.

WERLE, E., SCHNEIDER, C., RENNER, M., VÖLKER, M., FIEHN, W. 1994: Convenient single-step, one tube purification of PCR products for direct sequencing. Nucleic Acids Res. **22** (20): 4354–4355.

WHITE, T. J., BRUNS, T. D., LEE, S., TAYLOR, J. 1990: Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In INNIS, M. A., GELFAND, D. H., SNINSKY, J. J., WHITE, T. J. (eds.): PCR protocols, a guide to methods and applications. San Diego: 315–322.

WHITE, V. S. 1901: The Tylostomaceae of North America. Bull. Torrey Bot. Club. **28** (8): 421–444.

WIENS, J. J., BONETT, R. M., CHIPPINDALE, P. T. 2005: Ontogeny Discombobulates Phylogeny: Paedomorphosis and Higher-Level Salamander Relationships. Syst. Biol. **54** (1): 91–110.

WINTERHOFF, W. 2000: Epigäische Gasteromycetanae. In KRIEGLSTEINER, G. J. (ed.): Die Großpilze Baden-Württembergs. Bd. 2. Stuttgart: 103–183.

WRIGHT, J. E. 1987: The Genus *Tulostoma* (Gasteromycetes) – A World Monograph. Bibl. Myc. **113**. Berlin, Stuttgart.

WRIGHT, J. E., SUAREZ, V. L. 1990: South American Gasteromycetes IV. The genus *Abstoma*. Crypt Bot. **1**: 372–383.

YOON, K. S., MCLOUGHLIN, D. S. 1984: Basidiosporogenesis in *Boletus rubinellus*. I. Sterigmal initiation and early spore development. Amer. J. Bot. **71** (1): 80–90.

YOON, K. S., MCLOUGHLIN, D. S. 1986: Basidiosporogenesis in *Boletus rubinellus*. II. Late spore development. Mycologia **78** (2): 185–192.

ZELLER, S. M. 1943: North American species of *Galeropsis*, *Gyrophragmium*, *Longia*, and *Montagnea*. Mycologia **35**: 409–421.

ZELLER, S. M. 1947: More notes on Gasteromycetes. Mycologia **39**: 282–312.

ZELLER, S. M. 1948: Notes on certain Gasteromycetes, including two new orders. Mycologia **40** (6): 639–668.

ZELLER, S. M., SMITH, A. H. 1964: The Genus *Calvatia* in North America. Lloydia **27** (3): 148–186.

Supplemental material

TAB. 1: List of herbarium specimens and culture collections used in Chapter 1. Abbreviations in Collection ID refers to: HD = private collection Heinrich Dörfelt; MG = private collection Matthias Gube; BPI = Herbarium of the United States Departement of Agriculture, Beltsville, Maryland; CANB & CBG = Australian National Herbarium, Canberra, Australia; DSM: DSMZ, Braunschweig, Germany; GLM = Staatliches Museum für Naturkunde, Herbarium, Görlitz, Germany; JE = FSU Jena, Herbarium Haussknecht, Jena, Germany; MICH = University of Michigan Herbarium, Ann Arbor, Michigan; NY = Steere Herbarium, New York Botanical Garden, Bronx, New York; OSC = Oregon State University Herbarium, Corvallis, Oregon; W = Naturhistorisches Museum Wien, Herbarium, Vienna, Austria.

#	**Taxon determined**	**Original taxonomy (if differing)**	**Collection ID**	**Origin**
4	*Agaricus xanthodermus*		MG 060914_1	Germany, Thuringia, Jenapriessnitz
5	*Tulostoma brumale*		MG 061115_1	Germany, Thuringia, near Jena
6	*Endoptychum agaricoides*		HD MON 249	Mongolia, Chovd Aimak, Chovd
7	*Battarrea phalloides*		HD MON	Mongolia
14	*Vascellum pratense*		MG 060826_1	Germany, Saxony, near Bergen (Vgtl.)
25	*Gyrophragmium dunallii*		GLM 44519	Portugal, Algarve, Ilha de Tavira
26	*Endoptychum depressum*		NY 834535	U.S.A., California, Yuba Pass
27	*Disciseda bovista*		GLM 19708	Mongolia, Övör-Hangai Aimak, near Erdeni Cu
38	*Lycoperdon pedicellatum*		GLM 42625	Germany, Saxony, Neumühle
41	*Lycoperdon foetidum*	*Lycoperdon umbrinum*	GLM 46636	Germany, Saxony, MTB 5343
54	*Arachnion album*		BPI 736377	U.S.A., Virginia, Fairfax County
55	*Schizostoma mundkarii*		BPI 645636	Pakistan, West Pakistan, Fort Abbas
56	*Longula texensis*		BPI 728422	U.S.A., California, Los Angeles
58	*Schizostoma lacerum*		BPI 645664	Pakistan, West Pakistan, Fort Abbas
62	*Phellorinia herculeana*		CANB 742307.1	Australia, Western Australia, S of Koolyanobbing
67	*Montagnea haussknechtii*	*Montagnea arenaria*	CANB 649668.1	Australia, South Australia, Barrier Highway
68	*Montagnea haussknechtii*	*Montagnea arenaria*	CBG 9511851	Australia, South Australia, Eyre Peninsula
70	*Montagnea haussknechtii*		HD MON 60	Mongolia, Bajan-Ölgij Aimak, near Cengel
71	*Coprinus sterquilinus*		L. Nagy 01.10.2004	Hungary, Nyomásy
72	*Coprinus sterquilinus*		F. Doveri 03894-BIS	no locality
73	*Coprinus xerophilus*		L. Nagy 20.05.2005	Hungary, Ásetthalom
75	*Endoptychum arizonicum*	*Secotium arizonicum*	NY 834493	U.S.A., Texas, Cisco
76	*Endoptychum arizonicum*	*Secotium arizonicum*	NY 834495	U.S.A., Arizona, Sabino Canyon near Tucson
78	*Endoptychum agaricoides*		MICH 08095	U.S.A., Idaho, Owyhee County
79	*Endoptychum agaricoides*	*Endoptychum arizonicum*	MICH 28568	U.S.A., Arizona, Coconino County
80	*Coprinus xerophilus*	*Coprinus asterophorus* *Coprinus* fragments	NY 761539	U.S.A., Nevada, near Lovelock
81	*Montagnea arenaria*	*Coprinus asterophorus* *Montagnea* fragments	NY 761539	U.S.A., Nevada, near Lovelock
83	*Dictyocephalus attenuatus*		NY 449901	U.S.A., California, Lancaster
84	*Chlamydopus meyenianus*		NY 834498	U.S.A., Texas, near El Paso
109	*Schizostoma lacerum*		NY 834492	U.S.A., New Mexico, Dona Ana County
110	*Chlamydopus meyenianus*		NY 834499	U.S.A., Idaho, Owyhee County

111	*Endoptychum agaricoides*		NY 218152	U.S.A., Kansas, Manhattan
112	*Montagnea arenaria*	*Coprinus asterophorus*	NY 761538	U.S.A., Nevada, near Pyramid Lake
113	*Montagnea arenaria*	*Coprinus asterophorus*	NY 761537	U.S.A., Nevada, near Soda Lake
114	*Montagnea arenaria*		NY 048122	U.S.A., Utah, Dixie National Forest
115	*Montagnea haussknechtii*	*Montagnea arenaria*	NY 834496	U.S.A., California, San Bernardino County
119	*Agaricus bernardii*		MG 070805_1	Germany, Thuringia, near Seitenbrück
120	*Lepiota brunneoincarnata*		MG 061002_1	Germany, Baden-Wurttemberg, Tübingen
125	*Bovista plumbea*		MG 061202_7	Germany, Hesse, near Bad Sooden-Allendorf
133	*Agaricus rusiophyllus*		MG 060824_1	Germany, Thuringia, near Jena
138	*Agaricus* cf. *comtulus*		MG 070816_3	Germany, Thuringia, Jena
143	*Podaxis pistillaris*		HD AUS 210	Australia
144	*Podaxis pistillaris*		HD AUS 216	Australia
158	*Macrolepiota konradii*		MG 070905_20	Germany, Thuringia, near Seitenbrück
159	*Schizostoma lacerum*		HD AUS 94	Australia
170	*Lycoperdon perlatum*		MG 031102_1	Germany, Saxony, near Jonsdorf
171	*Lycoperdon echinatum*		MG 061024_8	Germany, Thuringia, near Jena
173	*Montagnea arenaria*		MICH 06614	U.S.A., Washington, Benton County
174	*Montagnea arenaria*		MICH 27885	U.S.A., Arizona, Apache County
175	*Montagnea arenaria*		MICH 28596	U.S.A., Arizona, Coconino County
176	*Montagnea arenaria*		MICH 53275	U.S.A., New Mexico, Dona Ana County
179	*Endoptychum arizonicum*		MICH 08131	U.S.A., Texas, Eastland County
180	*Endotychum agaricoides*		MICH 08133	U.S.A., Oregon, Wasco County
191	*Coprinus sterquilinus*	*Coprinus vosoustii*	JE Gröger 14.V.1989	Germany, Thuringia, Pößneck
196	*Phellorinia strobilina*		JE 08.67	former USSR area
197	*Coprinus comatus*		MG 051029_1	Germany, Thuringia, Coppanz
241	*Crucibulum laeve*		MG 040820_1	Germany, Thuringia, Jena
243	*Lycoperdon pyriforme*		MG 070315_1	Germany, Thuringia, near Jena
253	*Macrolepiota brunnea*		MG 071003_1	Germany, Lower Saxony, Hann. Münden
282	*Leucoagaricus littoralis*		MG 071015_7	Hungary, Nyomási
284	*Montagnea arenaria*		HD MON 22	Mongolia, Chovd Aimak, near Chovd
285	*Coprinus comatus*	*Coprinus sterquilinus*	DSM 3341	Germany
287	*Coprinus comatus*		DSM 1746	no locality
309	*Endoptychum depressum*		OSC 50031	U.S.A., Idaho, Valley County
310	*Endoptychum depressum*		OSC 56130	U.S.A., California, Plumas County
319	*Calvatia fragilis*	*Calvatia lilacina*	NY 068833	Australia, Australian Capital Territory, Canberra
325	*Chlamydopus meyenianus*		NY 449872	U.S.A., New Mexico, Otero County
326	*Battarraea phalloides*	*Battarea laciniata*	NY 384537	U.S.A., Arizona, Green Valley
345	*Secotium arizonicum TYPE*		NY 809153	U.S.A., Arizona, Tucson
347	*Schizostoma lacerum*		NY 449873	U.S.A., Arizona, near Phoenix
348	*Queletia mirabilis*		NY 384532	U.S.A., Pennsylvania, Trexlertown
350	*Battarraeoides diguetii*	*Battarea griffithsii* TYPE	NY 737973	U.S.A., Arizona, Tucson
351	*Endoptychum arizonicum*	*Secotium arizonicum*	NY 834494	U.S.A., Texas, Cisco
365	*Queletia turkestanica*		BPI 729809	Turkmenistan, Karakum
366	*Gyrophragmium dunallii*	*Gyrophragmium lusitanicum*	BPI 718222	Portugal, Lisboa
379	*Montagnea arenaria*		GLM 19673	Mongolia, Ömnögov' Aimak, near Ulan-Ereg
382	*Coprinus spadiceisporus*		Doveri 01296-DIS	no locality

383	*Gyrophragmium dunallii*	*Gyrophragmium inquinans* cf.	CANB 742313.1	Australia, Western Australia, S of Koolyanobbing
396	*Podaxis pistillaris*		JE Long 1938	U.S.A., New Mexico, between Albuquerque and Las Cruces
406	*Morganella fuliginea*		NY 398747	French Guiana, Saül, Limonade Trail
408	*Morganella subincarnata*		NY 398765	U.S.A., Massachusetts, Conway State Forest
416	*Abstoma townei*		NY 065575	no locality
436	*Tulostoma* cf. *cineraceum*		HD MON 59a	Mongolia, Bajan-Ölgij Aimak, near Cengel
437	*Tulostoma* cf. *cineraceum*		HD MON 59b	Mongolia, Bajan-Ölgij Aimak, near Cengel
438	*Tulostoma* cf. *cineraceum*		HD MON 59c	Mongolia, Bajan-Ölgij Aimak, near Cengel
439	*Tulostoma* cf. *cineraceum*		HD MON 80	Mongolia, Bajan-Ölgij Aimak, near Cengel
440	*Tulostoma* cf. *cineraceum*		HD MON 84	Mongolia, Bajan-Ölgij Aimak, near Cengel
441	*Battarea phalloides*		HD MON 89	Mongolia, Bajan-Ölgij Aimak, near Cengel
442	*Tulostoma* aff. *kotlabae*		HD MON 90	Mongolia, Bajan-Ölgij Aimak, near Cengel
443	*Tulostoma* cf. *cineraceum*		HD MON 91	Mongolia, Bajan-Ölgij Aimak, near Cengel
444	*Tulostoma* aff. *kotlabae*		HD MON 91a	Mongolia, Bajan-Ölgij Aimak, near Cengel
445	*Tulostoma* cf. *cineraceum*		HD MON 245	Mongolia, Chovd Aimak, Char nuur
446	*Tulostoma* cf. *evanescens*		HD MON 245a	Mongolia, Chovd Aimak, Char nuur
447	*Tulostoma* aff. *cretaceum*		HD MON 245b	Mongolia, Chovd Aimak, Char nuur
448	*Tulostoma* cf. *evanescens*		HD MON 245c	Mongolia, Chovd Aimak, Char nuur
449	*Tulostoma* aff. *brumale*		HD MON 246	Mongolia, Chovd Aimak, Char nuur
450	*Tulostoma* aff. *kotlabae*		HD MON 246a	Mongolia, Chovd Aimak, Char nuur
453	*Tulostoma melanocyclum*		MG 071020_4	Hungary, Fülöpháza
454	*Tulostoma brumale*		MG 071017_10	Hungary, Bugac
455	*Tulostoma brumale*		MG 071020_20	Hungary, Ladánybene
456	*Tulostoma brumale*		MG 071020_16	Hungary, Kunbaracs
457	*Tulostoma* aff. *kotlabae*	*Tulostoma* cf. *leiosporum*	MG 071016_8	Hungary, Szikra
458	*Tulostoma fimbriatum*		MG 071016_20	Hungary, Tőserdő
459	*Tulostoma fimbriatum*		MG 071019_3	Hungary, Nyír
460	*Tulostoma pulchellum*	*Tulostoma fimbriatum*	MG 071016_40	Hungary, Tőserdő
461	*Tulostoma kotlabae*		MG 071020_3	Hungary, Fülöpháza
462	*Tulostoma kotlabae*		MG 071017_11	Hungary, Bugac
463	*Tulostoma melanocyclum*		MG 071020_22	Hungary, Méntelek
464	*Tulostoma melanocyclum*		MG 071020_21	Hungary, Fülöpháza
465	*Tulostoma melanocyclum*		MG 071015_12	Hungary, Nyomási
466	*Tulostoma pulchellum*		MG 071016_9	Hungary, Szikra
467	*Tulostoma pulchellum*		MG 071016_25	Hungary, Tőserdő
468	*Tulostoma squamosum*		MG 071020_5	Hungary, Fülöpháza
469	*Tulostoma squamosum*		MG 071020_18	Hungary, Kunbaracs
471	*Tulostoma* aff. *cretaceum*	*Chlamydopus meyenianus*	BPI 863658	U.S.A., New Mexico, Las Cruces
480	*Mycenastrum corium*		MG 071015_8	Hungary, Nyomási
481	*Endoptychum agaricoides*		MG 071016_29	Hungary, Hantháza
482	*Endoptychum agaricoides*		MG 071015_3	Hungary, Nyomási
495	*Battarea phalloides*		HD Teutschenthal	Germany, Saxony-Anhalt, Teutschenthal
513	*Panaeolona* cf. *foenisecii*		MG 080701_1	Germany, Lower Saxony, Göttingen

542	*Tulostoma brumale*		JE Diedicke ex Henkel 1.-10.3.19	Germany, Thuringia, near Erfurt
543	*Tulostoma cretaceum* ex-TYPE		JE Long #9302 7.5.41	U.S.A., New Mexico, near Albuquerque
544	*Tulostoma fimbriatum*		JE Günther 9.4.88	Germany, Thuringia, near Hemleben
545	*Tulostoma kotlabae*		JE Gröger 4.9.78	Germany, Mecklenburg-Pomerania, near Göhren/Rügen
546	*Tulostoma polymorphum*		JE Long #10371 11.08.43	U.S.A., New Mexico, Albuquerque
547	*Tulostoma melanocyclum*	*Tulostoma sp.*	JE Schnittler&Günther 3.4.89 coll. mix.	Slovakia, near Bratislava
548	*Tulostoma brumale*	*Tulostoma sp.*	JE Schnittler&Günther 3.4.89 coll. mix.	Slovakia, near Bratislava
549	*Tulostoma brumale*	*Tulostoma sp.*	JE Walther 18.3.44	"Mazedonien, bei Saloniki, oberhalb Sarranada Eeliza, 200m"
550	*Tulostoma squamosum*	*Tulostoma granulosum*	JE Walther 18.5.44	"Bulg.-Macedonia, Opagneka-al, Ochrida"
551	*Macrolepiota procera*		MG 080906_1	Germany, Saxony, near Zentendorf
553	*Bovista tomentosa*		MG 080909_3	Germany, Thuringia, near Oberheldrungen
566	*Longula texensis*	*Gyrophragmium decipiens*	MICH 08701	U.S.A., California, Santa Barbara County
568	*Longula texensis*	*Gyrophragmium decipiens*	MICH 08700	U.S.A., Arizona, near Valentine
569	*Longula texensis*	*Gyrophragmium delilei*	MICH 08702	U.S.A., California, Los Angeles County
570	*Longula texensis*	*Gyrophragmium delilei*	MICH 08699	Mexico, Durango, Torreon de Canas
572	*Longula texensis*	*Gyrophragmium decipiens*	MICH 08705	U.S.A., California, Ventura County
573	*Longula texensis*	*Gyrophragmium delilei*	MICH 08694	U.S.A., California, Sequoia National Park
577	*Longula texensis*	*Gyrophragmium delilei*	MICH 08696	U.S.A., California, Kern County
578	*Endoptychum depressum*		MICH 08165	U.S.A., Idaho, Valley County
579	*Endoptychum depressum*		MICH 08166	U.S.A., Idaho
580	*Endoptychum depressum*		MICH 08171	U.S.A., Oregon, Clackamas County
581	*Endoptychum depressum*		MICH 08168	U.S.A., Oregon, Clackamas County
582	*Endoptychum depressum*		MICH 08170	U.S.A., California, Tuolumne County
583	*Agaricus campestris*		MG 080915_1	Germany, Thuringia, near Grobsdorf
584	*Agaricus semotus*		MG 080915_2	Germany, Thuringia, near Grobsdorf
585	*Leucagaricus leucothites*		MG 080916_1	Germany, Thuringia, near Grobsdorf
586	*Stropharia coronilla*		MG 080915_3	Germany, Thuringia, near Grobsdorf
599	*Longula texensis*	*Gyrophragmium inquinans*	BPI 704085	U.S.A., California, Console Springs
602	*Longula texensis*	*Gyrophragmium decipiens*	BPI 728427	Mexico, Baja California, Poso Gande
625	*Macrolepiota mastoidea*		MG 081006_1	Germany, Hesse, NP Kellerwald-Egersee

Lebenslauf

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Veröffentlichungen

Dörfelt, H., Gube, M. 2007: Secotioid Agaricales (Basidiomycetes) from Mongolia. Feddes Repertorium **118** (3-4): 103–112.

Gube, M. 2007: The gleba development of *Langermannia gigantea* (Batsch: Pers.) Rostk. (Basidiomycetes) compared to other Lycoperdaceae, and some systematic implications. Mycologia **99** (3): 396–405.

Schmidt, A., Gube, M., Schmidt, A., Kothe, E. 2009: In silico analysis of nickel containing superoxide dismutase evolution and regulation. Journal of Basic Microbiology **49**: 109–118.

Ebersberger, I., Gube, M., Strauss, S., Kupczok, A., Eckart, M., Voigt, K., Kothe, E., von Haeseler, A. 2009: A stable backbone for the fungi (manuscript in preparation, available from Nature Precedings http://hdl.handle.net/10101/npre.2009.2901.1.).

Gube, M., Dörfelt, H. 2009: Anatomy and ecology of the gasteromycetation process in Agaricaceae s. l. (in preparation for Feddes Repertorium).

Gube, M., Piepenbring, M. 2009: Preliminary annotated checklist of Gasteromycetes in Panama (accepted for publication in Nova Hedwigia after revision).

Gube, M., Thienes, M., Nagy, L., Kothe, E. 2009: Ten times angiocarpy – gasteromycetation events within Agaricaceae s. l. (Agaricales, Basidiomycetes) (in preparation for Molecular Phylogenetics and Evolution).

Hennicke, F., Gube, M., Kothe, E. 2009: *Schizophyllum* revisited: A new type of fruit body development (manuscript in preparation).

Völksch, B., Thon, S., Jacobsen, I., Gube, M. 2009: Pheno- and genotypic comparison of plant- and clinic-associated *Pantoea agglomerans* strains: assessment of their virulence potential (manuscript in preparation).

Beiträge für Fachtagungen

32. Internationale Tagung der Deutschen Gesellschaft für Mykologie, Tübingen (29.09.–07.10.2006)
Vortrag: GUBE, M.: Systematic aspects of the ontogeny of Lycoperdaceae (Basidiomycetes).

26. Konferenz Vogtländischer Mykologen, Bergen (Vogtland) 13.–16.09.2007)
Vortrag: GUBE, M.: Eine Einführung in die Molekularsystematik der Pilze.

World Fungi 2007, Córdoba, Spanien (10.–16.12.2007)
Poster: GUBE, M.: The systematic relationships of *Vascellum* (Agaricales, Basidiomycetes) inferred by developmental and molecular systematic studies.

33. Internationale Tagung der Deutschen Gesellschaft für Mykologie, Kassel 02.–07.10. 2008
Vortrag: GUBE, M., KOTHE, E.: Multiple events of Gasteromycetation within Agaricaceae (Basidiomycetes) from morphological and molecular phylogenetic points of view.
Poster: GUBE, M., KOTHE, E.: Systematic relationships of *Lycoperdon* subgen. *Morganella* inferred by molecular phylogenetic and morphological studies

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Jena, den 11.05.2009

Matthias Gube