

# *Anomalomyces panici*, new genus and species of Ustilaginomycetes from Australia

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**Abstract.** A new genus, *Anomalomyces*, is proposed to accommodate a peculiar, new smut fungus, *A. panici*, collected in Australia, on *Panicum trachyrhachis*. The new species shares some characteristics of both *Sporisorium* and *Macalpinomyces*, but is also unique in possessing two types of sterile cells. *Anomalomyces* is compared morphologically to the genera *Ustilago*, *Sporisorium*, and *Macalpinomyces*. Its relation to these genera is shown also by molecular analyses of ITS and LSU rDNA sequences. The problems of generic delimitation in this large group of smut fungi are discussed.

**Key words:** *Anomalomyces*, *A. panici*, ITS, LSU, *Macalpinomyces*, molecular analysis, smut fungi, *Sporisorium*, *Ustilago*

## Introduction and Discussion

A peculiar, new smut fungus was collected in Australia on the endemic *Panicum trachyrhachis* (comp. Zundel 1953; Vánky 2005: 217–250). Its morphological characteristics do not collectively fit with those of any known genus of smut fungus (comp. Vánky 2004). It deviates from *Sporisorium* in that the sori, which are produced in the ovaries, lack a columella and are traversed and divided into irregular and incomplete compartments by membranes of host tissue permeated by hyphae. Furthermore, the spore balls are unique in possessing a thick, darkly pigmented layer on the surface of the free wall of the outermost spores, as a result of the deposition of a pigmented substance on the external surface of young spore balls during development. The presence of two different types of sterile cells between the spore balls is a unique characteristic. The new fungus has

true spore balls, which can be observed in serial sections of the sori. It thereby differs from species of *Macalpinomyces*, which have spore balls that result from fragmentation and disintegration of spore masses, resulting in ‘pseudo’ spore balls, intermixed with sterile cells. Molecular analyses of ITS and LSU + DNA sequences were used to find its phylogenetic position amongst the smut fungi. The peculiar morphology and the DNA ITS analysis has lead us to consider that the new species is a member of a separate and new genus, for which we propose the name *Anomalomyces*.

## Materials and Methods

Sorus and spore characteristics were studied using dried herbarium specimens. Sori of various developmental stages were boiled in a mixture of distilled water and lactophenol

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with cotton blue, on a microscope slide, and hand sectioned with a razor blade under a stereo microscope. Thin sections showing the structure of sori and the development of spores, spore balls, and sterile cells were mounted in a droplet of lactophenol with cotton blue on a slide, covered with a cover glass, gently heated to eliminate air bubbles, and examined by a light microscope (LM) at various magnifications. For further study, mature spore balls were dispersed in a droplet of lactophenol on a microscope slide, covered with a cover glass, and gently heated to boiling point to rehydrate the spores. Under a stereo microscope, some of the spore balls were crushed by applying pressure on the cover glass with a soft piece of wood (matchstick) and examined by LM at 1000× magnification. For scanning electron microscopy (SEM), dry spore balls (partly squashed with a lancet), were placed on double-sided adhesive tape, mounted on a specimen stub, sputter-coated with gold-palladium, c. 20 nm, and examined in a SEM at 10 kV.

For molecular analysis, genomic DNA was extracted directly from the herbarium specimen. The methods of isolation and crushing of fungal material, DNA extraction, amplification, purification of PCR products, sequencing, and processing the raw data were those of Lutz *et al.* (2004). Amplification of the ITS 1 and ITS 2 regions of the rDNA including the 5.8S rDNA (ITS) was performed using the primer pair M-ITS1 (Stoll *et al.* 2003) and ITS4 (White *et al.* 1990). The 5'-end of the nuclear large subunit ribosomal DNA (LSU) was amplified using the primer pair NL1 and NL4 (O'Donnell 1993). DNA sequences were deposited in GenBank under accession numbers DQ459348 (ITS) and DQ459347 (LSU). Blast searches (Altschul *et al.* 1997) for both the ITS and LSU sequence revealed closest similarity to members of the *Macalpinomyces/Sporisorium/Ustilago*-group. To further elucidate the phylogenetic position of *Anomalomyces panici*, its ITS and LSU sequences were analysed against the combined ITS/LSU-dataset of Stoll *et al.* (2005). For this analysis, the dataset was reduced to one specimen per species. Additionally, those sequences from the blast searches which were within the first 15 hits but not yet included in the dataset of Stoll *et al.* (2005) (namely *Pseudozyma hubeiensis*, *Pseudozyma fusiformata*, *Pseudozyma* sp., uncultured fungus AY464868, uncultured fungus AY464860) were added. GenBank accession numbers are listed in Fig. 9. Sequence alignment was obtained using MAFFT 5.743 (Kato *et al.* 2005) with the FFT-NS-i option. Both manipulation of the alignment (length: 1608 bp, 671 variable sites) by hand and manual exclusion of any positions was avoided as recommended by Giribet & Wheeler (1999) and Gatesy *et al.* (1993), respectively. Phylogenetic relationships were estimated using a Bayesian approach of phylogenetic inference using a Markov chain Monte Carlo (MCMC) technique as implemented in the computer program MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). Four incrementally heated simultaneous Markov chains were run over 2 000 000 generations using the general time reversible model of DNA

substitution with gamma distributed substitution rates and estimation of invariant sites, random starting trees and default starting parameters of the DNA substitution model. Trees were sampled every 100th generation resulting in an overall sampling of 20 001. From these, the first 2001 trees were discarded (burnin = 2001). The trees sampled after the process had reached stationarity (18 000 trees) were used to compute a 75 % majority rule consensus tree to obtain estimates for the *a posteriori* probabilities of groups of species. This Bayesian approach of phylogenetic analysis was repeated five times to test the independence of the results from topological priors (Huelsenbeck *et al.* 2002). Based on the results of Stoll *et al.* (2005) the trees were rooted with *Moesziomyces bullatus* and *M. eriocauli*.

## Results

*Anomalomyces* Vánky, M. Lutz & R.G. Shivas, **gen. nov.**

*Pertinet ad classam Ustilaginomycetes R. Bauer, Oberw. et Vánky, soris in ovariis hypertrophicatis familiae Poaceae. Sori peridio cooperti, sine columella, membrana ex telis hostilibus hyphis permeatis formata in compartimentis divisi. Sporae pigmentiferae (brunneae, sine ullo transitu colorum violaceo vel rubello), glomerulos permanentes formantes. Sporae glomerulorum maxime externae strato atro substantiae pigmentiferae coopertae. Germinatio sporarum cum phragmobasidiis basidiosporas lateraliter et terminaliter producentibus. Cellulae steriles inter glomerulos sporarum typorum 2 formatae: unus eorum maiores, alter minores. Analyses moleculares generis novi cum typo Anomalomyces panici non obstantes.*

Member of the Ustilaginomycetes R. Bauer, Oberw. & Vánky, having sori in hypertrophied ovaries of Poaceae, covered by a peridium, columella absent. Sori divided into compartments by membranes of host tissue permeated by hyphae. Spores pigmented (brown, without violet or reddish tint), forming permanent spore balls. Outermost spores in the balls are covered by a layer of darkly pigmented substance. Spore germination results in phragmobasidia producing basidiospores laterally and terminally. Sterile cells between the spore balls of two kinds, large, thick-walled, and small, thin-walled. Molecular analyses do not exclude erection of a new genus for the selected **typus generis**:

*Anomalomyces panici* Vánky, R.G. Shivas & M. Lutz, **sp. nov.**

*Typus in matrice Panicum trachyrhachis Benth., Australia, Northern Territory, 100 km S urbe Darwin, Snake Creek, 13°13'31.8" S, 131°05'59.5" E, alt. cca. 140 m.s.m., 9.VI.2006, leg. M.J. Ryley, M.D.E. & R.G. Shivas. Holotypus in BRIP 47 952; isotypus in Herbario Ustil. Vánky, H.U.V. 21 366. Paratypus in matrice Panicum trachyrhachis (det. R. Booth & J. Thompson, BRI), Northern Territory, 10 km W urbe Batchelor, 13°02'54" S, 130°54'41" E, alt. cca. 140 m.s.m., 2.V.2005, leg. D.R. Beasley, T.S. Marney & R.G. Shivas, BRIP 46 421; isoparatypus in H.U.V. 21 084.*

*Sori in ovarii nonnullis inflorescentiae eiusdem, globoidei vel ovoidei, 1,5-3 × 2-3,5 mm, peridio crasso, primum viride serius brunneo, origine plantae nutrientis et fungali cooperti, quo maturo ab apice eius rupto irregulariter massam atrobrunneam, semiagglutinatum usque glomerulosopulveream glomerulorum sporarum cellulis sterilibus multis intermixtarum ostendentes. Columella absens sed sori membranis origine telae plantae nutrientis et hyphis permeatis in loculos incompletos irregularesque divisi. Glomeruli sporarum subglobosi, ovoidei, ellipsoidales usque subpolyedrice irregulares, 25-120 × 30-200 µm, atro-olivaceobrunnei vel opaci, e sporis pluries decem usque pluries centum, arete contiguus pressu valido separabilibus compositi. Sporae rotundatae, subpolyedrice vel polyedrice irregulares, 8-10,5 × 8-11 (-12) µm, pallide olivaceobrunneae; pariete aequali, tenui, cca. 0,5 µm crasso, levi, excepto superficie libera sporarum in glomerulis extimarum 1-2,5 µm crassa, atro-olivaceobrunnea, conspicue levi usque valde leniter punctato-verruculosa, in SEM 2 vel nonnullae verrucarum rotundarum, humilium in unum coalescentes figuram irregularem formantes. Germinatio sporarum cum 3-5-sept. phragmobasidiis 2,5 × 30-60 µm. In basidiis in sterigmatibus lateralibus et terminalibus basidiosporae multae fusiformes 0,8-1,5 × 8-13 µm formatae. In decursu germinationis successivae sporidiorum fusiformium catena parvorum et magis parvorum formata. Cellulae steriles inter glomerulos sporarum typorum 2 formatae: unus eorum maiores, alter minores, omnes singulae. Cellulae steriles typi 1. globosae, subglobosae, ovoideae, ellipsoidales vel parum irregulares, 7-12 × 8-15 µm, pallide olivaceobrunneae; pariete bistrato, aequali vel parum inaequaliter incrassato, 1,2-2,5 µm crasso, levi. Cellulae steriles typi 2. globosae, subglobosae, ovoideae, rotundato-subpolyedrice irregulares, non raro cum apice uno vel apicibus duobus subacutis, et sic lacrima- vel limoniiformes, 2,5-5 × 3-5,5 µm, mediocriter atro-olivaceobrunneae; pariete tenue (cca. 0,2-0,3 µm) levi, saepe cum appendice brevi, hyphali usque 5 µm longo.*

**Sori** (Fig. 1) in some ovaries of an inflorescence, globoid or ovoid, 1.5-3 × 2-3.5 mm, covered by a thick, at first green later brown peridium of host and fungus origin which ruptures irregularly at maturity from its apex disclosing the dark brown, semiagglutinated to granular-powdery mass of spore balls intermixed with numerous sterile cells. Columella lacking but the sori are divided into incomplete and irregular compartments by membranes of host tissue permeated by hyphae (Fig. 2). In the hyaline mass of sporogenous hyphae agglomerated groups of elongate spore initials appear, each with a rounded top (Fig. 3). These increase in size, become globoid (Fig. 4). During this early stage the spore balls become delimited by a 2-2.5 µm thick, olivaceous brown, continuous layer formed from the thickened external wall of the outermost spores. By maturation, the spores increase in size, become pigmented and polyangular by mutual pressure (Fig 5) whereas the hyaline fungal mass around the spore balls is gradually consumed, leaving fungal cells from which sterile cells develop. **Spore balls** (Figs 6-7) subglobose, ovoid, ellipsoidal to subpolyhedrally irregular, 25-120 × 30-200 µm, dark olivaceous brown or opaque, permanent, composed of

tens to hundreds of tightly packed spores which separate by hard pressure. **Spores** (Figs 6-7) rounded subpolyhedrally or polyhedrally irregular, 8-10.5 × 8-11 (-12) µm, pale olivaceous brown; wall even, thin, c. 0.5 µm thick, smooth, excepting the free surface of the outermost spores in the balls which is 1-2.5 µm thick, dark olivaceous brown, apparently smooth to very finely punctate-verruculose, in SEM two or several rounded, low warts often fuse forming an irregular pattern. **Spore germination** (Fig. 8; on slide, in humid chamber, at room temp., in one day) results in 4-6-celled phragmobasidia, measuring 2.5 × 30-60 µm. On the basidia, laterally and terminally, on sterigmata, numerous fusiform basidiospores are produced measuring 0.8-1.5 × 8-13 µm. By successive germination, the basidiospores give rise to a chain of successively smaller, fusiform sporidia. **Sterile cells** (Figs 6-7) between the spore balls of two types, one large and one small, both solitary. Sterile cells of the larger type are globose, subglobose, ovoid, ellipsoidal or slightly irregular, 7-12 × 8-15 µm, pale olivaceous brown; wall of two layers, even or slightly unevenly thick, 1.2-2.5 µm wide, smooth. Sterile cells of the smaller type are globose, subglobose, ovoid, rounded subpolyhedrally irregular, often with one or two subacute tips, then tear- or lemon-shaped, 2.5-5 × 3-5.5 µm, medium dark olivaceous brown; wall thin (c. 0.2-0.3 µm), smooth, often with a narrow, short hyphal appendage, up to 5 µm long.

On Poaceae: *Panicum trachyrhachis* Benth.

Distribution: Australia.

*Anomalomyces panici* has some characteristics of *Sporisorium*, namely the host plant belongs to the *Poaceae*, sori are covered by a peridium, the presence of true spore balls, and also sterile cells between the balls. However it differs from *Sporisorium* in that the multilocular sori lack columellae, the presence of a thick, pigmented layer of an unknown substance on the surface of the spore balls, and the presence of two kinds of sterile cells. *Anomalomyces panici* also has some characteristics of *Macalpinomyces*, namely the host plant is in the *Poaceae*, the sori are covered by a peridium, an absence of columellae, and the presence of sterile cells. It differs from *Macalpinomyces* by having the multilocular sori, true spore balls developed from coiled sporogenous hyphae, and two kinds of sterile cells. This mixture of characteristics indicates a close relationship to *Sporisorium* and *Macalpinomyces*, which was supported by the rDNA analyses. The different runs of Bayesian phylogenetic analyses that were performed yielded consistent topologies. We present the consensus tree of one run to illustrate the results (Fig. 9). All in all the results of Stoll *et al.* (2005) are confirmed although some of their groups are not resolved (e.g., *Ustilago-Sporisorium* group). That differences can be put down to differences in data handling (different alignment methods, no exclusion of any alignment positions in our analyses) and a different kind of depiction of results. We avoided to show groups which received an a posteriori probability less than 75 %. *Anomalomyces panici* clusters within the *Macalpinomyces/Sporisorium/Ustilago*-group in a close but unresolved relationship to the groups *Ustilago* s. str. and *Sporisorium* s. str. (each of

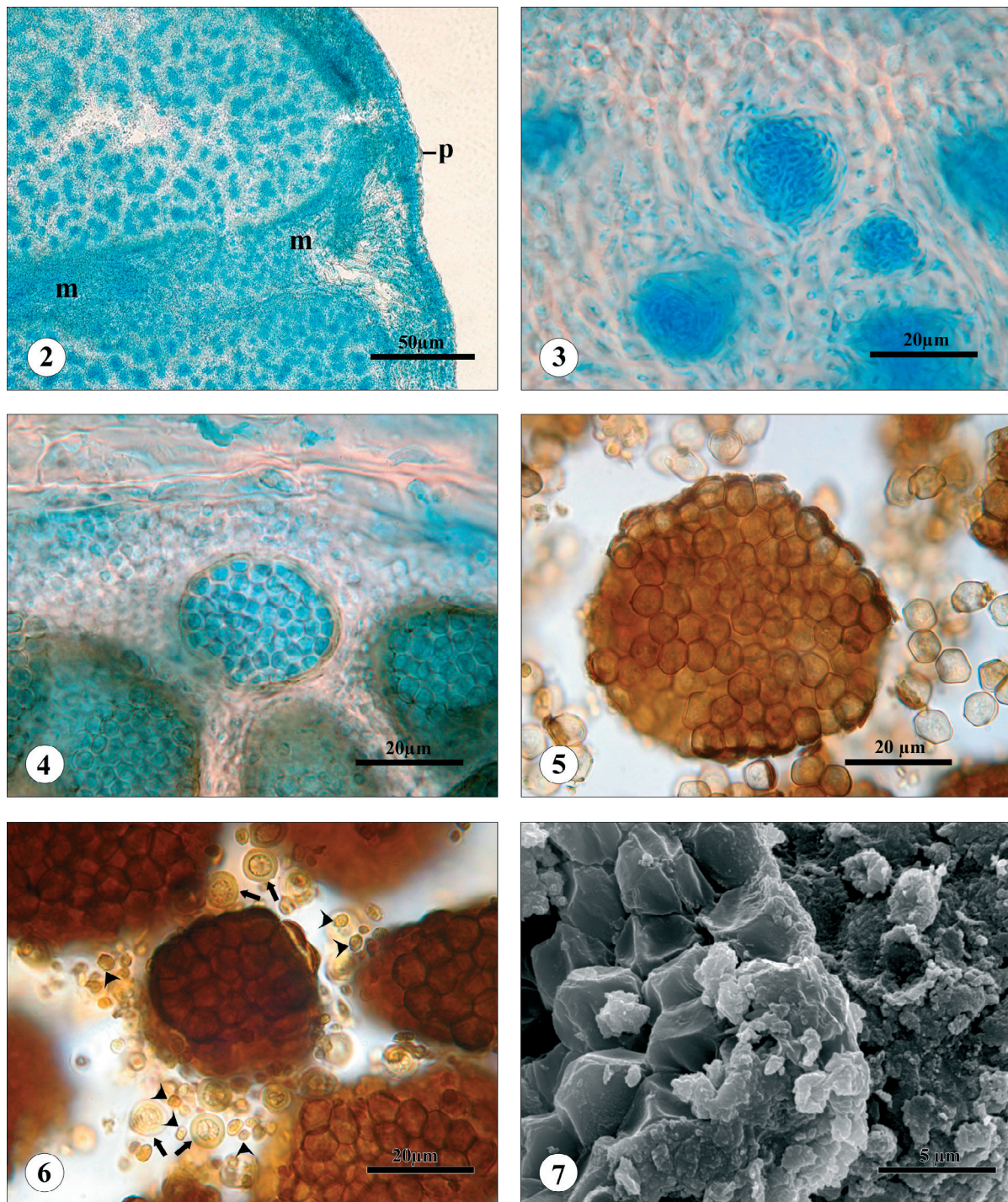
**Fig. 1.** Sori of *Anomalomyces panici* in some ovaries of *Panicum trachyrhachis* (type). Habit and enlarged three sori and some healthy spikelets. Bars = 1 cm for habit and 2 mm for enlargements



them containing the type species of the respective genus) and several *Macalpinomyces*, *Pseudozyma*, *Sporisorium*, and *Ustilago* species of uncertain affiliation. Concerning its relationship to *Macalpinomyces eriachnes*, the type species of *Macalpinomyces*, *Anomalomyces panici* is quite separated (Fig. 9).

The generic limits between *Ustilago*, *Sporisorium*, *Macalpinomyces*, and *Tranzscheliella* has become somewhat blurred in recent years owing to the discovery of intermediate forms in which one or several of the accepted generic features is absent. Molecular analyses (Stoll *et al.* 2003, 2005) rather pointed at the problem than they could help to resolve it.

The erection of small, often unispecific genera, for specimens presenting one or a few abnormal morphological characteristics, especially if unsupported by molecular data is generally not advantageous (comp. *Endosporisorium* Vánky, or *Lundquistia* Vánky). Conversely it is also disadvantageous to describe all new species to the *Ustilago/Sporisorium/Macalpinomyces* complex under the oldest generic name *Ustilago*, which logically would require the recombination of all species of *Sporisorium/Macalpinomyces* into *Ustilago*. Until this group has been re-assessed, possibly using new methods, a sound rearrangement is not possible.



**Fig. 2.** Section of a part of a young sorus of *Anomalomyces panici*, with the pericarp (p) and a membrane of host tissue (m) permeated by fungal filaments (in blue), dividing the sorus into two parts, filled with masses of sporogenous hyphae in which young spore balls are differentiating. Cut in lactophenol with cotton blue (from holotype), in LM. Bar = 50  $\mu\text{m}$ . **Figs 3-4.** Sections of young sori showing various developmental stages of the spore balls, spores and sterile cells of *Anomalomyces panici*, in lactophenol with cotton blue (from holotype), in LM. Bars = 20  $\mu\text{m}$ . **Fig. 5.** A spore ball and some spores of *Anomalomyces panici* (from holotype), in LM. Note the dark layer on the free surface of the outermost spores of the spore ball. Bar = 20  $\mu\text{m}$ . **Fig. 6.** Spore balls of *Anomalomyces panici* (from holotype), in LM. Between the balls two kinds of sterile cells: large, thick-walled (arrows), and small, thin-walled cells (arrowheads). Bar = 20  $\mu\text{m}$ . **Fig. 7.** Part of a ruptured spore ball of *Anomalomyces panici* showing smooth inner spores and rough, irregular free surface of the outermost spores, as well as some of the small sterile cells (from holotype), in SEM. Bar = 5  $\mu\text{m}$

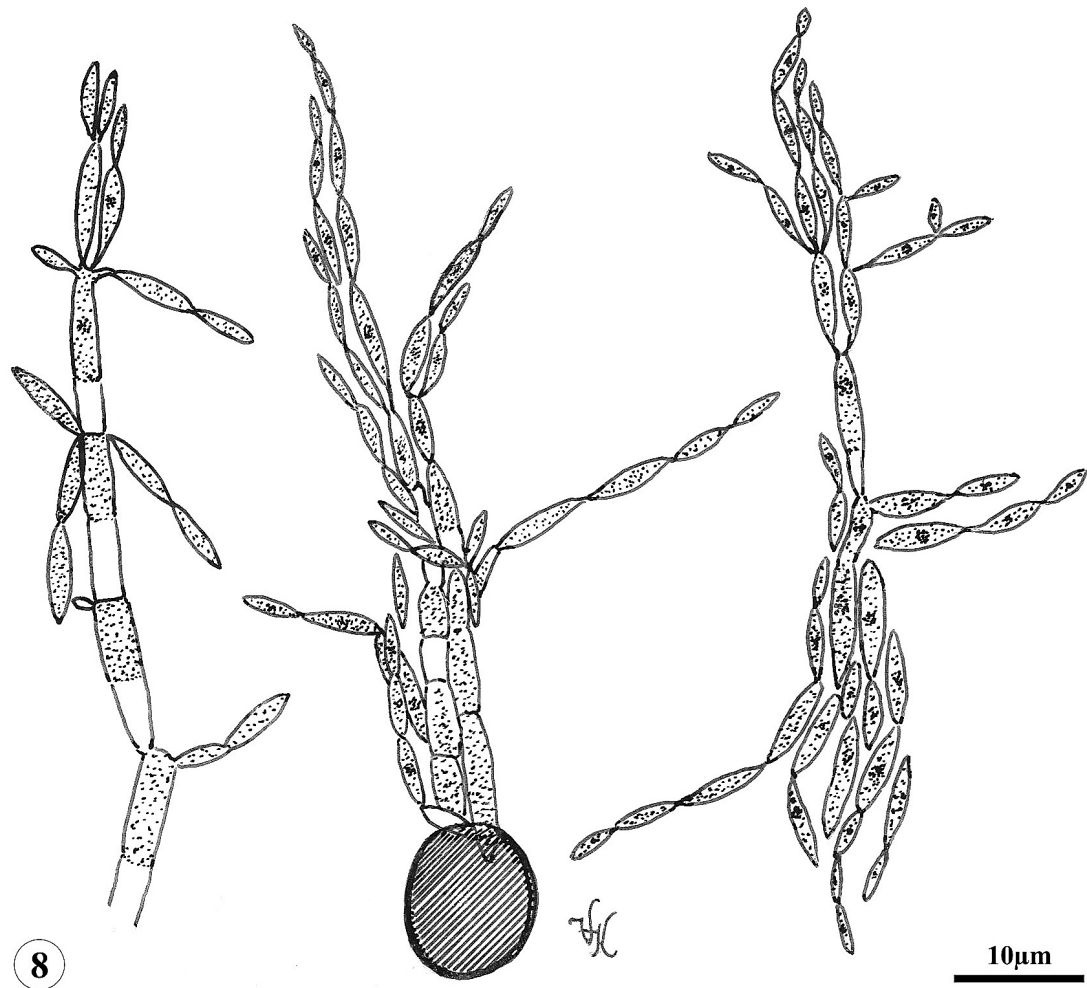


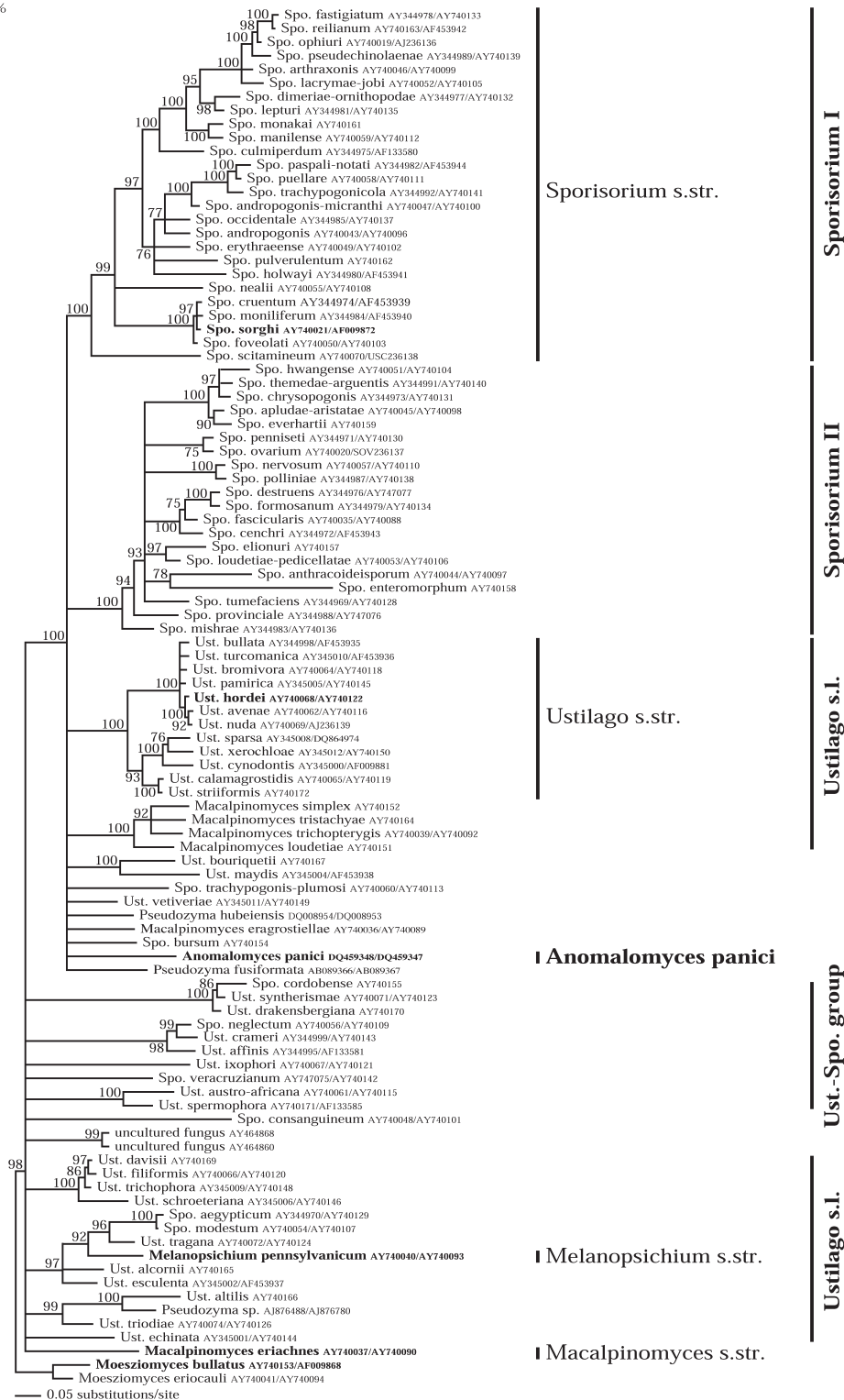
Fig. 8. Spore germination of *Anomalomyces panici* (on slide, in humid chamber, at room temp., in one day) results in phragmobasidia producing laterally and terminally fusiform basidiospores. Bar = 10  $\mu$ m

We suggest that it is best to follow the more or less established genera, which are primarily based on the combination of morphological characteristics, even if intermediate forms are identified, whether by morphological or molecular studies. However, when unusual populations are discovered, which cannot be classified into any of the well-established genera as in the case of *Anomalomyces*, and when molecular data are not contradictory with it, it is best to classify them into new genera. This was also the case with the establishment of the genus *Pilocintractia* Vánky (2004: 172) for which DNA analysis of a specimen of *Cintractia fimbristylidicola* showed an isolated position, supported by unique morphological characteristics. Within two years of its establishment, a second species of *Pilocintractia* was discovered (*P. adrianae* Vánky 2006: 54).

Many unispecific genera can become substantially larger, for example, *Yelsemia* J. Walker (2001: 225), unispecific when published, now has four known species. Sometimes knowledge about the host plant systematic and geographical location support these new groupings, for example both *Pilocintractia* species are on *Fimbristylis*

species from India. In other cases, the host plant and geographical location provide no clues, for example the type of the genus *Yelsemia*, *Y. arthropodii* J. Walker is on the monocotyledonous *Arthropodium* spp. (Liliaceae, s. lat., from Australia). Three further species are on dicotyledonous host plants. The second one, *Y. speculariae* (J.A. Stevenson) Vánky & R. Bauer is on *Triodanis* (Campanulaceae, USA). The third species, *Y. lowrieana* R.G. Shivas & Vánky, is on *Byblis* (Byblidaceae, Australia), whereas the fourth species, *Y. droserae* R.G. Shivas, Vánky & Athipunyakom is on *Drosera* (Droseraceae, Thailand and Australia). The wide phylogenetic range of host plants and geographical distribution of *Yelsemia* is explained by ultrastructure, which shows that *Yelsemia* is closely related to *Urocystis* Rabenh. ex Fockel (both within the Urocystales R. Bauer & Oberw.), which is a surprisingly homogenous genus, with c. 160 species, on both mono- and dicotyledonous host plants, all over the world. As we can see also from these few examples amongst the smut fungi, the criteria for classification varies from group to group.

hc, -2000, 75%



**Fig. 9.** Bayesian inference of phylogenetic position of *Anomalomyces panici*: Markov chain Monte Carlo analysis of an alignment of ITS and LSU base sequences using the GTR+I+G model of DNA substitution with gamma distributed substitution rates and estimation of invariant sites, random starting trees, and default starting parameters of the DNA substitution model. A 75 % majority rule consensus tree computed from 18 000 trees that were sampled after the process had reached stationarity is shown. The topology was rooted with *Moesziomyces bullatus* and *M. ericauli*. Numbers on branches are estimates for a posteriori probabilities. Branch lengths were averaged over the sampled trees. They are scaled in terms of expected numbers of nucleotide substitutions per site. Names of type species are printed in bold.

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## References

- Altschul, S.F., Madden, T.L., Schäffer, A.A., Zhang, J., Zhang, Z., Miller, W. & Lipman, D.J. 1997. Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. – *Nucleic Acids Research* **25**: 3389-3402.
- Gatesy, J., DeSalle, R. & Wheeler, W. 1993. Alignment-ambiguous nucleotide sites and the exclusion of systematic data. – *Molecular Phylogenetics and Evolution* **2**: 152-157.
- Giribet, G. & Wheeler, W.C. 1999. On gaps. – *Molecular Phylogenetics and Evolution* **13**: 132-143.
- Huelsenbeck, J.P., Larget, B., Miller, R.E. & Ronquist, F. 2002. Potential applications and pitfalls of Bayesian inference of phylogeny. – *Systematic Biology* **51**: 673-688.
- Huelsenbeck, J.P. & Ronquist, F.R. 2001. MRBAYES: Bayesian inference of phylogenetic trees. – *Bioinformatics* **17**: 754-755.
- Katoh, K., Kuma, K., Toh, H. & Miyata T. 2005. MAFFT version 5: improvement in accuracy of multiple sequence alignment. – *Nucleic Acids Research* **33**: 511-518.
- Lutz, M., Bauer, R., Begerow, D., Oberwinkler, F. & Triebel, D. 2004. *Tuberculina*, rust relatives attack rusts. – *Mycologia* **96**: 614-626.
- O'Donnell, K.L. 1993. *Fusarium* and its near relatives. – In: D.R. Reynolds & J.W. Taylor [eds]. *The fungal holomorph: mitotic, meiotic and pleomorphic speciation in fungal systematics*, pp. 225-233. CAB International, Wallingford.
- Ronquist, F.R. & Huelsenbeck, J.P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. – *Bioinformatics* **19**: 1572-1574.
- Stoll, M., Piepenbring, M., Begerow, D. & Oberwinkler, F. 2003. Molecular phylogeny of *Ustilago* and *Sporisorium* species (Basidiomycota, Ustilaginales), based on internal transcribed spacer (ITS) sequences. – *Canadian Journal of Botany* **81**: 976-984.
- Stoll, M., Begerow, D. & Oberwinkler, F. 2005. Molecular phylogeny of *Ustilago* and *Sporisorium*, and related taxa based on combined analysis of rDNA sequences. – *Mycological Research* **109**: 342-356.
- Vánky, K. 2002. *Illustrated Genera of Smut Fungi*. 2<sup>nd</sup> edn. APS Press, St. Paul, Minnesota, USA.
- Vánky, K. 2004. *Pilocintractia* gen. nov. (Ustilaginomycetes). – *Mycologia Balcanica* **1**: 169-174.
- Vánky, K. 2005. Taxonomic studies on Ustilaginomycetes – 25. – *Mycotaxon* **91**: 217-272.
- Vánky, K. 2006. Taxonomic studies on Ustilaginomycetes – 26. – *Mycotaxon* **95**: 1-65.
- White, T.J., Bruns, T.D., Lee, S. & Taylor, J.W. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. – In: M.A. Innis, D.H. Gelfand, J.J. Sninsky & T.J. White [eds]. *PCR protocols, a guide to methods and applications*, pp. 315-322. Academic Press, San Diego.
- Walker, J. 2001. *Yelsemia arthropodii* gen. et sp. nov. (Tilletiales) on *Arthropodium* in Australia. – *Mycological Research* **105**: 225-232.
- Zundel, G.L. 1953. The Ustilaginales of the world. – Pennsylvania State College School of Agriculture, Department of Botany Contribution **176**: 1-410.