The smut fungi (Ustilaginomycetes) of Eriocaulaceae. I. *Eriomoeszia* gen. nov.

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Abstract. A new genus, *Eriomoeszia,* is described for *Tolyposporium eriocauli* (*Moesziomyces eriocauli*) on *Eriocaulon.* It is compared with *Moesziomyces bullatus,* the type species of the genus *Moesziomyces,* found on *Echinochloa* and other grass genera.

Key words: *Eriocaulon, Eriomoeszia, Moesziomyces bullatus,* new genus, smut fungi, Ustilaginomycetes

Introduction

According to Heywood (1978: 281), the Eriocaulaceae, within the subclass Commelinidae, order Commelinales, is a largish family of herbaceous plants, usually with grass-like leaves. It comprises 13 genera and about 1200 species. It is centred in the New World, but found throughout the tropics and subtropics, usually on swampy or seasonally water inundated ground. Its systemic position varies considerably according to author. Takhtajan (1996: 18) places the Eriocaulaceae in the order Eriocaulales, superorder Commelinanae of the subclass Commelinidae. The Poaceae, according to the same author, are in the order Poales, superorder Poanae of the subclass Commelinidae. Bremer *et al.* (2003: 30) places the Eriocaulaceae under the order Poales of the subclass Commelinidae, as a sister group of the Xyridaceae.

Only six smut fungi have been described on members of Eriocaulaceae, five on species of *Eriocaulon* and *Syngonanthus,* and one on *Mesanthemum.* In this paper, only "*Tolyposporium*" *eriocauli* G.P. Clinton is treated.

A new genus, *Moesziomyces* Vánky (1977: 133), was proposed for a peculiar smut fungus, then known as *Tolyposporium bullatum* (J. Schröt.) J. Schröt., in the ovaries of *Echinochloa crus-galli* (L.) P. Beauv. (Poaceae). This smut was morphological different to the type of the genus *Tolyposporium, T. junci* (J. Schröt.) Woronin ex J. Schröt. on *Juncus bufonius* L. (Juncaceae). Host plant taxonomy also played a role in the decision to erect a new genus, and this was subsequently also supported by molecular analyses (comp. Begerow *et al.* 1998, Figs 2-3). Initially, three other similar smut fungi, parasitising various grass genera, were recombined into the genus *Moesziomyces.* These are: *M. evernius* (Syd.) Vánky, type on *Paspalum distichum* L., *M. globuligerus* (Berk. & Broome) Vánky, type on *Leersia hexandra* Swartz, and *M. penicillariae* (Bref.) Vánky, type on *Penicillaria spicata* Willd.

In a later study of the genus (Vánky 1986), it was not possible to construct a good key to differentiate the four species of *Moesziomyces;* the morphological differences being small, or possibly non-existent. Consequently, these smuts were united under the oldest name *M. bullatus,* the type of the genus. Molecular analyses will be necessary to demonstrate if this decision is correct. At the same time (Vánky 1986), based on morphological similarities of the spore balls, e.g., permanent spore balls in which the spores are separated and connected by sterile fungal cells, I recombined *Tolyposporium eriocauli* G.P. Clinton, type on *Eriocaulon septangulare* With. (Eriocaulaceae), as *M. eriocauli* (G.P. Clinton) Vánky.

Results and Discussion

During preparation of a world monograph of the smut fungi, I again studied the two *Moesziomyces* species and came to the conclusion that it is best to place them in two separate genera. This opinion is based partly on morphological and biological differences between the two species, and partly on host plant

taxonomy. There is a thin cortex of sterile cells surrounding the spore balls in *Tolyposporium eriocauli,* a feature not previously noted. As this layer is absent in *M. bullatus,* a new genus is proposed to accommodate *T. eriocauli:*

Eriomoeszia Vánky, **gen. nov.**

Sori *in ovariis plantae nutrientis familiae Eriocaulaceae, sine columella,* ***glomerulos sporarum*** *permanentes e massa sporarum arcte agglutinatarum cellulis sterilibus separatarum compositos et strato corticali cellularum sterilium circumdatos formantes.* ***Sporae*** *pigmentiferae (brunneae), non colore violaceo neque flavide-rubro tinctae.* ***Cellulae steriles*** *inter sporas pariete tenues, pigmentiferae (brunneae), inanes.* ***Germinatio sporarum*** *cum phragmobasidiis, basidiosporas producentibus.* ***Infectio*** *systemica.* ***Interactio*** *inter plantas nutrientes et parasitas per hyphas intracellulares.* ***Septa*** *mature sine poris.*

Typus generis: E. eriocauli.

Sori in ovaries of host plants belonging to the Eriocaulaceae, columella lacking, forming permanent **spore balls** composed of a mass of tightly agglutinated spores separated by sterile cells, surrounded by a cortical layer of sterile cells. **Spores** pigmented (brown), without violet or yellowish red tint. **Sterile cells** between the spores thin-walled, pigmented (brown), empty. **Spore germination** results in phragmobasidia producing basidiospores. **Infection** systemic. **Host-parasite interaction** by intracellular hyphae. Mature **septa** are poreless.

Type of the genus:

Eriomoeszia eriocauli (G.P. Clinton) Vánky, **comb. nov.**

Basionym: *Tolyposporium eriocauli* G.P. Clinton, Rhodora **3**: 82, 1901. — *Dermatosorus eriocauli* (G.P. Clinton) M.D. Whitehead & Thirumalachar, 1972: 128. — *Tolypoderma eriocauli* (G.P. Clinton) Thirum., in Thirumalachar & Neergaard, 1978: 191 (invalid name, *Tolypoderma* being a nomen nudum). — *Moesziomyces eriocauli* (G.P. Clinton) Vánky, 1986: 71. — Type on *Eriocaulon septangulare* (= *E. aquaticum*), USA, Massachusetts, at Ellis, 10 Sep 1900, G.P. Clinton (BPI 192 598; isotypes in Seymour & Earle, Econ. fgi., Suppl. C, no. 54, H.U.V. 7953!).

Sori (Figs 1-3) in all flowers of an inflorescence as obovoid, laterally flattened, often two lobed, or rounded three lobed bodies, the swollen capsules, up to 2 mm long, hidden by the perianth, covered by a thin membrane of host origin which ruptures easily disclosing the blackish brown, granular powdery mass of spore balls. Infection systemic. Both female and male flowers of an inflorescence are affected developing capsules (transvestitism) and replacing the ovaries by spore balls. Usually all inflorescences of an infected plant are affected. **Spore balls** (Figs 4, 7) ovoid or irregular, rarely globose, 65-160 × 70-200 (–250) µm, dark brown, opaque, composed of a mass of hundreds of spores separated by sterile cells which at same time also "glue" the spores together in the ball. A thin, hard, cortical layer of sterile cells covers the balls. **Spores** (Figs 4, 6, 9) globose to ovoid or almost subpolyhedral, 7-9 × 8-11 µm, pale yellowish brown; wall thin (in LM *ca* 0.5 µm, in TEM 1-2 µm), finely, densely, low verrucose as seen in SEM. **Sterile cells** (Figs 4, 9) between the spores varying in shape and size, irregularly polyhedral, up to 7 µm long, yellowish brown, empty at maturity; wall thin, 0.15-0.4 µm (measured in TEM), smooth. In squash preparation the sterile cells rupture irregularly and their fragments remain firmly attached to the spores as winged reticulations, spines or wrinkles. **Cortex** (Figs 4, 7, 11) formed of small, firmly united, relatively thick-walled, sterile cells arranged in a single, continuous layer, empty, in face view rounded, ovoid, elliptical or subpolygonally slightly irregular, 4-6.5 × 4-7.5 µm, dark yellowish brown, in side view 3-5 µm high, with four more or less flattened sides; lateral walls fused with those of the neighbouring cells, 0.5-0.8 µm thick, free wall in LM slightly convex or concave, much thinner, especially in its centre, in SEM finely verruculose, impressed. At a 40× magnification, the spore balls appear shiny due to the presence of the small-celled cortical layer. **Spore germination** (Clinton 1901: 80) results in septate basidia bearing laterally and terminally basidiospores.

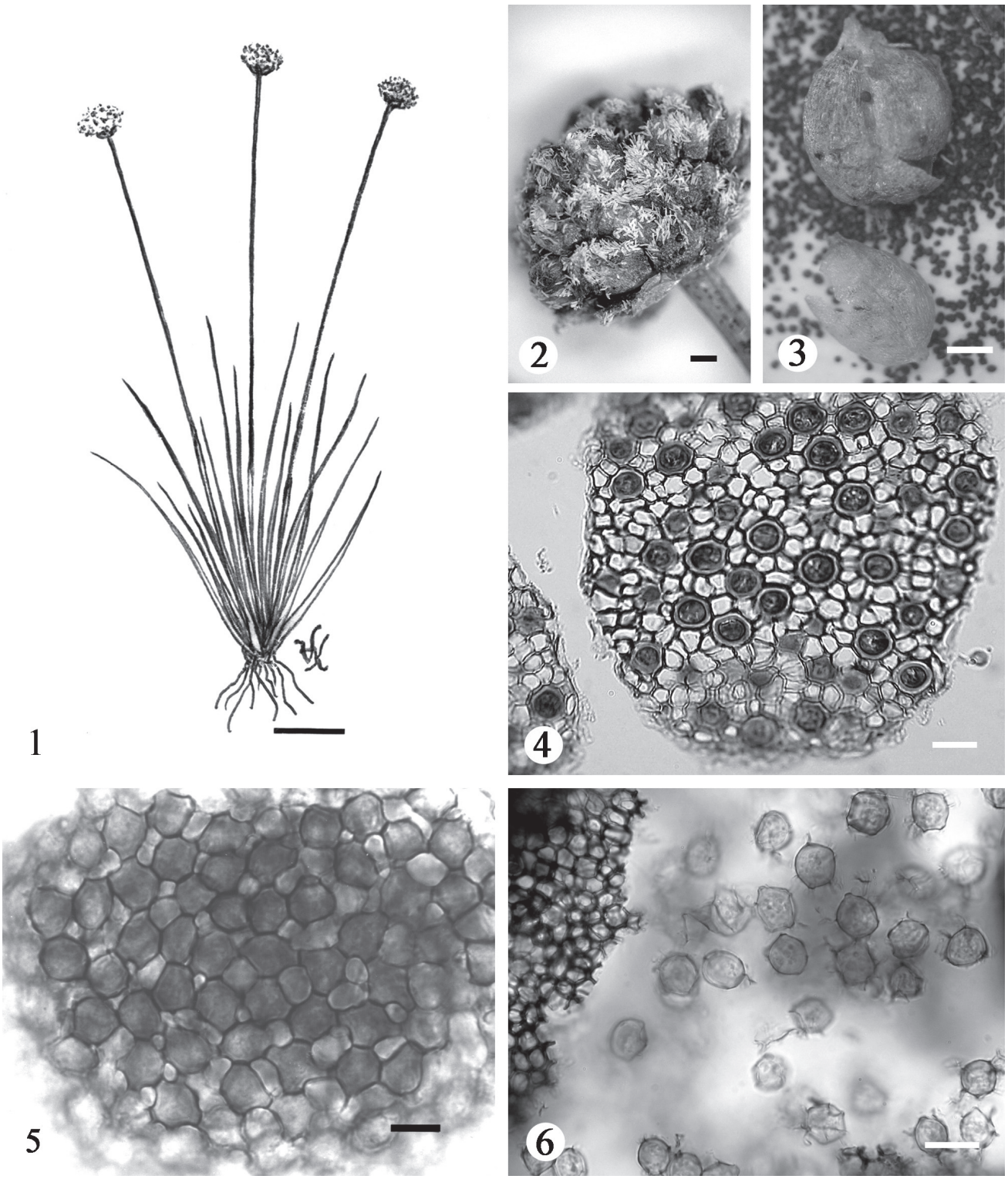
On *Eriocaulon aquaticum* (Hill) Druce (*E. septangulare* With., *E. articulatum* (Huds.) Morong), *E. cinereum* R. Br., *E. collinum* Hook. fil.

Distribution: S. Asia (India), N. America (USA). Certainly more widespread but overlooked.

Etymology: *Erio-* from the host plant family, Eriocaulaceae, *-moeszia* from the smut fungus genus *Moesziomyces,* which was named in honour of the great Hungarian mycologist, Dr. Gusztáv Moesz (1873-1946).

Whereas the differences between *Tolyposporium junci* on one hand, and *Moesziomyces bullatus* and *Eriomoeszia eriocauli* are striking (e.g., sterile cells absent in *T. junci*), the differences between the two latter species are more discrete but present. These differences, discussed below, are grouped into three categories: (1) morphological differences, (2) biological differences, and (3) phylogenetic differences, expressed also in host plant taxonomy and shown by molecular biological methods.

Fig. 1. Sori of *Eriomoeszia eriocauli* in three inflorescences of *Eriocaulon aquaticum* (type). Habit. Bar = 1 cm. **Fig. 2.** Sori of *Eriomoeszia eriocauli* in all swollen flowers of an inflorescence of *Eriocaulon aquaticum,* hidden by the perianths (type). Bar = 1 mm. **Fig. 3.** Two sori of *Eriomoeszia eriocauli* in the capsules of *Eriocaulon aquaticum* (type), one filled with dark spore balls, another empty. Bar = 1 mm. **Fig. 4.** Part of a sectioned and coloured spore ball of *Eriomoeszia eriocauli* on *Eriocaulon aquaticum* in LM (type). Thick-walled spores are separated by a layer of thin-walled, empty, sterile cells, which at the same time are al-



so connecting the spores in a ball. Note the thin cortex formed of a layer of small, flattened, empty, sterile cells. Bar = 10 µm. **Fig. 5.** Part of a young spore ball of *Moesziomyces bullatus* on *Leersia japonica* in LM (HUV 5218), in which the spores are connected to each other by peculiar prolongations of the spores. Bar = 10 µm. **Fig. 6.** A squashed spore ball of *Eriomoeszia eriocauli* on *Eriocaulon aquaticum* in LM (type), in which the spores are more or less separated because of the ruptured sterile cells. To the left a fragment of the cortex. Bar = 10 µm

Morphological differences, similarities

Due to modern, high power light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM), as well as applying special techniques, earlier unknown morphological and ultrastructural characters of the smut fungi became evident. *Tolyposporium junci,* "*T.*" *bullatum* and "*T.*" *eriocauli* share common ultrastructure, i.e., host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix, and poreless mature septa (Bauer *et al.* 1997). Consequently, ultrastructure cannot be used for further division on generic level (all three belonging to the order Ustilaginales). On the other hand, LM study of the spore balls revealed an earlier overlooked cortical layer surrounding the mass of spores and sterile cells of *Eriomoeszia eriocauli,* which was confirmed also by SEM pictures (Figs 7, 11). Such a cortex is lacking in *Moesziomyces bullatus* (Figs 8, 12). Furthermore, in the spore balls of *E. eriocauli* the spores are nearly always completely separated by a single layer of surrounding sterile cells. Interestingly, the same sterile cells, which are surrounding the spores, are concomitantly constituting parts of the surrounding cover of the neighbouring spores (Fig. 4). The spores in the balls of *M. bullatus* are often connected to each other by peculiar, wide prolongations of the spores (Fig. 5), a feature which is lacking in *E. eriocauli.* The sterile cells between the spores in the balls of *Moesziomyces* are scattered irregularly, not as in *Eriomoeszia.*

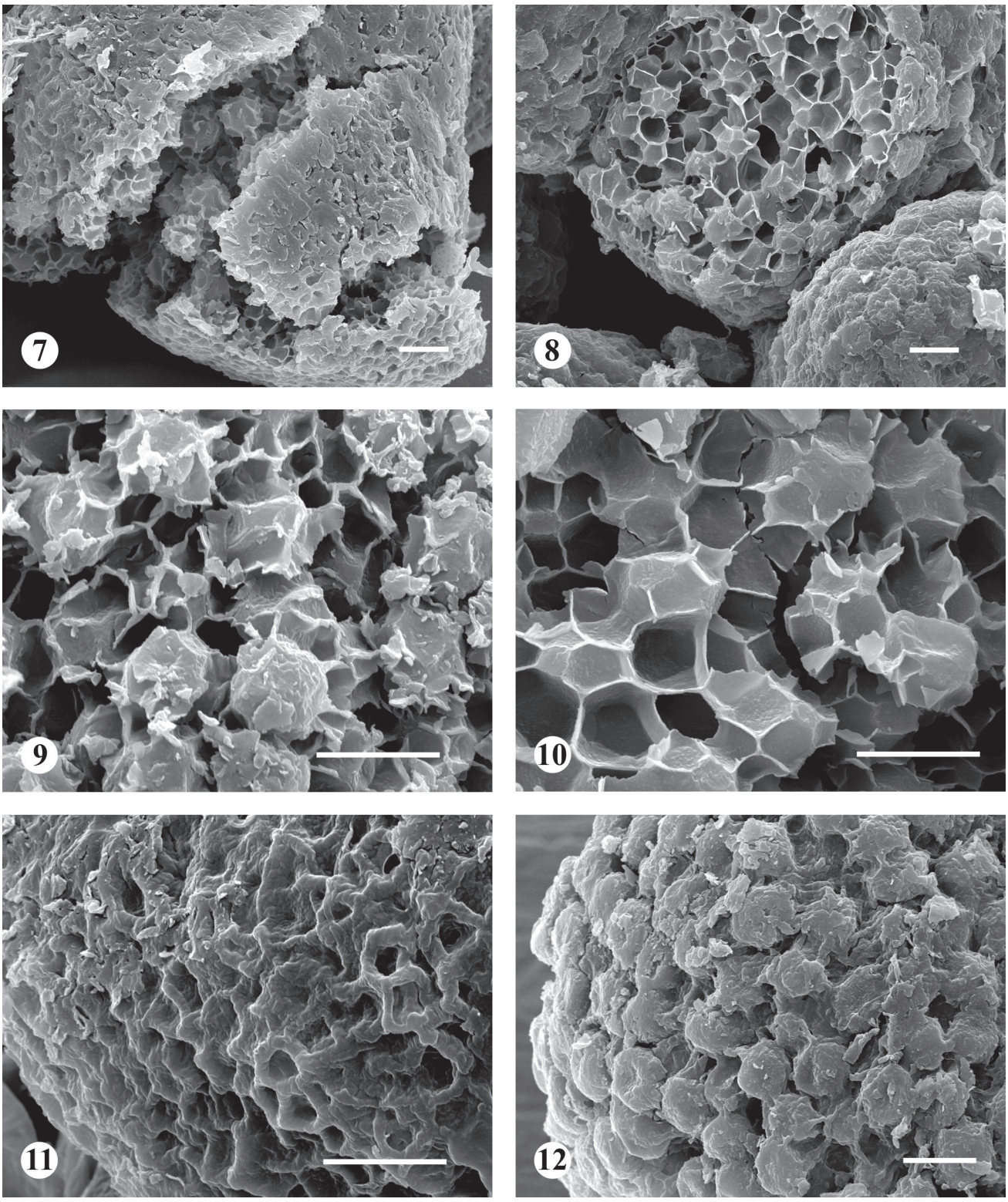
The two morphological differences between *E. eriocauli* and *M. bullatus,* viz. presence and absence of a cortical layer of the spore balls, and the different arrangement of the sterile cells between the spores in the balls, are considered to be important, qualitative differences, separating the two species. Another character, which is more evident, and to which earlier a great importance was attributed in separating *Moesziomyces* from all other genera (Vánky 1977, 1986) is the remnants of ruptured, thin-walled sterile cells, adhering to the spores of *Moesziomyces* when the balls are crushed (Figs 9, 10). These remnants were previously considered to be spore wall ornamentation. To appear such remnants the following three conditions are necessary: (i) spore balls in which the spores are separated by extremely thin-walled, fragile, sterile cells; (ii) the spores are relatively thick-walled, resistant to certain pressure; and (iii) the sterile cells are strongly adhering ("glued") to the spores on their contact surfaces. Nowadays, when with the help of molecular biology has revealed many cases of convergent evolution within the fungi, the idea is easily born: the similar spore ball structures in *M. bullatus* and *M. eriocauli* may also result from convergent evolution in these two smut fungi that parasitise systematically unrelated host plants which, with a few exceptions, all live in wet places. I would like to recall the very interesting case of convergent evolution within the smut fungi. The genus *Doassansiopsis* (Setch.) Dietel (with 12 known species), the single genus within the Doassansiopsiaceae Begerow, R. Bauer & Oberw., of the order Urocystales R. Bauer & Oberw. shares with the *ca* 40 species of the ten genera belonging to the Doassansiaceae (Azbukina & Karatygin) R.T. Moore ex P.M. Kirk, P.F. Cannon & J.C. David of the order Doassansiales R. Bauer & Oberw. the following characters: adapted to aquatic or paludal plants, and possessing pale coloured spores agglutinated in permanent spore balls (with a single exception). The balls of all these genera are composed of spores, sterile cells and/or hyphae in various arrangements. The arrangement of these components and the structure of the spore balls is used for generic delimitation (comp. Vánky 2002a: 8-9). In *Doassansia* Cornu (16 species), the spore balls are composed of a central mass of spores, surrounded by a layer of sterile cells. In the spore balls of *Doassansiopsis,* a central mass of sterile cells is surrounded by one or several layers of spores and a thin, outer layer of cortical sterile cells. These differences do not seem to be very important, because other characters of the spores and sterile cells are similar. This may explain why even such greatness of mind of mycology as the late Professor John Axel Nannfeldt (Uppsala, whose lucky pupil I was), and another pupil, the late Brita Lindeberg (1959: 22) considered *Doassansiopsis* to be a synonym of *Doassansia.* Ultrastructural (Bauer *et al.* 1997) and molecular studies (Begerow *et al.* 1998) revealed that these two genera are not only two good genera but they are not related, belonging to different families and orders. They are products of a convergent evolution, as an adaptation to aquatic or paludal host plants. The spore ball structure of *Eriomoeszia eriocauli* and *Moesziomyces bullatus,* containing empty sterile cells, is certainly also an adaptation to water or paludal host plants. Most *Eriocaulon* spp., *Leersia* spp., *Paspalum distichum* L., many *Echinochloa* spp. are such plants, but there are also exceptions (e.g., *Echinochloa crus-galli* or *Pennisetum glaucum* (L.) R. Br.).

Spore ball development may also be a useful character for differentiating two genera but, unfortunately, this was studied only for *M. bullatus* (Vánky 1986: 69, Fig. 2B, 1987: 72, Fig. C).

Biological differences, similarities

The flowers in Eriocaulaceae are unisexual, in dense heads, subtended by an involucre of bracts. Male and female flowers are mixed within each head. Contrary to earlier descriptions,

Fig. 7. Part of a spore ball of *Eriomoeszia eriocauli* on *Eriocaulon aquaticum* in SEM (type) with fissured cortex revealing a few spores inside the ball. Bar = 10 µm. **Fig. 8.** A broken spore ball of *Moesziomyces bullatus* on *Echinochloa crus-galli* in SEM (Vánky, Ust. exs. no. 35) with spores and empty sterile cells. Bar = 10 µm. **Fig. 9.** Part of a broken spore ball of *Eriomoeszia eriocauli* on *Eriocaulon aquaticum* in SEM (type) with spores and broken, empty, sterile cells. Bar = 10 µm. **Fig. 10.** A broken spore ball of



Moesziomyces bullatus on *Echinochloa crus-galli* in SEM (Vánky, Ust. exs. no. 35) with spores and empty sterile cells. Bar = 10 µm. **Fig. 11.** Part of the surface of a spore ball of *Eriomoeszia eriocauli* on *Eriocaulon aquaticum* in SEM (type), showing the small, tightly glued cortical cells with impressed outer wall. Bar = 10 µm. **Fig. 12.** Part of the surface of a spore ball of *Moesziomyces bullatus* on *Echinochloa crus-galli* in SEM (Vánky, Ust. exs. no. 35) showing the free surface of the spores and the lack of a cortical layer. Bar = 10 µm

I found that each flower in the head of infected *Eriocaulon* contain sori, independently of the host plant species. This can be explained by the phenomenon called "transvestitism", caused by *Eriomoeszia eriocauli.* In this case, each infected male flower develops a capsule in which the ovaries are replaced by spore balls, which fill the capsules. Only a thin layer of host tissue remains, the covering layer of the sori, similar to infected female flowers. The narrow and often also smaller sori are probably those that have developed in male flowers. Transvestitism is common also in some other groups of smut fungi, e.g., within the genus *Restiosporium* Vánky, on members of the Restionaceae s. lat.

Infection of the host plants by *Moesziomyces bullatus* is a local, floral infection, through the stigma and style, before the flowers are pollinated (Bhatt 1946, for the smut on *Pennisetum typhoides* (Burm. fil.) Stapf & C.E. Hubb.). In *Eriomoeszia eriocauli* the infection is a systemic one, because all flowers of an inflorescence, and all inflorescences of a plant are affected. Local or systemic infection can be used as a character to separate the two genera. In homogenous genera, the type of infection is the same, e.g., in *Anthracoidea* species it is always a local, floral infection. In contrast, spore germination cannot be used to separate these two genera because in both type species the pattern is similar: a phragmobasidium producing basidiospores.

Phylogenetic differences, similarities

Before publication of the new classification of the smut fungi and allied taxa (Bauer *et al.* 1997), generic delimitation was based mainly on morphological characters of the sori and spores and, when present, also of spore balls and sterile cells, as well as on the basidial characters (Vánky 1987: 3). When *Tolyposporium eriocauli* was transferred into the genus *Moesziomyces,* only 47 (+ 8 doubtful) smut genera were known (Vánky 1987). The similarity of the spore ball structure of *T. eriocauli* with that of *M. bullatus* was striking and very different from spore ball structures in any described genus. Consequently, the decision to transfer *Tolyposporium eriocauli* into *Moesziomyces,* based on a generally similar structure of the spore balls, was relatively easy, despite some doubts, caused by the host taxonomy: "The Eriocaulaceae has no near relatives and occupies a somewhat isolated position in the monocotyledons" (Heywood 1978: 282).

In 1997, the historical period "Zundel – New classificatory system" (1953-1997) of the smut fungi and related taxa came to an end and the "Present, molecular biological period" started (Vánky 2002b: 164). Many papers appeared after 1997, contributing to the progress, and bringing clarity into numerous details of the classification of these fungi, based on ultrastructural-, molecular-, and classical morphological characters (comp. Bauer *et al.* 1997, 1998, 1999a, b, 2000, 2001, 2006; Piepenbring & Bauer 1997; Vánky 1997a, b, 1999a, b, c, 2000, 2001a, b, 2004a, b; Vánky *et al.* 1997, 1998; Begerow *et al.* 1998, 2004; Piepenbring *et al.* 1999; Ershad 2000; Walker 2001; Denchev 2003; Bauer 2004; Weiss *et al.* 2004; Piatek 2005). At present, the number of recognised genera of "classical smut fungi" (those possessing teliospores) is 83.

Since 1997, for the delimitation of genera, in addition to macro-, micro-, and ultrastructural characters, molecular biological results are used, where such are available. With these techniques, natural relationships are shown better which not rarely are disguised by occurrence of such phenomena as "convergent evolution" or "host jumps".

In the excellent paper of Stoll *et al.* (2005), combined analyses of ITS and LSU rDNA sequences were utilised to resolve the phylogenetic relationships of 98 members of the smut genera *Lundquistia* (1 sp.), *Melanopsichyum* (1 sp.), *Moesziomyces* (2 spp.), *Macalpinomyces* (6 spp.), *Sporisorium,* and *Ustilago* (together the remaining 88 spp.). In their discussion (Stoll *et al.* 2005: 344) wrote: "*Moesziomyces* species are placed basal with sufficient bootstrap support (Fig. 1), thus justifying their use as outgroup for subsequent phylogenetic analyses. Monophyly of *Moesziomyces* is not supported by our analyses, although *M. bullatus* and *M. eriocauli* share a very peculiar morphology with fragments of sterile cells adhering to the teliospores (Vánky 1986, 1998)".

This means that *Moesziomyces* and *Eriomoeszia* are only distantly related to the *Ustilago-Sporisorium* complex, and these two groups represent most probably two evolutionary lines. Further molecular analyses, including that of other smut species and genera are necessary to reveal how much *Moesziomyces* and *Eriomoeszia* are related and to confirm or rebute the supposed heterogeneity of the two *Moesziomyces* species, based on morphology, biology, and host plant taxonomy (Tab. 1).

Table 1. The main differentiating characters of *Eriomoeszia* and *Moesziomyces*

Characters	Eriomoeszia	Moesziomyces
host family	on Eriocaulaceae	on Poaceae
infection	systemic, all flowers in the inflorescence being infected	infection local, affecting only some flowers in the inflorescence
spore balls	shiny; cortex present	spore balls not shiny; cortex absent
spores	regularly and completely separated by sterile cells	irregularly, often incompletely separated by sterile cells

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