The emended *Ustilaginaceae* of the modern classificatory system for smut fungi

Kálmán Vánky

Herbarium Ustilaginales Vánky (HUV), Gabriel-Biel-Str. 5, D-72076 Tübingen, Germany; e-mail: vanky.k@cityinfonetz.de

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Some of the higher taxa of the modern classificatory system for smut fungi are analysed. It is shown that the emended family of *Ustilaginaceae*, with its 29 genera unified by an identical ultrastructure, is heterogeneous. Based on classical morphological and ecological characters, including host taxonomy, several genera are excluded from this family and placed into other families. New families proposed are: *Clintamraceae*, *Dermatosoraceae*, *Farysiaceae*, *Geminaginaceae*, *Melanopsichiaceae*, *Uleiellaceae* and *Websdaneaceae*. The family *Cintractiaceae* was expanded to include also *Heterotolyposporium*, *Leucocintractia*, *Testicularia*, *Tolyposporium*, *Trichocintractia* and *Ustanciosporium*. A few genera with uncertain placement regarding their family, are mentioned. Spore colour in the classification of smut fungi is discussed. The generic name *Uleiella* J. Schröt. instead of *Ulea* J. Schröt. is preferred.

Key words: *Cintractiaceae*, *Clintamraceae*, *Dermatosoraceae*, *Farysiaceae*, *Geminaginaceae*, *Melanopsichiaceae*, new families, smut fungi, *Uleiellaceae*, Ustilaginomycetes, *Websdaneaceae*.

Introduction

A new classificatory system of smut fungi and allied taxa (Bauer *et al.*, 1997, Begerow *et al.*, 1997(1998), Vánky, 1999b) was proposed on the basis of ultrastructural characters of the septal pore and host-parasite interactions, molecular analyses (LSU rDNA sequences), and to a lesser extent, microscopic characters of the spores and spore balls. Currently in this system, the *ca.* 1450 known "classical" smut fungi (those possessing teliospores), are classified into two classes, three subclasses, eight orders, 19 families and 77 genera. Compared with earlier classifications, this new system is the most natural classification of the smut fungi and allied taxa so far. At the same time, the new classificatory system has stimulated the development of an even more natural classification by attempts to group smut fungi at the suprageneric level,

as revisions of existing genera. Examples are the unification of the genera *Sorosporium* F. Rudolphi and *Thecaphora* Fingerh. (Vánky, 1998a), and the splitting of the genus *Cintractia* s. lat. into several genera (Piepenbring *et al.*, 1999).

While working on the second edition of *Illustrated Genera of Smut Fungi* (Vánky, in prep.) it became obvious that the *Ustilaginaceae* L.-R. and C. Tul., emend. R. Bauer and Oberw. are a heterogeneous assemblage of morphologically and ecologically quite different genera. The study of species, which showed characters distinct from those of recognised genera of smut fungi, resulted in the description of several new genera, e.g. *Farysporium*, *Lundquistia*, *Pseudodermatosorus*, *Pseudotracya*, *Restiosporium* and *Ustanciosporium* (Vánky, 1999a,c, 2000, 2001).

The class Ustilaginomycetes R. Bauer, Oberw. and Vánky is characterised by host-parasite interactions with deposits of specific fungal vesicles, in contrast to the Urediniomycetes, where such deposits are lacking. Members of the Ustilaginomycetes with enlarged interaction zones and either poreless septa or septal pores with membraneous caps represent the subclass Ustilaginomycetidae Jülich, emend. R. Bauer and Oberw. Members of the Ustilaginomycetidae having poreless septa form the order Ustilaginales G.P. Clinton, emend. R. Bauer and Oberw. To the family *Ustilaginaceae* L.-R. and C. Tul., emend. R. Bauer and Oberw. belong those members of the Ustilaginales in which the parasitic hyphae are intracellular. Originally, in the emended *Ustilaginaceae* the following 21 genera were recognised (Bauer *et al.*, 1997: 1310): *Anthracoidea*, *Cintractia*, *Clintamra*, *Dermatosorus*, *Farysia*, *Franzpetrakia*, *Geminago*, *Glomosporium*, *Kuntzeomyces*, *Macalpinomyces*, *Melanopsichium*, *Moesziomyces*, *Orphanomyces*, *Pericladium*, *Schizonella*, *Sorosporium*, *Sporisorium*, *Thecaphora*, *Tolyposporium*, *Trichocintractia* and *Ustilago*. Members of these genera share the characters of intracellular hyphae, enlarged interaction zones and poreless septa.

LSU rDNA analyses showed that several higher taxa, established on the basis of ultrastructural characters, are heterogeneous (Begerow *et al.* 1997(1998)). *Glomosporium*, *Sorosporium* and *Thecaphora* were excluded from the *Ustilaginaceae* and placed under the *Glomosporiaceae* Cif., emend. Begerow, R. Bauer and Oberw. Besides molecular differences, "members of the *Glomosporiaceae* parasitise dicotyledons, whereas those of the *Ustilaginaceae* predominantly occur on monocotyledons. In addition, the *Glomosporiaceae* are holobasidiate, whereas the *Ustilaginaceae* are phragmobasidiate". Within the Urocystales R. Bauer and Oberw. three families have been recognised as a result of molecular studies: *Doassansiopsaceae* Begerow *et al.*, *Melanotaeniaceae* Begerow *et al.* and *Urocystaceae* Begerow

et al. (Begerow *et al.* 1997(1998)). Of these, the *Doassansiopsaceae* and *Urocystaceae* share common ultrastructure, a simple septal pore with two membrane caps and two non-membraneous inner plates closing the pore, as well as host-parasite interaction by haustoria. These two families have molecular differences, and the spores are colourless in the *Doassansiopsaceae* and pigmented in the *Urocystaceae*.

As shown above, the emended family of *Ustilaginaceae* is a heterogeneous assemblage of genera possessing the same ultrastructure. Further division of this family based on ultrastructure is not possible, but molecular data and classical morphological characters may help, best if they are combined. However, as long as sequence data are unavailable for all known species of a group, a phylogenetically-based classification system will also undergo changes. As more taxa are added to comparisons, even major branches may change position. As I have no access to molecular analyses, I have used morphological and ecological characters to divide the heterogeneous *Ustilaginaceae* into natural groups. Such an attempt is difficult and the results may be subject to changes when molecular data becomes available. The problem is that during phylogeny, morphological characters of the sori, spore balls, spores and basidia changed more than ultrastructural or molecular characters. Therefore, I selected only a few groups which appear to be distinct enough to propose a transfer.

Taxonomy

A new family for *Dermatosorus*

Dermatosorus K. Sawada ex L. Ling (1949: 267) was described for an ovaricolous smut fungus, *D. eleocharidis* Sawada ex Ling on *Eleocharis dulcis* Trin. from Taiwan. It has five known species, each on a different genus of the *Cyperaceae*. *Dermatosorus* is a homogeneous, natural genus. Based on its ultrastructure, it was classified into the emended *Ustilaginaceae*. However, most of the characters of *Dermatosorus* and those of *Ustilago*, the type of the *Ustilaginaceae*, are different. Typical for the genus *Dermatosorus* are:

- Host plants in the *Cyperaceae*, in the tropics and subtropics.
- Sori in considerably swollen ovaries, with peridium and columella, in some of the spikelets of the host plants, indicating a local, floral infection.
- Spore balls large, permanent, composed of a great number of spores surrounded by a cortex of empty, sterile cells.

- The spores are separated by small, empty compartments formed by the reticulum of the spore wall, with the meshes face to face (*cf.* also Piepenbring *et al.*, 1998: 173-175, Figs. 12, 21, 22).
- Formation and maturation of the spore balls and spores are also characteristic for this genus. The spore balls differentiate successively from the hyphal initials amassed over the columella, ripening from their distal part (*cf.* Langdon, 1977: 448, Figs. 1,2,4,5).
- Parasitic hyphae are intracellular, coated by an electron-opaque matrix.
- Mature septa are poreless.

The permanent spore balls with a cortex of empty cells and the empty spaces between the spores are certainly an adaptation to water dispersal and to resistance during dry periods. The spore balls float on the surface of water in the rainy period of the year, where the spores germinate easily, infecting flowers of young plants probably by basidiospores in water droplets splashed up by heavy rains.

The genus *Ustilago* (Pers.) Roussel (1806: 47), with *ca.* 230 known species, type *U. hordei* (Pers.: Pers.) Lagerh. on *Hordeum* (*Gramineae*), is characterised by:

- Host plants in the *Gramineae*.
- Sori in various parts of the host plants, at maturity bursting and exposing usually powdery, sometimes agglutinated, blackish-, or olivaceous-brown spore masses.
- Sterile cells absent.
- Spores single, small to medium-sized, pigmented (brown), usually ornamented (verruculose, echinulate or irregularly verrucose-reticulate, etc.), rarely smooth.
- Spore germination results in phragmobasidia producing laterally and terminally basidiospores or hyphae.
- *Ustilago* shares ultrastructure (poreless septa and intracellular hyphae coated by an electron-opaque matrix) with other genera in the emended *Ustilaginaceae* and in families which have already been separated from them (e.g. *Glomosporiaceae*).

Species of *Ustilago* are, with very few exceptions, restricted to terrestrial host plants, and are adapted to dispersal by wind through the powdery spore masses and the single, small, light spores. Rains, insects, animals, human beings may also contribute to spore dispersal but apparently without a clear and uniform adaptation of the fungus to such kinds of dispersal.

Based on the characters and differences between *Dermatosorus* and *Ustilago*, I propose to remove *Dermatosorus* from the *Ustilaginaceae* into a new family:

Dermatosoraceae **Vánky, fam. nov.**

Pertinent ad ordinem Ustilaginales G.P. Clinton, emend. R. Bauer and Oberw., cum hyphis intracellularibus et characteribus generis *Dermatosorus*. *Sori* in ovariis familiae *Cyperaceae*. *Peridium et columella* adsunt. *Glomeruli sporarum* permanentes, typici, compositi e cortice ex cellulis vacuis formato et e massa centrali sporarum pigmentiferarum per loculos vacuos e reticulis sporarum formatos separatarum. *Germinatio* sporarum cum phragmobasidiis, basidiosporas sessiles, hyalinas producentibus.

Typus familiae: *Dermatosorus* Sawada ex L. Ling, Mycologia 41: 267, 1949.

Member of the order Ustilaginales, having intracellular hyphae and the characters of the genus *Dermatosorus*: *Sori* in ovaries of *Cyperaceae*. *Peridium and columella* are present. *Spore balls* permanent, typical, composed of a cortex of empty sterile cells and a central mass of pigmented spores separated by empty compartments formed by the reticulum of the spores. *Spore germination* results in phragmobasidia producing sessile, hyaline basidiospores.

Type of the family: *Dermatosorus* Sawada ex L. Ling.

A new family for *Websdanea*

Another genus in the emended *Ustilaginaceae*, with dissimilar characters to *Ustilago* (and other genera in the *Ustilaginaceae*) is the unispecific *Websdanea* Vánky (1997: 184).

Type: *W. lyginiae* (Websdane, Sivasith., K.W. Dixon and Pate) Vánky, on *Lyginia barbata* (Labill.) R. Br., Australia. It is characterised by:

- Host plants in the *Restionaceae*.
- Sori in the stems producing hypertrophy of the covering tissues.
- Systemic infection; diseased plants remain sterile.
- Spore mass black.
- Spore mass formed of spore balls.
- Peridium, columella and sterile cells are lacking.
- Spore germination results in phragmobasidia on which basidiospores on sterigmata and also hyphae are produced.

To accommodate it, I propose:

Websdaneaceae **Vánky, fam. nov.**

Pertinent ad ordinem Ustilaginales G.P. Clinton, emend. R. Bauer and Oberw., cum hyphis intracellularibus et characteribus generis *Websdanea*. *Sori* in caulibus familiae *Restionaceae*. *Massa sporarum* nigra, e glomerulis sporarum composita. *Peridium, columella et cellulae* steriles absentes. Ad phragmobasidia basidiosporae cum sterigmatibus et etiam hyphae productae.

Typus familiae: *Websdanea* Vánky, Mycotaxon 65: 184, 1997.

Member of the order Ustilaginales, having intracellular hyphae and the characters of the genus *Websdanea*: *Sori* in stems of *Restionaceae*. *Spore mass* black, composed of spore balls. *Peridium, columella and sterile cells* are lacking. On phragmobasidia basidiospores on sterigmata and also hyphae are produced.

Type of the family: *Websdanea* Vánky.

Another smut genus on *Restionaceae* is *Restiosporium* Vánky (2000: 346), with about 10 species (several still unpublished). The sori develop in the ovaries, attacked male plants are transformed into female ones (transvestism), spore mass black, composed of spore balls. At present, *Restiosporium* is classified into the *Ustilaginaceae*. Further studies are needed to clarify to which family it belongs.

A new family for *Uleiella*

Of the 29 smut fungus genera (three with uncertain place), enumerated by Bauer *et al.* (2000: 67), under the emended *Ustilaginaceae*, one genus (*Uleiella*) is on a Gymnosperm (*Araucaria*). Twenty-five genera are restricted to monocotyledoneous host plants: *Cyperaceae* and/or *Juncaceae* (17 genera), *Gramineae* (6), *Restionaceae* (1), *Liliaceae* (1). Only three genera are on dicotyledoneous plants: 1. *Pericladium* Pass., with four known species, three on *Grewia* (*Tiliaceae*), one on *Piper* (*Piperaceae*), 2. the unispecific *Geminago* Vánky and R. Bauer on *Triplochiton* (*Sterculiaceae*) and 3. *Melanopsichium* Beck, with two species on *Polygonum* (*Polygonaceae*). Preparing a paper, dealing with the new classificatory system (Vánky, 1999b), it become clear to me that the genus *Ustilago* is restricted to host plants in the *Gramineae*. I am also convinced that members of the *Ustilaginaceae* are restricted to monocotyledoneous host plants. However, this has to be verified by molecular analyses because jumps to new host groups may have occurred.

Schröter (1894) described a peculiar smut fungus, and for it also a new genus, *Uleiella*, producing sori in the inflorescence of *Araucaria* (*Araucariaceae*, Gymnospermae).

Type: *U. paradoxa* J. Schröt. on *Araucaria imbricata* Pav., Brazil. Soon, a second species, *U. chilensis* Dietel and Neger was described, also on *A. imbricata* Pav., from Chile.

Almost all smut fungi (*ca.* 1450 species) occur on phanerogams, with only five exceptions, one species of *Exoteliospora* R. Bauer, Oberw. and Vánky (belonging to the *Melanotaeniaceae* Begerow, R. Bauer and Oberw.) on *Osmunda* spp. (Pteridophyta, *Osmundaceae*), two species of *Melaniella* R. Bauer, Vánky, Begerow and Oberw. (*Melaniellaceae* R. Bauer, Vánky,

Begerow and Oberw.) on *Selaginella* spp. (Lycophyta, *Selaginellaceae*), and the two species of *Uleiella*.

Surprisingly little is published about the curious and problematic genus *Uleiella*. There is a nomenclatural problem regarding the generic name of *Uleiella* J. Schröt., 1894 versus *Ulea* J. Schröt., 1892. According to the Index Nominum Genericorum, *Uleiella* J. Schröt. (1894) is a nomen novum superfluum pro *Ulea* J. Schröt. (1892), and this last name should be the valid one for this genus. In my opinion, Schröter knew very well how a new genus and species have to be described. In 1892 he had no intention to describe a new genus and species. At a meeting of the Society of the Silesian Culture, he enumerated many South American fungi, amongst them 12 new species including *Ulea paradoxa* n. sp. (for many of them mentioning only a name and the host plant). In connection with this fungus Schröter remarked that it produces brown, powdery spore masses consisting of large, brown spores on the base of the needles of an *Araucaria* and cannot be considered a *Uredineae*. To consider this a generico-specific description is contrary to Schröter's intention. This will be more evident if we compare it with the lege artis publication of "*Uleiella* Schröter gen. nov." and that of "*Uleiella paradoxa* Schröter sp. nov.", with detailed descriptions in Latin, with spore measurements, indication of the (type) specimen, etc., given by Schröter in 1894. In addition, there is a footnote in the second paper of Schröter (1894: 65) in which he wrote "Der in der vorläufigen Mittheilung Bot. Central-Blatt Bd. 50 pag. 42 angenommene Gattungsname *Ulea* musste geändert werden, da mir Herr Ule schrieb, dass derselbe bereits für eine Lebermoosgattung vergeben ist". (The in the preliminary notice used generic name *Ulea* had to be changed, because Mr. Ule wrote, that the same name was already given to a livermoss).

If *Ulea* J. Schröt. would be accepted as the valid name of this genus, one has to propose to reject it in the favour of *Uleiella*, because under this generic name both important, plant pathogenic species on *Araucaria* in South America are known. In addition, the name of the livermoss genus *Ulea* Müll. Hal. also has to be changed. Consequently, my opinion is that it is better to consider *Ulea* J. Schröt. and *Ulea paradoxa* J. Schröt. as nomina nuda. (As a result of a correspondence, Dr. Ellen Farr recently communicated to me that *Ulea* J. Schröt. can be considered a nomen subnudum and, consequently, an invalid name. Corresponding changes will also be made in the *Index Nominum Genericorum*).

The systematic position of *Uleiella* was obscure for a long time and still not all its aspects are satisfactorily solved. It was even thought to be a rust fungus, which was denied already by Schröter (1892: 42).

Furthermore, it is still not clear what the rounded, reticulate, pigmented propagules of the fungus with several units inside represent. They are certainly not true spore balls (Vánky, 1998b: 525-526). Are they spore agglomerates enclosed by a reticulate cover? Are they spores with (1-)several cells or, according to Thirumalachar (1949: 340-342) are they spores with "endospores"? Regarding spore formation and maturation of *Uleiella*, all that I found published is in a general paper of Dietel (1897: 23). He wrote that "spores mostly 4–12, formed inside an intensively yellow or yellowish-brown cover. The cover is formed by a coloured external layer and a gelatinous, colourless, inner layer. These spore cases are globoid or ellipsoidal and are produced singly at the end of hyphae" (translated from German).

Examination of the propagules of different ages, stained with cottonblue in lactophenol, shows small "spore complex" initials of 5-8 µm diam. already have a finely reticulate, 0.5-1 µm thick, yellow coloured wall and blue coloured contents. Inside the larger spore complexes, several small, blue coloured "spore" initials can be seen, separated by a more or less thick layer of a hyaline, homogenous mass. With age the spore complexes increase in size, the reticulate, covering layer becomes thicker (2.5-5.5 µm) and yellowish-brown coloured. The spores inside increase too, whereas the gelatinous mass around them successively diminishes. Under pressure, the reticulate cover ruptures and the "spores", with a *ca.* 0.5 µm, evenly thick, yellow wall surrounded by an unevenly thick, hyaline layer, pass freely through the cover.

Spore germination, described by Butin and Peredo (1986: 68), results in several, short, septate (retraction septa?) germ tubes (basidia) which soon assume an arborescent appearance producing successively, apically, numerous, ovoid, hyaline spores (basidiospores) which bud like yeast cells. The spores germinate still enclosed by the reticulate layer through which the basidia grow out.

Concerning the ultrastructure of *Uleiella*, one must deduce from the fact that it was classified under the *Ustilaginaceae* by Bauer *et al.* (2000: 69) that the mature septa are poreless and the parasitic hyphae are intracellular, coated by an electron-opaque matrix. Consequently, the place of *Uleiella* is within the smut fungi.

In conclusion, *Uleiella*, a homogeneous genus of two species is characterised by:

- Host plants in the *Araucariaceae* (Gymnospermae).
- Sori in the inflorescence, superficial, forming a naked, dark brown mass of "spore complexes", powdery when dry, slimy when wet.
- Spore complexes with one- to usually many spores held together by a pigmented, deeply reticulate cover (exospore?).

- Spore germination results in several, short, septate (retraction septa?) basidia which soon assume an arborescent appearance producing apically, successively, numerous basidiospores.
- Basidiospores hyaline, ovoid, with yeast-like budding.
- Parasitic hyphae intracellular, coated by an electron-opaque matrix.
- Mature septa poreless.

To accommodate this curious and unusual genus, I propose:

Uleiellaceae Vánky, **fam. nov.**

Pertinent ad ordinem Ustilaginales G.P. Clinton, emend. R. Bauer and Oberw., cum hyphis intracellularibus et characteribus generis *Uleiella*. Sori in inflorescentiis familiae *Araucariaceae* (Gymnospermae), intecti. *Massa sporarum* pigmentifera (atrobrunnea), pulverea, in superficie telarum hospitis. *Complexio sporarum* cum ornamento, uni- usque plerumque multisporales. *Sporae* leves, pallide flavidobrunneae. *Germinatio* sporarum basidio basidiosporas apicales, ovoideas, fermentiformes producenti.

Typus familiae: *Uleiella* J. Schröter, Hedwigia, Beiblatt 33: (65), 1894 (*Ulea* J. Schröter, Botaniches Centralblatt 50: 42, 1892, nom. subnud.).

Member of the order Ustilaginales, having intracellular hyphae and the characters of the genus *Uleiella*: *Sori* in the inflorescence of *Araucariaceae* (Gymnospermae), naked. *Spore mass* pigmented (dark brown), powdery, on the surface of host tissues. *Spore complexes* ornamented, with one- to usually many spores. *Spores* smooth, pale yellowish-brown. *Spore germination* results in a basidium producing apically ovoid, yeast-like basidiospores.

Type of the family: *Uleiella* J. Schröt.

A new family for *Melanopsichium*

One of the three smut genera on dicotyledoneous host plants, included in the *Ustilaginaceae* on the basis of their common ultrastructure, is *Pericladium* Pass. on *Grewia* (*Tiliaceae*) and *Piper* (*Piperaceae*). It was studied by the smut fungus team at the University of Tübingen (Bauer, Begerow, Vánky). The results, with taxonomic consequences and possible exclusion from the *Ustilaginaceae*, will be published separately.

Another genus in the emended *Ustilaginaceae* on dicotyledonous host plants is *Melanopsichium* Beck, with two species on *Polygonum* spp. (*Polygonaceae*). Typical for this genus are:

- Sori purplish-black, forming conspicuous, irregularly lobed galls in different organs of the host plants, elastic when young, viscid when humid, firmly indurate when dry, composed of hypertrophied host tissue containing numerous chambers filled with spores embedded in a hyaline, gelatinous matrix.

- Spores single, poorly pigmented (pale yellowish-brown to light chestnut-brown, without violet tint), with a well-developed gelatinous sheath.
- Spore germination results in one or two, septate basidia on which laterally and terminally ovoid to oblong, hyaline basidiospores are borne.

Melanopsichium, from temperate to tropical parts of the world, is adapted to resist frosty or dry periods by the spores enclosed in very hard sori. In humid conditions, the gelatinous substance, in which the spores are embedded, swells considerably and pushes the spore mass out to the sorus surface, sometimes looking like long worms. In ideal conditions, the released spores germinate producing local infections of the new generation of host plants.

To accommodate *Melanopsichium* Beck, I propose:

Melanopsichiaceae Vánky, **fam. nov.**

Pertinent ad ordinem Ustilaginales G.P. Clinton, emend. R. Bauer and Oberw., cum hyphis intracellularibus et characteribus generis *Melanopsichium*. *Sori* in organis diversis familiae *Polygonaceae* cecidia composita e telis hospitis unacum cellulis multis sporis impletis in matrice gelatinoso, hyalino inclusis formantes. *Sporae* singulae, pigmentiferae (pallide brunneae, sine ullo transitu coloris violacei), cum vagina bene evoluta, gelatinosa. *Germinatio* sporarum cum 1 vel 2 phragmobasidiis, basidiosporas ovoideas usque elongatas, hyalinas producentibus.

Typus familiae: *Melanopsichium* Beck, Annales des k. k. naturhistorischen Hofmuseums (Wien) 9: 122, 1894.

Member of the order Ustilaginales, having intracellular hyphae and the characters of the genus *Melanopsichium*: *Sori* in different organs of *Polygonaceae* forming galls composed of host tissue with numerous chambers filled with spores embedded in a hyaline, gelatinous matrix. *Spores* single, pigmented (pale brown, without violet tint), with a well-developed gelatinous sheath. *Spore germination* results in one or two phragmobasidia with ovoid to oblong, hyaline basidiospores.

Type of the family: *Melanopsichium* Beck.

A new family for *Geminago*

The unispecific *Geminago* Vánky and R. Bauer (in Vánky, 1996: 182).

Type species: *G. nonveilleri* (Zambett. and Foko) Vánky and R. Bauer, on the tree *Triplochiton scleroxylon* K. Schum. (*Sterculiaceae*), in Central Africa. It is a peculiar fungus and one of the few smuts to parasitise woody plants. *Geminago* is characterised by:

- Sori in all floral parts which are considerably hypertrophied and deformed, with dark brown, semipowdery spore mass produced centripetally in numerous, small cavities, embedded in superficial

layers of the host tissue which later rupture disclosing the spores. The cavities are lined by sporogenous hyphae and filled by spores. Mature sori have a peculiar, alveolar pattern, resembling an irregular honeycomb (*cf.* Zambettakis and Foko, 1971: 293, plate 1).

- Spores olivaceous-brown, more or less hemispherical, in pairs, tightly adhering on the whole flattened surface of the spores, later they may separate partially or completely.
- Spore wall uneven, smooth, in TEM the centre of the adhering surface shows a peculiar, irregular, radial pattern (Vánky, 1996: 182, Fig. 19).
- Spore germination results in septate, ramified basidia composed of variable numbers of cells. On the basidia, ovoid, elongated, fusiform, brown basidiospores are produced in chains or in groups, laterally or terminally (Zambettakis and Foko, 1971; Ofong, 1978).
- Parasitic hyphae intracellular, coated by an electron-opaque matrix.
- Mature septa poreless.

The floral bud is susceptible to direct infection (Zambettakis and Foko, 1971) by germinating spores, perhaps transported by wind, insects or by birds.

To accommodate this unusual smut fungus, I propose a new family:

Geminaginaceae Vánky, **fam. nov.**

Pertinent ad ordinem Ustilaginales G.P. Clinton, emend. R. Bauer and Oberw., cum hyphis intracellularibus et characteribus generis *Geminago*. *Sori* in floribus familiae *Sterculiaceae*, hypertrophiam et deformitatem provocantes. *Sporae* in cavitatibus multis telarum hospitis centripetaliter evolutae. *Massa sporarum* atrobrunnea, semipulverea, e paribus sporarum composita. *Sporae* pigmentiferae (olivaceobrunneae, sine ullo transitu coloris violacei). *Germinatio* sporarum phragmobasidiis basidiosporas pigmentiferas (brunneas) producentibus.

Typus familiae: *Geminago* Vánky and R. Bauer, in Vánky, Mycoscience 37: 182, 1996.

Member of the order Ustilaginales, having intracellular hyphae and the characters of the genus *Geminago*: *Sori* in the flowers of *Sterculiaceae* causing hypertrophy and deformation. *Spores* develop centripetally in numerous cavities within the host tissue. *Spore mass* dark brown, semipowdery, composed of pairs of spores. *Spores* pigmented (olivaceous-brown, without violet tint). *Spore germination* results in phragmobasidia producing pigmented (brown) basidiospores.

Type of the family: *Geminago* Vánky and R. Bauer.

A new family for *Clintamra*

Amongst the 29 genera of the emended *Ustilaginaceae* (Bauer *et al.*, 2000: 67), only one genus, the unispecific *Clintamra* Cordas and Durán (1976(1977): 1244) has host plants in the *Liliaceae* (*Nolina* spp.).

Type: *C. nolinae* (G.P. Clinton) Cordas and Durán on *Nolina microcarpa* Wats., USA. *Clintamra* is characterised by:

- Sori external on the surface of young leaves and inflorescence of *Liliaceae*, forming a blackish-brown, granular-powdery spore mass.
- Spores single, in pairs or in small groups, pigmented (brown).
- Spore germination results in a usually short, bifurcate, nonseptate basidium bearing two, apical, multiseptate basidiospores (Durán and Safeeulla, 1968, Cordas, 1971).
- Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix.
- Mature septa are poreless.

Besides the host plant family, this genus is differentiated from other genera in the *Ustilaginaceae* by the type of germination. For it I propose:

Clintamraceae Vánky, **fam. nov.**

Pertinent ad ordinem Ustilaginales G.P. Clinton, emend. R. Bauer and Oberw., cum hyphis intracellularibus et characteribus generis *Clintamra*. *Sori* externi, in superficie foliorum juvenilium et inflorescentiae familiae *Liliaceae*, tegmen nigrobrunneum massae sporarum granuloso-pulvereum formantes. *Sporae* singulae, in paribus vel in catervis parvis, pigmentiferae (brunneae). *Germinatio* sporarum basidiis brevibus, bifurcatis, basidiosporas 2, apicales, multiseptatas producentibus.

Typus familiae: *Clintamra* Cordas and Durán, Mycologia 68: 1244, 1976(1977).

Member of the order Ustilaginales, having intracellular hyphae and the characters of the genus *Clintamra*: *Sori* external on the surface of young leaves and inflorescence of *Liliaceae*, forming a blackish-brown cover of granular-powdery spore mass. *Spores* single, in pairs or in small groups, pigmented (brown). *Spore germination* results in a short, bifurcate basidium bearing two, apical, multiseptate basidiospores.

Type of the family: *Clintamra* Cordas and Durán.

Clintamra has a rather similar sorus and spore morphology, as well as spore germination, to the genus *Orphanomyces* Savile, a genus with three known species on the surface of young leaves of *Carex* species (*cf.* Vánky, 1987: 84-85). Unfortunately, nothing is known about the genetic relationship between these two genera.

A new family for *Farysia*

The genus *Farysia* Raciborski (1909: 354), with *ca.* 20 known species, is a natural genus. It is characterised by:

- Sori in single ovaries or ovarian pedicels (denoting a local infection through the stigma) of *Carex* species (*Cyperaceae*).
- When young, sori are covered by a fungal peridium.

- Mature spore mass olivaceous- to dark brown, dusty.
- Spore mass traversed by numerous, conspicuous, capillitium-like fascicles of sterile hyphae which function as elaters.
- Spores single, relatively small, variable in shape and size, produced in chains by the division of the sporogenous hyphae.
- Spore germination results in a septate, 4-celled basidium, usually in a 3 + 1 arrangement (the 4th cell remains included in the spore). On the basidia ovoid basidiospores, rarely long hyphae, are produced (Ingold, 1987: 356).
- Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix.
- Mature septa are poreless.

To accommodate *Farysia*, I propose:

Farysiaceae Vánky, **fam. nov.**

Pertinent ad ordinem Ustilaginales G.P. Clinton, emend. R. Bauer and Oberw., cum hyphis intracellularibus et characteribus generis *Farysia*. *Sori* in floribus nonnullis inflorescentiae specierum generis *Carex*, primo peridio cooperti, quo rupto massam pulveream, brunneam, fasciculis conspicuis hypharum sterilium capillitii instar perductam ostendentes. *Sporae* singulae, forma et magnitudine variae, pigmentiferae (brunneae), cum ornamento (verrrucosae), in catenis productae propter disjunctionem hyphae sporogenae. *Germinatio* sporarum phragmobasidio (plerumque 3 + 1-cellulari) basidiosporas ovoideas (raro etiam hypham) producenti.

Typus familiae: *Farysia* Raciborski, Bulletin International de l'Académie des Sciences de Cracovie, Classe des Sciences Mathématiques et Naturelles 1909(3): 354, 1909.

Member of the order Ustilaginales, having intracellular hyphae and the characters of the genus *Farysia*: *Sori* in some flowers of an inflorescence of *Carex* species, first covered by a peridium which ruptures disclosing the powdery, brown spore mass traversed by numerous, conspicuous, capillitium-like fascicles of sterile hyphae. *Spores* single, variable in shape and size, pigmented (brown), ornamented (verrucose), produced in chains by the division of the sporogenous hyphae. *Spore germination* results in a phragmobasidium (usually of 3 + 1 cells) on which ovoid basidiospores (rarely also a hyphae) are produced.

Type of the family: *Farysia* Racib.

Spore colour and its importance in classification of smut fungi (chemotaxonomy). The *Anthracoideaceae* and *Cintractiaceae*.

Another, theoretical possibility in splitting the heterogeneous family of *Ustilaginaceae* would be to use spore colour as a tool. Spore colour was extremely helpful in separating *Microbotryum* and *Bauerago* species from *Ustilago*. Based only on the presence of a more or less expressed violet colour

(mixed with a pale or dark brown colour) of the spores, 55 *Ustilago* species of dicotyledoneous host plants have been transferred into the genus *Microbotryum*, without using expensive and time-consuming ultrastructural and/or molecular methods (*cf.* Vánky, 1998c). In another case, based on the yellow or yellowish-red colour of the spore masses and spores, five single-spored *Ustilago* species on *Cyperaceae* and *Juncaceae* have been transferred into the new genus *Bauerago* within the *Ustilentylomataceae* (*cf.* Vánky, 1999b).

The colour of the spore masses and spores of the genera of the emended *Ustilaginaceae* helps differentiate two extreme groups: 1. genera with black spore masses (dark reddish- or blackish-brown spores) and 2. genera with pale to dark brown spore masses (light olivaceous- or reddish-brown spores). To divide smut fungi of the *Ustilaginaceae*, based on their colour, is not as easy as it was with violet-tinted *Microbotryaceae* or the yellow or yellowish-red *Bauerago*. Black and brown may vary in their quality and quantity resulting in a great variability of shade of colours of the spores of these smut fungi, as seen by light microscopy. However, smut fungi of *Cyperaceae* and *Juncaceae*, possessing black spore masses, are certainly more closely related to each other than to the genera possessing brown spores, e.g. *Farysia* (on *Cyperaceae*) or *Ustilago* and *Sporisorium* (on *Gramineae*).

Denchev (1997: 413) separated the genus *Anthracoidea* from the *Ustilaginaceae* by describing the *Anthracoideaceae*, based on the typical 2-celled basidia. The *Anthracoideaceae* has black spore masses and parasitise the monocotyledoneous *Cyperaceae*. Species of *Anthracoidea* are apparently homothallic, i.e. no fusion of basidial cells or basidia has been observed.

I proposed (Vánky, 2000: 344) to separate the *Cintractiaceae* from the *Ustilaginaceae*, also possessing black spore masses and parasitising *Cyperaceae*, but the basidia are 4-celled. Compatible cells of the basidia often fuse producing not only large, dicaryotic blastoconidia but also monocaryotic basidiospores, or sometimes both, even on the same basidium. The recognition of the *Cintractiaceae* seems to be supported also by molecular analyses (see Begerow *et al.*, 1997(1998), Figs. 2, 3; Begerow *et al.*, 2000, Figs. 1, 2; Bauer *et al.*, 2000, Figs. 33, 34). The molecular data show also that the analysed type species of *Leucocintractia* M. Piepenbr., Begerow and Oberw., *Trichocintractia* M. Piepenbr., and *Tolyposporium* Woronin, as well as *Heterotolyposporium piluliforme* (Berk.) Vánky, are related to *Cintractia axicola* (Berk.) Cornu, the type of *Cintractiaceae*. Indeed, these genera, and also *Testicularia* Klotzsch and *Ustanciosporium* Vánky (*Gymnocintractia* M. Piepenbr., Begerow and Oberw.) have several common characters:

- Host plants in the *Cyperaceae* and *Juncaceae*.

- Black colour of the spore mass (except for *Heterotolyposporium*, in which it is grey due to the mixture of dark spore balls with hyaline spores).
- Sori develop on the surface of the host plants, they are not embedded in host tissues, but often surrounded by a fungal peridium.
- Basidia transversely septate, 4-celled phragmobasidia.

I consider it better to place these genera into the *Cintractiaceae* than to leave them in the *Ustilaginaceae*.

Some of these genera are characterised by single spores, others by spore balls. However, ultrastructural and molecular studies demonstrated that the presence or absence of spore balls not always denotes or excludes a close relationship, as was thought earlier. For example, *Doassinga* Vánky *et al.* (1998), possessing single spores, belongs to the *Doassansiaceae* (Azbukina and Karatygin) R.T. Moore, emend. R. Bauer and Oberw., together with nine other genera, all forming spore balls. Or, some species of *Ustanciosporium* Vánky have single spores, while others form spore balls (*cf.* Piepenbring, 2000). What more, in the same species both spore balls and single spores are present concomitantly (e.g. *Ustacystis waldsteiniae* (Peck) Zundel, or *Clintamra nolinae* (G.P. Clinton) Cordas and Durán). In the unispecific *Testicularia* Klotzsch (on *Rhynchospora*) there are spore balls composed of a superficial layer of thick-walled, dark reddish- or chestnut-brown spores and a central mass of empty, fungal cells. The dark spores of *Testicularia* may indicate a relationship with the members of the *Cintractiaceae*. The presence of the spore balls, with a central mass of empty, sterile cells, might be a later adaptation to water dispersal. Molecular data are needed to elucidate closer relationships.

Even after the exclusion of several genera from the emended family of *Ustilaginaceae*, there still are genera which in one or another respect are peculiar and do not seem to fit in this family, being very different from *Ustilago* (e.g. *Farysporium* Vánky, *Kuntzeomyces* Henn. ex Sacc. and P. Sydow, *Moreaua* T.N. Liou and H.C. Cheng, *Orphanomyces* Savile, *Restiosporium* Vánky, and others). Studies, complemented with molecular analyses, may show that further genera have to be excluded from the present *Ustilaginaceae*, or rearrangements of genera will be necessary. Using molecular data, some heterogeneous genera, such as *Ustilago* (Pers.) Rosussel, or *Sporisorium* Ehrenb., will certainly be split into smaller, more homogenous and natural genera.

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