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THE GENUS *SPHACELOTHECA* (USTILAGINALES): CRITERIA FOR ITS DELIMITATION AND THE CONSEQUENCES THEREOF

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SUMMARY

The characteristics of *Sphacelotheca hydro-piperis* have been defined and criteria for the genus *Sphacelotheca* established. That genus is valid for some smuts of Polygonaceae. Studies of the ontogeny and mature structure of sori of *Sphacelotheca sorghi* and some other smuts of Poaceae currently included in *Sphacelotheca* have shown that these are markedly different from the type species of *Sphacelotheca* and should not be included in that genus. *Sporisorium*, a genus based on *Sporisorium sorghi* on *Sorghum*, is available for certain smuts previously placed in *Sphacelotheca*.

De Bary (1884) erected the genus *Sphacelotheca* de Bary to accommodate *Ustilago hydro-piperis* (Schum.) Schrot. (*Uredo hydro-piperis* Schum.), a smut of *Polygonum hydro-piper* L. He observed that while the sori of some other smuts such as *Sorosporium saponariae* Rudolphi and *Ustilago hypodytes* (Schlecht.) Fr. consisted only of spores, *Ustilago hydro-piperis* had a distinctly differentiated spore-receptacle. He described the sorus as having a thick outer wall of small, round, hyaline cells, an axile columella composed of cells similar to the outer wall and a dark spore mass lying between the columella and the sorus wall.

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De Bary gave a short description of sorus ontogeny in *Sphacelotheca hydropiperis* (Schum.) de Bary. We quote from the authorised English translation (de Bary, 1887) his description of how the peridium, columella and spores originate: '... each of these three portions grows from its base by addition of new tissue-elements, which are constantly being produced and pushed onwards from the basal formative tissue, and are differentiated and assume their ultimate form in the order in which they are produced.'

Many mycologists have failed to appreciate the significance of de Bary's data. There has been confusion and conflict of opinion about the limits of the genus *Sphacelotheca* and even its validity. Prillieux (1895) investigated the structure of sori of a smut of *Sorghum*, *Ustilago sorghi* Pass. and noted gross similarities of sorus structure between that smut and *Sphacelotheca hydropiperis*. He rejected the notion that the sorghum smut was possibly a species of *Sphacelotheca* because the anatomy of its columella differed greatly from that of *S. hydropiperis*. Dietel (1900) noted that de Bary had proposed a genus, *Sphacelotheca*, based on *S. hydropiperis*, but he still listed that smut as a species of *Ustilago*. Later Dietel (1928) accepted *Sphacelotheca* and remarked that some species of smuts on grasses had been included in it. Probably he was influenced by Clinton (1902, 1904) who had altered the diagnosis of *Sphacelotheca* in order to justify the inclusion in that genus of some smuts of the Poaceae whose sori had a fungal peridium, sterile cells among the spores, and apparent centripetal development of spores around a columella. Clinton knew of Prillieux's (1895) work and included the latter's paper in an annotated list of references to smut fungi (Clinton, 1904). Nevertheless he proceeded with the transfer of some graminicolous smuts to *Sphacelotheca*. Among them were two well known smuts of *Sorghum* spp., namely *Sporisorium sorghi* Ehrenb. and *Ustilago reiliana* Kühn.

Many species of graminicolous smuts have been placed in *Sphacelotheca* since Clinton's time. Fischer & Holton (1957), in their census of smuts on various hosts, recorded 123 species of *Sphacelotheca* on Poaceae out of a total of 137 on all hosts.

Some mycologists have accepted *Sphacelotheca* sensu Clinton tacitly, by describing species within that genus or reluctantly, as did Schellenberg (1911), who remarked that

he did so as a matter of expediency because relationships between *Ustilago* and *Sphacelotheca* were still to be resolved. Liro (1924) accepted *Sphacelotheca* for certain smuts of *Polygonum* spp. He suggested that further work was necessary before it could be certain that the transfer of certain graminicolous smuts to *Sphacelotheca* by Clinton and other authors was justifiable. Fischer (1953) and Fischer & Holton (1957) supported retention of *Sphacelotheca*, considering that the fungal peridium and basipetal formation of spores around a columella were characters sufficient to make it distinct from *Ustilago*. Other mycologists have not been favourable to acceptance of *Sphacelotheca*. McAlpine (1910) and Hirschhorn (1939) rejected *Sphacelotheca*, retaining the *Polygonum* smut in *Ustilago*. They did not consider the fungal peridium and columella to have generic value. McAlpine included in *Cintractia* a number of smuts which might have been placed in *Sphacelotheca* if he had accepted Clinton's (1902) opinion. Hirschhorn too favoured *Ustilago* and *Cintractia* for the disposition of certain smuts which in 1939 were included in *Sphacelotheca*. Savile (1953) looked on *Sphacelotheca* as a doubtful genus and suggested that it was a polyphyletic outgrowth from *Ustilago*. Nannfeldt (1959) rejected *Sphacelotheca*, believing that the species assigned to it had strong affinities with *Ustilago*.

Because de Bary's (1884) criteria for *Sphacelotheca* were altered by Clinton (1902) there are strong grounds for believing that smuts with characteristics very different from those by which de Bary recognised *Sphacelotheca* may at present be included in that genus. It is clear that the doubts and controversies concerning *Sphacelotheca* as a genus of smut fungi will not be resolved without new evidence being brought forward. Therefore specimens of some species of *Sphacelotheca* on Polygonaceae and Poaceae have been examined. New data on sorus ontogeny and the structure of mature sori of certain species of smuts are presented in this paper. The impact of these data on the taxonomy and nomenclature of smuts currently accepted as species of *Sphacelotheca* has then been considered.

SPHACELOTHECA SPP. ON POLYGONACEAE

De Bary's (1884) short account of *Sphacelotheca hydro-piperis* was confirmed and extended by Liro (1924). His important contribution was the observation that the spores are at first catenulate and separated by 'hyphenfragmenten'.

The latter are now referred to as disjunctors. Liro (1924) thought that Bubak, in 1912, had been the first to depict these structures, but illustrations by McAlpine (1910) show disjunctors associated with the spores. Neither Bubak (fide Liro (1924)) nor McAlpine mention disjunctors in their writings. Ciferri's (1938) statement that very small (1 - 4 μm , often 2 μm diam.), round to elongate sterile cells were mixed with spores of *S. hydropiperis* could possibly refer to disjunctors.

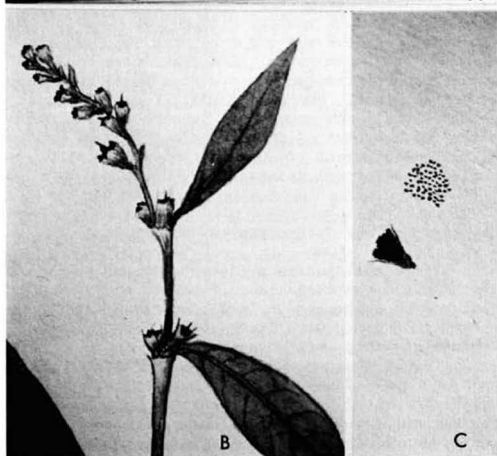
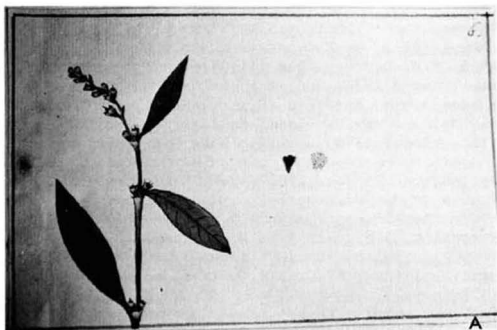
Specimens of some *Sphacelotheca* spp. on *Polygonum* spp. have been studied. One purpose was to determine whether soral characters consistent with those enumerated by de Bary when he erected the genus *Sphacelotheca* were in evidence. The other was to examine the accuracy of de Bary's account of sorus ontogeny. Because some authors (McAlpine, 1910; Hirschhorn, 1939; Savile, 1953) have considered that *Sphacelotheca* is not separable from *Ustilago*, some species of *Ustilago* on *Polygonum* spp. have been included for comparison with species which have been placed in *Sphacelotheca*.

Materials and methods

Schumacher's specimen of *Uredo hydropiperis* is no longer extant (H. Knudsen, private communication). Evidence of the structure of that fungus is provided by drawings, with annotation, by C.F. Schumacher, in *Flora Hafniensis, Fungi Delineati* (Fig. 1). That work, executed in about 1800, was never published. The manuscript is held now in the Botanical Central Library, University of Copenhagen. The following specimens of *Sphacelotheca* spp. and *Ustilago* spp. on *Polygonum* spp., listed by the names under which they were received, have been examined. Their taxonomy at the species level has not been analysed.

Sphacelotheca hydropiperis (Schum.) de Bary. On *Polygonum hydropiper* L.: Denmark, 18 Aug. 1878, E. Rostrup (C); Denmark 18 Oct. 1874, E. Rostrup (C); Denmark, 26 Sept. 1908, A. Lange (C); Denmark, 10 Sept. 1899, J. Jespersen (C); Germany, Sydow, *Ustilagineen*, no. 68, 12 Aug. 1894, P. Hennings (VPRI); Romania, 3 Sept. 1964, K. Vanky (DAR

Figure 1. *Sphacelotheca hydropiperis*. (A) Schumacher's drawing of *S. hydropiperis* in *Flora Hafniensis, Fungi Delineati* (unpublished); (B) and (C) enlargements of portions of (A).



23705); Britain, 1 Sept. 1940, G.C. Ainsworth (IMI 32365). On *Polygonum sagittatum* L. U.S.A., Sept. 1907, A.B. & F.C. Seymour (DAR 11101); U.S.A., 8 Sept. 1954, F.C. Greene (DAR 15368). On *Polygonum bistorta* L. Manchuria, 7 June 1925, P.H. Dorsett (DAR 11100). On *Polygonum* sp. Indonesia, 12 Apr. 1936, W.J. Lütjeharms (DAR 14835). *Sphacelotheca borealis* (Clint.) Schellenb. On *Polygonum bistorta* L. Switzerland, no date, H. Schinz (Krypt. exsicc. Vindob. 2003, duplicate as DAR 25976). *Sphacelotheca tropico-africana* Zundel on *Polygonum* sp. Congo, Africa, 16 Feb., 1927, D.H. Linder (TYPE, BPI). *Sphacelotheca* sp. On *Polygonum decipiens* R.Br. N.S.W., Australia, 14 Sept., 1969, J. Walker (DAR 19169); South Australia, 9 May, 1959, L.D. Williams (DAR 20450). *Ustilago bistortarum* (DC) Korn. On *Polygonum viviparum* L. Canada, 1 Aug., 1950, D.B.O. Savile & C.T. Watts No. 1232 (DAR 16106). *Ustilago anomala* Kunze. On *Polygonum hydropiper* L. Queensland, 10 April, 1976, R.F.N. Langdon (DAR 27755).

Each specimen was compared with Schumacher's illustrations of the whole sorus. Some sori were dissected manually and others were sectioned with a freezing microtome, both transversely and vertically. For microscopic examination material was mounted in lactophenol and stained with either cotton blue or acid fuchsin. Sori of *Ustilago anomala* Kunze of which living material was available were sectioned after embedding in wax.

Observations and interpretation

All of the specimens listed above as species of *Sphacelotheca* had the macroscopic features of *S. hydropiperis* as depicted by Schumacher. In all specimens except DAR 11100 spores in chains, with disjunctors, were found when basal regions of young sori were examined. The sori of specimen DAR 11100 were mature with most of the spores eroded from them. The remaining spores were separate from one another. Only a few with disjunctors attached were found. Some disjunctor remnants lay free in the slide mount. In all specimens, every sorus had a peridium and columella composed of hyaline, thick-walled cells. Spores still in chains were somewhat flattened where they were joined to adjacent spores by disjunctors. Mature spores which had disarticulated were subglobose and many no longer had disjunctors attached to them. In all specimens the columella was per-

sistent and protruded well beyond the eroded spore mass in many sori. The length of the columella in many cases exceeded by several millimetres the length of the fruits of the host. Evidently growth of the sorus is indeterminate and ceases only when floral parts senesce. The columella, except at its base, is free of admixture with host tissues. Only remnants of the funicle and ovule are included there and the greater part of the columella is composed of fungal cells pushed upwards past the stub of host tissue. The peridium, more fragile than the columella, is often eroded together with the spore mass as the sorus elongates. All specimens had the characters which de Bary (1884) gave as the criteria for *Sphacelotheca*. *S. austro-africana*, described by Zundel (1944) as destroying the inflorescence, does not involve the whole inflorescence in a single sorus. The sori are in individual flowers as is the case with the other species of *Sphacelotheca* on *Polygonum* species which have been examined. There were sufficient differences in spore ornamentation in some of the specimens to indicate that there is more than one species of *Sphacelotheca* on *Polygonum* species.

The specimen of *Ustilago bistortarum* examined is part of a collection which led Savile (1953) to comment on the possible invalidity of *Sphacelotheca* as a genus. The smut is a species of *Ustilago* as that genus was defined by Langdon & Fullerton (1975). It lacks a peridium and resembles species of *Sphacelotheca* only by its having dark, elongated bodies resembling columellae associated with the sori. They are mummified staminal filaments. Similar structures occur in some of the sori of *Ustilago anomala* from Australia. A study of the latter's sori confirmed that it is truly an *Ustilago*.

After a study of specimens which were received as *Sphacelotheca hydro-piperis* and which conformed to descriptions of that species, the following account of *S. hydro-piperis* has been prepared. Observations on the other species of *Sphacelotheca* showed that the ontogeny and the mature form of the sori were the same as that of *S. hydro-piperis*, apart from minor differences significant only at the species level.

Sphacelotheca hydro-piperis: Around small sori about 2 mm long the pericarp may be intact and still surmounted by the style. In the apical parts of larger, older sori the peridium and overlying tissues of the pericarp break up, exp-

osing the spore mass and columella. The components of the sorus develop from hyphae in the receptacle close to the base of the ovary. Hyphal walls gelatinize and the protoplasts differentiate as hyaline cells, which constitute the peridium and columella, or as dark spores (Fig. 2; A). From the soral meristem some of the cells are pushed outwards and upwards, lining the enlarging pericarp and forming the soral peridium. Others are pushed upwards to form the columella, a structure which at its base includes degraded vascular and other tissues, these being remnants of the funicle and the basal orthotropous ovule. Above the distal limits of host tissue the columella is composed only of hyaline, thick-walled, subglobose cells similar to those of the peridium. Between the columella and the peridium are spores, packed closely together but readily separable from one another. There is no gradation in maturity of spores between the columella and the peridium, nor are there any hyaline cells or hyphae in the spore mass. Continual hyphal growth adds cells to those formed first and which are pushed upwards as the sorus enlarges. Spores and the cells of the peridium and columella are formed in ascendant, sinuous, intertwined chains with disjunctors between the cells. Disjunctors are readily seen in chains of spores taken from the base of a sorus (Fig. 2; B, C) but have disappeared from many of the mature spores taken from the upper part of the sorus (Fig. 2; D). Distorted remnants of the disjunctors persist among columellar and peridial cells.

Discussion

Sorus ontogeny and characteristics of the mature sorus of *Sphacelotheca hydropiperis*, the type species of *Sphacelotheca*, have been elucidated. Now criteria for that controversial genus can be defined. Sori are bounded by a fungal peridium of hyaline cells overlying which are tissues of the ovary wall. Dark spores are formed in ascendant chains with disjunctors between the spores. The columella is formed of cells similar to those of the peridium. The components of the sorus develop from mycelium located in host tissue at the base of the sorus.

Sphacelotheca has sometimes been placed in synonymy with *Ustilago*. That action has never been based on critical, comparative studies. Hirschhorn (1939) reviewed the opinions of several authors on the status of *Sphacelotheca*

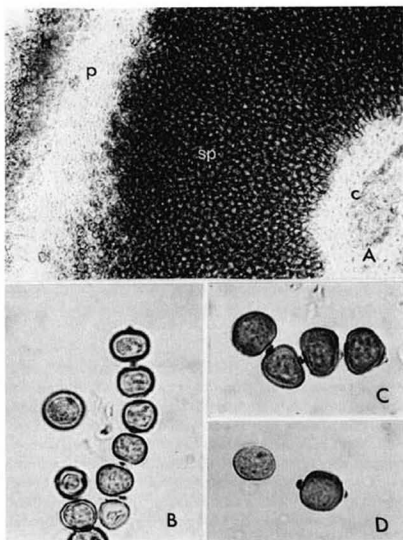


Figure 2. *Sphacelotheca hydropiperis*. (A) transverse section of sorus near base (x200). h, host tissue (pericarp); p, fungal peridium; sp, spores; c, columella with an inclusion of host tissues. (B) immature spores, catenulate and separated by disjunctors (x1000). (C) spores, near maturity (x1000). (D) mature spores (x1000).

in her report on some smuts from the Argentine. She concluded that the peridium and the columella should be rejected as generic characters because they are structures common to several genera. Noting that in species of *Ustilago* and *Sphacelotheca* the spores are separate from one another, she placed two species of *Sphacelotheca* (including *S. hydro-piperis*) in *Ustilago* and one (*S. sorghi*) in *Cintractia*. She accepted agglutination of the spores as characterising *Cintractia*, even though mature spores are readily separable from one another. Rejection of the columella as a generic character is not warranted. Langdon & Fullerton (1975) have studied the origin and structure of the columella in sori of some graminicolous species of *Sorosporium*. The columella in those species is very different in structure and function from the columella of species of *Sphacelotheca*. The columellae in the two genera are not homologous structures. Sporogenesis in *Ustilago* (Langdon & Fullerton, 1975) differs from that of *Sphacelotheca*. A common end point, spores separate from one another, does not justify placing *Sphacelotheca* in synonymy with *Ustilago*.

Doubts concerning *Sphacelotheca* as an acceptable genus have been dispelled. Consideration of the ontogeny of the soral components makes it clear that the peridium and columella are constant features of the sorus. They differ morphologically from analogous structures in some other genera. The spores, developing in chains with disjunctors, provide a distinctive character to ally with the columella and peridium as criteria for delimiting *Sphacelotheca*. We conclude that *Sphacelotheca* is soundly based and that some species of smuts of the Polygonaceae are correctly placed in that genus.

SPHACELOTHECA SPP. ON POACEAE

It is necessary to resolve whether certain smuts of the Poaceae are congeneric with the species of *Sphacelotheca* on Polygonaceae. Therefore sorus ontogeny and sporogenesis of four graminicolous smuts currently included in *Sphacelotheca* have been investigated. Those matters can then be considered in relation to the components of mature sori. A basis for an appreciation of the taxonomic position of these graminicolous smuts will then be available.

Materials and methods

The smuts studied and their respective hosts were as follows: *Sphacelotheca sorghi* (Link) Clint. on *Sorghum leiocladum* (Hack.) Hubb., *S. andropogonis* (Opiz) Bubak on *Bothriochloa bladhii* (Retz) S.T. Blake, *S. amphiphis* Syd. on *Bothriochloa decipiens* (Hack.) Hubb. and *S. vanderystii* (P.Henn.) Ling on *Hyparrhenia filipendula* (Hochst.) Stapf. The hosts are indigenous, perennial grasses of tropical and subtropical Queensland. In each the smut fungus is systemic. Naturally infected plants were transplanted from the countryside to garden beds at the University of Queensland where they were maintained as sources of smut sori.

The methods and techniques used in light and transmission electron microscope studies were the same as those described previously (Langdon & Fullerton, 1975). For observation of spore surfaces with a scanning electron microscope, spores from mature sori were fixed to stubs with double adhesive tape and coated with gold.

Observations and interpretation

Sphacelotheca sorghi

The inflorescence of *Sorghum leiocladum* is a panicle with spikelets in pairs, one sessile and the other pedicellate. In the sessile spikelet the lower floret is reduced to a lemma and the upper floret is hermaphrodite. The pedicellate spikelet is similar except that the upper floret is male. Sori form in both hermaphrodite and male florets. A mature sorus is subglobose to elongate, up to 3mm long (Fig. 3; A). Spores are slightly agglutinated and among them lie chains or groups of thick-walled, hyaline cells. There is a central columella composed of hyphae and host tissues and a peridium consisting of a hyphal sheath overlain by several layers of host cells.

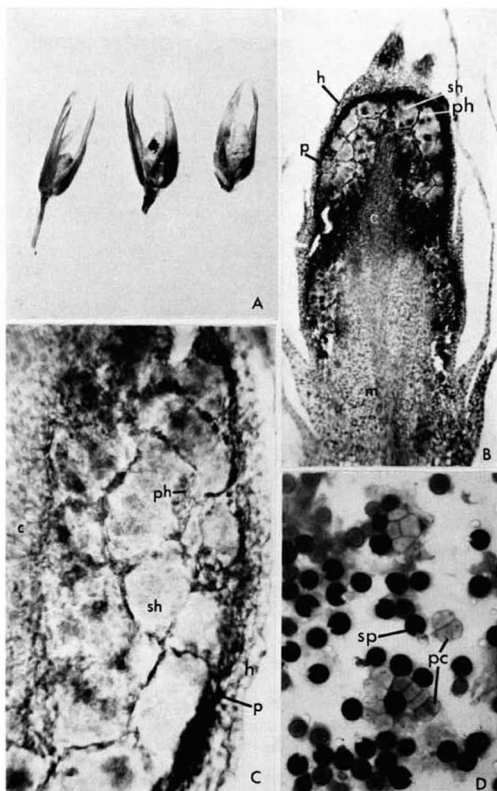
While tillers are in a vegetative state mycelium remains in juvenile tissues below the growing point. After flower initiation hyphae occupy positions close to the growing points of the panicle branches. Hyphae grow into spikelet primordia when the latter are less than 0.5 mm long, massing in each spikelet axis close to the level of the glume primordia. The particular position of this pocket of hyphae determines whether the lower floret is in-

cluded in the sorus or remains free. Glumes develop normally. Ovary primordia are seldom developed in hermaphrodite florets invaded by hyphae. Primordia of other floret structures have no further development after sorus initiation and their remnants remain at the apex of the sorus as it develops. A host meristem is initiated in the axis of the spiklet just below the pocket of hyphae. The sorus, a complex of host tissue and hyphae (Fig. 3; B), then develops by the contemporaneous growth of host and fungus.

Intercellular hyphae circumjacent to the periphery of a cell mass formed by the host meristem become confluent, separating a layer two or three cells deep from the central group of cells. Continual proliferation of host cells provides a columella, where parenchyma and vascular elements are differentiated, and layers of parenchymatous cells which invest the developing sorus. Contemporaneously with the development of new host tissues, hyphae close to the peripheral host cells form a sheath of elongate, thick-walled, vacuolate cells. Other hyphae grow inter- and intracellularly with tissues of the columella. Hyphae close to the host meristem increase in quantity and at the same time hyphae grow from the developing columella towards the peridium. In this mass of hyphae subglobose pockets of intertwined hyphae, which soon become sporogenous, are separated by a network of long-celled, non-sporogenous hyphae. The latter we term *partitioning hyphae* (Fig. 3; B, C).

The walls of sporogenous hyphae gelatinize and protoplasts swell and become subglobose. Karyogamy sometimes occurs before wall gelatinization is complete, sometimes while the protoplasts are enlarging. Spines are first evident when the spores are about 2 μm diam. When the spores are 6 μm diam. the first-formed spines are 0.8 μm long and a second series of spines up to 0.4 μm long has developed (Fig. 4). The secondary spines are more numerous than the primary spines (Fig. 5). They develop between and also

Figure 3. *Sphacelotheca sorghi*. (A) spikelets with sori (x4.5). (B) longitudinal section of young sorus (x75). m, soral meristem; h, host tissue overlying fungal peridium; p, fungal peridium; c, columella; sh, pocket of sporogenous hyphae; ph, partitioning hyphae. (C) detail of part of (B) (x225). h, host tissue overlying fungal peridium; p, fungal peridium; c, columella; sh, sporogenous hyphae; ph, partitioning hyphae. (D) spores (sp) and partitioning cells (pc) from a mature sorus (x550).



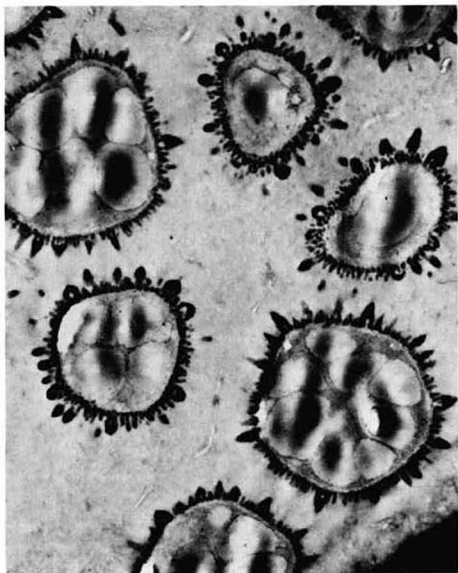


Figure 4. *Sphacelotheca sorghi*. Section through spores showing primary and secondary spines (x7000).

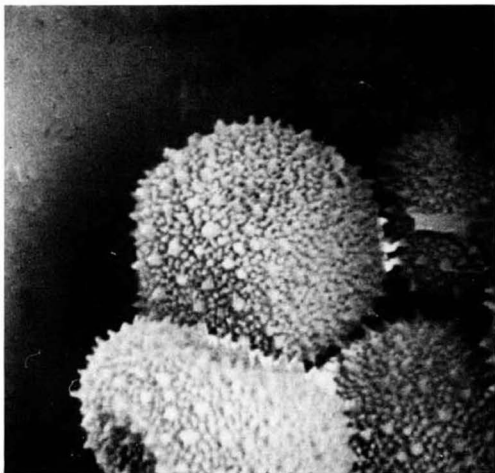


Figure 5. *Sphacelotheca sorghi*. Surface view of spores showing primary and secondary spines (x5400).

beneath the primary spines. In the latter position one to several secondary spines develop after apparent erosion of the spine base. The distal portions of primary spines remain intact. Lipid bodies are present in young spores and they enlarge as spores increase in size. As spores approach maturity their walls become pigmented. By then all of the gelatinous matrix has disappeared.

While sporogenous hyphae are forming spores the partitioning hyphae are modified. Single cells or several adjacent cells divide and enlarge, producing chains or irregular clumps of hyaline cells with smooth, thick walls. Each cell has a thin peripheral layer of cytoplasm, a nucleus and a large vacuole. We call these cells *partitioning cells* (Fig. 3; D).

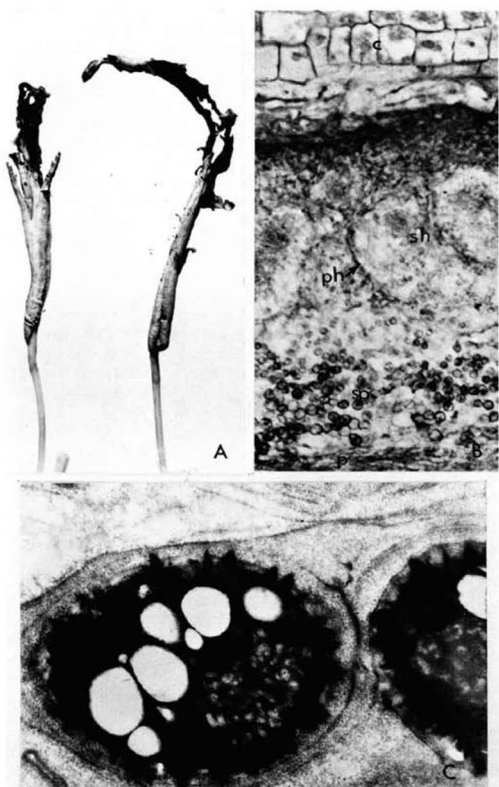
Spores mature first in distal parts of the sorus and close to the peridium. Progressive maturation of spores occurs in the direction of the columella. In older parts of the sorus transformation of the partitioning hyphae to groups of partitioning cells, and great expansion of the original pockets of sporogenous hyphae as spores mature, eliminate the pattern of pockets of young spores invested by partitioning hyphae which is so evident at earlier times.

Sphacelotheca andropogonis

The inflorescence of *Bothriochloa bladhii* has a number of racemes originating close to one another on a short axis. Smutted tillers exhibit a range of symptoms, from replacement of the whole inflorescence by a sorus to development of sori in the lower racemes only, with all or only part of a given raceme being smutted. The sori are long, cylindrical often branched, enclosed by a whitish peridium which eventually ruptures, exposing the spore mass and the columella (Fig. 6; A).

Hyphae in undifferentiated host tissue below the grow-

Figure 6. *Sphacelotheca andropogonis*. (A) sori (x3). (B) parts of longitudinal section of a sorus (x410). c, host cells of the columella; sh, sporogenous hyphae; ph, partitioning hyphae; sp, mature spores; p, peridium. (C) immature spores



ing point of a tiller enter embryonic floral parts soon after initiation of an inflorescence. Delayed entry may result in partial smutting of the inflorescence. Hyphae mass in intercellular positions at the base of each raceme. Just below that pocket of hyphae a host meristem is initiated. The processes of sorus formation and sporogenesis (Fig. 6; B, C) then follow the pattern described for *S. sorghi*.

Sphacelotheca amphiphis

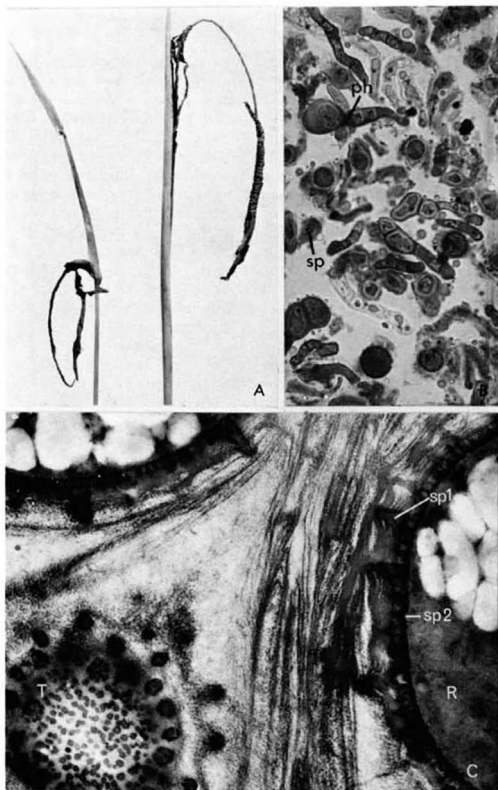
The inflorescence of *Bothriochloa decipiens* consists of several racemes originating close to one another on a short axis. On smutted tillers the inflorescence is replaced by a long cylindrical sorus (Fig. 7; A) at the tip of which are the distorted remnants of the young inflorescence.

Hyphae enter the base of the embryonic inflorescence and proliferate there. Closely adjacent to that pocket of hyphae and just above the topmost node of the tiller a host meristem develops. Sori develop by contemporaneous growth of hyphae and host tissue (Fig. 7; B, C), the processes being the same as those described for *S. sorghi*. The sorus at maturity protrudes beyond the uppermost leaf and extends downwards to the topmost node of the tiller.

Sphacelotheca vanderystii

The inflorescence of *Hyparrhenia filipendula* is a narrow panicle of paired racemes. In smutted plants each raceme is replaced by a sorus up to 1 cm long (Fig. 8; A). Hyphae grow into a young raceme when spikelet primordia are forming. The site of the soral meristem is just above the lowermost spikelet. Sorus development and sporogenesis (Fig. 8; B) follow the pattern described for *S. sorghi*. The distorted remnants of the lowermost spikelet can be

Figure 7. *Sphacelotheca amphiphis*. (A) sori (x1.7). (B) sp, immature spores and ph, partitioning hyphae partly transformed to partitioning cells (x660). (C) section through spores (x12,000). R, radial section, showing spl, primary spines; sp2, secondary spines. T, tangential section.



found on a slight lobe at the base of the sorus. The remnants of floral parts distal to the soral meristem at the time of its formation are carried at the apex of the sorus.

The origin and nature of partitioning cells, termed 'sterile cells' by earlier authors, have not previously been determined. Peck (1882) saw pale, irregular cells mixed with the spores of *Ustilago cylindrica* Peck (*Sphacelotheca andropogonis*, fide Fischer (1953)) but he made no comment on their origin. Clinton (1897) described cells in the sori of *Ustilago sorghi* which he believed had been derived from the peridium and mentioned various characteristics which tally with those of partitioning cells. In another paper Clinton (1902) said that a membrane of sterile cells enveloped the spore mass and that groups of these sterile cells are found within the spore mass. Clinton's observations are probably the origin of an oft repeated statement that sterile cells in the spore mass are derived from the peridium (Zundel, 1953; Fischer, 1953; Fischer & Holton, 1957; Ainsworth, 1965). Fischer & Holton (1957) described the sterile cells as empty, despite Clinton's (1897) observation that they may sometimes have contents. Our work has shown that those cells are nucleate.

Clinton (1897) described the formation of spores of the sorghum smut as being centripetal around a central columella. He mentioned that feature when he (1902) made alterations to the circumscription of *Sphacelotheca*. Fischer & Holton (1957) accepted centripetal spore formation as an important character for *Sphacelotheca*. However, evidence has been adduced earlier in this paper to show that *Sphacelotheca hydropiperis*, the type species, differs markedly from the graminicolous species of *Sphacelotheca* in its sporogenesis. The apparent centripetal formation of spores in *S. sorghi* and some other species of *Sphacelotheca* is a consequence of maturation of pockets of sporogenous hyphae which are being formed progressively around the columella. There is no pre-formed total mass of sporogenous hyphae which are converted to spores in the direction of the columella.

Khanna & Payak (1972), working with mature spores, observed that the spore walls of *Sphacelotheca reiliana* bore spines of two sizes. They deduced that the longer spines were formed by fusion of the distal parts of the shorter spines. We have observed two sizes of spine on the

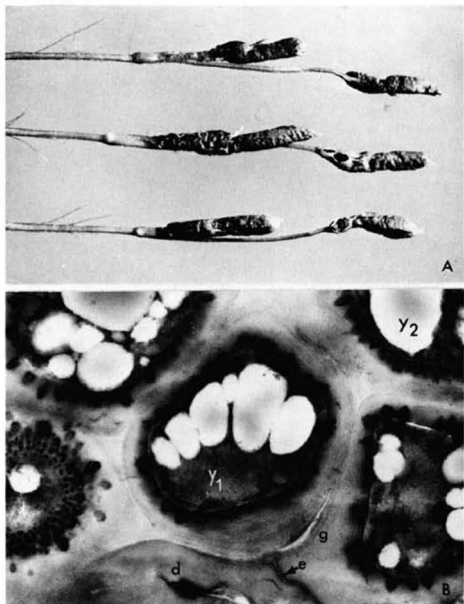


Figure 8. *Sphacelotheca vanderystii*. (A) sori (x7). (B) Spores at different stages of development (x7000). y1, young spores with primary spines; y2, older spore with primary and secondary spines; e, electron-transparent portion of hyphal septum; d, hyphal cell which has degenerated; g, gelatinized hyphal wall.

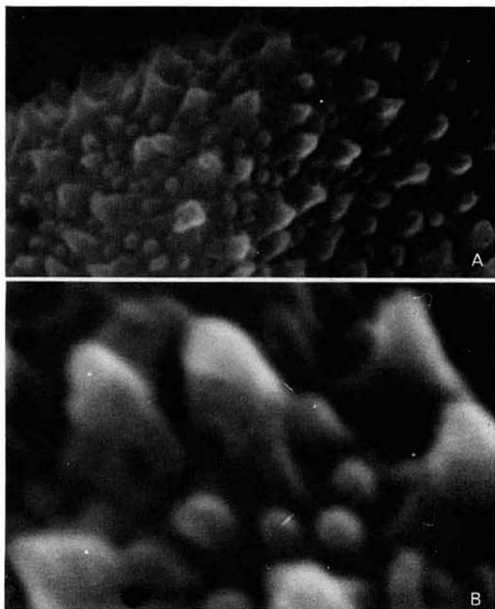


Figure 9. *Sphacelotheca reiliana*. (A) surface view of spore wall, showing primary and secondary spines (x31,200). (B) detail of (A) (x100,000).

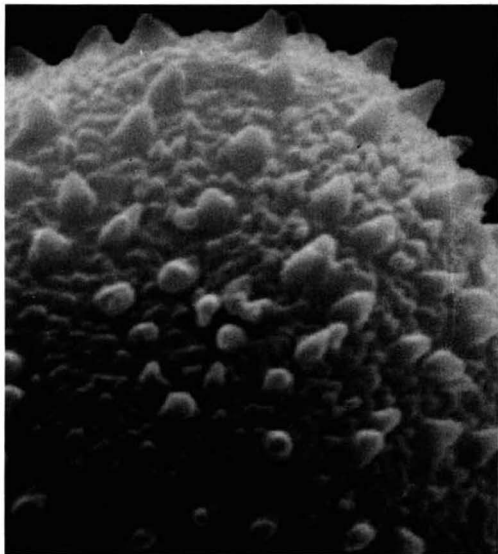


Figure 10. *Ustilago valentula*. Surface view of spore wall, showing two series of spines (x31,200).

walls of mature spores of *S. reiliana* (Fig. 9; A, B) and on both young and mature spores of the several species of *Sphacelotheca* on Poaceae whose sorus ontogeny has been studied. Sections of the spores show that the 'molar-like complexes' described by Khanna & Payak (1972) are the result of several small spines developing at the base of a larger spine formed earlier in the spore's development. Two-seriate spines may not be confined to species of *Sphacelotheca* on Poaceae. Spore walls of *Ustilago valentula* Syd. (Fig. 10) and *U. tricophora* (Link) Kunze (Fig. 11) show two series of spines in surface view at very high magnifications. Whether the structure of the spines of those species is similar to that of certain graminicolous smuts which have been placed in *Sphacelotheca* can be determined only with sections of spores in various stages of development.

The processes of formation of peridium, columella and spore mass are the same in the four smuts from grasses. The site of the soral meristem determines whether florets or all of the inflorescence are replaced by smut sori. The sori of the graminicolous species of *Sphacelotheca* are different in their ontogeny and mature structure from the sori of *Sphacelotheca hydrophiperis* on *Polygonum* spp. In Table 1 the characteristics of the smuts of the two groups of hosts are compared. The species from plants of the Poaceae and from *Polygonum* spp. cannot be regarded as congeneric.

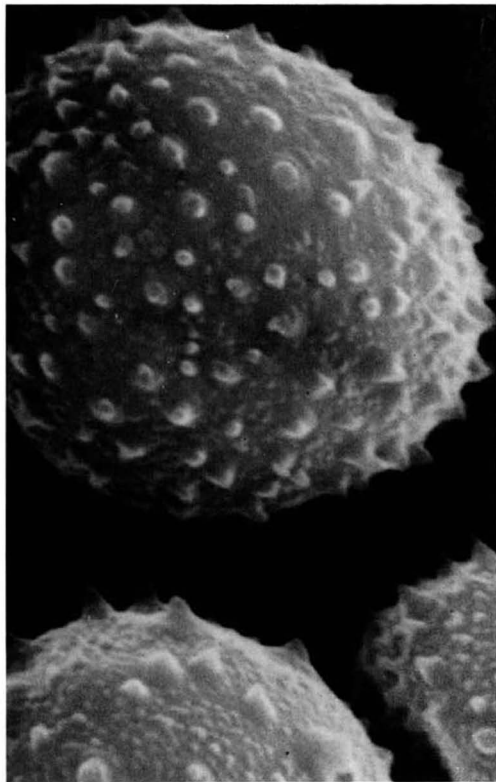
REPUTED SYNONYMS OF SPHACELOTHECA

Various authors have placed *Sporisorium* Ehrenb., *Endothlaspis* Sorokine and *Planetella* Savile in synonymy with *Sphacelotheca*.

Sporisorium Ehrenberg apud Link in Linne's Species Plantarum Ed. 4 (Willdenow's), Berlin, 6(2), 86, 1825.

The genus *Sporisorium*, based on *S. sorghi* Ehrenberg apud Link, was validly published. The host was *Sorghum*, collected in Egypt by Ehrenberg. Although extensive enquiries have been made, the type specimen has not been located, and it is concluded that it is no longer extant. The original description of the *Sporisorium sorghi* contains

Figure 11. *Ustilago tricophora*. Surface view of spore wall showing two series of spines (x31,200).



nothing that is inconsistent with Ehrenberg's collection being the same smut as that widely known today as *Sphacelotheca sorghi* (Link) Clint. In that belief we are supported by an opinion from the staff of the Commonwealth Mycological Institute, Britain, that *Sporisorium* was 'clearly based on what we all have been calling *Sphacelotheca sorghi*' (C. Booth, private communication).

The sorghum smut was transferred to *Sphacelotheca* as *S. sorghi* (Link) Clint. by Clinton (1902). He offered no explanation for moving the species from *Sporisorium*. It is noteworthy that the epithet *sorgi* was retained, indicating tacit acceptance that he was dealing with the sorghum smut collected by Ehrenberg. In a later paper Clinton (1904) included *Sporisorium sorghi* among synonyms of *Sphacelotheca sorghi*. That action is probably the reason for Dietel's (1928) listing of *Sporisorium* as a synonym of *Sphacelotheca*. However, *Sporisorium* was erected in 1825 and *Sphacelotheca* in 1884. Fischer (1953) and Zundel (1953) wrote *Sorosporium sorghi* instead of *Sporisorium sorghi* in their lists of synonyms of *Sphacelotheca sorghi*. That has no bearing on the synonymy since it is clearly a spelling mistake. Both authors gave the literature reference for *Sporisorium sorghi*. *Sporisorium* predates *Sorosporium* by four years.

Endothlaspi Sorokine Revue mycologique 12, 4-5, 1890.

Sorokine (1890) erected the genus *Endothlaspi* with two species, *E. melicae* Sorokine and *E. sorghi* Sorokine on *Melica ciliata* L. and *Sorghum cernuum* (Ard.) Rorn. respectively. He excluded those smuts from *Ustilago* because there was a hyphal peridium around each spore mass. Sorokine emphasised the absence of a columella in *Endothlaspi* and thereby distinguished his genus from *Sphacelotheca*. He considered the possibility that the smuts he studied might belong in *Testicularia* or *Doassansia*, rejecting the former because of the absence of hyphae within the spore mass of *Endothlaspi* and the latter because of its sterile cells around the spore mass were quite unlike those of the species placed in *Endothlaspi*. Clinton (1904), from a consideration of Sorokine's figures and description, decided that *Endothlaspi*, with a covering membrane of sterile cells, belonged with *Sphacelotheca*. He listed *Endothlaspi* as a synonym of *Sphacelotheca* but made no new combinations for the species of *Endothlaspi*. Ciferri (1928), without seeing Sorokine's specimens and with no reference to Clinton (1904) said that *Endothlaspi* could not be held distinct

Table 1

Comparison of soral characteristics of species of *Sphacelotheca* on Polygonaceae and Poaceae

	<i>Sphacelotheca</i> spp. on Polygonaceae	<i>Sphacelotheca</i> spp. on Poaceae
Peridium	hyaline, catenulate, subglobose cells	interwoven hyphae
Columella	hyaline, catenulate, subglobose cells; host tissue only at base; not a source of sporogenous or non-sporogenous hyphae.	an integrated structure composed of host tissue and hyphae; sporogenous and non-sporogenous hyphae growing from the hyphal component of the columella
Spore mass	spores developed from hyphae at the base of the sorus; spores at first catenulate with disjunctors, later free from one another; spores not mixed with other structures.	Spores developed from hyphae growing from the columella; sporogenous hyphae at first surrounded by partitioning hyphae, the latter later forming partitioning cells; spores free from one another, with partitioning cells mixed with the spores.

from other genera of the Ustilaginales in the absence of data on spore formation and germination. He assigned Sorokine's species of *Endothlaspis* to *Sphacelotheca* because the spore mass was enclosed by a fungal peridium, a character which he declared completely defined *Sphacelotheca*. He attached no importance to the columella as a generic character because he believed its presence or absence was dependent on the host organ in which a smut formed its spores. Ciferri made a new combination for the *Melica* smut and a new name for the *Sorghum* smut. In more recent years, various authors have accepted *Endothlaspis* as a synonym of *Sphacelotheca* (Ainsworth & Sampson, 1950; Fischer, 1953, Fischer & Holton, 1957).

Sorokine's specimens have not been located nor have we found any record of a smut of *Melica* which might possibly be conspecific with *Endothlaspis melicae*. The only evidence by which the nature of *Endothlaspis* can be judged is that provided by Sorokine's text and figures. The former is vague, the latter poorly executed. On one matter Sorokine was definite: '.... notre espèce diffère du *Sphacelotheca* en ce qu'elle n'a pas de colonne centrale.' Sorokine's data are difficult to interpret. Certainly they do not justify the description which Zundel (1953) concocted for *Endothlaspis melicae* or Zundel's acceptance of Ciferri's (1928) opinion that the species should be placed in *Sphacelotheca*. Zundel's account of the nature of the sorus and his description of the spores are speculative and his statement that the sorus has a central columella is directly opposed to Sorokine's observations. The characters of *Endothlaspis melicae* remain obscure.

The identity of *Endothlaspis sorghi* is by no means certain. Sorokine, after discussing the smuts of *Sorghum*, insisted that the smut he described was not the same as *Ustilago reiliana*. Fischer (1953), evidently accepting Ciferri's (1928) opinion, listed *Endothlaspis sorghi* as a synonym of *Sphacelotheca reiliana*. The latter has spores 9-13 μ m diam. in contrast to the former's 7-10 μ m.

Endothlaspis is poorly defined and its status is obscure. Its characteristics will become known only when the specimens studied by Sorokine (1890) are located and then prove to be adequate to reveal the mode of development and mature structure of the sori. Until more evidence is available there is no justification for regarding *Endothlaspis* as a synonym of *Sphacelotheca*.

Planetella Savile Can. J. Bot. 29, 326-327, 1951.

Thirumalacher & Whitehead (1975) transferred *Planetella lironis* Savile, the type species of *Planetella*, to *Sphacelotheca*, commenting that its sorus structure was identical with that of *Sphacelotheca*. Savile (1951) described well the sorus structure of *Planetella lironis*. After an examination of the type specimen we agree with Savile that *Planetella* is distinct from other genera. Thirumalacher and Whitehead were in error in placing *Planetella* in synonymy with *Sphacelotheca*.

TAXONOMY OF GRAMINICOLOUS SMUTS ASSIGNED TO *SPHACELOTHECA*

Clinton (1902) confused mycologists' interpretation of *Sphacelotheca* by including in it some smuts of the Poaceae. In the course of time features of those smuts rather than those of the *Polygonum* smut on which de Bary based *Sphacelotheca* have gained acceptance as the criteria for delimiting *Sphacelotheca*. Our detailed study of four smuts of the Poaceae shows that those smuts have characteristics very different from those by which de Bary (1884) defined *Sphacelotheca*. *Sporisorium sorghi* is the nomenclatural type of the smut currently known as *Sphacelotheca sorghi*. No reasons have ever been published for abandoning *Sporisorium* as a genus for the sorghum smut although the epithet *sorghi* has been retained to this day. *Sporisorium* was validly published and undoubtedly referred to the same sorghum smut as the one studied in detail in this paper. Our fruitless enquiries have led us to the conclusion that the type specimen of *Sporisorium sorghi* is no longer extant. Therefore, a neotype for that species is nominated below. The sorghum smut and other fungi with similar characteristics must be placed in *Sporisorium*. In the Ustilaginales, only *Ustilago* predates *Sporisorium*. The criteria for *Ustilago* were defined by Langdon & Fullerton (1975), and that genus is not acceptable as a repository for the grass smuts we have considered in this paper.

The characters by which mature specimens of species of *Sporisorium* can be recognised are the hyphal peridium, columella composed of host tissues and hyphae, and spores intermixed with partitioning cells. The latter can be seen readily if sorus contents are mounted in lactophenol containing acid fuchsin.

SPORISORIUM Ehrenberg in Link in Linné's Species Plantarum Ed. 4 (Willdenow's), Berlin, 6, (2), 86, 1825.

Sori replacing inflorescences or florets. Peridium of interwoven hyphae overlain by several layers of host tissue. Columella composed of host tissues permeated by inter- and intra-cellular hyphae. Hyphae growing from the columella of young sori differentiating as pockets of sporogenous hyphae enclosed by non-sporogenous partitioning hyphae, the precursors of partitioning cells. Spores at first somewhat agglutinated, later pulverulent, dark, single, globose to subglobose. Partitioning cells hyaline, subglobose, in groups or chains, intermixed with the spores.

Type species: *Sporisorium sorghi* Ehrenberg in Link in Linné's Species Plantarum, Ed. 4 (Willdenow's), Berlin, 6, (2) 86, 1825.

Sporisorium sorghi Ehrenberg in Link in Linné's Species Plantarum, Ed. 4 (Willdenow's), Berlin, 6, (2), 86, 1825. Synonyms: *Ustilago sorghi* Pass. in Thümen, Hedwigia, 12, 114, 1873; *Sphacelotheca sorghi* (Ehrenb.) Clint., J. Mycol. 8, 140, 1902.

Sori in florets, covered by a hyphal peridium overlain by host tissue. Columella central, composed of host tissues permeated by hyphae. Spores globose to subglobose, single, dark, minutely echinulate, up to 10 µm for longest dimension. Partitioning cells in groups or chains, hyaline. Specimens examined: On *Sorghum bicolor* (L.) Moench. (= *S. vulgare* Pers.). Italy, 1872, G. Passerini (Thümen, Herb. mycol. oeconomicum, no 63.) (B); Gatton, Queensland, 6 Apr. 1939, P.J. Skerman (BRIU 127); Urbana, Ill., U.S.A., 1895, G.P. Clinton (VPRI); Virginia, U.S.A., 15 Apr. 1902, C.R. Bail (ADW); Roseworthy, Sth. Australia, 29 Mar. 1915, C.F. Stephens (ADW). On *S. leiocladum* (Hack.) Hubb. Hirstglen, Queensland, 7 Mar. 1941, R.F.N. Langdon & D.A. Herbert (BRIU 341); Killarney, Queensland, 6 Jan. 1966, R.A. Fullerton (NEOTYPE, BRIU 2426). On *S. plumosum* (R. Br.) Beauv. Chillagoe, Queensland, 4 Apr. 1938, S.T. Blake (BRIU 1942).

Some changes in the synonymy given by Fischer (1953) are necessary. The epithet *sorghi* of 1825 is now to be attributed to Ehrenberg. Passerini (1873) used the epithet *sorghi* for a sorghum smut he described as a 'spec. nov.'

from his own collections in Italy. He made no reference to Ehrenberg's *Sporisorium sorghi* and evidently believed that the sorghum smut was previously unknown. Lindeberg (1959) noted that Passerini had used the epithet *sorghi* for what he regarded as a new species, but other authors have written their lists of synonyms to indicate that Passerini had transferred the species from *Sporisorium* to *Ustilago*.

It is unfortunate that the generic name of this smut, a cosmopolitan parasite of *Sorghum* spp., resembles another generic name in the same group of fungi. However, this situation is not unique in relation to plant names. Link (1825) cited the genus as *Sporisorium* Ehrenberg in litteris and evidently wished to attribute the specific epithet to Ehrenberg also. The epithet *sorghi* has been ascribed to Link in most instances where the species has been cited formally, but article 46, Rec. 46D of the International Code of Botanical Nomenclature gives support to the view that the genus and species should be attributed to Ehrenberg.

Sporisorium amphiphis (Syd.) Langdon & Fullerton comb. nov.

Basionym: *Sphacelotheca amphiphis* Syd. Annal. Mycol. 33, 232, 1935.

Specimens examined: On *Bothriochloa insculpta* A. Camus, Transvaal, South Africa, June 1931, L.C.C. Liebenberg (TYPE, PRE); on *B. decipiens* (Hack.) Hubbard, Esk, Queensland, Mar. 1967, R.A. Fullerton (DAR 25286).

Sporisorium vanderystii (P. Henn.) Langdon & Fullerton comb. nov.

Basionym: *Ustilago vanderystii* P. Henn. Ann. Mus. Congo Bot. V. 2, 86, 1907.

Synonym: *Sphacelotheca vanderystii* (P. Henn.) Ling Lloydia, 14, 104, 1951.

Specimens examined: On *Hyparrhenia rufa* (Nees) Stapf. Dembo, Belgian Congo, June 1906, H. Vanderyst B31 (LECTO-TYPE, BR). On *Hyparrhenia filipendula* (Hochst.) Stapf. Buaraba, Queensland, Feb. 1966, R.A. Fullerton (DAR 25284); Brisbane Queensland, 22 Mar. 1943, M.S. Clemens (BRIU 51) (part of specimen at BPI, det. Ling)

A full synonymy for this smut was given by Ling (1951) when making the combination *Sphacelotheca vanderystii* (P. Henn.) Ling.

Sporisorium reilianum (Kühn) Langdon & Fullerton comb. nov.
 Basionym: *Ustilago reiliana* Kühn In Rabenhorst, Fungi
 Europ. No. 1998, 1875.

Synonym: *Sphacelotheca reiliana* (Kühn) Clint. J. Mycol. 8.
 141.1902

Specimens examined: On *Sorghum bicolor* (L.) Moench. Rabenhorst, Fungi europaei, No. 1998 (TYPE, BPI); Sydow, Ustilagineen, no. 116, Germany, Sept. 1894 (BPI); Illinois, U.S.A., Sept. 1897, G.P. Clinton (BPI); Brookstead, Queensland, 13 Mar. 1951, R. Morwood (BRIU 743). On *Zea mays* L. Lawes, Queensland, Apr. 1960, N. Fox (BRIU 747). On *Hackelochloa granularis* (L.) Kunze. Townsville, Queensland, 20 Mar. 1938, S.T. Blake (BRIU 63); Sydow, Ustilagineen, no. 451, Pusa, India, 28 Sept. 1907, E.J. Butler (VPRI).

Fischer & Shaw (1953) have listed synonyms of *Ustilago reiliana*. This cosmopolitan smut of maize and sorghum was transferred to *Sorosporium* by McAlpine (1910) who was misled by the aggregations of spores in very young parts of the sorus. McAlpine recorded that 'sterile cells' were mixed with the spores. Our studies of the sorus have shown that the smut belongs in *Sporisorium*.

Sporisorium doidgeae (Zundel) Langdon & Fullerton comb. nov.
 Basionym: *Sphacelotheca doidgeae* Zundel Mycologia 22,
 131, 1930.

Specimen examined: On *Bothriochloa glabra* A. Camus. Natal, Africa, 26 Dec. 1911, E.M. Doidge (TYPE, PRE).

The smut of *Bothriochloa bladhii*, *Sphacelotheca andropogonis*, which was examined in detail has not been transferred to *Sporisorium* here. The type specimen has not become available to us and in the absence of the nomenclatural type we have refrained from making the transfer. We have seen the type specimen of *Ustilago ischaemi* Fckl. and our specimen of the *Bothriochloa* smut is conspecific with it. Fischer & Shaw (1953) have shown that *U. ischaemi* is a synonym of *Sphacelotheca andropogonis*. That smut is but one of scores of species which, judging by their descriptions, will probably be referable to *Sporisorium* when the type specimens are examined.

DISCUSSION

The status of the genus *Sphacelotheca* has now been resolved. Its validity is beyond doubt. Whether species of

Sphacelotheca are confined to the Polygonaceae has yet to be determined. There are many smuts of Poaceae and some of Cyperaceae which have been included in *Sphacelotheca*. Perusal of their descriptions suggests that many of them will prove to be species of *Sporisorium*.

It is unfortunate that de Bary's (1884) short account of the sorus ontogeny and mature structure of *S. hydropiperis* has been ignored. The extension of the circumscription of *Sphacelotheca* by Clinton (1902) which allowed gramminicolous smuts with sporogenous hyphae growing from a central columella to be included has led many later mycologists into error. Savile (1953), when discussing some smuts of *Polygonum* species, remarked that an ontogenetic study of the sori might resolve the problem of intergradation between *Ustilago* and *Sphacelotheca*. Probably no such intergradation exists. *Sphacelotheca* differs markedly in its soral ontogeny from *Ustilago* which, as Langdon & Fullerton (1975) have shown, has no fungal structures associated with its spore mass. Some smuts of the Polygonaceae are undoubtedly referable to *Ustilago*. The species *hydropiperis*, and probably some others, belong in *Sphacelotheca*. The way is now clear for a taxonomic revision of the smuts of the Polygonaceae.

We have studied *Sporisorium* spp. which, in the common parlance of mycologists, have sori either in inflorescences or in ovaries. The ontogeny of the sori is the same in each case. In soral meristems the host tissues associated with the fungal portions of the sorus are formed concurrently with the latter, and would not form in non-infected plants. Inflorescences are not destroyed except in the sense that their development is stopped when they are still very small. The sori of *S. sorghi* do not originate in ovaries but in rachillae of the florets. A similar origin has been reported for sori of *Sorosporium cryptum* McAlp. and *S. polycarpum* Syd. but the sori of *S. consanguineum* Ell. & Ev. are formed in ovaries (Langdon & Fullerton, 1975). For many smuts it may not be possible to determine the exact site of sorus initiation by an examination of mature specimens. In the absence of precise information it would be preferable to use the term floret smut rather than ovary smut. In the several species of *Sporisorium* the marshalling of host cells and fungal hyphae proceeds in the same manner irrespective of the site of the soral meristem. The particular host organ involved does not determine the nature of the sorus formed. In view of this, it is doubtful

whether smuts with the same characters but differing in the location of the sorus, for example in inflorescences or in florets, should be considered as separate species.

The sporogenous hyphae of *Sporisorium* spp. are converted to spores by processes similar to those involved in sporulation in species of *Ustilago* (Langdon & Fullerton, 1975). Clinton (1897), examining *U. sorghi* (*Sporisorium sorghi*), concluded that spore formation was different in that species from what was then known for species of *Ustilago*. He was considering the matter in the context of the order of events in the whole spore mass rather than in reference to the changes in sporogenous hyphae themselves. The latter he acknowledged to be similar to what he saw in *Ustilago zaeae* (*Ustilago maydis*).

In the youngest parts of sori of *Sporisorium* spp. clumps of agglutinated spores may be found. Being subglobose these spore aggregations may be mistaken for true spore balls and the smut then placed in *Sorosporium*. McAlpine (1910) transferred a smut of maize to *Sorosporium* as *S. reilianum* after finding globose to irregular spore aggregations in very young sori. He also recorded "sterile cells" mixed with the spores. Since the sori of some gramminicolous species of *Sorosporium* have fungal peridia and columellae his mistake is understandable. His erroneous conclusion concerning the generic position of the maize smut, now known to belong in *Sporisorium*, emphasises the need to combine data obtained from both developing and mature sori before a decision on the generic position of a smut is reached.

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SOME SPECIES OF TILLETIA FROM AUSTRALIA

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SUMMARY

The generic position of a smut sporing on leaf surfaces of *Phragmites australis* is discussed. This smut's characteristics have been compared with those of foliicolous species of *Orphanomyces* and *Clintonia*. The smut of *Phragmites* has been described as a new species of *Tilletia*. Two other species of *Tilletia* from Australia are discussed.

Tilletia nigrifaciens Langdon & Boughton sp. nov.

Sori nudi, in paginae foliorum. Sporae globosae, subinde subglobosae, fuscae, 18-24 μm diam.; exosporium reticulatum; vagina gelatinosa tenuis. Cellulae steriles globosae vel subglobosae, hyalinae, 16-32 μm diam., paries crassitie 1-4 μm .

Specimens examined: On *Phragmites australis* (Cav.) Trin. ex Stendel: Logan River, Queensland, Australia, 18 May 1974, R.F.N. Langdon, BRIU 2533 (TYPE); Broadbeach, Queensland, 26 Aug. 1964, D.J. O'Dowd, BRIU 2534; Broadbeach, Queensland, 26 May 1965, R.A. Fullerton, BRIU 2251.

Although *Phragmites australis* is widespread on stream banks and in marshes in south-eastern Queensland, its smut has been found at only two sites. The mycelium is perennial in the rhizomes of the host. Smutted plants which were moved from a riverine site to garden conditions in 1974 have produced smutted culms each year since.



Figure 1. Smutted culms of *Phragmites australis*. A. Non-flowering culms. B. Culms with inflorescences. (Scales in millimetres).

Infected plants are conspicuous. Dark masses of spores cover much of the adaxial surfaces of leaves on distal parts of culms when *Phragmites australis* is entering its flowering phase at the end of summer. Some smutted culms do not develop inflorescences (Fig. 1; A). Others do (Fig. 1; B), and the inflorescences range from normal to greatly reduced and distorted. Smutted leaves on the distal parts of non-flowering culms are crowded, small and distorted. In culms with inflorescences the internodes in distal parts are longer than those of non-flowering culms, and the leaves on which spores form are small and distorted.

Sori cover extensive areas of the adaxial surfaces of leaf blades. Rarely, sori of limited extent occur on adaxial surfaces of leaf sheaths, close to the ligule, and on the abaxial surfaces of leaf blades. Leaf tissue beyond the margins of sori remains green, and beneath the spore masses it is at first chlorotic and eventually necrotic. Streaks of dark, necrotic tissue extend beyond the soral areas in both directions, some reaching into the leaf sheaths.

A comparison of transverse sections of healthy and infected leaves (Fig. 2; F, G) shows that in the presence of the pathogen, the leaf is thicker. Most cells of the infected leaf increase in size, but the major effect is brought about by hypertrophy of the intercostal mesophyll cells and an interpolation of parenchyma cells between the veins and the adaxial sclerenchymatous girders. The veins, which in a healthy leaf are equidistant between the two epidermises, are near to the lower epidermis of the diseased leaf. Two major changes are apparent in the mesophyll which in the normal leaf consists of arm cells (Metcalf, 1960) richly provided with chloroplasts. In those parts of the leaf which underlie sori, the walls of the mesophyll cells are not invaginated. In these mesophyll cells, chloroplasts are initially infrequent and finally absent.

A noticeable feature of the adaxial epidermis of normal leaves is the regularly disposed groups of bulliform cells; these are absent from the diseased leaf. Guard cells occur in the appropriate places in the adaxial epidermis but they are not as big as those of the healthy leaf. In the abaxial epidermis they enlarge to match the other lower epidermal cells. The epidermal

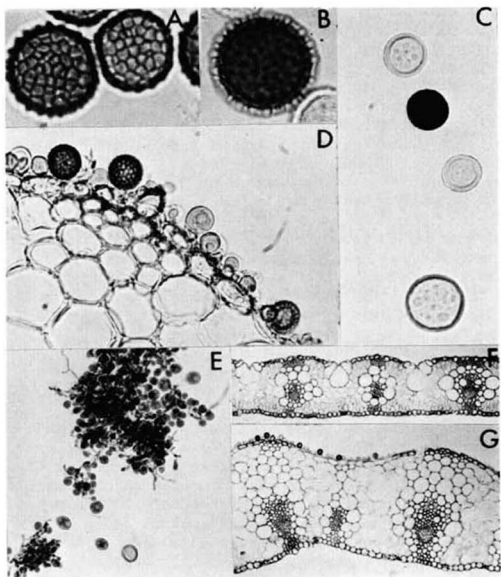


Figure 2. *Tilletia nigrifaciens*. A. Spores, surface view, (x1000). B. Spores, median optical section, (x1000). C. Spores and sterile cells, (x400). D. Sporulation on leaf surface, (x400). E. Mycelium from leaf surface showing mode of sporulation, (x400). F. Section of normal leaf of the host (*Phragmites australis*), (x63). G. Section of smutted leaf of host, (x63).

cells under a developing sorus appear intact (cf. *Clintonia nolinae*, (Cordas & Durán, 1976)) but those underlying a mature sorus are shrivelled and may eventually erode away. There is phloem degeneration in those parts of leaves on which sporulation occurs.

Sporulation begins when the leaves are very young and still rolled around one another. At this stage the leaf blades are still concealed by the sheaths of older leaves. Hyphae growing from the internal tissues of the leaf form a dense mat on the adaxial surface. Rarely there is limited emergence of hyphae onto an abaxial surface. The hyphae are freely branched. Apical portions of hyphal branches swell and are rapidly transformed to spores or sterile cells (Fig. 2; D). The latter are few relative to the number of spores formed.

Spores taken from living plants as well as spores kept on air-dried leaves in the laboratory for up to 1y have been incubated at various temperatures and in the presence of extracts of host tissues and of soil. No spores germinated. The same result was obtained with spores which had developed in the autumn (May, in Queensland) and had remained on the plants in the countryside until after the winter (September).

Quite recently the genera *Orphanomyces* Savile and *Clintonia* Cordas & Durán have been erected for certain smuts with sori associated with leaves. The species of *Orphanomyces* (Ustilaginaceae) bear spores in a crust outside the intact epidermis of leaves of systematically infected plants (Savile, 1974). A similar condition has been described for the type species of *Clintonia* (Tilletiaceae) (Cordas & Durán, 1976). Cordas & Durán supported the opinion offered by Savile that the external position of the sorus was grounds for excluding Clinton's (1904) species *nolinae* from *Melanotaenium* de Bary and for erecting a new genus for it. In the context of discussion about the species placed in *Orphanomyces* and *Clintonia* respectively there are quite reasonable grounds for the erection of those genera. Such actions do not necessarily constitute grounds whereby other smuts with external sori should be excluded from long existing genera. Cordas & Durán (1976) have accepted the principle of evolutionary parallels for sorus location. Although sori may occupy similar locations on the hosts, there are matters such as sporogenesis and the structures present in mature sori

which must be given due weight when a decision on the generic position of a smut is being made.

The smut of *Phragmites australis* has sorus location similar to that of species of *Orphanomyces* and *Clintamra*. Knowledge of the mode of germination of its spores is lacking and therefore it would not be possible to determine to which genus, *Orphanomyces* or *Clintamra*, the smut should be referred if the decision were to be based only on location of the sorus. There are some features of the smut of *Phragmites* which provide strong evidence that it should be placed as a species of *Tilletia*. These are as follows:- (i) the processes of sporulation (Fig. 2; E) conform to those described by Fischer von Waldheim (1872) and Fischer & Holton (1957) for *Tilletia*, (ii) sterile cells are associated with the spores in the sorus (Fig. 2; C), (iii) the spores are relatively large and have a gelatinous sheath (Fig. 2; A, B).

Savile (1974) did not describe how spores formed in *Orphanomyces arcticus* (Rostr.) Savile. Sporulation in *Clintamra nolinae* (Clint.) Cordas & Durán is different from that observed in the smut of *Phragmites*. Attempts to germinate the latter's spores are still being made. If germination were shown to be of the *Tilletia* type the case for including the smut of *Phragmites* in *Tilletia* would be strengthened. If perchance the germination were of the *Ustilago* type a reassessment of the smut's generic position would be necessary.

Tilletia eragrostidis Clint. & Ricker. J. Mycol. 11, 111, 1905.

Specimen examined: On *Eragrostis japonica* (Thurl.) Trin.: Clarke River, Queensland, 8 July 1954, S.T. Blake, BRIU 1485.

Dr. R. Durán of Washington State University, U.S.A., has compared our specimen of this smut with the type specimen and confirmed its identity. *Tilletia eragrostidis* has been reported previously only from U.S.A. The smut possibly has a wider circum-Pacific distribution than that now established. The sori, developed in ovaries, are less than 1mm long. Only a small number of florets in a panicle are smutted. The smut could be overlooked during field collecting. The specimen from Queensland was found by the late Dr. S.T. Blake on a herbarium specimen of the host during his taxonomic studies of Poaceae.

Tilletia texana Long. In Clinton, J. Mycol. 8, 149, 1902.

Specimen examined: On *Stipa setacea* R.Br. Ooline, Queensland 31 Mar. 1936, S.T. Blake, BRIU 40 (IMI 42693).

Herbert & Langdon (1941) recorded this smut as *Tilletia hypsophila* Speg. (= *T. hyalospora* Mass.). Durán & Fischer (1961) have commented on the extension of the host range and the geographic distribution of *T. texana* resulting from their determination of the identity of the specimen from Queensland.

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INDEX OF TAXA IN THE GENUS PSILOCYBE

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SUMMARY

A list of 390 specific, varietal, and form epithets previously described or considered in the genus Psilocybe is given. We tentatively exclude 210 taxa, since they belong to different genera in the modern concept, are synonyms, doubtful species, or nomina nuda.

Fourteen new combinations, based on type studies, are made from Psilocybe into Agrocybe (2), Melanotus (1), Naematoloma (3), and Psathyrella (8). Hallucinogenic species (73) are marked with an asterisk.

The abbreviated bibliographic reference codes used in the present paper are based in part on the system used by Donk in his book CHECK LIST OF EUROPEAN POLYPORES (1974).

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BIBLIOGRAPHIC REFERENCE CODES

- (AB) Ann. Bot.
 (ABA) Ann. Mus. nac. Buenos Aires
 (AEC) An. Esc. nac. Ci. Biol., México
 (AgM) Agaricaceae of Michigan (Kauffman)
 (Am) Annls. mycol.
 (ANS) Ann. Rep. N.Y. State Museum
 (BB) Br. Basid. (Rea)
 (BBr) Bull. Jard. bot. Brx.
 (BCo) Bol. Acad. nac. Ci. Córdoba
 (BF) Brit. Fung.-Fl. (Masse)
 (BFi) Bidr. Finl. Nat. Folk (Karsten)
 (Bl) Blätterpilze (Ricken)
 (BMH) Bull. N.Y. Mus. nat. Hist.
 (BmI) Bull. misc. Inf., Kew
 (BNb) Bull. N.Y. bot. Gard.
 (BnH) Beiheft nov. Hedwigia
 (BNS) Bull. N.Y. State Museum
 (Bro) Brotéria
 (BS) Beiheft Sydowia
 (BSb) Bolm. Soc. broteriana
 (BSF) Bull. Soc. mycol. Fr.
 (BSM) Bol. Soc. Mex. Mic.
 (BTC) Bull. Torrey bot. Club
 (Ch) České houby (Velenovský)
 (ChE) Les Champ. d'Europe (Heim)
 (ChM) Les Champ. halluc. du Mexique (Heim & Wasson)
 (CiM) Ciencia, México
 (CJV) Champ. du Jura et Vosges (Quélet)
 (CM) Česká Mykol.
 (CrA) Compt. r. Acad. Sc., Paris
 (Cza) Champ. sup. zone alpine, Parc Nat. Suisse
 (D) Darwiniana
 (DAB) U.S. Dept. Agric. tech. Bull.
 (Bba) Denkschrift bayer. bot. Ges.
 (DCs) Dict. iconogr. Champ. sup. (Laplanche)
 (DM) Derm. et Mel.
 (EBJ) Bot. Jahn. (Engler)
 (FAC) Fl. Anal. Champ. sup. (Kühner & Romagnesi)
 (FaD) Fl. agar. Dan. (Lange)
 (Fic) Fl. ital. crypt. (Fungi)
 (Fl) Flora
 (FP) Führer Pilzkunde (Kummer)
 Fries 1821-1823 Syst. Myc.
 (FuF) Fungi of the Faeröes (Möller)
 (G) Grevillea
 (H) Hedwigia
 (Ho) Hoppea
 (IBF) Illustr. Brit. Fungi (Cooke)
 (IcM) Iconographia Mycol. (Bres.)
 (Ih) Iheringia (Bot.)
 (Im) Icones mycologicae (Boudier)
 (JaR) J. agr. Research
 (JFA) J. Fla. Acad. Sc.
 (JJB) J. Jap. Bot.
 (JLS) J. Linn. Soc. (Bot.)
 (JMS) J. Elisha Mitch. Sc. Soc.

- (JMy) J. Mycology
 (KB) Kew Bull.
 (KK) Kleine Kryptogamenflora II, b/2, 1967
 (L) Lilloa
 (LH) Les Champ. qui croissent en France (Gillet)
 (Ll) Lloydia
 (M) Mycologia
 (MG) Medd. Grønland
 (Myc) Mycotaxon
 (Myp) Mycopath. Mycol. appl.
 (NAP) N. American species of Pholiota (Smith & Hesler)
 (NBF) Not. Br. Fungi (Masse) (Masse)
 (Nca) Naturaliste canad.
 (Ned) Not. Roy. bot. Gard., Edinb.
 (NH) Nova Hedwigia
 (NIC) Nouv. Invest. Champ. halluc. du Mexique (Heim)
 (NPF) Nat. Pfl. Fam. (Engler & Prantl)
 (NT) Nat. Tijdschrift
 (Pe) Persoonia
 (PFl) Proc. Fla. Acad. Sc.
 (PMi) Pap. Mich. Acad. Sc.
 (RM) Revue Mycol. (Paris)
 (SAW) Sitzungsber. K. Akad. Wiss., Wien
 (SF) Syll. Fung. (Saccardo)
 (Sy) Sydowia
 (SyF) Symb. Fenn. (Karsten)
 (TBS) Trans. Br. mycol. Soc.
 (TmJ) Trans. mycol. Soc. Jap.
 (TPR) Trans. Proc. Roy. Soc. So. Austr.
 (TSn) Trans. Sapp. nat. hist. Soc.
 (VZB) Verh. K. K. Zool. Bot. Ges., Wien
 (ZP) Zeitschrift für Pilzk.
 (ZPk) Zeitschrift für Pflanzenkr.

CHECK-LIST OF TAXA IN THE GENUS PSILOCYBE (Fr.) Kumm.
 = DECONICA W.G. Smith ex Karst.

- acadiensis A.H. Smith 1946 (JMS 62): 192
acutipilea (Deconica) Speg. 1889 (BCo 11): 381 = Psilocybe
acutipilea (Speg.) Guzmán *?
acutissima Heim 1959 (RM 24): 106
acutiuscula (Deconica) Sing., in LE herb. = Kuehneromyces
vernalis (Peck) Sing. & Smith 1946 (M 38): 518
acutopapillata, P. yungensis var., Sing. & Smith 1958
 (M 50): 295; nom. nud.
aerugineomaculans (Höhnelt) Sing. & Smith 1958 (M 50): 273 =
Psilocybe subaeruginascens Höhnelt
aggericola Sing. & Smith 1958 (M 50): 142 *
aggregata Clel. & Cheel 1918 (TPR 42): 134; doubtful sp.
agnata (Britz.) Sacc. 1887 (SF 5): 1047; doubtful sp.
agraria (Fr.) Karst. 1879 (Bfi 32): 505; doubtful sp.
agrariella Atk. 1909 (Am 7): 374 = Psathyrella
agrariella (Atk.) A.H. Smith
alachuana Murr. 1942 (Ll 5): 155 = Simocybe alachuana
 (Murr.) Sing.

- albida, P. caerulescens var., Heim 1967 (NIC): 170 =
P. caerulescens Murr. var. caerulescens
albobrunnea Beeli 1938 (BBr 15): 42 = Psathyrella
candolliana (Fr.) Maire
albobrunnea Lutz 1907 (BSF 54): 191; doubtful sp.
albofimbriata (Naucoria) Rick 1930 (Bro 24): 110 =
Psilocybe sp.
alboquadrata (Berk.) Sacc. 1887 (SF 5): 1043; doubtful sp.
aleuriata Heim & Remy 1926 (BSF 41): 459; doubtful sp.
alnetorum Sing. 1952 (L 25): 332
ammophila (Dur. & Lév.) Gill. 1878 (LH): 587 = Psathyrella
ammophila (Dur. & Lév.) Orton
andina Guzmán 1977 (Myc) in press
anellariiformis (Murr.) Sing. 1973 (BS 7): 82
angulata (Batsch ex Pers.) Sing. 1961 (Pe 2): 7
angulata-olivacea, P. mexicana f., Heim & Cailleux 1967
(NIC): 140 = P. mexicana Heim f. mexicana
angustispora A.H. Smith 1946 (JMS 62): 193
antillarum (Fr.) Sacc. 1887 (SF 5): 1052 = Panaeolus
antillarum (Fr.) Dennis
apelliculosa Orton 1969 (Ned 29): 118
appendiculata Rick 1920 (Bro 18): 62
araucana Sing. 1969 (BnH 29): 239 *
arenulina (Peck) Sacc. 1887 (SF 5): 1057 = Psathyrella
arenulina (Peck) A.H. Smith
areolata (Klotz.) Sacc. 1887 (SF 5): 1047 = Psathyrella
velutina (Pers. ex Fr.) Sing.
argentina (Speg.) Sing. 1969 (BnH 29): 241
argentipes Yokoyama 1976 (TmJ 17): 349 *
arrosus, Ag. (Psilocybe) Schulz. 1876 (VZB): 418; doubtful
sp.
asperospora Clel. 1934 (TPR 58): 212 = Panaeolus
foeniseccii (Pers. ex Fr.) Kühn. ?
atomatoides Thom & Lathrop 1925 (JaR 30): 625; doubtful sp.
atomatoides (Peck) Sacc. 1887 (SF 5): 1048 = Psathyrella
atomatoides (Peck) A.H. Smith
atrobrunnea (Lasch) Gill. 1878 (LH): 586
atrorufa (Schaeff. ex Fr.) Quél. 1872 (CJV): 117 =
Psilocybe montana (Pers. ex Fr.) Kumm.
australiana Guzmán & Watling 1977 (Ned) in press *
australis (Deconica) Horak 1967 (D 14): 363 = Psilocybe sp.
aztecorum Heim 1957 (RM 22): 78 *
baecystis Sing. & Smith 1958 (M 50): 141 *
bifrons (Berk.) P. Henn. 1900 (NPF 1 (1**)): 235 =
Psathyrella bifrons (Berk.) A.H. Smith
bipellis (Quél.) Pereira-Coutinho 1931 (BSB 7): 340 =
Psathyrella bipellis (Quél.) A.H. Smith
blattariopsis (Speg.) Sing. 1950 (L 23): 214 *?
bolivarii Guzmán 1968 (CiM 26): 25 *
bonetii Guzmán 1968 (AEC 17): 9 *
borealis Guzmán 1977 (BSM 11) in press
brasiliensis Guzmán 1977 (Myc) in press *
brevipes, P. atrorufa f., Kill. 1936 (DbA 20): 78
brevispora, P. mexicana var., Heim 1956 (CrA 242): 1393 =
Psilocybe muliercula Sing. & Smith

- brunneocystidiata Guzmán & Horak 1978 (Sy 30) in press *
bryophila (Deconica) Peck 1893 (ANS 46): 106 =
Psilocybe montana (Pers. ex Fr.) Kumm.
bulbosa (Peck) A.H. Smith 1948 (M 40): 694
bulbosulus, Ag. (Psilocybe) Schulz. 1876 (VZB): 417; doubtful
 sp.
bullacea (Bull. ex Fr.) Kumm. 1871 (FP): 71
caeruleoannulata Sing. ex Guzmán (Myc) in press *
caerulescens Murr. 1923 (M 15): 20 *
caerulescens (Naematoloma) Pat. 1907 (BSF 23): 78 =
Psilocybe cubensis var. caerulescens (Pat.) Sing. &
 Smith
caerulescens, Ag. semilanceata var., Cke 1881-91 (IBF): 605,
 pl. 573 = Psilocybe cookei Sing. non Sacc.
caerulescens, P. cubensis var., (Pat.) Sing. & Smith 1958
 (M 50): 269
caerulescens, P. semilanceata var., (Cke.) Sacc. 1887
 (SF 5): 1051 = P. semilanceata (Fr. ex Secr.) Kumm.
 var. semilanceata
caerulescens (Stropharia) Imai 1932 (TSn 12): 148 =
Psilocybe venenata (Imai) Imazeki & Hongo
caerulipes (Peck) Sacc. 1887 (SF 5): 1051 *
caesioannulata Sing. 1965 (Myp 26): 165 *
caespitosa, P. squalidella var., Peck 1906 (ANS 59): 55 =
Naematoloma squalidellum (Peck) A.H. Smith
caespitosa (Berk.) Sacc. 1887 (SF 5): 1053 = Psathyrella sp.
caespitosa Murr. 1923 (M 15): 5
californica Earle 1904 (BNb 3): 301 = Psilocybe crobula
 (Fr.) Lange ex Sing. ?
callosa (Fr.) Quél. 1872 (CJV): 257 *?
camptopoda (Peck) Sacc. 1887 (SF 5): 1057 = Psathyrella
camptopoda (Peck) A.H. Smith
candidipes Sing. & Smith 1958 (M 50): 141 *
canificans Cke., in Sacc. 1887 (SF 5): 1047 = Psilocybe
canofaciens Cke.
canobrunnea (Fr. ex Batsch) Quél. 1872 (CJV): 257; doubt-
 ful sp.
canofaciens Cke. 1885 (G 14): 1; doubtful sp.
canoruber (B. & C.) Sacc. 1887 (SF 5): 1052 = Agaricus sp.
carbonaria Sing. 1965 (Myp 26): 166 *?
caricicola Orton 1969 (NEd 29): 119 = Melanotus
caricicola (Orton) Guzmán, comb. nov.
castaneicolor Murr. 1923 (M 15): 19 = Psathyrella
conopilea (Fr.) Pears. & Dennis
castaneifolia Murr. 1923 (M 15): 17 = Psathyrella
castaneifolia (Murr.) A.H. Smith
castanella Peck 1888 (BNS 1): 7 = Psilocybe crobula
 (Fr.) Lange ex Sing. ?
catervata Mass. 1892 (BF 1): 378 = Psathyrella catervata
 (Mass.) Orton
cavipes House 1919 (BNS 205-6): 40; doubtful sp.
ceres (Cke. & Mass.) Sacc. 1891 (SF 9): 140; doubtful sp.
cernua (Vahl ex Fr.) Quél. 1872 (CJV): 147 = Psathyrella
cernua (Vahl ex Fr.) Moser
chilensis Sing. 1965 (Myp 26): 168

- chondrodermus (B. & Br.) Sacc. 1887 (SF 5): 1048 =
Psathyrella chondrodermus (B. & Br.) A.H. Smith
chrysocystidiata Sing. 1973 (BS 7): 82
cinchonensis (Psathyra) Murr. 1918 (M 10): 33 = Psilocybe
mammillata (Murr.) A.H. Smith
citrina Mass. 1901 (BmI 175-7): 162 = Psathyrella sp.
clivensis (B. & Br.) Sacc. 1887 (SF 5): 1055 =
Psathyrella clivensis (B. & Br.) Orton
cokeri Murr. 1923 (M 15): 12 = Psathyrella cokeri (Murr.)
A. H. Smith
cokeriana Smith & Hesler 1946 (JMS 62): 193
collybioides Sing. & Smith 1958 (M 50): 141 *
colombiana Guzmán 1977 (Myc) in press *
compta (Fr.) Sacc. 1887 (SF 5): 1050 = Ag. (Psilocybe)
comptulus B. & Br. ?
comptulus, Ag. (Psilocybe) B. & Br. 1861 (NBF): 376, #917;
doubtful sp.
conica (Psathyra) Peck 1901 (BMH 54): 153 = Psilocybe sp.
conissans Peck 1908 (BNS 122): 132 = Psathyrella
conissans (Peck) A.H. Smith
cookei Sacc. (non Sing.) 1887 (SF 5): 1043; doubtful sp.
cookei Sing. (non Sacc.) 1973 (BS 7): 84 = Psilocybe
semilanceata (Fr. ex Secr.) Kumm. var. semilanceata
coprinifasciens (Roll.) Pouz. 1953 (CM 7): 140
coprophila (Bull. ex Fr.) Kumm. 1871 (FP): 71
cordispora Heim 1959 (RM 24): 103 *
cordobensis Sing. 1973 (BS 7): 83
corneipes (Fr.) Karst. 1879 (BFI 32): 504; not a Psilocybe.
crobula (Fr.) Lange ex Sing. 1961 (Sy 15): 70
cubensis (Earle) Sing. 1948 (Sy 2): 37 *
cyanescens (Geophila) (Maire) Kühn. & Romagn. 1953 (FAC):
337 = Psilocybe mairei Sing.
cyanescens Wakef. 1946 (TBS 29): 141 *
cyanescens (Stropharia) Murr. 1941 (M 33): 279 = Psilocybe
cubensis (Earle) Sing.
cylindrispora Pears. 1950 (TBS 33): 306; doubtful sp.
cystidiosa Peck 1913 (BNS 167): 46 = Psathyrella
cystidiosa (Peck) A.H. Smith

deformata, P. squalidella var., Peck 1912 (BNS 157): 98 =
Naematoloma udum (Pers. ex Fr.) Karst.
delita (Britz.) Sacc. 1887 (SF 5): 1046; doubtful sp.
depauperata (Pholiota) (Sing. & Smith) A.H. Smith 1968
(NAP): 121 = Psilocybe sp. ?
desertorum Vel. 1921 (Ch 3): 589; doubtful sp.
dichroa (Pers.) Karst. 1879 (BFI 32): 504 = Psilocybe
atrobrunnea (Lasch) Gill.
dichroma (B. & C.) Sacc. 1887 (SF 5): 1057 = Psathyrella
dichroma (B. & C.) A.H. Smith
diconica, P. yungensis var., Sing. & Smith 1958 (M 50): 142*
digressus Peck 1895 (BTC 22): 205 = P. coprophila (Bull. ex
Fr.) Kumm. ?
discordabilis (Britz.) Sacc. 1895 (SF 11): 72; doubtful sp.
discordans (Britz.) Sacc. 1887 (SF 5): 1049; doubtful sp.
dispersa Heim 1957 (ChE 2): 465 = Naematoloma dispersum
(Fr.) Karst.

- distorta-intermedia, P. mexicana f., Heim & Cailleux
1967 (NIC): 140 = P. mexicana Heim f. mexicana
dumontii Sing. ex Guzmán 1977 (Myc) in press *
dunicola (Speg.) Sing. 1968 (Myp 34): 137
- ecbola (Fr.) Sing. 1969 (BnH 29): 254 = Psilocybe inquilina
(Fr. ex Fr.) Bres.
- echinata Clel. 1934 (TPR 58): 212; doubtful sp.
- elongata, P. zapotecorum var., Heim 1960 (CrA 250): 1158 =
P. zapotecorum Heim var. zapotecorum
- elongata (Pers.) Lange 1939 (FaD 4): 78 = Naematoloma
elongatipes (Peck) Sing. ?
- elongatipes (Peck) Sacc. 1887 (SF 5): 1046 = Naematoloma
elongatipes (Peck) Sing.
- ericaea (Pers. ex Fr.) Quél. 1873 (CJV): 349 =
Naematoloma ericaeum (Pers. ex Fr.) Sing.
- eucalypta Guzmán & Watling 1977 (NEd) in press *
- examinata (Deconica) (Britz.) Sacc. 1895 (SF 11): 73;
doubtful sp.
- exerrans (Britz.) Sacc. 1887 (SF 5): 1056; doubtful sp.
- exigua, (Stropharia) merdaria var., Möller 1945 (FuF 1):
196 = Psilocybe merdaria (Fr.) Ricken
- fagicola Heim 1959 (RM 24): 438 *
- farinacea Rick ex Guzmán (Myc) in press *
- farinulenta (Schaeff. ex Fr.) Sacc. 1916 (Fic 15): 829 =
Psathyrella cernua (Vahl ex Fr.) Moser ?
- fasciata Hongo 1957 (JJB 32): 144 *
- ferrugineo-lateritia (Vogl.) Sacc. 1891 (SF 9): 141;
doubtful sp.
- fibrillosa (Pers.) P. Henn. 1900 (NPF 1 (1**)): 235 =
Psathyrella fibrillosa (Pers.) Maire, in Maire & Wern.
- fimetaria (Orton) Watling 1967 (Ll 30): 150 (= Psilocybe
fimetaria (Orton) Sing.)*
- fimicola Guzmán 1977 (Myc) in press
- flaccescens, Ag. (Psilocybe) Schulz. 1876 (VZB): 418;
doubtful sp.
- flammuliformis Sing. 1969 (BnH 29): 247
- floccipes Kill. 1936 (DbA 20): 78; doubtful sp.
- floridana Murr. 1944 (PF1 7): 126 = Psathyrella sp.
- foeniseccii (Pers. ex Fr.) Quél. 1872 (CJV): 117 =
Panaeolus foeniseccii (Pers. ex Fr.) Kühner
- fortunata (Cke.) Sacc. 1887 (SF 5): 1056 = Panaeolus
antillarum (Fr.) Dennis
- frustulenta (Fr.) P. Henn. 1900 (NPF 1 (1**)): 235 =
Psathyrella frustulenta (Fr.) A.H. Smith
- fuegiana (Horak) Sing. 1969 (BnH 29): 256
- fuliginosa (Murr.) A.H. Smith 1948 (M 40): 697
- furdadonensis Guzmán 1977 (Myc) in press *
- fuscofolia Peck 1912 (BNS 157): 100 = Psathyrella
fuscofolia (Peck) A.H. Smith
- fuscofulva Peck 1888 (BNS 1): 7 = Psilocybe atrobrunnea
(Lasch) Gill.
- galericulata-convexa, P. mexicana f., Heim & Cailleux 1967
(NIC): 138 = P. mexicana Heim f. mexicana
- galericulata-viscosa, P. mexicana f., Heim & Cailleux 1967
(NIC): 143 = P. mexicana Heim f. mexicana
- gastonii, P. caerulipes var., Sing. 1958 (Sy 12): 236 *

- gilletii Karst. 1879 (BFI 32): 509 = Naematoloma sp.
goniospora (B. & Br.) Sing. 1961 (Sy 15): 70
gossypina (Bull.) P. Henn. 1900 (NPF 1 (1**)): 235 =
Psathyrella gossypina (Bull. ex Fr.) Konr. & Maubl.
graminicola (Orton) Sing. 1973 (BS 7): 83
grandis-gibbosa, P. mexicana f., Heim & Cailleux 1967
(NIC): 145 = P. mexicana Heim f. mexicana
granulata Naveau 1923 (NT 5): 85; doubtful sp.
graveolens Peck 1913 (BNS 167): 47
- hebes (Fr.) Sacc. 1887 (SF 5): 1054 = Psathyrella
obtusata (Fr.) A.H. Smith
heliophila, P. caerulescens var. mazatecorum f., Heim 1958
(ChM): 141 = P. caerulescens Murr. var. caerulescens
helobia (Kalchbr.) P. Henn. 1900 (NPF 1 (1**)): 235;
doubtful sp.
helvola (Schaeff.) Mass. sensu Rea (BB): 362; doubtful sp.
henningsii Jungner 1906 (ZPk 16): 131; doubtful sp.
heterosticha (Fr.) Sing. 1969 (BnH 29): 248
hoogshageni Heim 1959 (RM 24): 104 *
horaki Guzmán 1977 (Myc) in press
hydrophila (Bull. ex Fr.) Gill. 1878 (LH): 583 =
Psathyrella hydrophila (Bull. ex Fr.) R. Maire
hygrophila, P. spadicea var., Mass. 1892 (BF): 374 =
Psathyrella hydrophila (Bull. ex Fr.) R. Maire ?
hyperella (Fr.) Kühn. & Romagn. 1953 (FAC): 339; doubtful
sp.
inconspicua Guzmán & Horak 1978 (Sy 30) in press *
inquilina (Fr. ex Fr.) Bres. 1931 (ICM): 18, pl. 863
insiliens (Britz.) Sacc. 1887 (SF 5): 1049; doubtful sp.
insipidus, Ag. (Psilocybe) Schulz. 1881 (VZB 30): 487;
doubtful sp.
interjungens (Britz.) Sacc. 1887 (SF 5): 1055; doubtful sp.
iodoformica Pat. 1924 (BMH 6): 531; doubtful sp.
isauri Sing. 1958 (Sy 12): 237 *
jujuyensis Sing. 1973 (BS 7): 82
kumaenorum Heim 1967 (RM 32): 206 *
- larga Kauffm. 1918 (AgM): 279 = Psathyrella larga (Kauffm.)
A.H. Smith
lateritia (Murr.) A.H. Smith 1948 (M 40): 698 = Psilocybe
montana (Pers. ex Fr.) Kumm. ?
latispora Murr. 1923 (M 15): 10
lazoii Sing. 1969 (BnH 29): 242
leechii A.H. Smith 1946 (JMS 62): 196 = Agrocybe leechii
(A.H. Smith) Watling
libertatis (Deconica) (Batsch. ex Fr.) Sacc. 1887 (SF 5):
1059; doubtful sp.
limicola (Peck) Sacc. 1887 (SF 5): 1054 = Psathyrella
limicola (Peck) A.H. Smith
limophila (Peck) Peck 1912 (BNS 157): 104 = Psathyrella
limophila (Peck) Guzmán, comb. nov.
liniformans Guzmán & Bas 1977 (Pe) in press *
lipophila (Oudem.) Sacc. 1902 (SF 16): 125; doubtful sp.
lonchophorus, Ag. (Naucoria) B. & Br. 1871 (JLS 11): 544 =
Psilocybe sp.

- longingua Sing. 1959 (M 51): 578
longipes, P. agraria var., Kill. 1936 (DbA 20): 72;
 doubtful var.
longipes, P. atrorufa f., Kill. 1936 (DbA 20): 77
longispora Murr. 1945 (JFA 8): 197 = Naematoloma
longispora (Murr.) A.H. Smith
longispora, P. mexicana var., Heim 1956 (CrA 242): 1393 =
Psilocybe aztecorum Heim
luteonitens (Vahl ex Fr.) Parker-Rhodes 1951 (TBS 34): 364
lysiophylla (Fr.) Sacc. 1887 (SF 5): 1045; doubtful sp.

macrocystis Heim 1956 (CrA 242): 1392; nom. nud.
macrosperma, P. aqualidella var., Peck 1912 (BNS 157): 98 =
Naematoloma udum (Pers. ex Fr.) Karst.
macrospora, P. merdaria var., (Möller) Sing. 1969 (BnH 29):
 243
mairei Sing. 1973 (BS 7): 84 *
major, P. hebes f., Bres. sensu Kill. 1936 (DbA 6): 75 =
Psathyrella sp. ?
mammillata (Murr.) A.H. Smith 1948 (M 40): 700 *?
marthae Sing. 1969 (BnH 29): 255
maxima Vel. 1921 (Ch 3): 584; doubtful sp.
mazatecorum, P. caerulescens var., Heim 1957 (RM 22): 78 =
Psilocybe caerulescens Murr. var. caerulescens
merdaria (Fr.) Ricken 1915 (Bl): 251
merdicola Huijsman 1961 (Pe 2): 93
mesospora Sing. 1969 (BnH 29): 245
mexicana Heim 1957 (RM 22): 77 *
microrhiza (Lasch) P. Henn. 1900 (NPF 1 (1**)): 235 =
Psathyrella microrhiza (Lasch) Konr. & Maubl.
microsperma Speg. 1919 (BCo 23): 402 = Psathyrella
microsperma (Speg.) Guzmán, comb. nov.
microspora, P. semilanceata var., Sing. 1969 (BnH 29): 247
 = Psilocybe pelliculosa Sing. & Smith
minor, P. fatua f., Pereira-Coutinho 1934 (BSb 9): 209 =
Psathyrella fatua Fr.
mixaensis Heim 1959 (RM 24): 104 *
modesta (Peck) A.H. Smith 1948 (M 40): 700
moelleri Guzmán 1977 (Myc) in press
montana (Pers. ex Fr.) Kumm. 1871 (FP): 71
muliercula Sing. & Smith 1958 (M 50): 142 *
murcida (Fr.) Karst. 1879 (BFI 32): 507; doubtful sp.
musci Clel. & Cheel 1918 (TPR 42): 131; doubtful sp.
muscorum (Orton) Moser 1967 (KK): 239
mutabilis Karst. 1890 (SyF 29): 101 = Naematoloma sp.
mutans McKnight 1971 (BTC 98): 4
myosotis, Ag. (Psilocybe) Fr. 1821-23: 290 = Pholiota
myosotis (Fr.) Sing.

naematolomiformis Guzmán 1977 (BnH) in press
naviculata-viscosa, P. mexicana f., Heim & Cailleux 1967
 (NIC): 144 = P. mexicana Heim f. mexicana
nemophila (Fr.) Gill. 1878 (LH): 586; doubtful sp.
neocaledonica Guzmán & Horak 1978 (Sy 30) in press *
nigrella Peck 1910 (BNS 139): 28
nigripes, P. caerulescens var., Heim 1957 (RM 22): 79 *
nitidipes (Peck) Morgan 1907 (JMy): 253; doubtful sp.

- nolitangere (Fr.) P. Henn. 1900 (NPF 1 (1**)): 235 = Psathyrella nolitangere (Fr.) Pears. & Dennis
notha (Deconica) (Britz.) Sacc. 1887 (SF 5): 1060;
doubtful sp.
- nothofagensis Guzmán & Horak 1978 (Sy 30) in press
novae-zelandiae Guzmán & Horak 1978 (Sy 30) in press
nuciseda (Fr.) Rea 1922 (BB): 366; doubtful sp.
- obscura Peck 1897 (BTC 24): 144 = Psathyrella obscura
(Peck) Guzmán, comb. nov.
- obtusata (Fr.) Kumm. 1871 (FP): 71 = Psathyrella obtusata
(Fr.) A.H. Smith
- obtusissima Kauffm. & Smith 1932 (PMi 17): 194
- ochraeiceps Kauffm. 1925 (PMi 5): 143 = Naematoloma
dispersum (Fr.) Karst.
- ochreatus, Ag. (Psathyra) B. & Br. 1871 (JLS 11): 555 =
Psilocybe sp. ?
- oedipus Mass. 1899 (BmI 153-4): 178
- olivaceotincta Kauffm. 1925 (PMi 5): 144 = Naematoloma
olivaceotincta (Kauffm.) A.H. Smith
- ombrophila, P. caerulescens var., Heim 1973 (RM 37): 183 =
P. caerulescens Murr. var. caerulescens
- omnium-sanctorum Sing. 1969 (BnH 29): 249
- orizabensis Murr. 1918 (M 10): 29 = Psathyrella orizabensis
(Murr.) A.H. Smith
- pallidisporea (Murr.) A.H. Smith 1948 (M 40): 701
- palmigena (B. & C.) Sacc. 1887 (SF 5): 1049 = Psathyrella
palmigena (B. & C.) Guzmán, comb. nov.
- panaeoliformis Murr. 1923 (M 15): 12
- papuana Guzmán & Horak 1978 (Sy 30) in press *
- papyracea (Bolt.) Lange 1939 (FaD 4): 78 = Psathyrella sp.
- parabilis (Deconica) Britz. 1883 (DM): 174; doubtful sp.
- particularis Britz. 1883 (DM): 174; doubtful sp.
- parviducta (Britz.) Sacc. 1895 (SF 11): 72; doubtful sp.
- paupera Sing. 1955 (Sy 9): 404 *
- peckianum (Hypholoma) Kauffm. 1918 (AgM 1): 258 =
Psilocybe sp.
- pediades, Ag. (Psilocybe) Fr. 1821-23: 290 = Agrocybe
pediades (Fr.) Fayod
- peladae Sing. 1969 (BnH 29): 254
- pelliculosa (A.H. Smith) Sing. & Smith 1958 (M 50): 280 *
- pellosperma Vogl., per Laplanche 1894 (DCs): 299;
doubtful sp.
- pennata (Fr.) Pereira-Coutinho 1931 (BSb 7): 340 =
Psathyrella pennata (Fr.) Konr. & Maubl.
- percevalii (B. & Br.) Orton 1969 (NED 29): 80
- pertinax (Fr.) Sacc. 1887 (SF 5): 1044; doubtful sp.
- peruviana Sing. 1959 (M 51): 583
- phillipsii (Geophila) (B. & Br.) Kühn. & Romagn. 1953
(FAC): 339 = Melanotus phillipsii (B. & Br.) Sing.
- phoenix (Fr.) Gill. 1878 (LH): 583; doubtful sp.
- phyllogena (Peck) Peck 1912 (BNS 157): 99
- physaloides (Bull. ex Mérat) Quéf. 1872 (CJV): 256;
doubtful sp.
- pintonii Guzmán 1977 (Myc) in press *

- plana Rick 1930 (Bro 24): 113 = Psathyrella plana (Rick) Guzmán, comb. nov.
- plutonia (B. & C.) Sacc. 1887 (SF 5): 1056 *
- polycephala (Paulet ex Fr.) Peck 1912 (BNS 157): 55 = Psathyrella polycephala (Paulet ex Fr.) A.H. Smith
- polytrichi (Fr.) Sacc. 1887 (SF 5): 1046 = Naematoloma polytrichi (Fr.) Konr.
- polytrichi, P. uda var., Gill. 1878 (LH): 586 = Naematoloma udum (Pers. ex Fr.) Karst.
- polytricophila (Peck) A.H. Smith 1948 (M 40): 703
- praelonga, Ag. (Psilocybe) antillarum var., Fr. sensu Murr. 1918 (M 10): 33 = Panaeolus antillarum (Fr.) Dennis ?
- praetervisa Sing. 1969 (BnH 29): 244
- pratensis Orton 1969 (NED 29): 120
- pteridophytorum Sing. 1959 (M 51): 582
- pulicosa (Mont.) Sacc. 1887 (SF 5): 1056 = Psathyrella pulicosa (Mont.) Guzmán, comb. nov.
- pyrispora (Murr.) A.H. Smith 1948 (M 40): 703
- quebecensis Ola'h & Heim 1967 (Nca 94): 574 *
- recognita (Britz.) Sacc. 1895 (SF 11): 72; doubtful sp.
- reflexa-conica, P. mexicana f., Heim & Cailleux 1967 (NIC): 138 = P. mexicana Heim f. mexicana
- rhodophae (Mont.) Sacc. 1887 (SF 5): 1050 = Psathyrella rhodophae (Mont.) Guzmán, comb. nov.
- rhombispora (Britz.) Sacc. 1895 (SF 11): 72
- rhombispora (Stropharia) Höhnelt 1903 (Am 1): 393 = Psilocybe sp.
- rhomboidospora (Deconica) Atk. 1909 (Am 7): 368 = Psilocybe sp.
- rugosa Vel. 1921 (Ch 3): 586; doubtful sp.
- sabulosa Peck 1897 (BTC 24): 144
- sarcocephala (Fr.) Gill. 1878 (LH): 586 = Psathyrella sarcocephala (Fr.) Sing.
- scatigena (Deconica) (B. & C.) Sacc. 1887 (SF 5): 1058 = Psilocybe sp.
- schoeneti Bresins. 1976 (Ho 35): 104
- sclerotifera (Speg.) Sing. 1969 (BnH 29): 240 *?
- scobicola (B. & Br.) Sacc. 1887 (SF 5): 1048 = Naematoloma scobicola (B. & Br.) Guzmán, comb. nov.
- sellae Bres. & Matt. 1908 (AB 7): 145; doubtful sp.
- semilanceata (Fr. ex Secr.) Kumm. 1871 (FP): 71 *
- semistriata (Deconica) Peck 1898 (ANS 51): 291 = Psilocybe montana (Pers. ex Fr.) Kumm.
- semivestita (B. & Br.) P. Henn. 1900 (NPF 1 (1**)): 235 = Psathyrella semivestita (B. & Br.) A.H. Smith
- semperviva Heim & Cailleux 1958 (RM 23): 352 *
- senex Peck 1888 (ANS 41): 70 = Psathyrella senex (Peck) A. H. Smith
- septembris (Sing.) Sing. 1973 (BS 7): 83
- sepulchrorum (Deconica) Zoll. 1847 (F1): 306; doubtful sp.
- serbica Moser & Horak 1969 (ZP 34): 138 *
- sierrae Sing. 1969 (BnH 29): 240 *
- silvatica (Peck) Sing. & Smith 1958 (M 50): 277 *
- simulans (Karst.) Sacc. 1887 (SF 5): 1055; doubtful sp.

- singeri Guzmán 1977 (BnH) in press *
sordida (Deconica) (Speg.) Sing. 1950 (L 23): 214 =
Agrocybe sp.
spadicea (Schaeff. ex Fr.) Kumm. 1871 (FP): 71 =
Psathyrella spadicea (Schaeff. ex Fr.) Sing.
spadiceo-grisea (Fr.) Boud. 1905-10 (Im 4): 68 =
Psathyrella spadiceo-grisea (Fr.) Maire
sphagnicola A.H. Smith 1946 (JMS 62): 197
squalens (Fr.) Sacc. 1887 (SF 5): 1054; doubtful sp.
squalidella (Peck) Peck 1893 (ANS 46): 55 =
Naematoloma squalidellum (Peck) A.H. Smith
squamosa (Pers. ex Fr.) Orton 1969 (NED 29): 80
squarrosipes Sing. 1959 (M 51): 580
stagnina (Fr.) Lange 1957 (MG 148): 65 = Phaeogalera
stagnina (Fr.) Kühn. 1972 (BSF 88): 144
stercicola Clel. 1927 (TPR 51): 305 = Naematoloma sp.
strictipes Sing. & Smith 1958 (M 50): 141 *
stuntzii Guzmán & Ott 1976 (M 68): 1261 *
subaeruginascens Höhnelt 1914 (SAW 123): 78 *
subaeruginosa Clel. 1927 (TPR 51): 305 *
subagraria Atk. (Am 7): 375 = Psathyrella subagraria
(Atk.) A.H. Smith
subammophila Clel. 1927 (TPR 51): 306; doubtful sp.
subbrevipes A.H. Smith & Hesler 1946 (JMS 62): 195
subcaerulipes Hongo 1958 (JJB 33): 44 *
subcoprophila (Britz.) Sacc. 1895 (SF 11): 72
subcubensis Guzmán 1977 (Myc) in press *
subericaea (Fr.) Sacc. 1887 (SF 5): 1045 = Naematoloma
subericaeum (Fr.) Sing.
subhyperella Sing. 1973 (BS 7): 83
submaculata Atk. 1909 (Am 7): 375 = Psathyrella
submaculata (Atk.) A.H. Smith
subuda (Britz.) Sacc. 1895 (SF 11): 72 =
Naematoloma udum (Pers. ex Fr.) Karst. ?
subuda Clel. 1934 (TPR 58): 212; doubtful sp.
subviridis (B. & C.) Sacc. 1887 (SF 5): 1051 =
Naematoloma subvirida (B. & C.) A.H. Smith
subviscida (Peck) Kauffm. 1918 (AgM): 275
subyungensis Guzmán 1977 (Myc) in press *
sullivantii (Mont.) Sacc. 1887 (SF 5): 1047 =
Psathyrella sullivantii (Mont.) Guzmán, comb. nov.
- taediosa (Kalch.) Sacc. 1887 (SF 5): 1044; doubtful sp.
tasmaniana Guzmán & Watling 1977 (NED) in press *
tegaris (Schum. ex Fr.) Gill. 1878 (LH): 585;
doubtful sp.
tenax (Geophila) (Fr.) Kühn. & Romagn. 1953 (FAC): 338;
doubtful sp.
testaceo-fulva (Britz.) Sacc. 1887 (SF 5): 1049;
doubtful sp.
thrausta (Schulz. ex Kalch.) Bon 1969 (BSF 85); pl. 182
tibetensis Mass. 1906 (BmI 4): 93 = Agrocybe tibetensis
(Mass.) Guzmán, comb. nov.
- togoënsis P. Henn. 1891 (EBJ 14): 353; doubtful sp.
tomentosa (Murr.) A.H. Smith 1948 (M 40): 705
torpens (Fr.) Pereira-Coutinho 1931 (BSB 7): 340 =
Psathyrella torpens Fr. ?

- tortipes Speg. 1898 (ABA 6): 151 = Naematoloma tortipes (Speg.) Guzmán, comb. nov.
- tortipes Speg. sensu Rick 1961 (Ih 8): 438 = Naematoloma subumbonatescens (Murr.) Sing.
- tristis P. Henn. 1901 (H 40): 330; doubtful sp.
- tropicalis (Deconica) Speg. 1891 (BCO 11): 429 = Agrocybe tropicalis (Speg.) Guzmán, comb. nov.
- tuberosa (Karst.) Sacc. 1905 (SF 17): 90 = Psathyrella sp.
- turficola Favre 1939 (BSF 55): 196 = Psilocybe atrobrunnea (Lasch) Gill.
- uda (Pers. ex Fr.) Gill. 1878 (LH): 586 = Naematoloma udum (Pers. ex Fr.) Karst.
- umbonata, P. squalidellus var., Peck 1912 (BNS 157): 98 = Naematoloma squalidellum (Peck) A.H. Smith
- umbonatescens (Stropharia) (Peck) Sacc. 1887 (SF 5): 1021 = Psilocybe luteonitens (Vahl ex Fr.) Parker-Rhodes
- umbrospora Vel. 1921 (Ch 3): 586; doubtful sp.
- unicolor Peck 1900 (ANS 53): 845 = Psathyrella camptopoda (Peck) A.H. Smith
- urticicola (B. & Br.) P. Henn. 1900 (NPF 1 (1**)): 235; doubtful sp.
- uruguayensis Sing. ex Guzmán 1977 (Myc) in press
- uspanapensis Guzmán 1977 (BnH) in press *
- vaccinii, P. agrariella var., Charles 1931 (DAB 258): 12; doubtful var.
- valdiviensis Sing. 1969 (BnH 29): 251
- vanhoeffenii (P. Henn.) Sacc. 1912 (SF 21): 219; doubtful sp.
- velifera (Geophila) Favre 1955 (Cza): 204 = Psilocybe crobula (Fr.) Lange ex Sing. ?
- venenata (Imai) Imazeki & Hongo 1957 (JJB 32): 146 *
- venezuelana Dennis 1961 (KB 15): 137
- vernalis Vel. 1921 (Ch 3): 587; doubtful sp.
- vialis Murr. 1923 (M 15): 11 = Naematoloma vialis (Murr.) Guzmán, comb. nov.
- vicina (Fr.) Sacc. 1887 (SF 5): 1056; doubtful sp.
- virescens Mass. 1892 (BF): 367; doubtful sp.
- vomiticola, P. coprophila var., Kill. 1936 (DbA 20): 76
- washingtonensis A.H. Smith 1946 (JMS 62): 199
- wassonii Heim 1958 (RM 23): 119 = P. muliercula Sing. & Smith
- weldeni Guzmán 1977 (BnH) in press *
- wrightii Guzmán 1977 (Myc) in press *
- xeroderma Huijism. 1961 (Pe 2): 94
- yungensis Sing. & Smith 1958 (M 50): 142 *
- zapotecorum Heim 1957 (RM 22): 77 *
- zonalis Vel. 1921 (Ch 3): 589; doubtful sp.

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PSILOCYBE MAMMILLATA IN FLORIDA

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SUMMARY

Psilocybe mammillata a probably hallucinogenic fungus, is reported for the first time from the United States (Florida). It was previously known only from Jamaica. Discussions of the relationships of this species with P. fagicola, P. yungensis, P. cordispora, P. plutonia and P. hoogshageni are presented. All of these related species are known from Mexico or South America.

Psilocybe mammillata (Murr.) Smith has until now been known only from a subtropical forest at an elevation of 1,500 m, in Jamaica, where it was collected by Murrill and was described by him as Atylospora mamillata Murr. (Murrill, 1918). Later in the same paper he changed this species to the genus Psathyra. Smith (1948) studied Murrill's type and concluded that it was a Psilocybe. He also found that Psathyra cinchonensis (Murr.) Murr. (= Atylospora cinchonensis Murr.), from the same locality was synonymous with it. Studies on the types (in NY) of both of Murrill's species made by the senior author of the present paper confirmed the above synonymy.

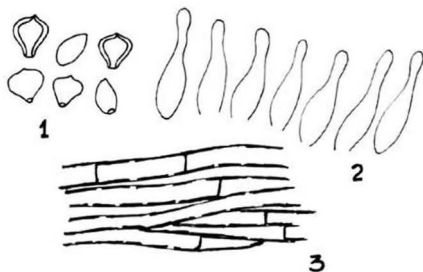
Psilocybe mammillata was collected by Thiers in Florida in 1958 and has been studied by the senior author. Thiers' material checks well with the type (Murrill 608, NY). This is the first record of P. mammillata in the United States and only the second report of this species in the literature.

The material studied from Florida: Thiers 5067 SFSU, Florida, Highlands Hammock State Park, Aug. 6, 1958, gregarious in humus along trail, has the following features: Pileus 10-15 mm broad and 10-15 mm high, conic-apiculate, brown, darker with age; stipe crooked, reddish brown with white spots toward the subbulbous base; both pileus and stipe seem slightly bluing to darker. The spores are (4.9) 5.5-6.5 (8) x 4.4-5.5 x 3.5-4 μ m, rhombic to subtriangular in face view, subelliptic in side view; walls thick, brown to yellowish in KOH, with a broad germ pore (Fig. 1). Cheilocystidia 12-17 x 4-5.5 μ m, abundant, forming a sterile band at the edge of the lamellae, hyaline, fusoid-ventricose with long necks 3.3-5 x 1-2.5 μ m (Fig. 2). Pleurocystidia none or similar to the cheilocystidia, near the edge of the lamellae. Subhymenium hyaline to brownish to brown-orangish, hyphae not incrusted, 3.3-5.5 μ m in diameter. Lamellar trama parallel, brownish to brownish orange, hyphae thick-walled, 6-15 μ m in diameter, irregularly incrusted (Fig. 3). Epicutis differentiated as a subgelatinous, thin layer of subhyaline to brownish-orange, incrusted hyphae. Hypodermium similar to the lamellar trama. Clamp connections common.

This fungus is closely related to the following hallucinogenic fungi: *P. fagicola* Heim, *P. yungensis* Sing. & Smith, *P. cordispora* Heim, and *P. hoogshageni* Heim, and with the probably hallucinogenic species *P. plutonia* (B. & C.) Sacc. It differs from these species, however, in the size of the spores and in shape and size of the cheilocystidia as in shown in Table 1.

All species related to *P. mammillata* have rhombic or subrhombic, thick-walled spores, conic or papillate pilei and context with brown-orangish pigment incrusted on the walls of the hyphae, and all grow in subtropical forests in America. These relationships have been established from a study of the types (in PC, MICH, NY and FH) and from an analysis of the related bibliography (Heim, 1959; Heim & Wasson, 1958; Singer & Smith, 1958; Smith, 1948 and Dennis, 1961) as well.

Psilocybe fagicola is only known from the State of Hidalgo in Mexico (Heim 1959) and differs from all of the above mentioned species, including *P. mammillata*, in the more or less rhizomorphic base of the stipe. *P. yungensis*, described from Bolivia (Singer & Smith, 1958) and from the State of Oaxaca in Mexico (Heim & Wasson, 1958), differs from the others in the irregular form of the cheilocystidia, which do not have necks. *P. cordispora*, *P. hoogshageni* and *P. plutonia* differ from *P. mammillata* in the size of the spores and cheilocystidia; the first two species are known only from the State of Oaxaca in Mexico (Heim & Wasson, 1958), and the last from Cuba and Venezuela (Dennis, 1961).



Figs. 1-3. *Psilocybe mammillata* (Murr.) Smith. 1. Spores. 2. Cheilocystidia. 3. Tramal hyphae. All from Thiers 5067.

Of the fungi mentioned so far, *P. fagicola*, *P. yungensis*, *P. cordispora* and *P. hoogshageni* are known to be hallucinogenic, but the hallucinogenic properties of *P. mammillata* and *P. plutonia* have not yet been demonstrated. The close resemblance of these two species to the others, however, as well as the dark color of their pilei and stipes seemingly resulting from the bluing of fresh specimens, make it very probable that they also are hallucinogenic.

Table 1. Comparison of *Psilocybe mammillata* (1) with its related species: *P. fagicola* (2), *P. yungensis* (3), *P. cordispora* (4), *P. plutonia* (5) and *P. hoogshageni* (6)

	spores	cheilocystidia
1	(4.9-)5.5-6.5(-8) μm long.	12-17 x 4-5.5 μm
2	(4.9-)5.5-6(-6.5) μm long.	6-13 x 2.5-3.3 μm
3	(4.4-)5-6(-6.6) μm long.	16-27.8 x 4-5 μm
4	(5-)5.5-7(-8.8) μm long.	25-35 x 5-6 μm
5	(3.7-)4.5-6.7 μm long.	20-30 x 5-10 μm
6	(4.9-)6.5-7.7(-9.6) μm long.	16.5-27 x 4.4-6.6 μm

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HOST-GENUS KEYS TO THE HYPODERMATACEAE OF CONIFER LEAVES

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SUMMARY

Universal keys to the described hypodermataceous fungi attacking conifer leaves are presented. They are arranged alphabetically by host-genus. Host species are listed under the keyed-out fungus species. Pertinent literature is cited which enables one to find taxonomic descriptions of the fungus species. The keys make diagnosis of hypodermataceous fungi more rapid.

INTRODUCTION

The keys, originally adapted from Darker's (1932) fungus species keys, have been arranged by host genus and have been modified to keep pace with taxonomic developments. Although we have retained the commonly used family name, Hypodermataceae, it may be more phylogenetically correct to place these species in the tribe Hypodermateae of the Rhytismataceae (Korf 1973).

The keys follow Darker's (1967a) species concepts and include all those described. Taxonomic descriptions of species can be found in Darker (1932, 1967a) or in the references cited in the key after the species. Measurements given in parenthesis are consistent deviations recorded from published sizes.

After each keyed-out species, the hosts are listed, except where this list would be long, such as with *Lophodermium pinastri*. Hosts, in addition to the taxonomic

citings, are derived from Teng (1936), Durrieu (1957), Benito Martinez and Torres Juan (1965), Ouellette and Magasi (1966), Czabator et al. (1971), Shaw (1973) and our own records. Some personal comments by Darker on certain species are included as footnotes.

One should examine conifer leaves carefully for Hypodermataceae, because frequently other fungi are associated with Hypodermataceae, or fungi may be mistaken for Hypodermataceae. Ziller (1968) summarized these for Abies and Ziller and Funk (1973) for Pinus. To these, we add Darkera (Whitney et al. 1975) which occurs on Abies or Picea, and Lophophacidium (Reid and Cain 1962) on Picea. In addition, Hypodermataceae in different geographic areas likely have other fungal associates.

Abies

- (1) Ascomata nervisequious (averaging more than 5 times longer than wide); parasitic (2)
- Ascomata elliptic to elongate (averaging less than 5 times longer than wide); saprophytic.....(10)
- (2) Spores 2-fusoid to 2-clavate (Isthmiella)..... (3)
- Spores not 2-fusoid to 2-clavate (except rarely in Virgella robusta)..... (5)
- (3) Asci 4-spored, 14-16 μ wide; pycnidia lacking
Isthmiella quadrispora
 (on A. lasiocarpa)
- Asci 8-spored, 20-30 μ wide; pycnidia in epiphyllous concolorous blisters (4)
- (4) Spores 35-45 μ long with isthmus 1-1.5 μ wide; pycnidia tend to be either side of the midrib
 Isthmiella abietis
 (on A. lasiocarpa)
- Spores 45-55 μ long with isthmus 3-4 μ wide; pycnidia tend to be along the midrib.... Isthmiella faullii
 (on A. balsamea)

- (5) Spores 27-36 μ long, rarely slightly constricted in the middle.....Virgella robusta
(on A. amabilis, A. concolor, A. grandis, A. magnifica)
- Spores 68-110 μ long, not constricted in the middle.....(6)
- (6) Asci 4-spored; pycnidia punctiform.....Lirula punctata
(on A. amabilis, A. concolor, A. grandis,
A. lasiocarpa, A. mariesii, A. procera)
- Asci 8-spored; pycnidia in epiphyllous rows.....(7)
- (7) Spores 6-7 μ wide; pycnidia in 2 concolorous rows..... Lirula mirabilis
(on A. balsamea)
- Spores 2-5 μ wide; pycnidia in one row.....(8)
- (8) Pycnidial blisters in one concolorous row, rarely furcate; Europe, Japan; asci 95-135 μ long, spores 2-2.5 x 68-75 μ Lirula nervisequia
(on Abies spp.)
- Pycnidial blisters in one light brown to black row; North America; asci longer, 130-208 μ , spores wider..... (9)
- (9) Pycnidial blisters dark, becoming light to concolorous after sporulation; western North America; ascomata 0.5-1 mm wide, dark grey..Lirula abietis-concoloris
(on A. amabilis, A. concolor, A. grandis,
A. lasiocarpa, A. procera)
- Pycnidial blisters light, becoming dark after sporulation; eastern North America; ascomata 0.4-0.6 mm wide..... Lirula nervata
(on A. balsamea)
- (10) Spores 3-4 μ wide; subepidermal...Lophodermium decorum
(on A. grandis, A. lasiocarpa)
- Spores 1.5-3.0 μ wide; subcuticular or intraepidermal..... (11)

- (11) Follows nervisequious Hypodermataceae preventing or inhibiting formation of their hysterothecia; pycnidial states undescribed.....(12)

Not known to follow or inhibit other Hypodermataceae; pycnidial states described.....(13)

- (12) Ascomata amphigenous, black, subcuticular; spores 1.5-2.0 x 85-96 μ , septate in mature ascus when boiled in lactic acid; paraphyses uncinately-contortedLophomerum autumnale
(on A. amabilis, A. balsamea, A. concolor, A. lasiocarpa, A. magnifica, A. procera)

Ascomata hypophyllous, dark grey, intraepidermal; spores 2-2.5 x 95-120 μ , not septate in mature ascus; paraphyses not uncinatelyLophodermium consociatum
(on A. amabilis)

- (13) Ascomata subcuticular, elongate, over 2 mm long; mature paraphyses conspicuously helical, not swollen at tips..... Lophodermium uncinatum
(on A. amabilis, A. lasiocarpa)

Ascomata intraepidermal, elliptic, less than 2 mm long; mature paraphyses not conspicuously helical, slightly swollen at tips; not known on A. amabilis (14)

- (14) Ascus 12-16 μ wide; hysterothecia on evenly discolored needles without bands or lines, rarely amphigenous, 0.3-0.4 x 0.5-0.7 mm; pycnidia black Lophodermium lacerum
(on A. balsamea, A. grandis)

Ascus 10-12 μ wide; hysterothecia on light bands delimited by black lines, usually amphigenous, 0.4-0.8 x 0.6-1.9 mm; pycnidia concolorous with black margin..... Lophodermium piceae
(on A. alba, A. balsamea, A. concolor, A. lasiocarpa)

CedrusLophodermium cedrinum(on C. atlantica)Chamaecyparis

Ascomata subepidermal; asci 5-5.5 x 50-60 μ ; spores
0.5-0.7 x 40-50 μ Lophodermium chamaecyparisii
(on C. obtusa)

Ascomata subcuticular; asci 15-17 x 110-130 μ ;
spores 2-3 x 70-90 μ Lophodermium juniperi
(on C. thyoides)

Cunninghamia

(1) On cone scales; spores 13-25 μ long, soon septate;
paraphyses straight..... Hypoderma handelii
(on C. lanceolata)

On foliage; spores 24-72 μ long, non-septate;
paraphyses may be uncinatate or forked.....(2)

(2) Ascomata linearly arranged; spores bifusiform
2.5-6.5 x 24-45 μ .. Soleella cunninghamiae (Saho and
Zinno 1972)
(on C. lanceolata)
(= Bifusella cunninghamicola Ogimi
and Korf 1972)

Ascomata randomly arranged; spores
tapered 1.5-2 x 56-72 μ Lophodermium petrakii
(on C. lanceolata)

Fitzroya

Hypoderma pilgerodendri
(Butin 1970)

(on F. cupressoides)

JuniperusLophodermium juniperi

(on J. communis, J. horizontalis, J. sabina,
J. scopulorum, J. virginiana)

Larix

Fruiting on fallen needles; ascus 8-spored, 9-11 μ wide; spores 1.5-2 μ wide; conidia bacillar; paraphyses uncinatae; hysterothecia generally scattered
..... Lophodermium laricinum
(on L. decidua, L. laricina)

Fruiting on overwintered, attached needles; ascus mostly 4-spored, 20-24 μ wide; spores 6-6.5 μ wide; conidia elongated pyriform; paraphyses straight; hysterothecia more or less in a continuous row
..... Hypodermella laricis
(on L. laricina, L. occidentalis)

LibocedrusLophodermium juniperi

(on L. decurrens)

Picea

- (1) Spores distinctly 2-fusoid, 8-8.5 μ wide; asci 24-28 μ wide..... Isthmiella crepidiformis
(on P. engelmannii, P. glauca, P. mariana)

Spores filiform to clavate-filiform, 1-3.5 μ wide; asci less than 24 μ wide..... (2)

- (2) Ascomata regularly nervisequious (typically more than 5 times longer than wide); spores 2.5-3.5 μ wide..... (3)

Ascomata elliptic or elongate, never nervisequious; spores narrower..... (4)

- (3) Asci 100-132 (180) μ long; ascospores 56-68 (125) μ long..... Lirula macrospora
(on Picea spp.)

- Asci 80-100 μ long; ascospores 25-35 μ long
 Lirula brevispora
 (Ziller 1969)
 (on P. engelmannii, P. glauca)
- (4) Spores septate in mature ascus (Lophomerum Ouellette
 of Magasi)..... (5)
- Spores aseptate in mature ascus..... (6)
- (5) Ascomata subcuticular..... Lophomerum septatum
 (on P. sitchensis)
- Ascomata intraepidermal..... Lophomerum darkeri
 (on P. glauca)
- (6) Ascomata subepidermal; clypeus 165-180 μ thick; asci
 145-165 μ long; one collection from California
 only..... Lophodermium crassum
 (on P. breweriana)
- Ascomata intraepidermal; clypeus 75-100 μ thick;
 asci 110-130 μ long; common and cosmopolitan; small
 hysterothecia generally produced on fallen foliage
 Lophodermium piceae
 (on Picea spp.)

Pilgerodendron

- Asci > 175 μ long; 8-spored... Hypoderma pilgerodendri
 (Butin 1970)
 (on P. uriferum)
- Asci < 175 μ long; 4-spored.....Hypoderma heterosporum
 (Butin 1970)
 (on P. uriferum)

Pinus

- (1) Ascomata inconspicuous to invisible, appearing brown
 to concolorous with needle surface.....(2)
- Ascomata conspicuous, appearing brown, dark grey
 to black.....(9)

- (2) Ascomata small, 0.20-0.25 mm wide, dark brown, sub-epidermal; ascospores 20-23 μ long, slightly constricted in middle..... Ploioderma pedatum (on P. radiata)

Ascomata wider, light brown to concolorous, subhypodermal; ascospores 23-90 μ long, not constricted in middle..... (3)

- (3) Ascospores 68-90 μ long (4)

Ascospores 23-60 μ long (5)

- (4) Ascomata 0.2-0.3 mm wide, brownish black, frequently fused laterally into compound hysterothecia Lophodermella conjuncta (on P. nigra, P. sylvestris)

Ascomata 0.3-0.6 mm wide, concolorous with needle surface, not fused laterally.. Lophodermella cerina (on P. contorta, P. elliottii, P. ponderosa, P. taeda)

- (5) Ascomata 0.4-0.8 mm long, concolorous, at maturity usually forming shallow depressions or may be erumpent; ascospores (4) 6-8 x 45-60 μ Lophodermella concolor (on P. banksiana, P. contorta, P. sylvestris)

Ascomata averaging over 1 mm long, darker than needle, at maturity often forming depressions; ascospores 2.5-6 x 23-53 μ (6)

- (6) Ascus width 14-18 μ ; parasitic on 5-needle pines; ascospores 4-6 x 42-50 μ Lophodermella arcuata (on P. albicaulis, P. lambertiana)

Ascus width 11-15 μ ; parasitic on 2- and 3-needle pines; ascospores 2.5-5 x 23-53 μ (7)

- (7) Ascomata width 0.55-0.68 mm; paraphyses septate, 2-3.5 μ diameter..... Lophodermella morbida (Staley & Bynum 1972) (on P. attenuata, P. ponderosa)

- Ascomata width 0.28-0.44 mm; paraphyses simple,
1 μ diameter.....(8)
- (8) Ascomata 2-20 mm long; asci 4- to 8-spored; spores
4-5 x 27-35 μ Lophodermella sulcigena
(on P. mugo, P. nigra, P. sylvestris)
- Ascomata 1-8 mm long; asci 8-spored; spores 3-4 x 40-
50 μ (ascomata often strongly erumpent!)
..... Lophodermella montivaga*
(on P. contorta, P. flexilis, P. monticola,
P. radiata, P. sylvestris)
- (9) Spores distinctly 2-fusoid or 2-clavate.....(10)
Spores not distinctly 2-fusoid or 2-clavate.....(13)
- (10) Parasitic on 5-needle pines; ascomata 0.4-0.9 mm wide,
subcuticular, lacking paraphyses
..... Bifusella linearis
(on P. albicaulis, P. flexilis, P. monticola,
P. strobus)
- Parasitic on 2- and 3-needle pines; ascomata 0.15-
0.30 mm wide, subepidermal, with paraphyses...(11)
- (11) Spores distinctly constricted in middle, 40-60 μ
long; paraphyses septate..... Soleella striiformis
(on P. coulteri, P. pinaster, P. sabiniana,
P. torreyana)
- Spores faintly constricted in middle, 20-52 μ long;
paraphyses septate or simple.....(12)
- (12) Spores 4-6 x 36-52 μ ; asci 125-180 μ long
..... Ploioderma lowei
(Czabator 1976)
(on P. elliottii)
- Spores 4-8 x 20-30 μ ; asci 108-128 μ long
..... Ploioderma pedatum
(on P. radiata)

* "May prove to be synonymous with L. sulcigena"
(G.D. Darker).

- (13) Spores septate in mature ascus..... (14)
 Spores not septate in mature ascus..... (16)
- (14) Asci 18-24 x 125-180 μ ; spores 4-6 μ wide..... (12)
 Asci 30-60 x 140-300 μ ; spores 6-18 μ wide..... (15)
- (15) Asci 40-60 x 280-300 μ ; spores 10-18 x 175-210 μ ;
 reported from Spain only....Elytroderma hispanicum*
 (on P. halepensis)
 Asci 30-45 x 140-240 μ ; spores 6-8 x 90-118 μ ; reported
 from North America only..... Elytroderma deformans
 (on Pinus spp.)
- (16) Asci characteristically 4-spored; spores over 4 μ
 wide..... (17)
 Asci characteristically 8-spored; spores varying in
 widths..... (18)
- (17) Asci 24-30 x 164-189 μ ; spores 8-11 x 28-32 μ ; sub-
 hypodermal..... Ploioderma hedgcockii
 (on Pinus spp., eastern North America)
 Asci 14-15 x 125-160 μ ; spores 4-4.5 x 33-45 μ ;
 subepidermal..... Davisomycella limitata
 (on P. radiata)
- (18) Ascomata lacking paraphyses; spores wide, 7.5-14 μ
 Bifusella pini
 (on P. flexilis, P. monophylla)
 Ascomata with paraphyses; spores narrow, < 7 μ wide
 (19)
- (19) Spores 3-7 μ wide (20)
 Spores 0.8-3 μ wide (33)

* "Probably synonymous with Elytroderma deformans as suggested to Torres" (G.D. Darker).

- (20) Spores under 60 μ long; slightly 2-clavate in some species..... (21)
- Spores over 60 μ long, not constricted in the middle..... (30)
- (21) Ascomata entirely subcuticular; pycnidia black, appearing similar to ascomata..... (22)
- Ascomata subepidermal (partly subcuticular in Meloderma desmazierii); pycnidia rare and concolorous..... (23)
- (22) Spores large, 6-7 x 35-45 μ Hypoderma mexicanum*
(Wolf 1951)
(on P. leiophylla)
- Spores small, 4-6 x 24-36 μ Bifusella saccata
(on P. albicaulis, P. edulis, P. flexilis)
- (23) Width of paraphyses 2-3.5 μ (24)
- Width of paraphyses 0.5-1.5 μ (25)
- (24) Spore sheath narrow, 2-4 μ (7)
- Spore sheath wide, 7 μ (30)
- (25) Ascomata light in color; spores frequently 2-clavate
..... Ploioderma pedatum
(on P. radiata)
- Ascomata dark; spores not constricted in the middle
..... (26)
- (26) Ascospores broadly clavate (Davisomycella)..... (27)
- Ascospores bacillar to fusiform, or slightly constricted in the middle (Meloderma, Ploioderma)
..... (28)

* "May be synonymous with Bifusella saccata" (G.D. Darker).

- (27) Ascomata on narrow brown zone in middle of green needle; asci 150-195 μ long; spores 24-38 μ long; subepidermal.... Davisomycella lacrimiformis (on P. attenuata)

Ascomata not on brown zone of green needle; asci 87-102 μ long; spores 36-56 μ long; subcuticular in middle but subepidermal at margin
..... Davisomycella hiratsukae
(on P. pumila)

- (28) Ascospores 4-6 x 36-52 μ (12)

Ascospores 3-6 x 24-38 μ (29)

- (29) Ascomata elliptic, "surrounded typically by a narrow grayish zone"; primordium of slit obvious, bordered by papillate, concolorous cells; subepidermal to subcuticular; on 2-, 3- and 5-needle pines..... Meloderma desmazierii (on Pinus spp.)

Ascomata elongate-fusoid, not surrounded by a grayish zone; no obvious primordium of slit; subepidermal; on 2- and 3-needle pines..... Ploioderma lethale (on Pinus spp., southeast U.S.A.)

- (30) Ascomata irregularly sinuous to bi-furcate; slit band distinct; paraphyses 2-3 μ wide; ascospores filiform, 3-4.5 x 120-170 μ
..... Davisomycella ponderosae
(Staley 1964; Dubin & Staley 1969)
(on P. ponderosa)

Ascomata elliptic to fusiform, mostly on tawny areas of living needle; slit band not distinct; paraphyses 1-1.5 μ wide; ascospores clavate, 60-130 μ long..... (31)

- (31) Ascomata subepidermal to subhypodermal; spores attenuated in lower half..... Davisomycella medusa (on P. contorta, P. jeffreyi, P. ponderosa)

Ascomata subepidermal; spores not attenuated in lower half..... (32)

- (32) On 1+ needles (needles 1 to 2 years old); asci maturing from May* onward..... Davisomycella ampla*
(on P. banksiana, P. contorta)
- On 2+ needles (needles 2 to 3 years old); asci maturing from July* onward.. Davisomycella montana*
(on P. contorta)
- (33) Ascomata with well-defined primordium of slit, subepidermal; on 2-, 3- and 5-needle pines.....(34)
- Ascomata without conspicuous primordium of slit; known on 5-needle pines only.....(36)
- (34) Ascomata long, 1-45 mm; frequently sinuous or bifurcate.....(30)
- Ascomata short, 0.8-2.0 mm; elliptic.....(35)
- (35) Labial band, pycnidia present. Spores not tapered and gelatinous sheath absent
..... Lophodermium pinastri
(on Pinus spp.)
- = L. pini-pumilae**
(with asci 7-11 x 67-104 μ)
= L. pini-excelsae**
- Labial band, pycnidia absent. Spores tapered with gelatinous sheath..... Davisomycella fragilis
(Darker 1967b)
- (on P. banksiana)
- (36) Ascomata 0.6-0.85 mm long; subcuticular; clypeus 15-37 μ thick; asci 11-13 μ wide; spores 2-3 μ wide; pycnidia conspicuous.... Lophodermium nitens
(on Pinus spp.)

* D. montana may prove to be synonymous with D. ampla: they are morphologically indistinguishable from each other and both were observed to mature in May in British Columbia on 1+ to 5+ year-old needles. See Ziller and Funk 1973.

** "Probably synonymous with Lophodermium pinastri" (G.D. Darker); but see Millar and Watson 1971, and Staley 1975, for additional information.

Ascomata 0.9-1.75 mm long; subepi- to subhypodermal;
 clypeus 60-75 μ thick; asci 8-9 μ wide; spores
 0.8-1.0 μ wide; pycnidia unknown
 Lophodermium durilabrum
 (on P. monticola)

Podocarpus

Hypoderma podocarpi
 (Butin 1970)

(on P. nubigenus, P. salignus)

Thuja

Asci sessile, 4-spored; spores 1.5-2 x 85-115 μ
 Lophodermium thujae
 (on T. occidentalis)

Asci pedicellate (pedicel 65-100 μ long), 8-spored;
 spores 3-4 x 19-25 μ Hypoderma thujae
 (on T. occidentalis)

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NIEBLA, A NEW GENERIC NAME FOR THE LICHEN GENUS DESMAZIERIA (Ramalinaceae)

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SUMMARY

The new generic name Niebla Rundel & Bowler is proposed to replace the genus name Desmazieria Mont., a homonym for the earlier described genus Desmazeria Dumortier (Poaceae). Thirteen taxa are transferred from Desmazieria and Ramalina into Niebla. One of these is the new combination Niebla robusta (R.H. Howe) Rundel & Bowler whose basionym is Ramalina combeoides Nyl. var. robusta R.H. Howe.

NIEBLA Rundel et Bowler, gen. nom. nov.

Desmazieria Mont., Ann. Sci. Nat. 18: 303. 1852.

Ramalina section Desmazieria (Mont.) Stizenb., Bericht
Thätigkeit St. Gallisch. naturw. Gesellsch. 176.
1862.

Ramalina section Corticatae Stnr. Oesterr. Botan.
Zeitschrift 54: 351. 1904.

Ramalina section Ellipsosporae series Desmazierae (Mont.)
R.H. Howe, Bryologist 16: 67. 1913.

Ramalina subgenus Desmazieria (Mont.) Du Rietz, Svensk.
bot. Tidskr. 20(2): 1926.

Desmazieria section Desmazieria series Cylindrica Follm.
& Hun., Willdenowia 5: 207. 1969.

Desmazieria section Desmazieria series Complanata Follm.
& Hun., Willdenowia 5: 207. 1969.

The generic name Desmazieria was proposed in 1852 by Montagne in honor of J.B.H.J. Desmazières (1796-1862), a French botanist. However, this generic name is a homonym

of a previous name, Desmazeria Dumortier, and is therefore illegitimate. Dumortier described the grass genus Desmazera in 1822 in honor of the same J.B.H.J. Desmazières. The following year he corrected the spelling to Desmazeria. Despite the opinions of Follmann (1976), the lichen genus Desmazieria Mont. is clearly an orthographic variant of the earlier Desmazeria Dumortier (Poaceae). It is very clear from the International Code of Botanical Nomenclature, therefore, that Desmazieria Mont. is a later homonym and is invalid. Since none of the species we consider to be included in this genus is the type of a validly described genus, we propose the new name Niebla for this group of species. Niebla comes from the Spanish word for fog or mist, an appropriate epithet for the ecological habitat of this group.

A world monograph of Niebla in preparation will discuss the generic limits of this group in detail (Rundel and Bowler, in prep.). Briefly, Niebla differs from Ramalina sens. str. by having principally palisade cell lines in the exterior cortex usually overlying supportive tissue, with chondroid supportive strands free in the medulla. The pycnidia in this genus are black and usually abundant. The spores are bilocular as are all genera in the Ramalinaceae. There are several variations in cortical type, ranging from a single layered cortex immersed in a gelatinous matrix, to a faint palisade array blending into a very thick supportive layer. Chondroid strands are not present as major structures in the medulla of some species aggregates. This anatomical variation is discussed in detail in our forthcoming monograph, and does not warrant further generic separation in our opinion. The majority of species of Niebla also share distinctive chemical similarities. Many species which have been placed in Desmazieria Mont. belong in Ramalina sens. str. or allied genera. Therefore, we propose here only new combinations for validly published taxa of Desmazieria and Ramalina which fit within our concept of Niebla. Complete discussions, keys, synonymies, and descriptions of new taxa will be included in our monograph.

Niebla bourgeana (Mont.) Rundel & Bowler, comb. nov.
 Basionym: Ramalina bourgeana Mont., Plant. Canar.
 1118. 1845. Synonym: Desmazieria bourgeana (Mont.)
 Follm., Philippia 3/2: 86. 1976.

Niebla cephalota (Tuck.) Rundel & Bowler, comb. nov.
 Basionym: Ramalina ceruchis (Ach.) De Not. f.
cephalota Tuck., Synops. N.A. Lich. 1: 21. 1832.
 Synonym: Desmazieria cephalota (Tuck.) Follm. & Hun.,
 Willdenowia 5: 208. 1969.

Niebla ceruchis (Ach.) Rundel & Bowler, comb. nov.
 Basionym: Parmelia ceruchis Ach., Method. Lich. 260.
 1803. Synonym: Desmazieria ceruchis (Ach.) Trev.,
 Flora 54: 51. 1861.

- Niebla combeoides* (Nyl.) Rundel & Bowler, comb. nov.
 Basionym: Ramalina combeoides Nyl., Bull. Soc. Linn. Normand., Ser. 2, 4: 107. 1870. Synonym: Desmazieria combeoides (Nyl.) Follm. & Hun., Willdenowia 4: 227. 1966.
- Niebla flaccescens* (Nyl.) Rundel & Bowler, comb. nov.
 Basionym: Ramalina flaccescens Nyl., Bull. Soc. Linn. Normand., Ser. 2, 4: 109. 1870. Synonym: Desmazieria flaccescens (Nyl.) Follm. & Hun., Willdenowia 5: 208. 1969.
- Niebla homalea* (Ach.) Rundel & Bowler, comb. nov.
 Basionym: Ramalina homalea Ach., Lich. Univ. 598. 1810. Synonym: Desmazieria homalea (Ach.) Mont., Ann. Sci. Nat. Bot., Ser. 3, 18: 304. 1852.
- Niebla josecuervoi* (Rundel & Bowler) Rundel & Bowler, comb. nov. Basionym: Desmazieria josecuervoi Rundel & Bowler, Bryologist 75: 505. 1972.
- Niebla maciformis* (Del.) Rundel & Bowler, comb. nov.
 Basionym: Parmelia maciformis Del., Descr. Egypte 2: 288. 1813. Synonyms: Ramalina maciformis (Del.) Bory, Dict. class. Hist. nat. 14: 458. 1828. Desmazieria maciformis (Del.) Follm., Philippia 3/2: 87. 1976.
- Niebla pulchribarbara* (Rundel & Bowler) Rundel & Bowler, comb. nov. Basionym: Desmazieria pulchribarbara Rundel & Bowler, Bryologist 75: 505. 1972.
- Niebla robusta* (R.H. Howe) Rundel & Bowler, comb., sp. et stat. nov. Basionym: Ramalina combeoides Nyl. var. robusta R.H. Howe, Bryologist 16: 106. 1913. Holotype: Palmer s.n. 1890, Agiabampo, Mexico (US!).
- Niebla tigrina* (Follm.) Rundel & Bowler, comb. nov.
 Basionym: Ramalina tigrina Follm., Willdenowia 4: 227. 1966. Synonym: Desmazieria tigrina (Follm.) Follm. & Hun., Willdenowia 5: 208. 1969.
- Niebla subwebbiana* (Nyl.) Rundel & Bowler, comb. nov.
 Basionym: Ramalina scopulorum R. subwebbiana Nyl., Bull. Soc. Linn. Normand., Ser. 2, 4: 158. 1870. Synonym: Ramalina subwebbiana (Nyl.) Hue, Nouv. Arch. Mus. III. 2. 267. 1890.
- Niebla webbii* (Mont. in Webb.) Rundel & Bowler, comb. nov.
 Basionym: Ramalina webbii Mont. in Webb, Hist. Nat. Iles Canar. 3(2): 100. Pl. 6, fig. 4. 1840.

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ON CALOCYBE NAMES

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SUMMARY

The combinations *Calocybe fallax*,
C. cyanea, *C. cyanella* and *C. rubra* are
validated.

INTRODUCTION

Kühner (1938: 211) proposed the generic name *Calocybe* for eight species but did not publish a latin description. Since that time several species have been described in the genus or transferred to it. Donk (1962: 42-43) noted that *Calocybe* Kühner was invalid as a nomen nudum.

Combinations published in *Calocybe* prior to 1962 (when Donk validated the generic name) whether spp. nov. or comb. nov. are also invalid (see Article 43, Stafleu et al. 1972). Fortunately most of the names of species placed in *Calocybe* Kühner have since been validated in *Calocybe* Kühner ex Donk by Donk (1962) and Singer (1962).

A comparison of the list of species compiled by Singer (1975) in the genus *Calocybe* with the names itemized in the Index of Fungi since 1962, reveals four invalid names and one illegitimate name. The four are *Calocybe cyanea* Sing., *C. cyanella* Sing., *C. fibrillosa* Singer and *C. rubra* Rick ex Sing. *Calocybe fibrillosa* is now considered a species of *Lyophyllum* by Singer (in Sydowia, in press). The fifth species actually has a valid name in *Calocybe*, namely *C. naucoria* (Murr.) Singer (1962:47). It was probably not listed in the Index of

Fungi because it was not designated as a new combination. However, the combination is used there and it fulfills all of the requirements for a new combination including proper citation of the basionym. Unfortunately, as explained below there is an earlier legitimate epithet for this species which should have been used.

Peck described *Agaricus fallax* in 1873. Murrill (1914), realizing that Peck's name was a later homonym of *A. fallax* Lasch (1829) and therefore illegitimate, published the new name *Melanoleuca naucoria* Murr. for Peck's species. It was Murrill's name that Singer (1962) transferred to *Calocybe*. However, as Smith (1942) noted, Saccardo (1887: 115) had previously transferred Peck's name to the genus *Tricholoma*. According to Art. 72 (Stafleu et al. 1972), a purported new combination of a valid epithet from an illegitimate name is to be treated as a new species. Hence, the legitimate name for this species is *T. fallax* Sacc. This name predates *Melanoleuca naucoria* Murr. *Agaricus (Tricholoma) fallax* Pk. was published first by Peck (1873) based on a paper presented to the Buffalo Society of Natural Sciences and not in the 25th report on the N.Y. State Museum of Natural History as indicated by Saccardo (1887). Peck (1875: 72) notes this in the 25th report. *Calocybe fallax* (Peck) Singer (1942) is not valid because of the invalidity of the generic name at the time.

The following new combination and new species are now proposed:

Calocybe Kühner ex Donk

Calocybe fallax (Sacc.) Singer ex Redhead & Singer *comb. nov.*

Basionym: *Tricholoma fallax* Saccardo 1887. Syll. Fung. 5: 115 (ut "(Peck) Sacc.")

≡ *Agaricus fallax* Peck (1873: 44), nom. illeg., non Lasch (1829: 524);

≡ *Calocybe fallax* (Peck) Singer (1942: 119) nom invalid.

≡ *Melanoleuca naucoria* Murr. (1914; 15);

≡ *Calocybe naucoria* (Murr.) Singer (1962: 47)

Calocybe cyanea Singer ex Redhead & Singer sp. nov. Basionym:

"*Calocybe cyanea* Singer" 1948. Pap. Mich. Acad. Sci. Arts & Lett. 32: 126 (nom. invalid).

Calocybe cyanella Singer ex Redhead & Singer sp. nov. Basionym:

"*Calocybe cyanella* Singer" 1948. Pap. Mich. Acad. Sci. Arts & Lett. 32: 124 (nom. invalid).

Calocybe rubra Rick in Singer ex Redhead & Singer sp. nov. Basionym:

"*Calocybe rubra* Rick in Singer" 1948. Pap. Mich. Acad. Sci. Arts & Lett. 32: 126 (nom. invalid).

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* This date is based on a list of publication dates of Peck's reports distributed by G.C. Ainsworth in 1964.

MYCOTAXON

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NOTES ON CLAVARIOID FUNGI. XVI. CLAMPLESS TAXA IN CLAVULINOPSIS.

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ABSTRACT

Clavaria longispora is described from fresh material, and the problem of clampless states in *Clavulinopsis* is reviewed.

Corner (1967) described *Clavaria longispora* from dried specimens at BPI. Petersen (cf. Petersen & Olexia, 1969) examined the type specimen, concluding that it represented a clampless *Clavulinopsis*, and strongly indicated its close similarity to *Clavulinopsis laeticolor* (Pk.) Pet. This assumption was born of experience, not fact, in that my only exposure to such forms had been through *C. laeticolor*, and even though the spore dimensions of *Clavaria longispora* did not accurately match those of *Clavulinopsis laeticolor*, the association was promoted, even with some force.

Recently, however, a fresh specimen of *Clavaria longispora* (Knoxville, TN, 30.x.77, coll. O. Mundt, TENN no. 40469) was given me, affording an opportunity to note color and habit as well as microscopic characters. This specimen may be described as follows:

Fruit bodies (fig. 1) up to 3 cm long, up to 2 mm thick, simple, gregarious to densely caespitose in groups up to 15, often geniculate or sinuous; stipe hardly distinguishable from hymenial area, concolorous with it; club "salmon orange*" to "capucine orange" (Royal Horticultural Society color chart: orange group 28C-D, 29A); apex tapering gradually when young, in maturity broadening somewhat to hemispherical, concolorous with club until withering slightly in age, and then becoming "burnt sienna." Taste and odor none. On soil beneath grass.

Tramal hyphae hyaline, parallel, without clamp connections, of two general width ranges. Basidia 40-50 X 6-8 μ m, clavate, without clamp connections, of two kinds; a) thin-walled, with homogeneous contents, and b) thick-walled, often with one or more adventitious septa (fig. 3)

* colors in quotes from Ridgway (1912)

and multiguttulate contents, the guttules refringent under phase contrast; sterigmata (1)-2-(3-4), divergent, somewhat cornute, up to 8 μm long (when 2 per basidium).

Spores (fig. 2) 8.1-9.6 (11.1) X 3.7-4.8 (5.9) μm (see Table 1 for statistics), elongate-ovate to amygaliform, smooth, hyaline; contents homogeneous to multiguttulate (at maturity?), the guttules refringent under phase contrast; wall thin; hilar appendix papillate, up to 0.7 μm long.

Identification of this specimen prompted a reexamination of the taxon, especially in light of my criticism (Petersen & Olexia, 1969) of Corner's (1967) assumption that the fruit bodies of the type "seem to have been pink when fresh." Of those specimens reported in 1969, several were available for study, or drawings of spores and other structures had been retained, and all of this was again digested. The following conclusions can be reported:

1. *Clavaria longispora* (type specimen) and the collection described above are conspecific, and represent clampless fruit bodies of *Clavulinopsis gracillima* (Pk.) Pet. (= *Clavaria luteo-alba* Rea).

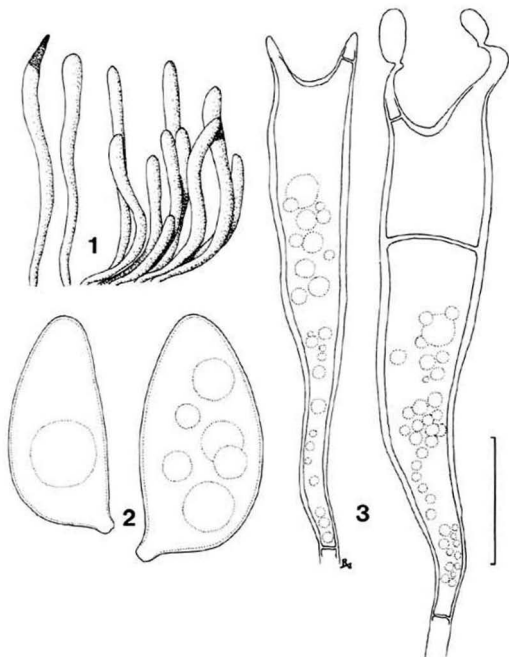
2. No other specimens reported by me (cf. Petersen & Olexia, 1969:1137) were contaxic with these two collection, but represented a clampless state of *Clavulinopsis laeticolor*. Table 1 shows spore statistics in support of this conclusion, especially if combined with fruit body colors reported previously.

3. Thick-walled basidia have been noted in both taxa. They are not uncommon, and have been reported also in *Clavulinopsis corniculata* (Petersen, 1971). Until observing nearly mature spores on such basidia in the collection described above, such basidia were thought to be sterile, but now seem fertile, at least occasionally.

Several taxa of *Clavulinopsis* now have been reported to produce clampless fruit bodies: *C. laeticolor*, *C. corniculata* (Fr.) Corner (Maas Geesteranus, 1976), *C. gracillima*, *C. fusiformis* (Sow. ex Fr.) Corner, *C. amoena* (Zoll. & Mor.) Corner and *C. subtilis* (Fr.) Corner (for the latter three, cf. Corner, 1970:64, but without documentation). Full documentation is available to support the association between *Clavaria longispora*, *Clavulinopsis gracillima* and *C. luteo-alba* (Corner, 1967; Petersen, 1967; Petersen & Olexia, 1967, 1968), and between the clamped and clampless states of *C. laeticolor* and *C. pulchra* (Pk.) Corner (Petersen, 1965, 1968; Petersen & Olexia, 1967).

That the clampless state of *Clavulinopsis gracillima* has been given a name in *Clavaria* opens the question of such practice in general: should the clampless states of *Clavulinopsis corniculata* and *C. laeticolor* also be named in *Clavaria* (Subg. *Clavaria*)? I think not, for at least two reasons.

First, if such forms are really anamorphic (i.e. do not exhibit a perfect state) they deserve only anamorphic names, not names in a teleomorphic genus (i.e. exhibiting a perfect state, such as *Clavaria*). To give them teleomorphic names would be to confuse the issue and to wreck havoc on Art. 59 of the ICBN. Second; although the absence of clamp connections would consign such forms to *Clavaria* (if karyogamy and



Figs. 1-3. *Clavaria longispora* Corner. Fig. 1. Fruit bodies. Fig. 2. Spores. Fig. 3. Thick-walled basidia. Standard line = 5 μ m for spores, 10 μ m for basidia, 1.5 cm for fruit bodies. TENN 40469.

Table 1.
Spore data for *Clavulinopsis* specimens

Specimen	Dimensions	\underline{E}^1	\underline{E}^m	\underline{L}^m
<i>C. longispora</i> ^{2,5} (type)	9.2-10.7 X 4.6-5.0	1.93-2.31	2.07	9.98
<i>C. longispora</i> ⁵ (TENN no. 40469)	8.1-11.1 X 3.7-5.9	1.77-2.20	1.95	9.03
<i>C. gracillima</i> ³ (type)	8.2-9.9 X 3.9-5.0	1.93-2.31	2.07	9.16
<i>C. luteo-alba</i> ⁴ (type)	7.4-9.6 X 4.1-4.8	1.75-2.00	1.87	8.23
<i>C. laeticolor</i> (type)	5.9-6.7 X 4.4-5.2	1.14-1.33	1.24	6.15
<i>C. pulchra</i> ³ (type)	4.8-7.4 X 3.7-5.7	1.04-1.60	1.34	5.93
<i>C. laeticolor</i> ^{2,5} (Minnesota)	7.5-9.2 X 5.0-6.4	1.31-1.73	1.43	8.16
<i>C. laeticolor</i> ^{2,5} (RHP 1817)	6.4-8.2 X 5.0-5.7	1.19-1.50	1.33	7.06
<i>C. laeticolor</i> ^{2,5} (RHP 1277)	6.7-9.3 X 5.2-6.7	1.20-1.57	1.36	7.67
<i>C. laeticolor</i> ^{2,5}	6.0-6.7 X 4.6-6.0	1.06-1.36	1.19	6.49

¹ \underline{E} = length \div width; \underline{E}^m = average \underline{E} ; \underline{L}^m = median length.

²Reported previously (Petersen & Olexia, 1969), but remeasured.

³Reported previously (Petersen & Olexia, 1967), but remeasured.

⁴Reported previously (Petersen, 1967), but remeasured.

⁵Clampless fruit bodies.

meiosis were present), their affinities are obviously with *Clavulinopsis* through hyphal construction and fruit body morphology. To give them names in *Clavaria* would be to undermine these genera on assumed phylogenetic grounds.

Finally, uncovering such associations raises at least two additional possible ramifications. First; two-spored taxa in *Clavaria* should be surveyed carefully, perhaps to reveal more clampless states of *Clavulinopsis* masquerading under names in *Clavaria*. Second; consideration should be given to clamped, clampless, and partially clamped taxa in *Ramaria* to reveal the mechanism at work there. Surely clues may be gained on this entire problem from work already accomplished in the Agaricales.

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A NEW SPECIES OF TAENIOLELLA HUGHES

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ABSTRACT

A new species of *Taeniolella* which differs from known species in wall ornamentation is described as *T. bilgramii*.

Hughes (1958) described the genus *Taeniolella* with *T. exilis* (Karst.) Hughes as the type species. The genus accommodated dematiaceous hyphomycetes which produce phragmosporous conidia in chains from conidiogenous cells on non-specialized conidiophores. He transferred the names of 14 species from other genera. Ellis (1971, 1976) described and illustrated 12 species. In this communication an undescribed species is reported.

It differs distinctly from these species in the wall ornamentation of the conidia. It is named in honour of Professor K. S. Bilgrami, whose contributions to fungi are well-known.

TAENIOLELLA BILGRAMII S. S. & S. M. Reddy, sp. nov.

Coloniae punctiformes, pulvinatae, olivaceobrunneae; mycelium immersum, subhyalinum, ramosum, septatum, 2.0-2.5 μm crassum; conidiophora semimacronemata, mononemata, caespitosa vel sparsa, plerumque brevia, simplicia, 7.5-57.5 (medio 18.5), pro more 12.5-25.0 μm longa, 1.25-2.5 (medio 2.0), pro more 2.5 μm crassa, simplicia, raro basim versus ramosa, subhyalina, levia, continua. Cellulae conidiogenae monoblasticae, integratae, terminalis determinatae, ellipsoideae, olivaceo-virides, leves, 17.5-58 μm longae, 1.75-3.0 μm crassae; conidia in catenulis longis, acropetalis, simplicibus vel ramosis producentes. Conidia in catenulis longis conjunctis, frequentes difficiliter secedentia acrogena, recta vel flexuosa, fusiformia, 7.5-60.0 (medio 27.5) μm longa, 3.75-10.0 (medio 5.4) μm crassa, 1-5-septata, tunica incrassata, sinuata, lumine constricto, frequenter prominulis dentiformibus tuberculata.

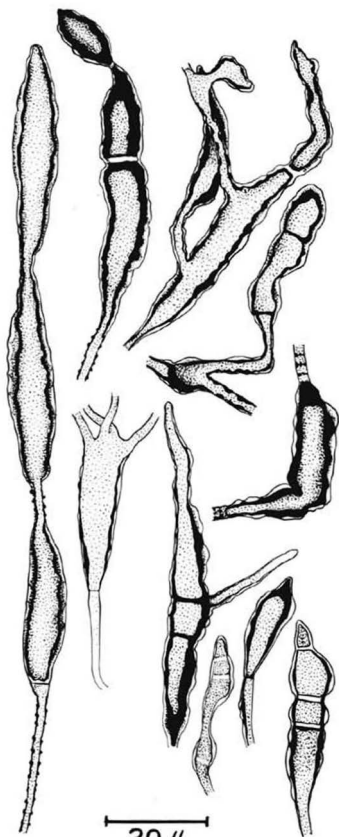


Fig. 1

Colonies punctiform, pulvinate, olivaceous-brown; mycelium immersed, subhyaline, branched, septate, 2.0-2.5 μm thick, conidiophores semi-macronematous, mononematous, caespitose or scattered, simple, 7.5-57.5 (av. 19.5) μm , usually 12.5-25.0 μm long and 1.25-2.5 (av. 2.0) μm , usually 2.5 μm wide, simple, rarely branched near the base, subhyaline, smooth, aseptate. Conidiogenous cells monoblastic, integrated, terminal, determinate, ellipsoidal, olivaceous-green, smooth, 17.5-58.0 μm long \times 1.75-3.0 μm wide, producing conidia in long acropetal, simple or branched chains (FIG. 2). Conidia in long chains often seceding with difficulty, acrogenous, straight or flexuous, fusiform, 7.5-60.0 μm long (av. 27.5 μm) and 3.75-10.0 μm wide (av. 5.4 μm), 1-5-septate, conidial wall thick (leaving narrow lumen), sinuate, often tuberculate with irregularly den-

FIG. 1. Camera lucida drawings of conidia and conidiophore of *T. bilgramii*.



FIG. 2. Photomicrograph showing the conidiophore and conidia of *T. bilgramii* ($\times 380$).

tate ornamentation (FIG. 1).

Collected on phyllodes of *Agave americana* Linn., Osmansagar, Hyderabad, 23rd Oct. 1976, S. S. Reddy. Specimen deposited in herbarium of the Botany Department, Kakatiya University, Warangal as KUMH 697 (HOLOTYPE) as well as CMI, Kew, England as IMI 209947 (ISOTYPE).

ACKNOWLEDGMENT

Thanks are due to Prof. U. B. S. Swami, Head, Department of Botany, Kakatiya University, Warangal, for encouragement.

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MYCOTAXON

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BOOK REVIEWS

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ON J. CRAMER'S MYCOLOGICAL PUBLICATIONS

In twenty years, from 1956 to 1977, the publisher J. CRAMER has contributed greatly to the diffusion of literature in botanical sciences, including mycology and lichenology, in the fields of taxonomy and floristics. More than 20 entitled series or collections of botanical books have been published or are still continued, more than half of them under the editorship of J. Cramer himself, the others being edited by scientists. These series each consist of a few to as many as 105 volumes. In addition to these, a number of books published separately, not in series, bring J. Cramer's contribution to botany to about 800 volumes.

In addition, J. Cramer assumes responsibility for publishing several journals. NOVA HEDWIGIA, a journal of cryptogamy, started in 1959 and including now 28 volumes of about 900 pages each, is the best known. The specific contributions of Cramer to mycological publishing is important enough to detail it here.

In 1967 Cramer initiated and still continues BIBLIOTHECA MYCOLOGICA, a series containing both ancient and recent mycological works. The 60 volumes of this series are mostly of significant scientific value, though variable in size and importance. When voluminous, they are cloth bound, when smaller, paperback. Reprinting of older books is usually of high quality. Recent papers are either typeset or offset from authors' copy. The appearance of such offset printing depends greatly upon the authors' manuscripts. Some authors clearly need more skill in preparing their camera-ready manuscripts, taking advantage of the suggestions and facilities the publisher certainly is able to provide. Among possible improvements, I'd suggest improving the clarity by subdivision into chapters by using, *e.g.*, various sizes of typeface or transfer letters adequately spaced for headings, and the general economy of space (particularly the avoidance of double-spaced typing!). The high price of some of the books could have been halved by intelligent attention to such details by the authors, or by more stringent typing requirements by the publisher. In this series recent works by Klebs, Horak, Clemençon and Sundberg, as well as reprints of works by Hennings and by Murrill are in preparation.

Two other mycological series are also published by J. Cramer. DIE PILZE MITTELEUROPAS consists of 5 volumes published from 1956 to 1967. FUNGORUM RARIORUM ICONES COLORATAE, a series started in 1966 with D. A. Reid's beautiful book, "Coloured illustrations of rare and interesting fungi," is continued, and now contains 8 volumes. Both series have caught the attention of mycologists and of University and State libraries for their high quality - especially of their illustrations.

Two reprinted collections issued by J. Cramer must be mentioned: the journal ANNALES MYCOLOGICI (1903-1944), of 44 volumes, and RABENHORST'S

KRYPTOGAMENFLORA VON DEUTSCHLAND, ÖSTERREICH UND DER SCHWEIZ, I. PILZE (1884-1920), reprinted in 1963, in 10 volumes.

Beyond these five series of books on mycology, 19 of the 55 volumes issued as BEIHEFTE ZUR NOVA HEDWIGIA deal with mycology. Also, 29 mycological papers of shorter length have been separately reprinted from NOVA HEDWIGIA. Cramer also printed ZEITSCHRIFT FÜR PILZKUNDE from 1968 to 1972, and MYCOLOGIA MEMOIRS vol. 6.

A number of important books have, however, been published separately from any series, works of Fuckel, Karsten, von Höhnelt, Zycha, Dennis, von Arx, Singer, Karling, and others. There are 21 such books of broad, nearly textbook, scope, dealing with large groups of fungi.

For lichenology, J. Cramer's contribution is the publication of two volumes in DISSERTATIONES BOTANICAE, 6 as BEIHEFTE ZUR NOVA HEDWIGIA, 9 in BIBLIOTHECA LICHENOLOGICA started in 1973, and 7 as reprinted papers from NOVA HEDWIGIA, plus 10 volumes published separately. A journal, HERZOGIA, organ of the bryological-lichenological workgroup for central Europe, edited by Follmann, Frey, Koppe and Poelt, has been issued by Cramer since 1969.

Not including periodicals, J. Cramer has published 147 items in mycology and 22 in lichenology, beginning in 1956. Some, not previously reviewed in these pages, are detailed here.

CHYTRIDIOMYCETARUM ICONOGRAPHIA, by John S. KARLING, xiv + 414 p., 175 pl., 4°, cloth bound, 1977. J. Cramer. Price, DM 200.-

A subtitle modestly qualifies this book as "an illustrated and brief descriptive guide to the chytridiomycetous genera with a supplement of the Hyphochtriomycetes." The descriptive characters, sexual reproduction, life history and ecology of each of the 174 genera of these two classes of fungi are critically presented and illustrated. The style, far from being straight technical, is agreeable and fluent, and the illustrations, of excellent full-page line drawings facing the text, make this book very attractive and will contribute greatly to a larger knowledge of these often neglected fungi. One can find here again the excellence of a monograph such as Thaxter's on the Laboulbeniaceae.

NOVA SCOTIAN BOLETES, by Darryl W. GRUND and Kenneth A. HARRISON, in Bibliotheca Mycologica vol. 47, 283 p., 80 fig., 68 b. & w. pl., 8°, cloth bound, 1976. J. Cramer. Price, DM 60.-, standing orders, DM 48.-

This book presents the descriptions of 80 species of boletes of Nova Scotia, Canada, based on freshly collected material. The study of the boletes of such a restricted area assumes greater value in view of the unique kind of floristic *carrefour* which this peninsula represents. The genera considered are *Boletus*, *Boletellus*, *Boletinellus*, *Fuscoboletinus*, *Gyroporus*, *Pulveroboletus*, *Strobilomyces*, *Suillus* and *Tylopilus*. The genus *Leccinum* is recorded with only 4 species at this stage, for it needs more investigation. Taxa are described technically by morphology, anatomy and macrochemical tests. Basidia, basidiospores and cystidia of each taxon are illustrated, and carpophores of many species are represented by quality photographs. The book is made of practical use by provision of a clear synopsis of the family Boletaceae, a well-constructed dichotomous key based on accessible characters and an excellent and detailed synoptic key to the species. Some new taxa are described and new combinations made.

GENETISCHE REGULATION DER FRUCHTKÖRPER-BILDUNG BEI HÖHEREN BASIDIOMYCETEN; MONOKARYOTISCHE FRUCHTEN BEI POLYPORUS CILIATUS, by Ulf STAHL, in Bibliotheca Mycologica vol. 50, 105 p., 16 fig., 8°, paperback, 1976. J. Cramer. Price, DM 30.-, standing orders, DM 24.-

This thesis, carried out under Prof. K. Esser's direction, consists of two parts. In the first, an analysis of mechanisms underlying the A and B incompatibility factors in tetrapolar systems leads to the distinction of these factors as *regulating* components in sexual morphogenesis from the *regulated* set of genes which, in each partner, codifies sexual morphogenesis itself. Further analysis of the four main patterns of control by A and B factors, only one of which results in a clamped fertile dicaryon, shows that these factors are gene-complexes acting specifically in the regulation of partner genomes. This is demonstrated in the second part through the mating of compatible and incompatible monocaryotic strains of *Polyporus ciliatus* which the author skilfully segregated and analysed up to definition of their genotype and production of monocaryotic fructifications. A *stimulating* and *inhibiting* mechanism of the incompatibility factors exists which determines dicaryotic *vs.* monocaryotic fructification.

GENETISCHE KONTROLLE DER PHENOLOXYDASE "LACCASE" DES ASCOMYCETEN PODOSPORA ANSERINA, by H. PRILLINGER, in Bibliotheca Mycologica vol. 51, 148 p., 31 fig., 14 tab., 8°, paperback, 1976. J. Cramer. Price, DM 40.-, standing orders, DM 32.-

This dissertation, carried out under Prof. K. Esser's direction, deals with the genetical analysis of laccase-deficient mutants of *Podospora anserina*, essentially a biochemical experimental investigation of the genetic characterisation of the fungal mutants. Such a specialized study might attain a broader audience if it were published in an appropriate journal rather than in Bibliotheca Mycologica.

THE GENUS LEPTONIA ON THE PACIFIC COAST OF THE UNITED STATES, including a study of the North American types, by David L. LARGENT, 286 p., 24 b.& w. phot. pl., 8°, cloth bound, 1977. J. Cramer. Price, DM 80.-, standing orders, DM 64.-

Following Romagnesi's treatment of the rhodophylloid fungi in one genus, *Rhodophyllus*, these fungi are now separated into six genera, *Claudopus*, *Pousarella*, *Alboleptonia*, *Nolanea*, *Entoloma* and *Leptonia*. *Entoloma* and *Pousarella* have been investigated by Hesler and Mazzer respectively in recent years. The author summarizes here 10 years of collecting and herbarium studies of *Leptonia* in the United States, and especially on the west coast. One hundred forty-two taxa are described carefully and documented with accurate redescriptions of the type material of the accepted epithet and of its synonyms. Illustrations of carpophores, cuticle structure, cystidia and spores are given by means of black and white photographs, but only for a few taxa; no line drawings are given. The dichotomous keys are scattered through the book at each subgenus, section and subsection, but there is fortunately a good synoptic key to guide the reader. An account, more detailed than just a short paragraph, on the segregation and diagnosis of the genus *Leptonia* from the other rhodophylloid genera might have been justified and informative. This book is an important contribution to taxonomy: it is the first one devoted to *Leptonia*, with 24 new species, 19 new varieties and 2 new forms described, 48 new combinations and 1 new name proposed.

COMPLÉMENTS À LA "FLORE ANALYTIQUE," by R. KÜHNER and H. ROMAGNESI, in *Bibliotheca Mycologica* vol. 56, 484 p., ill., with index by C. BAS, 8°, cloth bound, reprinted 1977. J. Cramer. Price, DM 100.-, standing orders, DM 80.-

The reprinting of the 9 serial papers published by Kühner and Romagnesi from 1954 to 1958 in different French periodicals as supplements to their "Flore Analytique" is a fortunate idea, for it brings together all these additional data on *Rhodophyllum*, *Lactarius*, the Pleorotaceae, Marasmiaceae, Tricholomataceae, *Cortinarius*, *Inocybe*, the Naucoriaceae, Coprinaceae, Lepiotaceae and Volvariaceae, and provides an index for them.

LE GENRE AMANITA PERSOON, by J. E. GILBERT, in *Bibliotheca Mycologica* vol. 53, 186 p., 13 × 19 cm, paperback, reprinted 1976. J. Cramer. Price, DM 40.-, standing orders, DM 32.-

This little book is an interesting document for mycologists interested in *Amanita*, for it shows the species concepts current in France in 1918. The 30 species of the three subgenera, *Amanita*, *Amanitopsis* and *Limacella*, were so vaguely or controversially described at that time that the author accepted no fewer than 68 infraspecific taxa to accommodate the divergent opinions. The then current use of such a system of synonymising taxonomic concepts (misapplied names and description references) as well as correctly applied names, instead of synonymising epithets as unequivocally based on type material, is the only explanation for the development of such an intricate and loose taxonomy.

A TAXONOMIC AND NOMENCLATORIAL STUDY OF THE GENUS AMANITA SECTION AMANITA FOR NORTH AMERICA, by David T. JENKINS, in *Bibliotheca Mycologica* vol. 57, 106 p., 12 col. phot., 22 b. & w. phot., 8°, paperback, 1977. J. Cramer. Price, DM 60.-, standing orders, DM 48.-

Eleven species and seven varieties of one of the six sections of *Amanita* are described here, supported by some type re-examinations. A new variety of *Amanita muscaria* is proposed. This is the total scope of this paper, which regrettably shows numerous defections in preparing the author's typed, camera-ready copy. e.g., missing punctuation, spelling or typing errors, inconsistent, incomplete or erroneous literature citations, chronologically mixed nomenclature, use of unexplained abbreviations, and consistent misplacing of the reference to the illustrations under the entry "type material." Not all color photographs are of high quality, nor are all of the black and white photographs; none are provided with a scale.

Criticism has been leveled at Cramer for the high price of many of the books he publishes. Part of the high cost is unquestionably caused by necessarily small press runs for highly technical papers such as this. Cramer has provided me with a cost breakdown for publication of this book, from which one finds that 82% of the production costs are consumed by the printing and paper costs of the six colored plates! The purchaser pays nearly \$20 of the approximately \$25 cost for 12 small color pictures of uneven quality. The author himself assumed responsibility for the high cost of his thesis publication by deciding that color plates were an essential. Once having made that decision, the author could have cut costs by cropping and grouping photos (both color and black and white), by avoiding the repeating of species names, nomenclators and type citation caused by grouping type descriptions at the end of the book, by various other typing economies, particularly by single spacing (everything is double-spaced). But then the book would have been just a thin journal article, and the prestige of having published a "book" would be lost.

THE BOLETINEAE OF FLORIDA, with notes on extralimital species, by Rolf SINGER, in *Bibliotheca Mycologica* vol. 58, 305 p., ill., 8°, cloth bound, reprinted 1977. J. Cramer. Price, DM 60.-, standing orders, DM 48.-

This is 4 reprinted articles from *Farlowia* 2: 97-141, 1945, 2: 223-303, 1945, 2: 527-567, 1946, and the *American Midland Naturalist* 37: 1-135, 1947, which is completed with a general index. Contrary to Kuntze, who "amused himself by transferring practically all known species of *Boletus* which he copied from Saccardo, to *Suillus*" although "Personally, he has never seen any of them except perhaps *Boletus edulis* in his kitchen," (Singer, p. 279), the author undoubtedly did see all of those he described and commented on so accurately. This book is a milestone in the study of boletes.

LOWER PLANTS OF THE INDIAN SUBCONTINENT. A collection of papers by Indian scientists. *Beihefte zur Nova Hedwigia* vol. 47, 648 p., ill., 8°, paperback, 1977. J. Cramer. Price, DM 200.-, standing orders, DM 160.-

About half of this book deals with taxonomic and developmental mycology and with plant pathology. Among the 28 papers attention is drawn to those on coprophilous fungi (*Thielavia* and *Chaetomidium*) by Lohda, on *Hypocrea* by Kar and Maity, on the Chaetomiales by Mukerji and Saxena, on *Meliola* by Srinivasulu, on aquatic pyrenomycetes by Tilak and Kulkarni, on ascocarp development of *Tryblidaria* by Anahosur and of *Tryblidiella* by Seshadri and Muthappa. There are also some papers of much lower quality. The figures on p. 217 should be on p. 624. The other half of the volume deals with the algal flora of Indian soils.

FUNGORUM LIBRI BIBLIOTHECAE JOACHIM SCHLIEMANN, Books and Prints of Four Centuries, edited by Winfried UELLNER, 287 p., 8°, cloth bound, 1976. J. Cramer. Price, DM 60.-

The Joachim Schliemann Library is an outstanding collection of literature on fungi consisting of some 2000 titles. Its special value is seen in its wide range from the classics of mycology such as the major iconographies, to recent books, booklets, and journals, as well as unpublished manuscripts. This catalogue, which unfortunately lacks an introduction, provides titles with descriptions, references to biographies, bibliographic listings and reviews in modern journals. The book is interestingly illustrated with 34 facsimile plates of titlepages of old and rare works on mycology. The book is printed for the Elias Fries Gesellschaft für Pilzforschung, Hamburg.

PILZKUNDE, by J. A. von ARX, vi + 296 p., 122 fig., 8°, paperback, third ed., 1976. J. Cramer. Price, DM 29.50

Since the second (1968) edition of this book, Professor von Arx has made an extensive investigation on the taxonomy and systematics of the Endomycetes, especially on the Endomycetales. This order consists of 4 families. The Endomycetaceae is enlarged to include part of the Dipodascaceae and the Eremascaceae of 1968; the Ascoideaceae is the remainder of the Dipodascaceae; the Saccharomycetaceae includes now the Spermophthoraceae, and the Saccharomycodaceae is a recent family. These changes have been integrated into this new edition. This textbook is very well documented with abundant and up-to-date literature citations. The illustrations are profuse and demonstrative. The volume is reasonably priced, and is to be recommended to any student in mycology.

EPIPHYTISCHE FLECHTEN ALS BIOINDIKATOREN DER LUFTVERUNREINIGUNG dargestellt an Untersuchungen und Beobachtungen in Bayern, by Peter JÜRGENG, in *Bibliotheca Lichenologica* vol. 4, 164 p., 49 maps and fig., 8°, paperback, 1975. J. Cramer. Price, DM 50.-, standing orders, DM 40.-

EPIPHYTIC LICHENS AND AIR POLLUTION IN THE NETHERLANDS, by Toke DE WIT, in *Bibliotheca Lichenologica* vol. 5, 227 p., 126 maps and fig., 8°, paperback, 1976. J. Cramer. Price, DM 60.-, standing orders DM 48.-

These two ecological studies show clearly the relation between the regression of the epiphytic lichen flora and several kinds of air pollution, particularly pollution by SO₂, which results in the development of "epiphytic deserts" in large urban or industrial zones. The first paper concerns Bavaria, with München as a center; the other covers the whole of The Netherlands wherein six epiphytic deserts are in progress of formation. Up to 38 species of epiphytic lichens on 8 different tree species were investigated and their distributions mapped.

ONTOGENETISCH-SYSTEMATISCHE STUDIEN ÜBER ERIODERMA im Vergleich mit anderen cyanophilen Flechtengattungen, by Gerhard KEUK, in *Bibliotheca Lichenologica* vol. 6, 20 fig., 217 b.& w. phot. in 60 pl., 8°, paperback, 1977. J. Cramer. Price, DM 60.-, standing orders, DM 48.-

This is a detailed investigation on the thallus and apothecium structure in 7 genera of the Peltigeraceae, 3 of the Stictaceae, 1 of the Placynthiaceae, 3 of the Coccocarpiaceae and 4 of the Pannariaceae in the Lecanorales, in order to define an adequate position for the genus *Erioderma*. Developmentally and structurally, *Erioderma* appears to be most closely related to the Pannariaceae, close to *Parmeliella pycnophora*. Twelve species of the genus are then redescribed (but with too few of them - including the type species - based on studies of type material). This paper is certainly a valuable contribution to the knowledge of the Lecanorales and their taxonomy. The reader may be confused by the "dissertation" or "thesis" style of the paper with headings and subheadings all typed alike. (Several of the other books reviewed above have the same flaw.) The reader gets confused, loses his way, goes back to the contents, and wastes time in finding data in an unclearly structured text. In this reviewer's opinion, many theses must be restructured, and planned for book use, before ever being produced as a published text.

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This index includes genera, infrageneric taxa, species, and infraspecific taxa. New taxa are in CAPITALS, and the pages where they are published are in *italics*. Petersen's index to Bulliard's "Histoire des Champignons" is itself an index (pp. 132-165), as is Guzmán & Vergeer's index of *Psilocybe* (pp. 466-476), and the sectional epithets in Patrick's treatment of *Coprinus* are separately indexed (pp. 354-355). References to these indices are indicated by the notation "see". The list of epithets on pp. 84-126 is also not indexed here.

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Volume IV

- p. 362, l. 5, delete R.P. Southby, CMI 34813.
 p. 374, l. 41, for 1969). read 1969; Sun and Huppert, 1976).
 p. 384, l. 14, for CMI 34813 read R.P. Southby, CMI 34813
 p. 386, l. 33, for (Fig. 5E) read (Fig. 6E)
 p. 390, l. 3, for (Figs. 7A, 7D) read (Figs. 7A, 7D)
 p. 390, l. 26, for *M. striatosporus* read *M. striatosporum*
 p. 413, l. 26, for Gymnoascaceae read *Gymnoascaceae*
 p. 427, l. 11, for Alaska read South Pacific
 p. 431, l. 2, for (Figs. 13J-12L) read (Figs. 13J-13L)
 p. 452, l. 2, after are divided by add thickened septa suggesting double septa (Figs. 17H, 17I). Arthroconidia are cylindrical, cuneiform if terminal, discoid in end view, hyaline, later greenish-yellow, often with refractile end walls (Fig. 17K), 2-3 X 2-6µm, mostly 2-3 X 2.5-5.5µm. Chlamydo-spores are rare. No other spore state was observed.
- p. 456, l. 10, for (UAMH 1942 and 1943) read (UAMH 1842 and 1843)
 p. 456, l. 17, for UAMH 1941 read UAMH 1841
 p. 456, l. 18, for 1943 read 1843
 p. 456, l. 28, for (UAMH 1841, 1943 and 1975) read (UAMH 1841, 1843 and 1975)
- p. 458, l. 14, delete
 p. 458, l. 15, for (from Orr): UAMH 1941, Calif., Huppert (SFVH 129), Orr 0-3226)
 read UAMH 1841, originally from bronchoscopy specimen from patient with pulmonary disease not diagnosed as coccidioidomycosis, S. McMillen, Hektoen Institute, Chicago, (from Orr as Huppert SFVH 129, 0-3226)
- p. 458, l. 16, for UAMH 1942, Calif., Huppert (SFVH 130), (Orr 0-3283) read UAMH 1842, originally from bronchoscopy specimen from patient with pulmonary disease not diagnosed as coccidioidomycosis, S. McMillen, Hektoen Institute, Chicago, (from Orr as Huppert SFVH 130, 0-3283)
- p. 458, l. 17, for UAMH 1943, Calif., Huppert (SFVH 149), (Orr ?0-1088) read UAMH 1843, originally from sputum of patient with non-coccidioidal respiratory disease, S. Froman, Olive View Hospital, L.A., (from Orr as Huppert SFVH 149, ?0-1088)
- p. 460, l. 25, for (UAMH 1941, SFVH 129; read (UAMH 1841, SFVH 129;
 p. 460, l. 26, for UAMH 1942, SFVH 130; UAMH 1943, SFVH 149) read UAMH 1842, SFVH 130; UAMH 1843, SFVH 149)
- p. 475, l. 39, for Fubalek, A. read Hubalek, Z.
 p. 481, l. 27, insert Sun, S.H. and M. Huppert. 1976.
 A cytological study of morphogenesis in *Coccidioides immitis*. *Sabouraudia* 14(2):185-198.
- p. 488, l. 15-
 l. 29, for Fig. 21 read Fig. 22

Volume VI

- p. 130, l. 44, for *acetabulum* read *acetabulum*
 p. 227, l. 41, for *corticola* read *corticolum*
 p. 233, l. 5, for *SCHIZOXYLON HIPPOPHAES* read (*SCHIZOXYLON HIPPOPHAES*)
 p. 241, delete last line
 p. 259, l. 13, for *venezuela* read *venezuelae*
 p. 343, l. 29, for (p. read (p. 352).
 p. 375-377, throughout, for *lundelli* read *lundelli*

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