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NOTES ON RESUPINATE HYMENOMYCETES—II*

The tulasnelloid fungi

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SUMMARY

1. Discussed are the tulasnelloid fungi, i.e. *Tulasnella* and other groups considered related by the author and also possessing spores capable of exhibiting repetition and not becoming septate.

2. The author rejects the designation epibasidia and considers the sterigmata in *Tulasnella* and *Gloeotulasnella* as being merely strongly inflated, a view already widely accepted.

3. He rejects the families Tulasnellaceae and Ceratobasidiaceae and includes them and the other tulasnelloid fungi in the Corticiaceae, which is still a heterogeneous group. Possible relations with other families are discussed.

4. The term pleurobasidia is introduced.

5. *Botryobasidium* Donk is restricted to species with spores not exhibiting repetition. Two new genera are proposed for segregates, *Uthatobasilium* Donk and *Thanatephorus* Donk. The new combination *Thanatephorus cucumeris* (Frank) Donk is published for the well-known parasitic species often called *Hypochnus solani* Prill. & Delacr.

SECONDARY BASIDIOSPORES.—Basidiospores exhibiting repetition (i.e. spores each capable of producing a secondary one on a sterigma-like outgrowth) are usually considered to be a sure indication of the heterobasidious[1] nature of the species showing this phenomenon. It is of general occurrence in some of the families now often referred to as Heterobasidiae, for instance Auriculariaceae and Tremellaceae.

The production of this type of secondary spores is usually referred to as 'germination by repetition.' 'Repetition' or renovation is what occurs: the basidiospores repeat themselves; but the term 'germination,' in my opinion, is incorrect here: the basidiospores repeat themselves without the actual process of germination setting in.

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[1] From Heterobasidiae; antonym, Homobasidiae.

Forcibly discharged spores (ballistospores[2]) are sticky spores (= slime spores, as opposed to dry spores[3]). They stick to objects with which they come into contact, but the violent discharge makes it possible for them to be carried away by the wind over considerable distances before they stick and, given the right conditions, germinate. Like the primary basidiospores the secondary (basidio)spores under consideration are ballistospores. The capacity for repetition would seem to give such basidiospores as have gone astray another chance. This may well be the reason why one so often finds spores exhibiting repetition on fruit-bodies when examining them for microscopical details: detached mature spores sticking to their fruit-bodies had bad luck. It follows that the so-called promycelia on which the secondary basidiospores are formed must be functionally, and may be expected to be structurally, quite similar to the sterigmata on which the true basidiospores are formed. (In liquids, an unfavourable medium, the sterigmata on the basidiospores often grow out anomalously to threads of often great length and may or may not produce abortive secondary spores.)

The fact that true sterigmata from which spores are forcibly discharged may be formed in undisputable basidiomycetes on structures other than the basidial body, namely on basidiospores and again on secondary basidiospores, is in itself highly interesting. It shows that one may be justified in regarding it as a basidiomycetous feature even in those cases where no basidia are formed. This is the view adopted when the Sporobolomycetaceae are included in the basidiomycetes, and this same view supports the assignment of the Tilletiales to that class. In the case of the Ustilaginales not only the homology of the so-called promycelium with the transversally septate basidium is, in my opinion, highly questionable, but these fungi also lack any indication of forcibly discharged spores: if they are to be regarded as basidiomycetes this view might be based on similar characters (mycelia) as would make basidiomycetes of Taphrinales (*Taphrina* Fr.).[4]

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[2] A term published by Derx (*1948*: 468). The mechanism of discharge of the spores of basidiomycetes was subjected to extensive researches by Buller. Compare also Prince (*1943*). Violent spore discharge, not necessarily homologous, occurs also among Entomophthorales and in the hyphomycete *Nigrospora sphaerica* (Sacc.) Mason (Webster, *1952*).

[3] See Mason (*1937*: 77).

[4] Compare Kniep (*1928*) and Lohwag (*1934*: 247-248). Stempell (*1935*: 255) stated that "Spiegelbild-Erzeugung" had been established for *Ustilago hypodytes* (Schlecht.) Fr. and he referred to Boss (*1927*), but I could not find any grounds for this statement in Boss's paper. Stempell (*1935*: 256) also reported that in several species of *Taphrina* forcibly discharged spores had been observed. It would appear that he took this information from a paper by Wieben (*1927*), but in this case, too,

In *Tulasnella* and related fungi the basidiospores are not known to produce anything in the line of 'conidia' but secondary basidiospores. Neither do the spores become septate. This is quite different from what is observed in Auriculariaceae and Tremellaceae if these families are taken as a whole.[5] There, other types of conidia, often in addition to secondary basidiospores, are regularly produced by the basidiospores in cultures. It seems promising to study more carefully their relation to the production of secondary basidiospores.

On the other hand it is remarkable that in certain groups producing such other kinds of conidia, whether or not accompanied by septation of the basidiospores, repetition seems to be entirely absent or rare as far as our present knowledge goes. This applies to the Homobasidiae (no septation[6]), to the heterobasidious families of Hymenomycetes, Septobasidiaceae, Dacrymycetaceae,[7] and to the Exobasidiaceae.

Among the holobasidious[8] fungi repetition of basidiospores is rare.[9] It is known to occur in *Tulasnella* J. Schroet. and *Gloeotulasnella* Höhn. & L., *Ceratobasidium* D. P. Rog., some species referred to *Botryobasidium* Donk (*Pellicularia* Cooke sensu D. P. Rog.), and a very small number of species placed by their authors in *Corticium* Fr. (non S. F. Gray) and *Peniophora* Cooke (= *Corticium* S. F. Gray). These fungi may for the present be referred to as the tulasnelloid fungi.

Heim once stated that the basidiospore of *Tulasnella* is "dépourvue des charactères d'asymmétrie" (*1949*: p. 14, and figures) and incomplete-

nothing definite was remarked on this point by the latter author. Stempell's "Myzel II" of *Entyloma calendulae* (Tilletiales) is taken by Derx (*1948*: 466) to represent a species of *Itersonilia* Derx, and thus as not belonging to *Entyloma* Bary at all. I have not yet come across any definite indication that violent spore discharge occurs in *Taphrina*, although some of Miss Wieben's illustrations would suggest that it might be present in that genus. Even assuming that her observations were correct and, in addition, interpretable as covering cultures showing the phenomenon of violent spore discharge, it is still doubtful, in view of the method by which the cultures were obtained, whether she really studied non-contaminated cultures of *Taprina*, rather than (admixtures with) species of *Sporobolomyces* Kluyver & Niel. Recently, Lodder & Kreger-van Rij (*1952*) concluded "that the formation of conidia in *Taphrina* resembling the spores of *Sporobolomyces* is not proved and needs further confirmation."

[5] Several species of these families show a behaviour similar to the tulasnelloid fungi: no other kinds of secondary spores, no septa.

[6] A few exceptions as to cross-walls have been reported.

[7] Bulat (*1953*) recently reported that sporobolomycetous colonies had developed in his cultures of *Dacrymyces ellisii* Coker; they showed all the characteristics of the genus *Tilletiopsis* Derx. He also found ellipsoid to obovoid conidia borne singly or in clusters of two or more on very short sporophores. These conidia "gave evidence of being forcibly projected from their sporophores; however, no mechanism for this type of spore discharge could be ascertained." The spores of the *Tilletiopsis*-like colonies are quite different from the basidiospores. Bulat did not report that the basidiospores exhibited renovation.

[8] From Holobasidiae; antonym, Phragmobasidiae.

[9] *Vuilleminia* is as yet insufficiently studied in this respect.

ly developed (p. 9). It must be emphasized in this connection that the basidiospores are quite normally developed and show the asymmetry coupled with violently discharged basidiospores.

THE TULASNELLA STERIGMA.—*Tulasnella* and the later described genus *Gloeotulasnella* have attracted considerable attention especially from phylogenetically-minded authors. The principal reason lies in the curious sterigmata which are greatly swollen bodies, storing the contents of the basidium before producing the spores and becoming separated from the basidial body by cross-walls; in addition these sterigmata may be the site of a nuclear division. The *Tulasnella* sterigma was first described by the Tulasnes (*1872*: 227 *pl. 10 fs. 3-5*) for a species they called "*Corticium incarnata* Fr. (*pinicola*)" and which today is identified with *T. violea* (Quél.) Bourd. & G. At the same time they depicted the repetition of the spores.

The sterigmata of *Tulasnella* have been diversely interpreted:

(i) as sterigmata (Tulasne, *1872*; Schroeter, *1888*; Brefeld, *1888*; Patouillard, *1888, 1900*; von Höhnel & Litschauer, *1906, 1908a*; Raunkiaer, *1918*; Burt, *1919*; Bourdot & Galzin, *1928*; Donk, *1931, 1954*; Talbot *1954*: 255-261),[10]

(ii) as one-spored basidia on a swollen support, the four of them being comparable with the four-celled *Tremella* basidium which, too, was looked upon as consisting of four one-spored basidia (tentatively suggested by Patouillard, *1888*; Boudier, *1896*),

(iii) as sessile basidiospores (Juel, *1897, 1915*; Gäumann, *1926*), and

(iv) as epibasidia, a term stretched to cover now sterigmata now metabasidia (Neuhoff, *1924*; Rogers, *1932, 1933, 1934*; Martin, *1944, 1952*).

After the cytology of the basidia of *Tulasnella* had become known, the second interpretation ceased to find serious support. Rejecting unconditionally Neuhoff's terminology of the parts or stages of the basidium as inapplicable and as fogging the understanding of homologies and, finally, passing the now generally abandoned interpretation of sessile spores, I adhere to the term sterigmata. In so doing *Tulasnella* and *Gloeotulasnella* remain directly comparable with other closely related holobasidious groups. For a recent discussion of this problem, see Talbot (*1954*).

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[10] The Tulasnes already spoke of sterigmata, "qui simulent de grosses spores avant de s'allonger pour devenir fertiles"; and Schroeter, of " . . . Sterigmen, welche . . . den Theilbasidien der Tremellineen gleichen . . ." These authors thus foreshadowed interpretations (ii) and (iii).

Rogers (*1934*: 164, 166, 169) has expressed the opinion that the *Tulasnella* basidium is the one in which the ascopore stage is most completely retained in basidial ontogeny and that it is to be held as the most primitive. Its 'epibasidia' would represent to a greater or less degree the ascospores themselves. Moreover, he postulates the rise of the basidiomycetes from some such resupinate forms as *Ascocorticium* Bref. Linder (*1940*: 442-444)) pointed out that there are no corresponding chiastic ascomycetes from which to derive the chiastic *Tulasnella* basidium. For other or similar speculations on the derivation of the basidium from the ascus, see Lohwag (*1937*) and Heim (*1949*).

In a short note recently published Donk (*1954*) suggests that all sterigmata that forcibly discharge their spores, even the tiniest ones, start their existence as blown-out buds (protosterigmata). The latter, usually without much interruption, form the pointed tips (spicula) from which the basidiospores develop. In some cases, however, the protosterigmata become strongly developed and 'autonomous' and some time elapses before they start producing their spores; they sprout by secondary protosterigmata which immediately produce spicula: *Tremella, Tulasnella.* Among the protosterigmata, the ovoid spore-like stages of *Tulasnella* and *Gloeotulasnella* are remarkable only by virtue of their unusual development and not by being something specific to these two genera. I do not really believe that they would represent the ascospores themselves.

In this connection it seems worthwile to draw attention to a variation in shape of the sterigmata of *Ceratobasidium anceps* (Bres. & Syd.) H. S. Jacks., a species of a genus closely related to *Tulasnella* as will be discussed below, but with sterigmata not so strongly inflated as in the latter genus. Mrs. Gregor (*1935*) found that the protuberances formed on the basidia as the beginning of the sterigmata (protosterigmata) gradually elongate, after which their apices taper to a point (spicula) while the middle portion often becomes somewhat swollen. This is the normal condition. However, in some cases this swelling is considerable and rather basal and abruptly narrows into the terminal portion of the sterigma. This reminds one of "*Corticium*" *grisellum* Bourd. as described by Bourdot & Galzin (*1928*: 223), who found the "stérigmates droits, rigides, plus ou moins renflés en petit bulbe à la base." This verbal picture also applies to the sterigmata of one of the basidia of *C. anceps* as depicted by Mrs. Gregor (*1935*: *f. 1D*).

THE GROUPS CONSTITUTING THE TULASNELLOID FUNGI.—The first genus of the fungi under discussion was described almost simultaneously by three different authors, *Tulasnella* J. Schroet. (*1888*), *Prototremella* Pat. (*1888*), and *Pachysterigma* Olsen apud Bref. (*1888*).[11] The feature that attracted the attention of these authors was the strongly swollen sterig-

[11] This is the chronological order of publication; cf. Costantin (*1889*).

mata; the repetition of the spores was stressed by Brefeld and still more so by Patouillard, who rated it an even more important character than the unusual sterigmata. Later on the genus *Gloeotulasnella* von Höhnel & Litschauer (*1908b*) was introduced for the gloeocystidiate species with typically strongly inflated sterigmata. It was redefined by Rogers (*1933*: 181-182, 194), who transferred certain non-gloeocystidiate species to it, the mucous to waxy-gelatinous trama being the main character of his emendation, against the arid to somewhat waxy trama in *Tulasnella*.

Tulasnella and *Gloeotulasnella* are now often considered to constitute a special family of Heterobasidiae, viz, Tulasnellaceae, established by Juel (*1897*: 21).[12, 13, 14] For a taxonomic review of the family in this restricted delimitation and other particulars, see Rogers (*1933*); for cytological investigations, see Juel (*1897*) and Rogers (*1932*).

An important step in connection with the tulasnelloid fungi was taken by Bourdot & Galzin (*1911*; *1928*: 238) when they isolated a taxon they called *Corticium* sect. *Botryodea* Bourd. & G.[15] In their remarks they drew attention to the often considerable development of the sterigmata and the repetition of spores in certain species, both of which features reminded them of *Tulasnella*.

> "Le stérigmata dans [*Corticium flavescens* Bonord., *C. frustulosum* Bres. et *Hypochnus solani* Prill. & Delacr.] offre une anomalie fort suggestive: il est quelquefois renflés, fusoide ou ovoide (en spore sessile), exactement comme dans *Tulasnella* et certaines spores produisent une conidie obovale par un promycélium court ventral ou apical."—Bourdot & Galzin (*1911*: 247).

They also drew attention to the strong development of the sterigmata of *Corticium sterigmaticum* Bourd., which "accentue les rapprochements indiqués entre les *Tulasnella* et plusieurs espèces du groupe *Botryodea*."

This group was considered to represent a good genus and called *Botryobasidium* by Donk (*1931*: 116). It was characterized, in agreement

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12 The genus *Muciporus* Juel is based on species of *Tulasnella* grown over a resupinate species of *Poria* Pers. ex S. F. Gray *sensu lato*; it has been abandoned. Bourdot & Galzin (*1928*: 65) provisionally described "*Peniotulasnella conspersa* p.t.," a fungus with the structure of *Odontia conspersa* Bres. "avec basides à peu près sûrement tulasnellées." It has not been redescribed and will be left out of consideration.

13 Gäumann (*1926*) combined this family with two unrelated ones, Vuilleminiaceae and Brachybasidiaceae, to form the order Tulasnellales.

14 The earliest name for this family is Tomentellaceae Bref. The genus *Tomentella* Bref. is different from Patouillard's and Karsten's.

15 A corresponding group was isolated as *Tomentella* subsect. *Botrytes* Bourdot & Galzin (*1928*: 481), afterwards converted into a distinct genus, *Botryohypochnus* Donk (*1931*: 118). Moreover, Bourdot & Galzin (*1928*: 243) brought the monotypic genus *Hypochnella* J. Schroet. [*H. violacea* (Auersw.) ex J. Schroet.] into relation with their section *Botryodea*. In both these groups no repetition of the basidiospores has been observed, as is the case in a number of species of *Corticium* sect. *Botryodea*.

with Bourdot & Galzin, primarily by characters of the hyphae (large diameter, strongly stainable in cotton blue, branching at right angles), structure (ascending hyphae rather short-celled, bearing the basidia in notable terminal clusters which cause the granular appearance of the fruit-bodies), and the basidia (short-cylindrical to ovoid). The variation in the number of sterigmata was indicated ("with 2—8 thin or more or less inflated sterigmata"), as well as the fact that repetition of the basidiospores occured in some, and not in other, species (Donk, *1931*: 115). This genus was already recognized before by Brefeld (*1888*) and called *Tomentella* "Pers.," but this name is preoccupied.

Botryobasidium was treated twice by Rogers (*1935; 1943*). In his first essay he excluded some species such as *Corticium sterigmaticum* and *C. cornigerum* Bourd., referring them to *Ceratobasidium* (see below). In his second monograph he introduced *Pellicularia koleroga* Cooke into the genus. This necessitated the change of the generic name *Botryobasidium* to *Pellicularia* Cooke. The latter name is interpreted by Donk (*1954*) as a perfect example of a name based on an inseparable mixtum compositum (nomen confusum) and, hence, he rejects it as impriorable. In case one would still prefer to select one element of the mixture as *typus sensu stricto*, the choice must be the spores (identifiable as belonging to a pervading hyphomycete) rather than the hyphae (of a hymenomycete) previously selected by Rogers, if it be permissible to leave a (presumably) hypothetical gelatinous medium, very strongly emphasized by Cooke, out of account. (No repetition of basidiospores has been reported for the species now sometimes assembled under the denomination of "*Pellicularia koleroga.*")

As already briefly indicated, *Botryobasidium* is a group comprising a majority of species with normal (i.e. thin and rather small) sterigmata and with spores not exhibiting repetition, as well as species with stout sterigmata, in development intermediate between the *Tulasnella* and normal sterigmata, and with spores that do exhibit repetition. Such characters as (i) the occurrence of repetition of the spores in certain species, (ii) the plump basidia, (iii) the strongly developed sterigmata in certain species, and (iv) the general structure (arrangement of hyphae and basidia), all induced Donk (*1931*: 115) to transfer *Botryobasidium* to the Tulasnellaceae. He was aware of the fact that the family thus became almost superfluous: " . . . in so doing the most important character of the family grows blurred."

This cannot be doubted: according to current views *Botryobasidium* contains two elements, a 'heterobasidious' and a 'homobasidious' one. The

first embraces those groups of species called by Rogers "*Pellicularia*" *flavescens* (Bonord.) D. P. Rog. (inclusive of *Hypochnus fusisporus* J. Schroet.) and "*P.*" *filamentosa* (Pat.) D. P. Rog. (inclusive of *Hypochnus solani* Prill. & Delacr.); the second is made up of the rest of the genus. Let us call these groups A and B. In group A ('heterobasidious') the sterigmata are stout, sometimes about as long as (or even longer than) the basidial body; they are not typically curved outwards. In group B ('homobasidious') the sterigmata are relatively much shorter, even small or delicate, and horn-shaped, i.e. curved outwards. The sterigmata of both groups have been called sterigmata by Rogers. I, herewith, restrict *Botryobasidium* Donk (selected type species, *Corticium subcoronatum* Höhn. & L.) to this group B. For the species of group A two new genera are distinguished below, *Thanatephorus* Donk, parasitic, type species *Hypochnus solani* Prill. & Delecr., and *Uthatobasidium* Donk, saprobic, type species *Hypochnus fusisporus* J. Schroet. A third genus is considered for the "*Pellicularia koleroga*" complex.

The next genus, *Ceratobasidium* Rogers (*1935*: 4), was founded for some species with sterigmata as stout as or even stouter than in *Botryobasidium* group A (*Thanatephorus* and *Uthatobasidium*). However, this time the sterigmata were called 'epibasidia,' like previously the sterigmata of *Tulasnella*, implying that they were fundamentally different from the sterigmata of *Botryobasidium sensu lato* (inclusive of group A). None of the authors adhering to this view has bothered to explain to their embarrassed readers the differences between sterigmata and 'epibasidia' in the present case.[16] Actually there are no essential differences between these structures. Rogers, pending a better ordering of the "lower" basidiomycetes, left *Ceratobasidium* in the "Thelephoraceae,"[17] but said that it is not thelephoraceous.

A few words may be devoted here to a remarkable variation in the basidia of *Ceratobasidium anceps*. This species is capable of forming what may be called p l e u r o b a s i d i a. By this term are meant basidia that arise as lateral appendages of more or less repent hyphae. These basidia are not to be confused with those that are merely laterally sessile on their supporting hyphae and separated from these by septa across their bases.

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[16] "The basidia of *Ceratobasidium* are properly divisible into hypo- and epibasidium, the epibasidia being completely homologous with those of *Tremella* and *Tulasnella*, and not at all with the true sterigmata of the Homobasidiomycetes [inclusive of *Botryobasidium*]."—Rogers (*1935*: 3).

[17] Excluding *Thelephora* Ehrb. ex Fr. and a few related genera from the family Rogers had in mind, many authors now refer to the remainder as Corticiaceae.

Pleurobasidia are relatively broad at their bases, which appear to be two-rooted; the two spreading 'roots' are the hypha from which such a basidium arises and from which it is not separated by a cross-wall.

For *C. anceps* they were first drawn by Mrs. Gregor (*1935: f. 7*), who depicted four basidia in all, of which two are terminal, another one shows a faint sublateral inflation (the hyphal tip), while the fourth is definitely a pleurobasidium, although the hyphal termination beyond the base of the basidium is short and hardly more than a large wart (f. 7C). Afterwards this phenomenon was also observed and depicted for *C. anceps* by Jackson (*1949*: 244 *f. 1*): "Basidia short cylindric, broadly clavate, obovate or irregular . . ., often formed directly from hyphal cells when they have a truncate base drawn out at either side or to one side if formed terminally."

Recently a new genus has been published to accomodate a fungus with typical pleurobasidia, *Pleurobasidium* Arnaud (*1951*: 193 *f. 1 B, C*), type species, *P. telae* Arnaud. This fungus has a loose structure of distinct hyphae, according to the figure and to the fact that its author compared it with "*Hypochnus* Pat." The pleurobasidia are "un diverticule latérale d'une cellule terminale des ramifications ultimes"; they are quite short. The sterigmata do not remind one of those commonly found in *Ceratobasidium*, because they are thin and rather short. This may be due to Arnaud's lack of accuracy, for in all drawings of basidia in his paper not only the asymmetry of the basidiospores is ignored, but also all sterigmata are depicted as straight and stiff. In view of the very incomplete description it will be difficult without studying the specimen itself to decide whether *Pleurobasidium telae* might or might not be a species of *Ceratobasidium* in which pleurobasidia are a regular feature. It can hardly be *C. anceps* itself, for instance, because is was found "sur sac de toile grossière, pourissant sur le sol herbeux" and was thus apparently not parasitic.

Pleurobasidia are not so rare as Arnaud thought them to be. This may be learned from two papers by Jackson, who recorded them for the group of "*Peniophora*" *rimicola* (P. Karst.) Höhn. & L. (*1950a*) and for some forms of another, rather heterogeneous, series of species of Corticiaceae, but at least in part related to *P. rimicola* (*1950b*).[18] Rogers (*1935*: 32 *f. 16c*) was the first to mention the basidia of *P. rimicola* as "often with a bifurcate base" and to depict its pleurobasidium. It should be noted that in all the species in which they are found the basidia are not all invariably 'lateral' as seems to be the case in *Pleurobasidium telae*: on

[18] One species of the *Peniophora rimicola* group was published by Arnaud (*1951*: 194 *f. 1F*) as the type of a new monotypic genus, *Clitopilina striata* Arnaud. This fungus belongs to "*Corticium*" *pulverulentum* Lits. = "*Peniophora*" *pulverulenta* (Lits.) Jackson (*1950a*: 532 *f. 3*). Had Arnaud followed the basidia downwards he would have found them to be pleurobasidia, too!

the contrary they may often be 'normal,' i.e. terminal, or sessile. In exceptional cases pleurobasidia may even be found in young stages of species with a well developed subhymenium of ascending hyphae from which the basidia arise terminally at maturity.

Ceratobasidium was provisionally included in the Tulasnellaceae by Martin (*1944*: 12), but afterwards he proposed a special family, Ceratobasidiaceae, for it:

"The logical place for the family is at the base of the Tremellales. *Pellicularia* [= *Botryobasidium* s. lat.] and possible related forms should sometime constitute a coordinate family at the base of the homobasidiomycete series."—Martin (*1948*: 114).

I wonder. If all species of *Botryobasidium sensu lato* had sterigmata (instead of 'epibasidia') the logical conclusion would be rather:

1. Epibasidia. Spores exhibiting repetition: Ceratobasidiaceae.
1. Sterigmata.
   2. Repetition: A-aceae.
   2. No repetition: B-aceae, or inclusion in Corticiaceae.

Would perhaps the answer be that after all the A-aceae ought to be transferred to the Ceratobasidiaceae, which would leave the B-aceae as the family to occupy the place at the base of the homobasidiomycete series? In that case the sterigmata of the A-aceae should first be rebaptized 'epibasidia' to remain consistent. It is gratifying to find that even the staunchest advocate of applying the term epibasidia to the sterigmata of *Tulasnella* and *Ceratobasidium* has shown signs of not always being able to distinguish with certainty between a sterigma and an epibasidium when he meets one: thus, Rogers (*1943*: 114), when discussing the sterigmata of "*Pellicularia*" *filamentosa* (Pat.) D. P. Rog. (= *Hypochnus solani*, etc.) added, "or epibasidia; the evidence is not clear." The same doubt he voiced in the case of "*Corticium*" *praticola* Kotila (Rogers, *1943*: 116).

The artificiality of separating *Ceratobasidium* from *Botryobasidium* by placing the two in different families was already pointed out by Jackson:

"In the opinion of the writer *Ceratobasidium* is too closely related to *Pellicularia* [= *Botryobasidium* s. lat.], as reviewed by Rogers . . ., to justify such a wide separation in the classification of Basidiomycetes. It would seem more logical to include *Pellicularia* in the family Ceratobasidiaceae and place that family at the base of the Homobasidiomycete series. The two genera approach each other closely, especially through the parasitic species."—Jackson (*1949*: 243).

For an excellent and recent treatment of the North Central American species of *Ceratobasidium*, see Martin (*1952*: 11-15 *text-pl. 1 fs. 1-2*).

Among the species actually included in the genus are a gloeocystidiate species (see also below) and one, *Ceratobasidium terrigenum* (Bres.) Wakefield (*1952*: 64 *f. 37*), not exhibiting repetition of the spores! It would seem that the latter fungus should be excluded again.

Finally, three species (spores exhibiting repetition) with gloeocystidia and not referable to *Gloeotulasnella* were described: *Ceratobasidium fibrillosum* (Burt) Rogers & Jackson (*1943*: 327; Martin, *1948*: 113 *f. 1*), *Peniophora heterobasidioides* Rogers (*1935*: 30 *f. 15*), and *Corticium pauxillum* Jackson (*1950*: 724 *f. 9*).

Summarizing, the groups of tulasnelloid fungi are (i) *Tulasnella*, (ii) *Gloeotulasnella*, (iii) *Ceratobasidium* (no gloeocystidia), (iv) *Thanatephorus*, (v) *Utatobasidium*, and (vi) the three gloeocystidiate species with more or less stout but not strongly inflated sterigmata. The problem before us is: are all these groups closely related or do they form a heterogeneous assemblage?; and, if they are related, where should they be attached to?

SYSTEMATIC POSITION.—The gradation in size and shape of the sterigmata from *Tulasnella* to *Peniophora heterobasidioides* (with the smallest sterigmata) seems complete enough, although not without something of a break between the sterigmata of *Tulasnella* and *Gloeotulasnella* and those of the rest of the tulasnelloid fungi. The *Tulasnella* sterigma (a) shows an extreme accumulative function (and thus is the most voluminous), (b) has a cross-wall across its base, separating it from the basidial body, and (c) is the site of a division of the transitory nucleus in certain, but not in all, species. There is every reason to believe that these characters are merely different aspects of the transfer from the basidial body to the sterigmata of a single physiological function (violent discharge of the spores), which has resulted in a highly developed autonomy of the sterigmata. This condition can easily be derived from that found among the other tulasnelloid fungi. Occasional cross-walls at the bases of the sterigmata have been reported for *Ceratobasidium* (Rogers, *1935*: 4). The less voluminous sterigmata in *Tulasnella* and the most inflated in the other tulasnelloid fungi reach each other very closely. The break does not seem at all impressive to me: it is just enough to assume that upon it rests the generic separation of *Tulasnella* and *Gloeotulasnella* from *Ceratobasidium*.

Between the sterigmata of *Ceratobasidium* and the three gloeocystidiate species, and *Thanatephorus* and *Uthatobasidium* on the one hand and the 'normal,' small sterigmata of the Corticiaceae on the other, there is hardly any break.

We now arrive at the point where the taxonomic importance of the repetition of basidiospores has to be evaluated. Is it a reliable specific feature or is it to be evaluated as a generic, or even a supergeneric, one? For classificatory purposes it seems at least a good specific feature, although it sometimes appears elusive. In the much studied *Hypochnus solani* (*Thanatephorus*), repeatedly cultivated on an extensive scale in the laboratory, it has for a long time escaped detection, but has of late occassionally been noticed. However, as a rule in herbarium specimens the presence or absence of the phenomenon can easily be established.

As a generic character repetition has not been rated high. Up till the present the homogeneity of *Botryobasidium sensu lato* has never been questioned, although it included species in which the spores do or do not exhibit repetition. Recently a species has been included in *Ceratobasidium* (*C. terrigenum*) that does not form secondary basidiospores. Some species showing repetition are known that nobody has cared so far to transfer to *Ceratobasidium* (*Peniophora heterobasidioides* and *Corticium pauxillum*). Still other species which, as to their other features would not seem greatly out of place somewhere among the tulasnelloid fungi, may have been kept outside that group on account of lack of repetition.

One thing is certain: if it is not deemed justifiable to divide *Botryobasidium sensu lato* into two or more genera with and without repetition, this character has to be given up as being of generic value as regards the tulasnelloid fungi and consequently its validity, too, has to be questioned in relation to *Ceratobasidium* and to the delimitation of, say, families (Tulasnellaceae, Ceratobasidiaceae).

Granting the thesis that some odd species may have been included that perhaps later on might be referred to other groups, the tulasnelloid fungi seem, in my judgment, too closely related *inter se* to be distributed over two or more families. Since, in addition, we have been unable to find any too clear demarcation line between them and some groups not exhibiting repetition, like *Botryobasidium sensu stricto*, it would appear a wise policy to merge the tulasnelloid fungi again into the amorphous mass of Corticiaceae. This is in agreement with the view of most modern mycologists, who never have cared to recognize Tulasnellaceae and Ceratobasidiaceae as well founded families.

Rogers (*1934*: 170) and Martin (*1944*: 14; *1952*: 15) think that *Corticium sterigmaticum*, in its regularly bifurcate basidia and in its elongate spores approaches the Dacrymycetaceae,[19] especially "*Ceracea* Cragin" =

[19] Unlike Martin, I would exclude this family from the Tremellales (Tremellaceae, Auriculariaceae). It seems to deserve treatment as an order of its own.

Cerinomyces Martin (*1949*).[20] Rogers even went so far as to state that except in length of the basidial body, there is no difference in form between the basidia of this species and those of the *Dacrymyces* type. This is emphatically not the case. In the Dacrymycetaceae the basidia are, even in their probasidial stage, narrow and slender (stichic), and the sterigmata are about as wide as the basidial body. In *Corticium sterigmaticum* the basidial body is relatively much wider (chiastic?) and shorter and the sterigmata more than half as narrow. The resemblance is merely superficial.

It seems more likely that the tulasnelloid fungi are related to the Tremellaceae, a view already repeatedly expressed, although the basis for such a conclusion appears rather slender as far as our present knowledge goes. The evidence could perhaps be summarized as follows:

(i) Repetition of spores is typical of both groups. In other groups of Heterobasidiae, Auriculariaceae excepted, it is rare (or doubtful).

(ii) There are several important points of agreement between the basidia of both groups; the position of the first division spindle of the diploid nucleus is the same (chiastic); there is a close resemblance between the general shape of the basidial body of *Ceratobasidium*, *Tulasnella*, and *Gloeotulasnella* and of several species of Tremellaceae; and the sterigmata of *Ceratobasidium*, *Uthatobasidium*, and *Thanatephorus* are often matched among Tremellaceae, especially among the not, or only slightly, gelatinous resupinate species.

(iii) Sometimes the resemblance is not restricted to the basidia only. *Ceratobasidium calospora* D. P. Rog., with remarkable, very long spores, is strongly reminiscent of *Sebacina calospora* Bourd. & G. Similar spores are also found in *Gloeotulasnella calospora* (Boud.) D. P. Rog.

(iv) If one were to eliminate the septa in the basidia of certain resupinate species of Tremellaceae, one would get species not distinguishable from the tulasnelloid series as far as present definitions run.

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[20] As suggested to me by Dr. John Eriksson and after a preliminary study of some collections, I now doubt whether *Cerinomyces* really belongs to the Dacrymycetaceae. It should perhaps be transferred to the neighbourhood of such species as *Corticium terrigenum* Bres. (no repetition; recently perhaps incorrectly transferred to *Ceratobasidium*), a species which in several respects resembles *Cerinomyces*, although it has four sterigmata per basidium. In *Cerinomyces* the young basidia are too broadly clavate to be identical with those of the Dacrymycetaceae. Moreover, in the latter family the constituent elements of the fruit-body are strongly gelatinified and more or less embedded in a gelatinous substance; the individual fruit-bodies are more or less, but always definitely, rooting; the spores generally become septate and produce a certain type of small conidia. This imposing combination of characters, to which several more could be added, is not matched in *Cerinomyces*, and to all appearances outweigh the superficial resemblance of basidia and sterigmata. I would tentatively refer *Cerinomyces* to the Corticiaceae.

CONCLUSION.—After the preceding discussion, it will not be surprising that in my opinion there are sufficient reasons for separating the species with repetition of the basidiospores from the rest of *Botryobasidium*. Other important reasons for so doing (not discussed in the present paper) are the presence or absence of characteristic mycelial formations and conidial stages.

Uthatobasidium Donk, *gen. nov.*[21]

Saprobicum. Fructificatio consimilis *Botryobasidio* sensu stricto natura et structura. Basidia brevia et compacta, paulum latiora hyphis sustinentibus; sterigmata relative magna, 2—4. Sporae renovantes. Status imperfectus *Rhizoctoniae* et conidiferus ignotus.

TYPE SPECIES.—*Hypochnus fusisporus* J. Schroet. Type distribution, Fuck., Fung. rhenan. exs. No. 2396, as *Hypochnus flavescens* Bonord.

Thanatephorus Donk, *gen. nov.*[22]

Parasiticus. Mycelium formans statum *Rhizoctoniae* consistens e fibrillis vel funiculis et (plerumque) sclerotiis. Fructificatio plus minusve similis *Botryobasidio* sensu stricto natura et structura sed hyphae ascendentes basidiferentes saepe minus evolventes. Basidia brevia et compacta, subcylindrica ad obovoidea, paulum latiora hyphis sustinentibus; sterigmata relative magna, 2—4(—5). Sporae renovantes. Status imperfectus conidiferus ignotus.

TYPE SPECIES.—*Hypochnus solani* Prill. & Delacr. = **Thanatephorus cucumeris** (Frank) Donk, *comb. nov.* (basinym, *Hypochnus cucumeris* Frank *in* Ber. dtsch. bot. Ges. 1: 62. 1883).

KEY TO THE GENERA OF TULASNELLOID FUNGI

1. Sterigmata strongly inflated, highly voluminous, separated from basidial body by septa. Saprobic.
   2. Fruit-body more or less gelatinous: the constituent elements embedded. Basidia usually rather long-stalked. Gloeocystidia present in most species. *Gloeotulasnella*
   2. Fruit-body arid-pruinose to waxy: the constituent elements not embedded. Basidia rather short-stalked. Gloeocystidia lacking. . . . . *Tulasnella*
1. Sterigmata often stout, but not strongly inflated, not separated from basidial body by septa. Saprobic or parasitic.
   3. Fruit-body not typically *Botryobasidium*-like in structure; in some species continuous, mucous-gelatinous, somewhat fleshy, or waxy, in others delicate, pruinose (somewhat waxy when fresh), or a tender weft. Basidia distinctly swollen (about 2—3 × as wide as supporting hyphae), many abruptly narrowed towards bases and distinctly (although often short-) stalked above basal septa (*Tulasnella*-like). Hyphae usually rather thin, 2—6(—9)μ wide (not counting

[21] *Οὖθαρ, -ατος*, udder.

[22] *Θανατηφόρος*, death-bringing.

inflations); clamps lacking or present. Gloeocystidia (whether or not protruding) present in some species. Saprobic, or (in one species) parasitic and forming sclerotia-like bodies. . . . . *Ceratobasidium*

3. Fruit-body *Botryobasidium*-like: floccose, under the lens granulose because of separate clusters of basidia borne on stout, erect, branched, short-celled, ascending hyphae (rarely reduced in some parasitic forms); neither mucous-gelatinous, fleshy, or waxy, nor continuous. Basidia plump and short, hardly swollen, their bases never constricted or substipitate, broadly attached (like in *Botryobasidium isabellinum*). Hyphae (rather) stout, 6—12 μ wide; clamps lacking. Gloeocystidia lacking.
   4. Saprobic; no *Rhizoctonia* stage. . . . . *Uthatobasidium*
   4. Parasitic; mycelium often soil-harboured and developing into a *Rhizoctonia* stage: tending to grow in fibrils or strands and usually forming sclerotia-like bodies. . . . . *Thanatephorus*

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