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TAXONOMIC PROBLEMS IN THE HETEROBASIDIOMYCETES

B. Lowly*

Summary

Certain taxonomic problems of long standing within the heterobasidiomycete complex are reviewed and recommendations for a rearrangement in the classification of tremellaceous fungi (sensu lato) are suggested whereby the subclass Heterobasidiomycetidae is erected and includes the holobasidiaceous Dacrymycetaceae and Ceratobasidiaceae as well as the Tulasnellaceae, the latter embracing such genera as *Metabourdotia* and *Pseudotulasnella*, which have incompletely divided basidia. The Ceratobasidiaceae as newly constituted, includes besides *Ceratobasidium* the genera *Oliveonia*, *Thanatephorus*, and *Uthatabasidium*. meta

The problem of the taxonomy of the genera *Tulasnella*, *Gloeotulasnella*, *Ceratobasidium* and *Cerinomyces* has been vigorously debated for over a decade. These genera, (among others,) share the distinction of occupying a position that may only be described as intermediate between the subclasses Heterobasidiomycetidae and Homobasidiomycetidae, hence the difficulty in assigning them unequivocally to either of these categories. Criteria are available that are meant to define the limits of these subclasses and to enable the taxonomist to reach a decision in accordance with his best judgment, but on occasion taxa are encountered that obstinately refuse to occupy a niche prepared for them, howsoever cunningly. The chief purposes of this paper are to review some of the opinions that have led to changes in basidiomycete taxonomy, with special reference to the complex of genera above named which occupy a precarious borderline position between the subclasses, and to propose a possible solution to this taxonomic problem of long standing. In an attempt to summarize the considerable body of opinion that has developed during the debate on pertinent issues, I have preferred to let authors speak for themselves and have intruded only such comments as have seemed necessary to carry the argument forward in a coherent manner. Before proceeding with the dialogue, however, it is important to recall briefly the background of the problems to be dealt with so that the argument may be followed not by the specialist alone but also by taxonomists whose interests may touch only lightly on the specific matters to be discussed. -and associated

The classification of the Basidiomycetes proposed by Fries (1874) was based on macroscopic characteristics which emphasized the configuration of the hymenium and in this work he divided the Hymenomyces into six "Ordines" (corresponding more or less to our Families) separated by a simple dichotomy as follows: "Hymenio effigurato: Agaricini (lamellato), Polyporei (poroso), Hydnei (aculeato); Hymenio laevigato: Thelephorei (horizontali intero), Clavarei (verticali amphigeneo), Tremel-linei (supero; gelatinosi)." Fries's indispensable studies, beginning with the publication of the first volume of his "Systema" (1821), dominated the field of taxonomic mycology, of which he was the founder, for more than half a century and their influence is still far-reaching today. Patouillard's "Hyménomycètes" of (1887) and especially his "Essai Taxonomique" (1900) are correctly considered to be the works that had the greatest influence in shaping subsequent taxonomic systems of the Basidiomycetes and which offered the first fundamental departure from the Friesian CO
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Taxonomía de los Heterobasidiomicetos

B. Lowy

Los Tremellales constituyen un conjunto heterogenico de los hongos lo cual se ha mantenido separado de los otros Basidiomicetos desde los tiempos de Patouillard y Brefeld a fines del siglo diezinueve. Son distinguidos por la gran variabilidad estructural de sus basidios, la manera unica en que germinan sus basidiosporas (por el proceso de repeticion), la condicion inflada de sus esterigmas y por los basidiocarpos mismos que en su mayor parte son gelatinosos o cerosos.

Se forma una subclase nueva - Metabasidiomycetidae - para contener taxa que son intermedios o transicionales (con basidios aseptados o solo parcialmente septados) entre las subclases Heterobasidiomycetidae y Homobasidiomycetidae. Estan colocadas en la nueva subclase las familias Tulasnellaceae, Dacrymycetaceae y Ceratobasidiaceae.

Se considera que la subclase Heterobasidiomycetidae constituye el grupo mas primitivo donde se encuentra taxa muy diversos en su morfologia y es entre los hongos saprobicos de esta subclase de que muy probablemente se ha formado por la evolucion el basidio estable de los Homobasidiomycetidae. La subclase Heterobasidiomycetidae esta caracterizada por sus basidios completamente septados en su madurez (el metabasidio) y incluye las familias Auriculariaceae, Hyaloriaceae, Phleogenaceae, Sirobasidiaceae y Tremellaceae.

Se presenta en este trabajo ciento cuarenta y cuatro especies conocido de la America Neotropical. Se muestra por primera vez la distribucion geografica de todas las especies de esta zona. Esta incluido en la parte sistematica, claves a las familias, generos y especies y se presenta tambien algunos fotos y dibujos que muestran las caracteristicas macroscopicas y microscopicas de los principales generos.

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Septate Holobasidia!

In response to a recent paper by Talbot (Taxon 17: 620-628. 1968) in which he discusses my proposal (Taxon 17: 118-127. 1968) for a re-classification of the heterobasidiomycetous fungi, the following comments will serve to further clarify my interpretation of the hetero- vs homo-basidiomycete taxonomic problem and to point out what I consider to be some shortcomings of Talbot's counterproposals.

Talbot considers it "against the principles of taxonomy to create a taxon . . . for intermediate forms". If this were conceded, an effective solution to a taxonomic problem would have to be discarded because of the rigidity of rules which have not anticipated that such a solution may exist. But it is a moot question whether or not a "principle" of taxonomy is involved. I would consider it more in the nature of a convention. When in spite of all efforts, a problem cannot be solved by conventional methods other useful approaches must be explored. In my judgement Occam's razor would seem to be the "principle" of choice.

A conspicuous example of an attempt to use a cytological criterion for the foundation of taxonomic categories in the Basidiomycetes was its application to the chiasmobasidium and the stichobasidium. This dichotomy proved to be unsound because spindle orientation in some species demonstrably did not conform to the definitions originally provided. I do not infer that this must be true in all cases. On the contrary, cytological evidence must continue to be sought and applied when appropriate to the better understanding of taxonomic problems. Talbot has already drawn attention to the possibility that the septa formed at the bases of sterigmata in

Tulasnella may turn out to be of the type he defines as "primary", "a hypothesis which would be tested by electron microscopy." Let us for a moment assume that this alternative eventually proves to be true. The basidium of Tulasnella would thereby be converted to a phragmobasidium and would be transferred to the "Phragmobasidiomycetes". If, however, it was found that the sterigmatal septum was "adventitious", the genus would then find its place among the "Holobasidiomycetes". It should be noted that according to this proposal, no other criterion whatever would be required to decide this taxonomic question--a matter of difference between classes! As opposed to the use of this single criterion; the occurrence of inflated sterigmata and the germination of basidiospores by repetition, two basic characteristics indisputable associated with Tulasnella, would not only be relegated to secondary importance but would be reduced to meaningless attributes.

The distinction between primary and adventitious septa rests on cytological evidence. In order to distinguish Talbot's phragmobasidium (which to the observer using light microscopy may appear to be septate but which in reality may be only adventitiously so and therefore merely an illusion) from a holobasidium, the taxonomist must first determine whether the septa have been formed as a result of nuclear division by ". . . constriction, true mitosis or meiosis" . . . or whether they are "formed in the absence of true mitosis or meiosis, . . . especially in association with changes in the local concentration of cytoplasm as it moves from one part of the fungus to another."

Let us examine the taxonomic consequences if we ignore the nature of the septum and simply apply the Patouillardian criteria without restriction.

Of the three principal criteria, two of them (inflated sterigmata and basidiospore repetition) apply directly to Tulasnella and we cannot escape the conclusion that Tulasnella viewed in this way is a heterobasidiomycete. In my earlier paper (1968) I considered Patouillard's criterion of basidial septation (regardless of type) as critical to the meaning of a heterobasidiomycete. Talbot states that "without specifying the kind of septation, this criterion is worthless." This conclusion is reached even though the criterion in Patouillard's sense has been one of the most successful devised for differentiating heterobasidia and every taxonomic system of merit since 1900 has taken it into account. Talbot's redefinition of the septum leads him to say that "a holobasidium can indeed be a divided basidium", the ambiguity of which scarcely needs additional comment. Yet Talbot finds the name "Metabasidiomycetidae" which I have chosen for a new subclass, "an unfortunate choice as it could remind one of the term metabasidium." What then is to be said of equating a "holobasidium" with a "divided basidium"? If by virtue of the kind of septum it produces, a basidium which is septate may nevertheless be termed a holobasidium (Tulasnella sensu Talbot) is not a certain confusion implicit here? It would seem desirable at least for the sake of clarity to adopt another term for such a basidium, perhaps hemiphragmobasidium, pseudophragmobasidium or even simulacrophragmobasidium, in order to avoid the inadmissible use of the term holobasidium in more than one sense.

In a previous paper Talbot (*Bothalia* 6: 262. 1954) defined the following terms which now require further comment. Holobasidium--"An unseptate basidium. It is most common in homobasidiomycetes, but is sometimes encountered in heterobasidiomycetes, e.g. in Ceratobasidium and Dacrymycetaceae." The inclusion at that time, of the Dacrymycetaceae and

Ceratobasidium (Ceratobasidiaceae) in the heterobasidiomycete complex, was a recognition of the basic correctness of Patouillard's approach. Removing these taxa to the "Holobasidiomycetes" (still less justified in the case of Tulasnella) is a reversal of Talbot's previous interpretation and it is in effect a reductio ad absurdum. Phragmobasidium--"A basidium which is divided by septa. The metabasidium is divided into a number of cells (usually four) by cruciate or parallel septa after meiosis, or in some instances the sterigmata are separated from the metabasidium by basal septa." ". . . antithesis of a holobasidium." There is no mention here of the kind of septa produced. Therefore, if Talbot's own criterion is applied to this definition, then it must be "worthless". But I seriously doubt that many taxonomic mycologists would so rate it. The reason they would not do so is that the definition as it stands is immediately comprehensible, directly applicable and unambiguous.

I also recognized that the septum sometimes formed in Ceratobasidium was of the "adventitious" type (loc cit p. 126), so I cannot be accused of overlooking what Talbot considers to be a point of fundamental importance. Let me pursue this by citing the following hypothetical circumstance. Assume that a species of Tremella was found to produce septa in a aberrant manner--that in fact the septa were "adventitious" (sensu Talbot) but that all other characteristics were those usually associated with conventional Tremella spp. In accordance with the cytological criterion, this Tremella, though it may have long, inflated sterigmata, basidiospores that germinate by repetition and be possessed of a highly gelatinous basidiocarp, would then (by Talbot's definition) be identified as a holobasidiomycete. Would mycologists be content with this disposition? Would it be correct? It is

very doubtful. No single criterion has yet been discovered which is both sufficient and necessary to delimit the heterobasidiomycetes. Their most fundamental attribute is variability of the basidium as opposed to the relative stability of the basidium in the homobasidiomycete complex and the establishment of the Metabasidiomycetidae is a reflection of this reality.

Talbot asks "how swollen must sterigmata be to indicate a Heterobasidiomycete?" Precise lower limits cannot be established but this is not an impediment since it is the combination of characters (as I have tried to define them for the Heterobasidiomycetidae and Metabsiciomycetidae) that must decide the question. Some species of Septobasidium, Platygløea and Helicogloea produce short, subulate sterigmata, but they are clearly recognizable as heterobasidiomycetes just the same.

Talbot's artificial class "Teliomycetes" was erected "principally on the basis that their teleutospores . . . are produced in sori rather than in typical basidiocarps." This really compounds the difficulties of his classification and was proposed to "avoid the necessity of dividing the Phragmobasidiomycetes into two subclasses", a rather arbitrary basis for establishing a new class.

Talbot has taken the precaution, quite correctly, of emphasizing that his proposals are "provisional", and made with "some diffidence". I believe his recommendations are untenable for the reasons indicated. It is for working taxonomists to decide which is the best course to follow.

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Neotropical Tremellales

B. Lowy

The Tremellales constitute a heterogeneous assemblage of fungi that has traditionally been separated from the homobasidiomycetes since the studies of Patouillard (1887) and Brefeld (1888), although the morphological diversity of tremellaceous basidia was first elucidated by Tulasne (1853). The major distinguishing characteristics of the Tremellales are the great structural versatility of the basidium, basidiospore germination by repetition, enlarged to grossly inflated sterigmata and a predominantly gelatinous or waxy basidiocarp.

A new subclass, Metabasidiomycetidae, is established to contain taxa that are transitional between the homobasidiomycete and heterobasidiomycete complexes and includes the Tulasnellaceae, Dacrymycetaceae and Ceratobasidiaceae.

The Heterobasidiomycetidae are interpreted as representing the more primitive group with highly diversified basidia including types from which the more stable holobasidium may have been derived and the subclass is reserved for taxa having completely divided basidia such as characterize the Auriculariaceae, Hyaloriaceae, Phleogenaceae, Sirobasidiaceae and Tremellaceae.

One hundred forty-four species are reported from neotropical America, 76 of which are restricted to the tropical zone. The geographical distribution of all species has been mapped and drawings showing pertinent microscopic details of representatives of the eight families treated are also presented.

Taxonomic Problems in the Heterobasidiomycetes and
Suggestions Toward a Solution

B. Lowy (Baton Rouge)

The problem of the taxonomy of the genera Tulasnella, Gloeotulasnella, Ceratobasidium and Cerinomyces has been vigorously debated for over a decade. These genera among others, share the distinction of occupying a position that may only be described as intermediate between the subclasses Heterobasidiomycetidae and Homobasidiomycetidae, hence the difficulty in assigning them unequivocally to either of these categories. Criteria are available that are meant to define the limits of these subclasses and to enable the taxonomist to reach a decision in accordance with his best judgment, but on occasion taxa are encountered that obstinately refuse to occupy a niche prepared for them, howsoever cunningly. The chief purposes of this paper are to review some of the opinions that have led to changes in Basidiomycete taxonomy, with special reference to the complex of genera above named which occupy a precarious borderline position between the subclasses, and to propose a possible solution to this taxonomic problem of long standing. In an attempt to summarize the considerable body of opinion that has developed during the debate on pertinent issues, I have preferred to let authors speak for themselves and have intruded only such comments as have seemed necessary to carry the argument forward in a coherent manner. Before proceeding with the dialogue, however, it is important to recall briefly the background of the problems to be dealt with so that the argument may be followed not by the specialist alone but also by taxonomists whose interests may touch only lightly on the specific matters to be discussed.

The classification of the Basidiomycetes proposed by Fries (1874) was based on macroscopic characteristics which emphasized the configuration of the hymenium and in this work he divided the Hymenomycetes into six "Ordines" (corresponding more or less to our Families) separated by a simple dichotomy as follows: "Hymenio effigurato: Agaricini (lamellato), Polyporei (poroso), Hydnei (aculeato); Hymenio laevigato: Thelephorei (horizontali intero), Clavarei (verticali amphigeneo), Tremellinei (supero; gelatinosi)." Fries's indispensable studies, beginning with the publication of the first volume of his "Systema" (1821), dominated the field of taxonomic mycology, of which he was the founder, for more than half a century and their influence is still far-reaching today. Patouillard's "Hymenomycetes" of (1887) and especially his "Essai Taxonomique" (1900) are correctly considered to be the works that had the greatest influence in shaping subsequent taxonomic systems of the Basidiomycetes and which offered the first fundamental departure from the Friesian approach. Nevertheless, Brefeld's "Untersuchungen" (1888) should not be lightly dismissed. Concerning it Patouillard (1900:2) said the following: "Depuis lors, les remarquables travaux de Brefeld sont venu confirmer notre maniere de voir et ses Autobasidiomycetes et Protobasidiomycetes correspondent sensiblement aux deux groupes que nous avions indiqués." Both men arrived independently at the same conclusion, namely that the Basidiomycetes should be divided into two groups, one for those having septate basidia, the other for those with aseptate basidia. It is Patouillard's (1887) terms, Heterobasidies and Homobasidies, that are still in use. In addition, Patouillard (1900) established the Aphyllorphoraces (Aphyllorphorales) from which he excluded the gilled fungi, the boletes and the "Cantharellies" of his Homobasidies.

Included in his Heterobasidies were the Families Auriculariaceae, Tulasnellaceae, Tremellaceae and Caloceraceae, a disposition that remained essentially unchallenged until a relatively recent date, and modern authors have adopted his Aphylophorales with little modification. But it was not until Bourdot and Galzin (1928) followed Patouillard's innovations that these were brought to the attention of mycologists outside of France.

Since what follows is mostly concerned with fungi having basidia that depart from the morphological types associated with typical Homobasidiomycetes, it is appropriate to draw attention to the brilliant work of the Tulasnes beginning with (1853) who published the first detailed studies which emphasized basidial variations that have since become the hallmark of the Heterobasidiomycetes. These include variations in septation and shape of the basidium (super-numerary sterigmata, for example, are illustrated in the 1853 paper) and the formation of "spores secondaires", the process later referred to by Patouillard (1900) as spore "germination par renovation", an expression now commonly designated in English as "germination by repetition", first published by Rogers (1933:183) at Martin's suggestion. Donk (1958:105) has expressed doubts about the propriety of using the word "germination" in this context. Brefeld (1888) also noted and illustrated the formation of "secundarspore" among his Protobasidiomycetes, adopting the terminology of Tulasne, and his further debt to Tulasne is evident from the frequency with which the latter is referred to in the "Untersuchungen". For his part, Patouillard (1900:2) acknowledges the importance of Tulasne's contributions in this way: "C'est a Tulasne que revient l'honneur d'avoir entrevu la valeur des

caracteres fournis par ces elements ou basides, et a une epoque deja lointaine, il indiqua la separation des Tremellines en un groupe special." Patouillard's classification of his Heterobasidies included two families, Auriculariaceae and Tremellaceae, with divided basidia and two families, Tulasnellaceae and Caloceraceae, (Dacrymycetaceae in the modern sense), with aseptate basidia. The two latter families were excluded from the Homobasidies in spite of the fact that Patouillard clearly identified them as having undivided basidia and in his remarks under "Tulasnellaces" (1900:26, 27) he offers the following justification for including them with the Heterobasidies: "Bien que n'ayant pas les basides munies de cloisons comme les deux familles precedentes, ce petit groupe est néanmoins inseparable des Heterobasidies, tant a cause de ses spores qui germent en se renouvelant, que par ses basidies si caracterisees par le volume enorme qu'acquierent les sterigmates avant de developper les spores." Present day observers agree that the mature basidium of the Tulasnellaceae have their sterigmata separated from the rest of the basidium by septa. But Patouillard's illustration (op. cit.:27) of Prototremella Tulasnei Pat. (= Tulasnella Schroeter apud Patouillard) shows aseptate basidia and no doubt he was in error on this detail. Had Patouillard observed the septa, his reasons for placing the Tulasnellaceae among the Heterobasidies could only have been fortified. But the more significant point is that even in the absence of septa in the basidium, he felt compelled, for the reasons stated, to identify the Tulasnellaceae with the Heterobasidies. Interestingly enough, there is currently no unanimity regarding the interpretation of the septa in tulasnellaceous basidia and this continues to be a critical point in arguments that have been advanced to justify classifying these fungi with the

Homobasidiomycetes. Donk (1964:213) deemphasized the importance of septa in the Tulasnellaceae and stated his opinion that "In Tulasnella the protosterigmata become separated from the basidial body by such adventitious septa across their bases." Also, "Such secondary septa in the basidial body are now known to occur in some other species of Aphyllophorales and even in some agarics. Likewise incidental adventitious septa are formed under abnormal conditions, for instance in the sterigmata of Tulasnella and Dacrymyces when the basidia become immersed in water. In none of these cases does the presence of the secondary septa make it necessary to call the holobasidium a phragmobasidium." This is a recurrent theme to which we shall have occasion to return.

Patouillard (1887) included 11 genera in the Heterobasidies. Under Dacrymyces Nees he notes: "Basidies d'abord cylindriques puis fourchues, avec ou sans cloisons transversales, a deux sterigmates continus ou septes." Transverse septa are described and illustrated in the genera Guepiniopsis Pat. and Calocera Fr. (op. cit. Pl. IV, Figs. 8, 10, 11) and one is left with the impression that the presence of septa in these genera was considered to represent the normal condition. In 1900, however, Patouillard omits any reference to the occurrence of septa in these genera and his figures (1900: figs. 20, 21) show only aseptate basidia, which confirms with current interpretations. That is to say, that in the Dacrymycetaceae, the presence of septa in the mature furcate basidia are to be regarded as distinctly anomalous. Nevertheless they are significant because they may be thought of as an atavistic character which reflect the ancestral condition of the Dacrymycetaceae and their origin from a phragmobasidial prototype.

We may now make explicit what has already been implied regarding the diagnostic features of the Heterobasidiomycetes. Patouillard's classification underscored the following criteria. 1) Basidia septate, 2) Basidiospore reproduction "par renovation", 3) Basidia with swollen sterigmata, 4) Basidiocarp more or less gelatinous. These criteria do not have equal weight but are listed in what I consider to be the descending order of their importance. A leading question may now be asked. Must all the criteria be met for a fungus to be classified as a Heterobasidiomycete? I believe there would be unanimous agreement among taxonomists that if the first three criteria were met, the answer must be affirmative. The suggestion has never been made that species of Aporpium, Eichleriella, Phleogena, Tremellodendron or Septobasidium be removed from the Heterobasidiomycetes because they may lack a conspicuously gelatinous basidiocarp. On the other hand, the Family Dacrymycetaceae (sometimes elevated to the rank of Order) is certainly holobasidiaceous yet there is almost universal agreement that with few or no exceptions, it is to be excluded from the Homobasidiomycetes. Now should we encounter a genus that is neither phragmobasidious nor has a notably gelatinous basidiocarp but which demonstrated "repetition" of its spores and has swollen sterigmata, a question might arise regarding its most appropriate taxonomic position. Ceratobasidium (to be discussed below) is such a genus, so it is not surprising that conflicting opinions have been expressed concerning it.

With the creation of the genus Ceratobasidium, a new phase in the discussions of the heterobasidium vs holobasidium was begun. Ceratobasidium was established by Rogers (1935:4) who described it as follows. "Fructification resupinate, tenuous; subiculum scanty, the hyphae

distinct, loose; hypobasidia subglobose or short, stout claviform, aseptate, nor forming a compact hymenium; epibasidia stout, elongate, more or less cornuate or flexous, occasionally with an adventitious septum, spores germinating by repetition." Rogers also stated that "The affinities of the genus are with the former subclass (Heterobasidiomycetes) where at present it has no place, either among the Tremellaceae, the Tulasnellaceae or the Dacrymycetaceae. Neither is it thelephoraceous; but among the Thelephoraceae it may well be left until a better ordering of the lower basidiomycetes permits the more acceptable disposition of their numerous badly placed forms."

An attempt at a "better ordering" was soon to come and the pertinent details concerning it will shortly be presented. Meanwhile, it should be noted that the genera Ceratobasidium and Tulasnella have frequently been linked in discussions on the nature of the holobasidium-heterobasidium complex. Regarding Tulasnella, Rogers (1932:101) observed: "The autobasidiomycete affinities of Tulasnella, perhaps equally strong, have been recognized in some degree by all investigators of this genus." Elsewhere, Rogers (1933:181) comments: "The septation of the basidium and the germination of the basidiospores of all species by secondary spores mark the Tulasnellaceae as heterobasidiaceous." A few years later, Linder (1940:442) made the following pertinent comments. "If the Tremellaceae are briefly surveyed, it will be found that within the family there is considerable variation in the septation of the basidium, both as regards to orientation and to number of septa. Since one or two or even three of the longitudinal septa may be lost, there should be no reason why all the septa may not, and when this happens the resulting basidium is similar to that described by Rogers for

Ceratobasidium and Tulasnella." Further animadversions on the Ceratobasidium-Tulasnella relationship were made by Martin (1945:534). "The differences between the Tulasnella basidium and the cruciate-septate type, while very real, should not be overemphasized." and "...the resemblance of Ceratobasidium to the species of Pellicularia (Botryobasidium) make it possible to connect the genus with the whole series of Homobasidiomycetes. On the other hand, aside from the fact that the epibasida are not cut off from the hypobasidium by septa, they are in every respect so like the tulasnellas that in a recent treatment I felt justified in including them in the Tulasnellaceae."

The next stage in the peregrinations of Ceratobasidium was the severing of the genus from its former close association with Tulasnella with the establishment of the family Ceratobasidiaceae by Martin (1948:114) who on this occasion made the following observations. "I have long felt that the proper taxonomic position of Ceratobasidium would be to place it in a separate family and have hesitated only because I disliked to erect a monogeneric family. After ample time for consideration, however, I fail to see any other satisfactory solution and therefore formally propose: Ceratobasidiaceae fam nov." The characteristics of the family were diagnosed as follows. "Resupinate, corticioid fungi, with basidia clearly divided into hypo- and epibasidia; hypobasidia globose or short clavate, aseptate; epibasidia thick, more or less inflated at center, usually continuous with the hypobasidium, occasionally cut off by a basal septum; spores germinating by repetition.The logical place for the family is at the base of the Tremellales. Pellicularia and possible related forms should sometime constitute a coordinate family at the base of the Homobasidiomycete series." Shortly

thereafter, Jackson (1949:243) included the genera Ceratobasidium and Pellicularia in the new family Ceratobasidiaceae but differed from Martin's view regarding the appropriate position to which it should be assigned. "In the opinion of the writer, Ceratobasidium is too closely related to Pellicularia as reviewed by Rogers to justify such a wide separation in the classification of the 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 genera approach each other very closely, especially through the parasitic species." Martin (1952:12) then commented on Jackson's stand: "There can be no doubt of the close affinity of the two genera, but there can also be little question of the close relationship of Ceratobasidium to Tulasnella."

One of the chief obstacles in deciding the most appropriate taxonomic position for the fungi under discussion arises from differences in interpretation of sterigmata. When Neuhoff (1924) introduced the term "epibasidium" for the elongated, inflated, spore-bearing structures of tremellaceous fungi (sensu lato), opposing views were ~~seen~~ presented when it became apparent that a certain ambiguity existed in the manner in which the term was applied to basidial parts that were not strictly homologous, exemplified by the "epibasidia" of Auricularia and Tremella. It was therefore suggested by Talbot (1954) and Donk (1954, 1956, 1958) that the term be abandoned. Martin (1957) opposed this rather drastic recommendation and the question of the correct interpretation of sterigmata (epibasidia sensu Neuhoff) became a central point in the debate that followed. Now there appeared to be some doubt regarding the justification of the family Ceratobasidiaceae and Talbot (1954:259, 260) argued as follows. "If the sterigmata are called

epibasidia in Tulasnella and Ceratobasidium, but sterigmata in Pellicularia (which includes species such as P. flavescens with sterigmata no different from the Ceratobasidium epibasidia) one is bound to establish a special family Ceratobasidiaceae." The following observations in the same paper stress the matter of ambiguity of the Neuhoff terminology. "The genus Ceratobasidium is placed as a heterobasidiomycete with a primitive type of holobasidium. This assignation by Rogers and Martin is probably correct, as indicated by the germination of the basidiospores by repetition. But suppose the point were controversial and it could be held that these were homobasidia. If they were heterobasidia, Rogers' terminology provides for a hypobasidium surmounted by a number of stout epibasidia. If they were homobasidial, the same basidia would be said to consist of basidia with four stout sterigmata. Donk's terminology for both homo- and heterobasidia of this type is inflexible. For him the basidia of Ceratobasidium consist of a metabasidium and four sterigmata, no matter which subclass is to receive the genus."

I believe it is clear from the foregoing statements that the core of the arguments center around the transitional nature of the basidia (between heterobasidium and homobasidium) quite apart from the terms that may be applied to their various parts, and this has been recognized by all who have participated in these discussions. A further attack on the position of genera thought of by many taxonomists (probably the majority) as being best classified with the heterobasidiomycetes was made when Donk (1956:375) considered transferring the genus Cerinomyces, traditionally included in the Dacrymycetaceae to the Corticiaceae. He stated his position in the following way. "...I now doubt whether

Cerinomyces really belongs to the Dacrymycetaceae.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 fruitbody 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 provide 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 outweighs the superficial resemblance of basidia and sterigmata. I would tentatively refer Cerinomyces to the Corticiaceae." Finally, Donk (loc. cit.) "...rejects the families Tulasnellaceae and Ceratobasidiaceae and includes them and the other tulasnelloid fungi in the Corticiaceae, which is still a heterogeneous group."

A reaction to this proposal was not long in coming. Martin (1957: 25) states the case for the opposition as follows: "Because of what I regard as its close relationship to the Tulasnellaceae, and to the Dacrymycetaceae through Cerinomyces, I prefer to class Ceratobasidium with the heterobasidiomycetous fungi. Donk's suggestion that Cerinomyces should be removed from the Dacrymycetaceae to the Corticiaceae seems to me utterly fantastic and completely without merit.For the present, I merely repeat that while Ceratobasidium shows strong evidence of close relationship with both the Tulasnellaceae and Corticiaceae, it cannot be fitted, without undue violence, into either family. If this view is held (and I hold it), then there is nothing to do but place it in a special family. ...Despite the fact that Donk recognizes that the swollen, spore-like bodies which produce basidiospores in Tulasnella and

Gloeotulasnella are definitely cut off by septa from the basal portion before the basidiospores are produced, he is forced by his peculiar interpretation to call them holobasidia, that is, that they are divided undivided basidia. Surely, this is to make the distinction between phragmobasidia and holobasidia meaningless."

Further comment on the genus Cerinomyces came in the following year from Erikssen (1958:47): "There are more close affinities to the genus Ceratobasidium, sometimes placed in Corticiaceae, sometimes in Tremellaceae, therefore I hesitate to place the genus among the Dacrymycetaceae. It seems to be best placed in Corticiaceae. If the number of sterigmata were four, I am sure that nobody would consider it a dacrymycetaceous fungus.I have given Cerinomyces a place in Corticiaceae, but no doubt it is a matter of much uncertainty."

Eriksson further observes: "The difference between Ceratobasidium and species of Botryobasidium with related genera (esp. Uthatabasidium) is, however, very slight and can hardly be said to form a limit between two families or between two orders."

Why does Donk insist that the Tulasnella basidium is a homobasidium, when it clearly has its sterigmata (epibasidia) separated by septa from the rest of the basidial body?? It is a matter of definition. Donk (1958:97) explains: "In my opinion, in a phragmobasidium the basidial body becomes divided into cells by true cross-walls. In Auricularia the resulting cells are superimposed, in Tremella the basidia appear (usually) cruciately divided into four cells if viewed apically, or the cells may be less regularly arranged. In Tulasnella and Gloeotulasnella Höhn. & Litzch. the basidial body remains undivided, hence with my definition, I cannot call them phragmobasidia by any stretch of

imagination. I cannot accept a definition, like one implied by Martin, that calls for homologizing the septa separating the sterigmata from the basidial body in Tulasnella and Gloeotulasnella with the septa in the basidial body of Auricularia and Tremella."

Donk (loc. cit.) next turns his attention to intergrading forms between the heterobasidiomycetes and the homobasidiomycetes, observing that "the gap between Tulasnella and the Corticiaceae has become filled with an imposing number of intermediates and Tulasnella now stands but as an extreme term in an intergrading series, at least if one arranges these forms according to the degree of development of their sterigmata."

And in a later paper Donk (1964:225) remarks: "In my opinion the morphological differences between the Tulasnella, Ceratobasidium and Uthatabasidium sterigmata are too insignificant to justify placing these genera in three different families, although the Tulasnella basidium as a whole represents a strongly advanced "physiological" type." Donk (1964:261-262) now foresees the abolition of the family Ceratobasidiaceae and summarized his opinion as follows: "The introduction of the Ceratobasidiaceae as a distinct family from both the Tulasnellaceae and Corticiaceae rested on the emphasis of the walls across the bases of the sterigmata of the Tulasnellaceae, and on calling the sterigmata in Tulasnella and Ceratobasidium epibasidia and in the other "tulasnelloid fungi", like Thanatephorus and Uthatabasidium, sterigmata. I cannot find any reason for not calling them all sterigmata, and therefore there seems no good reason why the Ceratobasidiaceae (as delimited at present) should not be abolished."

The discovery of the tropical genera Metabourdotia Olive (1957) and of Pseudotulasnella Lowy (1964) which were found to have basidia

with only partial or fragmentary septa, called further attention to forms that are frankly intermediate between the subclasses and to the difficulty of placing them satisfactorily into either of these categories.

Olive (1957:429) described his new genus as follows: "Fructification resupinate, waxy-pruinose; gloecystidia present; basidia typically broadly clavate, septate apically, septa incomplete below; basidiospores germinating by repetition." Olive has the following comments to make on the taxonomic position of the genus: "The new genus is believed to occupy a position of primitiveness in the Ceratobasidiaceae, indicating a phylogenetic connection of this family with the Tremellaceae.

....Metabourdotia might just as logically be classified as an advanced member of the Tremellaceae and there can be little doubt of its affinity with that family.The discovery of Metabourdotia strongly supports the conclusion of Martin that the Ceratobasidiaceae are closely allied to the Tremellales. At the same time there can be little doubt that Jackson is correct in his statement regarding Pellicularia and Ceratobasidium that "the two genera approach each other very closely, especially through the parasitic species."

Lowy (1964:696-699) described the genus Pseudotulasnella as follows: "Fructification resupinate, waxy-gelatinous; gloecystidia lacking; probasidia subglobose, apically cruciately septate, incomplete septa below; mature basidia clavate-capitate, producing tulasnelloid sterigmata; basidiospores germinating by repetition." The following comments are also pertinent. "...it is evident that Pseudotulasnella bridges the gap between the Tulasnellaceae and the Tremellaceae. Moreover, Metabourdotia might easily be classified as a member of the Tremellaceae

rather than of the Ceratobasidiaceae where it is more or less arbitrarily placed by Olive. It would seem more at home in the Tremellaceae, having both elongated sterigmata and partially septate basidia, whereas its inclusion in the Ceratobasidiaceae may be justified on the basis of its sharing only one of these characteristics, namely the elongated sterigmata. The exclusion of fungi having septate or partially septate basidia from the Ceratobasidiaceae would also have the advantage of maintaining the family as a more homogeneous group. If Metabourdotia is so considered, it provides us with a significant link through which a transition from the Tremellaceae to the Tulasnellaceae by way of Tulasnella may have been effected, establishing at the same time, a convincing intermediate stage between the Tremellaceae and the Ceratobasidiaceae." I have since reconsidered my position on this matter and now believe that it would be more desirable to include Metabourdotia in the Tulasnellaceae rather than in the Tremellaceae because I would prefer to maintain the homogeneity of the Tremellaceae, including in it only taxa with completely divided basidia. Nevertheless, the relationship of Metabourdotia to the Tremellaceae remains close.

From this review, I believe it is apparent that a workable solution to the problem of intermediate forms is urgently needed. A proposal was offered by Talbot (1965:371) who summarized his recommendations in this manner. "The genera dealt with are divided among the Tulasnellaceae and the Corticiaceae, the family Ceratobasidiaceae being regarded as superfluous. The subclasses Heterobasidiomycetes and Homobasidiomycetes are not recognized, as it is impossible to suggest characters by which they may consistently be delimited. The characters normally used for delimiting these subclasses are, however, still regarded as of great importance for separating lower taxonomic categories."

I cannot concur in the suggestion that the two subclasses be abolished. This is not because the action seems too unorthodox, but because in my judgement it does not solve the problem. I am in accord with the view that the Heterobasidiomycetidae as presently constituted is too heterogeneous an assemblage (including as it does many intermediate forms) to be maintained as a completely effective entity, but there seems little merit in retrogressing to a pre-Patouillardian system and trying to breathe life into a fossilized scheme that has been abandoned by working taxonomists for half a century. While the evidence shows the inadequacy of the present taxonomic arrangement, notably in its inability to cope with fungi having such troublesome attributes as make their assignation to either of the existing subclasses difficult or impossible, the abolition of those subclasses is not in my opinion the desirable answer. As I see the problem, there are three courses of action that may be taken in an effort to solve this dilemma. 1) Alter the criteria applicable to the two subclasses in such a way as to admit taxa having intermediate characters. 2) Abolish the subclasses. 3) Erect a new subclass, admitting taxa having characters that are intermediate between the existing subclasses.

The first "remedy" (status quo) has been in effect for some time and is inadequate because no satisfactory way can be devised to avoid having fungi with intermediate or overlapping characters, from impinging on one or the other of the mutually exclusive subclasses. The second suggestion, that of the abolition of the subclasses proposed by Talbot, would have the effect of obscuring the differences that exist between them or at least of deemphasizing these differences to a degree that would be incompatible with the morphological realities. To establish a

new subclass, while not entirely free of objection (mostly from the standpoint of precedent) would seem to be the solution of choice. I therefore, recommend the following rearrangement of the Heterobasidiomycetes.

Subclass: Heterobasidiomycetidae - Taxa with completely divided basidia, having notably enlarged or swollen sterigmata; basidiospores germinating by repetition; basidiocarps frequently with a waxy or gelatinous texture. Examples: **Eutremellales:** Auriculariaceae, Hyaloriaceae, Phleogenaceae, Sirobasidiaceae, Tremellaceae; **Septobasidiales, Uredinales, Ustilaginales.**

Subclass: Metabasidiomycetidae - Taxa with incompletely divided or aseptate basidia, having notably enlarged or swollen sterigmata; basidiospores germinating by repetition; basidiocarps with or without a waxy or gelatinous texture. Examples: **Metatremellales:** Dacrymycetaceae, (Ceratomyces, Dacrymyces etc.), Tulasnellaceae (Gloeotulasnella, Metabourdotia, Pseudotulasnella, Tulasnella), Ceratobasidiaceae (Ceratobasidium, Oliveonia, Thanatephorus, Uthatabasidium).

Subclass: Homobasidiomycetidae - Taxa with undivided basidia, lacking notably enlarged or swollen sterigmata; basidiospores not germinating by repetition; basidiocarps mostly nonwaxy and nongelatinous. Examples: **Aphylophorales, Agaricales, Gasteromycetes.**

Summary of Recommendations

1) The subclass Heterobasidiomycetidae as here constituted becomes homogenous by virtue of the removal of the holobasidiaceous Dacrymycetaceae. The remaining families and orders are those that have more or less traditionally been included in the subclass. It may be objected that the removal of the Dacrymycetaceae from this subclass is a denial of the incontestably close affinities of that family with other Tremellales. It is not my intention to imply this, but neither can the holobasidiaceous nature of the family be overlooked. Just as it would be completely invalid to include the family with conventional homobasidiomycetes, I believe also that an impartial evaluation of the Patouillardian criteria as applied to the Dacrymycetaceae justifies its separation from Tremellales having septate basidia. It is for this reason that I propose to include the Auriculariaceae, Hyaloriaceae, Phleogenaceae, Sirobasidiaceae and Tremellaceae in the Eutremellales and the Dacrymycetaceae in the Metatremellales, along with the Tulasnellaceae and Ceratobasidiaceae as newly constituted. 2) The new subclass Metabasidiomycetidae contains taxa that have oscillated between the Heterobasidiomycetes and Homobasidiomycetes or have been considered as being frankly intermediate between them, or as in the case of the Dacrymycetaceae, would normally be included in the Heterobasidiomycetidae were it not for the aseptate condition of the basidia. The Tulasnellaceae are included here because the nature of the septa at the bases of sterigmata is interpreted as a transitional type of basidium, not in the same category as the basidia of other Heterobasidiomycetidae. This is certainly true of Tulasnella and Gloeotulasnella and while it may be insisted that Metabourdotia and

Pseudotulasnella have basidia with partial septa of quite a different nature from that found in Tulasnella, nevertheless their affinities lie closer to each other than any of them do to Ceratobasidium in which only rarely is an adventitious septum ever found. 3) The Ceratobasidiaceae is maintained and expanded to include, in addition to Ceratobasidium, the genera Oliveonia, Thanatephorus and Uthatabasidium which share in common unicellular basidia, enlarged sterigmata and germination of basidiospores by repetition. In my opinion this is by far a preferable alternative to the abolition of the family and the inclusion of its members in the homobasidiomycete complex. In a recent paper by Oberwinkler (1965:6) the closeness of Ceratobasidium to Uthatabasidium is further emphasized by pointing out again that they share the typically heterobasidiaceous manner of secondary spore formation.

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Abstract for XI International
Bot. Congress
Seattle.

Neotropical Tremellales

B. Lowy

The Tremellales constitute a heterogeneous assemblage of fungi that has traditionally been separated from the homobasidiomycetes since the studies of Patouillard (1887) and Brefeld (1888), although the morphological diversity of tremellaceous basidia was first elucidated by Tulasne (1853). The major distinguishing characteristics of the Tremellales are the great structural versatility of the basidium, basidiospore germination by repetition, enlarged to grossly inflated sterigmata and a predominantly gelatinous or waxy basidiocarp.

A new subclass, Metabasidiomycetidae, is established to contain taxa that are transitional between the homobasidiomycete and heterobasidiomycete complexes and includes the Tulasnellaceae, Dacrymycetaceae and Ceratobasidiaceae.

The Heterobasidiomycetidae are interpreted as representing the more primitive group with highly diversified basidia including types from which the more stable holobasidium may have been derived and the subclass is reserved for taxa having completely divided basidia such as characterize the Auriculariaceae, Hyaloriaceae, Phleogenaceae, Sirobasidiaceae and Tremellaceae.

One hundred forty-four species are reported from neotropical America, 76 of which are restricted to the tropical zone. The geographical distribution of all species has been mapped and drawings showing pertinent microscopic details of representatives of the eight families treated are also presented.

DEPARTMENT OF PLANT PATHOLOGY
WASHINGTON STATE UNIVERSITY
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Dear Sir:

Will you please send me a reprint of your paper
entitled: *Taxonomic Problems in the Heterobasidiomycetes.*
in *Taxon* 17:118-127.

Sincerely yours,

~~Jay N. Holliday Jr.~~
~~Jay N. Holliday Jr.~~

The University of Adelaide
WAITE AGRICULTURAL RESEARCH INSTITUTE

Glen Osmond, South Australia 5064

Dear

Dr Lowy

Date

18-2-69

I would be glad to receive a copy of the following publication:

Taxonomic problems in the heterobasidiomycetes.
Taxon 17: 118-127.

Yours sincerely,

J A Simpson
DEPT. OF Plant Pathology

Aug. 1968

This is to acknowledge, with thanks,
the receipt of a reprint of your recent
publication on Taxon.

With best personal regards,
Sincerely,

Lucella K. Overcomb
Mycologist -

Plant Research Institute
Research Branch
Central Experimental Farm

Institut de Recherches sur les Végétaux
Service de Recherches
Ferme Expérimentale Centrale

Ottawa, Ontario, Canada

ILLINOIS STATE UNIVERSITY
NORMAL, ILLINOIS
Department of Biological Sciences

5/27/68

Dear Doctor Lowy

I would greatly appreciate a reprint of your paper "Taxonomic problems in the heterobasidiomycetes."

which appeared in Taxon 17: 118-127 (1968)

✓
Yours very truly,

Robert J. Harris, Jr.

July 3, 1968

Dear Dr. Lowy:

If you have available for distribution copies of your recent article "Taxonomic Problems in the Heterobasidiomycetes" *Taxon* 17: 118-127 (1968), I would appreciate your sending me one very much.

Thank you.

Yours sincerely,
Ben Liles, Jr.
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Brookings, South Dakota 57006

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Dear Sir:

I would greatly appreciate receiving a reprint of the following: _____

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Yours truly,  G. SEMENIUK

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Thank you for your courtesy.

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