#### PERSOONIA

Published by the Rijksherbarium, Leiden Volume 7, Part 1, pp. 1-16 (1972)

# THE RELATIONSHIPS BETWEEN THE TREMELLALES AND THE APHYLLOPHORALES

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(With 10 Text-figures)

The relationships between the Tremellales and Aphyllophorales are discussed by comparison of the micromorphology of some species belonging to the following pairs of genera: Exidiopsis—Athelopsis, Basidiodendron—Dendrothele—Heterochaete, Myxarium—Oliveonia—Repetobasidium, Tremellodendropsis—Aphelaria, Uthatobasidium—Botryobasidium. A new combination is proposed in the genus Athelopsis.

The discovery that phragmo- and holobasidia are distinct structures has greatly advanced the classification in the lower Basidiomycetes. Some additional characters have led to the concept of two divisions, Phragmo- and Holobasidiomycetes, which for the occasion may be opposed to each other as follows:

Phragmobasidiomycetes (Fig. 1a)	HOLOBASIDIOMYCETES (Fig. 1b)
<ol> <li>Mature basidia septate.</li> <li>Sterigmata stout, mostly long and irregularly flexuous.</li> <li>Spores forming secondary spores.</li> <li>Walls of hyphae gelatinous; fruitbody greatly changing its shape on drying.</li> </ol>	<ol> <li>Basidia undivided.</li> <li>Sterigmata slender, relatively short and horn-like.</li> <li>Spores producing hyphal mycelium.</li> <li>Without gelatinous hyphal walls; living and dried specimens with more or less the same shape.</li> </ol>

Are these characters of value in separating subclasses? The following remarks on some species of either group touch upon this question.

There is no doubt that the genus Sebacina in the current broadly conceived sense is highly artificial. There are some well-founded arguments for splitting this taxon into a series of more natural genera. One of these would appear to be Exidiopsis (Bref.) A. Möll., based on Exidia effusa Bref. This species is characterized by all the features mentioned above as being typical of Phragmobasidiomycetes, i.e. septate basidia, flexuous sterigmata, spores forming secondary spores, gelatinized hyphae, and gelified fruitbodies when fresh. The basidia, which are globose or only slightly elongated and possess basal clamps seem to constitute an important character for

generic delimitation. Moreover, as distinct from *Exidia*, the fruitbody is strictly resupinate and usually the hymenium is smooth. With the circumscription of *Exidiopsis*, as emended by Wells (1961), the following unnamed species (see Fig. 2a) can be conveniently placed in this genus. This species differs however from typical

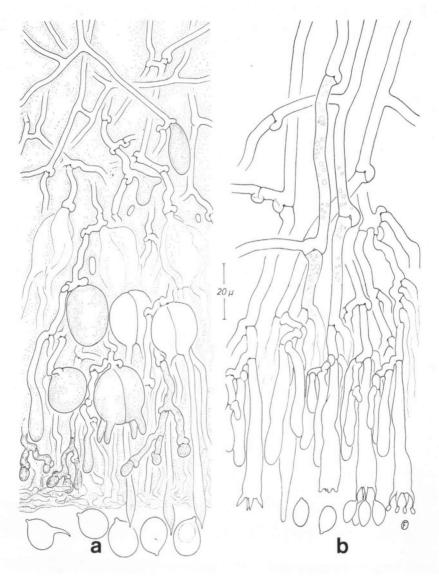


Fig. 1. Sections of hymenium and subhymenium, showing hyphal context, basidia, and spores. — a. Tremella mesenterica Retz. per Hook. — b. Corticium evolvens (Fr. per Fr.) Fr.

members of the genus in lacking a well-developed context, while the fruitbody is not gelatinous; the basidia arise on the surface, consequently the sterigmata sporulate directly in the air without first having had to grow through gelatinized tissue, a condition that explains their short horn-like shape rather well.

A homobasidial counterpart may be found within the genus Corticium in its traditional sense. Some of the members of Bourdot & Galzin's section Athele (1928: 206-211), transferred to the new genus Athelopsis (Oberwinkler, 1965: 48; accepted by Parmasto, 1968: 41), may well be compared with the species of Exidiopsis referred to above. The fungi (Fig. 2c) are adnate to the substratum, the non-effigurated hymenium lacks cystidia, the holobasidia commonly bear four sterigmata, and produce colourless, smooth, thin-walled spores. This general diagnosis of the 'Corticia' can be restricted even further. The basal hyphae are few and strongly interwoven, but they are not obviously gelatinous; the basidia are extremely short-cylindrical to subglobose with sterigmata of the common horn-like type.

Two points remain which should be mentioned. The first one is apparently easy

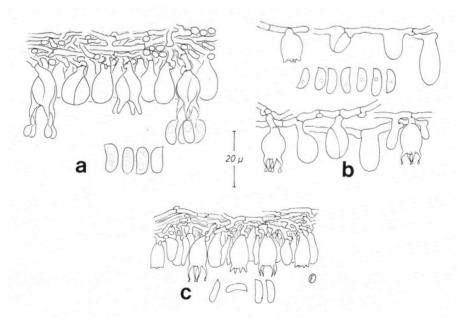


Fig. 2. Fruitbodies shown in section with spores. — a. Exidiopsis sp. — b. Coll. BFO 13845. — c. Athelopsis lembospora (Bourd.) Oberw.<sup>1</sup>

<sup>&</sup>lt;sup>1</sup> Athelopsis lembospora (Bourdot) Oberwinkler, comb. nov. (basionym: Corticium lembosporum Bourdot in Rev. Sci. Bourb. 32: 10. 1910).

to decide. The main and probably only difference of taxonomic importance at the moment between both species under discussion is the presence of phragmobasidia in the former and holobasidia in the latter. Another distinction may well be found in spore germination in that the spores of the *Exidiopsis* species may be expected to form secondary spores, whereas those of the *Athelopsis* species ought to germinate by producing hyphae.

The similarity indicated above, which might be explained by convergence, acquires a different slant by the find of a species which we collected in the Andes of Venezuela (Fig. 2b). The drawing shows a section of the whole fructification of the fungus, consisting of substrate-hyphae and some few, scattered basidia, which seem to belong to both the septate and the holobasidial type. Regrettably in this case, too, I have been unable to find germinating spores.

This species is likely to arouse theoretical speculations, but for the time being it seems more appropriate to look for other comparable taxa. For that purpose an additional structure of the fungus in question should not be overlooked. There are some elongate terminal bodies, whose nature is not clear, but which may be regarded as small cystidia. Within the genus *Bourdotia* s.l. (Fig. 3a) similar structures are to be found. Typically these are gloeocystidia which contain a yellow oleaginous substance.

A really interesting and highly characteristic group has been removed from *Bourdotia* in the original sense by Luck-Allen (1963) and transferred to an emended *Basidiodendron*. Well developed material (Fig. 3b) shows generative hyphae of ver-

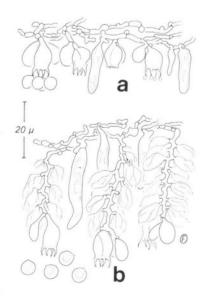


Fig. 3. Basidiodendron eyrei (Wakef.) Luck-Allen. — a. Section through a peripheral part of the fruitbody. — b. Section through the central part; with details of the young and old hymenium and spores.

tical growth which continue to produce apically mature basidia, surrounded by younger ones, while the exhausted basidia remain as calyx-like enveloping sheaths of the supporting hyphae.

I would like to draw attention to the basidial morphology in this genus, too. Some well-known species, for example Basidiodendron eyrei (Wakef.) Luck-Allen or B. caesio-cinereum (Höhn. & Litsch.) Luck-Allen show septate and undivided basidia in a single fructification. Thus, it is not surprising that von Höhnel & Litschauer (1908: 1116) had originally described B. caesio-cinereum as belonging to the genus Corticium, while Bourdot & Galzin (1912: 369), giving prevalence to the presence of gloeocystidia, transferred it to Gloeocystidium sensu von Höhnel & Litschauer, a

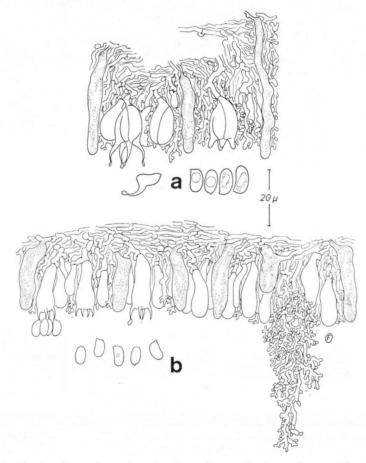


Fig. 4. Fruitbodies shown in section, showing substrate-hyphae, gloeocystidia, dendrophysoid hyphae and a hyphal peg (4b), basidia, and spores. — a. Basidiodendron cinereum (Bres.) Luck-Allen. — b. Dendrothele sp.

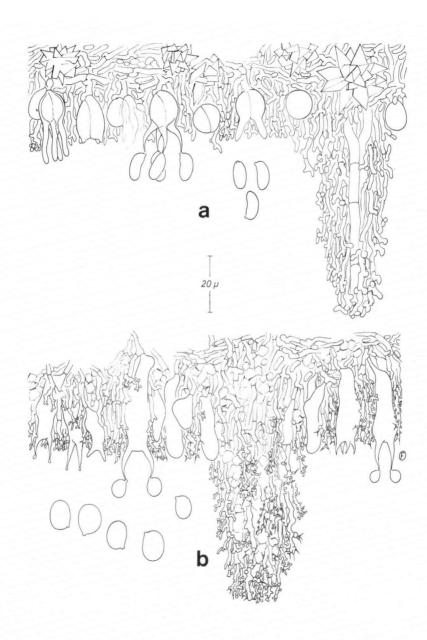


Fig. 5. Fruitbodies shown in section, with details of the hymenium, sterile teeth, and spores. — a. 'Heterochaete' sp. — b. Dendrothele griseo-cana (Bres.) Bourd. & Galz.

typically holobasidial genus. Similar arguments surely apply to Rick's *Basidiodendron luteo-griseum* (1938: 74; probably synonymous to *B. eyrei*, as already stated by Luck-Allen, l.c.), the type species of the genus *Basidiodendron*.

Apart from this, I would like to add some further details in comparing Basidiodendron cinereum (Bres.) Luck-Allen (Fig. 4a) with a species that might possibly be placed in the genus Dendrothele Höhn. & Litsch. (Fig. 4b). The latter genus is well defined by dendrophysoid hyphae which may form a primary layer, a sterile tissue, through which the basidia have to grow in order to reach the surface (catahymenium). Teeth made up of the same ramified hyphae are more or less characteristic. Size and shape of both basidia and spores seem to vary considerably according to the species. In some taxa gloeocystidia also occur. Leaving the sterile teeth aside, there are only two major morphological differences: phragmobasidia with the spores germinating by repetition, and holobasidia with the spores producing hyphae on germinating.

In addition to the preceding example there exist species without conspicuous gloeocystidia (Fig. 5b). The type species of the genus *Dendrothele*, *D. griseo-cana* (Bres.) Bourd. & Galz. (= *D. papillosa* Höhn. & Litsch.) shows the above mentioned characteristics; gloeocystidia seem to be rare or inconspicuous.

An equivalent micromorphology can be seen in some species currently referred to the heterobasidiomycetous genus *Heterochaete* (Fig. 5a). Some remarks may be made concerning the type species, *Heterochaete andina* Pat. The basal hyphae are loosely interwoven, non-gelatinized, partly thick-walled, with brown cell-walls. In contrast, the hyphae of the subhymenium, hymenium, and sterile teeth are more or less densely interwoven, while some are extremely thick-walled and have brown, plasmatic contents. At the apex, most of the sterile hyphae are dendritically ramified. The basidia have a basal stalk and develop diverging longitudinal septa.

It is obvious that *Heterochaete andina* and the fungus used for comparison with *Dendrothele griseo-cana* have little in common, except the cystidia-like, sterile hyphal pegs and cruciate-septate basidia. On the other hand this '*Heterochaete*' sp. and *Dendrothele* agree in hyphal construction and context, but their basidia belong to different types.

Whereas the species discussed above have effused fructifications, a second group includes clavarioid species (see Crawford, 1954; Reid, 1956; Corner, 1966). Corner (1970: 283) states that *Tremellodendropsis* "structurally knits *Aphelaria* with *Tremellodendron* and *Paraphelaria*."

The genus Tremellodendron, as typically represented by T. candidum (Schw.) Atk., differs from Tremellodendropsis by more or less globose basidia, lack of clamps throughout, and slightly thick-walled tramal hyphae. On account of basidial morphology it seems doubtful whether both genera are closely related. On the other hand there still remain points in need of investigation. In the first place Tremellodendropsis tuberosum (Grev.) Crawf. (Fig. 6a) is now a fairly well-known species with a curious method of basidial septation. The bases of the sterigmata are sunken into the apical

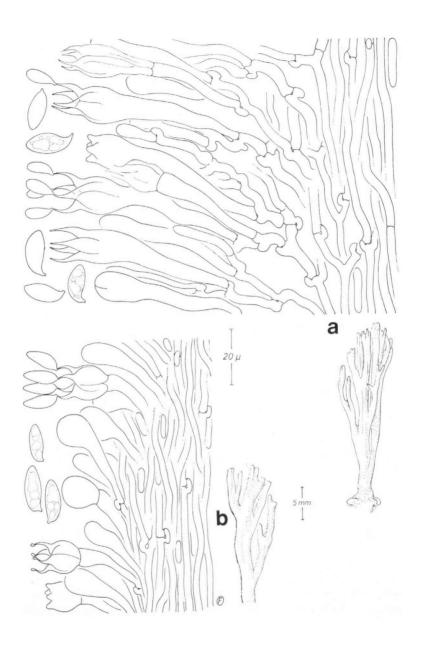


Fig. 6. Habit sketch of fruitbody and partial sections of hymenium and subhymenium. — a. Tremellodendropsis tuberosum (Grev.) Crawf. — b. Tremellodendropsis transpusio Crawf.

part of the basidial body. This means that the apex of the basidium is in part longitudinally septate. After spore discharge these septa diverge and may form what looks like a secondary transverse septum. Thus, the original basidium is divided into a basal stalk and in an effete apical part. In addition to this, Crawford (l.c.) was able to show that there also exist species like T. transpusio Crawf. (Fig. 6b), in which the terminal part of the basidium is septate in the normal tremellaceous manner, i.e. before producing the spores. There is a perfect correlation between Tremellodendropsis tuberosum and T. transpusio with respect to most of the other characteristics such as shape, consistency, and colour of fruitbodies; moreover in hyphal peculiarities (hyphae thin-walled, non-gelatinized, with clamp connections), shape of basidia (long-stalked, with an apical swollen part), and spores (navicular, smooth, and thin-walled) they are indistinguishable.

Secondly, there is a 'Pterula pusio' collected by Ramos (1204) in the Philippines, with tremellaceous basidia (Fig. 7b). It differs from the description given above in the following details: fruitbodies much more ramified, central hyphae somewhat thick-walled, all septa without clamps, spores subglobose. Aside from this, the basidial development seems to agree with that described for Tremellodendropsis transpusio. Besides Tremellodendropsis one should consider also Tremellodendron itself; but the type of this genus has non-stalked, globose basidia which are strongly different.

There also exists a third group, which may be of interest in this problem, the genus Aphelaria Corner, a derivative of the holobasidial Clavaria s.l. I have chosen Aphelaria guadelupensis (Lév.) Corner, of which a habit sketch and the hymenial micromorphology may serve for comparison with the collection Ramos 1204 (Fig. 7a). Except for the structure of the mature basidia there is a conspicuous agreement; but for the holobasidia, Aphelaria would be indistinguishable from the tremellaceous 'Pterula.'

In the Heterobasidiomycetes also holobasidial species are included, whose affinities and taxonomic positions have been hotly debated recently by some authors (Lowy, 1968 and 1969; Talbot, 1968 and 1970). I would like to delimit the discussion to the so-called Ceratobasidiaceae and to comparable species of the artificial Corticiaceae. I am fully aware of the fact that further taxa could be brought into discussion too. With regard to *Pseudotulasnella* (Lowy, 1964), I am convinced that this taxon is well placed within the Tulasnellaceae. Likewise I believe that much favours the treatment of *Cerinomyces* as a member of Dacrymycetaceae.

Ceratobasidiaceae, whose members so far known are corticioid species, show some characteristic features, such as often short-cylindric holobasidia with differently shaped sterigmata and spores forming secondary spores. The genus Oliveonia Donk (Figs. 8b, 9a) may be further characterized by the presence of cystidia. Moreover I would not be surprised if future investigations would re-establish Parker-Rhode's (1954: 325) invalidly published genus Hydrabasidium; it seems to me that Cejpomyces Svr. & Pouz. (Svrček & Pouzar, 1970: 5) could be the corresponding homobasidial taxon.

If we consider the basidia of Oliveonia s. str. to be slightly sphaero-pedunculate, then a counterpart in tremellaceous fungi can be found within the genus Myxarium.

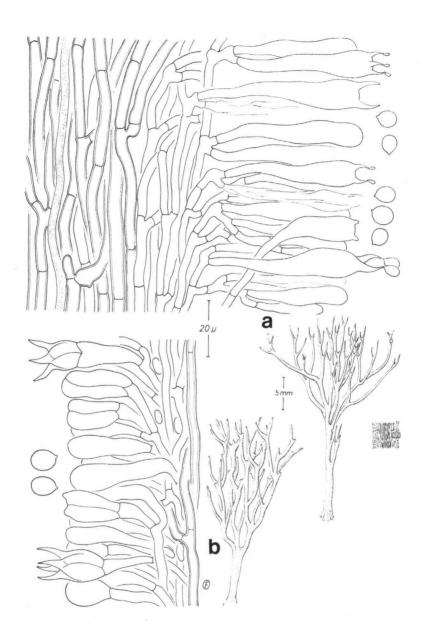


Fig. 7. Habit sketch of fruitbody and hymenial detail. — a. Aphelaria guadelupensis (Lév.) Corner. — b. 'Pterula pusio', Ramos 1204.

Such species (compare Fig. 8a) would fit in well with this description. It is obvious that the main difference between both species lies in the phragmo- against the holobasidium.

A second interpretation would describe the basidia as only short cylindric with an attenuate base. This would render it necessary to look for equivalent taxa in a different area of tremellaceous genera. There exist a few species in the genus Bourdotia in its old and artificial circumscription, which show close resemblance in morphological aspects. And finally the genus Metabourdotia Olive should be taken into consideration. In comparison with Oliveonia, some differences can be pointed out: the presence of few hyphidia, apparently true gloeocystidia, and the apically partially cruciate-septate basidia. Metabourdotia is in fact of great theoretical interest (Olive, 1957: 429; Talbot, 1965: 378-379; Lowy, 1968: 124-125; Rogers, 1971: 251-252). I do not intend to discuss once more either the problems or the different systematic conclusions. It seems more appropriate to consider the development of Oliveonia itself. The drawing discussed above (Fig. 8b) shows a section through a young fruitbody. In central portions of the same sample (Fig. 9a) which normally contain more developed stages, a thickening of the hymenium is the result of a basidial repetition. Such a behaviour was first shown to exist by J. Eriksson (1958: 67-70) in Corticium vile Bourd. & Galz. (Fig. 9b), for which a new genus Repetobasidium was subsequently proposed. This is apparently a homobasidiomycetous genus with holobasidia whose spores on germinating produce normal hyphae. Although spore germination has not been directly observed in this genus, the absence of secondary spores on the hymenial surface makes direct hyphal germination likely. Furthermore, repetobasidia have as yet not been reported from the genus Oliveonia. The only comment found in literature is a note by Talbot (1965: 381): "In a material of the

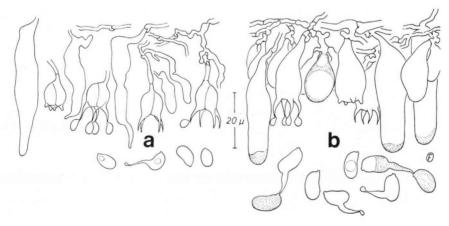


Fig. 8. Sections of fruitbodies in a young developmental stage. — a. Myxarium sp. — b. Oliveonia fibrillosa (Burt) Donk.

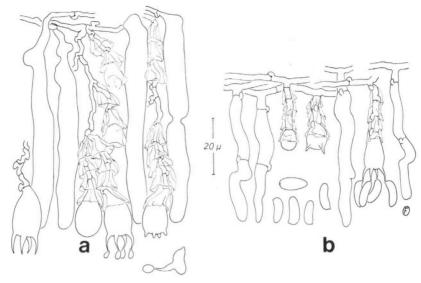


Fig. 9. Sections of fruitbodies. — a. Oliveonia fibrillosa (Burt) Donk. — b. Repetobasidium vile (Bourd. & Galz.) J. Erikss. var. macrosporum Oberw.

type species some of the probasidia had what appeared to be a partial or complete annulus of variable position..." I have little doubt that these are the envelopes of old basidia surrounding the younger ones, as I could easily prove in living material collected in Merida (Venezuela).

Additional reports on hetero- versus homobasidiomycetous taxa of recognized affinities should be mentioned. Two well-known genera need to be discussed briefly, Uthatobasidium Donk and Botryobasidium Donk (Figs. 10a, b), detailed information on which is to be found in Rogers, 1934: 174-175; 1971: 248-249; Linder, 1940: 442-444; Donk, 1956: 373-375; 1964: 225, 227-229, 258, 261-262; 1966: 255; Martin, 1957: 25; J. Eriksson, 1958: 47; Oberwinkler, 1965: 5-7; Talbot, 1965: 375-379; 1971: 224. These genera are similar in most details: effused, pruinose-arachnoid to hypochnoid fructifications composed of rather broad hyphae which branch at right or at least extremely wide angles. Basidia are short cylindrical and not or inconspicuously constricted. The generic separation is supported by basidia having normally four sterigmata and spores producing secondary spores in Uthatobasidium, and basidia having supernumerary sterigmata and spores forming hyphal mycelium from the beginning of their germination in Botryobasidium.

There is no doubt that the points mentioned in the beginning separating the Phragmo- and Holobasidiomycetes are not well-founded. The characters of fructifications and hyphae are extremely variable and occur in different groups of both taxa. But also basidia and spores of some genera and species of Tremellales and Aphyllophorales show great similarity in morphological respect.

There remain only two characters which may be combined to circumscribe the Heterobasidiomycetes: mature basidia septate or, if undivided, basidiospores forming secondary spores. The Homobasidiomycetes, on the other hand, include fungi with holobasidia whose spores never produce secondary spores.

The details shown above may indicate that this classification is still in need of improvement.

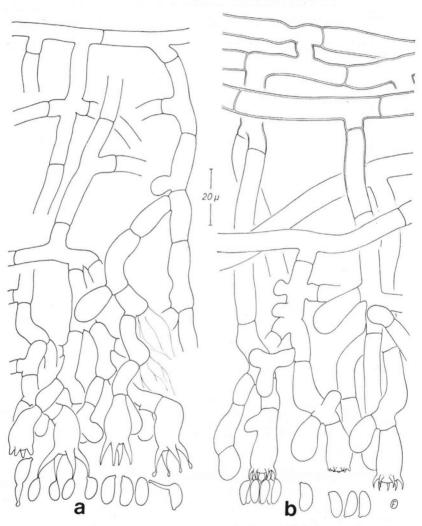


Fig. 10. Sections of fruitbodies. — a. Uthatobasidium sp. — b. Botryobasidium obtusisporum J. Erikss.

#### ACKNOWLEDGEMENTS

I am grateful to Dr. L. S. Olive, University of North Carolina, Chapel Hill, for the gift of some very important collections. For the loan of specimens I wish to express my sincere thanks to Dr. M. I. Lamb of the Farlow Herbarium, Cambridge, Massachusetts (FH); Dr. B. Lowy of the Mycological Herbarium, Louisiana State University, Baton Rouge (LSUM); the Director, Royal Botanic Gardens and Dr. D. A. Reid, Kew (K). I am highly indebted to the late Dr. M. A. Donk, to Dr. H. Merxmüller, Munich, and to my wife, Dr. Barbara Oberwinkler, for their helpful and detailed criticism.

### Collecting data of the species represented by drawings

Fig. 1a. Tremella mesenterica Retz. per Hook. Deutschland, Bayern; Grundübelau am Hintersee, bei Berchtesgaden, 820 m., 12.11.1961, F. Oberwinkler.

Fig. 1b. Corticium evolvens (Fr. per Fr.) Fr. Deutschland, Bayern; Halblech nordöstlich Füssen, 830-850 m., 23.3.1968, B. Mayr & F. Oberwinkler.

Fig. 2a. Exidiopsis sp. Venezuela, Dto. Federal; Baruta bei Caracas, ± 1300 m., 5.2.1969, B. & F. Oberwinkler 14558.

Fig. 2b. Coll. BFO 13845. Venezuela, Anden, Edo. Merida; El Valle nordöstlich Merida, ± 2300 m., 8.12.1968, B. & F. Oberwinkler 13845.

Fig. 2c. Athelopsis lembospora (Bourd.) Oberw. Venezuela, Dto. Federal; alte Strasze von Caracas nach La Guaira, 700 m., auf morschem Holz von Bathysa pittieri (Standl.) Steyerm. (Rubiaceae), 2.2.1969, B. & F. Oberwinkler 14537.

(Rubiaceae), 2.2.1969, B. & F. Oberwinkler 14537.

Fig. 3. Basidiodendron eyrei (Wakef.) Luck-Allen. Venezuela, Anden, Edo. Merida; Umgebung des Instituto Forestal Latino-Americano in Merida, 1800 m., 27.11.1968, B. & F. Oberwinkler 13733.

Fig. 4a. Basidiodendron cinereum (Bres.) Luck-Allen. Venezuela, Cordillera de la Costa, Edo. Aragua; Parque National Henri Pittier ("Rancho Grande") nördlich Maracay, 1100 m., 9.2.1969, B. & F. Oberwinkler 14633.

Fig. 4b. Dendrothele sp. Venezuela, Anden, Edo. Merida; La Mucuy oberhalb Tabay, östlich Merida,  $\pm$  2000 m., 3.9.1968, B. & F. Oberwinkler 12611.

Fig. 5a. Heterochaete sp. Venezuela, Anden, Edo Merida; Umgebung des Instituto Forestal Latino-Americano in Merida, 1800 m., 7.6.1969, B. & F. Oberwinkler 16019.

Fig. 5b. Dendrothele griseo-cana (Bres.) Bourd. & Galz. Venezuela, Anden, Edo. Merida; Umgebung des Instituto Forestal Latino-Americano in Merida, 1800 m., 12.11.1966, B. & F. Oberwinkler 13390.

Fig. 6a. Aphelaria tuberosa (Grev.) Corner Pellston Hills, Michigan, USA 10.8.1961, D. A. Reid (Royal Botanic Gardens Kew, K).

Fig. 6b. Tremellodendropsis transpusio Crawf. Venezuela. Anden, Edo. Merida; La Mucuy oberhalb Tabay, östlich Merida,  $\pm$  2200 m., 6.7.1969, B. & F. Oberwinkler 16167.

Fig. 7a. Aphelaria guedelupensis (Lév.) Corner (als Pterula aurantiaca P. Henn.), E. Ule, Appendix Mycothecae brasiliensis 10. Amazonas, Manáos. Ad solum humidum, 1902, E. Ule (Botanische Staatssammlung München, M).

Fig. 7b. 'Pterula pusio (Berk.) Bres.' Luzon. Rizal, Bosoboso, Max. Ramos 1204 (Botanische Staatssammlung München, M).

Fig. 8a. Myxarium sp. Deutschland, Bayern; Predigtstuhl bei Bad Reichenhall, 1400 m., 10,0,1962. F. Oberwinkler 2887a.

- Fig. 8b. Oliveonia fibrillosa (Burt) Donk Venezuela, Anden, Edo. Merida; Umgebung des Instituto Forestal Latino-Americano in Merida, 1800 m., 27.12.1968, B. & F. Oberwinkler 14101.
  - Fig. 9a. Oliveonia fibrillosa (Burt) Donk BFO 14101, compare Fig. 8b!
- Fig. 9b. Repetobasidium vile (Bourd. & Galz.) J. Erikss. var. macrosporum Oberw. Deutschland, Bayern; Funtensee im Steinernen Meer bei Berchtesgaden, 1600 m., 6.8.1963, F. Oberwinkler 5570, 5571a.
- Fig. 10a. Uthatobasidium sp. Venezuela, Anden, Edo. Merida; Umgebung des Instituto Forestal Latino-Americano, 1800 m., 1.10.1968, B. & F. Oberwinkler 12904.
- Fig. 10b. Botryobasidium obtusisporum J. Erikss. Venezuela, Anden, Edo. Merida; Umgebung des Instituto Forestal Latino-Americano in Merida, 1800 m., 9.1968, B. & F. Oberwinkler.

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