

## PERSOONIA

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## NOTES ON HYDNUMS—II

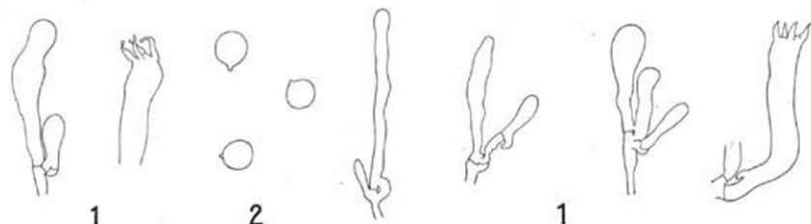
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(With 74 Text-figures)

This paper deals with a number of Hydnums, some of which seem not to have been reexamined since their publication. In a few cases the species appear to be Polypores, in others it is for various reasons impossible or inexpedient to indicate the generic relationship. Several names are reduced to synonymy. The following recombinations are proposed: *Deflexula sprucei* (Mont.), *Gloiodon nigrescens* (Petch), *Cyrodontium boveanum* (Mont. apud Decaisne), *G. versicolor* (Berk. & Br.), *Sarcodon carbonarius* (G. H. Cunn.), *S. martioflavus* (Snell & al. apud Snell & Dick), and *S. thwaitesii* (Berk. & Br.) Maas G.

*Ambustus*. — *Hydnum ambustum* Cooke & Massee apud Cooke in *Grevillea* 16: 32. 1887. — Type: "*Hydnum (Mesopus) ambustum* C & M [Australia] Victoria, Harkaway Range, 6/87. C. French" (K).

The type consists of three fruit-bodies with confluent pilei and stipes connate at the base. Pileus plano-convex, depressed in the centre, 1-1.5 cm across; surface smooth, glabrous except for some scattered remnants of a yellowish tomentum near the margin; fulvous along the margin, darker to almost black toward the centre; margin somewhat involute in places. Stipe central, solid, slender, equal (but flattened, divaricate, and widened near the apex in one of the specimens), about 1.5 cm long, 1-2 mm thick (up to 5 mm at the widened apex), glabrous, concolorous with the pileus above, blackened below. Spines reaching the stipe, subulate, up to 1.5 mm long, fulvous. Context fleshy, monomitic; hyphae thin-walled, inflating, with clamp-connections. Basidia cylindrical-clavate,  $36-50 \times 6.7-7.2 \mu$ , 4-spored, with clamp-connection at the base (Fig. 1). Spores (only immature ones seen, Fig. 2) globose, smooth, colourless,  $6.4-7.2 \mu$  diam., apiculus c.  $1 \mu$  long. Cystidia absent.



Figs. 1, 2. *Hydnum ambustum* Cooke & Massee apud Cooke (type). — 1. Basidia, the one in the centre apparently sterile. — 2. Spores. (Both figures  $\times 700$ .)

The specimens described above were either past their prime when collected or perhaps dried far too slowly, and both possibilities may account for what Cooke & Masee called the "scorched appearance" and for the glassy-horny consistency. No explanation can be offered why I failed to find mature spores. However, the microscopical characters indubitably determine the species as a true *Hydnum*, and I have no doubt that it is identical with *H. crocidens* Cooke which was published at a later date. As pointed out in the discussion under *H. crocidens*, I have as yet no definite opinion how that species might be distinguished from the *Hydnum repandum* complex.

At first some difficulty was experienced in finding the clamps at the base of the basidia of the material from Victoria. They seem to degenerate and disappear at an early stage of the development.

*Armeniacus*. — *Sarcodon armeniacus* Maas G., see under '*martioflavus*'.

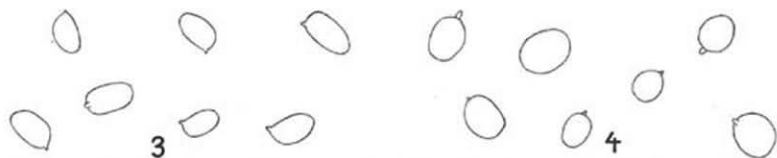
*Basi-asperatus*. — *Hydnum basi-asperatum* P. Henn., see under '*rawakensis*'.

*Boveanus*. — *Hydnum boveanum* Mont. *apud* Decaisne in Ann. Sci. nat. (Bot.), Sér. 2, 4: 194. 1835; Mont. *apud* Fr., Epicr. Syst. mycol. 513. 1838; Mont., Syll. Gen. Spec. Crypt. 173. 1856. — Type: "*Hydnum boveanum* Montag. / Sur des poutres dans le palais d'Ibrahim au Caire / Com. Cl. Bové" (PC).

A thin membrane bearing a mass of crowded spines is all that is left of the fungus described by Montagne. Where one would expect to find the fruit-body proper, the context is completely replaced by a thick layer of compacted fulvous powder. Spines up to 7 mm long, 0.3–0.4 mm thick, subulate, collapsed (probably from old age), and flattened and sulcate. Hyphae of the trama of the spines for the greater part badly collapsed, but in places still recognizable: of one kind only, up to 6.3  $\mu$  wide, thin-walled, septate, without clamp-connections, branched and with occasional connecting hyphae. Basidia collapsed. Spores (Fig. 3) ellipsoid, adaxially flattened, smooth, yellow-brown under the microscope, rather thick-walled, 3.8–5.4  $\times$  2.7–3.6  $\mu$ , with small, oblique apiculus. Cystidia and gloecystidia not seen.

The compact powdery layer mentioned above is made up of broadly ellipsoid to subglobose spores (Fig. 4), 3.6–4.9  $\times$  3.1–4.5  $\mu$ , yellow-brown and moderately thick-walled (the smaller ones) to dark brown and thick-walled (many of the larger ones), often with what seems to be a median, colourless, often very prominent apiculus, but occasionally without such a structure.

While there is no reason to believe that the specimen examined should be anything else than Bové's material (for those parts of Montagne's description that can be



Figs. 3, 4. *Hydnum boveanum* Mont. *apud* Decaisne (type). — 3. Basidiospores taken from a spine. — 4. Spores taken from powdery layer. (Both figures  $\times$  700.)

checked agree very well), it is difficult to imagine by what agent the pileus, after Montagne had described it, was completely destroyed and reduced to a powdery mass without there being left any trace of the original tissue. The symmetric shape of the spores, the median position of the apiculus (if it is an apiculus), the variable size of the latter, and its occasional absence suggest that the spores might be conidiospores or chlamydospores. Dr. M. A. Donk, in this connection, drew my attention to what seemed to be a similar kind of spores, viz. the "Gastérospores", which were stated by Heim & Malençon (1928: 69, fig. 5) to occur in the dissepiments of *Ganoderma rivulosum* Pat. & Har.<sup>1</sup> However, whereas these spores apparently developed in the living tissue of the fruit-body, the strange fact remains that the subglobose spores in *Hydnum boveanum* were produced after the specimen had been filed in the herbarium. Another difference is that these spores were not found to occur in the trama of the spines, which is homologous to the tissue of the dissepiments of a polyporous fungus. These considerations raise the question whether the spores under discussion belong to the species at all.

The hyphal structure of *Hydnum boveanum*, as far as can be made out, agrees with that of *Hydnum henningsii*, the type species of the genus *Gyrodontium*, while the basidiospores are exactly alike in size, shape, colour, and possession of a small, oblique apiculus. There can be no doubt, therefore, that the present species and *H. henningsii* are congeneric, but it seems advisable not to conclude yet that both are conspecific until better preserved material is available. Accordingly, the following recombination is here proposed: ***Gyrodontium boveanum*** (Mont. apud Decaisne) Maas G., *comb. nov.* (basonym, *Hydnum boveanum* Mont. apud Decaisne, l.c.).

*Carbonarius*. — *Hydnum carbonarium* G. H. Cunn. in Trans. roy. Soc. New Zeal. 85: 591, text-fig. 2, 2a, pl. 40 fig. 2. 1958; not *Hydnum carbonarium* Peck in Rep. N.Y. State Mus. nat. Hist. 40: 55. 1887. — Type: "*Hydnum carbonarium* G. H. Cunn., [New Zealand,] Otago Distr., Half Moon Bay, Stewart Island, Febr. 1948, J. M. Dingley" (Herb. Plant Diseases Div., New Zealand 17707).

The lack of zones in the context, the thin-walled, inflating hyphae, the strongly warted brown spores, and the absence of cystidia determine the present species as a true *Sarcodon* (*Hydnum* in Cunningham's sense), hence it is here transferred to that genus as ***Sarcodon carbonarius*** (G. H. Cunn.) Maas G., *comb. nov.* (basonym, *Hydnum carbonarium* G. H. Cunn., l.c.). The black exterior, the presence of clamp-connections, and the bluish discolouration of the hyphae in KOH solution indicate that the species belongs to that group, of which *Sarcodon atroviridis* (Morg.) Banker and *S. thwaitesii* (Berk. & Br.) Maas G. (p. 183) are further members. These last-mentioned species do turn black with age or when bruised, but they are more brightly coloured when young, and I believe this to be true for *S. carbonarius*, too. I have no doubt that Cunningham's description was based only on dried material, and

<sup>1</sup> It appears that time and again the formation of 'gasterospores' in *Ganoderma* has attracted the attention of mycologists. Among them Bose (1957) and Sarkar (1959) are mentioned whose papers refer to further literature on the subject.

I am convinced that the type (to judge from the specimen I had on loan) was already too far gone when it was collected, which accounts for its aforesaid black colour, the polished surface of the pileus, and the brittleness of the context. Cunningham's choice of the specific epithet is unfortunate in that '*carbonarius*', apart from being a later homonymous epithet (under *Hydnum*), suggests a quality which the fungus does not ordinarily possess. Even now the context is not black, as Cunningham described it, but of a dark olive colour and, being a *Sarcodon*, it is highly improbable that the context in the fresh condition should have been anything but fleshy.

*Sarcodon carbonarius* is urgently in need of a redescription from fresh material in order better to appraise the differences of this species from *S. atroviridis*. The criteria now used to distinguish *S. carbonarius* from *S. atroviridis* are the larger spore-size of the former and, rather as a last resort, the occurrence in two geographically widely separated regions.

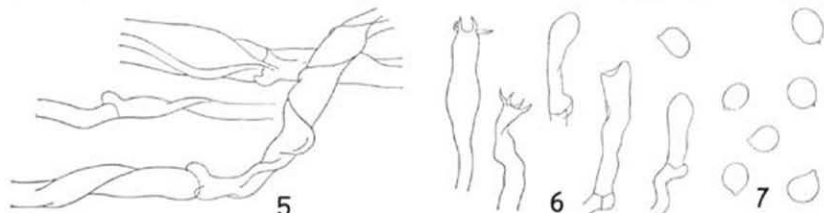
It should be pointed out that in lateral view the spores appear somewhat less broadly ellipsoid than indicated by Cunningham, being  $8.1-9.0 (-9.8) \times 6.3-7.2 (-7.6) \mu$ .

*Crassus*. — *Hydnum crassum* K. Harrison, Stip. Hyd. Nova Scotia 29, pl. 2 fig. 3. 1961. — Type: "Cape Split, Kings County, 10 Aug. 1958, K. A. H[arrison] 3548" (DAOM 53378).

The type consists of two half specimens: (i) a larger one which is yellow-brown in some places, dark brown in others and suffused with a very slight purplish hue; (ii) a smaller one which is mainly dingy ochraceous, but at one place distinctly lilaceous grey near the margin. The surface in both is cracked into areoles or adnate scales. The stipe is stocky, tapering to a pointed base which is whitish. The mature spines are chocolate brown. The context is yellowish (paler and with a greenish tint in the smaller specimen) and only a little darker in the base of the stipe.

The last-mentioned character excludes Groups 1 and 4 of the genus *Sarcodon*, and Group 2 may be left out of consideration as the hyphae possess clamp-connections. From the remaining characters the specimens are easily recognizable as belonging to *Sarcodon laevigatus*, which makes *Hydnum crassum* synonymous with the latter.

*Crocidents*. — *Hydnum crocidents* Cooke in Grevillea 19: 45. 1890. — *Dentinum crocidents* (Cooke) G. H. Cunn. in Trans. roy. Soc. New Zealand 85: 589. 1958. — Type:



Figs. 5-7. *Hydnum crocidents* Cooke (type). — 5. Generative hyphae from the context, showing clamp-connections at the septa. — 6. Basidia in various stages of development, with clamps at the base. — 7. Spores. (All figures  $\times 700$ .)

"*Hydnum crocidens* Cke / [Australia] Port Phillip / [C.] French / on ground / Aug. [18]90" (K).

Fruit-bodies solitary. Pileus plane, slightly depressed in centre, 2-3 cm across; surface apparently smooth when fresh, finely felted near margin, glabrous in centre, fulvous yellow-brown; margin somewhat involute in places, otherwise straight. Stipe central, solid, slender, equal, about 2.5 cm long, 2-4 mm thick; surface glabrous, concolorous or darker than the pileus. Spines reaching the stipe, moderately crowded, subulate, up to 2.5 mm long, orange-brown. Context fleshy, monomitic, made up of thin-walled, inflating hyphae, up to 12.5  $\mu$  wide, with clamp-connections at (all?) septa (Fig. 5). Basidia cylindrical-clavate, 45  $\mu$  or more long when mature, 5-7  $\mu$  wide, 4-spored, with clamp-connection at the base (Fig. 6). Spores broadly ellipsoid to subglobose, smooth, colourless, 6.7-8.1  $\times$  5.4-6.3  $\mu$  (Fig. 7). Cystidia lacking.

I have seen all the collections enumerated by Cunningham (Herbarium Plant Diseases Division, New Zealand) and both these and the type material have the habit of a small, sometimes even minute, *Hydnum repandum* var. *rufescens* (Fr.) Barla. However, particularly in the genus *Hydnum* it is unwise to decide on the identity of dried material without a reliable description of the specimens in the fresh condition. Unfortunately, some inaccurate or erroneous statements in Cunningham's account make me doubt the correctness of others. The following details are taken from his description:—

(1) "Pileus . . . polished, glabrous . . ."—It is true that in age the pileus becomes glabrous and shining from the centre outward, but initially it is completely covered with a fine felt. Remnants of this tomentum are still visible in Herb. PPD, New Zealand, Nos. 6386, 7341, 7379, and 16752.

(2) "Stems . . . sulcate, hollow . . ."—In the material examined the stipes are solid and do not give the impression of having ordinarily been marked with grooves when fresh.

(3) "Generative hyphae . . . without clamp connexions."—In all collections examined (No. 17721 was too badly dried and left out of consideration) the hyphae possess clamps at the septa.

(4) "Spores globose or subglobose, 5.5-7.5  $\mu$  diameter . . ."—Such globose spores are actually by far in the majority, but these represent, I believe, immature ones. Measurements on three different collections (Herb. PPD, New Zealand Nos. 4456, 5586, and 17720) yielded a wider range of the spore-size, viz. 6.3-8.1  $\times$  5.8-6.8  $\mu$ .

The discrepancies indicated above make me suspicious of the colours described by Cunningham (pileus "at first shining white", spines "ferruginous", context "ferruginous") which are radically different from the colour notes accompanying the collection from Wellington, Mt. Waiopahu (Herb. PPD, New Zealand, No. 533). These pencilled annotations (probably in Cunningham's own hand) read as follows:—

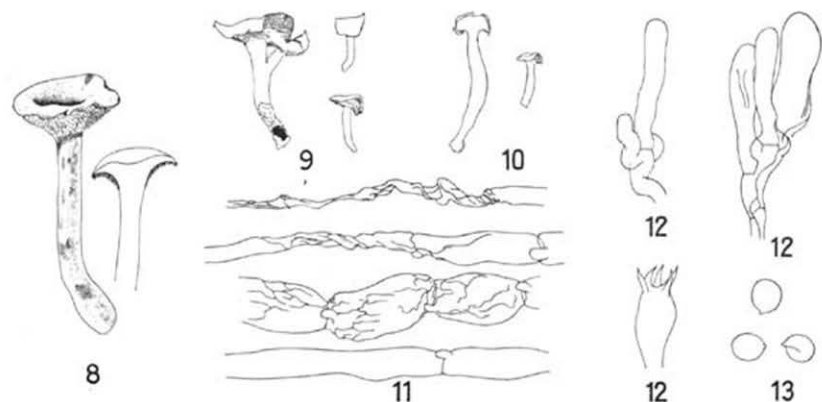
"P. cream plane. up to 4 cm diam. Stem excentric decurrent. colour of pileus. grooved. 2-4 cm long. 1 cm thick. Spines distinct at base awl-shaped acute, colour of pileus. about .5 cm long".

These notes are well in agreement with what Cleland (1934: 244) described as *Hydnum repandum*. The main parts of this description are here copied for facilitating comparison since Cleland's book may not be easily accessible.

"Pileus . . . 1.8 to 3.7 cm . . . , nearly plane . . . usually irregular, surface dull, edge turned in when young, fleshy, pallid with a buffy tint becoming Light Ochraceous Buff . . . Spines adnate with a decurrent tendency, . . . 3.5 to 10 mm long, crowded, unequal, entire, subulate to conical or blunt, buffy cream becoming Light Ochraceous Buff . . . Stem . . . 3.2 to 5 cm, moderately slender, equal or slightly attenuated upwards, solid, white or whitish, with ochraceous buff stains appearing. Flesh brittle, whitish, becoming near Ochraceous Orange . . . Taste none. Spores subspherical to irregular, whitish, 5.6  $\mu$ . Single or subcaespitose, on the ground".

Figure 55, accompanying Cleland's description, depicts two partly confluent fruit-bodies which remind one of a small *H. repandum* var. *repandum* rather than var. *rufescens*, and resemble several of the New Zealand collections, such as Herb. PPD, New Zealand, Nos. 5586, 7379, 17720, and 20105.

Taking stock of the material now available—(i) the type specimens, (ii) the collections from New Zealand, (iii) the pencil notes with one of them, and (iv) Cleland's description and illustration—I regard *Hydnum crocoides*, in contradistinction from Cunningham's opinion, as a member inseparable from the *Hydnum repandum* complex. I am, however, unable to say what status it would have within that complex or how it might be distinguished from the other members on account of its broad range of variability. Some extreme forms on one end of the range resemble minute specimens of variety *rufescens* as far as habit is concerned, while the extremes on the other end have all the characters of a small variety *repandum*. To add to the embarrassment, it should be noted that collections No. 7379 and No. 17720 each



Figs. 8–13. *Hydnum elatum* Masec. — 8. Habitus, after the water-colour (left) and pencil drawing (right) accompanying the type ( $\times \frac{1}{4}$ ). — 9. Specimens from bottom packet ( $\times \frac{1}{4}$ ). — 10. Specimens from top packet ( $\times \frac{1}{4}$ ). — 11. Hyphae of the context ( $\times 700$ ). — 12. Basidia in various stages of development ( $\times 700$ ). — 13. Spores ( $\times 700$ ).

contain both extremes. The one feature which may prove to be a differential character is that the basidia of *H. crocidens* consistently produce four sterigmata, whereas those of *H. repandum* not infrequently have five, more rarely even six.

*Hydnium ambustum* Cooke & Masee, which see for a description, proves to be identical, and as it was published three years prior to *H. crocidens*, it provides the correct name for the present species.

*Elatus*. — *Hydnium elatum* Masee in Bull. misc. Inf., Kew 359. 1914. — Type: "Hydnium elatum / Singapore / Botanic Gardens / on ground in garden jungle / colour above yellowish salmon / colour below dirty cream / 9 Oct. 1913 / Ethel M. Burkill / No. 183" (K).

Fruit-bodies solitary. Pileus (Figs. 8–10) plano-convex, depressed in centre, up to 6.5 cm across; surface smooth, finely felted, glabrescent, yellowish salmon; margin involute when young, becoming straight to wavy. Stipe central, solid, slender, straight with bent base, equal or somewhat enlarged below, up to 12 cm long, 1.3–1.5 cm thick, 2 cm at the base; surface smooth, felted, glabrescent, dirty white with scattered yellowish patches (according to the water-colour accompanying the type), brownish orange in one of the dried specimens. Spines decurrent, moderately crowded, subulate, up to 2 mm long, dirty cream. Context fleshy, monomitic, made up of thin-walled, inflating hyphae, 6–25  $\mu$  wide, with clamp-connections at all septa (Fig. 11). Basidia cylindrical-clavate, 8–9  $\mu$  wide when mature, 4–5-spored, with clamp-connection at the base (Fig. 12). Spores subglobose, smooth, 7.2–7.6  $\times$  5.4–6.5  $\mu$  (Fig. 13). Without cystidia.

The type, accompanied by a water-colour and a pencil drawing, consists of several specimens divided between two packets glued to the same sheet. On the label of the top packet is a line in a different hand (probably Miss Wakefield's) which reads, "*Hydnium elatum*, Mass. (= *H. ferreum* Lloyd)". The bottom packet contains a note by E. M. W[akefield] to state that "Mr. Masee described this as *H. elatum* from the figure only, for the specimen was in my possession at the time" (the words here spaced were underlined). It is unknown to me whether this note refers to the material of one or both packets. In the latter case it is hard to see how Masee could describe the pileus as "squamoso-diffractus" from the figure only which shows a perfectly smooth and uniform surface. One of the specimens from the top packet actually shows the surface of the pileus slightly cracked. On the other hand, Masee does seem to have been an imaginative observer, for neither the water-colour drawing nor the material give reason to describe the flesh as "fibrosa".

From the microscopical characters it is clear that the present species is a true *Hydnium*, while the colours, the central position of the slender stipe, and the decurrent spines are certainly reminiscent of *Hydnium repandum* var. *rufescens* (Fr.) Barla. The spores of *H. elatum*, however, seem to have a somewhat smaller maximum length and breadth than those given for *H. repandum* by Bourdot & Galzin (1928: 445), Coker & Beers (1951: 16), and Donk (1933: 15). Perhaps this character should not be given too much value as the spores measured may not have been quite mature, but then the habitus of the full-grown specimens of *H. elatum* is rather unusual for variety *rufescens*. As long as the *Hydnium repandum* group even in Europe

is still far from being satisfactorily unravelled, the best course for the time seems to leave the taxonomic rank of *Hydnum elatum* unchanged.

*Fragilis*. — *Hydnum fragile* Petch, see under 'scaber'.

*Gilvus*. — *Hydnum gilvum* Berk. in Lond. J. Bot. 3: 168. 1851. — Type: "*Hydnum gilvum* Berk. / Darjeeling" (K).

The type at Kew consists of two fruit-bodies torn from their base and a fragment glued to a piece of paper. Pileus plano-convex, fibrous-strigose, shining and sticky in places, coarsely strigose-hairy toward the margin, yellow-brown with the fibres more rufous. Spines crowded, subulate, reddish brown, shining, agglutinated. Context stringy, fairly soft, yellowish, not well preserved but clearly monomitic. Generative hyphae near the margin narrow, branched, septate, without clamp-connections, very thin-walled; those farther away from the margin gradually somewhat wider and with one clamp at each septum; the widest (up to 10  $\mu$ ) with two or three clamps and often an abortive side-branch at the septa, somewhat thick-walled. Interweaving and connecting hyphae present. Trama of spines monomitic. Generative hyphae much branched, septate, without clamp-connections. Hymenial elements badly agglutinated, interspersed with quantities of yellow-brown resinous matter. Gloecystidia present.

This belongs to the genus *Donkia* and *Hydnum gilvum* is a synonym of *Donkia pulcherrima* (Berk. & Curt.) Pilát. Under this name, the species would seem to be unreported from India.

*Glabrescens*. — *Hydnum glabrescens* Berk. & Rav. apud Berk., see under 'rawakensis'.

*Gleadonii*. — *Hydnum gleadonii* Masee in Bull. misc. Inf., Kew 166 "1899" [1901]. — Type: "26475 / *Hydnum Gleadoni*, Masee (sp. nov.). India, Dehra Dun, [18]98, coll. *F. Gleadon*, on dead wood" (K).

This is a polypore. Part of the dissepiments of the tubes are elongated into subulate laciniae which resemble the spines of a hydneous fungus. C. J. Humphrey made the following note on the label: "a true *Polystictus*, & must be called *P. Gleadoni*", whilst there is an additional note in Miss Wakefield's hand reading: "surely *P. funalis* or near".

In a paper on *Polystictus leoninus* Klotzsch (1950: 290), Chothia stated that "Masee's description of the fungus agrees closely with those of *P. leoninus* and *P. funalis* except in the character of spores . . ." He thought Masee's measurements of the spores were doubtful, in which case he considered *Hydnum gleadonii* (consistently spelled "*gleadowii*") to become a synonym of *Polystictus leoninus*. He concluded by saying that "Masee himself has endorsed on Kew specimens of *H. gleadowii* that the fungus is a true *Polystictus* . . ." It should be pointed out that it was Humphrey who wrote that note.

I am not in a position to offer an opinion in this matter, but can only add that I failed to find spores on the type.

*Henningsii*. — *Hydnum henningsii* Bres., see under 'versicolor'.



*Inquinatus*. — *Hydnellum inquinatum* Banker in *Mycologia* 5: 202. 1913. — Type: "*Hydnellum inquinatum* Banker / On ground under hemlocks / Indian Brook / Lake George, N.Y. / 3-8. 8. '06" (NY).

I once (Maas Geesteranus, 1957: 56) was in doubt as to whether *Hydnellum inquinatum* would be identical with *H. caeruleum*, reasoning that (i) it was hard to believe that Banker should have overlooked the bluish zones in the context of the pileus and the orange-brown colour in the stipe, and (ii) material in Herb. Donk, presented by Banker under the name of *H. inquinatum*, turned out to be a different species. This material is part of a larger collection (NY) and proves to be *Hydnellum velutinum* var. *spongiosipes*. The type, however, as well as a collection marked "Paratype" (No. 191 / Hebron, New Hampshire / *P[er]cy W[ilson]*, 14 VIII 1905; NY) are genuine *H. caeruleum*, but the three specimens of the type material are old, with the bluish zones in the context almost faded away and the originally bright orange-brown colour of the stipe dulled to a dark brown.

*Kummerae*. — *Hydnum kummerae* P. Henn. in *Bot. Jb.* 28: 321. 1900. — Type locality: East Africa, Usambara, Nguelo near Tanga.

The type (*Kummer* 51, July 1899) was preserved at Berlin, but lost during the last war.

Hennings himself indicated the relationship of *Hydnum kummerae* with *H. henningsii* Bres. (which in this paper is taken to be a synonym of *Gyrodontium versicolor*), but considered his species sufficiently distinct by "den fast hutförmigen, oberseits behaarten Fruchtkörper, sowie durch die cylindrischen stumpfen Stacheln . . ." The alleged differences may be immaterial, and even the different sizes of the basidia and spores as given by Bresadola and Hennings might be regarded as an expression of the variability of one and the same species.

Going by the description, *Hydnum kummerae* seems remarkably similar to another species, viz. *Gyrodontium boveanum*. For the time being the latter and *G. versicolor* are treated as two separate species, mainly because *G. boveanum* is incompletely known. It seems improbable that *Hydnum kummerae* should represent a third species; it is more likely that it is identical with either of the two species of *Gyrodontium* mentioned, but probably neither case can ever be proved.

*Martioflavus*. — *Hydnum martioflavum* Snell & al. *apud* Snell & Dick in *Lloydia* 25: 161. "1962" [11 Febr. 1963]. — Type: "*Hydnum martioflavum* Snell, Harrison & Jackson, Ste. Anne de la Pocatière, Quebec, 13 Sept. 1954, *H. A. C. Jackson & W. H. Snell*" (Herb. W. H. Snell 3011).

*Sarcodon armeniacus* Maas G. in *Nytt Mag. Bot.* 10: 169, figs. 1-4. 1 March 1963.

Barring such minor discrepancies as can be found in the texture of the surface of the pileus and the decurrence of the spines, the type and an additional collection of *Hydnum martioflavum* (Herb. W. H. Snell 3010) are identical with the type of *Sarcodon armeniacus*. Needless to say that *H. martioflavum* lacks clamp-connections, a character not mentioned by its authors.

Snell & al. indicated the size of the spores as  $4\text{--}5.5 \times 4\text{--}5 \mu$ , but I found the length to be somewhat greater,  $5.4\text{--}6.3 \times 3.6\text{--}4.9 \mu$ .

Following a different school of thought from that of Snell, *Sarcodon* is maintained as the correct name of the genus to which the present species belongs. Consequently, the species is hereby transferred to that genus as ***Sarcodon martioflavus*** (Snell & al. apud Snell & Dick) Maas G., *comb. nov.* (basonym, *H. martioflavum* Snell & al. apud Snell & Dick, l.c.).

*Merulioides*. — *Hydnum merulioides* Berk. & Br., see under '*versicolor*'.

*Modestus*. — *Hydnum modestum* Snell & Dick in *Lloydia* 25: 162. "1962" [1963]. — Type: "Peterson's Forest, Pleasant Creek, Sanpete Co., Utah, 30 July 1954, K. H. McKnight" (Herb. W. H. Snell 3192).

The pale dingy ochraceous colour of the spines prove that the specimens of the holotype are very young, but the spores are sufficiently developed to show a yellowish colour and an irregular outline. These characters, coupled with thin-walled, inflating hyphae of the context, determine the specimens as a species of the genus *Sarcodon*. The lack of clamp-connections, the colour of the context (which the authors described as "pallide olivaceo-cinerea"), and the lack of greenish or bluish colours in the base of the stipe, lead to Group 2 of that genus. This group contains the following species: *Hydnum badium* Pers. sensu Lundell, *Sarcodon bubalinus* (Pers.) Maas G., *S. martioflavus* (Snell & al. apud Snell & Dick) Maas G., *S. stereosarcinon* Wehm., and *Hydnum subfelleum* K. Harrison.

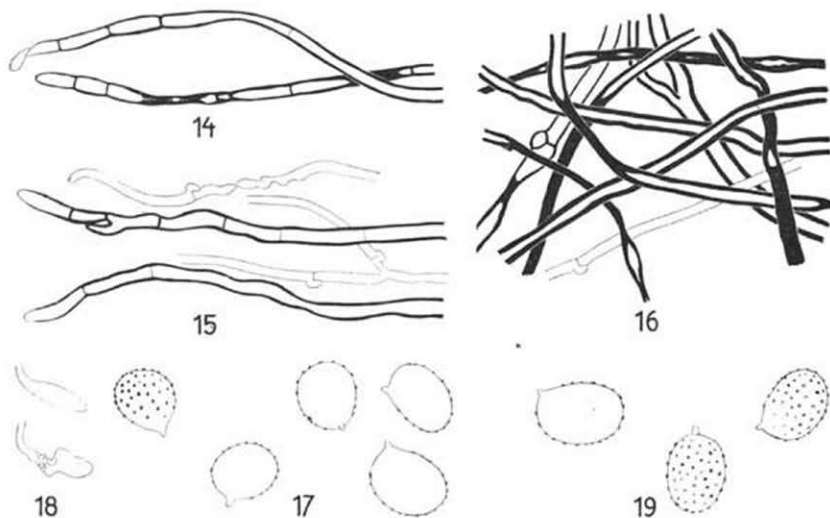
*Hydnum badium* differs from *H. modestum* in the yellow-brown pileus and the free scales. Both *Sarcodon martioflavus* (which see for particulars) and *S. stereosarcinon* are different from *H. modestum* in that the surface of the pileus is velutinous to granular or somewhat scurfy at first. *Sarcodon bubalinus* and *Hydnum subfelleum* are best discussed in the same breath. There is no doubt that both are very close, but I still hesitate to accept them as identical. Dismissing *Sarcodon bubalinus* for the time being leaves *Hydnum subfelleum* as the only species to be compared with *H. modestum*. However, comparison of the type specimens of *H. modestum* with the notes and water-colour drawings I once made of the type of *H. subfelleum*, fails to give a decisive solution. The pileus in both species is decidedly purplish and the surface (although Snell & Dick described it as "even, glabrous" in their species which, it should be remembered, was based on young fruit-bodies) is partly smooth and continuous, partly cracked into areoles and adnate membranous scales. The stipe is more yellowish in *H. modestum* than in *H. subfelleum*, and so is the context in the dried material. Odour and taste seem to differ in both species, but I fail to find more significant differences. I would not be surprised, therefore, if further collections should prove both species to be identical.

*Morgani*. — *Steccherinum morgani* Banker, see under '*rawakensis*'.

*Mülleri*. — *Hydnum mülleri* Berk., see under '*rawakensis*'.

*Nigrescens*. — *Hydnum nigrescens* Petch in Ann. R. bot. Gdns Peradeniya 7: 288. 1922. — Type: "*Hydnum nigrescens* Petch / 5110 / [Ceylon] Hakgala, April 1917" (K).

Fruit-bodies resupinate or partly reflexed, more or less orbicular, about 2 cm across, becoming laterally confluent and forming larger patches. Subiculum plushy, becoming matted and shining, light brown. Upper side of reflexed parts rough, pitted, in places with fasciculate 'hairs', the surface matted and fairly soft, brown. Spines, arising from the subiculum and the underside of the reflexed parts, crowded, subulate, up to 6 mm long, dark brown or with bluish bloom. Context not fleshy, but consisting of a homogeneous brown tomentum traversed by occasional black veins. Tomentum up to 3 mm thick, for the greater part made up of brown skeletal-like hyphae running in various directions and interspersed with few colourless generative hyphae which are often collapsed and hard to find. The skeletal-like hyphae, best studied in the plushy subiculum (Fig. 14) and in the 'hairs' on the surface of the reflexed portions (Fig. 15), where they form firmly cohering bundles, are  $2.7-3.6 \mu$  wide and thin-walled at their tip. They retain much the same width over a considerable distance when traced rearward, but their walls thicken rapidly to about  $0.9 \mu$  or even obliterate the lumen. In their radial arrangement (at least where they approach the surface of the fruit-body), the thick walls, the 'cloisons de retrait', and the lack of clamp-connections, these hyphae resemble true skeletal, but they differ from the latter in their occasional branching and the lack of a predominantly



Figs. 14-18. *Hydnum nigrescens* Petch (type). — 14. Skeletal-like hyphae from plushy subiculum. — 15. Generative and skeletal-like hyphae from a 'hair' of upper surface of fruit-body. — 16. Elements from tomentum of which fruit-body is made up. — 17. Spores, seen in Melzer's reagent. — 18. Tips of two gloecystidia. (Figs. 14-16, 18,  $\times 700$ ; Fig. 17,  $\times 2100$ .)

Fig. 19. *Gloiodon strigosus* (Sw. ex Fr.) P. Karst. — Spores, seen in Melzer's reagent,  $5.2-5.8 \times 4.2-4.5 \mu$  ( $\times 2100$ ).

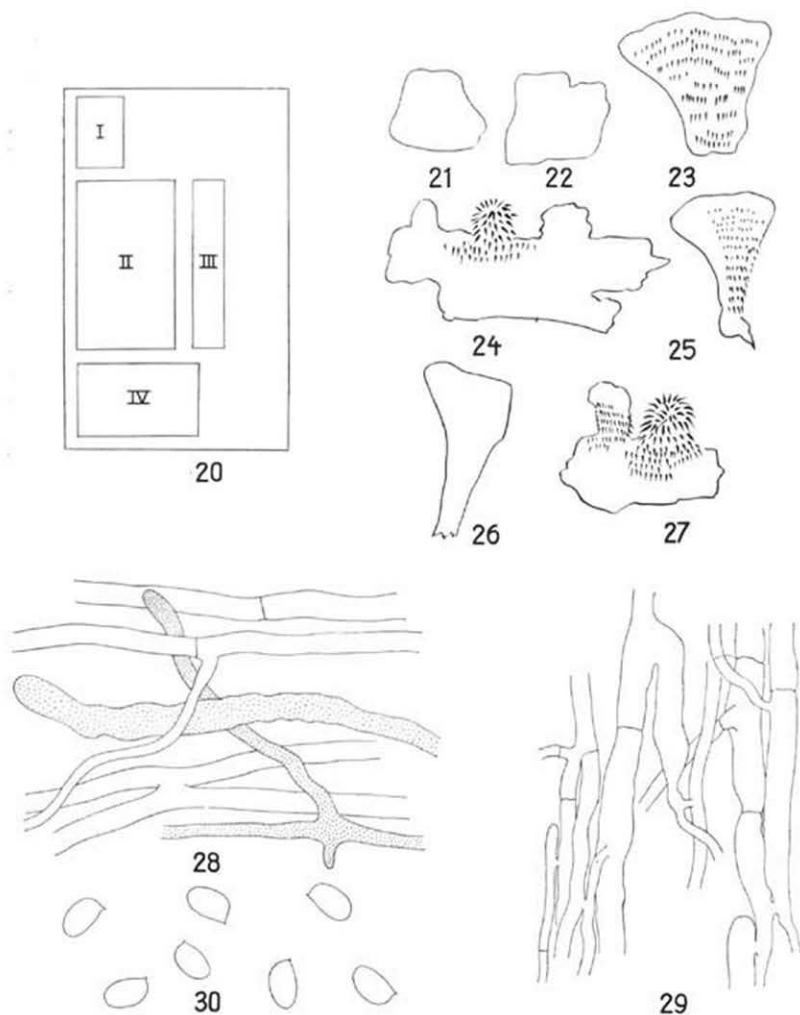
radial alignment deeper inside the tomentum (Fig. 16). Generative hyphae, at least the younger branches, 2.2–2.7  $\mu$  wide, very thin-walled (the cell-wall less than 0.5  $\mu$  thick), septate, with clamp-connections at every septum (Fig. 15), becoming wider and thicker-walled with age (Fig. 16). The construction of the spines is similar to that of the 'hairs' of the upper surface of the reflexed portions, only the generative hyphae are even more difficult to find. The hymenial elements are badly preserved. Basidia probably 4-spored. Spores subspherical to broadly ellipsoid, minutely rough to asperulate (ornamentation most clearly visible in the younger spores), with small oblique apiculus and central oil drop, colourless to pale brownish, strongly amyloid, 4.5–5.4  $\times$  3.6–4.5  $\mu$  (Fig. 17). Gloecystidia very hard to trace, the deflected portion projecting well beyond the collapsed hymenium, cylindrical to fusiform, very thin-walled, colourless, 15–18  $\times$  4–6.5  $\mu$  (Fig. 18).

In addition to the type, two more packets (Nos. 5582 and 3961) are glued to the same sheet. No. 3961 ("Hakgala, April 1914") is of particular interest as it contains a specimen with a well developed dimidiate pileus and with the 'context' up to 4 mm thick. This demonstrates that the growth form of the fungus is a variable character and in this connection a fourth collection has to be mentioned as it shows yet another aspect of the pileus. This collection is of additional interest in that it comes from far outside the type locality: Island of Enggano (west of South Sumatra), Buah-buah, 3 June 1936, *W. J. Lütjeharms 4136*, on decayed wood, c. 100 m alt. (L). The pileus in one of the specimens is nearly spatulate, 3 cm long and wide, and its surface is radiately wrinkled with broad and low ridges. Farther outward these ridges pass into coarse veins which toward the margin become reticulately connected. Some of the veins are raised above the surface and bear a terminal black spine, while in one part of the pileus the veins form separate tiers of small pileoli, each with their own system of spines hanging down from the underside.

The three collections from Ceylon and the one from Enggano all belong to the same species which, as it has all the characters of *Gloiodon*, is hereby transferred to that genus as ***Gloiodon nigrescens*** (Petch) Maas G., *comb. nov.* (basionym, *Hydnum nigrescens* Petch, l.c.).

The differences between *Gloiodon nigrescens* and *G. strigosus* are shown below:—

<i>G. nigrescens</i>	<i>G. strigosus</i>
Spines springing directly from the subiculum.  Reflexed portions showing a matted surface with few stiff hairs or no hairs at all.	Spines arising from ramifying processes which remain clearly visible as they are raised above the surface of the subiculum. Reflexed portions strongly strigose.



Figs. 20-30. *Hydnum polymorphum* Berk. & Br. (sensu lato). — 20. Type sheet with four packets. — 21-27. Contents of II. — 21, 22. Not closely examined. — 24-27. Species A. — 23, 28-30. Lectotype of *H. polymorphum*. — 28. Hyphae of context from near margin. — 29. Hyphae from spine. — 30. Spores. (Figs. 28 and 29,  $\times 700$ ; Fig. 30,  $\times 1400$ .)

*Pini*. — *Boninohydnum pini* S. Ito & S. Imai, see under '*versicolor*'.

*Polymorphus*. — *Hydnum polymorphum* Berk. & Br. in J. Linn. Soc. (Bot.) 14: 59. 1873. — Type: "178. *Hydnum polymorphum* B. & C. / Ceylon (Peradenia) G. H. K. T[hwaites] Nov. 1867" (K).

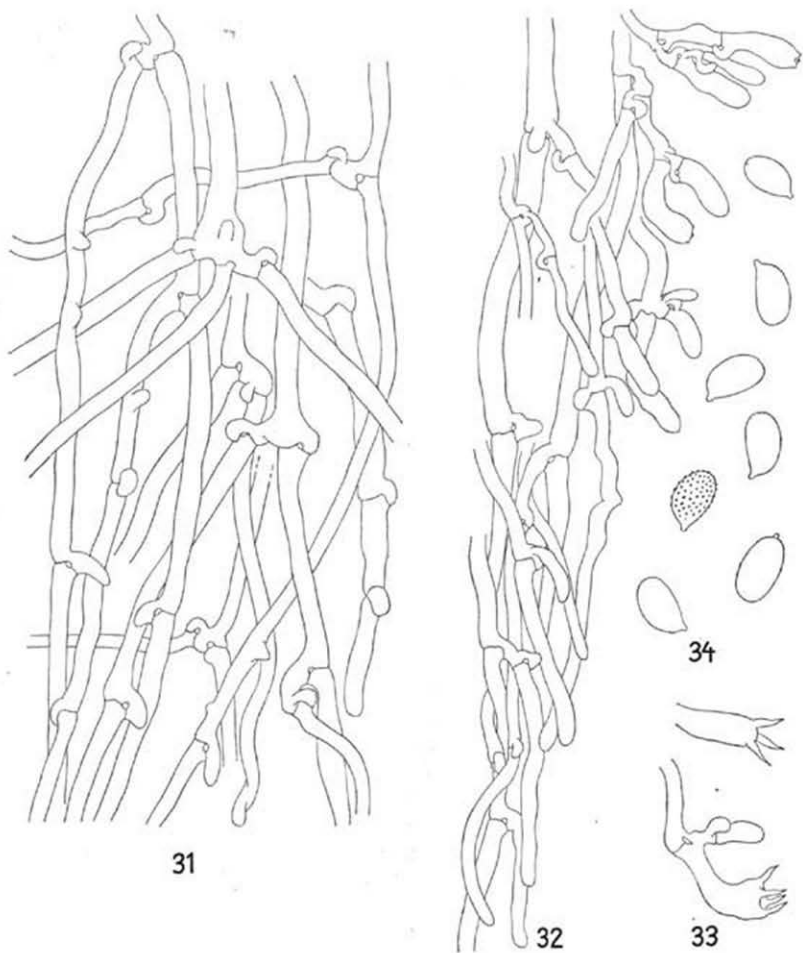
This is a somewhat complicated case and one of the difficulties, a minor one, was caused by Berkeley himself who erroneously labelled the material "*Hydnum polymorphum* B. & C". A graver error is that Berkeley thought the material consisted of a single species, whereas in fact it contains two.

On the sheet are glued four packets of variable size here numbered I, II, III, and IV (Fig. 20). No. I has nothing to do with the present species, being some Polypore from the Neilgherries. No. II contains several fragments (Figs. 21-27). Figure 23 is marked with a pencil line which outside the packet points to the words "Cf. *H. meruloides*" written in a hand unknown to me. Packets III and IV are both labelled "*Hydnum polymorphum*" (heavily pencilled) and "178. Dup." (in a thin handwriting), and they contain several slices of what apparently was a single pileus. In the upper right hand corner of packet IV Banker wrote in pencil: "These specc are identical with *Hydn. versicolor* B. & Br. and bear the same number. H. J. Banker". On account of the identical hyphal structure, I have no doubt that the contents of III and IV and the material represented by Figure 23 are conspecific (Species B), while Figs. 24-27 represent another species (A). Figs. 21 and 22 may also belong to Species A, but of that I am not certain. According to Article 9 of the Code, in case of the type sheet containing "parts belonging to more than one taxon, the name must remain attached to that part (*lectotype*) which corresponds most nearly with the original description". Unfortunately, it is not possible to decide which species (A or B) fits the original diagnosis best, as is shown by the following annotations:—

Cuneiforme [A, B], e mycelio communi effuso oriundum [A, in part only], postice radiatogulosum [A, B] umbrinum [B], antice farinaceum luteum marginatum [A, B]; aculeis acutis [A, B] quandoque furcatis [A] farinosis [A] vel subgelatinosis [B] (no. 178).

Under these circumstances the material depicted in Fig. 23 is here chosen as the lectotype of *Hydnum polymorphum*. The specimen represents a species which, as will be shown presently, is identical with *Gyrodontium versicolor*. This makes *Hydnum polymorphum* a synonym of that species and leaves us with Species A which seems undescribed.

The type of *Hydnum polymorphum* is a single segment glued with its back to a piece of paper. Hymenial surface badly soiled. Spines crowded. Context yellowish, monomitic. Generative hyphae (Fig. 28) 3.1-6.3  $\mu$  wide (up to 7.2  $\mu$  wide when filled with oily matter), colourless, thin-walled (cells-walls less than 0.5  $\mu$  thick), branched, anastomosing, septate, without clamp-connections. Hyphae in trama of spines similar, without clamps (Fig. 29). Basidia collapsed, gelatinized. Spores (Fig. 30) ellipsoid, adaxially flattened, smooth, yellow-brown under the microscope, fairly thick-walled, (4.3-4.5-5.4(-5.6)  $\times$  2.9-3.4  $\mu$ , with small oblique apiculus. Cystidia lacking.



Figs. 31-34. '*Hydnum*' species A. — 31. Hyphae from near margin of subiculum. — 32. Detail near tip of spine. — 33. Mature basidia. — 34. Spores. (Figs. 31-33,  $\times 700$ ; Fig. 34,  $\times 1400$ .)

The description of Species A is as follows: —

There are two pairs of fragments (Figs. 24 and 27, and Figs. 25 and 26). In the former pair pieces of leaf-litter appear covered with patches of a yellow-brown subiculum from which arise blunt protuberances, up to 1 cm tall and wide, and shaggy from crowded spines of the same colour. The latter pair consists of two yellow-brown wedge-like segments, of which the one in Fig. 25 shows the hymenial surface covered with spines. The segments are 4–4.5 cm long and up to 2 cm broad. In spore characters and also anatomically the two pairs are identical, but it is not now apparent what the natural position of the specimens in Figures 25 and 26 was, or how they developed from stages as pictured in Figures 24 and 27. The subiculum and context, which are spongy when soaked, are monomitic (Fig. 31). Hyphae from near the margin of the subiculum 2.7–6.3  $\mu$  wide, thin-walled (cell-walls less than 0.5  $\mu$  thick), with clamp-connections at all septa, frequently branching from a clamp. Hyphae from the trama of the spines similar, 2.7–4.5  $\mu$  wide (Fig. 32). Basidia (Figs. 32, 33) 27–30  $\times$  6–8  $\mu$ , with four sterigmata 6.3–6.7  $\mu$  long, and with basal clamp-connection. Spores (Fig. 34) ellipsoid, minutely prickly-verrucose, colourless with yellowish oily contents, non-amyloid, 5.4–7.5  $\times$  3.4–3.8  $\mu$ .

From the anatomical description and figures the species should be easily recognizable when found again. It seems undescribed and there is no genus to accommodate it. However, for a new genus to be described, the material should not only be in perfect condition but also consist of a number of complete fruit-bodies, of which the position of the various parts need not be guessed.

*Pumilus*. — *Hydnum imbricatum* f. *pumilum* Roum. in Rev. mycol. 12: 119. 1890. — Type locality: France, Central Pyrenees, Sode.

This is a nomen nudum, no description being supplied.

*Pygmaeus*. — *Hydnum pygmaeum* Yasuda in Bot. Mag., Tokyo 35: (220). 1921. — *Sarcodon pygmaeus* (Yas.) S. Ito, Mycol. Fl. Japan 2 (4): 184. 1955. — Type locality: Japan, Kyushu.

Yasuda's description runs as follows (translated): —

Fruit-body rather small, stalk central, rather soft, 15–22 mm high. Pileus thin, funnel-shaped, diam. 5–12 mm, height 5–13 mm, thickness 0.5–1.2 mm; outer surface rather dark brown, with soft dense hairs, without concentric rings. Context rather thin, wood-coloured. Stalk rather slender and long, surface smooth, dark brown to black, 7–14 mm long, 0.5–1.5 mm thick. Inner surface [of pileus, apparently] with soft dense spines, very light brown, 0.4–1.0 mm long. Spores globose, uncoloured, with spines, 4  $\mu$ .

Another description, mentioning the greyish purple colour of the pileus when fresh, was published by Lloyd (1922: 1107) who also furnished a photograph (pl. 189 fig. 2038).

The type of the present species may still be in existence, but thus far I have received no information on its whereabouts. Yasuda's description, however, leaves no doubt as to the identity of the species. The characters of the spores are those of a *Phellodon*. Of the European and North American species (as far as I know the latter), *Phellodon alboniger*, *P. cokeri*, *P. confluens*, *P. niger*, and *P. putidus* may be ruled out on account of the smooth surface of the stipe. *Phellodon tomentosus* differs from the



present species by the lighter colours and concentric rings of its pileus. *Phellodon delicatus*, which has about the same size as *Hydnum pygmaeum*, is different on account of the colours of the pileus which Coker & Beers described as "whitish drab or darker brownish drab", while the pileus, moreover, is not funnel-shaped. *Phellodon ellisianus* requires no further discussion, as Harrison (1961: 20, 21) recognized it as a synonym of *P. melaleucus*. This leaves only the latter species to be considered, and from the original description it is sufficiently clear that *Hydnum pygmaeum* is just another synonym of *Phellodon melaleucus*.

*Rawakensis*. — *Hydnum rawakense* Pers. apud Gaud. in Freyc., Bot. Voy. Monde 175. 1827. — *Mycoleptodon rawakensis* (Pers. apud Gaud.) Pat., Essai taxon. Hym. 117. 1900. — *Steckerinum rawakense* (Pers. apud Gaud.) Banker in Mycologia 4: 312. 1912. — Type: "*Hydnum rawakense* / Ded. Gaudichaud" (L 910.262-648; part in PC).

*Hymenium reniforme* Berk. & Curt. in J. Linn. Soc. (Bot.) 10: 325. 1868. — *Mycoleptodon reniformis* (Berk. & Curt.) Pat., Essai taxon. Hym. 117. 1900. — *Steckerinum reniforme* (Berk. & Curt.) Banker in Mem. Torrey bot. Cl. 12: 127. 1906. — Type: "301 / *Hydnum reniforme* B. & C. / Cuba / Wright (Curtis)" (K).

*Hydnum mülleri* Berk. in J. Linn. Soc. (Bot.) 13: 167. 1872. — Type: "*Hydnum mülleri* B. / [Australia] Tweed [River], Guilfoyle" (K).

*Hydnum glabrescens* Berk. & Rav. apud Berk. in Grevillea 1: 97. Jan. 1873; apud Berk. & Br. in J. Linn. Soc. (Bot.) 14: 59. Apr. 1873. — Type: "1634 / *Hydnum glabrescens* B. & R. / Sept. in putrid logs of *Carya* (all I have to spare) [North America] S[outh] C[arolina]. H. W. R[avenel]" (K).

*Hydnum basi-asperatum* P. Henn. in Hedwigia 36: 199. 1897. — Lectotype: "743 / *Hydnum basi asperatum* P. Henn. / [Brazil] Pr. St. Catharina / Auf Baumstamm am Bugerbach / Blumenau / April / [18]88" (Herb. Ule, HBG). — Isotype: "*Hydnum basiasperatum* P. Henn. n. sp. / H. rawacensi aff. / E. Ule 743" (Herb. Schroeter, BRSL).

The type of *Hydnum rawakense* consists of a sector of a pileus and, confluent with its base, a fragment of another pileus, both glued to a sheet of paper with their spines downward. Pileus laterally sessile, semicircular, flat except for a few low and broad concentric corrugations, the margin somewhat involute; surface smooth, glabrous except for traces of a tomentum at the base and along the margin, fulvous at the base, more yellow-brown farther outward, with darker concentric zones and minute spots (where the tomentum has collapsed and turned into innate squamules); remnants of the tomentum yellow-brown. Spines crowded, subulate, up to 1.5 mm long, corneous, brown. Context thin, tough, fibrous, without apparent zones, yellow-brown, dimitic, made up of generative hyphae (with clamp-connections at the septa) and skeletal.

As the hymenium in the type is almost completely destroyed, the description of this part has been made after material from New-Zealand (Auckland: Piha, Waitakere Ranges, Sept. 1949, J. M. Dingley; Herb. P.D.D., New Zealand, No. 17724).

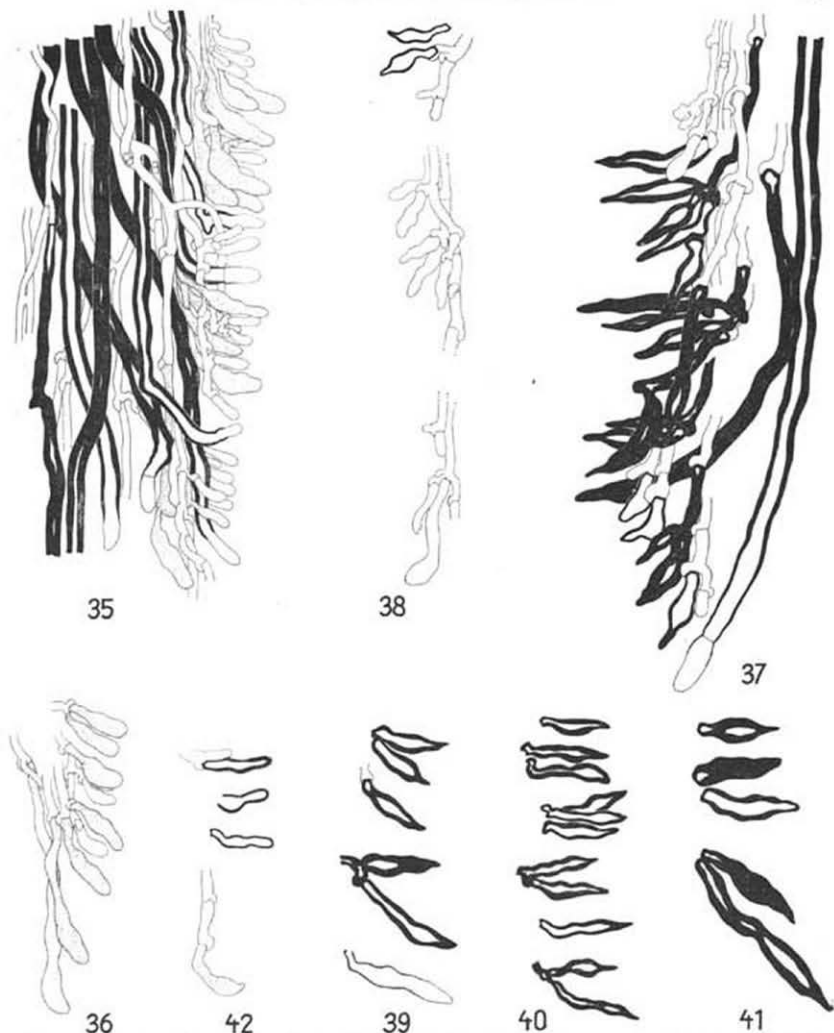
Trama of the spines dimitic. Generative hyphae and basidia with clamp-connections. The tips of the skeletals farthest from the axis of the spine bent outward, forming tramal cystidia which terminate in the hymenial layer or project beyond it; these cystidia usually more or less covered at the apex with crystalline matter dissolving in KOH solution (Fig. 35, illustrating the situation at about 650  $\mu$  back from the tip of the spine, shows the cystidia after removal of the crystals). The generative hyphae of the hymenium and/or the subhymenium (the exact position being hard to make out in squashed mounts) produce a second type of cystidia (dotted in Figs. 35-36) which are clavate or fusiformly swollen (up to 6  $\mu$ ), thin-walled, and filled with oily matter. The cystidia originating as side-branches are short-stalked, those produced at the end of a generative hypha having a stalk of variable length (up to 60  $\mu$ ).

Examination of several spines of the type eventually resulted in the find of a few thin-walled cystidia, in addition to a great number of tramal cystidia, which proved the material from New Zealand and the specimen in Persoon's Herbarium to be identical.

As may be gathered from Banker (1912: 312) and Cunningham (1958: 597), *Steccherinum rawakense*, although not reported from Africa,<sup>2</sup> has a very wide distribution in the tropics, while it is recorded by Cunningham as far south of the equator as Auckland, New Zealand, and by Miller (1935: 363) and Miller & Boyle (1943: 52) as far north as Iowa, United States. The descriptions given by Cunningham and by Miller and Miller & Boyle present an interesting difference in that Cunningham mentioned only the occurrence of "rudimentary cystidia" (i.e. the "terminal ends of skeletal hyphae"), while Miller & Boyle described thick-walled, fusiform, pointed hymenial cystidia. As the descriptions of these authors agree in other respects it seemed indicated to investigate further into this matter. For this purpose material of the first Regnell expedition (Brazil, Matto Grosso, Sante Anna da Chapada, 20 II 1894, *G. A:n Malme*, No. 535; UPS) was used. A detail of a spine (about half-way between its base and tip), with the exclusion of most of the basidia, is reproduced in Figure 37. Figures 35 and 37 are in such a marked contrast that they may easily be taken to represent two different species, but the following discussion purports to show that actually the same species is involved.

Two details in Figure 37 call for special attention. First, the gradual transition from true skeletals to hymenial cystidia indicates that the latter are nothing but shortened skeletals. This implies that the hymenial cystidia do not differ essentially from the tramal cystidia (the terminal ends of skeletal hyphae), being a modification owing to their position in the spine. A similar transition from cystidia to skeletal hyphae was described by Boidin & Ahmad (1963: 35, fig. A) in *Duportella tristicula* Pat. Secondly, it is noteworthy that not all of the hymenial cystidia are equally thick-walled, the younger ones farther down the spine tending to have thinner walls. An illuminating case is exemplified by Figure 38 (drawn from the same specimen) which, with the exclusion of all other elements, shows a number of thin-walled

<sup>2</sup> However, Lloyd (1913, Lett. 48: 9) published a note from which may be derived that he had seen specimens from Madagascar.



Figs. 35-38. *Steccherinum rawakense* (Pers. apud Gaud.) Banker. — 35, 36. (Herb. P.D.D., New Zealand, No. 17724). Detail of spine, showing generative and skeletal hyphae, basidia, tramal cystidia, and (dotted for greater clarity) thin-walled hymenial cystidia. — 37, 38 (1st Regnell Exp. No. 535). Detail of spine, showing thick-walled hymenial cystidia which farther down the spine pass into thin-walled cystidia. (All figures  $\times 700$ .)

Fig. 39. *Hydnum reniforme* Berk. & Curt. (type). — Hymenial cystidia ( $\times 700$ ).

Fig. 40. *Hydnum basi-asperatum* P. Henn. (lectotype). — Hymenial cystidia ( $\times 700$ ).

Figs. 41, 42. *Hydnum glabrescens* Berk. & Rav. — 41 (Ravenel No. 1634, type). Hymenial cystidia. — 42 (Thwaites No. 385). Hymenial cystidia. (Both figures  $\times 700$ .)

cystidia toward the tip of a spine and two moderately thick-walled ones farther back from the tip. The thin-walled cystidia are not filled with oily matter, but otherwise resemble those of Figure 35 in shape.

The thickening of the cell-walls of the hymenial cystidia as these grow older is probably nothing out of the ordinary. It also occurs in other groups of fungi, and in this connection a comparison is recommended with Corner's illustrations of the hymenial area in *Polystictus microcycclus* (Lév.) Cooke in which the thickening of the cell-walls of similar elements is shown (Corner, 1935: figs. 12, 13).

The cystidia in the type specimens of *Hydnum reniforme* (from Cuba; Fig. 39), *H. basi-asperatum* (from Brazil; Fig. 40), and *H. glabrescens* (from South Carolina, U.S.A.; Fig. 41) all resemble those of Figure 37 in being more or less fusiform, thick-walled, and pointed. However, one of the cystidia, the youngest, in *Hydnum reniforme* is still thin-walled.

A collection from Ceylon, which Berkeley identified with his *Hydnum glabrescens*, possesses apart from a few thin-walled cystidia (only one shown in Figure 42) mainly moderately thick-walled cystidia which are not pronouncedly fusiform and have blunt tips.

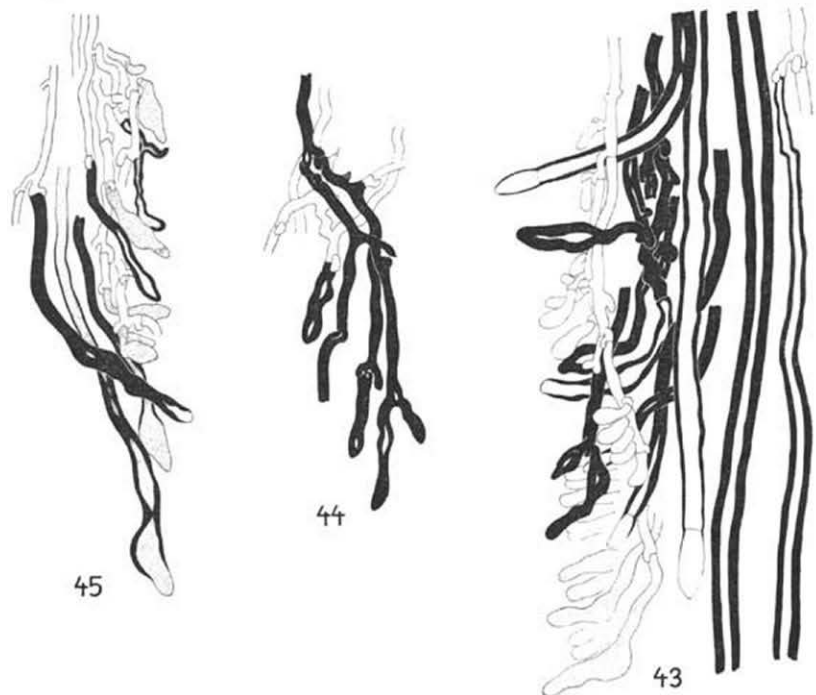
*Hydnum mülleri* (from Tweed River, New South Wales, Australia; Fig. 43) also possesses thick-walled and, farther down the spines, thin-walled cystidia (the latter should have been drawn farther separated from the former, according to their actual position on the spine). The thick-walled hymenial cystidia differ from those of Figure 37 in having rather more rounded tips, but otherwise they are similar and likewise pass gradually into the tramal cystidia. Another detail of importance is that not only the terminal ends of the hyphae (generative or skeletal) undergo a change in the hymenial region, but also large portions of the generative hyphal system farther back in the subhymenium. Figure 43 and 44 clearly show the hyphae to be partially very thick-walled or even solid.

Finally, a collection identified by Cunningham as *Steccherinum rawakense* (Auckland: Waipoua, Dec. 1951, M. E. Lancaster; Herb. P.D.D., New Zealand, No. 10984) is taken as an example to demonstrate the modification of the cystidia in the hymenial region. Figure 45 shows in the same spine the gradual change from a skeletal hypha to a thick-walled hymenial cystidium on the one hand, and intermediate forms between skeletal and thin-walled hymenial cystidia on the other.

From the examples discussed above it is, in my eyes, apparent that from a region possibly centred between New Guinea (approximately the type locality of *Hydnum rawakense*) and New Zealand (where *Steccherinum rawakense*, P.D.D. 17724 comes from), in various directions and in gradual steps, the hymenial cystidia of *Steccherinum rawakense* alter in outward appearance to culminate in entirely different-looking structures in South America and adjacent parts of North America. The potentiality of the hymenial cystidia to become thick-walled with age, remaining latent in one region, becomes manifest in varying degrees in others, while in another again the early thin-walled stage is largely suppressed. For the gradual change of a certain character in a species, J. Huxley (1938: 219) introduced the term cline. This par-

ticular kind, denoting the gradient from one end of the distributional area of the species to the other, has been called geocline.

The presence of true hymenial cystidia was not mentioned in the anatomical description of *Steccherinum* (Maas Geesteranus, 1962: 403), and might, therefore, lead to questioning the correctness of the inclusion of *Hydnum rawakense* in that genus. However, renewed examination of the spines in a number of European collections of *Steccherinum ochraceum*, including collection L958.319-049, brought to light that thin-walled hymenial cystidia of the type as shown in Figure 36 (but without oily contents, which may be of minor importance) do occur. It is now hard to explain how these structures could have passed unnoticed. In view of the incompleteness of the previous anatomical characterisation of *Steccherinum* and the variable aspect of the hymenial cystidia, it is necessary to give an emended description:—



Figs. 43, 44 *Hydnum mülleri* Berk. (type). — 43. Detail of spine, showing among others thick-walled and thin-walled hymenial cystidia. — 44. Generative hyphae which are partially solid. (Both figures  $\times 700$ .)

Fig. 45. *Steccherinum rawakense* (Pers. apud Gaud.) Banker (Herb. P.D.D., New Zealand, No. 10984). — Detail of spine showing tramal cystidia, thin-walled hymenial cystidia, and intermediate structures ( $\times 700$ ).

*STECCHERINUM* S. F. Gray (emend. descr.). — Context pliable to rigid, tough, not (visibly) zoned, pallid to white, dimitic, consisting of generative and skeletal hyphae. Generative hyphae branched, septate, with clamp-connections, thin-walled. Skeletals arising from the generative hyphae, either as a terminal continuation or as a side-branch, thick-walled, not septate. Trama of the spines also dimitic. Basidia with clamp-connections. Cystidia of tramal and hymenial origin, either clearly separated or showing various transitions; those of tramal origin being the terminal ends of skeletal hyphae curved outward and mostly thick-walled except at the tip which may be encrusted with crystalline matter; the cystidia of hymenial origin originating from generative hyphae in the (sub)hymenial region and either thin-walled or very thick-walled or again thin-walled when young, becoming thick-walled with age.

Hymenial cystidia are certain to be found in *Irpex* also. Some of the cystidia in Figure 13 (Maas Geesteranus, 1963: 454) are clearly intermediate between tramal and hymenial cystidia.

Banker (1912: 312) considered the specimen of *Hydnum rawakense* (collected by Gaudichaud, not C. Sandreud) he had found at Paris "to be in all probability the type of the species". I presume this is actually a portion of the specimen at Leiden.

Cunningham (1958: 597) gave the type locality of *Hydnum rawakense* as Sarawak, Borneo, but that is an error. Gaudichaud collected the type on the Island of Rawak (also spelled Lawak) which is a mere speck just off the north coast of the Island of Waigeo, north-west of Vogelkop Peninsula, New Guinea.

The type of *Hydnum reniforme* consists of two specimens and a fragment, still exhibiting the dense, partially collapsed surface tomentum.

Of *Hydnum mülleri* there are two packets, of which I prefer to indicate the one bearing the annotation "Tweed. *Guilfoyle*" as containing the type. This type consists of at least two confluent pilei with the upper surface glued to a piece of paper and badly destroyed by insects along the margin, but with a profusion of well-preserved spines.

The type folder of *Hydnum glabrescens* contains two different collections, one annotated "No. 385" and marked "Typus" in a different hand, the other bearing the number 1634 on a label which is obviously Ravenel's. As already explained by Banker (1912: 316) it is the latter packet which contains the type of *Hydnum glabrescens*. No. 385, as may be gathered from Berkeley's account in Grevillea, must have been collected by G. H. K. Thwaites in Ceylon. When he was at Kew, Banker found some more collections from Ceylon, all of which he did not hesitate to identify with *Steccherinum morgani* Banker, maintaining that this latter species was different from the "South Carolina plant of Ravenel, No. 1634", which he identified with *S. rawakense*. It has been reduced to the synonymy of that species by Miller (1935: 363) and Miller & Boyle (1943: 52).

I have no opinion as yet on *Hydnum guaraniticum* Speng., of which I did not see the type.

It was Banker again who (1912: 313) showed the truth about the "curious mare's-

nest" *Hydnum basi-asperatum*.<sup>3</sup> However, he was not correct in thinking that the material of this species at Berlin represented the type. Hennings (l.c., p. 190) stated that he gave an enumeration of Basidiomycetes "welche, zum grossen Theil vom E. Ule gesammelt, sich im Herbar des verstorbenen Professors Dr. Schröter in Breslau vorgefunden haben". From this it may be surmised that Ule's collection was distributed after it had been named, one of the isotypes being sent to Berlin. The latter material was destroyed during the last war, which leaves, as far as I know, the isotypes at Hamburg and Wrocław (Breslau). Of these I prefer to indicate the collection at Hamburg as lectotype, owing to its more complete annotations, but otherwise the material in Schroeter's herbarium at Wrocław is in no way inferior.

*Reniformis*. — *Hydnum reniforme* Berk. & Curt., see under '*rawakensis*'.

*Ridleyi*. — *Calodon ridleyi* Masee in Bull. misc. Inf., Kew 5. 1908. — *Hydnum ridleyi* (Masee) Trott. *apud* Sacc., Syll. Fung. 23: 472. 1925 ("*Rydleyi*"). — Type locality: Singapore.

Masee's diagnosis ("Pileus suberosus . . . Sporae subglobosae, verrucosae, brunneae . . .") suggests that the species is a *Hydnum*, but to judge from a copy of the original drawing, it might just as well be a species of *Sarcodon*. The species may even be brought in relation with *Sarcodon thwaitesii*, but there can be had no certainty until the type is discovered. Up till now this has not been located in the herbaria of both Kew and Singapore.

*Scaber*. — *Hydnum fragile* Petch in Ann. R. bot. Gdns Peradeniya 7: 287. 1922; not *Hydnum fragile* Pers. ex Fr., Syst. mycol. 1: 417. 1821; not *Hydnum fragile* Fr. in Öfers. svensk VetAkad. Förh. 8: 53. 1851. — *Hydnum scabrum* Petch in Ann. R. bot. Gdns Peradeniya 10: 134. 1926 (name change). — Type: "*Hydnum fragile* Petch [*fragile* crossed out and rewritten *scabrum*] / [Ceylon] Peradeniya, Dec. 1913, No. 3994" (K).

The type at Kew consists of two portions of a pileus roughly 6 cm long and wide. Near the basal part they are covered with spines which toward the margin are more and more conspicuously arranged in radial rows. Besides, the spines are more flattened and several spines in the same row are connected by an elevated line, thus rendering the hymenium toothed-lamellate. At the very margin the spines are wholly replaced by lamellae, several of which are reticulately connected.

The features described above are reminiscent of the hymenial configuration in some Polypore, and Dr. M. A. Donk in this connection suggested some relationship with *Hirschioporus*. The duplex nature of the context and its dimitic structure, the presence of cystidia crowned with a head of crystalline matter which disappears in a KOH solution, and the colourless spores are all characters corroborating this suggestion. However, the small size of the spores, given by Petch as  $3-5 \times 3 \mu$ ,

<sup>3</sup> Lloyd (1918: 801) told the same story in his own words, but omitted to mention his source of information.

may prove an obstruction to the inclusion of the present species in that genus.

On the sheet is a note in pencil in Miss E. M. Wakefield's hand which reads: "cfr. *H. duriusculum* Lloyd".

*Serpuloides*. — *Hydnum serpuloides* P. Henn., see under '*versicolor*'.

*Sinclairii*. — *Hydnum sinclairii* Berk. in Hooker, Handb. New Zeal. Fl. 756. 1867. — *Phellodon sinclairii* (Berk.) G. H. Cunn. in Trans. Roy. Soc. New Zeal. 85: 590. 1958. — Type: "*Hydnum sinclairii*, B. / New Zealand / 1860 / Dr. Sinclair" (K).

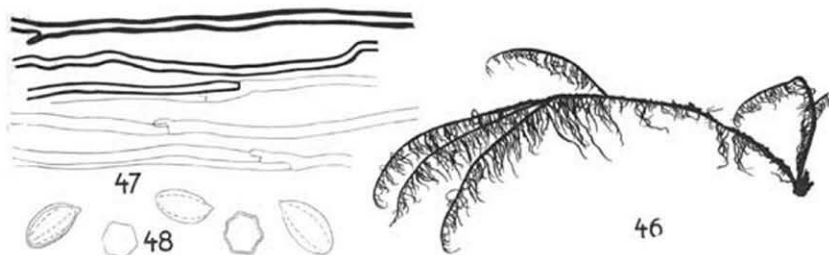
Several of the collections cited by Cunningham were received on loan and compared with the type. Cunningham's description, although good in general lines, needs a few supplementary and corrective remarks.

*Phellodon sinclairii* is a well-defined, independent species which comes close to *P. melaleucus* on account of the glabrous surface and dark colour of its stipe, but which has the black and hard context in common with *P. niger*. The stipe, which may be as long as 35 mm, has a tendency to proliferate, producing pointed processes. The latter may remain awl-shaped and sterile or broaden into flattened divisions bearing spines on the underside. The pileus, too, may proliferate and is sometimes deeply lacerated, which results in a profusion of narrow slips. The surface of the pileus in most cases is radiately fibrillose to striate, sometimes even rugulose or ridged (not sulcate). Near the margin, shallow concentric depressions may cause a structural zonation, but there may also occur a colour-zonation owing to an alternation of dark olive and blackish zones. Apparently, the superficial felt is very thin, collapsing very soon behind the growing margin, but in one collection (Otago Distr., Tapanui, Black Gully, Apr. 1957, S. D. & P. J. Brook; Herb. P.P.D., Auckland, No. 17715) this tomentum is still visible as a dingy whitish marginal rim. The spines, which Cunningham described as black with an olivaceous tinge, are ash grey when mature.

*Sprucei*. — *Hydnum sprucei* Mont., Syll. Gen. Spec. Crypt. 173. 1856. — *Pterula sprucei* (Mont.) "McGinty" / Lloyd, Mycol. Writ. 5: 865. 1919 (not validly publ.). — Type: "*hydnum (Merisma) Sprucei* Montg. / São Gabriel / supra ligna putrida. Junio, 1852" (PC).

The type consists of two complete fruit-bodies and two fragments. Fruit-bodies delicate, subfasciculately branched from a short stem, main branches patent, filiform, simple or dividing once or twice, up to 32 mm long, 0.5 mm wide near their base, tapering to 0.1 mm at their tip, floccose-tufted above and on the sides, producing on the underside secondary branches in one or two rows (Fig. 46). Secondary branches up to 6 mm long, subulate, simple or with short side-branches projecting at right angles, covered on all sides with the hymenium. Context horny when dried, dimitic, consisting of very firmly cohering generative and skeletal hyphae (Fig. 47). Generative hyphae up to 3.6(-4.9)  $\mu$  wide, very thin-walled (cell-walls less than 0.5  $\mu$ ), branched, septate, with clamp-connections, giving rise to the skeletal which are 1.8-3.6  $\mu$  wide, thick-walled but not solid (cell-walls 0.5-1  $\mu$ ), straight, flexuous, or kinked, with occasional excrescences and rarely with a side-branch. The floccose-tufted covering composed of the ends of the generative hyphae. Hymenium not thickening, composed of basidia only, of which not a single mature one was found, clavate, up to 15  $\mu$  wide (with a clamp at their





Figs. 46–48. *Hydnum sprucei* Mont. (type). — 46. One of the fruit-bodies of the type collection ( $\times 2$ ). — 47. Generative and skeletal hyphae ( $\times 700$ ). — 48. Spores ( $\times 700$ ).

base?). Spores (Fig. 48) numerous, subamygdaliform, smooth, with 5–7 longitudinal ribs, colourless,  $12.8\text{--}14.8 \times 7.9\text{--}9.0 \mu$ , with somewhat thickened wall, apiculus c.  $1 \mu$  long.

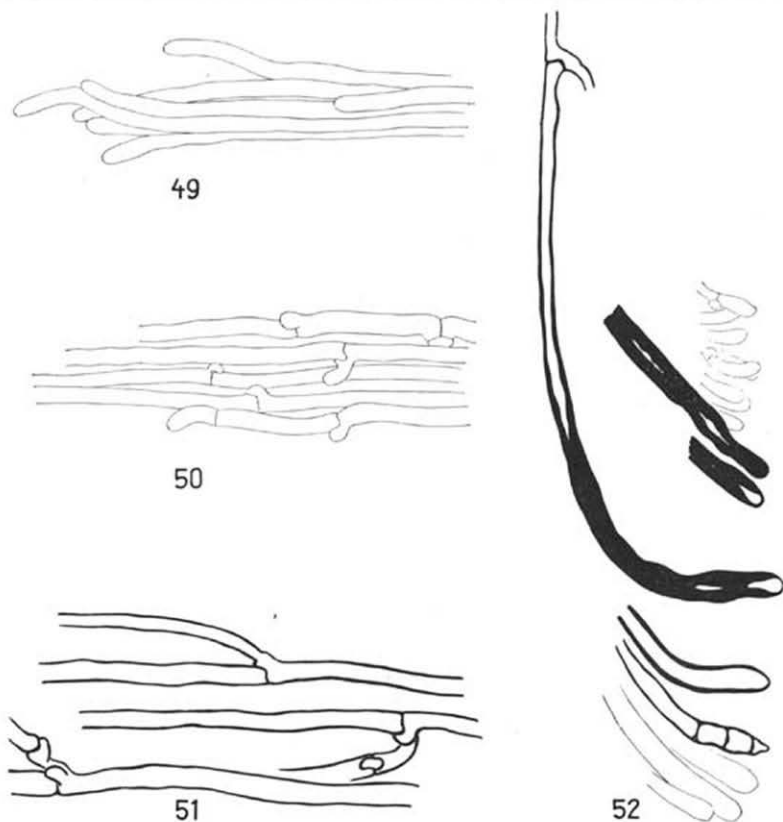
To judge from the characters described above (such as the filiform branches, the dimitic context, the smooth and colourless spores, the absence of cystidia, and the occurrence on wood), the present species obviously is a member of the genus *Deflexula* as defined by Corner (1952: 275). Further characters, such as the way the secondary branches are born on the underside of the main branches, and the size of the amygdaliform spores, indicate that *Hydnum sprucei*, in spite of a somewhat different outward appearance, is identical with and provides an earlier name for *Deflexula pennata*.

The genus *Deflexula* as emended by its author comprises two series of species which seem well distinguishable. One series, including the type species *D. fascicularis* (Bres. & Pat.) Corner, may be characterized by a thickening hymenium and globose spores, and the second by a not thickening hymenium and ellipsoid (amygdaliform, fusiform, ovoid, obovoid) spores. These characters may prove of generic value, but a formal separation of the two groups would appear premature as no definite information is available on the nature of the hymenium in *D. vanderystii* (P. Henn.) Corner (of the first group) and in *D. subsimplex* (P. Henn.) Corner (of the second group). *Hydnum sprucei*, which would enter the second group, is therefore retained in *Deflexula* as ***D. sprucei*** (Mont.) Maas G., *comb. nov.* (basonym, *Hydnum sprucei* Mont., l.c.), while *Pterula pennata* P. Henn. and *Deflexula pennata* (P. Henn.) Corner are reduced to its synonymy.

*Stereoides*. — *Hydnum stereoides* Cooke in Grevillea 20: 90. 1892. — Type: "No. 1660 / [*Stereum* crossed out] *Hydnum stereoides* / [Malaya, Perak] Gunong Batu Puteh / 1891 / L. Wray jr." (K).

The type is composed of numerous imbricated pilei attached with narrowed base to pieces of wood and bark. Pileus flabelliform, deeply lacerated or divided into several cuneate lobes, up to about 1.5 cm long, of a peculiar horny aspect; upper surface smooth, sometimes glabrous, sometimes scantily covered with radially

arranged, short, white or yellow fibrils which especially along the margin may be more numerous, forming a narrow zone of thin tomentum, while in a few cases there are two to three tomentose zones separated by concentric glabrous areas; black-brown near the base, chestnut near the margin; lower surface sterile for a distance of up to several millimeters; margin upturned, wavy, fimbriate or torn. Spines crowded, 0.2–0.3 mm long, subulate, brittle, brownish flesh-colour, with a white bloom from protruding cystidia. Context horny, 0.3–0.4 mm, dark brown, monomitic. Generative hyphae (Figs. 49–51) firmly coherent, thin-walled (at least at the margin and in the upper parts of the context; cell-walls less than  $0.5 \mu$ ), with clamp-connections at all septa, unbranched near the margin, sparingly branched



Figs. 49–52. *Hydnum stereoides* Cooke (type). — 49. Generative hyphae from margin of pileus. — 50. Same hyphae, about  $100 \mu$  rearward, showing clamp-connections, one of the latter budding into a side-branch. — 51. Hyphae about 1 mm back from margin, showing ramification. — 52. Detail of spine, showing cystidia and basidia. (All figures  $\times 700$ .)

farther back, 2.7–4.5  $\mu$  wide at the margin, very gradually widening to about 5.5  $\mu$ . Hyphae in the lower parts of the context have appreciably thicker cell-walls, up to 1.5  $\mu$ . Trama of the spines neither truly monomitic nor dimitic (Fig. 52). Generative hyphae similar to those of the context, but toward their tips curving outward and terminating as cystidia, 3–5.5  $\mu$  wide. The cystidia at the tips of the spines are very thin-walled to moderately thick-walled, those higher up the spines very thick-walled to solid; the latter resembling skeletal hyphae. Basidia with basal clamp-connection. Whether the spores seen belong to the present species cannot be stated with certainty.

*Hydnum stereoides* fits in with none of the genera I have studied up till now and may well represent an undescribed genus. A full description, however, must be postponed until better preserved material is available and the identity of the spores is beyond doubt.

*Subpallidus*. — *Hydnum subpallidum* Snell & Dick in *Lloydia* 25: 162. "1962" [1963]. — Type: "*Hydnum subpallidum* Snell & Dick, Black Fox Mountain, near McCloud, Siskiyou Co., Calif., 10-8-58 (?), *Kay Scott*" (Herb. W. H. Snell 3171).

The tuberculate brownish spores and the thin-walled, inflated hyphae of the context determine the species as a *Sarcodon*. On account of the white context (somewhat flushed with vinaceous in the stipe) and the presence of clamp-connections, the species belongs to Group 3 of that genus. The smooth, adnate scales of the pileus rule out *S. imbricatus* (L. ex Fr.) P. Karst., which leaves *S. laevigatus* (Sw. ex Fr.) P. Karst. as the only possibility.

Snell & Dick compared their species with *S. laevigatus*, from which they found it to differ in (i) the depressed pileus perforated into the stipe, (ii) the shorter spines, (iii) the whiter stipe, and (iv) the smaller spores.

Ad (i). — *Sarcodon imbricatus* is the species best known for the phenomenon described as "pileus perforated into the stipe", and here the perforation often is a sign of old age or appears after a spell of wet weather. Now, from an anatomical point of view, perforation of the pileus is a sign of loosening of the context, and that is a feature shared by several other species of *Sarcodon* I know, including *S. laevigatus*.

Ad (ii) and (iv). — In the present case, shorter spines and smaller spores are no independent characters. The specimens of the holotype are only half-way mature, which accounts for the shortness of the spines, their pale colour, the comparative scantness of the spores, and the size of the latter which Snell & Dick found smaller than in *S. laevigatus*.

Ad (iii). — There is nothing unusual in the fact that the stipe darkens with age. The white colour of the stipe in *Hydnum subpallidum* is in keeping with the immature condition of the type specimens. Also, apart from the age, there is the individual variability depending on the fruit-body's exposition to daylight. The specimens may well have been collected in a dark corner.

My conclusion is that *Hydnum subpallidum* represents an immature state and possibly somewhat pale form of *Sarcodon laevigatus*.

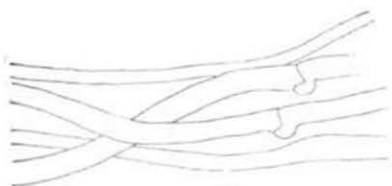
*Tapeinus*. — *Hydnum tapeinum* Masee in Bull. misc. Inf., Kew 171. "1899" [1901] ("*tapienum*"). — Type: "*Hydnum tapeinum* Mass. / Malay Peninsula / State of Selangor / Aug. 1897 / 75 / H. N. R[idley] (and an illegible word or name which may stand for a second collector)" (K).

A single pileus. Pileus fan-shaped, convex in the central portion and along the margin, deeply depressed in the intervening area, about 60 mm long and 65 mm wide, tough, 4 mm thick at the basal part, which is broken off, thinning out to about 0.2 mm at the strongly involute margin. Surface azonate, glabrous, finely innate-fibrillose and minutely radiately rugulose, holding dirt and grains of sand, fissured near the margin, dull, dingy ochraceous yellow-brown, somewhat more fulvous toward the margin and with tiny spots of that colour scattered over the whole of the surface. Spines probably decurrent, crowded, subulate, straight, often two or more connate, up to 4 mm long, corneous-translucent and reddish brown, with scurfy whitish apices. Context firm, fibrous, homogeneous throughout, azonate, pale yellow-brown, not staining in KOH solution, non-amyloid, odourless, monomitic, consisting of generative hyphae. The hyphae at some 10 mm distance from the margin and close under the surface are 3.6–6.3  $\mu$  wide, very thin-walled (cell-walls less than 0.5  $\mu$ ), occasionally branched and anastomosing (not drawn), and with clamp-connections at all septa (Fig. 53). Farther down in the context the side-branches become more numerous, the hyphae attain a width of 5.4–6.7  $\mu$ , and the thickness of the cell-walls increases to 1–2  $\mu$  or lumina of the hyphae may become obliterated in places (Fig. 54). In the basal portion of the pileus the hyphae are up to 8  $\mu$  wide, thick-walled, and frequently branched. The side-branches often form intricate knots of anastomoses and more (transverse) side-branches which serve to connect the radially arranged hyphae (Fig. 55). The hyphae in the spines lack transverse connecting hyphae, but branching and anastomosing are frequent, and clamp-connections occur at all septa. The axial hyphae reach a width of 4.5  $\mu$  and are moderately thick-walled, becoming increasingly narrower and thinner-walled toward the sides of the spines, eventually to develop the tortuous hyphae of the subhymenium (Fig. 56). The hymenium is not developed. Cystidia-like elements (10–25  $\times$  2–5  $\mu$ , very thin-walled) which project beyond the collapsed subhymenial tissue, both on the sides and near the tip of spines, may or may not be true cystidia, which is impossible to determine in this material. As all attempts to trace these

#### EXPLANATION OF FIGURES 53–60

Figs. 53–56. *Hydnum tapeinum* Masee (type). — 53. Thin-walled hyphae from close under the surface of the pileus. — 54. Thicker-walled and more branched hyphae from deeper parts of the context. — 55. The side-branches, in their turn producing branches and forming anastomoses, serve to connect the radially arranged hyphae. — 56. Detail of a spine, showing hyphae from the axial part (right) to the subhymenium (left). (All figures  $\times$  700.)

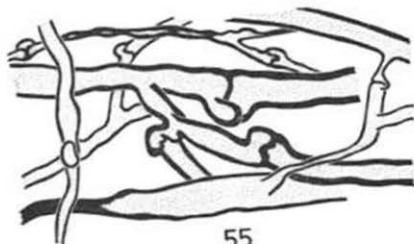
Figs. 57–60. *Hydnum aitchisonii* Berk. (type). — 57. Hyphae from the context, at about 7 mm distance from the margin of the pileus and close under the upper surface, 3.6–4.5  $\mu$  wide, thin-walled (cell-walls less than 0.5  $\mu$  thick), septate, with clamps, occasional side-branches and anastomoses. — 58. Hyphae from deeper down the context, up to 6.3  $\mu$  wide, cell-walls 0.9–2.7  $\mu$  thick, in places obliterating the lumen. — 59. Hyphae from near the base of the pileus, inflated in places, up to 14.5  $\mu$  wide, very thick-walled (cell-walls 1–3  $\mu$  thick) or solid. — 60. Detail of a spine. Hyphae frequently branched, septate, clamped at all septa; 3.6–4.5  $\mu$  wide, moderately thick-walled to solid in the axis; 1.8–2.7  $\mu$  wide and very thin-walled toward the sides. Subhymenium of very tortuous, narrow hyphae. (All figures  $\times$  700.)



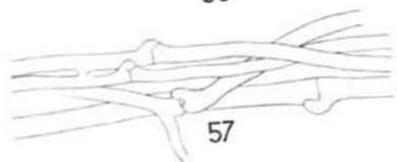
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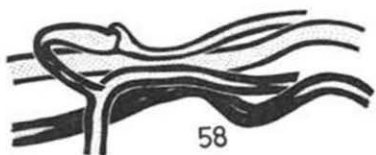
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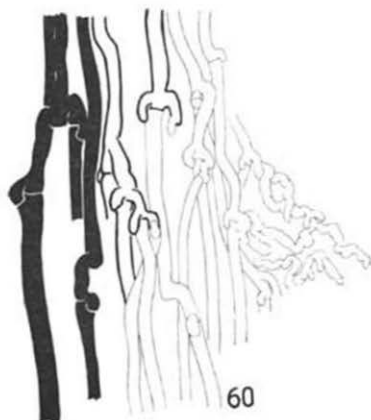
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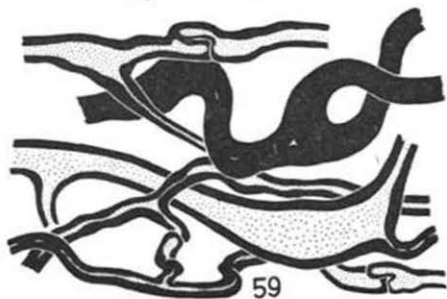
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56



59

Figs. 53-60

elements rearward failed, I am unable to say in what part of the spine they have their origin.

The similarity in outward appearance of *Hydnum tapeinum* and *H. aitchisonii* is extraordinary and at first led me to regard them as conspecific. The hyphal characters (with the exception of the questionable cystidia-like outgrowths) certainly agree with those of the genus *Mycoleptodonoides* Nikol. and resemble those of *M. aitchisonii* (Berk.) Maas G. However, there are certain discrepancies which make me hesitate actually to declare them conspecific.

The hyphal structure of *Mycoleptodonoides aitchisonii* is reproduced in Figs. 57-60, and on comparing these with Figs. 53-56, the following differences may be enumerated: (i) the hyphae deeper in the context seem to be more often solid in *M. aitchisonii* than in *H. tapeinum*; (ii) inflated hyphae are much in evidence in the former species, particularly in the basal portion of the pileus, but little pronounced in the latter; (iii) the axial hyphae in the spines in the former species are often completely solid, whereas those of the latter are moderately thick-walled at the most; (iv) the tips of the spines in the former are smooth and glabrous, those of the latter scurfy from the projecting cystidia-like outgrowths.

It is possible of course, that these differences are accidental and of an individual rather than specific nature, but until I have seen fully mature material from the State of Selangor, I am not quite prepared to identify *Hydnum tapeinum* with *Mycoleptodonoides aitchisonii*.

*Thwaitesii*. — *Hydnum thwaitesii* Berk. & Br. in J. Linn. Soc. (Bot.) 14: 58. 1873. — *Phaeodon thwaitesii* (Berk. & Br.) P. Henn. in Nat. PflFam. 1 (1\*\*): 149. 1898. — Lectotype: "*Hydnum thwaitesii*, B. & Br. / [Ceylon] Peradeniya / Aug. 1868 / [*Thwaites*] No. 735" (K).

One of the three packets containing the syntypes from Peradeniya bears the annotation (by Thwaites): "This is the only example I have found of this species unless it can possibly be a state of No. 728. — The colour but little altered in drying". This material, consisting of two slices of the fungus, is here chosen as the lectotype, as it best exhibits the habit and size of the species. A fourth packet, on which the words "*Hydnum thwaitesii* / 735 Dup." are written in pencil, contains slices of a completely different species; possibly representing No. 728 to which Thwaites referred?

A second sheet bears two more packets of the same species, one from Neilgherries (mentioned by Berkeley & Broome), and the other from the Botanic Gardens at Singapore, collected on 4 May 1920. The half specimen in the latter packet is in perfect condition and accompanied by the following note: —

Singapore 5702. Pileus fleshy, above dark purple, context greyish, 10 cm diam. Stipe central, outside dark purple, context greyish, 7 cm long. Tubes (!) greyish, discrete, readily breaking from hymenophore when dry, 1 mm long. Growing in the ground.

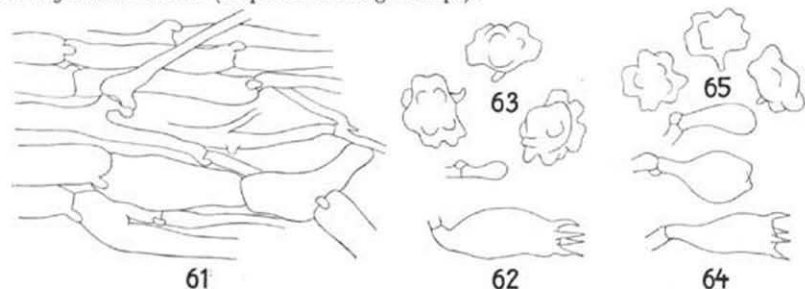
The following redescription of the species is chiefly based on the latter material, supplemented with data taken from both the material and the diagnosis of the type.

Pileus conical to convex, about 55 mm across, covered with a fine tomentum which becomes areolate, and from centre outward seems to collapse to form a glabrous, shining surface; greyish lilac (type) to dark purple (Singapore 5702) when fresh, blackish olive when dried. Stipe central, solid (Berkeley & Broome's "stipite . . . cavo . . ." is probably accidental), tapering downward, 60 mm long, 14 mm wide at the apex, 10 mm at the base, minutely tomentose, glabrescent, dark purple (Singapore 5702) when fresh, blackish when dried. Spines not decurrent, about 1 mm long, subulate, apparently white (type) to greyish (Singapore 5702) when young, dark brown from the spores when dried. Context fleshy, not zoned, greyish (Singapore 5702) when fresh, dark rufous brown (type) to black (Singapore 5702) when dried. Taste and odour unknown. Hyphae of the context (Fig. 61) of one kind only, inflating, thin-walled, branched, septate, with clamp-connections, 2–12.5  $\mu$  wide. Hyphae of the trama of the spines similar. When soaked in KOH solution both the context of the pileus and the trama of the spines rapidly stain the surrounding fluid red-brown, while the crystalline matter remaining on the hyphae dissolves and turns blue-green to ink blue. Basidia (Figs. 62, 64) with clamp-connections at the base when young, 4-spored, clavate, 28–30  $\times$  10–11  $\mu$  (type) or 25–27  $\times$  10–13  $\mu$  (Singapore 5702). Spores (Figs. 63, 65) irregular in outline, roughly tuberculate, yellowish brown, 8.1–9.4  $\times$  5.8–7.2  $\mu$  (type) or 7.6–8.0  $\times$  5.4–6.3  $\mu$  (Singapore 5702) (warts included). Cystidia lacking.

To judge from the hyphal structure and the spore characters, this is a true *Sarcodon*, and the species is accordingly transferred to that genus as *Sarcodon thwaitesii* (Berk. & Br.) Maas G., *comb. nov.* (basionym, *Hydnum thwaitesii* Berk. & Br., l.c.).

The very dark colour of the fruit-body may seem unusual in *Sarcodon* at first sight, but appears to be no isolated case and not even restricted to that genus. The combination of such characters as (i) blackening of the fruit-body, (ii) bluish green discolouration of the hyphae in an alkaline solution, and (iii) thin-walled, inflating generative hyphae is known to occur also in two other members of the Thelephoraceae, viz. the monotypic genera *Boletopsis* Fayod and *Polyzsellus* Murrill.

Within *Sarcodon*, the blackening of the fruit-body and the bluish green discolouration of the hyphae in an alkaline solution are common to *S. atroviridis* (Morg.) Banker and *S. carbonarius* (G. H. Cunn.) Maas G. (both with clamp-connections) and *S. fumosus* Banker (a species lacking clamps).



Figs. 61–65. *Hydnum thwaitesii* Berk. & Br. — 61. Hyphae from context of pileus (Singapore 5702;  $\times$  700). — 62, 64. Basidia (62: type; 64: Singapore 5702; not quite  $\times$  700). — 63, 65. Spores (63: type; 65: Singapore 5702; not quite  $\times$  1400).

*Sarcodon thwaitesii* differs from *S. atroviridis* in the different colours of the context both fresh and dried; from *S. carbonarius* in the different colour of the context in the dried condition; and from both in the much smaller, very crowded spines.

The Rijksherbarium possesses two Malaysian collections (Island of Enggano, Buah-Buah, 2 June 1936, *Lütjeharms 4081*; 5 June 1936, *Lütjeharms 4274*) which I do not hesitate to refer to the present species although they are much smaller than either the type or the specimen from Singapore. The determining characters are the black colour of the fruit-bodies, the very short and crowded spines, the presence of clamp-connections, and the bluish green discolouration of the hyphae in a KOH solution. From the field notes accompanying these collections the probable colour change of the fruit-bodies may be reconstructed.

	<i>Lütjeharms 4081</i>	<i>Lütjeharms 4274</i>
pileus	fairly dark purple	dark grey, nearly black
stipe	not mentioned	somewhat purple
spines	purple	brown
context	purple	greyish
spores	6.3-7.6(-8.1) × 4.9-5.4 μ.	7.0-8.1 × 5.4-6.0 μ.

Not only was *Lütjeharms 4081* collected a few days earlier than *Lütjeharms 4274*, but judging from the brown colour of the spines and the slightly larger spores, the latter collection would seem to be the older. It thus appears that the purple colour in *S. thwaitesii* is most pronouncedly in evidence in young specimens, passing into black (the surface of the pileus), grey (the context), and brown (the spines) when growing older.

*Uleanus*. — *Hydnum uleanum* P. Henn. in *Hedwigia* 36: 198. 1897. — Lectotype: "*Hydnum uleanum* P. Henn. [in Hennings's hand] / "*Polyporus* / Auf einem Baumstamm, VIII[18]85, Itajahy, Brazil / *E. Ule 490*" [Ule's handwriting] (Herb. Schroeter, BRSL).

The type, consisting of one larger and two smaller confluent pilei, is badly pressed but otherwise in satisfactory condition, and perfectly recognizable from its microscopical features. The context is monomitic. The generative hyphae at the margin of the pileus and in the spines, as well as the basidia, lack clamp-connections. However, clamps do occur in the older portions of the context, and in the widest hyphae, on opposite sides of the septa or even in whorls. Finally, the presence of (i) a brownish oily substance in most of the hyphae, (ii) connecting and interweaving hyphae, and (iii) gloecystidia readily determines the type as *Donkia pulcherrima* (Berk. & Curt.) Pilát.

Bresadola (1916: 231) identified *Hydnum uleanum* with *H. helvolum* Zipp. ex Lév., whilst Lloyd (1916: 7) regarded the latter as "an analogue, probably a thin form



of *Hydnium pulcherrimum*". Both authors were in error. From the hyphal structure it is apparent that *Hydnium helvolum* is different from *H. pulcherrimum* and not even generically related.

Hennings designated two different collections from Brazil in Schroeter's herbarium as the types of his *Hydnium uleanum*, one from Sta. Catharina near São Francisco (*Ule 492*), the other from Itajahy (*Ule 490*). If there were duplicates of these syntypes at Berlin, they have gone lost. It is not known what happened to *Ule 492* at Wrocław (Breslau), but *Ule 490* is still extant and hereby chosen as the lectotype.

*Versicolor*. — *Hydnium versicolor* Berk. & Br. in J. Linn. Soc. (Bot.) **14**: 59. 1873. — Type: "*Hydnium versicolor* B. & Br. / No. 178, Peradeniya, July 1868 / The whole plant, when fresh, of a beautiful bright yellow colour, except the growing edges which are pure white" (K).

*Hydnium meruloides* Berk. & Br. in Trans. Linn. Soc., Ser. 2, **2**: 63, pl. 13 fig. 4. 1883. — *Irpex meruloides* (Berk. & Br.) Lloyd, Mycol. Writ. **4** (Lett. 51): 3, 1914 ("*meruloides*"; nomen nudum). — Type: "*Hydnium meruloides* B. & Br. / Brisbane No. 246. F. M. Bailey" (K).

*Hydnium henningsii* Bres. in Bull. Soc. mycol. France **6**: xlviii, pl. 9 fig. 2. 1890; Iconogr. mycol. **22**: pl. 1061 fig. 1. 1932. — *Gyrodontium henningsii* (Bres.) Pat., Essai taxon. Hym. 117. 1900. — Type: "*Hydnium Schiederm.* Heufl. var. *Kamerunensis* Bres. [cf. also Sacc., Syll. Fung. **9**: 210. 1891; specific and varietal epithets crossed out and rewritten:] *Henningsii* Bres. / Kamerun ad ligna ? / Leg. Joh. Braun / comm. Hennings" (S).

*Hydnium serpuloides* P. Henn. in Verh. bot. Ver. Brandenb. **40**: 122, pl. 1 fig. 3. 1898. — *Gyrodontium serpuloides* (P. Henn.) Reid in Kew Bull. **17**: 267, fig. 1 (1). 1963. — Type: not seen (S).

*Boninohydnium pini* S. Ito & S. Imai in Trans. Sapporo nat. Hist. Soc. **16**: 127. 1940. — Type: "*Boninohydnium pini* S. Ito & Imai / Bonin Islands, Chichishima, Omura / 14 XI 1936. leg. S. Ito, S. Imai & K. Hino" (Herb. Faculty Agric., Sapporo).

Of the names enumerated above and here considered synonymous, *Hydnium henningsii* was selected by Donk (1956: 79) as the type species of *Gyrodontium* Pat. In the following lines a full description of the microscopical structures of this species is given, followed by those of the other types.

If the figure of *H. henningsii* published by Bresadola was drawn from nature, the type specimen at Stockholm represents only a small portion of the original material. The specimen is a shapeless fragment, measuring roughly 2 × 2 cm, with bits of wood attached to it on one side, and bearing spines on the opposite side. Most spines seem not fully developed as they are rounded at the apex, while quite a few are broken off. The longest undamaged spine measures 1.5 mm, its width ranging between 0.1 and 0.3 mm. The spines are covered with a yellow-brown to fulvous powdery layer. The context of the fruit-body and the trama of the spines are hard, glassy, and nearly black. Contrary to expectation, the microscopical structures are surprisingly well preserved. Context monomitic, composed of generative hyphae and connecting hyphae (Fig. 66). Generative hyphae (in the one slide made) up to 6.3 μ wide, thin-walled, septate, without clamp-connections,

branched, anastomosing. Connecting hyphae 2–3  $\mu$  wide, probably nothing but modified side-branches (Fig. 66a). Trama of the spines made up of the same elements (Fig. 67). Hyphae up to 6.3  $\mu$  wide in the axis of the spines, somewhat thick-walled; hyphae becoming narrower toward the sides of the spines, eventually giving rise to much branched and very tortuous subhymenial hyphae, 1  $\mu$  wide. Basidia (Fig. 68) slender, clavate, 22–27  $\times$  5.4–6.3  $\mu$ , 4-spored, without basal clamp-connection, sterigmata 2.7–3.6  $\mu$  long. Spores (Fig. 69) ellipsoid, adaxially flattened, smooth, yellow-brown under the microscope, rather thick-walled, 4.5–5.6(–6.3)  $\times$  2.7–3.4(–3.6)  $\mu$ , with small oblique apiculus. Cystidia and gloecystidia absent.

The description of the type of *Hydnum versicolor* is as follows: —

To a piece of paper are glued several slices of a fruit-body. The abhymenial side of some of these slices is covered with dirt and grains of sand, but in others it is collapsed to a smooth brown surface, and from this it may be deduced that at least part of the fruit-body, presumably near the margin, was easily separable from the substrate. The flesh is up to 6 or 7 mm thick in places, fairly soft and dirty white to pallid. The spines are crowded, up to 9 mm long, subulate, longitudinally grooved, dark brown. The context is a perfect replica of that of *H. henningsii*, only it is so badly preserved that, except for a few scattered fragments, which would be meaningless in a drawing, the hyphae fail to be restored to their original shape, even after prolonged boiling in KOH solution. Generative hyphae up to 6.3  $\mu$  wide, septate, branched, anastomosing, thin-walled, without clamp-connections. Connecting hyphae abundant, with all intergrading forms to side-branches, arranged in all directions (which accounts for the spongy nature of the context), some as narrow as 1.3  $\mu$ . Hyphae in the spines more compacted, parallel to the axis of the spines. Hymenium collapsed. Spores (Fig. 70) ellipsoid, adaxially flattened, smooth, yellow-brown under the microscope, rather thick-walled, 3.8–4.5  $\times$  2.7–2.9  $\mu$ . Cystidia and gloecystidia not seen.

*Hydnum merulioides* was described as a sessile-pileate form and this caused Cunningham (1953: 280) to identify it with *Hydnum cirrhatum* Pers. ex Fr. However, two of the chief differences which separate this species from *H. merulioides* are the presence of gloecystidia in the hymenium and clamp-connections at all septa. The redescription of *H. merulioides* follows: —

The type consists of two overlapping lobes of a specimen of which it is hard to decide whether it is truly pileate or only loosened from its substrate. The overall size is about 35  $\times$  40 mm. The flesh is 2–3 mm thick, yellowish white. The spines are overgrown with mould and broken in some places, but well discernible in others, crowded, up to 4 mm long, subulate, dark brown. Context moderately well preserved, monomitic, consisting of generative and connecting hyphae, completely resembling those in *H. henningsii* (Fig. 71). Generative hyphae up to 7.2  $\mu$  wide, septate,

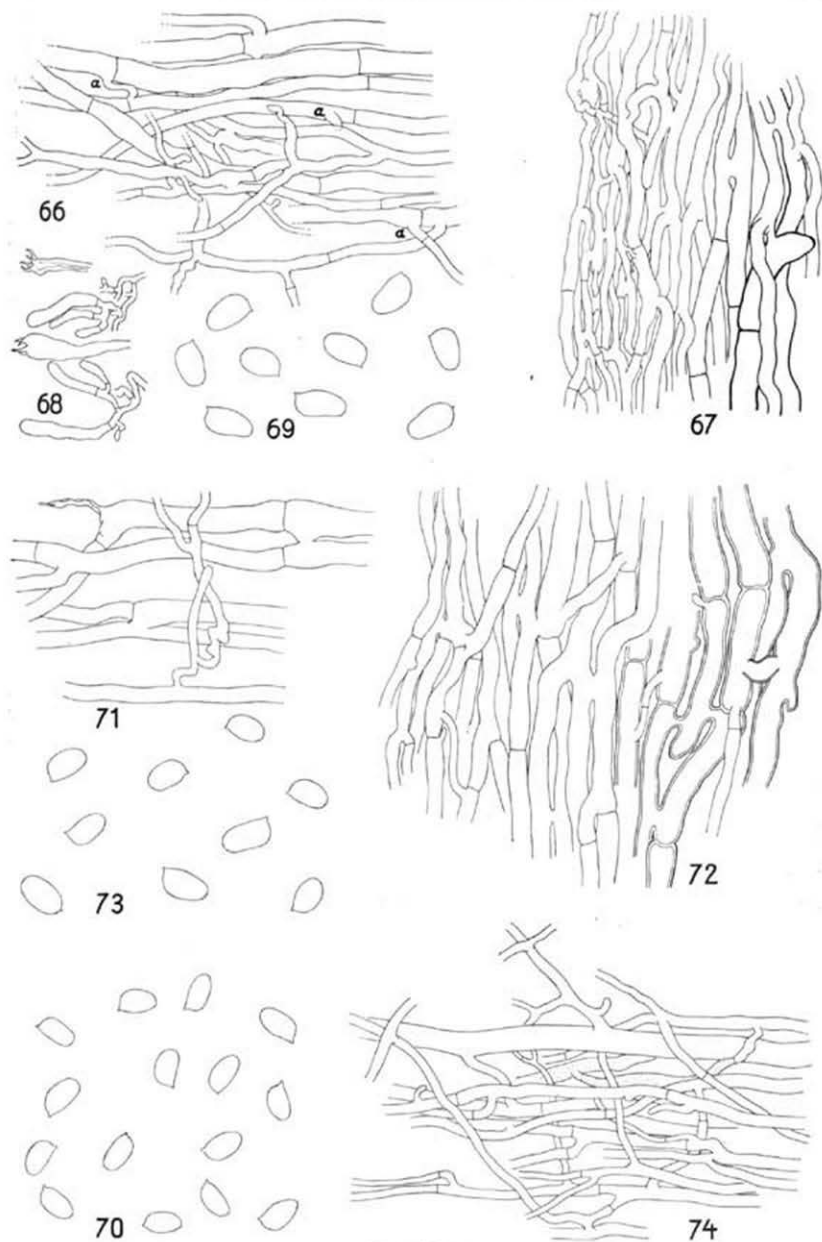
#### EXPLANATION OF FIGURES 66–74

Figs. 66–69. *Hydnum henningsii* Bres. (type). — 66. Context composed of generative hyphae and connecting hyphae (a). — 67. Detail from spine. — 68. Basidia. — 69. Spores. (Figs. 66–68,  $\times$  700; Fig. 69,  $\times$  1400.)

Fig. 70. *Hydnum versicolor* Berk. & Br. (type). — Spores ( $\times$  1400.)

Figs. 71–73. *Hydnum merulioides* Berk. & Br. (type). — 71. Hyphae from context. — 72. Detail from spine. — 73. Spores. (Figs. 71 and 72,  $\times$  700; Fig. 73,  $\times$  1400.)

Fig. 74. *Boninohydnum pini* S. Ito & S. Imai (type). — Hyphae from context ( $\times$  700.)



Figs. 66-74

branched, anastomosing, thin-walled, without clamp-connections. Trama of the spines somewhat better preserved (Fig. 72), the hyphae parallel to the axis of the spines, closely coherent, frequently anastomosing, branched, septate, without clamp-connections, up to  $6.3 \mu$  wide and fairly thick-walled in the axis, as narrow as  $2.7 \mu$  and thin-walled towards the periphery. Hymenium collapsed and gelatinized. Spores (Fig. 73) ellipsoid, adaxially flattened, smooth, yellow-brown under the microscope, rather thick-walled,  $4.4-4.9(-5.4) \times 2.7-3.1 \mu$ . Cystidia and gloeocystidia not seen.

Although *Boninohydnum pini* was described as a sessile-pileate species, all that was sent of the type material were three bits of wood, to which adhered some shreds of floccose-felted, yellowish white subiculum and context with no trace of spines. Yet, this sufficed for making the following description: —

Context monomitic consisting of generative and connecting hyphae (Fig. 74). Generative hyphae up to  $9 \mu$  wide, septate, branched, anastomosing, thin-walled, without clamp-connections.

Comparison of the original diagnoses and the descriptions given above shows that *Hydnum henningsii*, *H. versicolor*, *H. meruloides*, and *Boninohydnum pini* have the following characters in common: (i) they are wood-inhabiting, (ii) the flesh is thick and yellowish white, (iii) the context is monomitic, consisting of generative and connecting hyphae; (iv) the generative hyphae lack clamp-connections; (v) the hymenium is yellow to orange; (vi) the spores are smooth, yellow-brown under the microscope, rather thick-walled, of the same shape, and so little different in size as to form a continuous series. It is considered of minor importance that some of the species were described as pileate, others as resupinate. From this it is concluded that the names mentioned above actually refer to one and the same species, for which the following recombination is proposed: **Gyrodontium versicolor** (Berk. & Br.) Maas G., *comb. nov.* (basionym, *Hydnum versicolor* Berk. & Br., l.c.).

In this connection it is convenient here to discuss *Hydnum serpuloides* P. Henn. Reid (1963: 268) regarded *Gyrodontium henningsii* and *G. serpuloides* as closely related species, but found the former different on account of "(1) growth form (2) colour (3) shape of needles and (4) tough, fleshy texture."

Ad (1). — As stated above, not much weight should be attributed to growth form; it probably also depends to some degree on external factors.

Ad (2). — The colour of the spines is a variable character and depends on the maturity of the spores. When the spines in Bresadola's figure of *H. henningsii* are paler than those of *H. serpuloides* as described by Hennings, it may be pointed out that this is quite natural as the spines in the type of *H. henningsii* give the impression of being immature.

Ad (3). — The shape of the spines can rarely be used as a distinguishing character, and this is especially true if they are not fully developed.

Ad (4). — There is no evidence that Bresadola's description of *Hydnum henningsii* was based on field notes of the collector. When, therefore, the texture was described as "carnoso-lentus", this may well be put down to the author's "disciplined imagination guided by intuition" (Dennis, 1960: xvii). Bresadola's guess may

have been correct, but even so it is very hard to distinguish *H. henningsii* ("carnosolentus") from *H. serpuloides* ("carnosum") by the nature of the context.

From the preceding discussion it may be gathered that the differences indicated by Reid are not considered to have specific value. Reid described the hyphal structure of a specimen of *Gyrodontium serpuloides* from Melbourne, Australia. Allowing for some anomalies in the Australian material, probably owing to the fruit-body having developed in a mine, his description demonstrates that the hyphal structures of *Hydnium serpuloides* and *H. henningsii* are alike. In my opinion, therefore, there is no doubt that *Hydnium serpuloides* is conspecific with *H. henningsii* and hence with *Gyrodontium versicolor*.

Another synonym of *Gyrodontium versicolor* is *Hydnium polymorphum* which is discussed separately (p. 166).

It is possible that *Hydnium boveanum* (p. 156) is yet another name for the present species, in which case it would be the oldest name, but some of its characters make it advisable to keep the two species temporarily apart.

*Washingtonianus*. — *Hydnium washingtonianum* Ell. & Ev. in Proc. Philad. Acad. 323. 1894. — Type: "No. 214. *Hydnium washingtonianum* E. & E. / Tracyton, Kitsap Co., Wash. / Dec. 27, 1893 / on ground in deep coniferous woods / Adella M. Parker" (NY).

The type is a smallish specimen which has the pileus "slightly depressed in the center". The context is monomitic made up of inflating, thin-walled, septate hyphae with clamp-connections. The spores are subglobose, smooth, colourless, with small oblique apiculus,  $7.2-8.1 \times 6.3-6.7 \mu$ . These characters suffice to identify the specimen as *Hydnium repandum* L. ex Fr. The fairly short and thick stipe (about 9 mm thick near the apex, as opposed to the 3 millimeters mentioned by the American authors), the colour of the pileus ("pale orange"), and that of the spines ("nearly white when fresh") give further evidence of the specimen belonging to variety *repandum*. Ellis & Everhart were well aware of the close affinity of their species to *H. repandum*, but thought it to be different "in its decurrent aculei and tougher substance". I am unable to assert the latter statement, and as far as the decurrence of the spines is concerned, it is often true but by no means a rule that in variety *repandum* the spines do not reach the apex of the stipe. *Hydnium washingtonianum*, therefore, is here formally reduced to the synonymy of *Hydnium repandum* var. *repandum*.

*Hydnium decurrens* is a herbarium name used by the American authors on a slip of paper inside the packet, but afterwards apparently abandoned in favour of the epithet '*washingtonianum*'.

*Wellingtonii*. — *Hydnium wellingtonii* Lloyd, Mycol. Notes 7: 1200, pl. 247 figs. 2468, 2469. 1923. — Type: New Zealand, District Wellington, York Bay, *E. H. Atkinson 628* (Lloyd 27122, not seen; BPI).

Cunningham (1958: 590) remarked that: "Part of a collection from York Bay was forwarded to C. G. Lloyd, who named it *Hydnium wellingtonii* . . ."

I have seen the collection from York Bay, correctly identified by Cunningham as *Hydnium crocidens* ("Dentinum"), and refer to that name for further particulars.

## REFERENCES

- BANKER, H. J. (1912). Type studies in the Hydnaceae. II. The genus *Steccherinum*. In *Mycologia* 4: 309-318.
- (1913). Type studies in the Hydnaceae. III. The genus *Sarcodon*. In *Mycologia* 5: 12-17.
- BOIDIN, J. & AHMAD, S. (1963). The position of *Duportella tristicula* Pat. (Basidiomycetes: Thelephoraceae). In *Biologia* 9: 33-38.
- BOSE, S. R. (1957). Gasterospores (Chlamydospores) in tropical *Ganoderma*. In *Sydowia*, Beih. 1: 176-178.
- BOURDOT, H. & GALZIN, A. (1928). Hyménomycètes de France. Sceaux.
- BRESADOLA, G. (1916). Synonymia et adnotanda mycologica. In *Ann. mycol.*, Berl. 14: 221-242.
- CHOTHIA, H. P. (1950). *Polystictus leoninus* Klotzsch, a wound parasite. In *Ind. For.* 76: 290-291.
- CLELAND, J. B. (1934). Toadstools and mushrooms and other larger fungi of South Australia. Adelaide.
- COKER, W. C. & BEERS, A. H. (1951). The stipitate Hydnums of the Eastern United States. Chapel Hill.
- CORNER, E. J. H. (1952). Addenda clavariacea I. Two new Pteruloid genera and *Deflexula*. In *Ann. Bot.*, Ser. 2, 16: 269-291.
- (1953). The construction of Polypores—1. Introduction: *Polyporus sulphureus*, *P. squamosus*, *P. betulinus* and *Polystictus microcycloides*. In *Phytomorphology* 3: 152-167.
- CUNNINGHAM, G. H. (1953). Revision of Australian and New Zealand species of Thelephoraceae and Hydnaceae in the Herbarium of the Royal Botanic Gardens, Kew. In *Proc. Linn. Soc. New S. Wales* 77: 275-299.
- (1958). Hydnaceae of New Zealand. Part 1.—The pileate genera *Beenakia*, *Dentinum*, *Hericum*, *Hydnum*, *Phellodon* and *Steccherinum*. In *Trans. roy. Soc. New Zealand* 85: 585-601.
- DENNIS, R. W. G. (1960). British cup fungi and their allies. London.
- DONK, M. A. (1933). Revision der niederländischen Homobasidiomycetae-Aphylophoraceae II. In *Meded. Nederl. mycol. Ver.* 22.
- (1956). The generic names proposed for Hymenomycetes—V. "Hydnaceae". In *Taxon* 5: 69-80, 95-115.
- HEIM, R. & MALENÇON, G. (1928). Champignons du Tonkin recueillis par M. V. Demange. In *Ann. Cryptog. exot.* 1: 58-74.
- HUXLEY, J. (1938). Clines: an auxiliary taxonomic principle. In *Nature* 142: 219-220.
- LLOYD, C. G. (1913). Determination of specimens sent by Henri Perrier de la Bathie, Madagascar. *Mycol. Writ.* 4: (Lett. 48).
- (1918). Rare or interesting fungi received from correspondents. *Mycol. Writ.* 5: 801.
- (1922). *Hydnum pygmaeum* from A. Yasuda, Japan. *Mycol. Writ.* 7: 1107, pl. 189 fig. 2038.
- MAAS GEESTERANUS, R. A. (1962). Hyphal structures in Hydnums. In *Persoonia* 2: 377-405.
- (1963). Hyphal structures in Hydnums. IV. In *Proc. Kon. Nederl. Akad. (Ser. C)* 66: 447-457.
- MILLER, L. W. (1935). The Hydnaceae of Iowa IV. The genera *Steccherinum*, *Auriscalpium*, *Hericum*, *Dentinum* and *Calodon*. In *Mycologia* 27: 357-373.
- MILLER, L. W. & BOYLE, J. S. (1943). The Hydnaceae of Iowa. In *Univ. Iowa Stud. nat. Hist.* 18 (2).
- REID, D. A. (1963). New or interesting records of Australasian Basidiomycetes: V. In *Kew Bull.* 17: 267-308.
- SARKAR, A. (1959). Developmental anatomy and differentiation of tissue systems of *Ganoderma lucidum* (Leyss, ex Fr.) Karst. In *Φυτον* 13: 89-104.

## MELANCONIUM LINK EX FRIES

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(With one Text-figure and one Plate)

*Melanconium atrum* Link ex Schlechtendal, monotype species of *Melanconium* Link ex Fries, is described and illustrated from a collection in Persoon's herbarium, herein designated as the lectotype.

### INTRODUCTION

As a result of the examination of type and authenticated collections of microfungi in European herbaria, Hughes (1958) adopted the name *Melanconium* Link (1809) for imperfect fungi with brown dictyospores developing in basipetal succession from the more or less undifferentiated hyphae of semi-immersed stromata. These fungi had previously been referred to the somewhat ill-defined hyphomycete genera *Trimmatostroma* Corda and *Coniothecium* Corda. In Hughes' revision, *Trimmatostroma* Corda (1837) was treated as a facultative synonym of *Melanconium*.

The accepted concept of *Melanconium* for the last 150 years has been unambiguous, the name having been employed for acervular fungi with elliptical brown unicellular conidia. It has been deduced and generally accepted, though not formally designated, that *Melanconium* is the type genus of the family Melanconiaceae Corda (1842) in the order Melanconiales Berkeley (1860; as "Melanconici"<sup>1</sup>). Thus Hughes' interpretation of the genus as a Hyphomycete and the redispotion of one of its well-known species, *M. bicolor* Nees ex Schlecht. as "Coelomycetes Genus 2, mihi ignotum", has presented some taxonomic and nomenclatural problems. If Hughes is correct, they are problems which of necessity revolve around the fate of species which had formerly been assigned to *Melanconium*.

Before the obligatory rearrangement of names implied by Hughes' reassessment of genera, it was felt that the re-examination of Link's material was absolutely necessary. Therefore an account of observations and subsequent conclusions is presented below.

### HISTORY OF MELANCONIUM AND ITS TYPE SPECIES

Link (1809) erected the genus *Melanconium* with a single species *M. atrum*, the only host specifically stated by name being *Fagus*. The generic character runs as follows:

"Stroma globosum subepidermide plantarum mortuarum latens. Sporidia superne effusa, subglobosa, non septata, nuda, libera."

<sup>1</sup> As an "order" of "Fam. III.—Coniomycetes."

The single species was well illustrated for that period and briefly described as follows:

"Unica species nondum descripta *M. atrum*, stromate globoso subtus sulco notato, sporidiis per epidermidem acervatim procumbentibus nigris. In ramulis fagineis alliisque mortuis et exsiccatis frequens. . . ."

Nees (1816) added a second species, *M. bicolor*: the host was not named. von Martius (1817) however described this fungus from dead branches of *Quercus*. According to the "International Code of Botanical Nomenclature", 1961, Art. 13, the starting point for 'Fungi caeteri' is 1 Jan. 1821 (Fries, "Systema Mycologicum" 1). In this publication Fries (1821, p. xl) included *Melanconium* Link as Genus 1 in Subordo II, Stilbospori. However no species were listed and no descriptions given. Despite this, Fries, by giving the authority for the genus as Link, is automatically adopted as the post starting point authority for the name which therefore becomes *Melanconium* Link ex Fries.

The first authors after Fries (1821) to take up the genus appear to have been Ficinus & Schubert (1823) who gave descriptions for three species—"M. betulinum Kz.", "M. discolor Kz.", and "M. juglandinum Kz. msc." No reference was made to the earlier described species, except by the author's citations.

Schlechtendal (1824) is taken as the validating authority for *M. atrum* since he appears to be the earliest of the few authors to have considered this first species to be distinct after the starting point date. Steudel, later in 1824, listed five species which included *M. atrum*; he excluded *M. arundinis* Pers. The latter name was a nomen novum for *Stilbospora sphaerosperma* Pers. published by Persoon (1818, p. 134).

When Link (1825) enlarged his genus with several newly described species, he reduced *M. atrum* and *Stilbospora microsperma* Link to synonymy with *M. conglomeratum* (Link ex Steud.) Link (basionym, *Stilbospora conglomerata* Link). Most later authors including Chevallier (1826), Duby (1830) and more notably Fries (1829) accepted Link's synonymy. Since attempts to obtain material of *S. conglomerata* have been quite unsuccessful, it seems the preferable course to reject Link's synonymy which had subsequently been taken up by Fries, and adopt the name *M. atrum* Link ex Schlechtendal. This is at least affixed to a firm lectotype (see later). Sprengel (1827) was the exception among later authors in that he enumerated five species and maintained *M. atrum* on its own. No descriptions were given and no reference to Link's synonymy was made.

Several authors used the genus in its original sense and by 1837 at least 23 names had been referred to *Melanconium*. Following Link's reduction of *M. atrum* to synonymy the name quickly dropped out of use and has rarely appeared, it at all, in the rather infrequent subsequent accounts of the genus. The most recent treatment is that of Wehmeyer (1941) who dealt more specifically with the correlated perfect states of *Melanconium* and *Coryneum* Nees ex Fries.

Corda (1837) included *Melanconium* in the Caeomataceae (as "Caeomaceae") but later (1842) he referred it to the newly proposed family Melanconiaceae, the name obviously being derived from *Melanconium*. Later, Berkeley (1860) proposed



the order Melanconiales (as "Melanconiei") for ten genera of acervular fungi in which the "Perithecium [is] obsolete, or altogether wanting." The Melanconiales now includes at least 100 accepted genera and together with the Sphaeropsidales with 600 accepted genera has been incorporated into the class Coelomycetes Grove (1919).

#### TYPIIFICATION OF MELANCONIUM ATRUM

Material disposed in Persoon's Herbarium (in Herb. L.) as *Melanconium atrum* Link is composed of three separate sheets, the collections on each consisting of two small fragments of wood and bark. The sheets bear the Herb. L. loan number L.2445 No. 1 (accession numbers L 910.258-835), L.2445 No. 2 (L 910.258-844), L.2445 No. 3 (L 910.258-833) respectively.

Dr. C. R. Metcalfe of the Jodrell Laboratory, Royal Botanic Gardens, Kew, has determined the identity of the host plants in the three collections and reports as follows: —

L.2445 No. 1: Beech (*Fagus sylvatica*)

L.2445 No. 2: Willow (*Salix* sp.)

L.2445 No. 3: Willow (*Salix* sp.)

The bark structure of No. 1 agreed very well with that of Beech in one of our reference slides.

Luckily No. 3 still had a small piece of wood attached, and we could identify this as Willow without any difficulty, No. 2 would have been difficult if we had not been able to identify No. 3 but the bark structure in No. 2 is identical with that in No. 3.

In addition to the mounted material, the three sheets also bear labels showing various kinds of aged handwriting. Dr. M. A. Donk has kindly commented upon the nature of these annotations as follows: —

L.2445 No. 1 (L 910.258-835), '*Melanconium atrum*' I would ascribe to Link, but am not quite sure, but I think Link is correct.

L.2445 No. 2 (L 910.258-844), '*Melanconium atrum*': no suggestion; 'Dd. Link' was written by Persoon.

L.2445 No. 3 (L 910.258-833), '*Melanconium atrum*' was undoubtedly written by Link; 'ab ipso Linkio' was added by Persoon.

A composite deduction from this information suggests that the three collections in Persoon's Herbarium were sent from Link. Collection L.910.258-835 also bears the note "Link in hb. Pers". Although the writing may not belong to Link it indicates that the specimen again originated from him. Furthermore, since the substrate has been identified as *Fagus sylvatica* and the fungus agrees both with Link's description and his illustration, it is proposed to, designate L 910.258-835 as the lectotype collection of *M. atrum*. Justification for rejecting L 910.258-844 and L 910.258-833 as possible lectotypes or even paratypes is that (i) the fungi present on these two collections do not correspond with Link's figure, and (ii) the hosts have been determined

as *Salix* spp. It must be mentioned however that there is difficulty in equating Link's material with his rather brief and by modern standards vague description. The illustration however leaves no doubt in one's mind as to what he meant by *Melanconium*. The collections L 910.258-844 and L 910.258-833 may well be the specimens referred to by Link as 'other dead or dry branches'. The fungi present on them

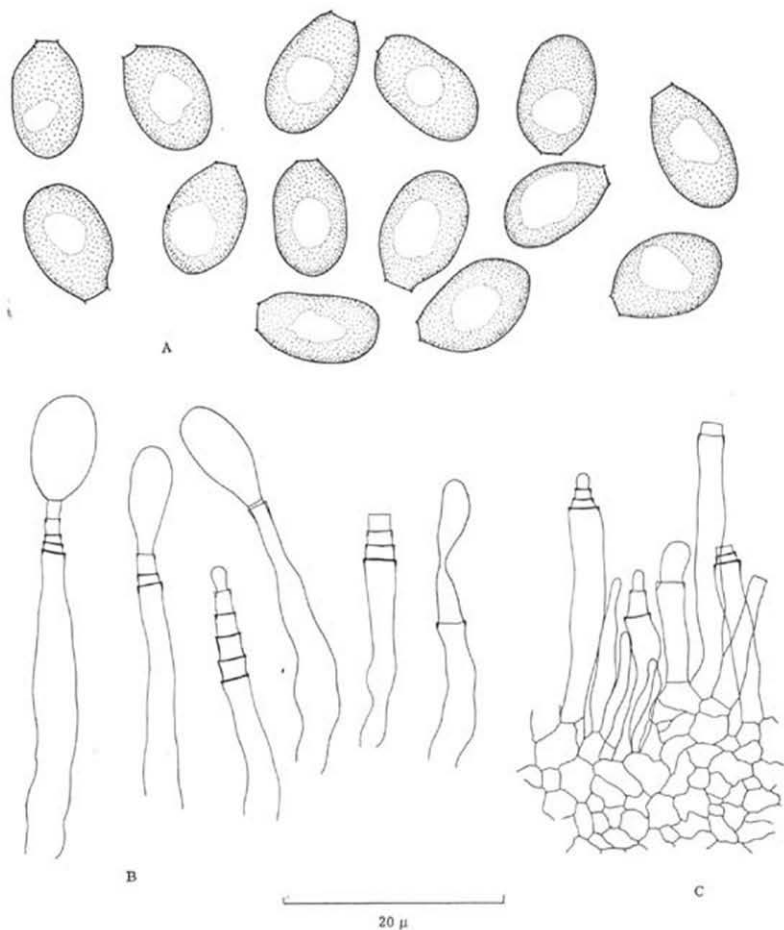


Fig. 1. — *Melanconium atrum*. A. Conidia. B. Separated annellophores. C. Vertical section of conidiophore bearing stroma.

may be placed in the '*Coniothecium-Trimmatostroma* complex'. It is highly probable that they are the specimens which Hughes examined and upon which he based his interpretation of *Melanconium*.

*MELANCONIUM* Link ex Fries, *Systema Mycologicum* 1: xl. 1821.

*Melanconium* Link in *Magaz. Ges. naturf. Freunde, Berlin* 3: 9. 1809

Fungi Imperfecti (Deuteromycetes), Melanconiales, Melanconiaceae.

*Acervuli* immersed, composed of hyaline to subhyaline, septate, branched hyphae restricted to the basal region of the fructification; spore mass irregularly erumpent; no well-defined ostiole.

*Conidiophores* hyaline to subhyaline, unbranched, 0-multiseptate, with several terminal annellations. Paraphyses absent.

*Conidia* formed as single blastospores at the apex of each conidiophore which after liberation of the first conidium proliferates through the ruptured apex to form additional conidia at successively higher levels, unicellular, brown.

Monotype species: *M. atrum*.

*MELANCONIUM ATRUM* Link ex Schlechtendal, *Flora berolinensis* 2, Cryptogamia: 136. 1824.

*Melanconium atrum* Link in *Magaz. Ges. naturf. Freunde, Berlin* 3: 9. 1809.

*Acervuli* abundant, immersed, scattered, at first lenticular and completely covered by the bark, later erumpent by a central ragged papillate opening, becoming wider and splitting irregularly, 0.5-1.5 mm diam.; immersed hyphae subcortical, hyaline to subhyaline, thin-walled, septate, branched, loosely aggregated to form a pseudo-parenchymatic stroma which is restricted to the basal region of the fructification. *Conidiophores* formed from the upper stromatic cells, erect, subhyaline, cylindrical, aseptate, with 1-5 terminal annellations, 10-30 × 2.5-4 μ. *Conidia* formed singly at the apex of each conidiophore which after liberation of the first conidium proliferates through the ruptured apex to form additional conidia at a higher level, elliptical, smooth-walled, unicellular, mid-brown, often with a central olivaceous guttule, base truncate with a marginal frill, 10-12 × 6.5-7.5 μ.

Specimen examined: On bark of *Fagus sylvatica* (Herb. L. 910.258-835). Lectotype of *Melanconium atrum*. (IMI 102914).

The presence of subhyaline to pale brown annellophores in *M. atrum* corresponds with a similar report by Hughes (1953) that the *Melanconium* states of *Melanconis juglandis* (Ell. & Ev.) Graves and *M. stilbostroma* (Fr.) Tul. bear annellate sporogenous cells. Far from being restricted to *Melanconium*, this phenomenon is evident in a number of other Coelomycete genera including *Cryptomela* Sacc., *Anaphysmene* Bubák, *Stilbospora* spp., *Hendersonia* (auctt.) spp., and *Septogloeum* spp.

It is a pleasure to acknowledge the invaluable assistance of Dr. C. R. Metcalfe in determining the substrata of *M. atrum*. Thanks are also due to Dr. M. B. Ellis and Mr. F. C. Deighton for their guidance and advice, and to Dr. M. A. Donk who kindly made available collections in his keeping and provided helpful comments on the 'scrispits'.

## REFERENCES

- BERKELEY, M. J. (1860). *Outlines of British fungology*. London.
- CHEVALLIER, F. F. (1826). *Flore général des environs de Paris, selon la méthode naturelle* 1. Paris.
- CORDA, A. C. J. (1837). *Icones Fungorum hucusque cognitorum* 1. Prague.
- (1842). *Icones Fungorum hucusque cognitorum* 2. Prague.
- DUBY, J. E. (1830). *Aug. Pyrami de Candolle Botanicon gallicum seu Synopsis plantarum in flora gallica descriptarum*, Ed. 2, 2. Paris.
- FIGINUS, H. D. A. & C. SCHUBERT (1823). *Flora der Gegend um Dresden. Zweite Abtheilung: Kryptogamie*. Dresden.
- FRIES, E. M. (1829). *Systema mycologicum* 3 (1). Gryphiswaldae.
- GROVE, W. B. (1919). Mycological notes.—IV. *In J. Bot.*, Lond. 57: 206–210.
- HUGHES, S. J. (1953). Conidiophores, conidia and classification. *In Canad. J. Bot.* 31: 577–659.
- (1958). Revisiones Hyphomycetum aliquot cum appendice de nominibus rejiciendis. *In Canad. J. Bot.* 36: 727–836.
- LINK, H. F. (1809). *Observationes in ordines plantarum naturales. Dissertatio I<sup>ma</sup>*. *In Magaz. Ges. naturf. Freunde Berlin* 3: 3–42.
- (1825). *Gymnomycetes*. *In C. Linn. Sp. Plant.*, Ed. 4 (olim cur. Willdenow), 6 (2). Berolini.
- MARTIUS, C. F. P. VON (1817). *Flora cryptogamica erlangensis sistens vegetabilia e classe ultima Linn. in agro erlangensi hucusque detecta. Norimbergae*.
- NEES VON ESENBECK, C. G. D. (1816). *Das System der Pilze und Schwämme*. Würzburg.
- PERSOON, C. H. (1818). *Traité sur les Champignons comestibles*. Paris.
- SCHLECHTENDAL, D. F. L. VON (1824). *Flora berolinensis* 2, *Cryptogamia*. Berolini.
- SPRENGEL, K. P. J. (1827). *Caroli Linnaei Systema Vegetabilium*, Ed. 16, 6 (1). Gottingae.
- STEUDEL, E. G. (1824). *Nomenclator botanicus. Stuttgardiae & Tubingae*.
- WEHMEYER, L. E. (1941). A revision of *Melanconis*, *Pseudovalsia*, *Prosthecium*, and *Titania*. *In Univ. Mich. Stud. (Sci. Ser.)* 15: 1–161.

## EXPLANATION OF PLATE 3

Fig. 1. — *Melanconium atrum*. Vertical section of young acervulus showing formation of conidia beneath the bark of the host.

Fig. 2. — *Melanconium atrum*. Vertical section of a mature acervulus showing basal conidiophore-bearing region and irregular rupture of host tissue.

A CONSPECTUS OF THE FAMILIES OF APHYLLOPHORALES

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The author gives a recapitulation of the families of the Aphyllorphorales. He is inclined to recognize 21: the families he is not (yet) prepared to uphold are discussed. The synonymy of the order and the families above the rank of genus is listed, but it is avowedly incomplete. The treatment of each family does not go further than the mention of the included genera, but through selected references cited for each genus in a special list, an introduction to the separate genera is provided. An introductory chapter contains some general remarks and discusses a number of terms used in connection with the treatment of the families. New taxa are, Brachybasidiales, Hericiaceae, Punctulariaceae, Asterostromatoideae, Pteruloideae, while the name Septobasidiales Couch is validly published and the new combination *Serpula mollusca* (Fr.) Donk is made.

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<sup>1</sup> The abbreviations after the family names are those used in the "Alphabetical enumeration of genera" at the end of this paper.

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### Preface

There was a time when Fries's classification of the Hymenomycetes was considered adequate and even now deviating from it often arouses suspicion in the mind of some mycologists. At the other extreme radical changes are often too eagerly accepted without much critical examination. That there is a need of a thoroughly revised classification is evident and as far as the Agaricales are concerned it has been supplied by Singer (1962) in a detailed manner down to the species level. This is not the case with the Aphylophorales. No revision of Patouillard's classification published in 1900, has been undertaken and the elaboration of the Friesian system by Killermann (1928) is totally inadequate for present use.

As long as it remains impossible to offer an advanced new classification, the only solution for improving the still current elaboration of the Friesian classification is to compromise and introduce into it those innovations one is prepared to accept. This is what I have tried to do. As well as proposed treatments of some new families, I have included more or less revised versions of concepts of taxa published by Patouillard and later authors, and also the remnants of the artificial Friesian classification. It was not possible to go further than give a brief outline of each accepted family and a rough indication of the genera thought referable to it. This is largely due to the fact that many genera are not yet satisfactorily delimited and others are still singularly artificial. A splitting up of the Aphylophorales into more or less natural genera is in progress, but this process is severely hampered by the great mass of insufficiently described species which, therefore, cannot yet be assigned to more properly defined genera.

Anyone voluntarily undertaking the task of outlining the current state of rapid but haphazard progress in the classification of a big group of fungi is liable to be accused of grossly overrating his own ability to fulfil the job. Moreover, he has to make many questionable decisions in groups of which he has no specialist knowledge in order to complete the scope of the work: in these times of specialization the field in which he is a stranger is likely to be bigger than the one in which he has worked more intensively. I plead guilty on all these counts, and I am prepared to accept a lot of criticism because it will almost certainly be justified.

The present paper is divided into three parts. "General considerations" at first sight looks like a general discussion of the Aphyllophorales, but this is emphatically not the case. After some introductory remarks a reasoned terminology follows; this takes into account only such terms as are to be encountered in the family diagnoses and the keys sampling the genera. Many topics of importance are lacking simply because they have not been touched on in the "Special part", or were not in need of separate comments.

The "Special part" is the chapter to which the title of this paper refers. Here the families are briefly reviewed one by one and on the whole the smaller families are considered in greater detail than the bigger ones. This is especially true of the two biggest families, the Corticiaceae and the Polyporaceae, both still highly artificial in their composition. A more elaborate revision is planned of both and for present purposes the Polyporaceae in particular are only very briefly considered. What I aimed at was a concise review presenting a somewhat personal interpretation of what has actually been achieved without introducing unpublished new views except perhaps in developing a few new interpretations that were latent in the work of other authors or of my own. In short, a starting-point for future discussion.

A few words are needed to explain the treatment of the synonymy of the taxa of higher rank than genus. It may look impressive to the casual reader, but it is certainly not exhaustive. At a given stage I merely assembled what I had gathered in this respect without having tried to complete it. The presentation of this synonymy was a problem in itself: how to bring order into a mixture of scientific precision, human slovenliness, and lack of discipline. I shall not dwell more fully on this subject except to say that I have included names under which taxa were first published even if they were inadmissible. From an historical point of view the taxonomic recognition of a group is often much more important than the introduction of the first correct name for it. Synonyms placed between square brackets are inadmissible as far as the "International Code of Botanical Nomenclature" (1961) is concerned.

The alphabetical order of the families will perhaps attract attention. However, since the interrelations of most of the families are as yet obscure any other sequence (except in a few cases) would hardly have been an improvement.

The third part, entitled "Alphabetical enumeration of the genera (exclusive of the polypores)", is added as a guide to selected literature on the individual

genera. The cited references will usually lead to generic conceptions most closely agreeing with my present views. The enumeration will also show which generic names I consider to be merely synonyms. I have tried to make it complete as far as validly published names are concerned.

ACKNOWLEDGEMENT.—I herewith express my indebtedness to Mrs. Y. M. Butler who has carefully read the manuscript and by her linguistic advice has greatly improved the English text.

## I. GENERAL CONSIDERATIONS

INTRODUCTION.—The classification of the Hymenomycetes from Linnaeus's to our times has been greatly influenced by two factors, the rapid increase in the number of species that became known, and the general tendency to be dissatisfied with artificial grouping.

The increase of described species that had to be accommodated in the accepted Friesian classification was so enormous that its genera became much too big and unwieldy. To ease this situation some authors (P. A. Karsten, Quélet, Murrill) resorted to raising generic subdivisions to generic rank which was, incidentally, a tribute of praise to Fries's classification below the generic level. The really personal innovations of these 'splitters' keeping to the Friesian tradition were relatively few and only some have stood the test of time unaltered.

What was primarily needed was a re-examination of the taxonomic value of the characters used as basic. The first really important critics of the Friesian tradition were Fayod (1889) (for the agarics only) and Patouillard (1900). The dissatisfaction with the traditional classification grew from the uneasy feeling that many of the accepted genera and their grouping were artificial, and that new characters had to be used to improve the situation. In the biggest group of the Hymenomycetes, the agarics, the work of laying new foundations, started by Fayod and Patouillard, has been taken up and continued in the first place by Kühner & Romagnesi (1953) for the European species and by Singer (1962) on a world-wide scale. Agaricologists are fortunate in having comprehensive surveys of the agarics by these authors to refer to and, what is still more important, their works have been conceived from different angles so that they will, in the end, become mutually corrective.

The Aphyllophorales have been less lucky. After Patouillard, the giants in this field were Bourdot & Galzin (1928), who completely renovated the study of these fungi but hardly went beyond Patouillard's system of classification of 1900. Yet, their indispensable work, moulded as it was according to that system, did much to focus attention on Patouillard's classification not only in France but also outside that country. A big retarding factor from a taxonomic point of view was Lloyd, later in his life one of the most ardent new species hunters in the worst tradition.

Any evolution of a scheme of classification evolves from the correlative work of taxonomists who roughly can be divided into 'lumpers', 'splitters' and, of course, 'conservatives'. These last are not only content to accept genera that are admittedly



quite heterogeneous but they also act as if the demands of a natural classification cannot be met or, at least, are of no importance. Lloyd was a conservative in this sense of the word. His attitude was furthered by the work of some of his fellow country-men such as Murrill and Banker, who were to him unforgiveable splitters. The terror Lloyd spread among North American mycologists and abroad by ridiculing everything that reminded him of taxonomic innovation in the systematics of fungi, and of the bigger Aphyllophorales in particular, has not yet been completely overcome. His slipshod taxonomic methods were accepted as standard by some of his correspondents.

The search for new characters to improve the Friesian classification of the Aphyllophorales is now in full progress. One trouble is that the taxonomist who finds a given character useful in certain groups, often tends to overemphasize its importance and is often too eager to apply it on too wide a scale. Telling examples are the position of the nuclear division-spindles in the basidium (Juell, Maire, van Overbeem), the amyloidity of the spores, absence and presence of clamps, and, more recently, characters derived from cultures. The golden rule in the taxonomy of big groups is to be on one's guard when applying a character found useful in one group to another one. Basidia with two sterigmata are invariably a reliable aid in recognizing a species of Dacrymycetales, but in the genus *Mycena* two-spored basidia may be useful on not more than the specific level and in quite a number of cases even this character fails. Quite recently an author stated of two species he previously placed in one genus, that since clamps were absent in one of them, the species appeared to belong to different phylogenetic groups. In the Septobasidiales and the Hymenochaetaeaceae the complete absence of clamps stamps this feature as one of prime importance as far as these groups are concerned, but it is easy to point out instances in other groups where it even fails to help to characterize species. The features on which a natural classification is based must have been dictated by the objects that are being classified, not by preconceived notions of the taxonomist. Of course, this rule is easier to formulate than to follow.

The modern classification of the Aphyllophorales needs more and more characters to be taken into consideration to be able also to evaluate similarity correctly; resemblances may point either to relationship or to its reverse, 'convergence'. Among the Aphyllophorales a coralloid fruitbody was formerly considered a sure indication of taxonomic relationship. Now we approach this character with more caution. It is not accepted on its own as a valid characteristic but only in conjunction with several other correlated characters. It no longer causes surprise when two plants, both with coralloid fruitbodies, prove to belong to different groups.

What we really need in our pursuit of a better classification is an increasingly bigger repertoire of characters from which to draw. However, every character added to the repertoire now and considered of general importance requires an enormous amount of detailed observation. For instance, how many separate observations will be needed before the presence or absence of clamps can be really satisfactorily used in the family diagnoses of the Aphyllophorales? The answer is thousands and

thousands. Recently Kotlaba & Pouzar (1963) have paid renewed attention to the absorption of Cotton Blue by membranes, especially in the spores of the Hymenomyces. How many specimens and species will have to be tested in this respect before we know how to take advantage of this feature in the various groups of Aphyllophorales? The answer depends much on the state of the naturalness of the accepted genera. If the genera were all 'natural', testing one species of each might perhaps be sufficient for orientation. But which of the bigger genera are really 'natural'?

And here we come to a fundamental point of this discussion. For the correct naming of a species an artificial classification need not be a hindrance, but for the elaboration of a natural system it is imperative that these species are classed into natural genera. And even when this ideal situation is finally realized, the construction of a natural system at higher levels may pose its own, perhaps insurmountable, difficulties. As long as the naturalness of the majority of genera remains under discussion, attempting an improved classification will be a thankless task. Is the number of natural genera among the Aphyllophorales already big enough to attempt this? I would say it is: improvement of an artificial system has to start early. Gradually the naturalness of the classification will be increased, but never more than that.

**HISTORICAL.**—Briefly summarized it may be stated that the few Linnaean genera of what later became known as the Hymenomyces became families and these families appeared artificial. It turned out to be necessary to try and replace this artificial classification by a more natural one. The most important authors in this process in relation to the Aphyllophorales are Persoon, Fries, and Patouillard.

The real author behind many of the Friesian conceptions and classification is Persoon, but we call them Friesian because Fries was responsible for their maintenance and improvement, and for the enormous influence exercised by that classification. It became the traditional one and has been perpetuated through Saccardo's "Sylloge Fungorum" into our times. The following is Fries's own and last summary of his classification of the Hymenomyces (1874: 1).

Hymenomyces sequentes distinguimus ordines:

A. *Hymenio effigurato*

- I. lamellato = AGARICINI. Gen. I—XX.
- II. poroso = POLYLOREI. Gen. XXI—XXX.
- III. aculeato l. varie protuberante = HYDNEI. Gen. XXXI—XLI.

B. *Hymenio laevigato*

- IV. horizontali infero = THELEPHOREI. Gen. XLII—XLVII.
- V. verticali amphigeneo = CLAVARIEI. Gen. XLVIII—LIV.
- VI. supero; gelatinosi = TREMELLINEI. Gen. LV—LXIII.

This summary shows that the scope of the Aphyllophorales as adopted in the present paper roughly corresponds to Fries's 'orders' (families) II to V, and that in these groups he included about 34 genera to be found in Europe. (The number of genera that Fries recognized but which did not occur in Europe was very low.)

The first, and only important, classification of the Hymenomycetes that broke with the Friesian tradition was Patouillard's. An excerpt of it follows. This survey only takes into consideration Patouillard's 'Aphyllophoracés' to which is added his 'Tribu des Cantharellés' which he placed in his 'Agaricacés'.

- Tribu des Clavariés 39.<sup>2</sup>
  - Série des Théléphores 40 [*Cotylidia* or *Bresadolina*]
  - Série des Clavaries 40, 45
  - Série des Physalacries 40, 45
- Tribu des Porohydnes 39, 51
  - Sous-tribu: Cyphellés 51, 52
  - Sous-tribu: Odontiés 51, 58
    - Série des Odonties 58
    - Série des Corticies 58, 64
    - Série des Stéréums 58, 69
  - Sous-tribu: Porés 51, 75
    - Groupe: Les Polypores vrais 76, 77
      - Série des Polypores 76, 77 [*Albatrellus*]
      - Série des Leucopores 77, 79 [*Polyporus*]
      - Série des Leptopores 77, 83 [*Tyromyces* or *Postia*]
    - Groupe: Les Fomes 77, 86
      - Série des Trametes 77, 87
      - Série des Igniaires 77, 96 [*Phellinus*]
      - Série des Placodes 77, 102 [*Fomes*]
    - Groupe: Les Mérules 77, 106
    - Groupe: Les Fistulines 77, 109
  - Sous-tribu: Hydnes 51 113
    - Série des Mucronelles 114
    - Série des Hydnes 114, 115
    - Série des Echinodonties 114, 117
    - Série des Phylactéries 114, 117 [*Thelephora*]
    - Série des Astérostromes 114, 120
- Tribu des Cantharellés 123, 126

The number of genera Patouillard recognized amounted to 85 inclusive of the 5 genera which he referred to the 'Cantharellés'.

Because many of the generic names Patouillard used are now replaced by nomenclaturally more correct ones, the above scheme does not readily reveal in all cases the type genera after which he named his taxa, some of the modern names of the genera have been added in the above excerpt between square brackets.

The classification adopted in the present paper has been primarily derived from Patouillard's.

<sup>2</sup> The numbers indicate the pages in Patouillard's "Essai" (1900).

**THE FRUITBODY.**—As a rule the truly stalked fruit-body, however variable it may be, is within a given species, always stalked, although the stalk may be reduced to a knob or disc or otherwise very short. Spuriously stalked fruitbodies occur in species in which the fruitbody shows a wide variation in development and may also occur in sessile or even more or less appressed or effused modifications. An example of this kind is *Abortiporus biennis* (Bull. per Fr.) Sing. In contrast to such species the fruitbody of *Polyporus* sensu stricto is truly stalked. If in the stalked or sessile fruitbody the hymenophore is one-sided (unilateral) the fruitbody is pileate and the portion bearing the hymenophore is called the cap (pileus). The stalk (stipe) may be inserted at the margin of the cap (lateral)<sup>3</sup> or its place of insertion be completely surrounded by the hymenophore (eccentric or central). If the cap is attached by its abhymenial side, the point of attachment (which may be drawn out into a stalk) is called the vertex. I suggest that caps spreading over the substratum by the whole of their abhymenial side should be called appressed. (Among the agarics this condition has been called resupinate.) Such caps often become secondarily and loosely connected with the substratum over their appressed (abhymenial) side. If they are partially appressed and partially directed away from the substratum in their upper portion they are called appressed-reflexed.

The clavarioid (simple or branched) fruitbody bears an amphigenous hymenium. Corner (1950: 1-10) distinguishes between radial and flattened branching; in the former instance the branches are formed on a broadly rounded or truncate apex. An extreme case of radial branching is the pyxidate one, typical of *Clavicornia*. In the other type of branching, the apex "flattens and widens, as the tip of a screwdriver, becoming ligulate, spatulate, and cuneate, or flabelliform, and along the knife-edge 'growing-point' so formed new growing-points appear at regular intervals to give a palmate or flabellate polychotomy." (Flattened branching may also be conceived as proliferation along the margin of a cap when there is a characteristically one-sided hymenium present.) In some genera (*Lachnocladium*, Hymenochaetaeaceae; *Thelephora*, Thelephoraceae) both types of branching occur. Finally branching may be adventitious or false, viz. non-apical: a branch of this type "arises by a local proliferation of hyphae at any part of the surface of the fruit-body and grows out as a new branch."

While in most of the above mentioned cases the fruitbody has a well-defined point of attachment, the flattened effused fruitbody is primarily and evenly attached to the substratum throughout its extension.<sup>4</sup> Usually the distinction between it and the appressed fruitbody secondarily attached to the substratum is not difficult

<sup>3</sup> Actually the lateral stalk is not so easy to define and a rather complicated notion.

<sup>4</sup> It seems desirable to drop the term resupinate because it has different meanings partially depending on the group of Hymenomycetes. The true and original meaning (inverted, bottom up) applies rather to an agaric cap, sessile, with its abhymenial side more or less pressed against the substratum and, by extension, to completely appressed fruit-bodies. To reserve the term to what is here called effused is hardly in order.

to establish. In the latter the fruitbody often shows a distinct crust-like and/or tomentose layer bordering the abhymenial side so that the appressed fruitbody can be easily and cleanly separated when and where it has become secondarily attached. Sometimes effused fruitbodies may become effused-reflexed too. It is often difficult, if not impossible, to distinguish consistently between truly effused and resupinate (appressed) fruitbodies or portions of fruitbodies, but it may be useful in the future to try and distinguish more clearly between the two types.

Since a very important feature used to classify the Hymenomycetes was the shape of the fruitbody and since this feature still plays an important role, it is of interest to study those examples in which the species forms two different kinds of fruitbody each of which, when found isolated, would be likely to be referred to a different family. Such dual fruitbodies tend to eliminate the traditional boundaries especially between the Corticiaceae and the Clavariaceae. The earliest example of this kind to be described among the Corticiaceae was perhaps *Cristella fastidiosa* (Pers. per Fr.) W. Brinkm., "émettant quelquefois vers les bords et à la surface des émergences éparses subulées ou laciniées" (Bourdot & Galzin, 1928: 230). Another example to be described was that of *Corticium bombycinum* f. *ramulosum* Bourd. *apud* Donk, 1931: 143 [= *Hypochnium bombycinum* (Sommerf.) John Erikss.] which I described as follows (translated from the Dutch): "Fruitbody, especially toward the centre, covered by patent or somewhat appressed, dendroidly branched hymenial excrescences, tangled, coalescent, crowded, often with fringed tips, 8-10 mm long." Later on, I found corresponding forms of *Hyphoderma setigerum* (Fr.) Donk, and more recently a similar form was described and depicted as the type of the genus *Corticirama* Pilát. In all these instances the proliferations were apparently neither clearly negatively nor positively geotropic enough to qualify as very good clavarioid fruitbodies.

Much more strongly clavarioid outgrowths are sometimes formed by *Sebacina incrustans* (Pers. per Fr.) Tul. which typically is an effused species encrusting the soil and everything it meets; however, it is not corticiaceous and belongs to the Tremellineae. It may sometimes produce strongly developed, upright, self-supporting branches which simulate a clavaria and it has been determined as *Clavaria laciniata* Schaeff. *sensu* Bull. This form comes very close to *Tremellodendron* Atk. As that genus it may not only form clavarioid fruitbodies but also imitate a stalked sterium by forming stalked and more or less pileolate fruitbodies. Some such forms were included in what was called *Sebacina bresadolae* Lloyd (1925: 1362 *pl.* 342 *f.* 3243) and Wells (1962: 359) even thought that "the description and illustration presented by Lloyd indicated that the species should be referred to *Tremellodendron* Atk.", to which conclusion I would not, however, subscribe.

A still more striking example was described by Corner (1950: 536) for *Pterulcium*, a genus closely related to *Pterula* but distinguished from it by developing, besides the truly negatively geotropic *Pterula* fruitbody, an effused patch covered with a normal fertile hymenium when it faces downward; this patch generally accompanies the clavarioid fruitbody but sometimes it may occur separately. While the

clavarioid fruitbody has a dimitic context with skeletal, the corticioid patch is devoid of skeletal and monomitic. If these two types of fruitbody were not known to be expressions of the same species, one of them would undoubtedly be classed with *Pterula* (Clavariaceae) and the other with *Corticium* (Corticaceae). It must be the endeavour of the taxonomist to look through these disguises and to establish the really fundamental characters, truly a seemingly hopeless task in this instance. Yet, the taxonomist has already overcome some difficulties of this kind: the recognition of the close relationship between the corticioid genus *Ramaricium* and the clavarioid genus *Ramaria* by Eriksson (1954) is an example.

There are other clavarioid species known with a corticioid fertile patch. Thus the type of *Parapterulicium* (*P. subarbusculum* Corner) looks like a typical species of the Pteruloideae (Clavariaceae) but it does perhaps not belong to that subfamily because of its floccoso-coriaceous context. The components of the hymenial layer strongly remind one of the resupinate genus *Vararia* and from the description of the corticioid patch on the underside of twigs and petioles it would seem to be typical of that genus. The proof might depend on whether or not the context turns reddish in Melzer's solution as in typical species of *Vararia*.

Finally, in connection with corticioid, fertile patches at the base of stalked fruitbodies, attention is drawn to *Amylaria* (Bondarzewiaceae) and *Sparassis simplex* D. Reid (Sparassidaceae).

The normal condition in the Hymenomycetes (ballistospores!) is that the one-sided hymenophore faces downward; the opposite condition appears to be very rare: an example is the fertile patch on the ground from which the erect fruitbody of *Sparassis simplex* arises. In some other cases the young sessile or stalked fruitbody is so orientated that the hymenium is directed upward but it usually becomes re-orientated downward when reaching maturity through the unequal growth of the fruitbody (*Rimbachia*, *Arrhenia*). Besides inverted hymenophores mention should be made of inverted fruitbodies. When these have an amphigenous hymenium, as in certain Clavariaceae (*Myxomycidium*, *Hormomitriaria*, *Mucronella*), they are (or appear to be) positively geotropic.

THE HYMENOPHORE.—This term has been used in two different senses, (i) for the whole cap or even the whole fruitbody that produces a hymenium, and (ii) for that portion of the fruitbody directly adjacent to the hymenium and usually responsible for the various 'hymenial' configurations. In this paper *hymenophore* is used in the second, narrow sense. When the 'hymenium' is smooth (as in *Stereum hirsutum*), it is preferable to state that the hymenophore itself is smooth. Singer (1962) would write 'without a hymenophore'. In *Stereum hirsutum* and similar instances the hymenophore is a thin layer bearing the hymenium; it is rather a theoretical concept, because it is not structurally distinct. (When a distinct subhymenium is differentiated from the context of the fruitbody, the hymenophore borders this subhymenium.) In a typically developed agaric it is the lamellate hymenophore that bears the smooth hymenium. If the context of the effigured

hymenophore (to which the term 'trama' is often restricted<sup>5</sup>) is separated from the hymenium (plus subhymenium) by a thin layer of special structure (as may be the case in certain agarics), this latter is called the hymenopodium in agreement with Fayod. The usefulness of the term hymenophore is best demonstrated by scrutinizing the common expression, 'the hymenium is lamellate'. If one admits this expression as correct the term hymenium would acquire a double meaning, that of hymenium proper and of hymenium plus hymenophore.

It is usually the hymenophore that determines the configuration of the hymenium proper. The latter may be spread over gills, teeth, or dissepiments of tubes. These are all definite structures and together they form the effigured hymenophore. But this is not always the case: it may also happen that the hymenium itself produces a characteristic configuration. The morphogenetic factor appears in this case to be hyperextension of the hymenium caused by the abundant intercalary production of (turgescient) basidia. This results in the hymenium being thrown into folds. When the fruitbody dries up the folds may disappear completely [*Athelia bispora* (J. Schroet.) Donk] or they may be replaced by a reticulate system of folds which are not the same as the original folds of the fresh condition [*Merulius rufus* Pers. per Fr., *Serpula himantoides* (Fr. per Fr.) P. Karst., *S. molluscus*<sup>6a</sup>]. In certain cases it may be that the folds of the fresh fruitbody are more or less retained unaltered upon drying. This last happens when they are very strongly developed, either as gill-like folds (*Cantharellus cibarius* Fr.) or as rather deep tubes [*Merulius taxicola* (Pers.) Duby].

Fries made the configuration of the hymenium his first character for subdividing the Hymenomycetes (cf. p. 204). He recognized as principal types the lamellate, tubulate, toothed, and smooth 'hymenium'. It will be profitable to add the folded hymenium as a special type, which, however, must be understood to be a mere modification of the smooth hymenophore. When the folds were reticulately connected (in dried specimens) Fries referred the species to the Polyporei (*Merulius sensu lato*), when the principal folds were radially developed he classed the species with the Agaricini (*Cantharellus* in part).

By recognizing the essential difference between the folded hymenium of the *Cantharellus cibarius* type and the true gills of the agarics, it is possible to draw a clearer distinction between the Cantharellaceae and the Agaricales. The gill-like folds of the former are fertile on the edge; true gills are not only definite structures but also may be either fertile or sterile on the edge; in the latter case the edge is often marked (even in poorly developed gills) by sterile elements concentrated along

<sup>5</sup> For me 'context' and 'trama' denote precisely the same idea. Like Singer (1962: 49) I prefer to speak of 'hymenophoral context (trama)' instead of only 'trama' unlike those authors who reserve the latter term for only that portion of the context that makes up part of the hymenophore.

<sup>6a</sup> *Serpula mollusca* (Fr.) Donk, *comb. nov.*; basionym, *Merulius molluscus* Fr., *Syst. mycol.* 1: 329. 1821.

it, or particular to it, compared with the elements making up the hymenium over the sides of the gills.

The second character Fries used to subdivide the Hymenomycetes was the position of the hymenophore. In this connection he distinguished the 'hymenium horizontale inferum' from the 'hymenium verticale amphigenum', the amphigenous hymenium being typical of his Clavariacei. It is more exact to replace 'inferum' by 'unilaterale', for the one-sided hymenophore does not always strictly face downward. For instance in effused or appressed-reflexed fruitbodies growing on a vertical substratum the hymenophore of the non-reflexed portions is directed sideways. It would appear that in very rare cases among the Aphyllophorales and Agaricales the hymenophore is directed upward. See also page 208.

**THE HYMENIUM.**—The hymenium of the Hymenomycetes is best known in the agarics mainly through Buller's extensive studies (1922; 1924) which, however, were concerned with only one hymenial maintype. Its most notable characteristic is the presence of what looks like a 'static' subhymenium that generates all hymenial elements including past and future ones. There is a steady replacement of the exhausted hymenial elements by new basidia and new sterile elements (if present): these are added through a process of intercalation and arise from the same subhymenial layer at about the same height as their predecessors.

Among the Aphyllophorales this type is often replaced by a variant in which the new basidia are formed at increasingly higher levels than the older, maturing and exhausted ones; the hymenium thus gradually and noticeably increases in thickness. The branches of the subhymenium that produce these young basidia penetrate between the older basidia. In species with more or less thick-walled spores and true thickening hymenia, spores will usually be found included throughout the hymenium. Thus we arrive at two types of euhymenia, the non-thickening and the thickening ones. In euhymenia the basidia and their sterile homologues and derivatives (hymenial cystidia) are the first and principal elements to build up the hymenium. I am fully aware that completely non-thickening hymenia are rare if existing at all, and that it would be more truthful in most cases to speak of less and more thickening hymenia. Exceptionally fine drawings of typical thickening hymenia have been published by Corner (1950) for various clavariaceous fungi, and by Eriksson (1950) for many species of *Peniophora* sect. *Coloratae* Bourd. & G. (= *Peniophora* sensu stricto).

The euhymenium has been opposed to the hyphidial hymenium (Donk, 1957: 4), which was recently rechristened *catahymenium* (Lemke, 1964: 218). This latter term is here adopted because the hyphidia may be freely mixed with gloecystidia (see p. 233).

The catahymenium comes into being before the first basidia are formed: it originally consists of hyphidia which may be supplemented by more or less numerous gloecystidia (*Aleurodiscus*). The hyphidia are either the tramal ground-tissue itself, composed of upright, more or less branched hyphae (*Scytinostroma*), or secondary



products particular to the basidial region (*Laeticorticium*, *Vararia*). Enclosed between the sterile elements, or even below them, the deep-seated basidia are initiated as offshoots that have to work their way to the surface of the fruitbody in order to be able to produce their spores in the air. At first, when the basidia are still few in number, this condition can be easily demonstrated. The number of basidia may increase without obscuring the fact that they are scattered organs in the basidial region constituting a diffuse or discontinuous hymenium. However, during periods of intense sporulation, the basidia may become so numerous and the sterile elements relatively so scarce that a euhymenium is simulated, especially when the sterile elements (hyphidia) are not very striking.

The hyphidial region, or catahymenium, may either be a definite outer layer of the fruitbody (*Laeticorticium*) or it may coincide more or less completely with the fruitbody itself (*Vuilleminia*). In some cases the hymenium may even quickly develop into a true thickening one that leaves the hyphidial region completely behind (*Lachnocladium*).

I am fully aware of the fact that it will be impossible to refer all species of Aphyllophorales to the types of hymenia sketched above: the number of intermediate conditions will appear to be large and there will be some left-overs that are not readily assigned to any of these hymenial types. A case in point is the hymenium of typical species of *Xenasma* [*Corticium tulasnellodeum* Höhn. & Litsch.; the group of *Peniophora rimicola* (P. Karst.) Höhn. & Litsch.]. In these species the fruitbody consists of repent, narrow hyphae glued together in a thin film in which the individual hyphae can hardly be made out as distinct elements. At the surface of such a film the basidia and (if present) the cystidia protrude as more or less scattered bodies (pleurobasidia; see p. 218) with their basal portions more or less deeply hidden in the hyphal mass. Since the fruitbody increases in thickness by new hyphae growing over the surface and these new hyphae will at some time produce new crops of basidia, the hymenium is in principle a thickening one although one would not readily suspect this from a section.

The same is true when, in the deeper portions of the thickening hymenium, the collapsed basidia quickly disintegrate and are replaced by the strongly inflated cells of a cellular subhymenium. Here, although the actual, active hymenium may not readily impress one as a thickening one, the increase in thickness of the cellular subhymenium indicates that this is so. In many Corticiaceae with a dense subhymenium of ascending, not swollen hyphae, the so-called filamentous (ramose) subhymenium is often nothing more than the old portions of a thickening hymenium from which the basidia have disappeared.

**FUNCTIONS AND PARTS OF THE BASIDIUM.**—The basidium is the seat of several important functions in the life cycle of the Basidiomycetes. In order, these functions are: the zeugite function (karyogamy), the gonotokont function (meiosis), and the propagative function (spore production). The last task is in itself a compound one in most basidiomycetes because the basidium does not only produce

the spores but also violently discharges them. In the holobasidium all these functions are performed by a single cell.

In typical haploid cycles the basidium may start with a single nucleus and then, of course, karyogamy does not occur.<sup>6</sup> Yet even in these haplo-parthenogenetic forms the behaviour of this nucleus and its divisions retain many of the characteristic features of the normal cytological course; the single original nucleus swells before division to a considerable size, comparable to the swelling of the diploid nucleus in the normal cycle, and the position and length of the division spindles are remarkably identical too. This swelling of the nucleus before entering upon division appears to be an important feature of the basidium.

In agreement with the nuclear behaviour it has been proposed to call *probasidium* that part or stage of the basidium in which karyogamy occurs, and *metabasidium* that part or stage in which the enlarged (diploid or haploid) nucleus divides. The two organs may be largely overlapping (club-shaped basidium) or completely separate (*Helicogloea*, *Auriculariineae*).

In the Aphyllophorales (holobasidious) the second extreme is not met with. In the *Cantharellus* basidium (which is stichic) the probasidium is a nearly cylindrical, only slightly club-shaped organ that elongates while becoming the metabasidium. The diploid nucleus remains at about the middle of the basidium where it also divides. In this case the probasidium, after elongating as a whole, is completely replaced by the metabasidium. In the club-shaped *Agaricus* basidium (chiastic) the probasidium also elongates as a whole, but here the diploid nucleus first migrates into the top before it divides.

In the urniform basidium (*Sistotrema*) the probasidium is a swollen, vesicular organ that emits a tube into which the diploid nucleus migrates and divides stichically (but see p. 221). This tube is morphologically easily distinguished from the original probasidium. The utriform basidium is similar but usually the tube is less clearly set off from the probasidium, it may become longer (and in fact generally is of variable length) and swells somewhat at the apex where the diploid nucleus divides chiastically (as far as is known). It is often difficult to distinguish between the club-shaped and the utriform basidium because the 'tube' may not be strongly contrasted with the probasidium and the middle portion of the basidium is then hardly constricted. These basidial types are more extensively reviewed under the next heading.

According to the definitions given it may be thought preferable to call the basal portion of the urni- and utriform basidia 'probasidium' and to restrict 'metabasidium' to the prolongation. However, although these basidial types are *dimerous* (with two parts) there is no reason, as far as I can see, to assume that the mature basidial body does not *act* as a single unit during the production of the spores. Hence one may prefer to identify the whole of the mature basidial body with 'the

<sup>6</sup> It has also been reported for some species that basidia developing on haploid mycelium were regularly binucleate and that in later stages the basidia contained a large fusion nucleus (cf. for instance Biggs, 1938: 71, for "*Peniophora*" *ludoviciana* Burt).

stage in which the diploid nucleus divides' and call it accordingly as is also done in the typical stichic club-shaped basidium. If it is desired to use special designations for the two portions of the dimerous basidium of the two types under discussion, they may be indicated as the probasidial or basal vesicle and the metabasidial or apical extension (prolongation, outgrowth). In certain phragmobasidious fungi, as for instance in quite a number of species of *Septobasidium* with a persistent probasidium, the pro- and metabasidium are not only clearly differentiated morphologically, they are also different organs acting more or less independently of each other. In these cases the metabasidium is usually divided into four units each producing a spore and violently discharging it; the probasidium has no part in these tasks.

The rule that in the Aphyllophorales spores are produced by the basidial body has only few exceptions. The most remarkable one is found in the *Tulasnella* basidium where this function is delegated to and divided among the sterigmata.

The basidia of the Aphyllophoraceae are without exception holobasidious: no septation occurs in the metabasidium in connection with the divisions of the diploid nucleus. This is unlike the phragmobasidium, where true septa divide the metabasidium either longitudinally or transversely into cells. Septa may occasionally be encountered but if so they are secondary (false or adventitious) septa, formed independently of nuclear divisions. In *Tulasnella* the protosterigmata become separated from the basidial body by such adventitious septa across their bases (see also p. 224). In *Clavulina* "the secondary septum, which cuts off the completely vacuolate distal half, or third, of the basidium after spore-discharge, is a constant and noteworthy feature. In some species it is followed by several more septa formed successively in the proximal part as the protoplasm withdraws" (Corner, 1950: 65). Such secondary septa in the basidial body are now also 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 submersed in water. In none of these cases does the presence of the secondary septa make it necessary to call the holobasidium a phragmobasidium. If one considers the basidiospores as part of the basidium, the formation of secondary or true septa in the basidiospores does not make basidia phragmobasidia either.

In all Aphyllophorales, except perhaps *Digitatispora* (cf. p. 225), the spores are produced apically as ballistospores on distinct sterigmata. The spores are usually produced in groups of four, but in the same hymenium they may be produced in threes and twos and even, exceptionally, singly. Two-spored basidia occur as a specific or varietal character in various groups. When combined with stichic basidia (and some other distinctive marks) this feature may become highly significant, as in the Dacrymycetales; it also helps to characterize the family Clavulinaceae, and may eventually lead to the separation of another family based on *Clavulicium* (see Corticiaceae).

The production of more than four spores per basidium has as yet not been used as a distinguishing feature for any family of the Aphyllophorales. It is rare and

usually occurs in conjunction with stichic basidia (*Hydnum*, only genus of the Hydnaceae sensu stricto, 2-6; *Cantharellus*, 3-7; *Sistotrema*, 2-8, usually more than 4, sterigmata per basidium). It is worthy of note that in all these cases the presence of more than four sterigmata per basidium is of variable occurrence even within a single hymenium or within a genus; some species of *Sistotrema* for instance have not more than four sterigmata; e.g. *S. hirschi* (Donk) Donk.

Other instances of the number of sterigmata exceeding four were reported for *Tulasnella* (in certain species "five or more", Rogers, 1933: 194; usually four), *Botryobasidium*, *Sistotremastrum*, *Paulliticium*, *Koleroga* (rarely), some species of Clavariaceae (q.v.), and some odd species of *Corticium* (residual genus). Except for *Tulasnella* (chiastic basidia) little is known for certain about the position of the first nuclear division spindle in the basidium in these cases. (For a remark on *Sistotremastrum*, see p. 221; for *Clavaria falcata* sensu Juel, see p. 222). A fifth sterigma is occasionally seen in various species, for instance in *Thanatephorus cucumeris* (Frank) Donk. On the whole it can be concluded that in most families of Aphyllophorales and Agaricales the number of four is only very exceptionally exceeded.

For a more thorough discussion on the basidium in general, see Talbot (1954: 249-263 fs. 1-3).

**THE SHAPE OF THE MATURE BASIDIA.**—The basidium of the Aphyllophorales lacks true septa formed before spore formation (is holobasidious), produces its sterigmata apically and typically is more or less club-shaped.

I have chosen as the central type for discussing the variations in shape of the holobasidial body the one that may be called typically *club-shaped*. It is neither short nor long, it gradually widens toward the apex and is widest at the base of the hemispherical dome by which it is terminated; the base (whether subtended by a clamp or not) is rather wide, perhaps half the width of the greatest apical diameter. Usually the gradual widening from the base toward the apex increases slightly more rapidly from just below the middle onward (*Athelia*). The first division spindle of the diploid nucleus in such an ideal basidium is situated where the apex is widest and its orientation is perpendicular to the basidial axis (transverse division; chiastic basidia).

If this typical club-shaped type is considerably shortened so that it becomes less than twice as long as broad and if it also becomes narrower at the base the obovoid basidial type is produced which occurs in *Paulliticium*, *Oliveonia*, and several *Tulasnella* species. Rarely the basidium may be so short that it is nearly globose. Often these short basidia appear stalked above the basal septum and then they are more or less pear-shaped or even sphaero-pedunculate. Short basidia have been called barrel-shaped if they have a broad base. If the typical club-shaped basidium becomes drawn out along its long axis it becomes slender club-shaped and often more or less flexuous toward the base.

The sphaero- and pyro-pedunculate basidia encountered in certain genera of the Corticiaceae (*Tulasnella*, *Oliveonia*) deserve a special paragraph. They remind

one strongly of the basidia of certain tremellaceous fungi just before the septa are formed, for example: *Heterochaetella* (Bourd.) Bourd. & G., *Stylinella* A. Möll., and *Pseudotremellodendron* D. Reid. Normally, it would seem, in the basidia of these fungi a transverse septum cuts off the stalk and the thus separated apical portion becomes cruciately septate. (In the species with clamps the 'basal' septum is clampless but the next septum has a clamp.) The sphaero-pedunculate holobasidium is usually (but not invariably) correlated with formation of secondary basidiospores and these two features together very strongly suggest that at the level of the 'tulasnelloid fungi', and some other genera not producing ballistospores (cf. p. 228), we are confronted with 'incipient' or 'reduced' Tremellineae. The question of intermediate forms between the Aphyllophorales and the Tremellineae is also briefly touched on page 243.

An interesting variant of the slender club-shaped basidium is the one in which the first division-spindle of the diploid nucleus occurs in the middle of the basidium, and is orientated more or less along the long axis, instead of occurring in the more pronounced apical swelling of the chiasitic basidium. These stichic basidia tend to be relatively narrower and more cylindrical than the typical club-shaped chiasitic basidium. Examples: *Clavulina*, Cantharellaceae, *Hydnum sensu stricto*, *Clavulicium*. For further details, see page 221.

Compared with the preceding basidial types the *u r n i f o r m* basidium appears quite distinct. It starts as a swollen vesicle that emits apically a cylindrical, rather short tube which hardly swells at its extreme apex. On maturity the apex usually flattens and produces a crown of often 6-8 tiny sterigmata. Cytological details have been published by Kühner (1947) and Boidin (1958b: 269 *textpl.* 6 f. 14). The vesicle is the seat of fusion of the basidial synkaryon into the diploid nucleus. The diploid nucleus migrates into the tube but not as far as the apex; it divides somewhere in the basal half of the tube. The first division spindle is apparently usually longitudinally orientated but it may also be oblique or even transverse. Boidin insists upon calling this basidial type stichic too, since in this case he prefers to emphasize the place of the division. In any case this type seems well enough marked to be singled out under the special term of 'urniform' basidium.

This restriction of the term calls for the introduction of a new one for basidia that are otherwise similar, especially as to the initial vesicle sending out a tube in which the first division spindle is situated. The principal difference is that the spindle is orientated as in the chiasitic club-shaped basidium being apical and usually more or less transverse. The apex of the mature basidium is slightly, but distinctly, swollen but is often narrower than the initial vesicle at the base of the basidium. Since these basidia, in their average shape, strongly resemble certain cystidia in the agaric genus *Drosophila* Quél. [= *Psathyrella* (Fr.) Quél.] which Romagnesi (1939: 126) has called *utriform*,<sup>7</sup> it is now proposed to call them

<sup>7</sup> Illustrations showing the range of variation in this type of cystidium were published by Kühner & Romagnesi (1953: f. 461). Jossierand (1952: 329) discussed the etymology of the term 'utriform'.

utriform basidia. Examples: *Galzinia* (cytology still unknown), *Coniophora* (Lentz, 1957).

Utriform basidia are usually rather variable within the same hymenium: at one end of the scale of variation, the two swollen portions are close together and hardly distinguishable from each other except by a faint constriction; at the other end of the scale there may be a rather long and narrow flexuous tube separating them. A remarkable deviation from the standard type occurs when, apparently accidentally, the tube does not arise apically but from the side of the vesicle and the two portions of the basidium thus contrast more strongly than usual [see Rogers, 1944: 97 fs. 13b, c, *Galzinia pedicellata* Bourd.; Eriksson, 1958: f. 17d, *Scytinostroma praestans* (H. S. Jacks.) Donk]. The main difference from the typical club-shaped basidium is that in the utriform basidium the initial basidial vesicle is not narrow club-shaped and does not elongate as a whole into the metabasidium but produces a more or less contrasting proliferation. Yet it is often difficult to distinguish between the two, especially in those cases where the mature utriform basidium is only faintly narrowed at its middle. We know too little about the cytology in most genera to be quite sure that in *Hyphoderma* the basidia are really utriform, but the two aberrant cases illustrated by Eriksson (1958: f. 23d) for *H. definitum* (H. S. Jacks.) Donk strongly suggest this.

The basidium of *Vuilleminia comedens* (Nees per Fr.) Maire appeared for some time to be distinct enough to place it in a genus and family of its own. Here follows an excerpt of Maire's account of it (1902: 81-82):

"Si l'on examine au microscope une coupe du champignon, on remarque dès le premier abord la rareté des basides, leur longueur et leur dissémination au milieu du tissu stérile . . . Les basides se forment très profondément . . . ; elles ne sont d'abord que les cellules terminales binucléées de ramifications spéciales. Ces cellules terminales, de forme cylindrique grossissent un peu, . . . leurs deux noyaux se fusionnent de très bonne heure et la jeune baside ainsi formée s'allongeant . . . et se renfle à son sommet en une ampoule semblable à une jeune probaside de Trémelle, où se trouve placé son noyau, qui grossit . . . Puis l'ampoule émet un tube de germination à son sommet . . . ; ce tube s'insinue au milieu des filaments du tissu stérile. Le noyau y pénètre bientôt et déforme souvent le tube plus étroit que lui . . . Puis celui-ci s'épanouit à l'extérieur en une grosse ampoule où passe le noyau . . . La première division . . . est apical en même temps que transversal . . . La baside développe alors quatre grands stérigmata arqués et divariqués . . . Les basides mûres allongées à travers toute la croute de tissu stérile peuvent atteindre depuis leur base jusqu'à leur sommet 80 à 100  $\mu$  . . ."

At the time Maire described this basidium type it was very remarkable indeed, but now that the Corticiaceae have become better known it hardly appears to me to be more than an extreme variation of the utriform basidium. The two essential elements are there: the swollen probasidium and the prolongation with the swollen apex in which the diploid nucleus divides chiasmatically (in contradistinction to the urniform basidium). As in other genera (*Laeticorticium*) the basidium is of deep origin and has to work its way to the surface of the fruitbody through a strongly developed layer of sterile tissue (hyphidia). The big size of the sterigmata and their appearance are matched by those of *Aleurodiscus* in which genus also the basidia

are often more or less utriform although much less so than in *Vuilleminia* where the basidium has to pass through a dense gelatinous tissue. As to its basidial morphology, *Vuilleminia dryina* (Pers.) Donk (cf. Bourdot & Galzin, 1928: 336), with its 'dry' fruitbody, is in many respects intermediate between *V. comedens* and *Aleurodiscus*. I do not support a family Vuilleminiaceae if it is solely to be based on the shape of the basidium of the one genus *Vuilleminia*.

A remarkable example of basidial variation was first reported by Linder (1934) for *Myxomycidium guianense* Linder (pendent, simple, clavariaceous fruitbodies) in which species he found two types of basidium. One was typical of the chiasitic club-shaped type and the other of the utriform type except for the fact that the tube-like proliferation was apparently not formed until after the completion of nuclear division. Linder's discussion shows that he attached great importance to the basidial behaviour in what he called the 'proliferative' basidia; he excluded *Myxomycidium* from the Clavariaceae and was strongly inclined to enter it in the Vuilleminiaceae (which in this paper are merged into the Corticiaceae). At that time the utriform basidium was hardly known from genera other than *Vuilleminia* (a genus with effused fruitbody).

It now seems as if this basidial variation must be interpreted as a mere adaption to a peculiarity of the fruitbody rather than as a fixed and phylogenetically important character. The fruitbody of *M. guianense* is subjected to an extreme final stage of liquefaction: "with increasing age, the fruiting body enlarged apically and became ... considerably softer, until finally it became so watery at maturity that it was almost impossible to touch it without its flowing around one's finger and leaving the stipe behind." This rapid increase in the volume of the basidiferous portion of the fruitbody, expressed in a progressively rapid extension of the surface, would appear to be the clue to the aberrant basidial behaviour, as was previously suggested by Martin and Corner. During the course of their development the basidia have to be able to produce their ballistospores beyond the surface of the fruitbody. There are indications that this requires several rigorous adaptations. (i) Although the hymenium of the smaller fruitbodies is originally composed of a single layer of club-shaped basidia, it soon develops into a very rapidly thickening one (Linder, l.c., pl. 39 f. 24), (ii) the stalk of the probasidium may elongate considerably, (iii) the not yet fully developed basidia may emit a tubular outgrowth, which may become very long, thus giving rise to utriform-like basidia, and (iv) exceedingly long sterigmata may be formed which are strongly reminiscent of the *Tremella* sterigmata when they grow out hypha-like before they reach the surface of the gelatinous fruitbody. (In *M. yakusimense* Kobayasi, 1954: 46 f. 37, some of the basidial adaptations are even more accentuated, i.e. very long stalks and the tubular outgrowth may emit still another tube.) The fact that Linder drew 'normal', curved sterigmata of the same length on each basidium he depicted would seem to suggest that, in *M. guianense*, the basidial apices manage to reach the surface of the fruitbody and the sterigmata to develop in the air. In *M. yakusimense* one gets the impression that most of the depicted basidia were completely embedded and that the sterigmata

(one branched) continued the race toward the ever expanding surface of the fruit-body by elongating. Martin (1938: 437) found in *M. flavum* G. W. Mart. both what appeared to be normal sterigmata and some that were cylindrical and considerably longer. "It seems reasonable to suppose" he wrote of the basidia with 'hypobasidium'-like bases and cylindrical sterigmata that they "represented nothing more than adaptations to the increasing thickness of the gelatinous envelope, making it necessary for both basidia and sterigmata to be longer if the spores are to be borne at the surface."<sup>8</sup> From some of his figures (fs. 21, 23) one would conclude that the reduction division of the diploid nucleus may occur in the outgrowths of the probasidia and that this and the utriform modifications of the basidium are true to the utriform type.

I cannot agree with Kobayasi (op. cit., p. 47) that the long sterigmata and the utriform basidia are indicative in this genus of primitiveness and of an intimate relation with 'Heterobasidiae'. The resemblance to the *Vuilleminia* basidium, which impressed Linder, are in my opinion merely a matter of 'convergence'; the deviations from the normal chiasitic club-shaped basidium would seem of secondary importance only. Finally, Heim proposed the family "Myxomycidiaceae" which he considered intermediate between the "Protoclavariales" (= Dacrymycetales) and the Aphyllophorales, but the few characters he enumerated for the new taxon are hardly valid. See further page 224.

I do not doubt that the metabasidium of those Auriculariineae with a persistent probasidium is homologous with the tube emitted by the probasidium of the utri- and urniform basidium. However, I would not go so far as Olive (1954: 797) who derives *Sistotrema* (urniform basidia) by way of *Galzinia* (utriform basidia) from such auriculariaceous basidia merely because of the observation of some incidental, and presumably adventitious, cross-walls and some abnormal types of spore-production. Neither does the derivation of the *Sistotrema* basidium from that of *Sebacia*, as suggested by Linder (1940: 443 f. 6), seem likely. The differentiation of the probasidium into a dimerous organ upon further development is apparently not a very fundamental phenomenon in most groups and in a number of cases at least appears to be hardly more than an adaptation to some particular circumstance. *Myxomycidium* would seem a *casé* in point.

The last basidial type to be discussed is the pleurobasidium (Donk, 1956a: 370; 1957: 2) which has also been called a 'basidium with a bifurcate base'. These basidia are not merely laterally more or less sessile on hyphae; they are, rather, lateral extensions of hyphae which are broad at their base and not separated by a cross-wall. The hypha from which a pleurobasidium arises forms its 'bifurcate' base which appears as two opposite horizontal 'roots'.

Typical pleurobasidia develop from more or less repent hyphae; they do not

<sup>8</sup> Martin (op. cit., p. 435) also stated, "sterigmata . . . when borne near the surface acicular, curved, short . . . when borne deeper within the gelatinous mass longer, . . . cylindrical, resembling epibasidia [viz. hyphae-like protosterigmata]." One would suggest that the basidia with short, curved sterigmata really protruded into the air with their apices.



develop from an ascendant subhymenium. They can be found, as an exceptional development, for instance in *Boletopsis* and *Albatrellus* where the basidia originate from hyphae repent over the inner surface of the tubes. One would theoretically, therefore, expect to come across some pleurobasidia among the first basidia of corticiums with a strongly thickening hymenium the initials of which arise directly from a basal layer of repent hyphae. This is indeed the case in, for instance, at least some species of *Peniophora* sensu stricto where later basidia develop terminally on ascending branches penetrating into the thickening hymenium. However, where there is no thickening hymenium in this sense, and the new basidia are formed on new repent hyphae overgrowing their predecessors, pleurobasidia may be the predominant type throughout the basidiferous stage of the fruitbody. The manner in which the fruitbody increases (new repent hyphae over its surface) also accounts for another characteristic of the pleurobasidium, viz. the fact that its base is often hidden in the surface layers of the fruitbody and is difficult to find. Moreover, the pleurobasidial hymenium is often one in which the basidia (and in some species also the cystidia) protrude as more or less scattered bodies from the stroma that represents the fruitbody proper.

From these considerations one would conclude, therefore, that as a taxonomic feature pleurobasidia should not be overrated; they may be expected everywhere where basidia are born on repent hyphae, although in certain species the tendency to form them may be either strongly pronounced or suppressed and even completely absent. In *Paullicorticium*, for instance, many of the basidia are formed on repent hyphae but they do not develop as pleurobasidia: they are formed on (very) short side-branches and have a narrow base with a septum across it.

NUCLEAR SPINDLES IN THE BASIDIUM.—The normal nuclear phenomena occurring in the basidium are briefly that the two conjugate nuclei (dikaryon) fuse into a diploid nucleus, this then proceeds to divide twice or thrice producing four or eight haploid nuclei which either all pass through the sterigmata into the spores or some may remain back and then degenerate. The position of the division spindles has been of interest to the taxonomist since Van Tieghem and Juel (1898) first drew attention to the fact that two main basidial types could be distinguished in connection with them. These are basidia in which the first division spindle is longitudinal and those in which it is transverse. In the stichic basidium this division spindle is not only longitudinal but in addition is situated at about the middle of the basidium. In the chiasitic basidium this spindle is transverse and located in the dome-shaped top of the basidium.

Maire (1902) followed Juel in considering this distinction a first-rate taxonomic character and after studying a number of additional species proposed a new classification of the Basidiomycetes which became widely known as it was adopted in text-books by Lotsy (1907) and Gäumann (1926). This classification was radically different from the then current ones and was not favourably received by taxonomists for various reasons. The number of investigated species on which it was based was

much too small, and adding further examples was a time consuming labour during the first decades of this century and proceeded very slowly and quite incidentally (Juel, 1916, as far as the Aphylophorales were concerned). Of too many genera nothing at all was known in this respect and hence it was almost impossible satisfactorily to elaborate Maire's academic scheme into one for practical or even taxonomic use. The result was that the position of the basidial division spindles was completely ignored by most taxonomists, even at the generic level. One of the arguments against its use (if these were mentioned at all) was that one or more of the division spindles may be oblique and, hence, that intermediate stages occur. At least in some cases this apparent obliqueness was due to technical deficiencies. However, in other cases, as in more or less globose or broad-topped probasidia, the swollen apex leaves room for considerable variation in the position of the first division spindle. This has led to an extreme underestimation of its value as a taxonomic character: "I do not believe the much-quoted distinction between chiasmo- and stichobasidia is of any fundamental significance" (Martin, 1938: 437). There are indications that such a complete rejection is being revised by at least some of the more recent authors.

The few authors who did not want to neglect the presumed fundamental difference between the two basidial types tried to avoid the cumbersome cytological investigation by looking for correlated features. Juel listed some of these and van Overeem (1923) added others. Apart from the cytology, the latter author thought that the species with stichic basidia could be recognized by the basidial shape (more cylindrical, elongating considerably, and at maturity far-protruding), the hymenial type (thickening hymenium with embedded spores), the number of sterigmata per basidium (variable, originally eight, then six, and finally two), the shape of the sterigmata (strongly developed, divergent, and curved), and the spores (globular and firm-walled in the clavarioid species). Donk (1933: 66-70) criticized some of these assertions. For instance, he pointed out that thickening hymenia (which he then called protohymenial) also occurred in chiasmo species such as *Coniophora* and *Gyrophana* (= *Serpula*). According to Corner (1957), in the tropical form of *Craterellus cornucopioides* (L. per Fr.) Pers. (of which the basidia may be expected to be stichic as in the European forms) the hymenium is non-thickening.

In his classification of the Dutch Aphylophorales, Donk (1933) emphasized on the one hand that he had arrived at his conclusions on morphological grounds as opposed to cytological ones and that he was not prepared to follow Maire by combining all groups with stichic basidia into a single taxon. On the other hand he did not want to disregard the position of the nuclear spindles altogether because it appeared to him that it represented a welcome set of 'supporting' characters, indicative of differences in basidial shape otherwise easily overlooked or difficult to establish. He separated the Phylacteriaceae (as Phylacterioideae; = Thelephoraceae, emended) from the Cantharellaceae (as Cantharelloideae) because he did not believe them to be closely related; and he refused to place a so-called stichic species [*Peniophora quercina* (Pers. per Fr.) Cooke] into a different genus from a

chiastic species (*Radulum laetum* Fr.) on these grounds alone. In the mean time it has been found that the species of the Thelephoraceae which have now been investigated are all chiastic and not stichic as Maire stated of the few he had examined: they therefore differ in this respect from the Cantharellaceae. It has also been established that *Peniophora quercina* and *Radulum laetum* both belong to the same, somewhat aberrant, type. (In the present paper the Cantharellaceae is divided into three families, the Cantharellaceae *sensu stricto*; the Hydnaceae, perhaps too closely related with the preceding for separation; and the Clavulinaceae.)

During the last few decades the methods of investigating the nuclear cytology of the basidium have become simpler and quicker, and many details have been added to our knowledge particularly by Boidin (in various papers, but mainly, 1958b) and Penancier (1961). Boidin (1951a) has slightly altered the definitions making them more precise.

In the *s t i c h i c* basidia the first division is situated at the middle of the basidium and is generally longitudinal; the second divisions are spaced from each other and are never both apical, they often occur at two different levels and their direction is not fixed.

Boidin emphasized particularly the position rather than the direction of the first spindle. In the basidia of *Trechispora niveo-cremea* (Höhn. & Litsch.) Park.-Rh. [= *Sistotrema niveo-cremeum* (Höhn. & Litsch.) Donk]<sup>9</sup> he found transverse as well as longitudinal first spindles but he called the species stichic because they were always in the middle; the second divisions occurred at different levels but again rather toward the middle.

In the *ch i a s t i c* basidium the first and second spindles are apical and mostly transverse; the second divisions occur parallel to each other and at the same level.

Boidin (1951a) also proposed an additional term, "hémichiastobasidié" (*h e m i c h i a s t i c*), for a somewhat intermediate condition in which the first spindle is situated at some distance from the top of the basidium and is variously orientated, mostly strongly obliquely in comparison with the chiastic basidium; the second divisions are as perfectly apical and transverse as in typical chiastic basidia. It would seem that the hemichiastic basidium may be subordinated as a subtype to the chiastic, with which it is connected by intermediates.

The investigated species are divided as follows among the families and genera as these are accepted in the present paper. The numbers after the generic names indicate the number of investigated species.<sup>10</sup>

<sup>9</sup> This species has been transferred to the genus *Sistotremastrum* which was segregated from *Sistotrema* because its basidia do not pass through the typical urniform basidial stages. However, Boidin's figures (1958b: *textpl.* 6 *fs.* 14-16), if drawn from correctly determined material, strongly suggest that he did study a species with urniform basidia; he insisted of this species, that "il est certain cependant que cette espèce se rapproche beaucoup plus des *Trechispora* [= *Sistotrema*] que d'aucun autre espèce de *Corticium*." In the following list I have included Boidin's fungus under *Sistotrema*.

<sup>10</sup> About ten species have been omitted, mainly Clavariaceae. This was done because the determinations were thought to be doubtful and their generic position could not be inferred

## Stichic.—

Cantharellaceae.—*Cantharellus* (4), *Craterellus* (1).Clavulinaceae.—*Clavulina* (3).Corticaceae.—*Clavulicium* (1), *Sistotrema* (2).<sup>11</sup>Hydnaceae.—*Hydnum* sensu stricto (1).

## Chiastic (inclusive of hemichiastic).—

Agaricales: former 'Cyphellaceae'.—*Calyptella* (2), *Cyphellopsis* (1), *Lachnella* (1), *Mniopetalum* (1).Bankeraceae.—*Bankera* (1), *Phellodon* (1).Clavariaceae.—*Clavaria* (3), *Clavariadelphus* (3), *Clavulinopsis* (4), *Mucronella* (1), *Myxomycidium* (3), *Pistillaria* (4), *Ramariopsis* (1), *Typhula* (5).Coniophoraceae.—*Coniophora* (1?), *Serpula* (2, inclusive of *Leucogyrophana*, 1).Corticaceae.—*Aleurodiscus* (2), *Amylocorticium* (2), *Athelia* (6), *Auriculariopsis* (1), *Corticium*, residual genus (3), *Cristella* (3; 1 hemichiastic; 1 hydnaceous species), *Dacryobolus* (1, hemichiastic), *Digitatispora* (1), *Gloeocystidiellum* (4; 2 hemichiastic), *Hyphoderma* (7), *Hyphodontia* (6; 1 hemichiastic; 4 hydnaceous species); *Hypochnicium* (2), *Laeticorticium* (1, hemichiastic), *Merulius* (2), *Mycocacia* (2), *Odontia*, residual genus (2), *Peniophora* (14, all hemichiastic), *Phanerochaete* (13; 2 hemichiastic; 3 hydnaceous species), *Phlebia* (2), *Sarcodontia* (1), *Scytinostroma* (1, hemichiastic), *Thanathephorus* (1), *Tulasnella* (3 or 5), *Vuilleminia* (1).Ganodermataceae.—*Ganoderma* (1).Fistulinaceae.—*Fistulina* (1).Gomphaceae.—*Gomphus* (1), *Ramaria* (10).Hericiaceae.—*Hericum* (2), *Laxitextum* (1).Hydnaceae (residual).—*Steccherinum* (2).Hymenochaetaceae.—*Hymenochaete* (2, hemichiastic?).Polyporaceae.—*Coriolus* (1), *Grifola* (1), *Lenzites* (1), *Trametes* (1), & 3 other species.Schizophyllaceae.—*Henningsomyces* (1), *Plicaturopsis* (1), *Schizophyllum* (1). — For former 'Cyphellaceae', see above under Agaricales.Sparassidaceae.—*Sparassis* (1).Stereaceae.—*Amylostereum* (1), *Chondrostereum* (1), *Lopharia* (1), *Stereum* (4).Thelephoraceae.—*Boletopsis* (1), *Hydnellum* (6), *Sarcodon* (3), *Thelephora* (1), *Tomentella* (1).

Corner (1957: 267) considers the stichic basidium "as an adaptation of the meiotic sporangium to its own excrecence from a congested surface, and not as a primitive mark." This may be so but is not very evident if one remembers that in all similar circumstances in chiastic basidia the first division occurs in the apical, exerted portion and hence is presumably not subjected to any congestion. In this connection it may be also recalled that the first division spindle may be longitudinal even in species with loose tufts of basidia (*Kordyana*, Exobasidiales). The point here is that if the stichic basidium of the *Cantharellus* type is to be considered an adaptation, it is necessary to explain why the diploid nucleus did not migrate to the exerted apex of the basidium.

It is likely that the position of the spindles is more or less determined not only by their length but also by the resistance offered by the cytoplasm (and its inclusions such as vacuoles and other bodies). A long spindle in a narrow tube will have to

because insufficient details for recognition were added. One of them is *Clavaria falcata* Fr. sensu Juel (type of *Stichoclavaria* Ulbr.) which was thought to be stichic but this conclusion rests on a very slender basis.

<sup>11</sup> See also foot-note 9.

divide longitudinally. Taking into consideration the difficulty in predicting whether a basidium is stichic or chiasitic, the direction of the longest spindle offers a clue for tracing differences in basidial form which otherwise would remain at most suspected instead of proven. Because the spindles of the second and third divisions are shorter, they may be expected to be less constant as to their direction and this has been found to be actually the case. Yet, they have appeared to be still of some significance, for instance, as to their level in the basidium.

As is the case with most taxonomic characters, the shape of the individual basidia is subject to variation within certain limits; where this variation is considerable (as in catahymenia and/or thickening hymenia) it is not surprising that the cytology of the basidium also shows some measure of variation. Occasional 'abnormal' or 'intermediate' spindle positions should not lead to too hasty conclusions as to their lack of taxonomic value.

**THE STERIGMATA.**—The typical sterigma of the Aphyllophorales originates as a minute, more or less rounded bud which soon grows out into a tapering, slender tip which produces the ballistospore. The bud has been termed *protosterigma*, and the pointed tip *spiculum* (Donk, 1954). It may be assumed that even the tiniest sterigma starts as a nipple- to knob-like protuberance that rapidly produces the spiculum. The typical, full-grown sterigma of the Aphyllophorales (and Agaricales) is a *curved* organ. Variations on this typical sterigma will be briefly mentioned, since 'aberrant' sterigmata have been used as important taxonomic characters.

In cases where (i) the spores produced at the tip of the sterigmata are ballistospores and (ii) the developing sterigmata are not completely embedded in the fruitbody,<sup>12</sup> the curvature of the full-grown sterigma is one of the most constant characteristics of the basidium.

The concurrence of curved sterigmata and ballistospores is an empirically well-established fact. Equally, when the basidiospores are not violently discharged the sterigmata producing them invariably lack this curvature (compare the Gasteromycetes, for instance species of *Lycoperdon*). A remarkable instance in which this correlation is demonstrated is *Xenolachne* D. P. Rogers (1947; Tremellineae). In this genus the basidiospores are not forcibly discharged and break off by mechanical disturbance from long, exceedingly slender, stiff, straight sterigmata. Similar cases are not known from the Aphyllophores.

Completely embedded basidia (i.e. including the developing sterigmata) are of common occurrence in the Tremellales but rare among the Aphyllophorales. If in the latter the fruitbody is gelatinous or mucous-waxy, the top of the mature basidium nearly always protrudes beyond the surface to form its spores in the air. Such basidia are usually of the utriform type and individually of variable length

<sup>12</sup> Not taken into consideration are one-spored basidia which among the Aphyllophorales occur only as variations of usually two- or more-spored basidia.

depending on the distance of their probasidia from the surface. In the Tremellales the basidial body itself remains embedded and the sterigmata, which are of variable length, grow toward the surface. In one genus placed in the Clavariaceae, viz. *Myxomycidium*, it would seem that both methods rarely may occur in combination: basidia as well as sterigmata may be of variable length and the latter may develop in a manner strongly reminiscent of the hypha-like sterigma in *Tremella*. This case is more extensively reviewed above (p. 217).

Strongly developed protosterigmata, but not due to their basidia being embedded, are rare among the Aphyllophorales. They occur in the so-called tulasnelloid series, a small set of genera all of which exhibit secondary basidiospore formation (Donk, 1956a; 1958). Thus in *Ceratobasidium*, *Uthatabasidium*, and *Thanatephorus* the protosterigmata grow out as finger-shaped rather strongly developed tubes that become tipped by spicula and often somewhat fusoidly swollen when starting to produce spores. In *Tulasnella* (inclusive of *Glootulasnella*) the sterigmata develop in three phases. First, they grow out into the swollen, spore-shaped bodies which have attracted so much attention (protosterigmata). Secondly, after these voluminous, ovoid bodies have reached their maximum size and gone through an outwardly stationary period (in some species a nuclear division has been reported) they emit an outgrowth that varies from rather conical and short to rather finger-shaped and long. Finally these outgrowths (secondary protosterigmata) each produce a spiculum on which the forcibly discharged basidiospore is formed.<sup>13</sup>

The sterigmata in *Uthatabasidium* and *Thanatephorus* have been called sterigmata by some authors who called the protosterigmata in *Tulasnella* and *Ceratobasidium* epibasidia. This use of the comprehensive term epibasidia has led to an unusual situation. *Tulasnella* (and *Glootulasnella*) has been put into a special family on account of its spore-like 'epibasidia' and *Ceratobasidium* into another special family, also characterized by 'epibasidia' but which are not, in this case, separated by a septum across their base as in *Tulasnella*, while *Uthatabasidium* and *Thanatephorus* (both as portions of a bigger genus *Pellicularia* sensu D. P. Rog.) are placed among the Thelephoraceae (Corticaceae) because they would possess sterigmata.

Since I can neither accept a term that covers protosterigmata (*Tulasnella*, *Ceratobasidium*; *Tremella*) and metabasidia which are morphologically separated from their probasidia as in *Auricularia*, nor a terminology that does not homologize the sterigmata of *Tremella* with those of *Auricularia*, I have abandoned this confusing term epibasidium altogether (Donk, 1931: 78-81 fs. 3-5). I also, unlike Martin (1957: 25), refuse to call the *Tulasnella* basidium a phragmobasidium (Donk, 1958: 96) because of the adventitious septum across the base of the protosterigma (see also p. 213).

The cross-wall dividing the basidial body from the protosterigmata in *Tulasnella* appears to be a consequence of the fact, that, collectively, the protosterigmata have

<sup>13</sup> It is likely that in certain species of *Tulasnella* the basidia with their protosterigmata are, or gradually become, embedded; this would explain their often long secondary protosterigmata which have to reach the surface of the embedding matrix.

taken over the spore-discharging function of the basidial body; each of them presumably acts as if it were a monosporous basidium. This situation is analogous to that in many true phragmobasida where each basidial cell acts as a monosporous holobasidium. In my opinion the morphological differences between the *Tulasnella*, *Ceratobasidium*, and *Uthatabasidium* sterigmata are too insignificant to justify placing these genera in three families, although the *Tulasnella* basidium as a whole represents a strongly advanced 'physiological' type.

The first hymenomycete to be described among the marine fungi, *Digitatispora marina* Doguet (1962; 1963), is also remarkable in other respects. The basidia are of the chiasitic, club-shaped type, although rather slender. Each produces four cylindrical, tube-like outgrowths of considerable length each of which normally divides apically into three similar, spreading outgrowths of about the same length but somewhat more slender. ('Abnormal spores' have also been reported.) These spores are dispersed by passively breaking off at their bases when the fruitbodies are flooded by the sea. Doguet calls these structures basidiospores which may be correct but nevertheless still appears questionable. Truly sessile spores are known among the Gasteromycetes where active spore discharge does not occur. In the case of *Digitatispora* the 'spores' are also passively freed from their support but the homology is not self-evident.

I pose the thesis that these 'spores' are in reality sterigmata acting as diaspores. Their initials are hypha-like outgrowths resembling the branched hypha-like developing protosterigmata which have been incidentally observed in many Tremellales and in *Myxomycidium yakusimense* (see pp. 217-218). Protosterigmata behaving as diaspores are occasionally seen in *Tulasnella*, and are typical of *Sirobasidium* Lagerh. & Pat. (Bandoni, 1957). The detached protosterigmata retain the ability to produce basidiospores by forming secondary protosterigmata tipped by basidiospore-bearing spicula, or by directly producing spicula. It is conceivable that the 'spores' of *Digitatispora* may produce ballistospores upon germination under certain circumstances as yet unknown.

Doguet considers *Digitatispora* "proche des Corticiums". If this view is not accepted by placing this genus in the Corticiaceae (artificial sense) as is done below, the alternative would be to place it in a family of its own.

For some remarks on the number of sterigmata per basidium, see page 213.

THE SPORES.—The study of the basidiospores has been gradually intensified since the time when descriptions of their shape and size became an integral part of the specific description. However, the number of spore characters taken into consideration in the descriptions of the families of the Aphylophorales in the present paper has remained relatively low. Such familiar characters as colour of spores (not really a microscopic one), shape, size, and ornamentation are rarely mentioned in descriptions mainly because the families are currently either artificially or too comprehensively conceived. A faithful inclusion of such characters would clutter up the descriptions with features varying within broad limits and very much the

same for several families. The smaller and more natural the families become the more it may be expected that this situation will improve.

As in the Agaricales, the colour of the spores should be carefully noted from good spore prints which, however, are not always so easily obtained as in the gill-fungi. The colour is almost invariably located in the spore-wall, exceptionally it may be in the contents as in *Clavaria helicoides* Pat. & Demange, where the yellow pink colour of the massed spores is due to the cytoplasm (Corner, 1950: 243).

Although the germ-pore so typical of many agarics (which is not always the place of germination) is lacking among the Aphylophorales, certain spore-types possess definite spots from which the mycelium germinates. In *Ganoderma* (one of the genera of Ganodermataceae) this is the apex which is originally a bulging, lens-shaped to conical portion of the outer wall. This soon collapses and causes the spore to appear apically truncate. Favoured spots for germination are through the apiculus at the base of the spore or at the undifferentiated spore-top.

The terminology of the several layers that may form the agaric spore-wall has become intricate and, apparently, irrational. It is to be hoped that a reassessment of these terms will be made when it becomes necessary to take them into consideration also for some groups of Aphylophorales. At the moment little is known about the layered structure of the spore-wall in this order. When two layers appear distinct the spores are mentioned in this paper as being double-walled and a distinction is made between the inner and the outer layer. The most complicated spore-wall is found in the Ganodermataceae (which see for a brief discussion). If there are still more layers to account for I have, for the present, made use of such indications as innermost and outermost layer, reserving the terms inner layer (e n d o s p o r i u m) and outer layer (e x o s p o r i u m) for the two principal, most evident ones.<sup>14</sup>

The chemical nature of the spore-wall has become more and more important in the Aphylophorales. It has become essential to establish whether a spore-wall is amyloid or non-amyloid and also its affinity for Cotton Blue (cyanophily) (see p. 239).

A difficult problem is the correct assessment of the value of the septation of the spores. Normally the spores of the Aphylophorales do not become septate upon germination but the formation of cross-walls during this process has occasionally been reported. More important, it would appear, is the appearance of septa shortly after discharge of the spore (or perhaps even shortly before that event) and before germination sets in. The next item to establish is the nature of the septa, whether or not they are formed in connection with nuclear divisions, i.e. whether or not they are true or secondary septa. A cross-wall laid down at the middle of the long axis of the spore will probably be a true septum.<sup>15</sup> In *Vuilleminia comedens* (Nees

<sup>14</sup> The terms epi- (or exo-)sporium and endosporium were used by De Bary (1884: 107). Singer (1962: 72) recently insisted, correctly, on the use of the ending -sporium instead of -spore.

<sup>15</sup> Brefeld (1888: 30 pl. 2 f. 2) recorded the germinating spore of *Radulum laetum* Fr. [= *Peniophora laeta* (Fr.) Donk] as forming a cross-wall at the middle and germinating with



per Fr.) Maire (Corticiaceae) both types occur simultaneously (Maire, 1902: *pl. 2 fs. 12, 13*). *Waitea circinata* Warcup & Talb. (Corticiaceae) often shows one or two septa in the spores.

Such facts, especially with a knowledge of the cytological background, are of value in connection with a reassessment of the status of the Dacrymycetales (stichic, 2-spored basidia; spores often septate). I am becoming more and more convinced that this order is not related to the Auriculariineae and Tremellineae, but that it is a rather small, highly characteristic, offshoot of some group of Corticiaceae such as, perhaps, those in which *Clavulicium* (stichic, 2-, rarely 1- or 3-, spored basidia) or *Cerinomyces* (position of nuclear spindless in the basidium unknown, 2-spored basidia) belong.

SECONDARY BASIDIOSPORES.—Among the hymenomycetes a number of species form basidiospores capable of producing a secondary spore on a sterigma-like outgrowth. The formation of this type of secondary spore is usually referred to as 'germination by repetition'. Renovation or 'repetition' certainly occurs since the basidiospore repeats itself, but in my opinion the term 'germination' is incorrect here, because the process of germination does not actually set in in these cases. The agreement between the formation of the primary basidiospore on its sterigma and the secondary basidiospore on its sterigma-like support is so great that if one insisted on calling the latter process 'germination' one would logically have to call the spore-production of the basidium 'germination' which would not be correct.

Basidiospores exhibiting repetition are now almost unanimously considered to be a sure indication of the 'heterobasidious' nature of the species showing this phenomenon. Such a view needs qualification. Secondary basidiospores are of general occurrence in most of the genera of the Tremellales (including the Auriculariineae), but the ability to form them is by no means a constant feature of all genera of that order. It does not occur, for example, in *Phleogena* Link ('dry' spores not violently discharged), which is so well known from cultures that repetition of its basidiospores would certainly have been reported if it existed. Moreover, quite typical repetition of basidiospores is not certainly known from the Dacrymycetales<sup>16</sup> as far as I am aware and seems to have been very rarely observed in the Septobasidiales. Thus, it will not do to state that the 'Heterobasidiales' are invariably characterized by their basidiospores exhibiting repetition, even if one restricts this group to the taxa with phragmobasidia producing ballistospores.

On the other hand if all Hymenomycetes capable of producing secondary ballistospores were to be included in one taxon, not only a part (although a very big majority) of the phragmobasidious 'Heterobasidiales' would be present but also a small series of holobasidious genera, viz. *Tulasnella* (inclusive of *Gloeotulasnella*), *Cerato-*  
secondary spores which, from his figures, quite possibly represent secondary basidiospores. It would seem that some error crept in and that he observed in this case true 'heterobasidious' spores of a quite different species.

<sup>16</sup> Not taken into account, Bulat in *Mycologia* 45: 40-45. 1953.

*basidium*, *Oliveonia*, *Thanatephorus*, and *Uthatabasidium*. This series has been called 'the tulasnelloid fungi' by Donk (1956a). It follows from the above considerations that if one wants to insist on regarding the tulasnelloid series as 'heterobasidious' by definition, one will be forced, either (i) to doubt the heterobasidious nature of a portion of the 'Heterobasidiae' sensu stricto (with phragmobasidia) which would not qualify as heterobasidious because they lack the ability to form secondary basidiospores, or (ii) to postulate that the other holobasidious hymenomycetes cannot be excluded *a priori* as non-heterobasidious (homobasidious) simply because they do not show repetition of basidiospores. In short this latter character is a very important feature but hardly a guide for unfailingly establishing the 'heterobasidious' nature of any single group of hymenomycetes: if it is lacking we cannot be sure that the fungus is non-heterobasidious. It is also not self-evident that the tulasnelloid series is a natural group.

The occurrence of secondary basidiospores among the holobasidiomycetous hymenomycetes has been estimated as a first rate character, important enough to be emphasized in delimiting families. The Tulasnellaceae and the Ceratobasidiaceae are now upheld by some authors mainly because both exhibit repetition of basidiospores and possess 'epibasidia' (see also p. 224). Other authors (Donk, 1956a), who are not willing to agree that there is a clear-cut distinction between these 'epibasidia' and true sterigmata, are less sure about the family rank but tentatively admit repetition of basidiospores (not without some reluctance for fear of ascribing still too much value to it) as a character of generic importance. Some of the considerations that lead to this latter opinion are the following. First, *Thanatephorus* (*'Hypochnus solani'* is an example) and *Uthatabasidium* are morphologically so similar to some other genera such as *Botryohypochnus* and certain species of *Botryobasidium*, which lack repetition of basidiospores, that even the generic separation of all these four genera is not generally accepted; putting them into different families (Olive, 1957)—without supplementary evidence—seems to me far-fetched. Secondly, even within the 'Heterobasidiae' proper (phragmobasidious) the presence or absence of repetition of ballistospores is not used for dividing, for instance, the Tremellineae into families. In terms of one current trend of phylogenetic thought any one of the following theses might be defended: (i) holobasidious derivatives of the Heterobasidiae need not be characterized by secondary basidiospore formation; (ii) Heterobasidiae may have been derived from two different groups of holobasidious hymenomycetes, one lacking and one possessing secondary basidiospore formation; (iii) secondary basidiospore formation is a character that manifests itself somewhat erratically within the alliance of the 'Heterobasidiae'; one would thus expect to find holobasidious Heterobasidiae lacking this character.

It may be objected that in the tulasnelloid series the basidial type is so strongly reminiscent of certain tremellaceous basidia (except for the absence of septa) that it must be put into a separate family or families. In answer to this it may be pointed out that similar basidia are to be found in other holobasidious genera outside the tulasnelloid series, for instance in *Koleroga*, *Paullicorticium*, and *Repetobasidium*. (It

is not denied here that these genera may be related to the tulasnelloid series.)

After these remarks it will be obvious that I find it difficult to support the Tulasnellaceae (see also p. 225) and the Ceratobasidiaceae as distinct families, or if so only as artificial ones. The number of such families should be kept as low as possible.

**STERILE ELEMENTS IN THE HYMENIUM.**<sup>17</sup>—These have nearly all been called 'cystidia' but it is proposed to restrict this term primarily to all sterile elements in the hymenial layer produced by, or with, the subhymenium (basidiferous tissue) and homologous with the basidia. To avoid misunderstanding with the more comprehensive use of the term it will be desirable to call these *hymenial cystidia*. Other sterile elements which penetrate from the context (trama) through the subhymenium into, and often protruding beyond, the hymenium will be called *false or tramal cystidia*. Bodies similar to, and homologous with, cystidia may also occur in the non-hymenial surfaces of the fruitbody. This is especially true of the Agaricales; in the Aphyllophorales they are of little importance.

One category may be called *hyphidia*.<sup>18</sup> These are sterile elements produced by the hyphae of the context (trama) and retaining their hyphal nature by not becoming more or less characteristically inflated, as basidial homologues and other hymenial elements do and to which the term cystidia is generally restricted. Typical hyphidia are produced *in advance* of the first basidia and form a superficial layer that gradually becomes converted into a catahymenium. (The basidia may eventually become predominant and even finally superimpose over it a typical thickening

<sup>17</sup> The best modern discussions on this subject are those by Romagnesi (1944), Lentz (1954), Talbot (1954), and Singer (1962: 40-54).

<sup>18</sup> Hyphidia (Donk, 1956b: 3) have also been called 'paraphyses', 'pseudoparaphyses', 'paraphysoids', and the like, terms preferably to be restricted to the Ascomycetes, where they are used in no less bewildering confusion. Their abolition (inclusive of the shortened suffix '-physes') for hymenial elements of the Hymenomycetes would certainly clear the air, and this is why the term hyphidia was proposed. Lohwag (1941: 39) by definition, reserved 'paraphyses' for the young basidia replacing the exhausted ones, but then proceeded to extend its use also to cover various other, permanently sterile, elements in the hymenium. Lowy (1954: 302) called the hyphidia 'dikaryoparaphyses', a term afterwards shortened to 'dikaryophyses'. Singer (1962: 63) thought that they should be called 'pseudophyses', but this is against current usage: this term had previously been restricted to, and is still in use for, a special type of organ of Hymenomycetes, viz. the moniliform gloeocystidia as they occur in *Aleurodiscus* (von Höhnelt & Litschauer, 1907: 795). Since these bodies are to be excluded from the hyphidia (because they are really gloeocystidia), conserving 'pseudophyses' for hyphidia only would add to the confusion. Moreover, the simultaneous use of both 'pseudophyses' and 'pseudoparaphyses' for different sterile hymenial bodies will no doubt be unacceptable to many mycologists. This twin use was recently defended by Singer & Gamundi (1963: 149). The 'pseudoparaphyses' they had in mind are the pavement cells so typical of the hymenium of most species of *Coprinus*, an application previously proposed by Romagnesi (1944: 13; called brachycystidia below). The objection that 'hyphidium' had been previously introduced for 'spermatium' (lichens) is not valid now, because that term has become completely obsolete.

hymenium; see p. 211). The hyphidia are very varied in their characters and many terms have been invented to cope with this diversity; often, however, a short descriptive phrase is preferable. It seems desirable to exclude from the hyphidia all bodies belonging to the gloeocystidial system, which have a pronounced tendency to inflate in the hymenial region; and also hyphocystidia (see below) and similar bodies.

Most hyphidia belong to the generative hyphal system. They are either ascending, little or not modified terminal hyphae, or abruptly and more strongly modified terminal bodies particular to the hymenial region. Hyphidia that are hardly more than unmodified and unbranched or little branched hyphal ends may be called *haplo* hyphidia; strongly branched types, are called *dendro-* and *dicho-*hyphidia, the latter typical of *Vararia*, *Parapterulicium*, *Lachnocladium*. A remarkable type is that of the bottle-brush hyphidia (*acantho* hyphidia) so conspicuous in *Aleurodiscus*. In this connection it should be recalled that the (moniliform, torulose, or beaded) pseudophyses in the strict, original sense have appeared to be gloeocystidia and, hence, must be kept dissociated from the true hyphidia (cf. Lemke, 1964: 218).<sup>19</sup>

In rapidly thickening hymenia, hyphae can be seen that penetrate between the collapsing and mature basidia: they develop basidiferous branches and others that will branch again, and so on. Although these hyphae resemble hyphidia, they are in reality 'generative hyphae' producing basidia rather than typical 'hyphidia'.

Cystidia may be divided into classes according to various sets of characters, e.g. shape (club-shaped, fusiform, utriform, &c.); thickness of the walls (*lepto-*cystidia with thin walls; *lampro* cystidia with thick, glassy, often breakable walls); contents (oily: *gloeocystidia*), and so on.

It must be understood that true hymenial cystidia may closely simulate tramal cystidia (see below) if they become buried below the functioning (outside) layer of the hymenium. This is the case in species having a strongly thickening hymenium (see p. 210); cystidia formed with the basidia (hymenial cystidia) in thickening hymenia become engulfed by the continuously increasing hymenium. They may either be perishable and collapse and disintegrate like the exhausted basidia if they are and remain thin-walled; or they may continue their development and, for instance, produce a thick, glassy, and often crystal-encrusted wall. In this latter case the oldest cystidia (originally contemporaneous with the first basidia), which are closest to the trama, mark the original level of the hymenial basis (e.g. *lampro-*cystidia of *Peniophora* s. str. which are the true and original metuloids). It has also

<sup>19</sup> When introducing the term 'hyphidia' I did not expressly exclude the pseudophyses, but this is no valid reason completely to reject the term 'hyphidia' as well as such compounds as *dendro-* and *acantho*hyphidia. Compare: "It should be pointed out that hyphidia, as I propose to apply that term, is to be restricted to hyphal elements, and not to include basidia and their derivatives [viz. hymenial cystidia], although intermediates do occur" (Donk, 1956b: 3). This becomes more precise when it is amended thus, '... not to include basidia and their derivatives, and gloeocystidia in general...'

been observed that in some species, hymenial gloeocystidia that become engulfed may elongate and keep pace with the increase of the hymenium. Fine illustrations showing this situation were published by Corner (1950: fs. 36, 141) for a species of *Lachnocladium* and one of *Clavulina*.

It has to be kept in mind that an old, strongly thickening hymenium consists of two strata, (i) the actual, active, hymenium which is superficial and may be comparatively thin, and (ii) the so-called subhymenium which may be many times thicker than the actual hymenium. As stated, the oldest lamprocystidia in *Peniophora* rest on the bottom of this subhymenium (that is, on the surface of the hymenophoral trama). This situation reminds one very much of that in many agarics for which the term lamprocystidia was introduced [e.g. *Pluteus cervinus* (Batsch per Fr.) Kummer, *Hohenbuehelia* S. Schulz, *Geopetalum* Pat., *Inocybe* (Fr.) Fr.]. There is as yet one unanswered question in this connection: Are these lamprocystidia always formed contemporaneously with the very first basidia? or (what seems more likely) do at least the older ones belong to the first elements of the subhymenium itself before the latter produces the hymenium? If one wants to restrict the adjective 'hymenial' to those cystidia that are produced simultaneously with the basidia, it might be useful eventually once more to separate the lamprocystidia from the metuloids, but too little is known at present about the true situation in many species to draw a clear distinction.

The term 'basidioles' has been used in three different senses. First, it has been applied to the young organs that may develop into either the typical basidia or into sterile cells closely resembling basidia; secondly, to only the latter category; and thirdly, to what other authors would call cystidioles. If the abortive basidia are more strongly developed than the fertile basidia they are often called cystidioles, but I can see no reason for not including the cystidioles with the leptocystidia and I incline to treat the sterile basidioles accordingly. Romagnesi (1944: 13) wanted to exclude both the sterile basidioles and the pavement cells of *Coprinus* (which he called pseudoparaphyses) from the cystidia. This seems inadvisable. The pavement cells (for which I suggest the term 'brachycystidia') are not found either among the Aphyllophorales or among most of the Agaricales. It is thus possible to find more than one kind of hymenial cystidium in the same hymenium.

The tramal cystidia form a very diverse group. They must not be confused with the deeply situated hymenial cystidia left behind by the thickening hymenium (see above). It seems reasonable to divide the tramal cystidia into three groups based on the hyphal systems from which they originate—the vascular and gloeocystidial hyphae; the skeletal hyphae; and the generative hyphae.

Cystidia which originate from clearly differentiated tramal gloeocystidial hyphae have been called pseudocystidia (Romagnesi, 1944: 14; Singer, 1962: 41). When Romagnesi introduced this term, he did so in connection with a discussion on the cystidia of the agarics only, and in that group the only hyphal system contributing truly tramal cystidia were the gloeocystidial hyphae. Had he also taken into consideration the Aphyllophorales, he might well have made the term more inclusive

by also calling the terminations of the skeletal hyphae in the hymenium pseudocystidia. This is what some authors are actually doing. If one accepts this extension of the term, 'pseudocystidia' become a very comprehensive term denoting tramal cystidia in general (whether or not inclusive of skeletal hyphidia). On the other hand some authors are restricting 'pseudocystidia' to 'gloeocystidia', but I can see no gain in replacing the latter, firmly established term particularly when it is used for both tramal and hymenial gloeocystidia.

The skeletal hyphae that bend or ascend toward the hymenium may terminate either in the subhymenium or in, or beyond, the hymenium. They may either form unmodified, or at least uninflated, ends or more or less strongly apically modified and more or less inflated ends: skeletocystidia. Sometimes (*Stereum sensu stricto*) the skeletocystidia may have the special contents of vascular hyphae.

There remains briefly to be mentioned those tramal cystidia that originate from generative hyphae deep in the context below the subhymenium; they penetrate into the hymenial region and often protrude beyond it. They may be very diverse organs (e.g. tramal gloeocystidia); if they retain many hyphal characters but are still distinct in one way or another they are called hyphocystidia. The latter may be robust, septate (and even clamped: Cunningham's septocystidia), and protrude beyond the hymenium. In some cases these cystidia are reminiscent of skeletocystidia, parts of a system of skeletal hyphae in which the skeletals themselves are not formed (*Hyphodontia* spp.). Occasionally noteworthy tramal elements do not establish any connections with the hymenial region (e.g. stephanocysts).

The gloeocystidial hyphae and gloeocystidia in a strict sense are represented among the Aphyllophorales by at least two modifications. Of one of these the contents turn bluish grey to blackish, at least in part, in contact with sulfovanillin. This reaction was first discovered for the Russulaceae, later on it was established for *Lentinellus* and *Auriscalpium* (viz. for the group now called Auriscalpiaceae). Romagnesi and Boidin (1951b; 1958b: 261) and still more recently Lemke (1964) encountered the same reaction among the Corticiaceae where it could be established for certain species of *Gloeocystidiellum*, all species tested of *Peniophora sensu stricto*, and *Scytinostroma portentosum* (Berk. & C. apud Berk.) Donk, as well as for most species of *Aleurodiscus*. In investigating various Aphyllophorales, Boidin preferred sulphuric-benzaldehyde instead of sulfovanillin. The specimens tested should preferably be fresh material or at least recently and well dried. At first sight one would conclude that the positive sulpho-aldehyde reaction is coupled with amyloid spores, but the correlation is very incomplete because *Peniophora* has non-amyloid spores and also many species possessing gloeocystidia as well as amyloid spores react negatively with sulfovanillin. The gloeocystidia reacting positively with sulpho-aldehydes have been called macrocystidia by Romagnesi (1944: 15). They are "characterized by a chemical feature, viz. the discoloration with acid-aldehyde solutions, and the weak absorption of cresyl blue

by its contents" (Singer, 1962: 41). The use of this term, even for the Russulaceae, is of doubtful value. Kühner & Romagnesi (1953) dropped the term altogether and it has not been taken up for the positively reacting species of the Corticiaceae by Boidin.<sup>20</sup> Moreover, the continued use of 'macrocystidia' for gloeocystidia merely because they are sulpho-aldehyde positive (darkening) is confusing also for etymological reasons, since they are not longer (or bigger) than the negatively reacting gloeocystidia. Lemke has shown that the moniliform sterile bodies often called pseudophyses (best known for several species of *Aleurodiscus*) are really gloeocystidia (moniliform gloeocystidia): these may be either sulpho-aldehyde positive or negative, depending on the species.

The second category of gloeocystidia is the one to which the use of the term 'gloeocystidia' has been restricted by certain authors. These bodies are sulpho-aldehyde negative. However, since it has become clear that at least in certain groups (*Russula*, *Aleurodiscus*, *Gloeocystidiellum* sensu lato) the two categories are clearly homologous, I believe that the restricted use of the term 'gloeocystidia' is not to be favoured. Singer (1962: 41), who excludes the 'macrocystidia' from his concept of gloeocystidia, gave the following definition: "the gloeocystidia can be recognized by the oily contents that are often very distinct but sometimes absent, and, more clearly, by the deep blue color they assume when stained with cresyl blue (excepting the walls which remain a pale violet color). This metachromatism [?] is, on the basis of what is known at present, an infallible sign that the bodies showing it are part of the gloeo-system or more precisely gloeocystidia." This definition is clearly based in the first place on what is known of the agarics. It is as yet not possible unconditionally to extend Singer's definition to the Aphyllophorales because too few details about the Cresyl Blue reaction in that group are known, but it is certainly worth while to keep it in mind.

Where, in this paper, vascular hyphae are mentioned this indicates either that their exact nature still needs clarification, or that they are different from the two types of gloeocystidia discussed above. Gloeocystidia are usually more or less inflated, often ventricose or even vesicular bodies clearly differentiated from the hyphae from which they originate not only in their contents but also in diameter and shape. In many species they may originate almost anywhere in the fruitbody (tramal and hymenial gloeocystidia). They may also be hypha-like, but if so those penetrating into the hymenium usually have 'gloeocystidia-like' terminations; the hypha-like portions are referred to as gloeocystidial hyphae (Singer's gloeovessels).

*S e t a e* is a term I reserve for certain organs typical of the Hymenochaetaceae. Usually they are stiff, simple, ventricose-pointed to fusiform, gradually tapering, with sharp-pointed apex (which may be hooked, uncinata), thick, brown (rarely

<sup>20</sup> It is worth while to point out that Singer (1962: 756) does not make the macrocystidia an absolute feature of the Russulaceae: "macrocystidia . . . commonly present, but in some species replaced by another type of pseudocystidia: gloeocystidia."

dark-reddish), smooth wall (perhaps slightly encrusted apically where the wall is thinnest), and turn much darker in KOH solution (h a p l o setae). They are usually formed in, or at least in connection with, the hymenium (and hence become secondarily embedded when there is a layered or strongly thickening hymenium). Occasionally they will be found elsewhere, on surfaces, like the surface of the cap for example, and then may be irregularly branched ('Anker-zellen'). Besides the embedded 'hymenial' setae, much bigger and often very long ones may be found embedded in the context (m a c r o setae). In a few small genera (*Asterostroma*, *Asterodon*) the setae occur throughout the context of the fruitbody as star-shaped bodies with several radiating branches (stellate setae or a s t e r o setae).

There are other organs that have been called setae, but to my knowledge there is no instance outside the Hymenochaetaeaceae that would qualify as typical setae. The organs called setae in *Boletochaete* Sing., some species of *Marasmius* Fr., and a few other Agaricales are better designated as setiform cystidia, perhaps they would even qualify simply as lamprocystidia.

M a r g i n a l h a i r s (the "poils marginaux" of Romagnesi 1944, which see for a very penetrating discussion in which they are differentiated from cystidia) do not play an important role among the Aphyllophorales. Where they are noteworthy they are almost certainly indicative of the agaric nature of the fruitbody, as in *Dictyopanus* Pat. and *Favolaschia* (Pat.) Pat. apud Pat. & Lagerh. Marginal hairs in the form of growing hyphal tips make up the sterile edges of gills or dissepiments of tubes in the Aphyllophorales. The axial, only somewhat differentiated, hyphae forming the sterile tips of teeth are homologous with 'marginal' hairs.

Classifying and naming the innumerable types of sterile organs currently called cystidia is no easy task and the terminology connected with them is chaotic. The above outline has tried to keep to rational bases for arranging them in groups and to preserve the terms most currently in use where this could be done without retaining highly ambiguous or confusing terms. One of the main factors detracting from the clarity of the scheme is that any one kind may vary enormously in itself and hence must be judged from average features. To mention an example: certain skeletocystidia (specialized, inflated terminations of skeletal hyphae) are usually quite typical and the hyphae that they terminate can often be followed far down into the trama. However, since skeletal hyphae may originate almost anywhere from the generative hyphae, some skeletals are likely also to originate quite near to, or even occasionally in, the hymenium. In such cases the skeletals may be reduced to the modified top and thus coincide with skeletocystidia or may even be strictly hymenial in certain individual cystidia. The hymenium is a morphogenetic field that tends to influence any organ that comes into contact with it. This is also shown in certain species of *Aleurodiscus* with bottle-brush hyphidia; when the basidia are formed one may encounter all intermediate stages between typical hyphidia, gloecocystidia, and basidia, even basidia with a ring of excrescences that are typical of the bottle-brush hyphidia round their middle [*Aleurodiscus oakesii* (Berk. & C. apud Berk.) Pat.].



**HYPHAL CONSTRUCTION AND HYPHAL SYSTEMS.**—A new approach to a better understanding of the Aphyllophorales fruitbody was inaugurated by Corner (1932a, 1932b, 1932c) when he published his first, now classical, studies on the hyphal construction of some species of polypores. He was the first person to study more than thin sections and stressed that to understand the more complex tissues they must be teased out with fine needles under a dissecting microscope to disentangle the hyphae. This kind of work requires considerable skill and is often time consuming which may account for the relatively few carefully worked out analyses of more intricately built fruitbodies which have been published, although it is now generally believed, however, that a proper understanding of the hyphal construction is essential to the elucidation of the taxonomy of the polypores and other groups of Aphyllophorales. For concise introductions, see Corner (1953) and Teixeira (1956; 1962).

What follows is merely a catalogue of terms with brief explanations and a few closing remarks.

In the trimitic fruit-body three systems of hyphae (also called hyphal series) are encountered. Basically there are the generative hyphae and from these the skeletal hyphae (skeletals) and the binding hyphae arise. In trimitic context, typical generative hyphae are thin-walled, septate; they usually have clamps. They have often more or less deteriorated in matured fruitbodies and if so they should be looked for in younger tissues such as the growing margins of the cap. Typical skeletals are unbranched, narrow, aseptate (but may show one to several secondary septa formed in their still growing terminal portion). Binding hyphae are much-branched, narrow, rarely septate, thick-walled, and of very intricate and limited growth; their main function appears to be to weave the skeletals together. While the skeletals originate in the growing margins of the fruitbody, the binding hyphae do not participate in that region and may be formed at a comparatively late stage of development of the fruitbody.

If only two of the above mentioned systems of hyphae are present the fruitbody is called dimitic. Here, two main types are distinguished (a) generative hyphae combined with skeletals, and (b) generative hyphae combined with binding hyphae. In the latter case the generative hyphae often show more or less thicker-walled intercalary segments from which the binding hyphae arise.

"Finally, many [species] have no distinction into skeletal and binding hyphae: all the hyphae of the fruit-body are identical in manner of growth and branching, so that they must be called monomitic. . . . The monomitic is the ordinary construction, but it is often difficult to assess because it has the potentialities of the others and grades into them. The radiating or longitudinal hyphae of the flesh, for instance, may be wider and less branched than the hyphae which weave between them, thus suggesting an incipient trimitic state. . . . Mere thickening of the hyphal wall is no proof of the presence of skeletal or binding hyphae."—Corner (1953: 153, 156).

The construction of the context of the cap may be different from that of the

hymenophore, and binding hyphae may be formed at a late stage of development. In *Ganoderma* it has been shown that skeletals are often branched towards their ends and participate in the function of the binding hyphae. These few examples of 'irregularities' may suffice to demonstrate that extreme care is needed in reaching conclusions about hyphal construction.

The presence of skeletals in dimittic context should be treated with great care as a feature characterizing taxa of a higher rank than genus or even species. Corner & Thind (1961) admit a number of species with skeletals in the genus *Ramaria* in which most species have a typically monomittic context. In *Pterulicium* (see also p. 207) the corticioid fertile patch is monomittic, but the pteruloid fruitbody arising from it is dimittic. (These two types of fruitbody may occasionally occur separately.) Skeletals appear to have 'independently arisen' in several of the families recognized in the present paper. The same seems true of the binding hyphae: those of *Laetiporus* are very different from those of *Polyporus sensu stricto* and hardly indicative of close relationship.

Cunningham (1947) gave a wider circumscription of the skeletals and divided them into a "long" and a "bovista" type. His long-type often represents the true skeletals; however, his bovista-type (so called because these hyphae resemble capillitium of the genus *Bovista*) should not be identified with skeletals but with binding hyphae as Corner (1953: 153) pointed out. Overholts (1953: 17-18), who like most authors studied the hyphae only superficially, often mentioned 'hyphal complexes': these, too, are the binding hyphae. He completely ignored the existence of Corner's studies.

As Corner has remarked, there clearly exists a reluctance in 'anatomizing' the fruitbody and the number of species (except many 'resupinates', of simple structure) really thoroughly known as to their hyphal structure is still low. Apart from Corner's own work in this field (1932a, 1932b, 1932c, 1953), excellent studies have been published for example by Teixeira (1956, 1958, 1961), Hansen (1958), and Maas Geesteranus (1962, 1963).

Generative hyphae may undergo very diverse modifications, for instance, in fleshy context, a good number (if not all) of them may become inflated. "Inflation means that the cells of the hyphae begin to enlarge behind the growing-point, and become wider and much longer, thus hastening the apparent growth, or increase in size, of the fruitbody. It is the usual method of growth in fleshy fungi" (Corner, 1950: 14). These inflated hyphae are the same as those which have been called fundamental hyphae (Kühner, 1926: 44 f. 12). Inflated hyphae usually remain thin-walled, but both in the Agaricales and the Aphyllophorales they may become firm- to rather thick-walled. They may also, on inflation, form secondary (false) septa "which as broad thin membranes, joint them into shorter sections which, in their turn, enlarge and become septate" (Corner, 1950: 14 f. 10). These secondarily septate inflated hyphae are typical of *Clavaria sensu stricto* and *Pseudocraterellus*, to mention the most important examples.

When inflation of generative hyphae has occurred in fleshy context, the hyphae

(if any) that did not inflate (and do not become otherwise modified) may be called the connective hyphae (Kühner, 1926: 44 f. 12), or if they develop into branched systems, interweaving hyphae (Corner, 1950: f. 8).

Among the Aphyllophorales a monomitic context with inflating hyphae has been described and depicted in detail for many Clavariaceae (Corner, 1950) and for fleshy hydnums like *Hydnum repandum* L. per Fr. (Maas Geesteranus, 1963: 449).

Many other modifications of generative hyphae are known. Since few of these have been used to help characterize families of Aphyllophorales this is hardly the place to discuss them *in extenso*. However, brief mention should be made of gelatinous tissue, in which the hyphal walls become more or less excessively gelatinized; and of generative hyphae that become strongly thick-walled. The latter, which I propose to call the sclerified generative hyphae, must not be confused with the skeletals. They differ in being septate and often also clamped. Sometimes they strongly resemble skeletals in form being long, straight, and of equal diameter throughout their length; these sclerified hyphae perhaps merit the term pseudo-skeletals. In certain species the sclerified generative hyphae are the only thick-walled hyphae in the context of the fruitbody where they may exist together with thin-walled generative hyphae. In other genera (*Mycoleptodonoides*) the hyphae of the monomitic context may become all more or less strongly sclerified (Maas Geesteranus, 1962: 392 fs. 32-34 for *M. vassiljevae* Nikol.). Sclerified generative hyphae may also be intermediate between the thin-walled generative hyphae (in space or time) and the skeletals (which then may be relatively short). Reid (1956: 637 f. 10) described the hyphal structure of *Irpex vellereus* Berk. & Br. as "apparently monomitic, consisting of thick-walled, freely branched . . . hyphae, . . . lacking clamps at the septa, and with narrow lumina. Cystidia very abundant, arising in the context of the needles as terminal modifications of ordinary thick-walled hyphae, curving into the hymenium . . ." Apparently we are dealing here with a context consisting of sclerified generative hyphae that give rise to 'skeletals', varying from short to rather long (25-127  $\mu$ ) and presumably comparable to the cystidia in the vertical subhymenial tissue of *Columnocystis* (cf. Boidin, 1958: 215). In this genus the cystidia are formed terminally on ascending generative hyphae rather than being terminal portions of the skeletal hyphae present in the context of the fruitbody. Although in these cases the cystidia do not issue from a system of skeletal hyphae, one is nevertheless tempted to refer to them as skeletocystidia (cf. p. 232).

In many fruitbodies additional kinds of hyphae may be encountered: vascular and gloecystidial. If these are to be regarded as hyphal systems *sui generis*, like the skeletal and the binding hyphae, rather than as modified generative hyphae, they should not be taken into account in defining the hyphal construction of the context. They are recognized by their specialized cytoplasmic contents as well as by their thin, or relatively thin, walls and the lack of septa. It has become customary to regard them as conducting vessels (ducts). However, there is no reason to accept that they are really comparable to the conducting elements of the phanerogams, serving as conductors of nutritive substances. This function is exercised by the

ordinary generative hyphae and by the capillary cavities between the hyphae. It is likely that the various specialized contents are the result of different processes of internal excretion or are partially destined to be rejected from the cells (cf. Lohwag, 1941: 372-408). In view of this, these depository and secreting vessels may be called vascular only because morphologically they normally lack the typical primary septa of the undifferentiated generative hyphae: they must not functionally be compared with the vascular ducts of the phanerogams. It may be recalled in this connection that the true conducting hyphae often do not all look the same; the variation depends on their age or on gradually acquired supplementary functions. The depositing of substances into thickened hyphal walls (like those of the skeletal hyphae) is now often regarded as an internal rejection of substances from the cell contents. A further discussion of the gloeocystidial hyphae will be found elsewhere (p. 232).

**CLAMP-CONNECTIONS.**—The value of clamps as a taxonomic feature differs from group to group, and may even appear erratic within rather small taxa of lower rank such as species. It is now generally believed that the presence of clamps is associated with 'diploid' or synkaryonic mycelia, but the reverse is not true: not only do haploid mycelia lack clamps, many 'diploid' mycelia do not form them either, depending on the taxon. Repeated isolation of 'monokaryonic' mycelia of various species from decays in trees suggests that such mycelia are common in nature. Maas Geesteranus (1962: 398) found that *Mycorrhaphium pusillum* (Brot. per Fr.) Maas G. differed from *Steccherinum adustum* Banker in hardly anything else but the lack of clamps in the former and their presence in the latter. The two could be conceived as vicarious subtaxa of the same species, the former occurring in Europe, the latter in North America. It follows that the absence of clamps in a fruitbody may be due, theoretically, to one of at least three factors: (i) the fruitbody being formed by a haploid mycelium, (ii) the species lacking clamps altogether, or (iii) the species in 'diploid' condition occurring in two 'forms', one clampless, one clamp-bearing.

Moreover, the pattern of distribution of clamps within the fruitbody often shows considerable variation, depending on the taxon. Usually they will be found at all septa, but if distal septa are formed they will be absent from these. Corner (1950: 40) distinguished a group of *Clavaria* species on account of the basidia having a wide loop-like clamp at the base, while no clamps are to be found elsewhere on the hyphae. In *Botryobasidium angustisporum* Boid. the basal hyphae have clamps at most septa while the basidia-bearing ones are generally without clamps, but in some collections the hymenial branches are found to bear clamps at all septa (Eriksson, 1958: 48). (*Botryobasidium* also embraces species lacking clamps altogether, and still others with clamps at all septa.) Depending on the species, the hyphae of the mycelial mat in cultures may lack septa in the advancing zone while they are clamped elsewhere.

Usually there is only one clamp per septum, but in a number of cases two opposite

clamps or a whorl of them is formed. In *Donkia pulcherrima* (Berk. & C.) Pilát the hyphae from the growing margin of the fruitbody lack clamps which however start to appear at some distance from the margin, at first one per septum, then two on opposite sides of a septum, and finally, in whorls of three to four on the widest hyphae (Maas Geesteranus, 1962: 384).

These few considerations may suffice to indicate that clamps must be treated with great care as a taxonomic feature. Yet there are groups of considerable size (as to their number of species) that seem invariably to form clamps at the primary septa, for instance the typically trimitic Polyporaceae. On the other hand the constant absence of clamps is a perhaps absolute feature in the Septobasidiales (over 200 species) and in the Hymenochaetaceae, q.v.

CHEMICAL FEATURES.—One of the first chemical tests that attained the reputation of being of high taxonomic standing in the systematics of the Hymenomycetes was the amyloidity or inamyloidity of the spore-wall. It also proved to be sometimes a most erratic one. Amyloid spore-walls may be particular to whole families (Agaricales-Russulaceae as to ornamentation; Hericiaceae), to certain genera, or to certain species, but in other groups it is totally unreliable above the specific level. Thus in *Mucronella* (even when taken in a much restricted and apparently homogeneous sense), *Scytinostroma*, *Aleurodiscus* (even when restricted) it breaks down as a generic character, some of the species of these groups having amyloid, and others, non-amyloid spore-walls. Among the Agaricales its importance has often been overrated at the generic level. Great caution has to be exercised to find out its real taxonomic importance within any given taxon. Species with amyloid spores are relatively few if compared with those having non-amyloid spores.

The use of Cotton Blue (in lactic acid) has attracted the attention of taxonomists studying the Aphyllophorales since Nannfeldt & Eriksson (1953) showed it to be a very helpful character in delimiting the Coniophoraceae. They found that in the double-walled spores of this family the inner wall strongly takes up Cotton Blue (and Congo Red). In the smaller-spored members of this family the spore-wall also strongly absorbs Cotton Blue, but it has not yet been possible clearly to distinguish between the two walls, which are tentatively supposed to be really present.

Shortly afterwards, Eriksson (1954) also discovered that the spore-wall (or at least its exterior layer and its ornamentation) in *Ramaricium*, *Kavinia*, and *Ramaria* became strongly stained by Cotton Blue too, while the same was subsequently found in other genera considered related (*Gomphus*, *Beenakia*). This feature was, in all these genera, correlated with other spore characters (more or less elongated shape, brown colour, with only few exceptions) and confirmed the existing surmise that most of them belonged to one family. The family has since been called Gomphaceae and now includes them all.

Quite recently Kotlaba & Pouzar (1963) proposed the terms cyanophily

and acyanophily to indicate positive and negative staining with Cotton Blue. This is in line with previous uses of the term in cytology which refers to nuclei that readily take a deep blue stain as cyanophilous. The two authors also considerably extended the number of species tested and confirmed that the layers of the spore-wall or different stages of age of spores may be differently affected. Moreover, it seems as if cyanophily of the spore-wall is correlated with dextrinoidity, at least in the Hymenomycetes, although the latter reaction proved to be more variable and less reliable than the blue stain. The dextrinoid (formerly, pseudoamyloid) spore-wall is one that turns more or less reddish- to rusty-brown in Melzer's reagent.

Kotlaba & Pouzar also found that cyanophily may be positive or negative within certain taxa now considered tolerably natural (*Phellinus*, *Inonotus*). As in the case of amyloidity, the taxonomist is again confronted with a feature of different reliability in different groups now considered natural.

For a note on some chemical characters of gloecystidia see page 232. In general the metachromatism of cell-walls with Cresyl Blue will no doubt acquire considerable importance in the future also in connection with the taxonomy of the Aphyllophorales, although perhaps not at the family level.

I have tentatively entered into the family character of the Gomphaceae the green-positive reaction of the fruitbody with a 10% watery solution of ferric sulphate,  $\text{Fe}_2(\text{SO}_4)_3$ . Melzer & Zvara (1928: 136) used ferrous sulphate,  $\text{FeSO}_4$ , in connection with *Russula*, where they found that it could provoke two positive reactions, (i) "plus ou moins rosé" (that is, pinkish grey, orange pink, or even pale yellowish grey) and (ii) green. Doty (1948: 174) used it in his studies on the clavariaceous fungi. The solution is applied to the surface in drops and when there is a positive reaction the wetted spot turns a dark (often almost blackish) olive-green, blue-green or green. Usually the reaction takes place within 30 seconds, but occasionally a longer time is required. The best results are obtained with fresh material, but well-dried herbarium material will usually react sufficiently if it is treated with a freshly made ferric sulphate solution. (However, my experience is still restricted.) It is necessary to obtain much more information from various other families before an opinion can be formed about the real value of this test. *Clavariadelphus* (at least its original species) reacts positively but I have left it in the Clavariaceae pending further studies.<sup>21</sup>

The colour of the context in several species belonging to various genera of Thelephoraceae (emended) as well as colour reactions in alkali solutions (appearance of a greenish colour) are indications that they have also a chemical relationship.

<sup>21</sup> The genus *Donkella* Doty (1950: 14) was based on *Clavaria corniculata* Schaeff. per Fr.; it was published with a generic description containing the remark "producing pigments which form dark or green colors with certain iron salts". Leathers (unpublished thesis) keyed its only species among the species not turning green with ferric sulphate. I find that dried specimens darken but hardly turn green in ferrous sulphate, and turn somewhat olive-greenish in ferric sulphate. Fresh material is needed before a definite conclusion can be drawn. I am not prepared to transfer the *Clavaria corniculata* group to the Gomphaceae.

This has been supported by the researches of Zopf and of Kögler & al. (1930) and of others, who extracted a substance from the fruitbody that has been called the telephoric acid. It has been demonstrated to be present in species of *Thelephora*, *Hydnellum*, and was also found by Sawada (cited by Imazeki, 1953) to occur in *Polyozellus*. Telephoric acid has been found also in species of *Lobaria* (Lichens). The chemical structure was established through synthesis by Gripenberg (1960). The occurrence of this substance throughout a single family of the Hymenomycetes is significant.<sup>22</sup>

The substance so characteristic of the Hymenochaetaceae deserves to be chemically more extensively analysed. Sections in water show that the hyphal walls contain a yellowish-brown substance that turns permanently dark brown in alkali solutions. (Sometimes sections first pass rapidly through a reddish discolouration.) This may be known as the xanthochroic reaction, after the denomination Xanthochroic series given to the group.

Some knowledge of the most important liquids for microscopical observation and of the much used micro- and macrochemical colour reactions is indispensable for the study of fungi to-day. The interested reader is referred to the following introductions: "Les réactions chimiques" (Josserand, 1952: 134-140), "Conseils techniques aux débutants. Principaux réactifs utilisés en mycologie systématique" (Kühner & Romagnesi, 1953: 487-493), "Stains, macrochemical color reactions and chemical analysis" (Singer, 1962: 77-97).

## II. SPECIAL PART

### APHYLLOPHORALES Rea<sup>23</sup>

Tulasnellinae Juel in Jb. wiss. bot. 32: 374. 1898; Herter in Krypt.-Fl. Brandenb. 6: 68. 1910 ("Tulasnellales"; "Reihe" as subdivision of "Ordnung"). — Type: *Tulasnella* Juel.

[Famille des Aphyllophoracés Pat., Essai tax. Hym. 34, 37. 1900. — Lectotype: *Polyporus* "Fr." sensu Pat. (lectotype: *Polyporus ovinus* (Schaeff.) per Fr.) = *Albatrellus* S. F. Gray]; → Aphyllophorales Rea; → Aphyllophoraceae Rea; Donk.

[Tribu des Porohydnes Pat., Essai tax. Hym. 39, 51. 1900; Bourd. & G., Hym. France 79, 143. "1927" [1928] (→ Porohydneae Talbot). — Lectotype: *Polyporus* "Fr." sensu Pat. (lectotype: *Polyporus ovinus* (Schaeff.) per Fr.) = *Albatrellus* S. F. Gray]; → Porohydneae Rea; → Porohydneae R. Heim.

[Protohymeniés Maire in Bull. Soc. mycol. France 18 (Suppl.): 80. 1902 ([ordo]). — Monotype: *Vuilleminia* Maire]; → Protohymeniales Lotsy.

[Cantharellinées Maire in Bull. Soc. mycol. France 18 (Suppl.): 83. 1902 ([subordo]). — Type: *Cantharellus* Adans. per Fr.]; → Cantharellinae Lotsy.

<sup>22</sup> Hegnauer (1962: 128) stated that it was also found in "*Polystictus*". I have been unable to find out either to what species this refers or from which source this example was taken.

<sup>23</sup> The nomenclature of taxa above the rank of family is not affected by the principles of priority and typification. Nevertheless I have mentioned and selected types (genera) because this is indispensable for relating the names to definite groups.

The synonyms pertaining to Hymenolichens are listed in connection with the Dictyonemataceae (see p. 298).

[Polyporinées Maire in Bull. Soc. mycol. France **18** (Suppl.): 99. 1902 ([subordo]). — Type: *Polyporus* [Mich.] Fr. per Fr.]; → Polyporineae Lotsy.

Protohymeniales Lotsy, Vortr. bot. Stammesgesch. **1**: 686. 1907 ≡ 'Protohymeniés Maire'.  
 Cantharellineae Lotsy, Vortr. bot. Stammesgesch. **1**: 684 ("Cantharellineen"), 686. 1907;  
 Rea, Brit. Bas. **5**, 540. 1922 (≡ 'Tribu des Cantharellés Pat.', see p. 248); ≡ 'Cantharellinées Maire'.

Polyporineae Lotsy, Vortr. bot. Stammesgesch. **1**: 686, 695. 1907; Herter in Krypt.-Fl. Brandenb. **6**: 68. 1910 ("Polyporales"; "Reihe" as subdivision of "Ordnung"); Bond. & Sing. in Ann. mycol. **39**: 44, 45. 1941 (lacking Latin description and reference); ≡ 'Polyporinées Maire'.

Aphylloraceae Rea in Trans. Brit. mycol. Soc. **3**: 63. 1909 (incidental mention) ≡ 'Famille des Aphylloracés Pat.'

Theleporineae Herter in Krypt.-Fl. Brandenb. **6**: 69. 1910 ("Theleporales"; "Reihe" as subdivision of "Ordnung"). — Type: *Thelephora* Ehrh. ex Fr.

Clavariineae Herter in Krypt.-Fl. Brandenb. **6**: 143. 1910 ("Clavariales"; "Reihe" as subdivision of "Ordnung"); Rea, Brit. Bas. **10**, 16, 704. 1922 (≡ 'Tribu des Clavariés Pat.', see p. 250). — Type: *Clavaria* "Vaillant" ≡ *Clavaria* [Vaill.] Fr.

Hydriaceae Herter in Krypt.-Fl. Brandenb. **6**: 168. 1910 ("Hydriales"; "Reihe" as subdivision of "Ordnung"). — Type: *Hydnum* "Linné" ≡ *Hydnum* L. per Fr.

Aphyllorales Rea, Brit. Bas. **1**, 10, 574. 1922 ≡ 'Famille des Aphylloracés Pat.'

Poro-hydriaceae Rea, Brit. Bas. **10**, 574. 1922 ≡ 'Tribu des Poro-hydriés Pat.'

Tulasnellales Rea, Brit. Bas. **2**, 19, 739. 1922. — Monotype: *Tulasnella* Juel.

Cantharellales Gäum., Vergl. Morph. Pilze 495. 1926. — Type: *Cantharellus* Adans. per Fr.

Polyporales Gäum., Vergl. Morph. Pilze 503. 1926. — Type: *Polyporus* [Mich.] Fr. per Fr.

Aphylloraceae Donk in Meded. Nederl. mycol. Ver. **18-20**: 125. 1931 ≡ 'Famille des Aphylloracés Pat.'

[Poro-hydriaceae R. Heim in Treb. Mus. Ci. nat. Barcelona **15**: 53. 1934 (nomen nudum); Talbot in Bothalia **6**: 5. 1951 (≡ 'Poro-hydriés Bourd. & G.'; lacking Latin description); ≡ 'Tribu des 'Poro-hydriés Pat.']

Phylacteriineae Bond. & Sing. in Ann. mycol. **39**: 44, 45. 1941 ≡ Phylacterioideae Donk (see p. 296).

Cyphellineae Bond. & Sing. in Ann. mycol. **39**: 44, 45. 1941 (nomen nudum); in Sovetsk. Bot. **1943** (1): 29-43. 1943 (lacking Latin description and reference). — Type: *Cyphella* Fr.

Corticineae Bond. & Sing. in Ann. mycol. **39**: 45. 1941 (nomen nudum); in Sovetsk. Bot. **1943** (1): 29-43. 1943 (lacking Latin description or reference). — Lectotype (not mentioned): *Corticium* Pers. per S. F. Gray.

Xanthochroales Corner, Monogr. Clav. **23**. 1950 (provisional name). — Lectotype: *Xanthochrous* Pat. [= *Coltricia* S. F. Gray].

Theleporales Corner, Monogr. Clav. **24**. 1950 (provisional alternative name) ≡ Theleporaceae Chev. (see p. 295).

Poriales Locq. in Bull. Jard. bot. Brux. **27**: 560, 561. 1957 ("Bondarzew"; with Latin description; lacking valid reference). — Holotype: "*Poria*" = "*Poria* (Fr.) Karst." sensu Bond., not *Poria* Pers. per S. F. Gray 1821.

An artificial order of holobasidioid Hymenomycetes, opposed to the Agaricales, forming distinct fruitbodies. Fruitbody developing centrifugally with one-sided hymenophore, or clavarioid with amphigenous hymenium, not developing within a universal veil, the hymenium not covered by a partial veil and exposed during the maturation of the basidiospores. Hymenophore smooth (hymenium may be folded), toothed, or tubulate, exceptionally, and then mostly imperfectly, lamellate. — Not included are the Brachybasidiales, Exobasidiales, and Dacrymycetales.

Saprobic, less commonly parasitic (quite exceptionally parasites in herbaceous living tissue).



The Aphyllophorales is essentially an artificial group that differs from the Exobasidiales and Brachybasidiales<sup>24</sup> in that its members are not internal parasites that produce their basidia in or on herbaceous portions of their host. If species of Aphyllophorales are internal parasites then they form distinct, external fruitbodies. In the typical Exobasidiales and Brachybasidiales true fruitbodies are lacking and the basidia are at most concentrated into bundles or layers. The few genera brought together in the Exobasidiales are perhaps not all really closely related. Some genera referred to this latter order (*Exobasidiellum* Donk, *Dicellomyces* L. Olive) are of doubtful systematic position and would perhaps not be out of place in the Aphyllophorales (artificial family Corticiaceae).

It is usually also easy to differentiate the Aphyllophorales from the Dacrymycetales, for instance by the basidia which do not combine the characters of being almost cylindrical (exceptionally urniform), stichic, two-spored, with rather stout to stout sterigmata. However, there are a few genera (*Clavulina*, *Clavulicium*, *Cerinomyces*) that have more or less similar basidia without being in other respects obviously dacrymycetaceous. *Cerinomyces* may be considered a border case and is perhaps a bridge between the Aphyllophorales and Dacrymycetales.

The separation from the Gasteromycetes is not difficult: in contrast to that order the Aphyllophorales produce their spores at the surface of the fruitbody: their ripening hymenium is exposed to the air. Moreover, their basidiospores are invariably ballistospores, with perhaps one exception, viz. *Digitatispora*, discussed in greater detail above (see p. 225).

Since the Aphyllophorales are holobasidious by definition one would not suspect any difficulties in drawing a sharp distinction between it and the phragmobasidious orders. Yet, here, too, a few exceptions are worth mentioning. Both the genera *Platyglœa* J. Schroet. = *Achroomyces* Bon. (Auriculariineae) and *Septobasidium* Pat. (Septobasidiales<sup>25</sup>), with auriculariaceous basidia, contain a few species in which the transverse septa are wanting and hence are 'holobasidious', with one apical sterigma.

Then there are the genera *Metabourdotia* L. Olive and *Tremellodendropsis* (Corner) D. A. Crawf. (Tremellineae). In both of these the basidia are more or less tremellaceous but not perfectly so, they vary more or less in the direction of the holobasidium. The second of these genera is clavarioid or, rather, more like a stalked 'Sterium'. The first is resupinate and recalls the 'tulasnelloid series' which is discussed

<sup>24</sup> **Brachybasidiales** Donk, *ordo nov.* — Basidiomycetes. In phanerogamarum foliis parasiticæ, per stomata erumpentes, supra stomata hymenia probasidialia semiglobosa formantes. Basidia maturitate constrictione in probasidium et metabasidium separata; metabasidium cylindricum, haud septatum, chasticum, sterigmatibus 2 apicalibus. — Typus: Brachybasidiaceae Gäum., Vergl. Morph. Pilze 487, 489. 1926 = *Brachybasidium* Gäum.

<sup>25</sup> **Septobasidiales** Couch *ex* Donk, *ordo nov.* — Septobasidiales Couch, Genus Septobasidium 65. 1938 (lacking Latin description). — Basidiomycetes, phragmobasidiis transverse septatis instructi, symbiontice cum Coccidiis conviventibus. — Typus: Septobasidiaceae Racib. in Bull. int. Acad. Sci. Cracovie (Sci. math. nat.) 3: 346, 359. 1909 = *Septobasidium* Pat.

above in connection with considerations on secondary basidiospores. However, it is not my intention to examine more fully on this occasion the tremellaceous basidia and its variations in the direction of the holobasidium.

Finally, it remains to pay attention to the demarcation between the Aphyllophorales and the Agaricales, the latter in a broadly conceived sense. I have found it impossible even faintly to suggest a formula for tentatively separating these two groups since the lack of gills, although typical of nearly all Aphyllophorales, is also to be found in an ever increasing proportion of the Agaricales. Moreover, one big group (Boletaceae) and various other minor ones now referred to the Agaricales possess a tubulate hymenophore, once the hallmark of the Polyporaceae (Aphyllophorales). A few examples: some of the agaric genera, like *Dictyopanus* Pat., *Mycenoporella* Overcem (*Filoboletus* P. Henn. sensu Sing.), and *Poromyцена* Overcem, have a tubulate hymenophore but in other respects are so evidently closely related to typical agarics [*Panellus* P. Karst. and *Mycena* (Pers. per Fr.) S. F. Gray] that they should be placed next to their agaric relatives. In some of the species the tubulate hymenophore is only a faintly disguised lamellate one, slightly modified by the radiating gills being tangentially connected by anastomoses. In other species, however, nothing remains of such a tendency and the hymenophore is typically tubulate as in most Polyporaceae.

As mentioned above, the complete lack of gills is not quite exceptional among the agarics. The hymenophore is then 'smooth', or in terms of the Friesian tradition, 'thelephoraceous'. In many cases (*Gloiocephala*) such agarics without or with underdeveloped gills are more or less easy to connect taxonomically with their nearest lamellate counterparts, but this is by no means always the case. Sometimes (*Phaeosolenia*, *Chromocyphella*) a combination of characters points more or less vaguely in the direction of certain genera without the connection being quite evident. The removal of genera or species with smooth hymenium from the Aphyllophorales to the Agaricales has not yet come to an end. The 'Cyphellaceae' particularly still contain several agaric elements not yet ready for removal because they are still insufficiently known or not yet packed into definable natural genera ready for transport. It may be that the Schizophyllaceae represent such an agaricaceous element among the Aphyllophorales, but no acceptable suggestion has been made about the group among the Agaricales to which this small family would be related. There would seem little objection however against placing it as a distinct family among the Agaricales until an acceptable taxonomic connection is suggested, rather than leaving it among the Aphyllophorales as is done below.

In the above cases various Agaricales were mentioned that deviated from their closest relatives by their hymenophore being either smooth ('thelephoraceous') or tubulate ('polyporaceous'). Quite recently the demarcation from the Aphyllophorales also broke down in connection with the 'hydneaceous' hymenophore. Maas Geesteranus (1963: 426) has united *Lentinellus* P. Karst. (with gills) with the genera *Auriscalpium* and *Gloiodon* (with teeth) into a single family, the Auriscalpiaceae.

The old genus *Cantharellus* long appeared intermediate between the 'Thelephorei' and the agarics, especially when it was still broadly conceived, inclusive of many species now referred to various genera of Agaricales: in it the hymenium with low radiating, flabellately branched folds seemed very gradually to pass into a frankly lamellate hymenophore with forked gills. At present the genus is commonly restricted to species with stichic basidia which do not occur among the agarics and most authors are now agreed that it belongs rather to the Aphyllophorales. The strong likeness between the fleshy, brightly coloured chanterelles and certain species of *Hygrophorus* Fr. is hardly more than another instance of convergence.

Patouillard (1900: 37, 122) considered the "Aphyllaphoracés" gymnocarpic and the "Agaricacés" hemiangiocarpic; the Gastromycetes he took to be truly angiocarpic. Moreover, he stated that in the agarics "la portion hyménifère est nettement délimitée dès le début et ne présente pas l'accroissement centrifuge que nous avons constaté chez les gymnocarpes." This point of view is an oversimplification of the situation. Even Patouillard himself included among the agarics gymnocarpic groups (for instance, his Tribu des Cantharellés), but it may well appear that after some shifting of the contents of the Aphyllophorales and Agaricales his hymenial criterion comes nearest to an acceptable brief formulation of the distinction between the two groups. For a more elaborate attempt at a circumscription of the Agaricales, see Singer (1962: 136-141).

This rapid survey of the difficulties of sharply distinguishing the Aphyllophorales from the Agaricales may suffice to demonstrate that at the moment at least the former must be conceived as artificially delimited. In my opinion, it will be gradually replaced by a series of more or less independent orders, this in contradistinction to the Agaricales which on the whole seems a reasonably homogeneous taxon perhaps consisting of only a few orders. Attention will be paid to the genera transferred to the Agaricales by mentioning them briefly under the several families of Aphyllophorales from which they were taken.

#### AURISCALPIACEAE Maas G.

Gloiodontoideae Donk in Meded. Nederl. mycol. Ver. 18-20: 190. 1931 ("Gloiodonoideae"). — Type: *Gloiodon* P. Karst.

Lentinellaceae Sing. in Ann. mycol. 41: 159. 1943 (nomen nudum). — Type: *Lentinellus* [P. Karst.].

Auriscalpieae Nikol. in Fl. Pl. crypt. URSS 6 (2): 199. 1961. — Holotype: *Auriscalpium* P. Karst.

Auriscalpiaceae Maas G. in Proc. Ned. Akad. Wet. (C) 66: 426. 1963. — Holotype: *Auriscalpium* S. F. Gray.

Fruitbody stalked and pileate, sessile, or appressed-reflexed (may rarely occur in completely appressed condition in *Gloiodon*); cap continuous or made up of a flattened system of branching strands, hirsute, becoming glabrous with age, or glabrous from the first; context usually tough, white or brownish, in section in the stalk toward the periphery, and in the pileus toward the upper surface (at least partially) bounded by a black-brown line, both in context of cap and of spines

and gills amyloid (rarely) or non-amyloid, dimitic with skeletal; hymenophore toothed or lamellate (gills lacerate-dentate).

Generative hyphae thin-walled, with clamped septa; skeletal thick-walled to almost solid, unbranched; gloecystidial hyphal system present, many hyphae terminating more or less as typical gloecystidia in the hymenium, darkening with sulpho-aldehyde solutions. Basidia clavate, 4-spored. Spores subglobose to ellipsoid, minute to small (2.5–8  $\mu$ ), colourless (white in a print); wall minutely echinulate, verruculose, or smooth, amyloid.

Lignicolous (or on fallen cones of conifers).

Genera.—

1. Hymenophore toothed.—*Auriscalpium* S. F. Gray, *Gloiodon* P. Karst. (fruitbody a flattened, branched system of strands embedded in a dense tomentum).
1. Hymenophore lamellate.—*Lentinellus* P. Karst.

When studying *Auriscalpium vulgare* S. F. Gray, Romagnesi (1953) drew attention to the fact that this hydneous fungus agreed remarkably well with the agaricaceous genus *Lentinellus* in some respects, viz. spore characters and chemical reactions of the gloecystidial hyphal system (see p. 232). Maas Geesteranus (1963: 429) showed that in many other respects, too, especially of hyphal structure, the resemblance was great and he felt bound to unite *Lentinellus* with the hydneous genera *Auriscalpium* and *Gloiodon* into a separate family. Since the distinction between Aphyllophorales and Agaricales is in the main artificial, one could express the situation by stating that he either transferred two hydneous genera to the Agaricales or one agaricaceous genus to the Aphyllophorales: he carefully did not commit himself in this regard.

This instance of blurring of the demarcation between the two orders is of great interest, because it is a still isolated one in which a genus with true gills could be confidently aligned with ostensibly typically non-agaricaceous genera with perfectly toothed hymenophore. These latter genera were traditionally classed in the Hydneae, now a strongly reduced family.

To be compared with the Hericiaceae, q.v.

#### BANKERACEAE Donk

Bankeraceae Donk in *Persoonia* 1: 405, 1961. — Holotype: *Bankera* Coker & Beers ex Pouz.

Fruitbody stalked and pileate, invariably and strongly smelling of Fenugreek (at least when dried); context fleshy or tough (i.e. more or less leathery to corky or even woody), white or coloured (may be black), monomitic; stalk typically central or eccentric, may be lateral; hymenophore toothed, the spines pointed, whitish or becoming greyish, but not brownish by deposited spores.

Hyphae of context thin- to slightly firm-walled, lacking clamps, inflating in fleshy portions; vascular hyphae may be present. Cystidia (inclusive of gloecystidia) lacking. Basidia clavate, chiasitic (known for 2 species), 2–4-spored. Spores globose, of even general outline, small (3–5  $\mu$  diam.), colourless (white in a print); wall shortly echinulate, non-amyloid.

Terrestrial and humicolous.

Genera.—*Bankera* Coker & Beers ex Pouz. (context fleshy), *Phellodon* P. Karst. (context toughish or tough to woody, zoned).

This small group was removed from the Thelephoraceae in its current radically emended sense. It had been included because of the strong resemblance to other genera with toothed hymenophore, *Bankera* recalling *Sarcodon*, and *Phellodon*, *Hydnellum*. The resemblance is so strong that several modern authors still combine the pairs into only two genera, *Sarcodon* and *Hydnellum*. However, the Bankeraceae lack precisely the two leading characters of the Thelephoraceae, viz. the uneven outline of the spores (which rarely may be almost even in some species of *Tomentella*) and their colour (which may be faint in *Boletopsis*, but hardly completely absent; "white, or pale tan or yellowish" in *Scytinopogon*, according to Corner, 1950: 647). It is for these reasons that I prefer to uphold the thesis that the Bankeraceae are an example of extreme convergence with certain genera of the Thelephoraceae, but not really closely related. It would be interesting to look into the presence or absence of thelephoric acid (cf. p. 241).

#### BONDARZEVIACEAE Kotl. & Pouz.

Bondarzewiaceae Kotl. & Pouz. in *Česká Mykol.* **11**: 163. 1957. — Holotype: *Bondarzewia* Sing.

Fruitbody polyporoid or clavarioid and branched, annual.

Gloeocystidia terminating in the hymenium lacking; vascular hyphae may be present. Spores globular to short-ellipsoid, rather small (5–8  $\mu$  long), colourless (may be pale ochre-yellow in a print); walls ornamented with conspicuous and strongly amyloid spines and crests.

Genera.—

1. Fruitbody clavarioid, flabellately branched with amphigenous or one-sided hymenium in oblique branches, may arise from a fertile resupinate *Corticium*-like patch.—*Amylaria* Corner.
1. Fruitbody more or less compound, big, with dorsiventral, lateral caps; hymenophore tubulate.—*Bondarzewia* Sing.

The two genera to which this family is reduced are very dissimilar in outward appearance but are classified together because of their spores which have been compared with *Russula* spores. It may be that the hyphal structure will confirm the relationship between the two genera but no sufficiently detailed analyses and drawings have as yet been published in this respect for mutual comparison, so that for the present the inclusion of *Amylaria* in this family is only provisional.

Following a suggestion by Corner, the genus *Hericium* (sensu lato) was originally also included in the family, but there are too many significant differences to merit this, and I take the Hericiaceae (q.v.) as being not very closely related.

#### CANTHARELLACEAE J. Schroet.

Merulioideae Pers., *Mycol. europ.* **2**: 2. 1825 ("Merulini"; [subordo] = subfam.); not Merulioideae S. F. Gray, *Nat. Arr. Brit. Pl.* **1**: 636. 1821 ["Merulideae"; [subfam.]; type: *Merulius* S. F. Gray, illegitimate name, = *Hygrophoropsis* (J. Schroet.) Maire, Agaricales]; not Merulioideae P. Karst. in *Bidr. Känn. Finl. Nat. Folk* **37**: xi. 1882 (type: *Merulius* Fr.). —

Type: *Merulius* [Haller] St.-Am. Apr. 1821, not *Merulius* Fr. Jan. 1, 1821; → *Phlebodermei* Pers.

[*Phlebodermei* Pers., *Mycol. europ.* 2: 2. 1825 ([subordo] = subfam.), alternative name ≡ *Merulioideae* Pers.]

Cantharellinae Fr., *Gen. Hym.* 8. 1836 ("Cantharellaei"; [subtrib.]). — Type: *Cantharellus* Adans. per Fr.

Craterelleae Payer, *Bot. crypt.* 108. 1850; Killerm. in *Nat. Pflfam.*, 2. Aufl., 6: 148. 1928 (typonym). — Type: *Craterellus* Pers.

[Cantharellinae Staude, *Pilze Mitteleurop.* xxv, 74. 1857 ("Abtheilung", uninferable rank). — Type: *Cantharellus* Adans. per Fr.]

[Fam. Cantharellidées Roze in *Bull. Soc. bot. France* 23: 51 (nomen nudum), 110. 1876. — Type: *Cantharellus* Adans. per Fr.]

Cantharelloideae P. Karst. in *Acta Soc. Fauna Fl. fenn.* 2 (1): 27. 1881 ("Cantharelleae"); Ulbr. in *Kryptfl. Anfänger* 1 (3. Aufl.): 84. 1928; S. Imai in *J. Fac. Agr. Hokkaido Univ.* 43: 4. 353. 1938 (typonym; "nom. nov." for "Cantharellaceae Rea ... p.p."; with Latin description). — Type: *Cantharellus* Adans. per Fr.

Cantharellaceae J. Schroet. in *Krypt.-Fl. Sches.* 3 (1): 413, 507. 1888 ("Cantharellacei"); Engl., *Syll. Vorl. Bot.*, *Grosse Ausg.*, 36. & *Kleine Ausg.*, 31. 1892; Lotsy, *Vortr. bot. Stammesgesch.* 1: 687, 688. 1907 (typonym; ≡ 'Familie des Cantharellacées Maire'); Rea, *Brit. Bas.* 9, 540. 1922 (→ Cantharelloideae S. Imai). — Type: *Cantharellus* "Adanson" [≡ *Chanterel* Adans.] ≡ *Cantharellus* Adans. per Fr.

[Fam. Ptychophyllei Qué., *Fl. mycol. France* 30. 1888. — Lectotype: "*Craterellus*, Qué." = *Craterellus* Pers. emend. Qué., inclusive of both *Craterellus cornucopioides* (L. per Fr.) Pers. & *Cantharellus cibarius* Fr.]

Cantharelleae Fayod in *Ann. Sci. nat. (Bot.) VII* 9: 302 ("Cantharellés"), 394. 1889; Murrill in *N. Amer. Fl.* 9: 163. 1910 ("Chantereleae"; type: *Chanterel* Adans.); Killerm. in *Nat. Pflfam.*, 2. Aufl., 6: 247. 1928 (typonym; ≡ Cantharellaceae J. Schroet.). — Type: *Cantharellus* Adans. per Fr.

[Tribu des Cantharellés Pat., *Essai tax. Hym.* 123, 126. 1900. — Type: *Cantharellus* Adans. per Fr.]; → Cantharellinae Rea (see p. 242).

[Familie des Cantharellacées Maire in *Bull. Soc. mycol. France* 18 (Suppl.): 83, 88. 1902. — Type: *Cantharellus* Adans. per Fr.]; → Cantharellaceae Lotsy.

Craterelleae Herter in *Krypt.-Fl. Brandenb.* 6: 141. 1910. — Monotype: *Craterellus* Pers.

Craterelloideae Ulbr. in *Krypt.-Fl. Anfänger* 1 (3. Aufl.): 84. 1928. — Type: *Craterellus* Pers.

Fruitbody either tubular becoming infundibuliform, membranous throughout, or centrally stalked and pileate; cap thick to membranous, fleshy to membranous-toughish; context monomitic; hymenophore wrinkled ("from the thickenings of the fruitbody medulla" in *Craterellus*), or smooth to more or less strongly folded; principal folds usually radially arranged and toward the margin flabelliformly branched, with cross-veins when well-developed, and blunt fertile edge (cf. p. 209).

Hypae generally thin-walled, inflating, with or without clamps, may become secondarily septate (consisting of rows of short, unbranched cells separating the branched cells). Hymenium showing little, to often excessive, thickening. Basidia slender club-shaped (rarely rather short), stichic, 2-8-spored. Spores subglobose, ovoid, ellipsoid, colourless (white to yellowish pale ochraceous or salmon in a print); wall smooth, non-amyloid.

Terrestrial, humicolous (may rarely occur on very rotten wood).

Genera.—*Cantharellus* Adans. per Fr., *Goossensia* Heinem., *Pseudocraterellus* Corner, *Craterellus* Pers.

Excluded.—

Agaricales.—*Arrhenia* Fr., *Campanella* P. Henn. (syn., *Laschia* [Fr. sensu] Pat.), *Cantharellula* Sing., *Clitocybe* spp., *Cymatella* Pat., *Geopetalum* Pat., *Hygrophoropsis*

(J. Schroet.) Maire apud Mart.-Sans, *Leptoglossum* P. Karst. (including *Leptotus* P. Karst.; syn., *Dictyolus* Quél.), *Nyctalis* Fr., *Rimbachia* Pat. (including *Skepperiella* Pilát?), *Trogia* Fr.

Corticaceae.—*Plicatura*.

Clavariaceae.—*Clavariadelphus* spp.

Gomphaceae.—*Chloroneuron*, *Gloeocantharellus*, *Gomphus* (syn., *Neurophyllum*).

Hericiaceae.—*Clavicornia* (at least in part).

Schizophyllaceae?—*Plicaturopsis*.

Stereaceae?—*Caripia*, *Skepperia*.

Thelephoraceae.—*Polyozellus*.

In the Friesian classification the species of this family with a more or less strongly folded hymenophore were placed in *Cantharellus* which in its turn was referred to the agarics. The species with a smooth to rugose hymenophore were placed in *Craterellus* of the Thelephorei (old sense). In fact the folds were equated with gills and *Cantharellus* became also the receptacle for quite a number of agaric species with true, but forked, gills and white spore-print. The greater part of its contents has been gradually excluded. A similar simplification was needed as regards *Craterellus*.

Patouillard (1900: 126) associated the still mixed genera *Cantharellus* and *Craterellus* with *Nyctalis*, *Trogia*, *Laschia* Fr. sensu Pat. (= *Campanella*), *Rimbachia*, *Hypolyssus* Pers. sensu Berk. (= *Caripia*), and *Neurophyllum* (= *Gomphus*).

Maire (1902: 88) was the first author to conceive a taxon (as "Famille des Cantharellées") exclusive of all these foreign elements and reduced to practically the above circumscription, characterized *inter alia* by stichic basidia. However, he associated this family with various others (placed together in his "Cantharellinées"), the contents of which were, for the greatest part wrongly, supposed also to have stichic basidia. Donk (1933: 5) greatly reduced the "Cantharellinées" (as *Cantharelloideae*) and retained the name both for the present family and for the Hydnaceae (with *Hydnum* sensu stricto) and the Clavulinaceae (with *Clavulina*). A more detailed discussion of the value of the position of the nuclear spindles in the basidia as a taxonomic character will be found on page 219.

As well as the narrow circumscription of the family adopted here, there is a more comprehensive one recently defended by Heinemann (1961) who proposed the subdivision of a suborder *Cantharellineae* into two families, viz. the *Cantharellaceae*, including besides the genera mentioned above, also *Polyozellus*, and the *Neurophyllaceae* with *Neurophyllum* (= *Gomphus*), *Chloroneuron*, and *Clavariadelphus*. In my opinion neither the *Gomphus* element (including *Chloroneuron*) nor *Clavariadelphus* (see *Clavariaceae*) nor *Polyozellus* (see *Thelephoraceae*) should be associated with the *Cantharellaceae*.

Although Corner (1957) emphasized many important characters shared by *Craterellus*, *Cantharellus*, and *Pseudocraterellus*, he was not convinced that they were closely related. He regarded *Craterellus* (restricted to the tubular-infundibuliform species) and *Cantharellus* (which in his circumscription absorbed many species of *Craterellus*) as an instance of parallel modification of the chiasitic basidium into a stichic one in two different alliances. *Cantharellus* he thought so closely related to

*Clavariadelphus* that he found it difficult to know where to draw a distinction. However, the differences appear more important than he assumed. *Clavariadelphus* lacks the truly pileate limb with inferior hymenium and (at least at first) curving downwards by epinastic growth. Unlike *Cantharellus* its fruitbody turns dark green in contact with ferric sulphate solution (at least in the typical species) and it has chiasitic basidia with four (not more) sterigmata. All this tends to stress the taxonomic remoteness from *Cantharellus* and the similarities may thus appear another striking example of what is often called 'convergence'. Corner's and my own views diverge, it would seem, because of a different emphasis. Corner is very much impressed by developmental differences, while I still consider the stichic basidia in this case of great importance (see p. 222), as has recently also been done by Boidin and Penancier (1961: 69). This is not to say that as soon as this family becomes more intensively studied in various additional respects, division of the taxon into two families (Craterellaceae Herter and Cantharellaceae) or into two subdivisions of lower rank may not be a good solution.

For a note on *Cantharellus* in relation with the Agaricales, see page 245.

#### CLAVARIACEAE Chev.

[Clavaceiformes Pers., Syn. Fung. xviii, 585. 1801 ([subordo] = subfam.). — Lectotype: *Clavaria* [Vaill.] L.]

[Clavariae Nees, Syst. Pilze 165. 1816; Syst. Pilze (Ueberbl.) 42. 1817 ("Circulus"). — Type: *Clavaria* "Pers." = *Clavaria* [Vaill.] L. emend. Pers.]

[Clavati Fr., Spec. Syst. mycol. 2. 1819; Syst. mycol. 1: lvi (subordo), 2, 461. 1821 (ordo = fam.). — Lectotype: *Clavaria* [Vaill.] Fr.; → Clavariaceae Duby; → subfam. Clavati Lindl.]

Clavarioideae S. F. Gray, Nat. Arr. Brit. Pl. 1: 598, 654. 1821 ("Clavariaceae"; [subfam.]); Endl., Gen. Pl. 35. 1836 ("Clavariaceae Fries"; subordo = subfam.; typonym); Rab., Deutschl. Krypt. Fl. 1: xix, 316. 1844 ("Clavariaceae"; [subfam.?]); P. Karst. in Bidr. Känn. Finl. Nat. Folk 25: 16, 326. 1876 ("Clavariaceae"). — Type: *Clavaria* "Micheli" = *Clavaria* [Vaill.] L. = *Clavaria* [Vaill.] Fr.]

[Trib. Clavulati Fr., Syst. Orb. veg. 90. 1825. — Lectotype: *Clavaria* "Vaill." = *Clavaria* [Vaill.] Fr.]

Pistillariaceae Fr., Syst. Orb. veg. 90. 1825 ("Pistillariini"); Reichenb., Consp. Regni veg. 12. 1828 ("Pistillarii"; name only). — Type: *Pistillaria* Fr.]

Clavariaceae Chev., Fl. Env. Paris 1: 102. 1826 ("Clavariaceae"; "ordre" = fam.); Dumort., Anal. Fam. Pl. 72, 73. 1829; Fr., Epicr. 570, 595, 607. 1838 ("Clavariaceae"; 'ordo' as subdivision of a family); Corda, Ic. Fung. 2: 35. 1838 & 5: 81. 1842 & Anl. Stud. Mycol. ciii, 171. 1842 (typonym); Bon., Handb. Mykol. 25, 165. 1851 ("Clavariaceae"); P. Karst. in Not. Sällsk. Fauna Fl. fenn. Förh. 9: 371. 1868 ("Clavariaceae Fr."); Sacc. in Syll. Fung. 5: 3. 1887 & 6: 690. 1888 ("Clavariaceae"). — Type: *Clavaria* "Vaill. . . Fr." = *Clavaria* [Vaill.] Fr.]

Clavariaceae Link in Abh. phys. Kl. Akad. Berl. 1824: 182. 1826 ("Clavariaceae"; [trib.]); Fr., Fl. scan. 338, 340. 1835 & Gen. Hym. 5, 17. 1836 ("Clavariaceae"); Payer, Bot. crypt. 107. 1850. — Type: *Clavaria* Vaill. = *Clavaria* [Vaill.] Fr.; → Clavarioideae Endl.; → Clavariaceae P. Karst.]

Clavariaceae Duby, Bot. gall. 2: 759. 1830 ("Clavariaceae") ≡ Clavati Fr.]

[Clavati Lindl., Veg. Kingd. 42. 1846 ("subordo" = subfam.; nomen nudum, also lacking reference); ≡ Clavati Fr.]

[Tribu des Clavariés Pat., Essai tax. Hym. 39. 1900. — Type: *Clavaria* [Vaill.] Fr.; → Clavariaceae Rea (see p. 242).]



- [Série des Clavaires Pat., Essai tax. Hym. 40, 45. 1900. — Type: *Clavaria* [Vaill.] Fr.]  
 [Série des Mucronelles Pat., Essai tax. Hym. 114. 1900. — Type: *Mucronella* Fr.]  
 [Eu-Clavariaceae Sacc. in Fl. ital. crypt. (Fungi; Hym.) 1218. 1916 ("Sect."). — Lecto-type: *Clavaria* "Vaill. . . Fr." = *Clavaria* [Vaill.] Fr.]  
 Stichoclavariaceae Ulbr. in Kryptfl. Anfänger 1 (3. Aufl.): 82. 1928. — Type: *Stichoclavaria* Ulbr.  
 [Famille des Myxomycidiacées R. Heim in Rev. Mycol. 25: 48. 1960 (lacking Latin description). — Monotype: *Myxomycidium* Mass.]  
 Mucronelleae Nikol. in Fl. Pl. crypt. URSS 6 (2): 208. 1961. — Holotype: *Mucronella* Fr.

Fruitbody erect, exceptionally growing downward, rarely curving downward or decumbent, simple or branched, usually stalked (rarely fertile down to base), the fruitbodies or branches terete in section or, if flattened, becoming so through fasciation or secondarily through excessive expansion of the hymenium (not flattened and dorsiventral); the simple fruitbody cylindrical, conical, or club-shaped, sometimes with truncate (to depressed) sterile top around which no pileate (dorsiventral) limb develops; the branched fruitbody with apical and radial, also adventitious, but not typically flattened, branching; context fleshy (often brittle) to subgelatinous, or tough (cartilaginous or horny when dry), white, pallid, or brightly coloured, mono- or dimitic; hymenial surface smooth or becoming longitudinally wrinkled, amphigenous, either extending over the top of the fruitbody or leaving sterile tip(s) or truncate apex.

Hyphae in monomitic context thin-walled, usually more or less inflating (rarely becoming rather thick-walled), with or without clamps, sometimes becoming secondarily septate; dimitic species, with non-inflating generative hyphae (thin-walled, with or without clamps) and with skeletal hyphae (which may be in part imperfect in some respects); vascular hyphae rare. Hymenium often thickening. Cystidia, except perhaps hymenial leptocystidia, rare. Basidia more or less typically club-shaped, chiasitic (as far as known),<sup>26</sup> 2-4- (rarely up to 6-8-)spored. Spores variable in shape, always even in general outline in side-view, colourless or with somewhat tinted contents (white or pale yellowish in a print); wall smooth, rarely with minute echinulations to coarse spines, non-amyloid, except (as far as known) in some species of *Mucronella*.

Terrestrial, often between mosses, or humicolous, rarely on rotten wood; sometimes mycelium associated with algae (phycophilous); the small species usually in portions of vegetable debris.

Genera.—

1. Hyphae non-inflating.
2. Context monomitic.—*Ceratellopsis* Konr. & Maubl., *Aphelaria* Corner sensu stricto (might be placed in the Stereaceae), *Phaeoaphelaria* Corner (conceivably pertaining to the Hymenochaetaceae?).
2. Pteruloideae Donk<sup>27</sup> (Corner's Pteruloid series). Context dimitic; skeletal colourless, typical (of unlimited growth, thick-walled, aseptate), rarely branched, usually in part less perfect (being intercalary segments, or with somewhat dilated tips branching into skeletal and/or generative hyphae). Fruitbody simple to much branched (branching apical or adventi-

<sup>26</sup> But compare *Clavaria falcata* Fr. sensu Juel, see page 222 (footnote).

<sup>27</sup> Pteruloideae Donk, *subfam. nov.* — Clavariaceae. Contextus dimiticus hyphis skeletalibus, hyphis generatis non inflatis. Fructificatio simplex usque valde ramosa, axibus generaliter gracilibus, attenuatis, lentis, in sicco corneis saepiusque tortis. Sporae hyalinae, leves. — Typus: *Pterula* Fr.

tious), the axes predominantly slender, attenuate, tough, drying horny and often twisted. Hymenial cystidia may be present. Spores pip-shaped, amygdali-form, oblong, aguttate; wall smooth.—*Allantula* Corner (fruitbodies developed on slender rhizomorphs as small sausage-shaped, intercalary swellings, generally curved, decumbent; skeletal hyphae only in the rhizomorphs), *Deflexula* Corner (fruitbodies in clusters pointing or curving downward; spores often longitudinally sulcate-angled), *Pterula* Fr.,? *Parapterulicium* Corner (fruitbody drying floccoso-coriaceous; dichohyphidia, cf. p. 208) and *Pterulicium* Corner (see p. 207) (both developing a *Corticium*-like patch which may be fertile). — Also here *Actiniceps* Berk. & Br. (*Dimorphocystis* Corner) (noteworthy types of cystidia)?

1. Hyphae more or less inflating (except perhaps in *Myxomycidium* and allied genera); context monomitic.
3. **Clavarioideae** S. F. Gray. Fruitbody negative geotropic (growing upward). Context usually fleshy, waxy, or gelatinous. Fruitbody simple or branched, exceptionally turning green in contact with ferric sulphate solution, in the bigger species terrestrial. Context monomitic; hyphae mostly more or less inflating, may become secondarily septate, sometimes appearing subdimitic because of strongly developed interweaving hyphae (which, however, are thin-walled and septate); clamps present, rare, or lacking, may be loop-like at base of basidia. Hymenial cystidia (leptocystidia) rare; gloecystidia and oleocystidia lacking. Spores non-amyloid as far as known.—*Araecoryne* Corner, *Clavaria* [Vaill.] Fr. (natural genus to which many unplaced species are appended), *Clavariadelphus* Donk, *Clavulinopsis* Overeem, *Tumidapexus* D. A. Crawf. (if different from *Clavulinopsis*), *Pistillaria* Fr., *Pistillina* Quéll., *Ramariopsis* (Donk) Corner, *Typhula* (Pers.) per Fr.
3. Fruitbody often directed vertically downward, i.e. pendent, or if otherwise orientated oleocystidia present; typically simple. Lignicolous, on rotten wood.
4. Context fleshy-waxy, not gelatinous. Spores amyloid or non-amyloid.—*Mucronella* Fr.
4. Context of head subgelatinous, waxy-firm to watery-gelatinous. Oleocystidia often present.—*Hormomitriaria* Corner, *Myxomycidium* Mass., *Pseudotyphula* Corner, related to *Physalacria* Peck (Agaricales?).

Excluded.—

Agaricales?—*Physalacria* Peck.

Bondarzewiaceae.—*Amylaria* is provisionally appended to this family.

Clavulinaceae.—*Clavulina*.

Gomphaceae.—*Kavinia*, *Lenzaria* sensu stricto, *Ramaria*.

Hericiaceae.—*Clavicornia* (at least in part), *Hericium*.

Hymenochaetaeae.—*Clavariachaete*, *Lachnocladium*.

Sparassidaceae.—*Sparassis* (*Masseola*).

Stereaceae?—*Caripia*.

Thelephoraceae.—*Thelephora* in part, *Scytinopogon*.

Tremellineae.—*Pseudotremellodendron* D. Reid, *Tremellodendropsis* (Corner) D. A. Crawf.

The Clavariaceae in the traditional sense has remained a convenient group which, on the whole, is easily set off from all other families that Fries recognized by its erect fruitbodies with amphigenous hymenium. However, in this broad sense it is by no means a natural family, as was recognized by Donk (1933) and Corner (1950). In his outstanding monograph Corner produced a great deal of order out of chaos. He emphasized several new characters which led to a better understanding

and delimitation of the genera. He also arranged the genera into a number of series. Some of these coincide with the portions into which the old family has been divided and which are distributed over a number of other families in the present paper, as is briefly indicated above. It should be pointed out, however, that another modern school of thought prefers a very comprehensive family rather than this splitting up.

Except for a relatively big proportion of still insufficiently known species, the remainder of the family is separated above into two main groups which (if found to be reasonably natural in the future) may eventually be given separate family status, and a few small genera of undecided classification. An element that has disappeared from the Clavariaceae in the present restricted sense is the one which has typically flattened segments with one-sided hymenium.

*Myxomycidium* (see also pp. 217, 224) may appear closely related to *Physalacia* and *Hormomitaria*; *M. flavum* possesses a type of cystidia that may well point in this direction. If one rejects the assignment of the genus to the Clavariaceae, the next thesis to be considered is whether or not *Myxomycidium* may belong to a small group of genera related to the Marasmiaceae (Agaricales), including the genus *Gloiocephala* Mass., with which *Physalacia* shows several points of agreement, a relation previously suggested and taken into consideration by some authors. Singer (1962: 406) included *Physalacia* as a reduced genus in the tribus mentioned.

Supernumerary sterigmata (exceeding four per basidium) are known to occur in some species mostly of still more or less doubtful taxonomic position: *Clavaria coronilla* G. W. Mart., *C. surculus* Berk. (type of *Lentaria*), *Clavulinopsis hastula* Corner, *C. septentrionalis* Corner, *Clavaria falcata* Fr. sensu Juel (type of *Stichoclavaria*; insufficiently described, see also pp. 222, 299), and *Typhula idahoensis* Remsburg. Of these *Clavaria surculus* is provisionally removed to the Gomphaceae as a representative of a much reduced genus *Lentaria*. In all these species the number of sterigmata per basidium may often be four—in some species even fewer.

For a note on phycophilous species, see Dictyonemataceae (p. 299).

#### CLAVULINACEAE Donk

Clavulineae Donk, Rev. niederl. Homob.-Aphyll. 2: 16. 1933. — Monotype: *Clavulina* J. Schroet.; → Clavulinaceae Donk.

Clavulinaceae Donk in Persoonia 1: 407. 1961 ≡ Clavulineae Donk.

Fruitbody erect (clavarioid), simple or often more or less branched, the branching radially or usually flattened with cristate tips, also adventitiously, more or less stalked, white or variously coloured but not dark-coloured, not turning dark-green in contact with ferric sulphate solution; context fleshy, brittle or fibrous, often toughish, monomitic; hymenium amphigenous or more or less one-sided at least in part (and then with sterile hymenium on upper side).

Hyphae thin- to somewhat firm-walled, more or less typically inflating especially toward the centre of fruitbody; clamps present or lacking. Hymenium distinctly, often strongly, thickening. Hymenial cystidia (becoming embedded or soon deteriorating) rare; gloeocystidia lacking. Basidia slender, appearing almost cylindrical but really narrowly club-shaped, apically never distinctly swollen, stichic, the

mature ones freely projecting, after spore-discharge usually becoming secondarily septate (usually 1, or more, secondary septa; cf. p. 213); sterigmata 2, rather stout and strongly curved as a rule. Spores subglobose, broadly ellipsoid, slightly wider than the basidia, with 1 (rarely more), large often very large, oil-drop, colourless (white in a spore print which may become more or less ochraceous in the herbarium); wall smooth, rather firm, non-amyloid.

Terrestrial and humicolous, rarely on vegetable debris.

Genus.—*Clavulina* J. Schroet.

At present the isolation of *Clavulina* is very much a matter of personal opinion. Donk (1933: 16) removed it from the Clavariaceae to associate it with the present families Cantharellaceae and Hydnaceae (sensu stricto) in one taxon. This was done mainly because of the stichic basidia characteristic of all three groups. The recent isolation of *Clavulina* as the sole representative of a distinct family is an expression of the conclusion that this genus might not be as closely related to *Cantharellus* and *Hydnum* sensu stricto as I originally thought, and it is a confirmation of faith in the taxonomic value of the stichic basidium (see p. 222). This belief has been strengthened in many respects by Corner's studies on the genus (1950). He pointed out several additional features by which the isolated position of *Clavulina* was underlined; most of these are incorporated in the above family description. Corner himself (1950: 27) showed considerable reluctance to dissociate *Clavulina* from *Clavaria* and *Clavulinopsis* (viz. from the typical Clavariaceae).

#### CONIOPHORACEAE Ulbr.

Xylophagaceae Murrill in *Torreya* 3: 7. 1903. — Holotype: *Xylophagus* Link per Murrill ≡ *Serpula* (Pers.) per S. F. Gray.

Xylophagoideae Murrill in *Torreya* 3: 7. 1903 ("Xylophageae"). — Holotype: *Xylophagus* Link per Murrill ≡ *Serpula* (Pers.) per S. F. Gray.

Coniophoraceae Ulbr. in *Kryptfl. Anfänger* 1 (3. Aufl.): 120. 1928; Donk in *Bull. bot. Gdns, Buitenz. III* 17: 474. 1948 (typonym). — Type: *Coniophora* DC. per Mérat.

Coniophoreae Killerm. in *Nat. PflFam.*, 2. Aufl., 6: 140. 1928; not "Series" Coniophoreae Nyl. in *Mém. Soc. Sci. nat. Cherbourg* 2: 10. 1854 (inadmissible term denoting rank; Lichenes). — Type: *Coniophora* DC. per Mérat.

Coniophoroideae Donk in *Meded. Nederl. mycol. Ver.* 18-20: 192. 1931. — Type: *Coniophora* "Pers. (ex DC.)".

Gyrophanoideae Imaz. & Toki in *Bull. Govt For. Exp. Sta., Tokyo* No. 67: 63. 1954 (lacking Latin description). — Type (by implication): *Gyrophana* Pat. = *Serpula* (Pers.) per S. F. Gray.

Fruitbody appressed or effused, reflexed or not reflexed, also sessile, or more or less distinctly stalked and pileate (abnormal fruitbodies may be formed in some species when growing in houses, mines, &c.); context from thin and almost arachnoid to thick-fleshy, white, pallid, or coloured but not brightly so, monomitic; hymenophore smooth, tuberculate, or toothed, or hymenium irregularly folded in various directions when fresh (drying with reticulately connected folds) up to tubulate (edges of tubes fertile), the surface usually strongly powdered by spores.

Hypphae of context of fruitbody thin-walled, or in some species intercalary segments thick-walled, the septa lacking clamps or clamped (clamps often in whorls in some species). Cystidia (septate, long or non-septate, hymenial) or gloeo-

cystidia rare. Hymenium usually considerably thickening. Basidia from short to usually slender club-shaped, the long basidia often somewhat flexuous, may be utriform, chiasitic, 2-4-spored; sterigmata rather big, curved. Spores ovoid to ellipsoid and then often somewhat bean-shaped, also spindle-shaped or amygdaliform, with even outline, yellowish-brown or darker, rarely appearing colourless (brown to cream-coloured in a print); wall rather thick, presumably always double (in the small-spored species this is not evident), both layers smooth, the inner strongly absorbing Cotton Blue (cyanophilous).

Lignicolous, humicolous.

Genera.—

1. Hymenophore smooth, tuberculate.—*Coniophora* DC. per Mérat, *Coniophorella* P. Karst. (septate cystidia), *Jaapia* Bres. (inclusive of *Coniobotrys* Pouz., and perhaps also *Suillosporium* Pouz.).
1. Hymenophore toothed.—*Gyrodontium* Pat.
1. Hymenium soon folded (upon drying becoming reticulately folded, 'meruloid', rarely more radially so) up to rather typically tubulate.—*Serpula* (Pers.) per S. F. Gray (inclusive of *Leucogyrophana* Pouz., *Meruliporia* Murrill; syn., *Gyrophana* Pat., *Merulius* Fr. pr. p. exclusive of type), *Podoserpula* D. Reid.

The average species of this family is recognizable by the combination of a number of rather striking features: brown, smooth, double-walled spores strongly colouring with Cotton Blue (in the bigger-spored species it is the inner wall which is cyanophilous), soft, monomitic context, and a strongly thickening hymenium.

#### CORTICIACEAE Herter<sup>28</sup>

Sistrematoideae S. F. Gray, Nat. Arr. Brit. Pl. 1: 597 ("Sistremadeae"), 648 ("Sistremideae"). 1824 ([subfam.]). — Type: *Sistotrema* "Persoon" sensu S. F. Gray = *Sistotrema* Fr. Jan. 1, 1821 (typonym), not *Sistotrema* Pers. per Nocca & Balbis 1821.

Merulieae Dumort., Anal. Fam. Pl. 73. 1829; J. Schroet. in Krypt.-Fl. Schles. 3 (1): 465-1888 ("Merulinei"; "Gruppe" = trib.); Engl., Syll. Vorl. Bot., Grosse Ausg., 39. & Kleine Ausg. 31. 1892 ("§"); P. Henn. in Nat. Pflfam. 1 (1\*\*): 152. 1898 (→ Merulioideae Killerm.); Lotsy, Vortr. bot. Stammesgesch. 1: 697; 700 ("Familie", presumably in error). 1907 (typonym; ≡ "Tribu des Méruliées Maire"). — Type: *Merulius* Fr.

[Fam. Les Cyphelles Payer, Bot. crypt. 105. 1850. — Type: *Cyphella* Fr.]

Cyphelleae Payer, Bot. crypt. 107. 1850; J. Schroet. in Krypt.-Fl. Schles. 3 (1): 433. 1888 ("Cyphellei"; "Gruppe" = trib.) & Killerm. in Nat. Pflfam., 2. Aufl., 6: 149. 1928; Lotsy, Vortr. bot. Stammesgesch. 1: 696, 698. 1907 (typonym; ≡ "Tribu des Cyphellées Maire"). — Monotype: *Cyphella* Fr.

Sistremateae Payer, Bot. crypt. 108. 1850 ("Systremateae"). — Type: *Sistotrema* Fr.

Merulieae P. Karst. in Rev. mycol. 3/No. 9: 19. 1881 ("Merulineae"; nomen nudum). — Type: *Merulius* Fr.

Merulioideae P. Karst. in Acta Soc. Fauna Fl. fenn. Förh. 2 (1): 32. 1881 (nomen nudum); in Bidr. Känn. Finl. Nat. Folk 37: xi. 1882 ("Merulieae"); Killerm. in Nat. Pflfam., 2. Aufl., 6: 171. 1928 (typonym; ≡ Merulieae P. Henn.); not Merulioideae S. F. Gray, Nat. Arr.

<sup>28</sup> The name Corticiaceae as it is used here is several times preoccupied, viz. by Tulasnelaceae Juel (1897), Vuilleminiaeae Lotsy (1907), Peniophoraceae Lotsy (1907), and Cyphelleae Lotsy (1907). However, I prefer to retain it for the present highly artificial assemblage as the name best suited because the other ones were, and often still are, applied to only relatively small portions of it, or not currently applied at all (Peniophoraceae).

Brit. Pl. 1: 596, 636. 1821 ["Merulioideae"; [subfam.]; type: *Merulius* S. F. Gray, illegitimate name, = *Hygrophoropsis* (J. Schroet.) Maire, Agaricales]; not Merulioideae Pers., Mycol. europ. 2: 2. 1825 ("Merulini"; [subordo] = subfam.; type: *Merulius* [Haller] St.-Am., illegitimate name). — Type: *Merulius* Fr.

[Familie der Tomentellen Bref., Unters. Mykol. 8: 4, 5. "1889" [1888]. — Type: *Tomentella* "Persoon (1799)" ex J.-Olsen apud Bref., nomen confusum based on basidiferous species and unrelated imperfect states]; → Tomentellaceae Warm.

Tomentellaceae Warm., Handb. syst. Bot. 110. 1890. — Type: *Tomentella* [J.-Olsen apud Bref.], nomen confusum based on basidiferous species and unre-lated imperfect states; ≡ 'Familie der Tomentellen Bref.'

Tulasnellaceae Juel in Bih. svenska VetAkad. Handl. (III) 23 (12): 21. 1897. — Type: *Tulasnella* J. Schroet.

[Sous-tribu Cyphellés Pat., Essai tax. Hym. 51, 52. 1900. — Type: *Cyphella* Fr.]

[Série des Corticies Pat., Essai tax. Hym. 58, 64. 1900. — Type: *Corticium* Fr. 1835, not *Corticium* Pers. per S. F. Gray 1821]; → 'Corticinés Bourd. & G.'

[Familie des Vuilleminiacées Maire in Bull. Soc. mycol. France 18 (Suppl.): 80. 1902. — Monotype: *Vuilleminia* Maire]; → Vuilleminiaceae Lotsy.

[Familie des Péniphoracées Maire in Bull. Soc. mycol. France 18 (Suppl.): 83, 84. 1902. — Monotype: *Peniophora* Cooke]; → Peniophoraceae Lotsy.

[Familie des Cyphellacées Maire in Bull. Soc. mycol. France 18 (Suppl.): 99. 1902. — Type: *Cyphella* Fr.]; → Cyphellaceae Lotsy.

[Tribu des Cyphellés Maire in Bull. Soc. mycol. France 18 (Suppl.): 99, 101. 1902. — Type: *Cyphella* Fr.]; → Cyphellaeae Lotsy.

[Tribu des Corticiés Maire in Bull. Soc. mycol. France 18 (Suppl.): 99, 104. 1902. — Type: *Corticium* [Pers. per S. F. Gray 1821]; → Corticieae Lotsy.

[Tribu des Méruliés Maire in Bull. Soc. mycol. France 18 (Suppl.): 99, 106. 1902. — Type: *Merulius* Fr.]; → Merulieae Lotsy.

Gloeoporoideae Murrill in Torreya 3: 7. 1903 ("Gloeoporeae"). — Holotype: *Gloeoporus* Mont. Vuilleminiaceae Höhn. in Oesterr. bot. Z. 54: 427. 1904 (not accepted); Lotsy, Vortr. bot. Stammesgesch. 1: 678, 679; 682 ("Vuilleminiaceen"); 686. 1907; ≡ 'Familie des Vuilleminiaceés Maire'.

Peniophoraceae Lotsy, Vortr. bot. Stammesgesch. 1: 687; 689 ("Peniophoraceen"). 1907 ≡ 'Familie des Péniphoracées Maire'.

Cyphellaceae Lotsy, Vortr. bot. Stammesgesch. 1: 695, 696. 1907; Herter in Krypt.-Fl. Brandenb. 6: 132. 1910; Romagn. in Rev. Mycol. 4: 149. 1939 ("Cyphelleae"); ≡ 'Familie des Cyphellacées Maire'.

Corticieae Lotsy, Vortr. bot. Stammesgesch. 1: 697, 698. 1907; Killerm. in Denkschr. bayr. bot. Ges. 15: 1; 12 ("Corticieen"). 1922 ("Gruppe" = trib.) & in Nat. Pflfam., 2. Aufl., 6: 136. 1928 (typonym; type: *Corticium* "Pers."); ≡ 'Tribu des Corticiés Maire'. Meruliaceae Rea, Brit. Bas. 10, 620. 1922; Sing. in Ark. Bot., Stockh. II 4: 377. 1959 (lacking description; reference to "Bond. & Sing., Sov. Bot. 1943, p. 35. 1943" where used as an already published family without author's citation, reference, or Latin description). — Type: *Merulius* Fr.

Corticieae Herter in Krypt.-Fl. Brandenb. 6: 70. 1910. — Type: *Corticium* "Pers."

[Sous-familie Tulasnellés Big. & Guill., Fl. Champ. France 2: 489, 512. 1913. — Type: *Tulasnella* Juel.]

Aleurodiscinae Pilát in Ann. mycol. 24: 206. 1926 ("Gruppe" = subtrib.). — Type: *Aleurodiscus* Rab. ex J. Schroet.; → Aleurodiscaceae Killerm.; → Aleurodiscaceae [?] Pilát. [Sous-tribu Corticinés Bourd. & G., Hym. France 144 ("Corticinés"), 167. "1927" [1928] ≡ 'Série des Corticies Pat.']; → Corticiinae Talbot.

Corticioideae Ulbr. in Krypt.-Fl. Anfänger 1 (3. Aufl.): 106. 1928. — Type: *Corticium* "Pers."

[Cystocorticioideae Ulbr. in *Kryptfl. Anfänger* 1 (3. Aufl.); 112. 1928. — Lectotype: *Gloeocystidium* "Karsten" sensu Höhn. & Litsch = *Gloeocystidiellum* Donk sensu lato.]

Aleurodisceae Killerm. in *Nat. Pflfam.*, 2. Aufl., 6: 142. 1928 ≡ Aleurodiscineae Pilát.  
Gloeoporeae Killerm. in *Nat. Pflfam.*, 2. Aufl., 6: 202. 1928. — Type: *Gloeoporus* Mont.  
Cyphelloideae Donk in *Meded. Nederl. mycol. Ver.* 18-20: 127. 1931. — Type: *Cyphella* Fr.  
Aleurodisceaceae [?] Pilát in *Bull. Soc. mycol. France* 49: 328. 1934 ("Aleurodiscineae", but presumably intended as the name of a family; nomen nudum); ≡ Aleurodiscineae Pilát.

Peniophoreae Greis in *Nat. Pflfam.*, 2. Aufl., 5a1: 267, 274, 275, 309. 1943 (lacking Latin description and reference). — Type (by implication): *Peniophora* Cooke.

Ceratobasidiaceae G. W. Mart. in *Lloydia* 11: 114. 1948. — Holotype: *Ceratobasidium* D. P. Rog.

Corticinae Talbot in *Bothalia* 6: 5. 1951 (lacking Latin description; "Corticinae") ≡ 'Corticinés Bourd. & G.'

Meruliinae Talbot in *Bothalia* 6: 5. 1951 (lacking Latin description; "Merulinae") ≡ 'Mérulinés Bourd. & G.'

[Hypochneae S. Ito, *Mycol. Fl. Japan* 2 (4): 104, 105. 1955 (lacking Latin description). — Monotype: *Pellicularia* Cooke sensu D. P. Rog. = *Koleroga* Donk.]

Botryobasidioideae (type: *Botryobasidium* Donk), Sistotremoideae (type: *Sistotrema* Fr.), Cristelloideae (type: *Cristella* Pat.), *Repetobasidioideae* (type: *Repetobasidium* John. Erikss.), Galzinioidae (type: *Galzinia* Bourd.), Tubulicrinoidae (type: *Tubulicrinis* Donk), Athelioideae (type: *Athelia* Pers.), Phlebioideae (type: *Phlebia* Fr.), Peniophoroideae (type: *Peniophora* Cooke), Hyphodermoideae (type: *Hyphoderma* Wallr.), Odontioideae (type: *Odontia* "Fr." exclusive of type species) John Erikss., *Stud. Swedish Heterob. Aphyll.* 18. 1958 (nomina nuda).

Odontioideae Nikol. in *Fl. Pl. crypt. URSS* 6 (2): 66. 1961. — Type: *Odontia* "Fr." sensu Nikol. = *Hyphodontia* John Erikss., not *Odontia* Pers. per S. F. Gray 1821, not *Odontia* Fr. 1835.

Odontieae Nikol. in *Fl. Pl. Crypt. URSS* 6 (2): 66. 1961. — Holotype: *Odontia* "Fr." sensu Nikol. = *Hyphodontia* John Erikss., not *Odontia* Pers. per S. F. Gray 1821, not *Odontia* Fr. 1835.

Sarcodontieae Nikol. in *Fl. Pl. crypt. URSS* 6 (2): 173. 1961. — Holotype: *Sarcodontia* S. Schulz.

Fruitbody strictly effused; context monomitic, rarely thin- and thick-walled hyphae mixed (typically dimitic with skeletals in some species), from arachnoid to membranous, cottony, waxy-pruinose, waxy to gelatinous, rarely rather tough (well-developed basal layer); hymenophore typically smooth, but also merulioid to tubulate when dry (edges of dissepiments fertile), or granular (granules fertile) to toothed (tips of teeth sterile), or with variously effigured, sterile tissue protruding beyond the hymenial surface; hymenium diffuse, interrupted, or continuous.

Sections through fruitbodies not showing the typical *Stereum*-like fruitbody construction (abhymenial crust-like layer, intermediate layer, and hymenium). Hyphae with or without clamps. Tramal and hymenial cystidia and/or hyphidia of various types may be present. Setae lacking. Eu- or cathymenium. Basidia usually club-shaped or slightly utriform, with 2-4 sterigmata, also urniform or more or less strongly utriform, stichic, chiastic, or hemichiastic, with 2-4, or -8 sterigmata; sterigmata mostly 'normal' and curved, in some genera 'aberrant' (see below). Spores even (not wavy or sinuose) in general outline, colourless or pinkish to lilac, still more rarely violaceous, bluish, or greenish; wall thin- or thick (inner layer, if distinct, neither coloured nor strongly absorbing Cotton Blue), smooth or not very distinctively ornamented, usually non-amyloid, in some groups or species amyloid.

Lignicolous, herbicolous, or humicolous, rarely terrestrial, saprobic or rarely parasitic.

*Included here but not covered by the family description.*—Fruitbody with reflexed portions (effused-reflexed or margin recurved all around), also cucullate or peltate, viz. more or less broadly attached at base only, rarely stalked (*Sistotrema confluens*, 'irpicoid' hymenophore), but context soft, typically monomitic: *Aleurodiscus* spp., *Auriculariopsis*, *Cytidia*, *Cytiliella*, *Corticium* spp., *Duportella* (context dimitic), *Gloeoporus*, *Merulius*, *Laeticorticium* sp., *Peniophora* spp., *Plicatura*; & compare the non-stalked, monomitic 'Stereaceae'.—Fruitbody more or less typically disk- to cup-shaped (viz. typically 'cyphelloceous'), with narrow base or stalk-like attachment: *Aleurodiscus* spp.—Fruitbody producing, or proliferating with, erect, self-supporting, cristate, sometimes more or less clavarioid, projections: *Cristella fastidiosa* (Pers. per Fr.) W. Brinkm., *Corticirama*, and individual modifications of certain species; & compare *Pterulium* & *Parapterulium* (Clavariaceae), *Amylaria* (Bondarzewiaceae).—Context consisting of thin- and clamped thick-walled hyphae mixed, viz. often some kind of skeletal hyphae present: *Aleurodiscus* spp. (inclusive of *Aleurocystidiellum*), *Fibricium*, *Gloeocystidiellum* sp., *Duportella*, *Scytinostroma*.

*Deviations from the 'smooth' hymenophore* as admitted in the above family description (all combined with monomitic hyphal systems) are related to the following groups.—Hymenophore tubulate (edge of dissepiments sterile): *Cristella* spp., *Echinotrema*, *Sistotrema* spp. (may be pileate or even stalked); & compare *Porogramme* (side of dissepiments sterile, only bottom of tubes fertile).—Hymenophore 'merulioid' or even appearing tubulate, but edges of dissepiments fertile: *Athelia* spp., *Gloeoporus*, *Merulius*, *Phlebia* spp., *Plicatura*.—Hymenophore toothed (strictly resupinate fruit-body): *Cristella* spp., *Dacryobolus*, *Hyphoderma* spp., most species of *Hyphodontia*, *Mycocia*, *Odontia* Fr. (residual genus; inclusive of 'Grandinia' spp.), *Sarcodontia*, *Sistotrema* spp.; & compare *Mucronella* (Clavariaceae).—Hymenophore with sterile tissue protruding beyond the hymenial surface: *Epithele*, *Gloiothele*, *Grammothele*, *Hymenogramme*, *Porogramme*.

Genera.—

1. Basidia inflated from a slender stalk, the inflated portion rather cylindrical, stichic, with (1)–2(–3) sterigmata.—*Clavulicium* Boid.; & compare *Cerinomyces* G. W. Mart., usually referred to the Dacrymycetales (position of nuclear spindles in basidia still unknown).
1. Basidia short and rather plump, obovoid, pear-shaped, subglobose and then more or less sphaero-pedunculate, barrel-shaped, (cf. p. 214), chiasitic as far as known, or, if rather slender, spores exhibiting repetition (capable of producing secondary basidiospores).
  2. Spores exhibiting repetition (cf. p. 227). Sterigmata spore-like bodies (obovoid to ellipsoid before spore-production, with septa across their bases) or big and finger-shaped and finally often subfusoidly inflated, or 'normal'.—*Tulasnella* J. Schroet. (inclusive of *Gloeotulasnella* Höhn. & Litsch.), *Ceratobasidium* D. P. Rog., *Oliveonia* Donk, *Thanatephorus* Donk (*Pellicularia* Cooke sensu D. P. Rog. in part), *Uthatabasidium* Donk.—Compare also page 224.
  2. Spores not exhibiting repetition. Basidia often with more than 4 sterigmata.—*Koleroga* Donk (*Pellicularia* Cooke sensu D. P. Rog. in part), *Botryohypochnus* Donk, *Botryobasidium* Donk in part, *Waitea* Warcup & Talb., *Paulliticium* John Erikss., *Repetobasidium* John Erikss.
1. Basidia of different shape. Spores not exhibiting repetition.
  3. Sterigmata 'normal'.
    4. Basidia either more or less typically urniform (known to be stichic in one or two species of *Sistotrema*; cf. pp. 212, 215, 221), often with supernumerary



sterigmata; or if not passing through an urniform state then with 4-8 sterigmata; not pleurobasidiosis.—*Sistotrema* Fr. (inclusive of *Trechispora* P. Karst. sensu D. P. Rog.), *Sistotremastrum* John Erikss., *Botryobasidium* Donk in part, *Echinotrema* Park.-Rh.

4. Basidia pleurobasidiosis (cf. pp. 211, 218) and/or cystidia originating from repent hyphae and 2-more-rooted; in a few species with supernumerary sterigmata.—*Xenasma* Donk, *Tubulicrinis* Donk.
  4. Basidia more or less typically club-shaped (rarely very slender) or utriform; sterigmata not exceeding 4 per basidium.
  5. Spores not coloured in a print.
    6. Hymenium neither a typical catahymenium nor basidia very pronouncedly utriform.—*Cristella* Pat. (inclusive of *Trechispora* P. Karst. sensu originario).—*Epithela* (Pat.) Pat.—*Athelia* Pers., *Byssocorticium* Bond. & Sing. ex Sing., *Amphinema* P. Karst., *Corticirama* Pilát (if not some abnormal condition; cf. p. 207), *Hypochnicium* John Erikss., *Hyphoderma* Wall., *Hyphodontia* John Erikss., *Tylospora* Donk, *Amylocorticium* Pouz., *Phlebia* Fr., *Mycoacia* Donk, *Sarcodontia* S. Schulz., *Cerocorticium* P. Henn., *Phanerochaete* P. Karst., *Merulius* Fr., *Cyrtidiella* Pouz., *Auriculariopsis* Maire, *Gloeoporus* Mont., *Fibricium* John Erikss., *Gloeocystidiellum* Donk in part.—*Dacryobolus* Fr.—*Gloiothela* Bres., *Grammothela* Berk. & C., *Hymenogramme* Mont. & Berk., *Porogramme* (Pat.) Pat.—*Plicatura*.
    6. Hymenium (at least at first) a more or less typical catahymenium (cf. p. 210); basidia often more or less utriform (cf. p. 216, 218), in *Galzinia* quite typically so but hyphidia not obvious.—*Galzinia* Bourd., *Vuilleminia* Maire (cf. pp. 216, 226), *Cyrtidia* Quél. s. str., *Aleurodiscus* Rab. ex J. Schroet. (cf. pp. 229, 233), *Dendrothela* Höhn. & Litsch., *Laeticorticium* Donk, *Scytinostroma* Donk (cf. also p. 278).
  5. Spores coloured in a print.
    7. Spores pink (to faint salmon) to pale lilac in a good print but neither amyloid nor voluminous. Basidia hemichastic. Gloeocystidia (darkening in sulpho-aldehyde solutions, see p. 232), hymenial cystidia (becoming deeply embedded), and hyphidia often present in various combinations.—*Peniophora* Cooke, *Duportella* Pat.; & compare *Aleurodiscus* for some species with amyloid and/or voluminous spores.
    7. Spores violaceous, bluish, greenish, rarely turning purplish in KOH solution.—*Hypochnella* J. Schroet., *Hypochnopsis* P. Karst., *Amaurodon* J. Schroet. if different.
  3. Sterigmata developing into long diaspores which apically bear spreading branches, breaking off, not (yet) known to produce (ballistospore) basidiospores. Marine fungus flooded by tide. Basidia slender club-shaped, chastic.—*Digitatispora* Doguet (cf. p. 225).
  1. 'Residual' genera.
    8. Surface of fruitbody 'smooth'.—*Corticium* Pers. per S. F. Gray (lacking gloeocystidia and cystidia), *Gloeocystidium* P. Karst. sensu Höhn. & Litsch. (with gloeocystidia), *Peniophora* Cooke [bis] (with cystidia; gloeocystidia may also be present).
    8. Surface distinctly granular to toothed.—*Odontia* Fr. (non Pers.; inclusive of residual *Grandinia* Fr.).
- Excluded.—
- Coniophoraceae.—*Coniophora*, *Coniophorella*, *Jaapia* (and *Coniobotrys*, *Suillosporium*), *Serpula* pr. p. (inclusive of *Leucogyrophana*, *Meruliporia* Murrill).

Gomphaceae.—*Ramaricium*.

Hericiaceae.—*Dentipellis*.

Hymenochaetaceae.—*Asterostroma*, *Hymenochaete* spp., *Vararia*.

Thelephoraceae.—*Kneiffiella*, *Tomentella*.

Fries's Thelephorei was conceived as the receptacle for those Hymenomycetes in which the dorsiventral fruitbody (irrespective of its shape) was provided with a smooth hymenophore, although the type species of *Thelephora* (viz. *T. terrestris* Ehrh. ex Fr.) had a warted hymenium (hence the generic name). Patouillard preferred to call the genus *Thelephora* (emended, but inclusive of its type species) by the name of *Phylacteria*, and reserved the name *Thelephora* for a group of species around *Thelephora pallida* Pers. per Pers. (type species of *Bresadolina* W. Brinkm.). His 'Série des Phylactéries' was a taxon that comprised not only genera with smooth, but also with toothed, hymenophores, and later on other authors added a polyporoid and a cantharelloid element. The correct name for this taxon, raised to the rank of a family, is Thelephoraceae, but the first few mycologists to treat Patouillard's series in that rank were loath to use this name because of its traditional implications and for some time they preferred the designation Phylacteriaceae. When finally the nomenclatural consequences were accepted and the Phylacteriaceae correctly called Thelephoraceae, a huge portion of the Friesian Thelephoraceae became deprived of this family name because only some of its genera went into the emended family. It has now become customary to call a good portion of what remained Corticiaceae. Moreover, it also had become customary to restrict this latter family in some respects, and thus most of the traditional Thelephoraceae became distributed over the Corticiaceae, Cyphellaceae, Stereaceae, and Thelephoraceae, while the last name gradually loses its mental association with 'smooth hymenium'.

The spreading of much of the residue over Corticiaceae and Stereaceae has no sound basis and has not led to even rational artificial families, for no clear-cut differences between the two can be given. The basic idea was that the Corticiaceae included the strictly resupinate groups and the Stereaceae those that were at least capable of producing caps (although completely resupinate individual fruitbodies might occur). This distinction cannot be upheld, but it sorts out at least the great majority of the contents of the two 'families' which are here maintained to comply with current usage for the lack of a better solution. In any case they are two nice examples of how extremely artificial taxa can be. The same applies to the Polyporaceae as here delimited and the residual Hydnaceae. Not until the combined contents of all these groups have been parcelled out into natural genera will a rearrangement be possible.

Since the basic formula for the Corticiaceae was 'strictly resupinate fruitbodies with smooth hymenophore', the exclusion of the resupinate Thelephoraceae (new sense), and more recently of still some other elements, required the addition, 'and with spores different *inter alia* from those of the Thelephoraceae, Coniophoraceae, Gomphaceae'. One would expect that it would not be difficult to keep an artificially delimited taxon intact. This is not true in this instance because the theoretical

'family' limits run clean through some of the more natural genera and closely related groups of genera. Therefore, it is necessary to admit several exceptions to keep certain genera and alliances unimpaired: hence the presence, in the above circumscription, of (i) a number of non-resupinate elements, and (ii) also such in which the hymenophore is not smooth but toothed, or also tubulate (poroid), or the hymenium folded (meruloid). Thus, even the two principal items contained in the original basic family character have gradually become encroached upon. Even so it is easy to mention some groups that remain arbitrarily separated. A point in case is *Stereum* sect. *Phellina* (Endl.) D. Reid (*Xylobolus*), Stereaceae, which in some respects reminds one of *Aleurodiscus*, Corticiaceae: acanthocystidia or -hyphidia; amyloid spores; dimitic hyphal construction (in all species of *Stereum* and in some of *Aleurodiscus*). In this case the presence of a euhymenium has been made binding for the Stereaceae, which excludes *Aleurodiscus* which has more or less cataphymenial fruitbodies.

Even after the exclusion of various odd genera (of which a recapitulation is given above), the Corticiaceae remains an assemblage of considerable diversity and size with about 60 definite genera and a respectable rest not yet disposed of. No less than six family names will be found listed in the above synonymy. Admitting some of these names as correct for the groups to which they are now sometimes applied would not reduce the contents of the Corticiaceae radically. Some of them were founded for one or two genera (Tulasnellaceae, Ceratobasidiaceae, Vuilleminiacae). The emended Meruliaceae would now consist only of *Merulius* (sensu stricto) and, as a recent addition, *Gloeoporus*. The Peniophoraceae has not found modern support at all. The Cyphellaceae, if it were to be maintained for cup-shaped fungi and at the same time for a natural taxon, would consist of hardly more than a portion of the genus *Aleurodiscus*; this family is more extensively discussed on page 290.

When the Tulasnellaceae was introduced there was much to support it, especially as long as the swollen sterigmata were considered to be sessile spores. Even after these 'spores' were recognized as sterigmata, they were so outstandingly different as to merit the retention of the group bearing them in a separate family. However, gradually a series of 'tulasnelloid fungi' (characterized by their capability to produce secondary basidiospores) were brought together in which the tendency to voluminous sterigmata was apparent, for instance, in the genus *Ceratobasidium*, which mainly differed from *Tulasnella* in the lack of walls across the bases of the sterigmata. If one takes the *Tulasnella* sterigmata as the ultimate expression of a tendency leading to an increase in the volume of the sterigmata (cf. p. 224) and, in addition, does not attach too much taxonomic value to the secondary basidiospores, as I do (cf. p. 228), then it becomes difficult to maintain the Tulasnellaceae either in a restricted or an emended sense on the basis of these characters. This is not to say that in the future there will be no room for a redefined family of Tulasnellaceae.

The introduction of the Ceratobasidiaceae as a distinct family from both the Tulasnellaceae and the 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 (cf. p. 224), and therefore there seems no good reason why the Ceratobasidiaceae (as delimited at present) should not be abolished. Occasional septa across the bases of its sterigmata have been reported. Compare also page 229.

The Vuilleminiaceae owes its existence to its remarkable basidia which were described by Maire. In my opinion we are dealing here with an extreme variation of the utriform basidium (cf. p. 216) and the family must be either expanded, or sunk again in the Corticiaceae, at least as long as no acceptable new definition for it is offered.

The Meruliaceae (after ceding a considerable portion to the Coniophoraceae) has nothing to support it but its folded hymenium (cf. p. 209), and this varies from often barely folded [*Merulius corium* (Pers. per Pers.) Fr.] to tubulate [*M. taxicola* (Pers.) Duby; *Gloeoporus*]. The assignment of the Meruliaceae to the Polyporaceae is a thing of the past (fertile edges of dissepiments) and its maintenance as distinct is hampered by the fact that its members appear to be very closely related to some genera in which the hymenium does not become folded (*Auriculariopsis*, *Cytidiella*, *Phanerochaete*) and others in which the fruitbody may be strictly resupinate (*Phanerochaete*). I am unable at the moment to suggest a more satisfactory character to support the retention of the family Meruliaceae but since most typical species of *Merulius* and *Gloeoporus* are effused-reflexed one might prefer to place it in the Stereaceae. This would be a highly unsatisfactory solution however because the hyphal system (monomitic) and fruitbody structure are not in the least *Stereum*-like.

Through Eriksson's studies on *Peniophora* sect. *Coloratae* (viz. *Peniophora* sensu stricto) and Boidin's on the same group, the emended genus *Peniophora*, together with *Duportella*, are emerging more and more as a natural group with a well-marked character, although containing several features with a rather wide range from a traditional point of view (effused to effuso-reflexed; with or without gloeocystidia, lamprocystidia, hyphidia; usually monomitic context, but dimitic in *Duportella*). I would not be surprised if in the near future the available name Peniophoraceae were to be restored to active duty.

As briefly discussed elsewhere in this paper (cf. p. 227) the Corticiaceae contains elements that are strongly reminiscent of certain Dacrymycetales (cf. also p. 243) and Tremellineae.

See also some remarks in the discussion of the Hericiaceae.

#### ECHINODONTIACEAE Donk

[Série des Echinodonties Pat., Essai tax. Hym. 114, 117. 1900. — Monotype: *Echinodontium* Ell. & Ev.]

Echinodontiaceae Donk in *Persoonia* 1: 405. 1961. — Holotype: *Echinodontium* Ell. & Ev.

Fruitbody appressed-reflexed, conchate, or dimidiato-sessile (up to unguiform); cap more or less concentrically sulcate, velutinous or tomentose; context corky to woody, distinctly coloured (e.g. orange-red); hymenophore toothed, may strongly increase in thickness, with paler, crust-like, hardening hymenium; the teeth rigid, 'stuffed'.

Hyphae of context seemingly dimitic with skeletal, but 'skeletal' may be sparingly branched and many bear well-formed clamps, coloured, a number terminating in cystidia. Euhymenium thickening, very compact, transparent in section. Cystidia at various levels, ventricoso-subulate to fusiform, becoming very thick-walled, hyaline to coloured (may resemble setae), encrusted or naked. Gloeocystidia lacking. Basidia club-shaped, 2-4 spored. Spores short-ellipsoid, rather small medium-sized (5.5-7.5  $\mu$ ), hyaline; wall thick, smooth, amyloid.

Lignicolous.

Genus.—*Echinodontium* Ell. & Ev.

Patouillard (1900: 117) thought that his 'Série des Echinodonties' (consisting of *Echinodontium* only) represented a genus among the hydroid fungi that corresponded with the polyporoid Hymenochaetaceae (his 'Igniaires'). This is not the case. Although the cystidia in *Echinodontium*, especially when more deeply coloured, may closely recall the setae of the Hymenochaetaceae, the resemblance is merely superficial. The fact that the thin-walled, and many of the thick-walled, hyphae have clamps is a decisive factor in keeping the two taxa apart. The thick-walled, short, amyloid spores also characterize this small family.

Some species of the Stereaceae remind one in some of their microscopic features (ovoid-ellipsoid spores with rather thick, amyloid wall; thick-walled cystidia) of *Echinodontium*, but in many other respects they differ considerably, and I am not (yet) prepared to see in them a stereoid element of the present family. The species I have in mind are the type and only species of *Laurilia* and "*Stereum*" *taxodii* Lentz & McKay apud Davids. & al.

The Hericiaceae (q.v.) also have amyloid, often somewhat thick-walled spores but the consistency of their context is very different and they have a strongly developed gloeocystidial system. Some of the genera have a toothed hymenophore and in this respect resemble *Echinodontium*, but only superficially so.

#### FISTULINACEAE Lotsy

Fistulinae J. Schroet. in Krypt.-Fl. Schles. 3 (1): 494. 1888 ("Fistulinei"; "Gruppe" = trib.); Engl., Syll. Vorl. Bot., Grosse Ausg., 40. & Kleine Ausg. 31. 1892 ("§"). — Type: *Fistulina* Bull.

[Famille des Fistulinacées Maire in Bull. Soc. mycol. France 18 (Suppl.): 111. 1902. — Monotype: *Fistulina* Bull. per Fr.]; → *Fistulinaceae* Lotsy.

Fistulinaceae Lotsy, Vortr. bot. Stammesgesch. 1: 695, 704. 1907 = 'Famille des Fistulinacées Maire'.

Fistulinoideae Donk in Meded. Nederl. mycol. Ver. 18-20: 126. 1931 (nomen nudum); Rev. niederl. Homob.-Aphyll. 2: 260. 1933. — Monotype: *Fistulina* Bull. per Fr.

Fruitbody pileate, laterally stalked (stalk may be short), annual; cap soon dorsiventral; stalk rooting; context fleshy, juicy and coarse-fibrous or fleshy

coriaceous, monomitic; hymenophore consisting of densely crowded free tubes, the individual tubes constricted at their bases to short stalks.

Hyphae of context consisting only of generative hyphae or mixed with vascular ones; generative hyphae, thin- to slightly thick-walled, with or without clamps; vascular hyphae, if present, with orange-reddish contents. Cystidia (and gloecystidia) lacking. Basidia club-shaped, chiasitic, 4-spored. Spores subglobose, short-ovoid, hyaline (white in a print) or faintly tinted (pale fulvous or reddish in a print, darker after some time); wall somewhat thickened or thin, smooth, non-amyloid.

Lignicolous.

Genera.—*Fistulina* Bull. per Fr., *Pseudofistulina* O. & K. Fidalgo.

Lohwag & Follner (1936) found that in *Fistulina hepatica* (Schaeff.) per Fr. the whole cap is initially covered by short-stalked cups which develop into long tubes on the underside. On the upper side these cups soon degenerate and eventually disappear. The two Austrian authors considered the fruitbody as coralloidly built, the cups being the terminations of the 'branches'.

Because of the densely crowded tubes forming the (compound) hymenophore the *Fistulinaceae* have long been considered as polyporaceous, but the tubes are merely crowded and mutually free from each other and in this and practically all other respects the *Fistulinaceae* are so dissimilar from the *Polyporaceae* that leaving them in that family would be completely unsatisfactory. The initial stages of the tubes are cup-shaped and strictly 'cyphelloid'. Hence, the assignment of *Fistulina* by some authors to the *Cyphellaceae* or *Cyphellineae*. The stalked fruitbody (minus the tubes) would be merely a strongly advanced stroma if compared with *Porothelium* (= *Stromatoscypha*), where it is membranous and 'resupinate'. Anatomical analysis leaves little doubt that there is only a very superficial likeness and that the *Cyphellaceae* as a whole is a purely artificial family which should be gradually dispersed rather than strengthened (see p. 290).

### Ganodermataceae Donk

[*Chromospori* Pat., *Hym. Eur.* 85 (description), 142. 1887 — Lectotype: *Ganoderma* P. Karst.]

*Ganodermatoideae* Donk in *Meded. Nederl. mycol. Ver.* 18-20: 126. 1931 (nomen nudum) & *Rev. niederl. Homob.-Aphyll.* 2: 229. 1933 ("Ganodermoideae"). — Monotype: *Ganoderma* P. Karst.

*Ganodermateae* Bond. & Sing. in *Ann. mycol.* 39: 58. 1941 (lacking Latin description). — Monotype: *Ganoderma* P. Karst.

*Ganodermateae* Imaz. in *Bull. Tokyo Sci. Mus.* No. 6: 99. 1932 ("Ganodermateae"). — Holotype: *Ganoderma* P. Karst.

*Ganodermataceae* Donk in *Bull. bot. Gdns, Buitenz. III* 17: 474. 1948. — Holotype: *Ganoderma* P. Karst.

Fruitbody sessile (sometimes with appressed, decurrent base) or stalked, annual or perennial; context pallid to dark brown or purplish-brown, trimitic; hymenophore one-sided, tubulate, often becoming stratified; tubes narrow; edges of dissepiments sterile; pores minute or small, nearly always regular.

Generative hyphae with clamps; skeletal may be branched in apical half; the binding hyphae may be rare. Cystidia and setae lacking. Basidia rather short,

swollen, 4-spored. Spores globular to ellipsoid, brown coloured (perhaps rarely only faintly so); walls complex, apart from very thin innermost and outermost layers, consisting of a firm, coloured inner layer provided with ornamentations piercing into or through the outer layer and a hyaline, comparatively thick outer layer; in one genus (*Ganoderma*) with an apical, conical or lens-shaped thickening which finally collapses and causes the spore to appear truncate.

Lignicolous.

Genera.—*Ganoderma* P. Karst. (sensu lato), *Amauroderma* Murrill (perhaps inclusive of *Lignosus* Torrend and *Whitfordia* Murrill: spores not seen by me).

This family is usually included in the Polyporaceae. It was introduced in the first place for those polypores with double-walled spores in which the inner layer was dark coloured and beset with an ornamentation piercing the hyaline outer one. At low magnifications such spores appear beset with spines at the surface.

The first mycologists to study the spores microscopically overlooked the outer, hyaline layer which fills up the spaces between the ornamentation of the distinctly coloured inner wall. It was Atkinson and later on Coleman (1927) who first laid the foundation of the correct understanding of the spore-wall structure. Their conclusions were recently confirmed and extended in details by means of electron-microscopic studies by Furtado (1962) and Heim (1962).

It was, in the first place, the unique structure of the spore-wall, as exposed by Coleman, that induced Donk to establish the present family (originally as a sub-family). The recent investigations cited above have shown that this structure is even more elaborate than was thought at the time of the conception of the taxon.

Heim concluded that the spore-wall showed considerable basic uniformity in the various species he had studied. He holds (i) that, because of this uniformity, Patouillard's comprehensive conception of *Ganoderma* (inclusive of *Amauroderma*) is correct; (ii) that there is consequently no room for placing it in a taxon of higher rank; and (iii) that the genus should be maintained merely as a member of Patouillard's 'Série des Placodes'. Ad (i). I shall not be surprised if, in the near future, not only *Amauroderma* is maintained as distinct from *Ganoderma* (inclusive of *Elfvigia*), but also some additional genera will be admitted on considerations other than the structure of the spore-wall. It appears that the hyphal structure of the fruitbody is less monotonous than might be thought from accounts so far published. It may also appear that even the spores of certain groups will offer useful features to support some of the segregates. Ad (ii) The fact of conceiving *Ganoderma* as a comprehensive genus does not necessarily lead to the conclusion that it should not form the sole representative of a taxon of higher rank. Ad (iii). Patouillard's 'Séries des Placodes' is such a heterogeneous mixture, that referring *Ganoderma* sensu lato back to it does not carry any positive taxonomic meaning. It may be that Heim thought in the first place of *Fomes fomentarius* (L. per Fr.) Fr. in which species the spore-wall is thin, simple, colourless, smooth, &c., but he failed to point out that these differences are of no taxonomic value above the generic level.

A number of Polyporaceae strongly remind one of *Ganoderma* by their truncate spores. However, these spores differ in the inner layer which lacks colour as well

as ornamentation and is relatively much thinner. Romell (1901: 20) simply included *Trametes ohioensis* Berk. in *Ganoderma*, remarking, "A typo *Ganoderm.* recedit haec species sporis subhyalinis . . . sed ob formam sporae aptissima in hoc genere locanda." Coker (1927: 133) agreed and Donk (1933: 230, 234) tentatively suggested inclusion in the 'Ganodermatoideae' also of the usually resupinate species of the group of *Poria medulla-panis* (Jacq. per Fr.) Cooke (Polyporaceae). This procedure was criticized by Overholts (1953: 45), who also pointed at some other species ("Fomes fraxinophilus, F. juniperinus, and F. ellisianus"), remarking that "in all of these, either constantly or at times, the spores have a truncate end, though they are not thick-walled."

Overholts's distrust of the association of *Ganoderma* with other species with somewhat similar and also truncate spores seems to have been well founded. From preliminary studies of the spores of *Perenniporia* and *Truncospora* (as well as a few other odd, non-European, species) I would now conclude that the truncation of the spores in these groups is of an entirely different nature from that in *Ganoderma*: it is not preceded by a lens-shaped or conical thickening of the outer wall. Moreover, although there is also a double wall in these pseudo-ganodermatoid spores, it would appear that there is no close further agreement in this respect either: the outer, most distinct, wall strongly absorbs Cotton Blue and then stands out as a kind of encasement; the inner wall is very thin, difficult to see, and remains uncoloured. In *Ganoderma* the situation is different (at least in the few species as yet tested): the outer wall remains hyaline and uncoloured while the coloured inner wall may become slightly darker and thus seems to absorb Cotton Blue. Recently Kotlaba & Pouzar (1963) stated that, in their experience, the cyanophily of the spore-wall was only apparent in the young uncoloured endosporium. These observations have still to be worked out more carefully and on a bigger scale, but on the whole they tend to support the maintenance of the Ganodermataceae as a distinct taxon because the gradual transition of its spore characters into those of the other polypores in the manner as indicated by Overholts is only seemingly true: in reality a sharp line of demarcation can be drawn. However, I do not want to overlook the possibility that species with less complex spores will become known and that these might tend to wipe out the distinction between the Ganodermataceae and certain groups of Polyporaceae (*Fomes*).

It is certainly incorrect to state that the apical truncation in the spores of *Ganoderma* is due to the presence of a germ pore, although it is known from White's studies (1919: 144 f. 1) that these spores germinate from the truncate end.<sup>29</sup>

Cunningham (1954: 47; 1955: 895) stated that clamps were lacking in *Elfvigia* P. Karst. (viz. the *Ganoderma applanatum* group) and (1954: 49) in *Amauroderma*. This is incorrect: as far as known all species of this family have clamped septa.

<sup>29</sup> Pilát (1942: 478) stated that "le pore germinative se trouve à la base de la spore". It seems hardly appropriate to see a germ pore in the channel between the spore contents and the sterigma.



As to the hyphal construction of the fruitbody, the few details given in the family description are primarily taken from Hansen's study (1958) of European species of *Ganoderma* and from a few other accounts scattered through the literature, although different interpretations have been published even for the same species. It is likely that the hyphal construction of certain extra-European species will not answer to the above characterization.

If one does not want to maintain this family on the basis of the short basidia and the quite remarkable spore structure, it will have to be associated, as far as I can see, with the Polyporaceae (and with *Trametes*, *Fomes* and related genera in particular) on account of the hyphal structure and several other features. Association of the Ganodermataceae and most of the Polyporaceae with the tubulate Hymenochaetaceae under a common family name (Mucronoporaceae) as was defended by Singer (1959: 372) is, in my opinion, unacceptable, because this implies an underestimation of the taxonomic isolation of the Hymenochaetaceae.

#### G O M P H A C E A E Donk

Ramariceae Donk, Rev. niederl. Homob.-Aphyll. 2: 103. 1933. — Type: "*Ramaria* (Holmskj. ex Fr.) Bon. em. Donk" ≡ *Ramaria* (Fr.) Bon. (name proposed for conservation), not *Ramaria* S. F. Gray.

Gomphoideae Sing. in Lloydia 8: 141. 1945 (lacking Lat. descr.). — Type: *Gomphus* (Pers. per Fr.) S. F. Gray.

[Tribu des Névrophyllés R. Heim in Revue Mycol. 19: 52. 1954. — Type: *Neurophyllum* Pat. apud Doass. & Pat.]

Neurophyllaceae Heinem. in Bull. Jard. bot. Brux. 28: 434. 1958. — Holotype: *Neurophyllum* Pat. apud Doass. & Pat. 1886, not *Neurophyllum* Torr. & Gray 1840 (Umbelliferae).

Gomphaceae Donk in Persoonia 1: 406. 1961. — Holotype: *Gomphus* (Pers. per Fr.) S. F. Gray.

Fruitbody effused, or stalked and pileate or coralloidly branched, the pileate species with flabelliform, turbinate to infundibuliform cap, either with one-sided hymenophore or in the coralloid species with amphigenous hymenium; context thin and loose to usually more or less fleshy and brittle to toughish, rarely gelatinous, white or pallid, monomitic or rarely rather imperfectly dimittic with skeletal; hymenophore smooth, wrinkled or more strongly folded (*Cantharellus*-like), also toothed.

Hyphae thin-walled, often inflating, may also become rather thick-walled, with clamps; in some species of *Ramaria* skeletal hyphae occur in the mycelium, rhizomorphs, or/and in the context of the fruitbody, the skeletal ending blindly in the flesh or, mostly, occurring as intercalary parts of generative hyphae and showing various imperfections. Hymenium thickening. Cystidia rare and then apparently hymenial leptocystidia; gloeocystidia quite exceptional. Basidia often slender club-shaped, chiasitic (as far as known), 2-4-spored. Spores almost invariably ellipsoid or more elongated, amygdaliform, subcylindrical, subsigmoid, of even general outline, ochraceous brown, rarely straw-coloured-olivaceous, cream, or practically colourless; wall roughened (with minute granules, warts, spines, ridges), rarely smooth, strongly absorbing Cotton Blue (cyanophilous), at least as to periphery and ornamentation, non-amyloid.

Terrestrial, more or less typically humicolous.

Genera.—

1. Fruitbody effused.
  2. Hymenophore smooth.—*Ramaricium* John Eriks.
  2. Hymenophore toothed.—*Kavinia* Pilát.
1. Fruitbody stalked.
  3. Fruitbody clavarioid, rarely truncate (subcantharelloid).
  4. Fruitbody branched.—*Ramaria* (Fr.) Bon., *Lentaria* Corner in part.
  4. Fruitbody simple.—Compare *Clavariadelphus* Donk (Clavariaceae)
  3. Fruitbody pileate.
    5. Hymenophore toothed.—*Beenakia* D. Reid.
    5. Hymenophore folded, cantharelloid.—*Gomphus* Pers. per S. F. Gray, *Chloroneuron* Murrill (spores straw-coloured-olivaceous, with ridges), *Gloeocantharellus* Sing. (gloeocystidia).

The above conception of this family is the result of a steady growth, which started when Maire remarked on the strong resemblance between the spores of some species now referred to *Gomphus* (cantharelloid) and *Ramaria* (clavarioid, branched). When Donk (1933) distributed the contents of the Friesian Clavariaceae over several taxa, he made of these two a special tribus, Ramariaceae. Then Eriksson (1954) described a corticiaceous genus *Ramaricium* and pointed out that it, and *Kavinia*, closely resembled *Ramaria* in both microscopical features and the affinity of the spores for Cotton Blue (cf. p. 239). This prompted Donk to extend the Ramariaceae with these genera and to raise it to family rank under the name of Gomphaceae. The fruitbody of *Kavinia* has been interpreted either as a crowd of small, simple clavarioid fruitbodies gregarious on a common subiculum, or as a resupinate hydnoaceous one. In the mean time Singer (1951: 733) had concluded that *Clavariadelphus* (clavariaceous, simple) was closely related to *Gomphus* (and some small taxa included in the latter by some authors). When I remembered that *Clavariadelphus* also turned dark green in contact with ferric sulphate solution (cf. p. 240) as did *Ramaria*, *Gomphus*, and *Kavinia*, I was tempted also to include *Clavariadelphus*, although it has smooth, almost colourless spores. In this respect it agrees with *Lentaria sensu stricto*, a genus hardly distinguishable from *Ramaria* and giving the same reaction. A recent addition to the family is made by Maas Geesteranus (1963: 437): *Beenakia*, with stalked, pileate, and hydnooid fruitbodies. The test with ferric sulphate solution may prove to be a valuable addition to the family character. (It has not yet been applied to *Ramaricium* and *Beenakia*.)

Heim's proposal (1954: 52) to concentrate the more or less cantharelloid element of this family (*Nevrophyllus* = *Gomphus sensu lato*, and *Clavariadelphus*) into a special tribus of the Cantharellaceae is not accepted here because *Gomphus* is certainly much more closely related to *Ramaria* than to the Cantharellaceae which is sufficiently distinguished by spore features (colour, lack of affinity for Cotton Blue), the lack of a positive reaction with ferric sulphate solution, and the stichic basidia.

The occurrence of skeletal in certain species of *Ramaria*, as described by Corner & Thind (1961), reminds one of the Pteruloideae (Clavariaceae). As in the latter group many of these skeletal are often more or less imperfect in one or two respects, but in the Pteruloideae the generative hyphae are not inflating.

HERICIACEAE Donk<sup>30</sup>

Hericiaceae Nikol. in Fl. Pl. crypt. URSS 6 (2): 212. 1961. — Holotype: *Hericium* Pers.

Fruitbody effused to effused-reflexed or pileate (may be attached at the vertex) or branched with a more or less outspoken tendency of the spines to grow downward, but also typically clavarioid and strictly growing upward; stalk may be present as a rooting base; hymenophore smooth or toothed; context fleshy to membranous (from cottony to toughish), white or pallid, amyloid in one genus, monomitic or perhaps rarely imperfectly dimitic with skeletal hyphae.

Hyphae all thin-walled or partially more or less thick-walled (walls rarely amyloid), with clamps, more or less inflated in fleshy portions. Euhymenium. Gloeocystidial hyphae present, terminating in the hymenium as gloeocystidia, not darkening with sulpho-aldehydes. Basidia club-shaped, chiasitic (as far as known), 4-spored. Spores typically globose to ovoid-ellipsoid and small to minute (3.5–6.5  $\mu$ ), colourless (white in a print); wall typically rather thick, smooth or with often scarcely discernible asperulation, amyloid.

Lignicolous, saprophytic, rarely parasitic.

Genera.—

1. Fruitbody fleshy, often big, with more or less strongly developed rooting base, branched (the branching may be strongly contracted) or the branching contracted and webbed to form a dorsiventral fruitbody.
2. Ultimate fertile branches (teeth) pointing downward (rarely spreading in various directions).—*Hericium* Pers. per S. F. Gray, *Creolophus* P. Karst.
2. Fruitbody typically clavarioid and growing upward.—*Clavicornia* Doty (at least in part).
1. Fruitbody different.
3. Hymenophore smooth.—*Laxitextum* Lentz, & compare *Gloeocystidiellum* in part (Corticaceae).
3. Hymenophore toothed.—*Dentipellis* Donk, *Steccherium* D. Reid.

At first Donk (1931: 160) removed *Hericium* in a broad sense (inclusive of *Dentipellis* and *Creolophus*) from the Hydneae and transferred it to the artificially conceived Corticiaceae (treated as a subfamily) because of agreement in microscopical details with the corticioid genus *Gloeocystidiellum*. More recently (Donk, 1962: 231), when the number of genera had increased, he spoke of a natural series of closely related genera that would be best included 'par enchainement' in the Corticiaceae; he was reluctant at that time to take the series out of that family because of the problem of where to draw the line between it and the remainder of the Corticiaceae. This problem is not yet satisfactorily solved but in the mean time still more genera could be added to the series (*Laxitextum*, *Steccherium*). Its disposition as a distinct entity had become more and more urgent and was also suggested by

<sup>30</sup> **Hericiaceae** Donk, *fam. nov.* — Aphyllophorales. Fructificationes typicae radicatae ramosae, ramificationibus laxis usque contractis, vel in pileum dorsiventralem conniventibus, aut coralloideo-erectae, aut ramificationibus ultimis modo dentium deorsum conversae; atypicae effusae usque appresso-reflexae, vel conchatae verticeque adfixae. Hymenophorum leve vel dentatum, euhymenio instructum. Systema hypharum in generibus centralibus monomiticum, hyphis inflatis fibulisque praesentibus. Hyphae gloeocystidiales et/vel gloeocystidia conspicua. Sporae hyalinae (accumulatae albae), parietibus levibus vel asperulatis, amyloideis. Lignicolae. — Typus: *Hericium* Pers. per S. F. Gray.

Reid (1963: 271) when he published *Steccherium*. The series is now made a distinct family with the provision that this is done on a tentative basis and with the hope that the limits with the Corticiaceae will eventually be more sharply defined.

The most typical group of this family consists of genera in which the fruitbody is in principle clavarioid and strongly branched. In some genera (*Heridium*, *Creolophus*) the fruitbody may originally tend to be more or less ageotropic but soon this trend is changed and the fertile branches grow downward and then are called teeth (hence the traditional inclusion among the Hydnaceae). Sometimes the downward trend sets in only imperfectly and then the clavarioid fruitbody produces branches which spread into various directions [cf. the form of *Heridium coralloides* (Scop. ex Fr.) S. F. Gray that has been referred to as *H. alpestre* Pers. by various authors]. *Clavicornia*, at least as far as *C. pyxidata* (Pers. per Fr.) Doty is concerned, seems to be a member of this alliance (gloeocystidia, amyloid spores, monomitic context) in which the fruitbody is strictly clavarioid in the sense that it grows upward without any tendency to positive geotropism.

After having isolated this kernel one is compelled to choose between restricting the Hericiaceae to this 'clavarioid' group or to let the microscopical features prevail. I have chosen the second alternative, which accounts for the inclusion of the other genera listed above.

The conspicuous gloeocystidial system is here taken to be of primary importance. This accounts for the exclusion of '*Heridium*' *bresadolae* (Quél.) Malenç. = *Mucronella fascicularis* (A. & S. per Fr.) Fr. (sensu Bres. 1903), which has amyloid spores and some vascular hyphae but apparently no gloeocystidial system. The exact position of *Mucronella* (in this paper tentatively kept in the Clavariaceae) is still to be determined. Some of its species have amyloid, and the others non-amyloid, spores.

*Amylaria*, which has strongly amyloid ornamentation on the spores, also lacks gloeocystidia and is provisionally included in the Bondarzewiaceae. *Heridium* was originally included in that family but in my opinion this is hardly its correct position.

The Auriscalpiaceae also possess a gloeocystidial system as well as amyloid spores, and two of its genera are hydroid. However, these points of agreement would appear to be sufficiently counterbalanced by other features such as the dimittic structure with skeletal and the gloeocystidial system reacting positively with sulphur-aldehyde solutions in the Auriscalpiaceae.

The Aphyllophorales with amyloid spores offer several very puzzling aspects. At first, when surveying them rather casually, one would conclude that they fall apart into several well-defined groups which do not appear to be mutually closely related. More careful scrutiny gradually changes this impression and a new image emerges for most of this mass, viz. of a protean-shaped rhizopod that withdraws or extends one or more of its 'feet' whenever a particular character is properly studied. The 'feet' represent groups or series which one is inclined to think of as clearly defined: somehow they seem to be mutually connected by a central body. When writing this down I see the following extensions: Auriscalpiaceae, Bondarzewiaceae (perhaps a compound one consisting of two, *Bondarzewia* and *Amylaria*), Echino-

dontiaceae, Hericiaceae, perhaps a small, 'resupinate' genus of Polyporaceae (unnamed), and, more doubtfully, *Vararia* and *Asterostroma* (Hymenochaetaceae). Some of these extensions seem to be rather definitely connected with the central core, mainly consisting of 'resupinates', and which is found lying over the limit-line of the Corticiaceae and Stereaceae. It may be that some of the extensions are not really connected with this core, but in these cases one would conclude that our knowledge is incomplete and, hence, their connection with the core out of focus.

The impression is strengthened if one associates the presence of gloeocystidia with the amyloid spore-wall, a combination found in several of the above mentioned groups. For instance, the hydroid genera of the Auriscalpiaceae remind one of the hydroid members of the Hericiaceae, but I do not yet see an uninterrupted connecting tract between the two. The hyphal construction of the Bondarzewiaceae is, on the whole, as yet poorly known, but the spores, with their peculiar ornamentation, are somehow reminiscent of those of the group of species around *Vararia dura* (Bourd. & L. Maire) John Erikss. (cf. Eriksson, 1954: 194; Hymenochaetaceae). The Echinodontiaceae may be connected through *Laurilia* with the stereoid element of the central core, although in this case too the real connecting tract is not very evident. As to the Hericiaceae, if they are broadly conceived, as they are above, the connection with the central core appears to be rather obvious, viz. through *Gloeocystidiellum* (effused, corticioid fruitbodies), and this is why I have long been reluctant to give this series a family name of its own. However, *Gloeocystidiellum* is not yet well defined and, in its present circumscription, is rather heterogeneous; some of its elements, that perhaps should be excluded, would link the series with *Aleurodiscus*. *Asterostroma* (cf. Eriksson, 1954: 195, for a discussion on the spores), I keep in the Hymenochaetaceae because of its setae. A possible point of contact of the Hymenochaetaceae (subfamily Vararioideae) with the 'central core' may be with *Scytinostroma* (cf. also p. 278).

In quite a number of instances the combination of an amyloid spore-wall and the presence of gloeocystidia is further strengthened by the fact that the spore-wall tends to be thickened and more or less ornamented. One is sometimes tempted to cut the Gordian knot and to ascribe a high taxonomic value to this combination of features and to make it the character of a family or order. Nothing would be more fallacious. In that 'central core' of resupinate genera all these features break down completely in various groups. An example is *Aleurodiscus* as quite recently restricted by Lemke (1964): some of its species lack gloeocystidia, others have not only thin spore-walls but also are devoid of any trace of ornamentation. The proposed restriction of *Aleurodiscus* to amyloid-spored species appears questionable: in any case one may well be disposed to admit that some groups with non-amyloid spores (*Cyphella* sensu stricto and others) are very closely related if not congeneric with *Aleurodiscus*. This corticioid element of the 'core' is now thought to be closely related to the stereoid one of which *Stereum* is an example (see p. 261). Other examples: the amyloidity of the spore-wall in *Vararia* runs from completely negative to com-

pletely positive, through some intermediate examples (cf. Eriksson, 1954: 194); and in *Scytinostroma* some species have amyloid and some non-amyloid spores. It is often thought that in many respects these two last genera are closely related to *Aleurodiscus*.

On the other hand the 'extensions' are all more or less sharply defined if the 'effused' genera are left out of consideration, and pending more complete knowledge of the corticioid and stereoid genera, it would seem practical policy to cut these series of genera off and treat them as distinct families, as far as they are easily definable.

#### HYDNACEAE Chev.

Hydnoideae Pers., Syn. Fung. xvii, 550. 1801 ("Hydnoidei"; [subordo] = subfam.; devaluated name). — Type: *Hydnum* L.

[Odontodermei Pers., Mycol. europ. 2: 150. 1825 ([subordo] = subfam.). — Lectotype: *Hydnum* L.; → Hydnoideae Pers. 1825.

Hydnoideae Pers., Mycol. europ. 2: 150. 1825 ("Hydnei"; [subordo] = subfam.), alternative name; Fr., Syst. Orb. veg. 80. 1825 ("Hydnei"; "subordo" = subfam.); P. Karst. in Bidr. Känn. Finl. Nat. Folk 25: 12, 286. 1876 ("Hydneae"); Nikol. in Fl. Pl. crypt. URSS 6 (2): 199. 1961 (typonym); not Hydnoideae S. F. Gray, Nat. Arr. Brit. Pl. 1: 597, 650. 1821 (type: *Hydnum* "Dillenius" [= L.] sensu S. F. Gray = *Sarcodon* P. Karst.); ≡ Odontodermei Pers.

Hydnaceae Chev., Fl. Env. Paris 1: 270. 1826 ("Ordre" = fam.); Fr., Epicr. 504, 595, 596. 1838 ("Hydnei") & Summ. Veg. Scand. 271 ("Hydnei"), 325 ("Hydnacci"). 1849 (ordo as a subdivision of a family); Corda, Ic. Fung. 3: 51. 1839, 5: 42. 1842, & Anl. Stud. Mycol. cv, 176. 1842 ("Hydnei"); Staude, Pilze Mitteleurop. xxiv ("Hydnei"), 44 ("Hydneae"). 1857; P. Karst. in Not. Sällsk. Fauna Fl. fenn. Förh. 9: 362. 1868 ("Hydnacci"; name only); in Medd. Soc. Fauna Fl. fenn. 5: 40. 1879 (name only) & in Bidr. Känn. Finl. Nat. Folk 37: xi. 1882 ("Hydneae Fr."); J. Schroet. in Krypt.-Fl. Schles. 3 (1): 450. 1888 ("Hydnacci"). — Type: *Hydnum* L. per Fr.

Hydneae Dumort., Anal. Fam. Pl. 73. 1829; Fr., Fl. scan. 338, 340. 1835 & Gen. Hym. 4, 12. 1836 ("Hydnei"); Endl., Gen. Pl. 1: 39. 1836 ("Hydnei"; typonym, ≡ Hydnoideae Fr.); Donk, Rev. niederl. Homob.-Aphyll. 2: 13. 1933; Nikol. in Fl. Pl. crypt. URSS 6 (2): 239. 1961 (typonym). — Type: *Hydnum* L. per Fr.

[Sect. Hydneae Duby, Bot. gallic. 2: 774. 1830 (inadmissible term denoting (rank) ≡ Hydnoideae Fr.)]

Hydninae Nikol. in Fl. Pl. crypt. URSS 6 (2): 302. 1961 ≡ Hydneae Donk.

Fruitbody pileate and stalked; hymenophore toothed; context fleshy, not zoned, white or faintly coloured, monomitic; stalk central to eccentric, well developed; spines typically terete, pointed.

Hyphae thin-walled, with clamps, inflating. Cystidia (and gloeocystidia) lacking. Basidia slender club-shaped, stichic, with 2-6 sterigmata; abortive basidia may be numerous. Spores subglobose, ovoid, to ellipsoid, small to medium-sized (4-10  $\mu$ ), colourless (in a print white or tinted yellowish; may turn 'buff yellow' in the herbarium), medium-sized; wall somewhat firm, smooth, non-amyloid.

Terrestrial, humicolous.

Genus.—*Hydnum* L. per Fr. (strongly reduced sense).

E x c l u d e d.—

Auriscalpiaceae.—*Auriscalpium*, *Gloiodon*.

Bankeraceae.—*Bankera*, *Phellodon*.

Clavariaceae.—*Mucronella*.

Coniophoraceae.—*Gyrodontium*.

Corticaceae.—*Cristella* spp., *Hyphoderma* spp., *Dacryobolus*, most species of *Hyphodontia*, *Mycocacia*, *Odontia* Fr. (residual genus, exclusive of type but inclusive of *Grandinia* spp.), *Sarcodontia*, *Sistotrema* spp.

Echinodontiaceae.—*Echinodontium*.

Gomphaceae.—*Kavinia*, *Hydnodon*, *Beenakia*.

Hericiaceae.—*Dentipellis*, *Stecchericium*, *Creolophus*, *Hericium*.

Hymenochaetaceae.—*Asterodon*, *Hydnochaete*, *Vararia* sp.

Polyporaceae.—*Irpex*.

Tremellaceae.—*Pseudohydnum* P. Karst. [*Tremellodon* (Pers.) Fr.].

Ascomycetes.—*Radulum* Fr.

Nomina dubia.—*Cystidiendron* J. Rick, *Grandinia* Fr., *Grandinochaete* J. Rick, *Irpicochaete* J. Rick., *Malacodon* Bataille, *Odontiochaete* J. Rick, *Radulochaete* J. Rick.

This family, in this very narrow sense, was first so defined by Donk (1933: 13, as a tribus) who associated it in one group of higher rank with the Cantharellaceae and Clavulinaceae, all having stichic basidia. In the mean time I have come to the conclusion that the Clavulinaceae form a rather independent group. The separation of *Hydnum* sensu stricto from the typical *Cantharellus* species into different families may not be merited but for the moment I am loath to merge the Cantharellaceae with the Hydneae under the latter name. For a discussion on stichic basidia see page 219.

In the Friesian classification the Hydneae comprised all hymenomycetes with a toothed hymenophore. Although many of the genera can be placed in various other families (including the present one), the residual portion is still significant. This situation necessitates the maintenance of an appendix to the re-defined family containing the genera of which the systematic (taxonomic or artificial) position is still uncertain.

### Appendix

#### Residual Hydneae, exclusive of type

[Sous-tribu Odonties Pat., Essai tax. Hym. 51, 58. 1900. — Type: *Odontia* Fr. 1835, not *Odontia* Pers. per S. F. Gray 1821.]

[Série des Odonties Pat., Essai tax. Hym. 58. 1900. — Type: *Odontia* Fr. 1835, not *Odontia* Pers. per S. F. Gray 1821.]

Unplaced genera of the former Hydneae. All strictly effused, monomitic species have been removed to the Corticiaceae. For an enumeration of those genera that have been assigned to other families, see above ("Excluded").

1. Context monomitic throughout.

2. Fruitbody stalked.—*Mycocleptodonoides* Nikol.

2. Fruitbody sessile.—*Donkia* Pilát, *Climacodon* P. Karst.

1. Context dimitic with skeletal, at least in part.

3. Context of teeth dimitic, of cap monomitic.—*Mycorrhaphium* Maas G.

3. Context dimitic throughout.—*Steccherinum* S. F. Gray.

1. Many as yet incompletely known species (fruitbody effused to stalked) of the traditional genus *Hydnum* L. per Fr. [bis].

In spite of the removal of many genera to other families, a residue remains which cannot be easily be accommodated, even provisionally, in such artificial families as

the Corticiaceae. This is not always because these genera are poorly known, but simply because the classification of the Aphyllophorales is not yet sufficiently advanced to allow them to be fitted in. The reorganization of the Aphyllophorales is being held up mainly because the Polyporaceae has yet to be revised.

#### HYMENOCHAETACEAE Donk

Boletoideae S. F. Gray, Nat. Arr. Brit. Pl. 1: 597, 639. Sept. 1821 ("Boletoideae"; [subfam.]). — Type: *Boletus* "Dillenius" [= L.] sensu S. F. Gray ('lectotype': *Boletus ignarius* L.; cf. Donk in *Persoonia* 1: 190. 1960), not *Boletus* L., Fr. Jan. 1, 1821.

[Série des Igniaries Pat., Essai tax. Hym. 77, 96. 1900. — Lectotype: *Phellinus* Quéf.]; → Igniariaceae R. Heim.

[Série des Astérostromes Pat., Essai tax. Hym. 114, 120. 1900. — Type: *Asterostroma* Mass.]; → 'Asterostromés Bourd. & G.'

[Sous-tribu Astérostromés Bourd. & G., Hym. France 143, 398. "1927" [1928] ≡ 'Série des Astérostromes Pat.']; → Asterostromeae Talbot.

[Astérostromellinés Bourd. & G., Hym. France 144, 394. "1927" [1928] (uninferable rank). — Type: *Asterostromella* Höhn. & Litsch.]; → Asterostromellaceae [?] Pilat; → Asterostromellinae Talbot.

Vararioideae Donk in Meded. Nederl. mycol. Ver. 18-20: 191. 1931. — Type: *Vararia* P. Karst.

Hymenochaetoideae Donk in Meded. Nederl. mycol. Ver. 18-20: 197. 1931; Rev. niederl. Homob.-Aphyll. 2: 236. 1933. — Type: *Hymenochaete* Lév.

Asterostromellaceae [?] Pilat in Bull. Soc. mycol. France 49: 34, 51. 1933 ("Asterostromellinae", but presumably intended as the name of a family; nomen nudum) ≡ ? 'Asterostromellinés Bourd. & G.'

[Igniariaceae R. Heim in Treb. Mus. Ci. nat. Barcelona 15: 61. 1934 (nomen nudum) ≡ 'Série des Igniaries Pat.'; no genus 'Ignarius' exists.]

Asterostromataceae Pilat in Bull. Soc. mycol. France 51: 414. 1936 ("Asterostromaceae"; nomen nudum). — Monotype: *Asterostroma* Mass.

Asterostromeae R. Heim in C.R. Acad. Sci., Paris 206: 1920. 1938 ("Asterostromae"; [trib. ?]; lacking Latin description and reference); Talbot in *Bothalia* 6: 5. 1951 (lacking Latin description); S. Ito in Mycol. Fl. Japan 2 (4): 106, 123. 1955 (lacking Latin description and reference); ≡ 'Sous-tribu Astérostromés Bourd. & G.'

Phaeoleae Bond. & Sing. in Ann. mycol. 39: 55. 1941 (lacking Latin description). — Monotype: *Phaeolus* Pat.

Inonoteae Bond. & Sing. in Ann. mycol. 39: 55. 1941 (lacking Latin description). — Type: *Inonotus* P. Karst.

[Mucronoporeae Imaz. in Bull. Tokyo Sci. Mus. No. 6: 102. 1943. — Holotype [!]: *Inonotus* P. Karst.

Hymenochaetaceae Donk in Bull. bot. Gdns, Buitenz. III 17: 474. 1948; Imaz. & Toki in Bull. Govt For. Exp. Sta., Tokyo No. 67: 24. 1954 (typonym). — Holotype: *Hymenochaete* Lév.

Asterostromelloideae Corner, Monogr. Clavaria 84. 1950 (lacking Latin description). — Type: *Asterostromella* Höhn. & Litsch.

Asterostromellinae Talbot in *Bothalia* 6: 5. 1951 (lacking Latin description) ≡ 'Asterostromellinés Bourd. & G.'

Asterostromeae Talbot in *Bothalia* 6: 5. 1951 (lacking Latin description); S. Ito, Mycol. Fl. Japan 2 (4): 106, 123. 1955 (lacking Latin description and reference); ≡ 'Sous-tribu Astérostromés Bourd. & G.'

Xanthochroideae Pinto-L. in Mem. Soc. broteriana 8: 167. 1952. — Type: *Xanthochrous* Pat. sensu Pinto-L. = *Inonotus* P. Karst.



Hymenochaetae G. Cunn. in Trans. roy. Soc. New Zeal. **81**: 174. 1953 (lacking Latin description). — Type: *Hymenochaete* Lév.

[Mucronoporaee Imaz. & Toki in Bull. Govt For. Exp. Sta., Tokyo No. 67: 25. 1954. — Holotype (!): *Phellinus* Quél.]

Varariae S. Ito, Mycol. Fl. Japan **2** (4): 105, 124. 1955 (lacking Latin description or reference). — Monotype: *Vararia* P. Karst.

Fruitbody appressed or effused and often partially reflexed, sessile, or stalked and pileate, may be attached at the vertex, also clavarioid and branched, annual to perennial; context varying from soft and loose, to fibrous and succulent, to often more or less toughish to leathery, or corky, woody, dark-coloured (various shades of brown, viz. rhubarb or darker), permanently darkening in KOH solution (may turn reddish first; xanthochroic reaction; exceptions few), monomitic or dimitic with skeletal; hymenophore smooth, tuberculate, toothed, tubulate (may vary to concentrically lamellate), but not radially lamellate.

Hyphae nearly always coloured, the generative ones in monomitic context either all of about the same width (often becoming somewhat thick-walled) or variable in width (the broadest may be firm-walled); in dimitic context generative hyphae thin-walled, the skeletal thick-walled; clamps lacking. Setae present in the great majority of species, but may be lacking, rarely star-like branched (asterosetae), usually simple; the latter may be of two types, viz. very long and big ones embedded in the trama (macrosetae), or the usual type found in connection with the hymenium, these protruding or (becoming) embedded. Dichohyphidia may be present, in a few genera also gloeocystidia. Basidia club-shaped, 2–4 spored. Spores colourless to distinctly brown coloured or sulfur- or greenish-yellow in a print (in the last two cases darkening to brown in KOH solution; hyaline spores may become coloured when remaining back in the tubes); wall thin to thick (and then often presumably double-walled), smooth, rarely ornamented, only in a few small groups amyloid.

Lignicolous, rarely terrestrial, several species parasitic (exceptionally on living leaves).

Genera.—

1. Dichohyphidia or asterosetae present, the latter not forming transitions to hymenial haplosetae. Spores often amyloid, smooth or ornamented. Gloeocystidia invariably present.
2. *Vararioideae* Donk. Dichohyphidia forming a dense layer over the sterile surfaces of the fruitbody; these surfaces completely or partially developing into a cathymenium which eventually may become superimposed by a waxy thickening hymenium. Setae lacking. Basidia may be more or less urniform. Spore-wall smooth and non-amyloid, or, in *Vararia*, often ornamented and amyloid in various degrees. Fruitbody cream-coloured, pallid, or from various shades of pale yellow, to dark-brown; fragments turn reddish in Melzer's reagent, hardly (or not) to distinctly darkening in dilute KOH solution.
3. Fruitbody resupinate; hymenial surface smooth, exceptionally granulariferous.—*Vararia* P. Karst.
3. Fruitbody clavarioid, branched; branches terete to flattened, the dorsal-ventral ones with one-sided hymenium; hymenophore smooth.—*Lachnocladium* Lév.
2. *Asterostromatoideae* Donk.<sup>31</sup> Asterosetae present, often very

<sup>31</sup> *Asterostromatoideae* Donk, *subfam. nov.* Hymenochaetaeae. Fructificatio effusa. Euhymenium. Gloeocystidia presentia. Contextus asterosetis instructus, maximis substrati proximitate, minoribus ad hymenium versus, hymenio ipso tamen deficientibus. — Typus: *Asterostroma* Mass.

variable, a number may resemble dichohypijidia, all situated in the context, the largest occurring in the basal region, decreasing in size toward the surface. Euhymenium lacking haplosetae. Fruitbody effused, with smooth surface. Spores more or less typically globose, *vide* Eriksson (1954: 193) smooth or in the majority of species echinulate (spines hollow), predominantly amyloid.—*Asterostroma* Mass.

1. Hymenochaetoidae Donk. Dichophyses lacking or, if present, also setae present; asterosetae exceptional, if present with transitions to, and replaced by, haplosetae in the hymenium; haplosetae and/or macrosetae usually present, but may be completely lacking. Euhymenium. Gloeocystidia lacking, or at least very exceptional. Spores smooth (exceptionally ornamented), non-amyloid as far as known.
4. Asterosetae in context, haplosetae in hymenium. Fruitbody effused; hymenophore toothed.—*Asterodon* Pat.
4. Haplo- and/or macrosetae present or lacking, no branched setae (except at abhymenial surfaces in a few species).
5. Fruitbody clavarioid or stereoid, stalked.—*Clavariachaete* Corner (setae present). — Compare *Phaeoaphelaria* Corner (Clavariaceae; setae lacking).
5. Fruitbody resupinate to pileate.
6. Hymenophore smooth, rarely granuliferous or warty.—*Hymenochaete* Lév.
6. Hymenophore raduloid to irpicoid.—*Hydnochaete* Bres.
6. Hymenophore tubulate; the radial dissepiments may be more or less obliterated, so that the hymenophore is typically to imperfectly concentrically lamellate. Polyporoid genera.—*Aurificaria* D. Reid, *Cyclomyces* Kunze ex Fr., *Coltricia* S. F. Gray (*Polystictus* Fr. sensu stricto), *Coltriciella* Murrill, *Flaviporellus* Murrill, *Inonotus* P. Karst., *Mucronoporus* Ell. & Ev. (*Onnia* P. Karst.), *Phaeolus* Pat., *Phellinus* QuéL., ? *Phylloporia* Murrill, *Xanthoporia* Murrill.

This is, in my opinion, a very well marked family. The group was first recognized by Patouillard (1900: 96) as "Série des Igniaires" and accepted by Donk (1933: 236; 1948: 474) in a somewhat emended circumscription by the inclusion of Patouillard's "Série des Astérostromes".<sup>32</sup> Thus emended the family includes genera with various kinds of hymenial configuration. Some authors (Imazeki & Toki, 1954: 24, 25) prefer two families here, based on the hymenial configuration, viz. Hymenochaetaceae ("hymenophorus aequalibus") and Mucronoporaceae ("hymenophorus inaequalibus, spinulosus, denticulatus, porosus"), but in my opinion such a disposition has little to recommend it. The present taxon is now also referred to as the 'Xanthochroic series' (Corner, 1948: 235; 1950: 22).

Most species are readily recognizable by the presence of setae that are believed to be unique in the Hymenomycetes (cf. p. 233). Although more or less similar bodies are known in other groups (for instance in *Marasmius*) it is safe to assume that in all these cases the resemblance is not complete. However, not all species of the Hymenochaetaceae possess setae while in some species they are very scanty. In these instances the combination of dark-coloured context turning

<sup>32</sup> Donk (1933: 236) also cited Patouillard's "Série des Echinodonties" as a synonym; this should be excluded (see p. 262).

permanently black (rarely at first dark reddish) in KOH solution, and the distinct and completely clampless hyphae form together a safe basis for the recognition of the polyporoid species. The dark colour (yellowish brown, reddish brown, or brown) is caused by pigmentation of the cell-walls. The absence of clamps was emphasized by Donk (1948: 474) when he established the family. Kühner (1950a) concluded that this character "est certainement une caractéristique de la plus haute importance de la série des Igniaries, car nous n'avons pas trouvé la moindre trace d'anses aux hyphes mycéliennes de toutes les espèces étudiées par nous . . . et dont le nombre dépasse la trentaine". Kühner (1950a, 1950b) also studied the behaviour of the mycelial nuclei of these species in culture. Corner (1950: 19) is of the same opinion: "The absence of clamps so distinguishes the Xanthochroic series . . . that their presence is proof that a species does not belong."

Nobles (1958b: 917) studied the cultural characters of about 40 polyporoid species, which proved to form such a homogeneous group that they were all placed (with the exception of *Phaeolus schweinitzii*) in a single division (her Key-section 65) which was not subdivided. This is very significant and may be taken as still another proof of the coherence of the group at least as far as the polyporoid species are concerned. I distrust her statement that "very rare clamp connections . . . have been observed in a number of species".

Another indication of the naturalness of the Hymenochaetaceae is the fact that all of the many species investigated in this respect appeared to produce extracellular oxidase in culture and are associated with white rots. Nobles (1958b: 902) listed only one exception, viz. *Polyporus schweinitzii* (genus *Phaeolus*), which she cited (Nobles, 1958a: 96, 97) as showing inconsistent reactions with the Bavendamm test and the gum guaiac test. This species is considered to be associated with a brown rot.

It seems quite likely that this family will be raised in rank and treated as an order consisting of a few families. In that case the Vararioideae and Asterostromatoideae would perhaps become families. How the rest should be subdivided is still difficult to predict: a mere breaking up according to the hymenial configuration (as was done by Imazeki) is not satisfactory. The trouble is that the generic conceptions are still insufficiently worked out in this family, and that most of the big genera (*Phellinus*, *Hymenochaete*) are still rather artificial and should become better known from a taxonomical point of view before too radical a reshuffling can be attempted.

In a sense, the Vararioideae, especially certain species of *Vararia*, conform poorly to the family character: not only are setae completely absent (as in some other genera or species of this family), but also the colour of the fruitbody may be almost pure white, the context may hardly, if at all, darken in KOH solution, and the spore-wall may be amyloid. The latter feature is shared only by most species of *Asterostroma*, as far as known. Gloeocystidia, which are typical of the Vararioideae, also occur in *Asterostroma*, but rarely elsewhere in the Hymenochaetaceae. This suggests that *Asterostroma* is a kind of link between the first and third subfamily recognized above. Dichohyphidia have also been reported for some tropical species of *Hymenochaete* (Corner, 1948: 244), but detailed information for comparison is

not yet available. However, this information supports the thesis that the dichomyphidia of the Vararioideae are modified hyphae and the more or less similar bodies which occur as variations of the variable asterosetae of *Asterostroma* are branched setae.

*Scytinostroma* (left in the Corticiaceae) has been thought to be closely related to *Vararia* by some authors: the context shows similar reactions with Melzer's reagent and dilute KOH solution, and the spores offer about the same variation in shape and in being amyloid in some, and non-amyloid in other species. Most of its species also have gloeocystidia. On the other hand there are marked differences. The usually well-developed context is worthy of note because of its narrow generative hyphae from which arise a system of abundant, thick-walled, strongly branched, non-septate, flexible hyphae which terminate at the surface of the fruitbody as dendrophyphidia; the generative hyphae of some of the species have clamps. *Scytinostroma* would seem more closely related to such corticiaceous genera as *Gloeocystidiellum*, which in its turn may well appear to belong to the Hericiaceae (see also p. 271).

#### POLYPORACEAE Corda

Daedaleoideae S. F. Gray, Nat. Arr. Brit. Pl. 1: 597 ("Daedaleoideae"), 638 ("Daedaleoideae"). 1821 ([subfam.]). — Monotype: *Daedalea* Pers.

[Porodermei Pers., Mycol. europ. 2: 34. 1825 ([subordo] = subfam.). — Lectotype: *Polyporus* [Mich.] Fr. per Fr.]

Polyporoideae Fr., Syst. Orb. veg. 79. 1825 ("Polyporei"; subordo = subfam.); Endl., Consp. Regni veg. 14. 1828 ("Polyporei"; nomen nudum); P. Karst. in Bidr. Känn. Finl. Nat. Folk 25: 11, 240. 1876 ("Polyporeae"); Donk in Meded. Nederl. mycol. Ver. 18-20: 126. 1931 (name only) & Rev. niederl. Homob.-Aphyll. 2: 110. 1933; Bond. & Sing. in Ann. mycol. 39: 58. 1941 (lacking Latin description and reference); Sing., Agar., 2nd Ed., 156. 1962 ("Bond. & Sing."; incomplete reference, lacking Latin description). — Type: *Polyporus* [Mich.] Fr. per Fr.

[Sect. Polyporeae Duby, Bot. gallic. 2: 781. 1830 (inadmissible term denoting rank) = Polyporoideae Fr.]

Polyporeae Fr., Fl. scan. 338, 339. 1835 & Gen. Hym. 4, 10. 1836 ("Polyporei"); QuéL., Ench. Fung. 164. 1886 ("Polypori"); J. Schroet. in Krypt.-Fl. Schles. 3 (1): 467. 1888 ("Polyporineae"; "Gruppe"); Engl., Syll. Vorl. Bot., Grosse Ausg., 39. & Kleine Ausg. 31. 1892 ("§"). — Type: *Polyporus* [Mich.] Fr. per Fr.

Polyporaceae Fr., Epicr. 408, 595, 603. 1838 ("Polyporei"; "ordo" as a subdivision of a family); Corda, Ic. Fung. 3: 49. 1839 ("Polyporei"); P. Karst. in Rev. mycol. 3/No. 9: 17. 1881 ("Polyporeae"); in Acta Soc. Fauna Fl. fenn. 2 (1): 28. 1881 (name only) & in Bidr. Känn. Finl. Nat. Folk. 48: 27, 275. 1887 ("Polyporineae"); J. Schroet. in Krypt.-Fl. Schles. 3 (1): 464. 1888 ("Polyporaceae"). — Type: *Polyporus* [Mich.] Fr. per Fr.

[Trib. Suberei QuéL., Ench. Fung. 153. 1886. — Lectotype: *Lenzites* Fr.]

[Ser. Mesopodes QuéL., Ench. Fung. 164. 1886. — Lectotype: *Caloporus* QuéL.]; → Mesopus QuéL.

[Ser. Pleuropodes QuéL., Ench. Fung. 167. 1886. — Lectotype: *Cerioporus* QuéL.]; → Pleuroporus QuéL.

[Ser. Apodes QuéL., Ench. Fung. 170. 1886. — Lectotype: *Placodes* QuéL.]; → Apus QuéL.

Daedaleae QuéL., Ench. Fung. 182. 1886 ("Daedalei"); Murrill in N. Amer. Fl. 9: 3. 1907. — Type: *Daedalea* Pers. per Fr.

[Ser. Mesopus Quél. *apud* Moug. & al., Fl. Vosges, Champ. in Louis, Dept Vosges 482. 1887 = Mesopodes Quél.]

[Ser. Pleuroporus Quél. *apud* Moug. & al., Fl. Vosges, Champ. in Louis, Dept. Vosges 483. 1887 = Pleuropodes Quél.]

[Ser. Apus Quél. *apud* Moug. & al., Fl. Vosges, Champ. in Louis, Dept. Vosges 485. 1887 = Apodes Quél.]

[Leucospori Pat., Hym. Eur. 83 (description), 133. 1887. — Lectotype: *Polyporus* "(Mich.) Karst." sensu Pat. = *Albatrellus* S. F. Gray.]

Lenziteae Fayod in Ann. Sci. nat. (Bot.) VII 9: 333 ("Lenzitinés"), 395 ("Lenziteineae"). 1889; Sacc. & P. Syd. in Syll. Fung. 14: 9. 1899 ([trib.], nomen nudum); Killerm. in Nat. PflFam., 2. Aufl., 6: 197. 1928. — Monotype: *Lenzites* Fr.

[Sous-tribu Porés Pat., Essai tax. Hym. 51, 75. 1900; Bourd. & G., Hym. France 144, 514. "1927" [1928]. (→ Poraceae Talbot). — Lectotype: "*Polyporus* Fr. . . pr. p." sensu Pat. = *Albatrellus* S. F. Gray.; → Poraceae R. Heim.

[Série des Polyposes Pat., Essai tax. Hym. 76, 77. 1900. — Type: "*Polyporus* Fr. . . pr. p." sensu Pat. = *Albatrellus* S. F. Gray.]

[Groupe . . . Les Polyposes vrais Pat., Essai tax. Hym. 76, 77. 1900. — Type: "*Polyporus* Fr. . . pr. p." sensu Pat. = *Albatrellus* S. F. Gray.]

[Série des Leucopores Pat., Essai tax. Hym. 77, 79. 1900. — Type: *Leucoporus* Quél.]

[Série des Leptopores Pat., Essai tax. Hym. 77, 83. 1900. — Type: *Leptoporus* Quél.]

[Groupe . . . Les Fomes Pat., Essai tax. Hym. 77, 86. 1900. — Type: *Ungulina* Pat.]

[Série des Trametes Pat., Essai taxon. Hym. 77, 87. 1900. — Type: *Trametes* Fr.]

[Série des Placodes Pat., Essai tax. Hym. 77, 102. 1900. — Lectotype: *Ungulina* Pat.]

Fomitoidae Murrill in Bull. Torrey bot. Cl. 32: 364, 490. 1905 ("Fomitidae"); not Fomitoidae Bond. & Sing. in Ann. mycol. 39: 53. 1941. — Type: *Fomes* (Fr.) Fr. sensu Murrill ('type': *Polyporus marginatus* Fr.).

Agaricoideae Murrill in Bull. Torrey bot. Cl. 32: 369. 1905 ("Agariceae"). — Type: *Agaricus* L. sensu Murrill = *Daedalea* Pers. per Fr., not *Agaricus* L. per Fr. 1821.

Poriceae Murrill in N. Amer. Fl. 9: 1. 1907 (for implied type genus, cf. Murrill in J. Mycol. 9: 89, 100. 1903); Killerm. in Nat. PflFam., 2. Aufl., 6: 174. 1928. — Type: *Poria* Pers.

Fomiteae Murrill in N. Amer. Fl. 9: 2. 1907. — Type: *Fomes* (Fr.) Fr. sensu Murrill ('type': *Polyporus marginatus* Fr.).

Daedaleae Murrill in N. Amer. Fl. 9: 3. 1907. — Type: *Daedalea* Pers. [per Fr.].

[Fam. Lenziteen R. Falck in HausschwForsch. 3: 44, 45. 1909. — Type: *Lenzites* Fr. sensu R. Falck = *Gloeophyllum* P. Karst.]

[Trib. Volvatae Murrill, North. Polyp. 60. 1914; West. Polyp. 2. 1915. — Holotype: *Cryptoporus* (Peck) Shear.]

Polystictaceae Rea, Brit. Bas. 10, 608. 1922. — Type: *Polystictus* Fr. sensu Rea [representative species: *Polyporus versicolor* (L.) per Fr.].

Trameteae Killerm. in Nat. PflFam., 2. Aufl., 6: 194. 1928. — Type: *Trametes* Fr.

Tyromycetaceae Donk, Rev. niederl. Homob.-Aphyll. 2: 141. 1933. — Type: *Tyromyces* P. Karst.

[Poraceae R. Heim in Treb. Mus. Ci. nat. Barcelona 15: 62. 1934 (nomen nudum) = 'Sous-tribu Porés Pat.']

Ungulinae R. Heim in Treb. Mus. Ci. nat. Barcelona 15: 62. 1934 (nomen nudum). — Type: *Ungulina* Pat.

Scutigerae Bond. & Sing. in Ann. mycol. 39: 44, 45, 47. 1941 (lacking Latin description). — Type: *Scutiger* Paul. per Murrill.

[Porioidae Bond. & Sing. in Ann. mycol. 39: 48. 1941 (lacking Latin description and reference; incorrectly derived); not Porioidae Bond., Trutov. Griby 35, 117. 1953. — Lectotype: *Fibuloporia* Bond. & Sing. (not validly published name), no genus *Poria* being admitted.]

- Tyromycetoideae Bond. & Sing. in Ann. mycol. **39**: 51. 1941 (lacking Latin description). — Type: *Tyromyces* P. Karst.
- Fomitoidae Bond. & Sing. in Ann. mycol. **39**: 53. 1941 (lacking Latin description); not Fomitoidae Murrill in Bull. Torrey bot. Cl. **32**: 364, 490. 1905. — Type *Fomes* (Fr.) Fr.
- Piptoporeae Bond. & Sing. in Ann. mycol. **39**: 53. 1941 (lacking Latin description). — Type: *Piptoporus* P. Karst.
- Ischnodermateae Bond. & Sing. in Ann. mycol. **39**: 54. 1941 (lacking Latin description). — Type: *Ischnoderma* P. Karst.
- Corioloideae Bond. & Sing. in Ann. mycol. **39**: 59. 1941 (lacking Latin description). — Type: *Coriolus* Quéf.
- Corioleae Bond. & Sing. in Ann. mycol. **39**: 59. 1941 (lacking Latin description). — Type: *Coriolus* Quéf.
- Oxyporeae Bond. & Sing. in Ann. mycol. **39**: 62. 1941 (lacking Latin description). — Type: *Oxyporus* (Bourd. & G.) Donk.
- Hirschoporeae Bond. & Sing. in Ann. mycol. **39**: 63. 1941 (lacking Latin description). — Type: *Hirschoporus* Donk.
- Trametiniae Imaz. in Bull. Tokyo Sci. Mus. No. 6: 72. 1943. — Holotype: *Trametes* Fr.
- Coriolineae Imaz. in Bull. Tokyo Sci. Mus. No. 6: 78. 1943. — Holotype: *Coriolus* Quéf.; → Corioloideae Bond. & Sing.
- Tyromycetinae Imaz. in Bull. Tokyo Sci. Mus. No. 6: 83. 1943. — Holotype: *Tyromyces* P. Karst.
- Piptoporinae Imaz. in Bull. Tokyo Sci. Mus. No. 6: 88. 1943. — Holotype: *Piptoporus* P. Karst.
- Fomitinae Imaz. in Bull. Tokyo Sci. Mus. No. 6: 90. 1943. — Holotype: *Fomes* (Fr.) Fr.
- Favolinae Imaz. in Bull. Tokyo Sci. Mus. No. 6: 93. 1943. — Holotype: *Favolus* "Fries" sensu Imaz. ("Typus: *F. alveolarius* Bosc. [= DC.] ex Fries").
- Polyporinae Imaz. in Bull. Tokyo Sci. Mus. No. 6: 96. 1943. — Holotype: *Polyporus* [Mich.] Fr. per Fr.
- Cryptoporeae Imaz. in Bull. Tokyo Sci. Mus. No. 6: 110. 1943. — Holotype: *Cryptoporus* (Peck) Shear ("Hubbard").
- [Trib. Poreae Talbot in Bothalia **6**: 5. 1951 (lacking Latin description) ≡ 'Sous-tribu Porés Pat., Bourd. & G.']
- Cladodendronoideae Pinto-L. in Mem. Soc. broteriana **8**: 159. 1952. — Monotype: *Cladodendron* Lázaro.
- Leptoporoideae Pinto-L. in Mem. Soc. broteriana **8**: 159. 1952. — Type: *Leptoporus* Quéf.
- Trametoideae Pinto-L. in Mem. Soc. broteriana **8**: 161. 1952. — Type: *Trametes* Fr.
- [Phraeochoideae Pinto-L. in Mem. Soc. broteriana **8**: 164. 1952. — Lectotype: *Gloeophyllum* P. Karst.]
- Cladomeroideae Pinto-L. in Mem. Soc. broteriana **8**: 165. 1952. — Type: *Cladomeris* Quéf. sensu Pinto-L. [representative species: *Polyporus giganteus* (Pers.) per Fr.].
- Mensularioideae Pinto-L. in Mem. Soc. broteriana **8**: 166. 1952. — Type: *Mensularia* Lázaro sensu Pinto-L. [only species, "*Ungulina ulmaria* (Sow.) Pat."].
- Porioideae Bond., Trutov. Griby 117. 1953 (lacking Latin description or valid reference). — Type: *Poria* "(Fr.) Karst." sensu Bond. (type: "*P. vulgaris* (Fr.) Cke sensu Rom."); → Porioaceae Locq.
- Caloporoideae Cejp, Houby **2**: 63 (& cf. p. 61). 1958 ≡ Cladodendronoideae Pinto-L.; (lacking Latin description; type changed by implication ? to *Caloporus* Quéf. 1886, not *Caloporus* P. Karst. 1881).
- Porioaceae Locq. in Bull. Jard. bot. Brux. **27**: 560. 1957 (nomen nudum; incomplete reference); Kreisel, Phytopath. Grossp. Deutschl. **140**. 1961 (lacking Latin description); ≡ Porioideae Bond.
- Corioloideae Bond. & Sing. in Publ. Inst. Micol. Univ. Recife No. 304: 6. 1961 ≡ Coriolineae Imaz.

Fruitbody extremely variable not only in shape (from truly stalked to effused, but never typically clavarioid except in abnormal specimens), but also in consistency, structure, and colour of context, annual or perennial; hymenophore one-sided, usually tubulate, rarely more or less radially (exceptionally concentrically) lamellate, or 'irpicoid' (viz., with flattened 'teeth' or ridges more or less reticulately or radially connected at their base by low dissepiments), may be layered when tubulate, the dissepiments sterile on edge from the first but for the rest fertile, the tubes not free from each other.

Context tri-, di-, or monomitic, if the prominent hyphae (skeletal) are distinctly coloured and darken in KOH solution then with clamped septa in the thin-walled hyphae, (when the context is white, pallid, or bright-coloured all hyphae may be clampless). Setae lacking. Basidia not typically urni- or utriform, chiasitic (as far as known), 2-4-spored. Spores neither as described for the Ganodermataceae and the Bondarzewiaceae nor bluntly and coarsely tuberculate, hyaline (white or perhaps rarely cream in a print); wall exceptionally ornamented, may be rarely pseudoamyloid, still more rarely amyloid.

Lignicolous or terrestrial, humicolous.

Genera. <sup>33</sup>—

*Albatrellus* S. F. Gray, *Grifola* S. F. Gray (inclusive of *Meripilus* P. Karst.), *Porodiscus* Murrill, *Hologloea* Pat., *Polyporus* [Mich.] Fr. (inclusive of *Polyporellus* P. Karst. = *Leucoporus* Quéll., *Favolus* Fr. 1828, *Hexagona* Pollini per Fr. 1825 sensu stricto, *Melanopus* Pat., *Echinochaete* D. Reid), *Pseudofavolus* Pat. (closely related to *Mycobonia*, Stereaceae), *Elmerina* Bres., *Xerotinus* Reichenb. (*Xerotus* Fr.), *Piptoporus* P. Karst., *Cryptoporus* (Peck) Shear, *Microporus* P. Beauv. per O.K., *Coriolus* Quéll., *Trametes* Fr. (inclusive of *Pseudotrametes* Bond. & Sing. ex Sing., *Pycnoporus* P. Karst., *Poronidulus* Murrill, &c.), *Corioloopsis* Murrill, *Scenidium* O.K. (inclusive of *Pogonomyces* Murrill, *Hexagona* auct. pr. p.), *Daedaleopsis* J. Schroet., *Globifomes* Murrill, *Fomes* (Fr.) Fr. (inclusive of *Phaeodaedalea* K. Fidalgo?), *Fomitopsis* P. Karst., *Lenzites* Fr., *Gloeophyllum* P. Karst. (whether or not inclusive of *Phaeocoriolus* Kotl. & Pouz., *Osmoporus* Sing.), *Laricifomes* Kotl. & Pouz., *Heterobasidium* Bref., *Ischnoderma* P. Karst., *Hirschioporus* Donk, *Trichaptum* Murrill, *Skeletocutis* Kotl. & Pouz., *Antrodia* P. Karst. (correct sense; syn., *Corioloellus* Murrill), *Irpex* Fr., *Chaetoporus* P. Karst., *Laetiporus* Murrill, *Postia* P. Karst. sensu lato (syn., *Tyromyces* P. Karst.), *Spongipellis* Pat. (inclusive of *Ipiciporus* Murrill, *Aurantiporus* Murrill), *Amylocystis* Bond. & Sing., *Climacocystis* Kotl. & Pouz., *Hapalopilus* P. Karst. (artificial sense), *Schizopora* Velen. (closely related, presumably, to *Hyphodontia* in part, Corticiaceae), *Chaetoporellus* Bond. & Sing. ex Sing. (restricted to type species), *Oxyporus* (Bourd. & G.) Donk, *Rigidoporus* Murrill (inclusive of *Leucofomes* Kotl. & Pouz.), *Hydnopolyporus* D. Reid, *Flaviporus* Murrill, *Ceriporia* Donk, *Lindtneria* Pilát, *Truncospora* Pilát, *Perenniporia* Murrill (*Poria* Pers. per S. F. Gray sensu stricto), *Poria* Pers. per S. F. Gray (residual genus), &c.

Excluded.—

1. Basidia not septate.
2. Hymenophore composed of crowded free tubes.—Fistulinaceae; certain genera

<sup>33</sup> This is not a complete list of genera. I have not yet been able to make up my mind about the character or circumscription of many of them. A considerable number of species could not be accommodated in any of the more or less natural genera now recognized. Several genera are still artificially conceived, often in addition to a restricted circumscription: these are in the first place the genera accepted by Fries, and *Poria* and other ones. The polyporoid fungi have not been taken into consideration in the alphabetical enumeration at the end of this paper.

- or species of the Schizophyllaceae and of the residual 'Cyphellaceae' (p. 288).
2. Hymenophore not composed of crowded free tubes.
  3. Fruitbody reminiscent of agarics, stalked to sessile or attached at the vertex; cap not zonate in any sense, usually more or less fleshy membranous, or gelatinous. Hymenophore often with imperfect tubes because the radial dissepiments more or less suggest gills. Spores may be amyloid.—Agaricales: Boletaceae (spores coloured, rarely almost colourless); *Campanella* P. Henn., *Dictyopanus* Pat., *Favolaschia* (Pat.) Pat. apud Pat. & Lagerh., *Filoboletus* P. Henn. (nomen dubium), *Marasmius* spp., *Mycena* spp., *Mycenoporella* Overeem, *Poromyceia* Overeem (all with colourless spores).
  3. Different.
    4. Edge of dissepiments sterile.
      5. Spores remarkable in one of the following respects.
        6. Spores with conspicuous amyloid projections. Fruitbody usually big and compound.—Bondarzewiaceae: *Bondarzewia*.
        6. Spores non-amyloid.
          7. Spores bluntly and coarsely tuberculate when mature.—Thelephoraceae: *Boletopsis*.
          7. Spores with compound wall, the main inner layer brown coloured, ornamented, the main outer one hyaline; often apically truncate.—Ganodermataceae.
      5. Spores different.
        8. Setae often present somewhere in the fruitbody, usually abundant in the hymenium. Context 'xanthochroic'. Clamps completely lacking.—Hymenochaetaceae: polyporoid genera.
        8. Setae lacking. If the context is dark coloured and darkens in KOH solution then with clamps on the generative hyphae.
          9. Hymenium lining only the bottom of the tubes, the dissepiments sterile.—Corticaceae: *Porogramme*.
          9. Basidia urniform; sterigmata may exceed 4 per basidium.—Corticaceae: *Sistotrema* spp., *Echinotrema*.
          9. Fruitbody effused; hyphae more or less typically ampullaceous at a number of septa. Spores ellipsoid, smooth or echinulate, small.—Corticaceae: *Cristella* spp.
    4. Edge of dissepiments fertile: hymenium continuous, more or less strongly meruloid, may even appear typically tubulate.
      10. Spores double-walled; inner wall often brown coloured, strongly absorbing Cotton Blue.—Coniophoraceae: *Serpula* (inclusive of *Leucogyrophana* and *Meruliporia* Murrill).
      10. Spores colourless, thin-walled.—Corticaceae: *Merulius* (inclusive of *Caloporus* P. Karst.), *Gloeoporus*, *Athelia* spp., *Phlebia* spp., &c.
  1. Basidia septate, tremellaceous.—Tremellineae: *Aporpium* Bond. & Sing. ex Sing.

As here conceived the Polyporaceae is merely a container of all 'polypores' not (yet) assigned to other families. That already many of its species have been removed can be seen from the above enumeration of excluded groups.

"... the family is a grade, or artificial assemblage, of fungi of diverse affinity, at a common level of developing tubes on the underside of the fruit-body. Some are related with clavarioid genera, others with stereoid, hydroid and, even, agaricoid. Indeed, because of this heterogeneous origin and because of their very intricate construction, I believe that the natural classification of the polypores will be the



hardest problem in the systematics of Basidiomycetes."—Corner (1953: 152).

Although it is possible to point to some coherent series of genera, I am not yet prepared to subdivide the 'family' into lesser natural taxa without retaining an unwieldy remnant of genera of uncertain position. I hope to return to the 'polypores' in greater detail on a future occasion.

Several attempts have been made to divide the above conglomerate into smaller families, and a rather small portion of it has sometimes been considered as belonging to the Agaricales. This latter question may be discussed in some detail first.

As long as the hymenial configuration was all-important in the classification of the Hymenomycetes, polyporaceous genera with more or less typically lamellate hymenophore like *Xerotus* Fr.  $\equiv$  *Xerotinus* Reichenb. (original sense) and *Lenzites* Fr. (wide sense) were of course assigned to the agarics, but not without comment. Thus, Fries (1874: 492) remarked under *Lenzites* (which he kept in the Agaricini), "Species Europaeae dimidiatae, sessiles, persistentes, lignatiles, tota facie *Daedalearum*", the latter genus being placed among the Polyporei. He considered *Daedalea* and *Lenzites* as intermediate between the two families (p. 495). There is no hesitation at present considering these genera as polyporaceous.

The first author to consider a group of more or less tubulate polypores as agaricaceous was Fries (Syst. Orb. veg. 76. 1825) who expressed himself in connection with *Favolus* (P. Beauv. per Fr.) Fr. (sensu Fries) in a manner that leaves no room for misunderstanding: "Genus certe Agaricoideum et lamellosum, quamquam lamellae, *A. involuti* instar, anastomosantes ad Polyporeos transitum indicant." Patouillard (1890) agreed; he actually transferred *Favolus* Fr. 1828 from the Polyporaceae to the agarics. In addition, he remarked that *Favolus* formed together with *Lentinus* Fr. a small distinct family comprizing one genus with gills and one with alveoles. However, it should be remarked that one of the main features on which Patouillard founded his conclusions, viz. the presence of hyphal pegs in both, is not tenable since hyphal pegs later appeared to be quite common in many groups of the polypores. Afterwards Patouillard (1900: 134-138) recognized among the Agaricaceae a "Série des *Lentinus*" in which he placed some genera now scattered over various groups of Agaricales and also *Lentinus* and *Favolus*.

One of the first authors to express the opinion that certain typical species of *Polyporus* sensu stricto were related to true agarics was van Overeem (1924: 3): "Zweifellos hängt die Gattung *Polyporus* phylogenetisch mit den grosssporigen *Pleurotus*-Arten zusammen. Mit anderen holzigen, kleinsporigen Gattungen der Polyporaceae hat sie phylogenetisch nichts zu tun." van Overeem restricted *Polyporus* to only the group of *Polyporus squamosus* (Huds.) per Fr. ("Sporen gross, farblos, glatt, länglich ellipsoidisch") of which he had more closely studied *P. udus* Jungh.; he referred the other groups of the genus, presumably including the *P. brumalis* and *P. varius* groups, to 'the small-spored genera which had nothing to do with it', which stamps his sweeping statement as unbalanced. If he had accepted a broader concept of *Polyporus* the same statement would have more closely anticipated a modern trend. The next year van Overeem (1925) expressed the opinion that

*Polyporus*, as emended by him, was agaricaceous and entered it with the big-spored species of *Pleurotus* (Fr.) Kumm. into the Pleurotaceae, a family he subordinated to the Agaricales. When studying the hyphal construction of *Polyporus squamosus*, Corner found that the originally monomitic context of the cap produced numerous binding hyphae at a relatively late stage of development of the fruitbody. In this connection he remarked (1953: 162) that "it is worth mentioning that the oblong spore and narrowly clavate basidia of *P. squamosus* resemble those of *Pleurotus*, in the Agaricaceae, some tropical species of which have similar, if less precise, binding hyphae. *P. squamosus*, as a favoloid polypore with inflating hyphae and early developed pores is probably related with these agaric forms."

After these and other preliminaries it is not surprising that recently several authors have once more transferred *Polyporus* to the Agaricales (Locquin, 1957; Singer, 1959: 378; 1962: 150 sqq.; Kreisel, 1961, and others), however, without making the slightest attempt to give redefinitions of the generic and the family character (Locquin, Singer, 1959, Kreisel) or providing completely inadequate ones (Singer, 1962). Singer transferred the genera *Polyporus* in a rather broad sense [inclusive of *Asterochaete* (Pat.) Bond. & Sing. = *Echinochaete* D. Reid], *Pseudofavolus*, and *Mycobonia* (smooth hymenophore with protruding hyphal pegs) as a tribus to the Agaricales, where he included them with the tribus *Lentinae* in the family Polyporoaceae. His comment is unsatisfactory and could not be otherwise because his and other current knowledge of for instance the hyphal construction in both the agaric and the polyporoaceous groups involved, is still too limited.

The only precise information we have in this respect about the agaric element has been contributed by Kühner (1929; 1963) for *Lentinus variabilis* (S. Schulz. ex Quél.) Quél. [= *L. cyathiformis* (Schaeff. per Fr.) Bres.] and *L. adhaerens* (A. & S. per Fr.) Fr.: these species, one would conclude, seem to possess a dimitic context with skeletal and thus come closer, presumably, to *Polyporus maculatissimus* Lloyd (cf. Reid, 1963: 290) than to *P. squamosus*, in which the context is dimitic with binding hyphae of the bovista-type (Corner, 1953: 157 *fs.* 8, 9). Does this indicate that *P. maculatissimus* and *P. squamosus* are not congeneric? At our present state of knowledge this question is difficult to answer in the affirmative. These few analyses could suggest that species with both skeletal and binding hyphae (*viz.* with strictly trimitic context) may well appear related to *Polyporus*; and the circumstance that the binding hyphae in *P. squamosus* appear at a late stage (not until the well-formed pileus is 9–12 cm in radius, or 12–20 cm wide, according to Corner) may even suggest close relationship to species with monomitic context. None of Singer's descriptions of the agaric and polyporooid genera of his Polyporoideae contains information bearing upon hyphal construction. Besides the above mentioned analyses only a few further adequate ones are available for some other species of *Polyporus*; these indicate that this genus contains in the main species with dimitic context with binding hyphae of the bovista-type, but several groups of the genus are still *terra incognita* in this respect. In view of this situation it is judicious to resort to the least disturbing arrangement and to maintain an artificial 'family' Poly-

poraceae in a broader sense among the Aphyllophorales until better founded solutions are possible. At this early stage in the investigation I am not prepared to undertake the task of those authors who already admitted a family of Polyporaceae sensu stricto among the Agaricales, but who have unanimously neglected to publish proper modern definitions or other workable directives for recognition of the family and the groups to be included.

Acceptance of a family of Polyporaceae as envisaged by the above mentioned authors would imply the exclusion from the family of a big portion of the polypores. Locquin suggested 'Poriaceae (= Porées)' (not validly published) for the comprehensive excluded part; in so doing he overlooked the existence of the names Ganodermataceae and Hymenochaetaceae. Kreisel took up the designation 'Poriaceae Locquin' (still not validly publishing it) but restricted it by excluding both the Ganodermataceae and the Hymenochaetaceae, as well as the Bondarzewiaceae.

Recently Singer has supplied another family name, Corioliaceae "fam. nov. Characteribus Coriolarum (subtribus, Imazeki, l.c. [34]) gaudet. Genus typicum: *Coriolus* Quélet." This may be valid nomenclature but is hardly sound taxonomy, since again it contributes nothing to a better understanding or characterization of either those Polyporaceae that were shifted to the Agaricales, or of the 'Corioliaceae', left in the Aphyllophorales. Quite a number of examples were listed of these 'Corioliaceae', but there is no explanation either as to why such genera as *Flaviporus*, *Xerotus*, *Oxyporus*, and *Whitfordia* were listed in connection with *Coriolus* from which they would seem to differ widely, or why certain other genera difficult to separate from *Coriolus* (such as *Trametes*) were left out. No family name was provided for the rest of the polypores which were not transferred to the Agaricales and the Corioliaceae. It would be easy to suggest a family name in advance for this residue before it is properly defined, but I can see no gain in providing names for groups which one is not yet able to characterize even approximately. Nomenclature has been called the handmaiden of taxonomy; it should not become its forerunner. It is my considered opinion that at present our knowledge is as yet insufficient to decide with confidence whether or not a family limit can be drawn between *Polyporus* and *Coriolus*. (I incline to the opinion that this cannot be done.) Too little is known of a vast group of species among which connecting links may appear to be hidden. It is quite possible that in the future, and after considerable careful and time consuming work, the Polyporaceae and the Corioliaceae (if they are to be separated at all), both in a strongly emended circumscription, will gradually be shaped into natural taxa. As discussed elsewhere (p. 267) I would not be surprised if in that case

<sup>34</sup> Subtribus Coriolarum Imazeki (1943: 78): "Fructificatio annua vel raro perennis, lignicola, sessilis vel effuso-reflexa; superficies pilei glabra vel hirsuta, frequenter subcutis formata, contextus coriaceus vel coriaco-suberosus, cum trama hymenophori subhomogeneous; hymenophorus tenui, tubulosus, sed facile deformatus (daedaloides, lamelliformis vel irpici-formis); sporae hyalinae, leves. / Typus: *Coriolus* Quélet." Genera: *Irpex* Fr. sensu Bond. & Sing., *Coriolus*, *Oxyporus* Donk, *Hirschioporus* Donk, *Antrodia* P. Karst. sensu Bond. & Sing.

some authors decided to place *Coriolus* and the Ganodermataceae into the same family (which would provide an earlier family name for the 'Corioliaceae').

Bondartsev & Singer (1941: 43-45, 47) introduced a new family, Scutigeraceae<sup>35</sup> for three of the genera retained here in the Polyporaceae, viz. *Scutiger* (in which they also included *Albatrellus*), and *Grifola* (which they called *Polypilus* P. Karst.), as well as a further genus, *Bondarzewia*, which more recently has been made the type of a distinct family (see p. 247). The character of the Scutigeraceae was very unsatisfactorily indicated as 'the fleshy "polypores" with white spores'. In later work (Bondartsev & Singer, 1943) entered into greater detail: Fruit-bodies with simple or compound, stalked caps, when compound arising from a common stump; consistency more or less fleshy; taste when old frequently somewhat bitter or adstringent; growing on the soil, at the base of stumps, or occasionally on tree trunks. Hyphae without clamps. Spores slightly apiculate, hyaline, thin-walled, and smooth, or occasionally with a definite, amyloid perispore in the shape of rollers. Cystidia and setae absent.<sup>36</sup> This characterization is still not very helpful and partly incorrect: clamps have been seen in some or all species of all four genera, and strongly apiculate spores are typical of, for instance, *Scutiger*. The family was referred to the suborder Clavariineae, which was not defined at all and only vaguely outlined by the mention of some examples. Several of the genera of the Clavariineae were believed to correspond to groups in the Scutigeraceae; thus, *Polyporus confluens* (*Albatrellus*) was regarded as only little different from *Hydnum repandum*, if one did not consider the effiguration of the hymenophore; it was thought remarkable that *Bondarzewia* had amyloid spores like '*Pleurodon*' (= *Auriscalpium* S. F. Gray) and *Hericium* Pers. per S. F. Gray; on the whole fleshy humus-lovers were stated to be common throughout the Clavariineae and it was implied that this was also the case with the Scutigeraceae; and for the multipileate forms of *Grifola* and *Bondarzewia* an analogue was found in some species of *Cantharellus* Adans. per Fr.!

All these points of agreement are hardly of great taxonomic importance. Both *Grifola* and *Bondarzewia* are rather wood-loving genera although the connection between the fruit-bodies and the woody substratum is not always obvious at once. Of *Scutiger* (restricted sense) I am not yet convinced that it is not connected in some way with tree-roots. It would be interesting to know whether or not the basidia of *Albatrellus confluens* are stichic as this might throw further light on its suggested connection with *Hydnum repandum*.

Singer (1962: 113) has come to the conclusion that "a careful revision of the tramal structure of all Strobilomycetaceae and Boletaceae . . . has established the fact that all boletes have more or less bilateral hymenophoral trama, a structure unknown in the Polyporaceae [sensu Singer] and polyporoid Aphyllophoraceae. White spore print also does not exist in the Boletaceae and Strobilomycetaceae . . ."

<sup>35</sup> Bondartsev (1953: 597) ascribed the family name to Murrill, but I have been unable to locate it in Murrill's publications.

<sup>36</sup> This description was adapted from an unpublished translation of the Russian paper made under the supervision of Dr. W. B. Cooke.

Yet, it is worth while to explore again carefully the differences between *Albatrellus* (stalked, fleshy, terrestrial polypores including some species with bluing flesh) and certain Boletaceae like *Gyroporus* Quél., with pale (yellowish) spores.

#### PUNCTULARIACEAE Donk<sup>37</sup>

Fruitbody appressed or appressed-reflexed, loosely attached; cap-like portion tomentose; context membranous, monomitic, on section showing a dark, thin abhymenial layer, a hyaline, somewhat gelatinous middle layer, and a compound, gelatinous hymenophore with hymenium; hymenial surface appearing strongly knobby when fresh, the crowded knobs tending to be radially elongated, the hymenophore consisting of cushions separated by sterile, narrow fissures filled up with amorphous mineral matter.

Hyphae with clamps, those of the abhymenial layer and its hairs, dark, distinct, thick-walled, those of the middle layer with gelatinous walls. Catahymenium: the mature basidia protruding beyond a compact layer of dendrohyphidia. Dendrohyphidia consisting of a hyaline, thick-walled stem and a brown knobby-branched terminal portion. Gloecystidia lacking or present. Basidia slender club-shaped, 4-spored. Spores ovoid, ellipsoid, adaxially flattened, colourless; wall thin, smooth, non-amyloid.

Lignicolous.

Genus.—*Punctularia* Pat. (inclusive of *Phaeophlebia* W. Cooke).

The two or three species of this remarkable genus have been placed in various Friesian genera. Patouillard was the first to discover that the knobs and folds (often likened to those of typical species of *Phlebia*) were not really what they appeared to be, but were distinct cushions covered by the hymenium and separated by narrow, sterile troughs. This led him to conceive *Punctularia tuberculosa* Pat. (the only species he admitted to his genus) as comparable to *Porothelium* (= *Stromatoscypha*) but with convex rather than concave individual fruitbodies, and to enter the genus as one of the cyphellaceous fungi. This was for lack of a better classification and has found little support, but it paid due respect to the singular construction of the (compound) hymenophore. Some years ago, when he restudied the genus, Talbot (1958: 143) also detected the great similarity between *Punctularia* and *Phaeophlebia* and I believe he was correct in combining the two into a single genus. He was also the first to recognize that "there might be a good case for the proposal of a new family to accommodate *Punctularia*".

By its abundant and densely crowded dendrohyphidia the hymenium reminds

<sup>37</sup> **Punctulariaceae** Donk, *fam. nov.* — Aphyllophorales. Fructificatio substrato appressa vel pro parte reflexa, sectione stratum abhymeniale obscurum tenue, deinde stratum medium hyalinum subgelatinosum, deinde hymenophorum compositum praebens. Hymenophorum in vivo tuberculatum tuberculis saepius radialiter elongatis fissurisque sterilibus angustis separatis. Stratum hymeniale (catahymenium) dendrohyphidiis inter se approximatis, basidiis per stratum dendrohyphidiorum prorumpentibus distincte exsertis. Basidia graciliter clavata, 4-sporea. Sporae ovoideae vel ellipsoideae, hyalinae, pariete tenui, levi, non-amyloideo. — Typus: *Punctularia* Pat.

one of several groups of Corticiaceae with a somewhat similar hymenium (catahymenium, see p. 210), and the only alternative solution to placing *Punctularia* in a family of its own, is to let it disappear again in the amorphous mass of Corticiaceae ('Thelephoraceae') or Stereaceae, where it is now usually relegated.

### SCHIZOPHYLLACEAE Quél.

[Fam. Schizophyllacées Roze in Bull. Soc. bot. France 23: 51 (nomen nudum), 108. 1876. — Monotype: *Schizophyllum* Fr. per Fr.]; → Schizophyllaceae Quél.

Schizophyllaceae Quél., Fl. mycol. France 365. 1888 ("Schizophyllei") ≡ "Schizophyllacées Roze".

Schizophylloideae P. Henn. in Nat. PflFam. 1 (1\*\*): 221. 1898 ("Schizophylleae"; → Schizophylleae Sing.); Sing., Agar., 2nd Ed., 178. 1962. — Type: *Schizophyllum* Fr. per Fr. Schizophylleae Engl., Syll. PflFam., 2. Aufl., 32. 1898 ("§. Schizophyllaceae"); Syll. PflFam., 4. Aufl., 42. 1904 ("§"); Sing. in Lilloa 22: 259. "1949" [1951] (≡ Schizophylloideae P. Henn.). — Type: *Schizophyllum* Fr. per Fr.

Porothelaceae Murrill in Mycologia 8: 56. 1916 ("Porotheliaceae"). — Holotype: *Porotheleum* (Fr. per Fr.) Fr.

Solenioideae W. Cooke in Beih. Sydowia 4: 14. 1961. — Holotype: *Solenia* Pers. [per Fr. 1821], not *Solena* Lour. 1790 (Cucurbitaceae).

Soleniae W. Cooke in Beih. Sydowia 4: 14. 1961. — Holotype: *Solenia* Pers. [per Fr. 1821], not *Solena* Lour. 1790 (Cucurbitaceae).

Porothleoideae W. Cooke in Beih. Sydowia 4: 127. 1961. — Holotype: "*P[orotheleum] fimbriatum* Pers. ex Fr.", type of *Porotheleum* (Fr. per Fr.) Fr.

Fruitbody in origin cup-shaped and attached at the vertex by a constricted, sometimes stalk-like base, may spread out over the substratum and become appressed with loose margin or develop more strongly at one side; in *Schizophyllum* forming 'gills' mainly by marginal proliferation in the form of radiating lobes ('gills' composed of two adjacent pileal margins which roll in in dry weather to cover the hymenium; in addition adventitious 'gills' may be formed), the lobes pressed together or digitately diverging; context toughish, soft and flabby when wet, dried specimens of *Schizophyllum* reviving when moistened, monomitic; hymenophore originally smooth, remaining so, or becoming rather radiately folded.

Hyphae thin- to thick-walled, not inflating, with clamps, at the outside of the cups rather loosely and radiately arranged and appressed. Euhymenium. Hymenial leptocystidia may be present. Basidia club-shaped, chiasitic, 2-4-spored. Spores broadly ellipsoid to cylindrical, adaxially slightly flattened to depressed, colourless (presumably white in a print), said to be yellow brown to brown under the microscope in one species; walls thin, smooth, non-amyloid.

Lignicolous rarely saprobic on herbs or leaves, *Schizophyllum* rarely parasitic on herbs or saprobic (also on horn, bones) or parasitic in animals and man.

Genera.—

1. Cups strongly proliferating and finally imitating an agaric with split gills.—*Schizophyllum* Fr. per Fr.
1. Cups not so proliferating.
  2. Hymenium more or less strongly folded.—*Plicaturopsis* D. Reid?
  2. Hymenium not really folded or at least (almost) smooth after drying.—*Stromatoscypha* Donk (fruitbodies in densely crowded colonies on a somewhat imperfectly dimitic stroma), *Henningsomyces* O.K. (fruitbodies scattered to densely crowded).

The basic fruitbody of this family may be conceived as a hollow cup attached at the strongly contracted vertex, with the hymenium lining the inside, and the hyphae becoming looser toward the abhymenial surface where they radiate appressedly from the base toward the rim. Such a fruitbody is typically 'cyphellaceous' in the traditional sense. This stage of the fruitbody may be retained or it may be radically modified during further development by one-sided expansion, and/or, as is the case in *Schizophyllum*, by a remarkable mode of marginal proliferation that becomes responsible for the formation of most of the so-called 'split gills'. The number of gills often become supplemented by an adventitious set, by means of radially arranged longitudinal eruptions from the context through the hymenial layer (or its initial). In principle the hymenium of *Schizophyllum* remains smooth. In *Plicaturopsis* the hymenium becomes folded by excessive extension of the hymenium, hence, these folds and the 'gills' in *Schizophyllum* are not comparable.

The ontogenesis of the 'gills' in *Schizophyllum* (cf. also Essig, 1922) is so peculiar that homology with the agaric gill is out of question. Assignment of the genus to the Agaricales on account of these structures alone is, therefore, not warranted. One might interpret the genus as one secondarily derived from 'reduced', cyphelloid agarics, but I am as yet not prepared to suggest the 'ancestral' group of agarics which would suit such a thesis.

These *Cyphella*-like genera differ from other similar ones that have been transferred to the Agaricales (like *Cyphellopsis*) by the fact that the outside is not clothed with 'hairs' (in the sense of clearly differentiated hyphal ends), but with somewhat modified hyphae which gradually intergrade into the context hyphae. In *Henningsomyces* many species produce dendroidly branched hyphal tips at the outside and along the rim of the cup.

It may well appear that I have made this originally monogeneric taxon artificial by adding the other genera mentioned above. This emendation is partly due to the circumstance that a receptacle was needed for a number of Cyphellaceae in the traditional sense, that could not (yet) be accommodated elsewhere.

### Appendix

#### Residual 'Cyphellaceae', exclusive of type

Fruitbody disk- to usually cup-shaped, or tubular, infundibuliform, attached at the vertex (abhymenial side) by a constricted basis or stalk, the individual fruitbodies directly seated on the substratum or on, or more or less sunk into, a common subicular layer; context (presumably always) monomitic. Hymenium smooth or with a few radiating folds when fresh but almost smooth when dry, rarely meruloid, lining the more or less concave to slightly convex disk.

Cystidia exceptionally present. Spores colourless or cream, reddish, or brown in a print; wall smooth, rarely asperulate.

Lignicolous or herbicolous.

Genera.—*Asterocyphella* W. Cooke, *Cytidia* Quél. in part (residual species, exclusive of type), *Glabrocyphella* W. Cooke (*Calyptella* Quél. as to type ?), *Mycobonia disciformis* G. Cunn. (protruding, sterile bristles of agglutinate hyphae), *Phaeodepas* D. Reid,

*Phaeoporotheleum* (W. Cooke) W. Cooke, ? *Rhodoarrhenia* Sing. (name not validly published), *Stromatocyphella* W. Cooke, *Woldmaria* W. Cooke, *Cyphella* Fr. [bis] (residual species of *Cyphella*, *Solenia* ≡ *Henningsiomyces*, and *Porotheleum*, exclusive of types); *Wiesnerina* Höhn. (disk convex, cystidiate).

Excluded from the 'Cyphellaceae' sensu lato.—

Corticiaceae.—*Cytidia*, *Cyphella* (type), *Aleurodiscus* (type), *Gloeosoma* Bres., and *Aleurocystis* Lloyd ex G. Cunn., all included in *Aleurodiscus* sensu lato (exceptionally big basidia and spores, the latter more or less subglobose, often amyloid; hyphidia of some kind usually present), *Auriculariopsis*, *Cytdiella*, *Plicatura*.

Punctulariaceae.—*Punctularia*.

Schizophyllaceae.—*Schizophyllum*, ? *Plicaturopsis*, *Stromatocypha* (*Porotheleum*), *Henningsiomyces*.

Agaricales.—

Comparable to *Resupinatus* (Nees) ex S. F. Gray.—*Stigmatolemma* Kalchbr.

Comparable to *Omphalina* Quél.—*Arrhenia* Fr., *Geotus* Pilát & Svrček, *Leptoglossum* P. Karst. (inclusive of *Leptotus* P. Karst.); *Mniopetalum* Donk & Sing. apud Donk.

Comparable to *Crinipellis* Pat.—*Calathella* D. Reid, *Lachnella* Fr., *Cyphellopsis* Donk (inclusive of *Pseudodasyscypha* Velen. ?), *Merismodes* Earle, *Flagelloscypha* Donk apud Sing.

Comparable to *Marasmius* Fr.—*Catilla* Pat.?, *Dendrocyphella* Petch.

Comparable to *Mycena* (Pers. per Fr.) S. F. Gray sensu lato.—*Calyptella* Quél., *Campanella* P. Henn., *Cellypha* Donk, ? *Favolaschia* (Pat.) Pat. apud Pat. & Lagerh. (amyloid spores), *Perona* Pers. (hymenium at outside of cup; nomen dubium).

Comparable to *Crepidotus* (Fr.) Staude.—*Pellidiscus* Donk, *Episphaeria* Donk.

Comparable to other dark-spored agarics.—*Chromocyphella* De Toni & Levi, *Phaeosolenia* Speg.

Patouillard (1900: 52) introduced the Cyphellaceae as a subtribus (Cyphellés). Through the work of Bourdot and Galzin and of Pilát, who treated it as a family, the taxon became generally accepted, and the above description could serve as the description of the broadly and artificially conceived family. When it was found that the type of *Cyphella* was a species of, or close to, *Aleurodiscus*, and the latter genus had expanded into one containing a cyphelloid element and also a considerable number of strictly resupinate species which it became customary to place among the Corticiaceae, the family Cyphellaceae became deprived of its name. W. B. Cooke (1961) took up the name Porotheleaceae Murrill for the broad concept minus *Aleurodiscus* and acted as if the family was an acceptable natural taxon. Lohwag & Follner (1936) concluded that *Fistulina* belonged to the Cyphellaceae, and Singer (1945) stretched the limits of the Cyphellaceae (as Cyphellineae) still more by also placing *Leptoglossum*, *Favolaschia*, *Campanella*, and *Rimbachia* into it. These later additions have not been generally accepted.

Another trend, this time one of demolition, was initiated by Donk who first excluded the type of *Cyphella* as a species of *Aleurodiscus*. Later he continued the process by removing several genera (emended or new ones formed of old species) either to the Corticiaceae or to the Agaricales. He is of the opinion that the Cyphellaceae (or Porotheleaceae) is an exceptionally artificial group that has no cause to exist and should be gradually liquidated. This process goes very slowly because of various factors. One of these is that many species appear to be strongly reduced



agarics with few salient features; this makes it difficult to establish which are their better developed agaric counterparts. Another factor is that most cyphellaceous species were inadequately described so that they must be redescribed one by one from a study of their types. The number of poorly described species has recently been considerably reinforced by W. B. Cooke (1961).

When I realized that *Schizophyllum* was in principle nothing but a highly modified cyphellaceous fungus I started to compare various other members of the Cyphellaceae with it and gradually became convinced that the Schizophyllaceae was another potential receptacle for at least some of the better known cyphellaceous genera. I have now acted in accordance with this conclusion, but I fully realize that the transfers to that family may have been too rashly made.

Altogether the 'Cyphellaceae' has gradually dwindled to its present insufficiently studied contents plus a few well described genera of uncertain taxonomic position (*Phaeodepas*, *Stromatocyphella* as recently emended by Reid, *Wiesnerina*). This residue is now appended to the Schizophyllaceae for the sake of convenience.

The 'family' character given above covers in the main the more traditional conception of the Cyphellaceae as accepted by W. B. Cooke. However, it is so worded that certain elements like *Punctularia* (which was admitted by Patouillard) and the corticiaceous element with more broadly attached fruitbodies (*Auriculariopsis*, *Cyrtidiella*, *Cyrtidia*), and also *Schizophyllum* are excluded. This also applies to such later introductions as *Fistulina*, *Favolaschia*, *Campanella*, and *Leptoglossum* (type group). The provision of the occasionally convex disk is made to accommodate *Wiesnerina*, and necessitates the remark that *Actiniceps* and *Pistillina* (both long-stalked) have been left in the Clavariaceae. The provision of the occasionally merulioid hymenium is made to accommodate *Rhodoarrhenia* and, if necessary, also *Plicaturopsis*, the latter provisionally assigned above to the Schizophyllaceae.

#### SPARASSIDACEAE Herter<sup>38</sup>

[Trib. Pileolati Fr., Syst. Orb. veg. 88. 1825; Gen. Hym. 36. 1836. — Lectotype: *Sparassis* Fr. per Fr.]; → Sparassideae Rab.

Sparassideae Rab., Deutschl. Krypt.-Fl. 1: xix, 330. 1844 ("Sparassidei Reichb."); [trib.]; Lotsy, Vortr. bot. Stammesgesch. 1: 695, 696. 1907 (typonym; ≡ "Tribu des Sparassidées Maire"); ≡ Pileolati Fr.

[Tribu des Sparassidées Maire in Bull. Soc. mycol. France 18 (Suppl.): 99. 1902. — Monotype: *Sparassis* Fr. per Fr.]; → Sparassideae Lotsy.

Sparassidaceae Herter in Krypt.-Fl. Brandenb. 6: 167. 1910 ("Sparassideaceae"). — Monotype: *Sparassis* Fr. per Fr.

Massecoleae Donk, Rev. niederl. Homob.-Aphyll. 2: 70. 1933. — Monotype: *Masseola* O.K. [≡ *Sparassis* Fr. per Fr.].

Fruitbody stalked, branching into a few, or a great mass of, flattened, more or less wavy lobes bearing the hymenium at the physiological underside in horizontally

<sup>38</sup> If *Sparassis* Fr. per Fr. 1821 is to be considered an orthographically different homonym of *Sparaxis* Ker-Gawl. 1804 (Iridaceae) than this family name has to be replaced by one derived from *Masseola* O.K.

orientated portions (abhymenial surface not covered by a crust-like layer) or amphigenously in ascending lobes; context tough-fleshy, shrinking and becoming somewhat cartilaginous upon drying, pallid, monomitic; hymenophore smooth; hymenium not becoming layered.

Hyphae thin-walled with a tendency to become firm- to thick-walled; clamps present (scarce to numerous, may occur only at the base of basidia); also vascular hyphae which may end in the hymenium. Basidia club-shaped, chiasitic, 2-4-spored. Spores short-ovoid, ellipsoid, rather small (5-9  $\mu$  long), colourless (pale cream or pale ochraceous-cream in a print); wall smooth, non-amyloid.

Lignicolous (stalk rooting) or humicolous (stalk arising from a corticioid patch covering vegetable debris).

Genus.—*Sparassis* Fr. per Fr. (If *Sparaxis* Ker-Gawl. is considered a homonym, then the correct name is *Masseola* O.K.)

*Sparassis* has been variously classified. After it had for some time been considered as belonging to the Clavariaceae, Cotton (1912) found that only the underside of the flattened branches of *Sparassis crispa* (Wulf.) per Fr. was covered by the hymenium; he thought, therefore, that the genus should be transferred to the neighbourhood of *Stereum* (Stereaceae). Buller (1922: 188-190 fs. 65-67) agreed; he affirmed that it was only the physiological underside that was fertile: a curled lobe would bear the hymenium at both sides, but only on the areas facing downward. In that remarkable species, *Sparassis simplex* D. Reid (1958: 439 f. 17, pl. 24 f. 1), in which the fruitbody arises from an effused fertile patch, the hymenium was stated to be amphigenous and spreading downward along the stalk over the patch. Assigning *Sparassis* to the Stereaceae would be the simplest solution, but this would not only entail the renaming of that family into Sparassidaceae (if *Sparassis* were not to be treated as a later homonym) but also add another strongly isolated element to that already desperately heterogeneous family. By its consistency and hyphal systems (monomitic, with inflating hyphae, and a vascular hyphal system), it seems better to put *Sparassis* either in the Clavariaceae as a special tribe (cf. Donk, 1933: 70) or close to the Clavariaceae as a distinct family.

#### STEREACEAE Pilát

[Thelephoroideae S. F. Gray, Nat. Arr. Brit. Pl. 1: 598, 652. 1821 ("Thelephoroideae"; [subfam.]); not Thelephoroideae Pers., Mycol. europ. 1: 109. 1822 (type: *Thelephora* Ehrh. ex Willd.). — Lectotype: *Stereum* Pers., no genus 'Thelephora' being either included or mentioned as a synonym.]

Auricularioideae Fr., Syst. Orb. veg. 64, 81, 363. 1825 ("Auricularini"; "subordo" = subfam.); not Auricularioideae Sacc. in Syll. Fung. 6: 760. 1888 (= "Auriculariae Bref." = Auriculariaceae J. Schroet.; type: *Auricularia* Bull. per Mérat). — Type: *Auricularia* Bull. sensu Fr. 1825 [= *Stereum* Pers. per S. F. Gray], not *Auricularia* Bull. per Mérat; → Auriculariae Reichenb.; Grev.; → Auriculariaceae Fr.

Auriculariae (?) Reichenb., Consp. Regni veg. 13. 1828 (nomen nudum; [subtrib. ?]) = Auricularioideae Fr.

Auriculariae Grev., Scott. crypt. Fl. 6: 29. 1828 ("Auricularini"); not Auriculariae Killerm. in Nat. Pflfam., 2. Aufl., 6: 106. 1828 (type: *Auricularia* Bull. per Mérat); = Auricularioideae Fr.

Auriculariaceae Fr., *Epicr.* 530, 606, 1838 ["Auricularini (S.O.V.)"; "ordo" = fam.]; *Bon.*, *Handb. Mykol.* 158, 1851 ("Auricularini"; *Auricularia* Bull. per Mérat not included); not Auriculariaceae J. Schroet. in *Krypt.-Fl.* Schles 3 (1): 383, 1887 (type: *Auricularia* Bull. per Mérat); ≡ Auricularioideae Fr.

[Trib. Frondini Quéf., *Fl. mycol.* France 1, 1888. — Lectotype: *Stereum* Pers.]

[Série des Théléphores Pat., *Essai tax.* Hym. 40, 1900. — Type: *Thelephora* "Fr." sensu Pat. (lectotype: *Thelephora pallida* Pers. per Pers.); → Thelephoreae R. Heim.

[Série des Stereums Pat., *Essai tax.* Hym. 58, 69, 1900. — Type: *Stereum* "Fr., Epicrisis" = *Stereum* Pers. per S. F. Gray; → Stereaceae R. Heim.

Stereaceae Killerm. in *Denkschr. bayer. bot. Ges.* 15: 1, 6, 1922 ("Stereaceae"; "Gruppe" = trib.); in *Nat. Pfl. Fam.*, 2. Aufl., 6: 143, 1928; R. Heim in *Treb. Mus. Ci. nat. Barcelona* 15: 58, 1934 ("Stereaceae"; nomen nudum; typonym; ≡ 'Série des Stereums Pat.'). — Type: *Stereum* Pers. per S. F. Gray.

[Stéréinés Bourd. & G., *Hym.* France 144, 365, "1927" [1928] (uninferable rank). — Type: *Stereum* "Fr. Epicr." = *Stereum* Pers. per S. F. Gray, 1821; → Stereinae Talbot.

Stereoidae Ulbr. in *Kryptfl. Anfänger* 1 (3. Aufl.): 115, 1928. — Type: *Stereum* "Fries" = *Stereum* Pers. per S. F. Gray.

Stereaceae Pilát in *Hedwigia* 70: 34, 1930; Singer in *Publ. Inst. Mycol. Univ. Recife* No. 304: 5, 1961 ("Bond. & Sing. Sov. Bot. 1943, p. 31, ex Sing."; typonym). — Type: *Stereum* Pers. per S. F. Gray.

Gloeostereae S. Ito & S. Imai *apud* S. Imai in *Trans. Sapporo nat. Hist. Soc.* 13: 11, 1933. — Monotype: *Gloeostereum* S. Ito & S. Imai.

Thelephoreae R. Heim in *Treb. Mus. Ci. nat. Barcelona* 15: 44, 1934 (nomen nudum), not Thelephoreae Dumort., *Anal. Fam. Pl.* 73, 1829 (type: *Thelephora* Ehrh. ex Fr.); ≡ 'Série des Théléphores Pat.'

Stereinae Talbot in *Bothalia* 6: 5, 1951 (lacking Latin description); ≡ 'Stéréinés Bourd. & G.'

Cladoderreae S. Ito, *Mycol. Fl. Japan* 2 (4): 105, 166, 1955 (lacking Latin description or reference). — Monotype: *Cladoderris* Fr.

Fruitbody appressed- or effused-reflexed (but often occurring in 'resupinate' condition), sessile or stalked, usually flattened throughout, with strictly one-sided hymenophore; cap often zoned (either colour- or tomentum-zones or both, also sulcate) but not invariably so; context in the majority of species in section showing an abhymenial darker crust-like layer (often bearing a hairy or spongy indumentum), an intermediate layer (a considerable portion may be occupied by hyphae curving toward the hymenium), and the hymenium (which may be layered), usually leathery, corky, to woody and dimittic with skeletal hyphae, exceptionally trimitic, in some small genera softer but fibrous, or gelatinous, and (presumably) monomitic; hymenophore smooth or flabellately ribbed, exceptionally more or less 'irpicoid'.

Generative hyphae thin- to somewhat thick-walled, with or without clamps; skeletal from nearly thin- to very thick-walled, the lumina may be filled with coloured sap, typically many curving towards the hymenium and terminating in the hymenium or more rarely in the sybhyemenium, with little, modified, uninflated ends or with more or less strongly modified and inflated ends (skeletalocystidia). Setae lacking. Hymenial cystidia of various types may be present. Basidia club-shaped, chiasitic, 2-4-spored. Spores colourless (white in a print); wall smooth, usually thin, amyloid or non-amyloid.

Lignicolous, or terrestrial in a number of the stalked species.

Genera.—

- Context dimittic with skeletal, rarely trimitic. Fruitbody appressed-reflexed (may occur in appressed or effused condition), sessile (attached at the vertex, but usually appearing lateral at maturity), or stalked; hymenophore smooth, tuber-

culate, flabellately ribbed, or rarely 'irpicoid' (in some species of *Lopharia*). Skeletals usually predominant in middle layer, typically many curving toward, and terminating in, the subhymenium or hymenium, with either little differentiated or more or less strongly modified tips (skeletocystidia), sometimes filled with a distinctive sap (bleeding), also occurring in a reduced form as long, hypha-like tramal cystidia in vertically constructed layers. Hymenial cystidia and gloecocystidia may be present. Lignicolous.

2. Fruitbody not typically stalked.—*Amylostereum* Boid., *Columnocystis* Pouz., *Cystostereum* Pouz., *Laurilia* Pouz., *Lopharia* Kalchbr. & McOw., *Stereum* Pers. per S. F. Gray (inclusive of *Xylobolus* P. Karst.). — Compare *Irpex* and *Chaetoporia* (Polyporaceae) and *Steccherinum* (residual Hydnaceae).
2. Fruitbody more or less typically stalked.—*Cymatoderma* Jungh., *Podoscypha* Pat.
1. Context monomitic (or supposed to be so).
3. Fruitbody appressed- to effused-reflexed (varying to resupinate) or sessile. Context leathery, subgelatinous, or gelatinous; hymenophore smooth. Lignicolous, rarely muscicolous.—*Chondrostereum* Pouz., *Stereophyllum* P. Karst. (name preoccupied), *Gloeostereum* S. Ito & S. Imai apud S. Imai (gelatinous).
3. Fruitbody stalked, clavarioid (may show a tendency to flattened branching) or pileate; cap flabelliform to infundibuliform (often incised), or turbinate; context tough, usually fibrous; hymenophore smooth or ribbed. Hyphae non-inflating. Often terrestrial.—*Bresadolina* W. Brinkm., ? *Caripia* O.K., *Cotylidia* P. Karst., ? *Skepparia* Bark. — Compare also *Aphelaria* Corner s. str. and *Phaeoaphelaria* Corner (Clavariaceae).
1. Prominent hyphal pegs (sterile bundles of more or less strongly agglutinate hyphae) protruding beyond the hymenium, resembling small teeth.—*Mycobonia* Pat. (closely related to *Pseudofavolus* Pat., Polyporaceae), *Veluticeps* (Cooke) Pat.

Excluded.—

Agaricales (stalked), related to *Marasmius* Fr., *Mycena* (Pers. per Fr.) S. F. Gray.—*Cymatella* Pat., *Delicatula* Fayod, *Discocyphella* P. Henn., *Eomyccenella* Atk., *Epicnaphus* Sing., *Gloiocephala* Mass., *Helotium* Tode per Leman, *Hymenogloea* Pat., *Manuripia* Sing., *Marasmius* spp., *Palaeocephala* Sing., *Perona* Pers., *Van-Romburghia* Holterm. ex Sacc. & P. Syd.—All these genera are based on stalked agarics with smooth or only occasionally folded hymenophore. — For species with attachment of fruitbody at abhymenial side, see 'Cyphellaceae' (p. 290).

Corticiaceae.—*Aleurodiscus* spp., *Auriculariopsis*, *Corticium* spp., *Cytidia*, *Cytdiella*, *Duportella* (context dimitic), *Merulius* (hymenium 'meruloid'), *Laeticorticium* sp., *Peniophora* spp., *Scytinostroma* spp.

Hericiaceae.—*Laxitextum* Lentz.

Hymenochaetaceae.—*Hymenochaete*, *Lachnocladium*.

Punctulariaceae.—*Punctularia* (inclusive of *Phaeophlebia*).

Sparassoideae.—*Sparassis* (*Masseola*).

Tremellaceae.—*Pseudotremellodendron* D. Reid & *Tremellodendropsis* (Corner) D. A. Crawf. (both excluded from *Aphelaria*), *Tremellodendron* Atk.

Some general remarks on this artificial 'family' and its separation from the Corticiaceae will be found on page 260. It was not possible to make a sharp demarcation between the two groups. Although the dimitic hyphal system (with skeletals) is predominant among the Stereaceae it cannot be too strongly emphasized because of (i) the existence of some groups of Corticiaceae with dimitic context, (ii) the existence of some groups with monomitic context closely imitating typical species

of *Stereum* when well developed (*Chondrostereum*<sup>39</sup>), and because transferring all monomitic species to the Corticiaceae would (iii) bisect some stereoid genera (like the rather heterogeneous genus *Lopharia*) and would (iv) also introduce a strong stalked element into the Corticiaceae (*Bresadolina*, *Cotylidia*, *Aphelaria*, &c.). These considerations and similar other ones have strongly tempted me to fuse the two 'families'. To be completely consistent, its fusion with the Polyporaceae and the residual Hydnaceae would be the next step. Therefore, from a purely practical point of view, to avoid too much lumping and to comply with a strong current tendency, the Stereaceae is maintained, but not without some important absentees as compared with Pilát's original conception.

### THELEPHORACEAE Chev.

[Gymnodermata Pers., Syn. Fung. xvii; 565 ("Gymnoderma"). 1801 ([subordo] = subfam.). — Lectotype: *Thelephora* Ehrh. ex Willd. = *Thelephora* Ehrh. ex Fr.]

[Hypochni Fr., Syst. mycol. 1: xliii, xlv. 1821 (uninferable rank). — Type: *Hypochnus* Fr. per Fr.]

Hydnoideae S. F. Gray, Nat. Arr. Brit. Pl. 1: 597, 650. 1821 ("Hydnidae"; [subfam.]); not Hydnoideae Pers. per Pers., Mycol. europ. 2: 150. 1825 (type: *Hydnum* L. per Fr.). — Type: *Hydnum* "Dillenius" [= L.] sensu S. F. Gray = *Sarcodon* Quéf. ex P. Karst.

Thelephoroideae Pers., Mycol. europ. 1: 109. 1822 ("Thelephorei"; [subordo] = subfam.); P. Karst. in Bidr. Känn. Finl. Nat. Folk 25: 14, 302. 1876 ("Thelephoreae"). — Type: *Thelephora* Ehrh. ex Willd. = *Thelephora* Ehrh. ex Fr.

[Fam. Papillariae Dumort., Comm. bot. 70; 82 ("Papillacie"). 1823. — Lectotype: *Thelephora* Ehrh. ex Fr.]

Thelephoraceae Chev., Fl. Paris 1: 84. 1826 ("Thelephoreae"; "Ordre" = fam.); Staudé, Pilze Mitteleurop. xxiv, 42. 1857 ("Telephorini"); P. Karst. in Acta Soc. Fauna Fl. fenn. 2 (1): 35. 1881 ("Thelephoraceae"; name only); Wint. in Rab. Krypt.-Fl., 2. Aufl., 1 (1): 318. 1882 ("Thelephorei"); J. Schroet. in Krypt.-Fl. Schles. 3 (1): 420. 1888 ("Thelephoreae"); Sacc. in Syll. Fung. 6: 513. 1888 ("Thelephoreae"; typonym, = Thelephoroideae Pers.); emend. Donk in Bull. bot. Gdns, Buitenz. III 17: 474. 1948. — Type: *Thelephora* Ehrh. ex Willd. = *Thelephora* Ehrh. ex Fr.; → Thelephorales Corner (see p. 242).

Thelephoreae Link in Abh. phys. Kl. Akad. Berl. 1824: 182. 1826 ("Thelephorei"; [trib.]); Dumort., Anal. Fam. Pl. 73. 1829 ("Terephoreae"); J. Schroet. in Krypt.-Fl. Schles. 3 (1): 421. 1888 ("Thelephorei"; "Gruppe" = trib.); Donk, Rev. niederl. Homob.-Aphyll. 2: 25. 1933 ("Thelephorineae"). — Type: *Thelephora* Ehrh. ex Fr.

[Fam. Erinacei Quéf., Ench. Fung. 1, 188. 1886. — Lectotype: "*Sarcodon*, Q." = *Sarcodon* Quéf. ex P. Karst.]

[Eu-Thelephoreae Sacc. in Syll. Fung. 6: 513. 1888 [trib.]. — Type: *Thelephora* "Ehrh. . . . emend. Fr."]

[Série des Phylactéries Pat., Essai tax. Hym. 114, 117. 1900. — Type: *Phylacteria* (Pers.) Pat.; → Phylacteriaceae R. Heim.]

[Famille des Phylactériacées Maire in Bull. Soc. mycol. France 18 (Suppl.): 83, 93. 1902. — Monotype: *Phylacteria* (Pers.) Pat.; → Phylacteriaceae Lotsy.]

Phylacteriaceae Lotsy, Vortr. bot. Stammesgesch. 1: 687, 691. 1907 (as synonym); Pilát in Bull. Soc. mycol. France 49: 328. 1934 (nomen nudum); Bond. & Sing. in Sovetsk. Bot. 1943 (1): 29-43. 1943 (nomen nudum); = 'Famille des Phylactériacées Maire'.

<sup>39</sup> On the other hand resupinate conditions of *Chondrostereum purpureum* (Pers. per Fr.) Pouz. may be typically corticiaceous.

Phylacterioideae Donk, Rev. niederl. Homob.-Aphyll. 2: 24. 1933. — Type: *Phylacteria* (Pers.) Pat. (as synonym of *Thelephora* Ehrh. ex Fr.); → Phylacteriineae Bond. & Sing. (sup. 242); → Phylacteriaceae Imaz.

Hydnelleae Donk, Rev. niederl. Homob.-Aphyll. 2: 46. 1933. — Type: *Hydnellum* P. Karst. (1879); → Hydnellinae Nikol.

Boletopsidae Donk, Rev. niederl. Homob.-Aphyll. 2: 64. 1933 ("Boletopseae"). — Monotype: *Boletopsis* Fayod.

Phylacteriaceae R. Heim in Treb. Mus. Ci. nat. Barcelona 15: 63. 1934 (nomen nudum); S. Ito, Mycol. Fl. Japan 2 (4): 170, 171. 1955 (typonym; lacking Latin description); ≡ 'Série des Phylactéries Pat.'

Boletopsidaceae Bond. & Sing. in Ann. mycol. 39: 45, 47. 1941 (lacking Latin description & reference). — Monotype: *Boletopsis* Fayod.

Sarcodontaceae Bond. & Sing. in Sovetsk. Bot. 1943 (1): 29-43. 1943 (nomen nudum). — Type (by implication): *Sarcodon* Quéf. ex P. Karst.

Phylacteriaceae Imaz. in Mycologia 45: 588. 1953 ("nom. nov."; with Latin description) ≡ Phylacterioideae Donk.

Polyozelleae Imaz. in Mycologia 45: 560. 1953. — Monotype: *Polyozellus* Murrill.

Tomentelloideae Svrček in Sydowia 14: 172. 1960. — Holotype: *Tomentella* Pat.

Hydnellinae Nikol. in Fl. Pl. crypt. URSS 6 (2): 239. 1961 ≡ Hydnelleae Donk.

Fruitbody strictly effused, effused-reflexed, or stalked and pileate or fertile portion divided into dorsiventral segments, or clavarioidly branched (with amphigenous hymenium); hymenophore smooth, warty, toothed, poroid or folded (*Cantharellus*-like), or imperfectly lamellate; context pallid or usually coloured and generally darkening and/or containing a substance that dissolves to become greenish in KOH solution, floccose to fibrillose, leathery, fleshy, monomitic.

Hyphae of context usually remaining thin-walled or some (in subicular portions of *Tomentella*) thick-walled, inflating in fleshy species; clamps present or lacking. Hymenium more or less typically thickening (less distinctly so in toothed and tubulate hymenophores). Cystidia (and gloecocystidia) lacking, or rarely present as hymenial leptocystidia or hyphae-like tramal cystidia. Basidia club-shaped, often flexuous and slender, chiasitic, 2-4-spored. Spores globular to somewhat ellipsoid, often uneven in general outline (which may be sinuose, wavy, or irregular by coarse tuberculous inflations), brownish (spore print distinctly coloured) to almost colourless (almost white and only faintly tinted; may be colourless in *Scytinopogon*); wall may bear (in addition to the irregularities in outline of the spores) small warts or spines, non-amyloid, in the typical genera not or hardly absorbing Cotton Blue (as far as known).

Mostly terrestrial or humicolous, also lignicolous.

Genera.—

1. Fruitbody strictly effused.
  2. Hymenophore smooth or warty, not typically toothed.—*Tomentella* Pat. (inclusive of *Pseudotomentella* Svrček and *Tomentellastrum* Svrček), *Kneiffella* P. Karst. (protruding hyphae-like cystidia of deep origin).
  2. Hymenophore typically toothed (teeth with sterile tips).—*Caldesiella* Sacc.
1. Fruitbody not strictly resupinate.
  3. Hymenophore smooth or warty, not typically toothed.—*Thelephora* Ehrh. ex Fr., *Scytinopogon* Sing. (spores hyaline or very pale coloured).
  3. Hymenophore toothed. Fruitbody stalked, often more or less centrally stalked.—*Hydnellum* P. Karst., *Sarcodon* Quéf. ex P. Karst. (fleshy species), *Hydnodon* Banker (spores coral pink in a print).
  3. Hymenophore tubulate.—*Boletopsis* Fayod.

3. Hymenophore folded (*Cantharellus*-like).—*Polyozellus* Murrill.  
 3. Hymenophore rather imperfectly lamellate (*Lenzites*-like).—*Lenzitopsis* Malençon & Bertault.

Excluded.—

Bankeraceae.—*Bankera*, *Phellodon*.

Corticiaceae.—*Botryohyphochnus*.

Polyporaceae.—*Lindtneria*.

Although it is difficult sharply to characterize this family it is undoubtedly essentially a natural one: a fine example of how a taxon can be built up 'par enchainement' rather than defining it by a sharp family character. Among the main features of this family, those of the spores are very important ones. Confusion with certain Gomphaceae, especially with those with short spores, is not unlikely in some cases, but in the latter family the spore-wall is never angular in general outline and strongly absorbs Cotton Blue.

Historically, the Thelephoraceae in the present circumscription is of importance because it was one of the very first modern families of Aphyllophorales that completely discorded with the Friesian tradition in the Hymenomycetes. When Patouillard (1900: 117) introduced it (as a "série") he admitted *Tomentella*, *Caldesiella*, *Phylacteria* (Pers.) Pat. (now called *Thelephora* sensu stricto), *Calodon* (= *Hydnellum*, inclusive of *Phellodon*), and *Sarcodon* (inclusive of *Bankera* and *Hydnodon*). It was only slowly that the family in this emendation became more generally accepted. A few additions were introduced afterwards, viz. *Polyozellus* and *Lenzitopsis*. Recently some retouching has been proposed: *Bankera* and *Phellodon* have been excluded and made a family of their own, viz. Bankeraceae (q.v.).

Corner (1950: 23), in his *Clavaria* monograph, thought *Scytinopogon* "... so similar to *Thelephora* s. str. (= *Phylacteria*) that, if the spores were fuscous, it would be congeneric."

There has been a tendency to raise this family to ordinal rank and to divide it into a number of families or to admit several tribes. Splitting has gone too far: for instance, *Boletopsis* and certain species of *Sarcodon* are so closely related that placing these two genera in different families on account of the different effiguration of the hymenophore is a relapse into the Friesian tradition in my opinion. The separation of the Tomentelloideae from the Thelephoroideae is another example of this kind because no clear distinction has as yet been made known between the two: *Thelephora terrestris* Ehrh. ex Fr., when it occurs in well developed but completely effused fruitbodies, is a true *Tomentella* in that condition. The limits between the two tribes, if accepted, would run through this (and a few other) species of *Thelephora*.

Malençon (1959) discussed the spore of the 'Phylactériés' and ascribed a peculiar apiculus to it. I have been unable to verify this point.

For a brief account on the correct family name, see under Corticiaceae (p. 260). For a note on the thelephoric acid, see page 241.

## Appendix

DICTYONEMATACEAE Tomaselli <sup>40</sup>

Hypochnaceae J. Schroet. in *Krypt.-Fl. Schles.* 3 (1): 415. 1888 ("Hypochnacei"); Engl., *Syll. Vorl. Bot., Grosse Ausg.*, 39. & *Kleine Ausg.*, 30. 1892. — Type: *Hypochnus* "Ehrenberg. Fries 1829".

Hypochnaceae Sacc. & P. Syd. in *Syll. Fung.* 14: 12. 1899 ([trib.]; nomen nudum). — Type: *Hypochnus* "Fr. '29" = *Hypochnus* Fr. ex Ehrenb.

[Hymenolichenes Sacc. in *Syll. Fung.* 6: 541. 1888 [trib.]; Sacc. & P. Syd. in *Syll. Fung.* 14: 12. 1899 ("Hymenolicheneae"); ≡ *Hymenolichenes* Mattiolo, see footnote 40].

Dictyonemataceae Tomaselli in *Arch. Bot., Forli* 25: 261. 1949; 26: 223. 1950. — Type: *Dictyonema* Ag.

Herpothallaceae Tomaselli in *Arch. Bot., Forli* 25: 261. 1949; 26: 223. 1950. — Monotype: *Herpothallon* Tobler.

Coraceae Tomaselli in *Arch. Bot., Forli* 25: 261. 1949; 26: 223. 1950. — Type: *Cora* Fr.

An artificial family comprising the lichenized Basidiomycetes, presumably all Aphyllophorales, the basidiomycetous nature of the fungous components being known (i) either from the occurrence of hymenia with holobasidia in most of them, (ii) or from the presence of clamp-connections in others, or (iii) merely presumed.

## Contents.—

1. Lichenized mycelium clearly differentiated from the non-lichenized fruitbody.— About half a dozen or more species of Clavariaceae.

<sup>40</sup> The following synonymy should properly have been incorporated in that of the name Aphyllophorales (p. 241), but it is given here to avoid too much disconnection from the group (Dictyonemataceae) for which these names were introduced before a correct family name was provided.

[*Hymenolichenes* Mattiolo in *Nuovo G. bot. ital.* 13: 265. 1881 (uninferable rank). — Lectotype: *Cora* Fr.]; → *Hymenolichenes* Sacc. (trib., see above); → *Hymenolichenes* Engl. (suborder).

*Basidiolichens* Engl., *Syll. PflFam.*, 2. Aufl., 42. 1898 ("Reihe" = ordo). — Lectotype: *Cora* Fr.

*Hymenolichenes* Engl., *Syll. PflFam.*, 2. Aufl., 43. 1898 ("Unterreihe" = subordo) ≡ *Hymenolichenes* Mattiolo.

*Basidiolichenes* Engl., *Syll. PflFam.*, 6. Aufl., 48. 1909 ("Nebenklasse" = classis) ≡ *Basidiolichenes* Engl. (ordo).

*Basidiolichenes* Engl., *Syll. PflFam.*, 8. Aufl., 75. 1919 ("Unterklasse" = subclassis) ≡ *Basidiolichenes* Engl. (ordo).

*Agarico-Lichenes* Mattick in *Ber. dtsh. bot. Ges.* 64: 99. 1951 ("Unterreihe" = subordo; nomen nudum). — Introduced for certain specimens of a species of *Russula* described by Kohl [in *Beih. bot. Cbl.* (2. Abt.) 24: 427. 1909].

*Polyporo-Lichenes* Mattick in *Ber. dtsh. bot. Ges.* 64: 99. 1951 ("Unterreihe" = subordo; nomen nudum). — Introduced for occurrences of algae on fruitbodies of polypores discussed by Tobler (in *Arch. Mikrobiol.* 13: 158. 1942; n.v.).

*Thelephoro-Lichenes* Mattick in *Ber. dtsh. bot. Ges.* 64: 99. 1951 ("Unterreihe"; nomen nudum). — Lectotype: *Cora* Fr.

*Clavario-Lichenes* Mattick in *Ber. dtsh. bot. Ges.* 64: 99. 1951 ("Unterreihe"; nomen nudum). — Introduced for *Clavaria* spp. described by Coker (in *Bot. Gaz.* 37: 62. 1904; viz. *Clavaria mucida* Pers.) and Palm (in *Svensk bot. Tidskr.* 26: 175. 1932; two unnamed species).



1. No such differentiation.—*Dictyonema* Agardh (inclusive of *Cora* Fr., &c.), *Rhipidonema* Mattirollo, ? *Corella* Wainio, *Herpothallon* Tobler.  
E x c l u d e d.—*Chlorocyphella* Speg. (parasymbiotic, deuteromycetous).

It is sometimes difficult for a mycologist who is used to interpreting a lichen as a consortium of a fungous and an algal component each entitled to its own name, to esteem the systematics of the lichens (starting-point date for nomenclature, 1753). As early as 1893 A. Möller concluded, after extensive research on the spot, that the fungous components of the type species of *Dictyonema*, *Cora*, and *Laudatea* were one and the same fungus in different environmental modifications and associated with two different algal species. To my knowledge his conclusions have never been refuted. Yet, it is still acceptable and current procedure among lichenologists to name this one fungus species when it is associated with two different species of algae not only as two distinct species but also to treat it as belonging to two distinct genera (or even families: Tomaselli, 1949; 1950), without the slightest attempt to contest Möller's thesis.

The fungous component of *Cora* has been referred to *Thelephora*, even by some modern lichenologists, presumably because the basidia and basidiospores were erroneously described by Mattirollo (1881: 254). Möller (1893), who studied them from living specimens reported them to be white in a print, and ovoid,  $6-7 \times 4 \mu$ , both in '*Dictyonema*' and '*Cora*'. Moreover, they are smooth and the basidia four-spored (Grassi, 1950: 384). No acceptable suggestions have as yet been made as to the correct taxonomic position of any of the fungous components of this group of lichens.

The other group, that may be termed the phycophilous Clavariaceae (Corner, 1950: 21), consists in the first place of *Clavaria mucida* Pers. per Fr., *C. coronilla* G. W. Mart. (both placed in *Lentaria* by Corner), *Clavulinopsis hastula* Corner, *Clavaria fossicola* Corner, and *C. helicoides* Pat. & Demange. Moreover, some species insufficiently described from a mycological point of view (no adequate descriptions of the fruitbody) should be added to this list. Corner distributed the species mentioned by name above over three genera: *Lentaria* (clamps present; on very rotten, sodden wood), *Clavulinopsis* (clamps present; on soil), and *Clavaria* (clamps lacking; on soil). On the other hand it would seem rash to put all phycophilous species of Clavariaceae into a distinct genus merely on account of their phycophily, first, because some of them seem to be allied to non-phycophilous species, and, secondly, because of several possibly related species the phycophily may be suspected but has not yet been confirmed or has even been denied. There is a possibility that the generic name *Stichoclavaria* Ulbr. (based on *Clavaria falcata* Pers. per Fr. sensu Juell) will have to be taken into consideration in this connection.

The occurrence of algae on a species of *Russula* (apparently incidental) and regularly on fruitbodies of more persistent fungi like polypores has led to the irresponsible publication of names like Agarico-Lichenes and Polyporo-Lichenes. That the hairy surface of certain polypore fruitbodies is an excellent substratum for algal growth is not surprising and is a generally known fact. No close application of the hairs (hyphae) or formation of haustoria has been reported in these cases, although Tobler paid attention to this possibility.

## GENERIC NOMINA CONFUSA

Of the following generic names the type species are here taken to be actually based on types consisting of two completely discordant elements erroneously supposed to represent single individual fungi.

For references to some informational details on the individual names, see the Enumeration at the end of the present paper.

- Gloeasterostroma* J. Rick  
*Heterobasidium* Mass. (not *Heterobasidion* Bref.)  
*Hypolyssus* Pers., see Excluded genera.  
*Langloisula* Ell. & Ev.  
*Muciporus* Juél  
*Pellicularia* Cooke  
*Peniophorella* P. Karst.

## GENERIC NOMINA DUBIA

(polypores not considered)

The type specimens of the following generic names are here held to be so insufficiently known that these names should not be taken into consideration for purposes of priority until more adequate information is available. In those cases in which no type specimen is known to exist, these names may usually be considered as having dropped out of current usage. In many cases taking up these names as correct, or their reduction to synonymy, is often a mere matter of renewed study of their types.

For references to some informational details on the individual names, see the Enumeration at the end of the present paper.

- Acrotamnium* Nees per Fr.  
*Aldridgea* Mass. (Coniophoraceae?)  
*Aldridgeiella* J. Rick  
*Alytosporium* (Link) per Link, type still to be selected.  
*Chaetocypha* Corda.  
*Coniophorafomes* J. Rick  
*Crystallocystidium* (J. Rick) J. Rick  
*Cyphellina* J. Rick  
*Cystidi dendron* J. Rick  
*Discocyphella* P. Henn.  
*Friesula* Speg.  
*Gloeopeniophorella* J. Rick  
*Grandinia* Fr.<sup>41</sup>

<sup>41</sup> Grandinieae Payer, Bot. crypt. 106. 1850. — Type: *Grandinia* Fr.

Grandiniaceae P. Karst. in Rev. mycol. 3/No. 9: 20. 1881 (nomen nudum). — Type: *Grandinia* Fr.

Grandinioideae P. Karst. in Acta Soc. Fauna Fl. fenn. 2 (1): 35. 1881 ("Grandinieae"). — Type: *Grandinia* Fr.

The selected type species of the generic name *Grandinia* Fr. is here considered a nomen dubium.

*Grandinochaete* J. Rick  
*Hydnellum* P. Karst. 1896 (non 1879).  
*Irpicochaete* J. Rick  
*Malacodermum* (Fr.) Léon March.  
*Malacodon* Bataille  
*Mycodendron* Mass.  
*Odontiochaete* J. Rick  
*Phaeoradulum* Pat.  
*Pseudoasterodon* J. Rick  
*Radulochaete* J. Rick  
*Skepperia* Berk.  
*Stereofomes* J. Rick  
*Stichoclavaria* Ulbr.  
 ? *Thelephorella* P. Karst.  
*Xenopus* Penz. & Sacc. (nomen anamorphosis?)  
*Xylodon* (Pers.) per S. F. Gray  
*Zygodesmus* Corda (nomen anamorphosis?)

EXCLUDED GENERA  
(polypores not considered)

The following list includes those genera that have been, or for some time were, placed among the Aphyllophorales. In a few cases the type species of a generic name was so treated, while the genus itself was excluded from its inception. Also added are some genera with smooth hymenophore or folded hymenium that have always been considered true Agaricales.

For references to some informational details on the individual names, see the Enumeration at the end of the present paper.

Abbreviations: D. = Deuteromycetes (non-basidiomycetous). — Ag. = Agaricales.

*Acurtis* Fr. (D.)  
*Arrhenia* Fr. (Ag.)  
*Aureobasidium* Viala & Boyer (D.)  
*Bonia* Pat. (Tremellales)  
*Calathella* D. Reid (Ag.)  
*Calyptella* Quél. (Ag.)  
*Campanella* P. Henn. (Ag.) (syn., *Laschia* [Fr. sensu] Pat.)  
*Catilla* Pat. (Ag.)  
*Cellypha* Donk (Ag.)  
*Ceracea* Crag. (D.)  
 [ *Cerinomyces* G. W. Mart. (Dacrymycetales ?) ]  
*Chlorocyphella* Speg. (Lichenes)  
*Chromocyphella* De Toni & Levi (syn., *Cymbella* Pat. apud Pat. & Doass., *Phaeocarpus* Pat.,  
*Phaeocyphella* Pat., *Phaeocyphella* Speg.)  
*Cymatella* Pat. (Ag.) (syn., *Discocyphella* P. Henn. ?)  
*Cyphellopsis* Donk (Ag.) [syn., *Maireina* (Pilát) W. Cooke, ? *Pseudodasyscypha* Velen.]<sup>42</sup>  
*Delicatula* Fayod (Ag.)

<sup>42</sup> *Cyphellopsidinae* Sing., *Agar.*, 2nd Ed., 402. 1962 ("ad int."; lacking Latin description). — Type: *Cyphellopsis* Donk.

- Dendrocyphella* Petch (Ag.)  
*Discocyphella* P. Henn. (Ag.)  
*Eomycenella* Atk. (Ag.)  
*Epicnaphus* Sing. (Ag.)  
*Episthaeria* Donk (Ag.)  
*Favolaschia* (Pat.) Pat. apud Pat. & Lagerh. (Ag.) (syn., *Porolaschia* Pat.)<sup>43</sup>  
*Flagelloscypha* Donk apud Sing. (Ag.)  
*Geotus* Pilát & Svrček (Ag.)  
*Gloiocephala* Mass. (Ag.)  
*Helotium* Tode per Leman (Ag.)  
*Hirsutella* Pat. (D.)  
*Hymenogloea* Pat. (Ag.) (syn., *Libellus* Lloyd).  
*Hypolyssus* Pers. (nomen confusum; Ag.)  
*Kordyanella* Höhn. (D.)  
*Lachnella* Fr. (Ag.)  
*Leptoglossum* P. Karst. (Ag.) (syn., *Corniola* S. F. Gray, *Dictyolus* QuéL., *Leptotus* P. Karst.)<sup>44</sup>  
*Manuripia* Sing. (Ag.)  
*Matruchotia* Boul. (D.)  
*Merismodes* Earle (Ag.) (syn., *Phaeocyphellopsis* W. Cooke)  
*Mniopetalum* Donk & Sing. apud Donk (Ag.)  
*Nyctalis* Fr. (Ag.)  
*Ordonia* Racib. (Septobasidiales)  
*Palaeocephala* Sing. (Ag.)  
*Pellidiscus* Donk (Ag.) (syn., *Phaeoglabrotricha* W. Cooke)  
*Peniophorina* Höhn. (D.?)  
*Perona* Pers. (Ag.)  
*Phaeosolenia* Speg. (Ag.)<sup>45</sup>  
*Phlebochora* Lévl. (Ag.)  
*Physalacria* Peck (Ag.) (syn., *Baumannella* P. Henn., *EOGARICUS* L. C. C. Krieger)<sup>46</sup>  
*Pleurotopsis* P. Henn. (Ag.) = *Resupinatus* Nees ex S. F. Gray  
*Pseudohydnum* P. Karst. (Tremellales) [syn., *Tremellodon* (Pers.) Fr.]

<sup>43</sup> Favolaschioideae Murrill in *Torreyia* 3: 7. 1903 ("Favolaschia"). — Holotype: *Favolaschia* (Pat.) Pat. apud Pat. & Lagerh.

<sup>44</sup> Tribu des Dictyolées Maire in *Bull. Soc. mycol. France* 18 (Suppl.): 99, 102. 1902. — Holotype: *Dictyolus* QuéL.; → Dictyoleae Lotsy; → Dictyolaceae Gäum.

Dictyoleae Lotsy, *Vortr. bot. Stammesgesch.* 1: 696, 698. 1907 = "Tribu des Dictyolées Maire".

Dictyolaceae Gäum., *Vergl. Morph. Pilze* 511. 1926; Ulbr. in *Kryptfl. Anfänger* 1 (3. Aufl.): 141. 1928 [*Dictyolus* "Pat." misapplied to monotypic genus consisting of *Cantharellus umbonatus* Gmel. per Fr., type species of *Cantharellula* Sing., Agaricales]; = "Tribu des Dictyolées Maire".

Leptotaceae Maire in *Treb. Mus. Ci. nat. Barcelona* 15: 58. 1933 (nomen nudum); Singer in *Lloydia* 8: 188. 1945 (lacking Latin description). — Type: *Leptotus* P. Karst.

<sup>45</sup> Phaeosoleniaceae W. Cooke in *Beih. Sydowia* 4: 14 ("Chromosoleniaceae"), 113. 1961. — Holotype: *Phaeosolenia* Speg.

<sup>46</sup> [Série des Physalacries Pat., *Essai tax. Hym.* 40, 50. 1900. — Type: *Physalacria* Peck]; → Physalacriaceae R. Heim.

Physalacriaceae R. Heim in *Treb. Mus. Ci. nat. Barcelona* 15: 50. 1934 (nomen nudum) = "Série des Physalacries Pat."

EOGARICACEAE L. C. C. Krieger in *Bull. Maryland Acad. Sci.* 3: 8. 1923. — Monotype: *EOGARICUS* L. C. C. Krieger (superfluous name change for) = *Physalacria* Peck.

- Pseudotremellodendron* D. Reid (Tremellales)  
*Ptychella* Roze & Boud. (Ag.) = *Agrocybe* Fayod, abnormal  
*Radulum* Fr. (Pyrenomycetes)<sup>47</sup>  
*Rimbachia* Pat. (Ag.)  
*Sarcopodium* Ehrenb. per Brongn. (D.)  
*Skepperiella* Pilát (Ag.) = *Rimbachia* Pat.?  
*Stigmatolemma* Kalchbr. (Ag.) (syn., *Rhodocyphella* W. Cooke)  
*Tremellodendropsis* (Corner) D. A. Crawf. (Tremellales) (syn., *Polyozus* P. Karst.)  
*Trogia* Fr. (Ag.)  
*Van-Romburghia* Holterm. ex Sacc. & P. Syd. (Ag.) = *Marasmius* Fr.?

### III. ALPHABETICAL ENUMERATION OF GENERA (exclusive of the polypores)

The following is an alphabetical enumeration of all validly published generic names based on species of Aphyllophorales, with the exclusion of the 'polypores', viz. the Polyporaceae, the Ganodermataceae, and the tubulate Bondarzewiaceae and Hymenochaetaceae.<sup>48</sup> Not included either are the genera that now make up the Brachybasidiales, Exobasidiales, and Cryptobasidiaceae; most of these genera have been included by some authors in the "Hypochneaceae".

This list aims at supplying some information on the genera by means of references and in this way to counterbalance the fact that they are merely mentioned by name in the Special Part. Preference is given to accounts that will contribute to taxonomic understanding of the genera rather than to mainly floristic treatments that aim at the naming of species. The references are of course of very different value, but I have tried to select the best available of those that define and describe the genera in closest agreement with my personal conceptions of them. Special attention is also paid to references to good illustrations of microscopic details. In some cases good descriptions of certain species (preferably type species) are chosen. Here and there references will be found to various other matters of importance to a better understanding of the genera or a special delimitation of them. Yet, the information thus assembled through these references on each of the genera is often very limited.

As to nomenclatural matters, mainly of typification, the reader is referred to

<sup>47</sup> *Raduleae* [?] Reichenb., *Consp. Regni veg.* 14. 1828 ("Radularii"; [subtrib. ?]; nomen nudum). — Type: *Radulum* Fr.

[Tribu des Radulées Maire in *Bull. Soc. mycol. France* 18 (Suppl.): 106. 1902. — Type: *Radulum* Fr.]; → *Raduleae* Lotsy.

*Raduleae* Lotsy, *Vortr. bot. Stammesgesch.* 1: 697, 699. 1907 ≡ "Tribu des Radulées Maire".

*Radulaceae* Gäum., *Vergl. Morph. Pilze* 511. 1929. — Type: *Radulum* Fr.

The type species of the generic name *Radulum* Fr. is an ascomycete, viz. *Eutypa hydnoidea* (Fr.) Höhn. The remaining species of the genus that are not yet referred to other genera are best at home in the residual genus *Odontia* Fr. (see p. 315).

<sup>48</sup> This also implies the exclusion from the list of names of genera incorrectly classed as polyporaceous and not referred back to one of the other families of the Aphyllophorales.

the series "The generic names proposed for Hymenomycetes—I–XIV" (Donk, 1951–63<sup>49</sup>).

Abbreviations and signs.—The names of the families of Aphyllophorales are reduced to their first few letters. These abbreviations are explained in the "Contents" on pages 199–200, where they are added to the full family names.

d.n., devaluated name;

nom. anam., nomen anamorphosis;

nom. cons., nomen conservandum; nom. cons. prop., nomen conservandum propositum;

nom. rejic., nomen rejiciendum; nom. rejic. prop., nomen rejiciendum propositum;

nom. conf., nomen confusum;

n.v.p., not validly published;

†, later homonyms, hence, not available;

→, transferred to.

*Acanthophysium* (Pilát) G. Cunn., Thel. Austr. New Zeal. 150. 1963, in part = *Aleurodiscus*, resupinate species.

† *Acia* P. Karst. = *Mycocacia*.

† *Aciella* (P. Karst.) P. Karst. = *Asterodon*.

*Acrotamnium* Nees, Syst. Pilze 74. 1816 per Fr.—Nomen dubium. *Fide* Hughes in Canad. J. Bot. 36: 733. 1958 ("=Basidiomycetes"); & cf. Donk in Taxon 11: 103. 1962 (nomenclature).

*Actiniceps* Berk. & Br. (Cl.).—Boedijn in Persoonia 1: 11. 1959; Corner, Monogr. Clav. 116, 400. 1952 (*Dimorphocystis*).

*Actinostroma* Kl. = *Cymatoderma*.

*Acutis* Fr. (nom. anam.) [*Entoloma abortivum* (Berk. & C.) Donk] (Cl. → Agaricales).

*Alectorolophoides* Earle = *Cantharellus*.

*Aldridgea* Mass. (Con.?).—Nomen dubium, *fide* Wakef. *apud* Donk in Taxon 6: 18. 1957.

*Aldridgeella* J. Rick in Brotéria (Ci. nat.) 3: 170. 1934.—Nomen dubium.

*Aleurocystidiellum* Lemke in Canad. J. Bot. 42: 277. 1964 (Cor.) = *Aleurodiscus*.

*Aleurocystis* Lloyd ex G. Cunn. in Trans R. Soc. New Zeal. 48: 234. 1956; Thel. Austr. New Zeal. 188. 1963 = *Aleurodiscus*.

<sup>49</sup> DONK, M. A. (1951–63): The generic names proposed for Hymenomycetes—I. "Cyphellaceae." In Reinwardtia 1: 199–220. 1951. — II. Hymenolichenes. In Reinwardtia 2: 435–440. 1954. — III. "Clavariaceae." In Reinwardtia 2: 441–493. 1954. — IV. Boletaceae. In Reinwardtia 3: 275–313. 1955. — V. "Hydnaceae." In Taxon 5: 69–80, 95–115. 1956. — VI. Brachybasidiaceae, Cryptobasidiaceae, Exobasidiaceae. In Reinwardtia 4: 113–118. 1956. — VII. "Theleporaceae." In Taxon 6: 17–28, 68–85, 106–123. 1957. — VIII. Auriculariaceae, Septobasidiaceae, Tremellaceae, Dacrymycetaceae. In Taxon 7: 164–178, 193–207, 236–250. 1958. — IX. "Meruliaceae" and *Cantharellus* s. str. In Fungus 28: 7–15. 1958. — [X]. The generic names proposed for Polyporaceae. In Persoonia 1: 173–302. 1960. — [XI]. The generic names proposed for Agaricaceae. In Beih. Nova Hedw. 5: iv & 320 & (i) pp. 1962. — XII. Deuteromycetes. In Taxon 11: 75–104. 1962. — XIII. Additions and corrections to Parts I–XI, XII. In Taxon 12: 113–123, 153–168. 1963. — [XIV]. The generic names proposed for Polyporaceae. Additions and corrections. In Persoonia 2: 201–210. 1962. — Parts I–IX, XII, XIII were brought together in a photo-reprint edition to which an "Index" was added, Weinheim, J. Cramer, 1964.

- Aleurodiscus* Rab. ex J. Schroet. (Cor.).—Höhn. & Litsch. in S.B. Akad. Wien (Math.-nat. Kl. I) **116**: 796. 1907, in part; Donk in *Persoonia* **1**: 65, 66. 1959; Lemke in *Canad. J. Bot.* **42**: 213. 1964.
- Allantula* Corner in *Ann. Bot., Lond.* II **16**: 270. 1952 (Cl.).
- Alytosporium* (Link) per Link.—Nomen dubium. Cf. Donk in *Taxon* **6**: 18. 1957; **12**: 156. 1963.
- Amaurodon* J. Schroet. in *Krypt.-Fl. Schles.* **3** (1): 461. 1888 (Cor.).
- Amphinema* P. Karst. (Cor.).—John Erikss. in *Symb. bot. upsal.* **16** (1): 111. 1958; M. P. Christ. in *Dansk bot. Ark.* **19**: 228. 1960.
- Amylaria* Corner in Balf.-Browne in *Bull. Brit. Mus. (Nat. Hist.) (Bot.)* **1**: 197. 1955 (Bo.).
- Amylocorticium* Pouz. in *Česká Mykol.* **13**: 11. 1959 (Cor.).
- Amylostereum* Boid. in *Rev. Mycol.* **23**: 345. 1958 (St.).
- Aphelaria* Corner (Cl., St.).—Corner, *Monogr. Clav.* 182. 1950 (*A. dendroides*); in *Ann. Bot., Lond.* II **17**: 347. 1953 (subgen. *Aphelaria*).
- Apus* (Nees) ex S. F. Gray = *Schizophyllum*.
- Araecoryne* Corner, *Monogr. Clav.* 32, 194. 1950 (Cl.).
- Arrhenia* Fr. (Ca., Cy. → Agaricales).—J. Favre, *Champ. sup. Parc nat. suisse* 37. 1955; Sing., *Agar.*, 2nd Ed., 276. 1962.
- Asterocyphella* W. Cooke in *Beih. Sydowia* **4**: 118. 1961 (Cy.).
- Asterodon* Pat. (Hym.).—Corner in *Trans. Brit. mycol. Soc.* **31**: 234. 1948.
- Asterostroma* Mass. (Hym.).—Corner in *Trans. Brit. mycol. Soc.* **31**: 241. 1948; John Erikss. in *Svensk bot. Tidskr.* **48**: 195. 1954 (spores).
- Asterostromella* Höhn. & Litsch. = *Vararia*.
- Athelia* Pers. (Cor.).—Donk in *Fungus* **27**: 12. 1957; John Erikss. in *Symb. bot. upsal.* **16** (1): 83. 1958; M. P. Christ. in *Dansk bot. Ark.* **19**: 137. 1960.
- †*Auricula* Lloyd = *Phaeophlebia* = *Punctularia*.
- Auriculariopsis* Maire (Cor.).—Donk in *Persoonia* **1**: 76. 1959.
- Auriscalpium* S. F. Gray (Au.).—Romagn. in *Bull. Soc. Natur. Oyonnax* **7**: 111. 1953; Maas G. in *Proc. Ned. Akad. Wet. (C)* **66**: 426. 1963.
- †*Auriscalpium* P. Karst. = *Auriscalpium* S. G. Fray.
- Bankera* Coker & Beers, *Stip. Hydn.* 33. 1951 ex Pouz. (Ba.).—Maas G. in *Fungus* **28**: 56. 1958; in *Proc. Ned. Akad. Wet. (C)* **66**: 434. 1963.
- Baumannella* P. Henn. = ? *Physalacria*, *fide* Corner, *Monogr. Clav.* 456. 1950.
- Beccaria* Mass. = *Beccariella* = *Cymatoderma*
- Beccariella* Ces. = *Cymatoderma*.
- Beenakia* D. Reid (Go.).—Maas G. in *Proc. Ned. Akad. Wet. (C)* **66**: 437. 1963.
- Boletopsis* Fayod in *Malpighia* **3**: 72. 1889 (Th.).—Donk, *Rev. niederl. Homob.-Aph.* **2**: 64. 1933.
- †*Bonia* Pat. = *Heterochaete* Pat. (Tremellineae).
- Boninohydium* S. Ito & S. Imai = *Gyrodontium*, *fide* Maas G. in *Persoonia* **3**: 190. 1964.
- Botryobasidium* Donk (Cor.).—John Erikss. in *Svensk bot. Tidskr.* **52**: 3. 1958; in *Symb. bot. upsal.* **16** (1): 47. 1958; Donk in *Fungus* **28**: 26. 1958; M. P. Christ. in *Dansk bot. Ark.* **19**: 69. 1960.

- Botryohypochnus* Donk (Cor.)—John Erikss. in Svensk. bot. Tidskr. **52**: 2. 1958;  
Donk in Fungus **28**: 24. 1958; M. P. Christ. in Dansk bot. Ark. **19**: 66. 1960.
- Bressadolina* W. Brinkm. in Ann. mycol. **7**: 289. 1909 (St.).—Boid. in Rev. Mycol.  
**24**: 201. 1959 (*Cotylidia pallida*).
- Buglossus* Wahlenb. per Wahlenb. = *Fistulina*.
- Byssocorticium* Bond. & Sing. ex Sing. (Cor.).—M. P. Christ. in Dansk bot. Ark.  
**19**: 159. 1960.
- Calathella* D. Reid in Persoonia **3**: 122. 1964 (Cy. → Agaricales).
- Caldesiella* Sacc. (Th.).—Bourd. & G., Hym. France 471. 1928; M. P. Christ. in  
Dansk bot. Ark. **19**: 302. 1960.
- Calodon* Quél. ex P. Karst. = *Hydnellum*.
- Caloporia* P. Karst. ≡ *Caloporus* = *Merulius*.
- Caloporus* P. Karst. = *Merulius*, fide Donk in Persoonia **2**: 227. 1962.
- Calyptrella* Quél. (Cy. → Agaricales).—D. Reid in Kew Bull. **15**: 261. 1961; Sing.,  
Agar., 2nd Ed., 329. 1962.
- Campanella* P. Henn. (Ca., Cy. → Agaricales).—Sing. in Lloydia **8**: 190. 1945;  
Agar., 2nd Ed., 325. 1962.
- Cantharellus* Adans. per Fr. (Ca.).—Corner in Beih. Sydowia **1**: 268. 1957; Heinem.  
in Bull. Jard. bot. Brux. **28**: 390. 1958.
- Cariþia* O.K. (St.?).—G. W. Mart. in Mycologia **30**: 438. 1938 (*Hypolyssus montagnei*);  
Corner, Monogr. Clav. 34. 196. 1950; Sing., Agar., 2nd Ed., 792. 1962.
- Catilla* Pat. in Bull. Soc. mycol. France **31**: 32. 1915 (Cy. → Agaricales).
- Cellypha* Donk in Persoonia **1**: 84. 1959 (Cy. → Agaricales).—Sing., Agar., 2nd Ed.,  
413. 1962; D. Reid in Persoonia **3**: 131. 1964.
- Ceracea* Crag. sensu Pat. & auctt. = *Arrhytidia* Berk. & C. (Dacrymycetales) &  
*Cerinomyces*.
- † *Ceratella* Pat. = *Ceratellopsis*.
- † *Ceratella* (Quél.) Big. & Guill. = *Clavaria*, residual genus.
- Ceratellopsis* Konr. & Maubl. (Cl.).—Corner, Monogr. Clav. 35. 198. 1952.
- Ceratobasidium* D. P. Rog. in Stud. nat. Hist. Univ. Iowa **17** (1): 4. 1935 (Cor.).—  
Donk in Fungus **28**: 17. 1958.
- Cerinomyces* G. W. Mart. in Mycologia **41**: 82. 1949 (Cor. or Dacrymycetales).—L.  
Kennedy in Mycologia **50**: 880. 1959; Parmasto in Eesti NSV tead. Akad. toim.  
**10**/Biol. **3**: 231. 1961.
- Cerocorticium* P. Henn. in Warb., Monsunia **1**: 138. [1899] (Cor.).—Höhn. & Litsch.  
in S.B. Akad. Wien (Math.-nat. Kl. I) **116**: 785. 1907 (*Corticium ceraceum*).
- Cerrenella* Murrill = *Hydnochaete* Bres., pileate forms.
- † *Chaetocarpus* P. Karst. = *Columnocystis*.
- Chaetocypha* Corda.—Nomen dubium. Cf. Donk in Reinwardtia **1**: 208. 1951.
- Chaetotyphula* Corner, Monogr. Clav. 207. 1950 (Cl.).
- Chanterel* Adans. per Murrill (variant spelling) ≡ *Cantharellus*.
- Chlorocyphella* Speg. = *Pyrenotrichum* Mont. Fide Santesson in Symb. bot. upsal. **12**  
(1): 41, 52. 1952, parasymbiotic Deuteromycetes, Lichens.



- Chloroneuron* Murrill (Go.).—R. Heim in Rev. Mycol. **19**: 51. 1954 (*Nevrophyllum viride*).
- †*Chlorophyllum* Murrill ≡ *Chloroneuron*.
- Chondrostereum* Pouz. in Česká Mykol. **13**: 17. 1959 (St.).—Lentz in Sydowia **14**: 127. 1960. — Cf. Boid. in Bull. Soc. linn. Lyon **28**: 219. 1959 (*Stereum purpureum*).
- Chromocyphella* De Toni & Levi (Cy. → Agaricales).—Donk in Persoonia **1**: 92. 1959; Sing., Agar., 2nd Ed., 669. 1962.
- Cilicia* Fr. = *Dictyonema*? Cf. Donk in Reinwardtia **2**: 435. 1954 (= *Cora*?).
- Cladaria* Ritgen = *Ramaria*. Cf. Donk in Reinwardtia **2**: 447. 1954.
- Cladoderris* Pers. ex Berk. = *Cymatoderma*.
- Clavaria* [Vaill.] Fr. (nom. cons.) (Cl.).—Corner, Monogr. Clav. 36, 241. 1950.
- Clavariachaete* Corner, Monogr. Clav. 42, 268. 1950 (Hym.).
- Clavariadelphus* Donk (Cl.).—Corner, Monogr. Clav. 42, 269. 1950.
- Clavariella* P. Karst. = *Ramaria*.
- Clavicorona* Doty (He.).—Corner, Monogr. Clav. 51, 285. 1950, at least in part.
- Clavulicium* Boid. in Bull. Soc. Hist. nat. Toulouse **92**: 280. 1957 (Cor.).—Boid. in Bull. Soc. linn. Lyon **23**: 229. 1954 (*Corticium pilati*).
- Clavulina* J. Schroet. (Clavul.).—Donk, Rev. niederl. Homob.-Aph. **2**: 16. 1933; Corner in New Phytol. **47**: 46. 1948 (basidia); Monogr. Clav. 59, 294. 1950.
- Clavulinopsis* Overeem (Cl.).—Corner, Monogr. Clav. 74, 342. 1950.
- Climacodon* P. Karst. (residual Hyd.).—Maas G. in Persoonia **2**: 378. 1962.
- Cnazonaria* Corda = *Pistillaria*, fide Corner, Monogr. Clav. 147. 1950.
- Columnocystis* Pouz. in Česká Mykol. **13**: 17. 1959 (St.).—Boid. in Bull. Soc. linn. Lyon **28**: 215. 1959.
- Coniobotrys* Pouz. in Česká Mykol. **12**: 32, 35. 1958 (Con.). = ? *Jaapia*.
- Coniophora* DC. per Mérat (Con.).—Bourd. & G., Hym. France 355. 1928; Lentz in Mycologia **49**: 534. 1957 (basidia).
- Coniophorafomes* J. Rick in Brotéria (Ci. nat.) **3**: 167. 1934.—Nomen dubium.
- Coniophorella* P. Karst. (Con.).—Wakef. & Pears. in Trans. Brit. mycol. Soc. **6**: 72. 1918.
- Cora* Fr.; Mattiolo in Nuovo G. bot. ital. **13**: 253. 1881 (wrong spores); Johow in Jb. wiss. bot. **15**: 363. 1884; A. Möll. in Flora **77**: 255. 1893; Grassi in Lilloa **24**: 384. 1950; (all, *C. pannonia*) = *Dictyonema*, fide A. Möll., l.c. (as to fungus component of type species).
- Coraeomyces* Ciferri & Tomasselli in Atti Ist. bot. Univ. Lab. critt. Pavia V **10**: 293. 1954 (n.v.p., lacking indication of type) = *Cora* = *Dictyonema*.
- Corallium* Hahn = *Ramaria*.
- Corella* Wainio (Di.).—Zahlbr. in Nat. PflFam., 2. Aufl., **8**: 261. 1926.
- †*Cornicularia* Bon. = *Clavulinopsis*. Cf. Donk in Reinwardtia **2**: 456. 1954.
- †*Corniola* S. F. Gray = *Leptoglossum*.
- Corticirama* Pilát in Beih. Sydowia **1**: 128. 1957 (Cor.).
- Corticium* Pers. per S. F. Gray.—Could be taken as the correct name for *Laeticorticium*; cf. Donk in Taxon **12**: 158. 1963. However, the name is suggested for use

- for a 'residual' genus of unplaced 'corticiums' whether in a narrow sense (lacking gloeocystidia and cystidia) or not (inclusive of species of '*Gloeocystidium*' and '*Peniophora*'), cf. Donk in *Taxon* **12**: 159 (in obs.). 1963.
- †*Corticium* "S. F. Gray" sensu Donk = *Peniophora*.
- †*Corticium* Fr. (Cor.). = *Phanerochaete*. Cf. Donk in *Taxon* **6**: 25. 1957 & **12**: 159 (in obs.). 1963; in *Persoonia* **2**: 223. 1962.
- Cotylidia* P. Karst. (St.).—Maire in *Ann. mycol.* **7**: 429. 1909 (*Podoscypha undulata*); Boid. in *Rev. Mycol.* **24**: 199. 1959, in part.
- Craterella* Pers. per S. F. Gray (nom. rejic. prop.) = *Bresadolina*.
- Craterellus* Pers. (nom. cons. prop.) (Ca.).—Corner in *Beih. Sydowia* **1**: 267, 270. 1957; Heinem. in *Bull. Jard. bot. Brux.* **28**: 429. 1958.
- Creolophus* P. Karst. (He.).—Donk in *Persoonia* **2**: 231. 1962; Maas G. in *Persoonia* **2**: 381. 1962.
- Cristella* Pat. (Cor.).—Donk in *Fungus* **27**: 19. 1957; in *Reinwardtia* **1**: 485. 1952 & cf. in *Taxon* **6**: 68. 1957 (typification).
- Cryptochaete* P. Karst. = *Peniophora*.
- Crystallocystidium* (J. Rick) J. Rick in *Iheringia (Bot.)* **4**: 79. 1959.—Nomen dubium.
- Cymatella* Pat. (Ca., "Th." → Agaricales).—Sing., *Agar.*, 2nd Ed., 326. 1962.
- Cymatoderma* Jungh. (St.).—Boid. in *Rev. Mycol.* **24**: 219. 1959; D. Reid in *Kew Bull.* **13**: 519. 1959.
- †*Cymbella* Pat. apud Doass. & Pat. = *Chromocyphella*.
- Cyphella* Fr. (nom. rejic.) = *Aleurodiscus*.
- Cyphellina* J. Rick in *Iheringia (Bot.)* **4**: 124. 1959.—Nomen dubium.
- Cyphellopsis* Donk (Cy. → Agaricales).—Donk in *Persoonia* **2**: 345. 1962; Sing., *Agar.*, 2nd Ed., 405. 1962; D. Reid in *Persoonia* **3**: 108. 1964.
- Cystidiendendron* J. Rick in *Lilloa* **9**: 218. 1943.—Nomen dubium.
- Cystostereum* Pouz. in *Česká Mykol.* **13**: 18. 1959 (St.).—John Erikss. in *Symb. bot. upsal.* **16** (1): 126. 1958 (*Stereum murraini*).
- Cytidia* Quél. (Cor.).—Donk in *Persoonia* **1**: 70. 1959.
- Cytidiella* Pouz. in *Česká Mykol.* **8**: 125. 1954 (Cor.).
- †*Dacrina* Fr. 1825 = *Dacryobolus*.
- Dacryobolus* Fr. (Cor.).—John Erikss. in *Symb. bot. upsal.* **16** (1): 115. 1958; M. P. Christ. in *Dansk bot. Ark.* **19**: 244. 1960.
- Dacryopsella* Höhn. = *Pistillina*, fide Donk in *Reinwardtia* **2**: 457. 1954.
- Deflexula* Corner, *Monogr. Clav.* 115, 394. 1950 (Cl.).—Corner in *Ann. Bot., Lond.* **II** **16**: 274. 1952.
- Delicatula* Fayod (Agaricales).—Kühner in *Botaniste* **17**: 94. 1926; Sing., *Agar.*, 2nd Ed., 370. 1962. Hymenophore may be smooth.
- Dendrocladium* (Pat.) Lloyd = *Ramaria*. Cf. Corner, *Monogr. Clav.* 83. 1950 & Donk in *Reinwardtia* **2**: 457. 1954.
- Dendrocycphella* Petch in *Ann. bot. Gdns Peradeniya* **7**: 289. 1922 (Cy. → Agaricales).
- Dendrothele* Höhn. & Litsch. in *S.B. Akad. Wien (Math.-nat. Kl. I)* **116**: 819. 1907 (Cor.).—Bourd. & G., *Hym. France* 337. 1928.

- Dentinum* S. F. Gray = *Hydnum*.
- Dentipellis* Donk in *Persoonia* 2: 232. 1962 (He.).
- Dicellomyces* L. Olive in *Mycologia* 37: 544. 1945; 39: 103. 1947.—Doubtful position (Exobasidiales?).
- Dichonema* Blume & T. Nees = *Dictyonema*, *vide* Hariot in *Bull. Soc. mycol. France* 7: 41. 1891.
- Dichostereum* Pilát = *Vararia* P. Karst.
- Dictyonema* Agardh (Di.).—Johow in *Jb. wiss. Bot.* 15: 380. 1884; Metzner in *Ber. dtsh. bot. Ges.* 52: 234. 1934 (*D. sericeum*).
- Dictyonematomyces* Ciferri & Tomaselli in *Atti Ist. bot. Univ. Lab. critt. Pavia V* 10: 293. 1954 = *Dictyonema*.
- Digitatispora* Doguet in *C.R. Acad. Sci., Paris* 254: 4336. 1962 (Cor.).—Doguet in *Bull. Soc. mycol. France* 78: 283. 1963; 79: 249. 1963.
- Dimorphocystis* Corner = *Actiniceps*, *vide* Boedijn in *Persoonia* 1: 12. 1959.
- Discocephella* P. Henn. ("Th." → Agaricales).—*Fide* Pat., *Essai tax. Hym.* 147. 1900 = *Cymatella*, but cf. Sing., *Agar.*, 2nd Ed., 415. 1962, who treats it as a nomen dubium.
- Donkella* Doty = *Clavulinopsis*.
- Donkia* Pilát (residual *Hyd.*).—Maas G. in *Persoonia* 2: 384. 1962.
- Dryodon* Quéf. ex P. Karst. = *Heridium*.
- Duportella* Pat. (Cor.).—Talbot in *Bothalia* 6: 46. 1951; Boid. & Ahmad in *Biologia* 9: 33. 1963.
- Echinodontium* Ell. & Ev. (Ech.).—Imaz. in *J. Jap. Bot.* 11: 514. 1935.
- Echinotrema* Park.-Rh. in *Trans. Brit. mycol. Soc.* 38: 367. 1955 (Cor.).
- EOGARICUS* L. C. C. Krieg. ≡ *Physalacia*.
- Eomycenella* Atk. (Agaricales) = *Mycena* (Pers. per Fr.) S. F. Gray? Cf. Sing., *Agar.*, 2nd Ed., 416. 1962.—Practically a nomen dubium.
- Epicnaphus* Sing. in *Sydowia* 14: 274. 1960 (Agaricales).—Sing., *Agar.*, 2nd Ed., 410. 1962. Hymenophore smooth.
- Episphaeria* Donk in *Persoonia* 2: 336. 1962 (Cy. → Agaricales).—Sing., *Agar.*, 2nd Ed., 666. 1962.
- Epithele* (Pat.) Pat. (Cor.).—Höhn. & Litsch. in *S.B. Akad. Wien (Math.-nat. Kl. I)* 115: 49. 1906 (*E. typhae*); Bourd. & G., *Hym. France* 245. 1928.
- Eriocladus* Lév. (nom. rejic. prop.) ≡ *Lachnocladium*.
- Etheiroidon* Banker (correct name for) ≡ *Odontia* Fr. sensu stricto = *Steccherinum*.
- Favolaschia* (Pat.) Pat. apud Pat. & Lagerh. (Cy. → Agaricales).—Sing. in *Lloydia* 8: 195. 1945.
- Fibricium* John Erikss. in *Symb. bot. upsal.* 16 (1): 112. 1958 (Cor.).
- Fistulina* Bull. per Fr. (Fi.).—De Seynes, *Rech. Vég. inf., Fist.* 1874; Lohwag & Follner in *Ann. mycol.* 34: 456. 1936.
- Flagelloscypha* Donk apud Sing. in *Lilloa* 22: 312. 1951 (Cy. → Agaricales).—Sing., *Agar.*, 2nd Ed., 414. 1962; D. Reid in *Persoonia* 3: 97. 1964.
- Friesites* P. Karst. = *Heridium*.

- Friesula* Speg. ("Th.").—Nomen dubium. — Cf. Sing. in *Lilloa* **23**: 123. 1950.
- Galzinia* Bourd. (Cor.).—D. P. Rog. in *Mycologia* **36**: 99. 1944; L. Olive in *Mycologia* **46**: 794. 1954; John Erikss. in *Symb. bot. upsal.* **16** (1): 70 (in obs.) f. 16. 1958.
- Geotus* Pilát & Svrček in *Česká Mykol.* **7**: 9. 1953 (Ca. → Agaricales), an *Leptoglossum*?
- Glabrocypbella* W. Cooke in *Beih. Sydowia* **4**: 45. 1961 (Cy.).
- Gliocoryne* Maire *apud* Guinier & Maire = *Pistillaria*.
- Gloeasterostroma* J. Rick in *Brotéria* (Ci. nat.) **7**: 75. 1938 (nom. conf.), *vide* J. Rick in *Iheringia* (Bot.) **4**: 116. 1959, "Gloeocystidia enim ibi notata nihil aliud sunt quam Ascomycetes parasiticus, probabiliter *Woronina*."
- Gloeocantharellus* Sing. in *Lloydia* **8**: 140. 1945 (Go.).
- Gloeocystidiellum* Donk (Cor.).—Donk in *Fungus* **26**: 8. 1956; John Erikss. in *Svensk bot. Tidskr.* **52**: 14. 1958.
- Gloeocystidium* P. Karst. = *Dacryobolus*.
- Gloeocystidium* P. Karst. sensu Höhn. & Litsch. (Cor.).—Suggested for use as the name of a 'residual' genus for unplaced gloeocystidiate 'corticiums', lacking cystidia, if kept distinct from *Corticium* Pers. per S. F. Gray, q.v. Cf. Donk in *Fungus* **26**: 10. 1956.
- Gloeopeniophora* Höhn. & Litsch. = *Peniophora*.
- Gloeopeniophorella* J. Rick in *Broteria* (Ci. nat.) **3**: 47, 173. 1934.—Nomen dubium.
- Gloeoporus* Mont. (Cor.).—L. Hansen in *Friesia* **5**: 253. 1956 (*Polyporus dichrous*).
- Gloeoradulum* J. Rick in *Iheringia* (Bot.) **5**: 183. 1959 (n.v.p.)—Nomen dubium.
- Gloeosoma* Bres. in *Ann. mycol.* **18**: 51. 1920 = *Aleurodiscus*.
- Gloeostereum* S. Ito & S. Imai *apud* S. Imai in *Trans. Sappora nat. Hist. Soc.* **13**: 11. 1933 (St.).
- Gloeotulasnella* Höhn. & Litsch. (Cor.); D. P. Rog. in *Ann. mycol.* **31**: 194. 1933 = *Tulasnella*, *vide* L. Olive in *Mycologia* **49**: 668–671. 1957.
- Gloiocephala* Mass. (Cl. → Agaricales).—Sing. in *Sydowia* **14**: 260. 1960; Agar., 2nd Ed., 407. 1962; Bas in *Persoonia* **2**: 77. 1961. Hymenophore often smooth.
- Gloiodon* P. Karst. (Au.).—Maas G. in *Proc. Ned. Akad. Wet. (C)* **66**: 430. 1963.
- Gloiothele* Bres. in *Ann. mycol.* **18**: 44. 1920 (Cor.).
- Gomphora* Fr. = *Gomphus*.
- Gomphus* Pers. per S. F. Gray (Go.).—A. H. Sm. & Morse in *Mycologia* **39**: 499. 1947 (*Cantharellus* sect. *Gomphus*); R. Heim in *Rev. Mycol.* **19**: 51. 1954 (*Neurophyllum*).
- Goossensia* Heinem. in *Bull. Jard. bot. Brux.* **28**: 424. 1958 (Ca.).
- Grammothele* Berk. & C. (Cor.).—Pat., *Essai tax. Hym.* 62. 1900; Talbot in *Bothalia* **6**: 59. 1951.
- Grandinia* Fr.—Nomen dubium, *vide* Donk in *Taxon* **5**: 77. 1956.
- Grandiniella* P. Karst. in *Hedwigia* **34**: 8. 1895 = ? *Phanerochaete*, *vide* Donk in *Taxon* **6**: 72. 1957.
- Grandiniochaete* J. Rick in *Ann. mycol.* **38**: 59. 1940.—Nomen dubium.
- Grandinioides* Banker = *Mycobonia*.
- Gyrodontium* Pat. (Con.).—D. Reid in *Kew Bull.* **17**: 267. 1963 (*G. serpuloides* & al.); Maas G. in *Persoonia* **3**: 187. 1964. (*Gyrodontium versicolor*).

- Gyrophium* Kunze ex Krombh. = *Cora* = *Dictyonema*.  
*Gyrophana* Pat. = *Serpula*.  
 †*Gyrophora* Pat. ≡ *Gyrophana* = *Serpula*.  
*Haematostereum* Pouz. = *Stereum*.  
*Helotium* Tode per Lemm (Agaricales).—Nomen dubium. Cf. Donk in Beih. Nova Hedw. 5: 122. 1962; Sing., Agar., 2nd Ed., 416, 799. 1962. — Name also applied to Discomycetes.  
*Henningsomyces* O.K. (Sch.).—D. Reid in Kew. Bull. 15: 269. 1961; in Persoonia 3: 118. 1964.  
*Heptasporium* Bref. = *Sistotrema*.  
*Hericium* Pers. per S. F. Gray (He.).—Donk in Persoonia 2: 231. 1962; Maas G. in Proc. Ned. Akad. Wet. (C) 66: 444. 1963.  
 †*Hericium* Fr. = *Hericium* Pers. per S. F. Gray, *vide* Donk in Taxon 5: 80. 1956.  
 †*Hericius* Juss. per Lam. = *Hericium* Pers. per S. F. Gray.  
*Herpothallon* F. Tobler in Flora 131: 446. 1937 (Di.).  
*Herpothallonomyces* Ciferri & Tomaselli in Atti Ist. bot. Univ. Lab. critt. Pavia V 10: 292. 1954 = *Herpothallon*.  
 †*Heterobasidium* Mass. (nom. conf.), *vide* Burt apud Lloyd (cf. Donk in Taxon 7: 73. 1957) based on some sterile stereum strands on which a little peziza was growing.  
 †*Heteromyces* L. Olive = *Oliveonia*.  
 †*Himantia* (Fr.) Zoll. = *Corticium* Pers. per S. F. Gray (residual genus).  
*Hirneola* Fr. 1825 (nom. rejic.) = *Mycobonia*.  
*Hirsutella* Pat. (nom. anam.).—Deuteromycetes (non-basidiomycetous), cf. Spere in Mycologia 12: 62. 1920; Mains in Mycologia 43: 691, 696. 1951.  
*Holocoryne* (Fr.) Bon. = *Clavaria*.  
*Holomitriaria* Corner, Monogr. Clav. 96, 410. 1950 (Cl.).—Corner in Ann. Bot., Lond. II 17: 34. 1953.  
*Hydnellum* P. Karst. (1879) (Th.).—Coker & Beers, Stip. Hydn. 56. 1951; Pouz. in Česká Mykol. 10: 68. 1956; Maas G. in Fungus 27: 50. 1957; in Persoonia 2: 388. 1962.  
 †*Hydnellum* P. Karst. in Hedwigia 35: 173. 1896.—Nomen dubium.  
*Hydnochaete* Bres. in Hedwigia 35: 287. 1896 (Hym.).  
 †*Hydnochaete* Peck = *Asterodon*.  
*Hydnochaetella* Sacc. ≡ *Hydnochaete* Peck = *Asterodon*.  
*Hydnodon* Banker (Th.).—Coker & Beers, Stip. Hydn. 83. 1958 (*Pseudohydnium*); Maas G. in Proc. Ned. Akad. Wet. (C) 66: 447. 1963.  
*Hydnofomes* P. Henn. = *Echinodontium*.  
*Hydnophysa* Clem. ≡ *Hydnofomes* = *Echinodontium*.  
*Hydnoporia* Murrill in N. Amer. Fl. 9: 3. 1907 = *Hydnochaete* Bres., *vide* Banker in Mycologia 6: 232. 1914.  
*Hydnopsis* (J. Schroet.) Rea = *Caldesiella*, *vide* Donk in Taxon 5: 97. 1956.  
*Hydnotrema* Link ≡ *Sistotrema* Fr.  
*Hydnium* L. per Fr. (Hyd.).—Donk, Rev. niederl. Homob.-Aph. 2: 13. 1933; Coker &

- Beers, Stip. Hyd. 15. 1951; Maas G. in *Persoonia* 1: 132. 1959; in Proc. Ned. Akad. Wet. (C) 66: 449. 1963.
- Hymenochaete* Lév. (nom. cons. prop.) (Hym.).—Burt in Ann. Missouri bot. Gdn 5: 301. 1918.
- Hymenochaetella* P. Karst. = *Hymenochaete*.
- Hymenogloea* Pat. (Agaricales).—Sing. in *Sydowia* 14: 275. 1960; Agar., 2nd Ed., 411. 1962. Hymenophore smooth.
- Hymenogramme* Mont. & Berk. (Cor.).—Pat., Essai tax. Hym. 60. 1900 (*H. javensis*).
- Hyphoderma* Wallr. (Cor.).—Donk in *Fungus* 27: 13. 1957; in *Persoonia* 2: 220. 1962; John Erikss. in *Symb. bot. ups. sal.* 16 (1): 95. 1958; M. P. Christ. in *Dansk bot. Ark.* 19: 199. 1960.
- Hyphodontia* John Erikss. in *Symb. bot. ups. sal.* 16 (1): 101. 1958 (Cor.).—M. P. Christ. in *Dansk bot. Ark.* 19: 216. 1960.
- Hypochnella* J. Schroet. (Cor.).—Wakef. in *Trans. Brit. mycol. Soc.* 5: 127. 1915 & Bourd. & G., *Hym. France* 243. 1928 (*H. violacea*).
- Hypochnicium* John Erikss. in *Symb. bot. ups. sal.* 16 (1): 100. 1958 (Cor.).—M. P. Christ. in *Dansk bot. Ark.* 19: 211. 1960.
- Hypochnopsis* P. Karst. (Cor.).—Wakef. in *Trans. Brit. mycol. Soc.* 35: 43. 1952 (*Coniophora mustialaensis*).
- Hypochnus* Fr. ex Ehrenb. (if not considered a nomen ambiguum, presumably correct name for) = *Herpothallon*.
- †*Hypochnus* Fr. per Fr. = *Tomentella*.
- Hypodrys* Pers. per Pers. = *Fistulina*.
- Hypolyssus* Pers. (nom. conf.). Agarics parasitized by *Hypomyces* (Fr.) Tul. and *Byssonectria* P. Karst. Cf. Donk in *Taxon* 6: 80. 1957.
- Hypolyssus* Pers. sensu Berk. = *Caripia*.
- Hyponevis* Paul. (d.n.) = *Merulius* Haller = *Merulius* [Haller] St.-Am. Cf. Donk in *Taxon* 12: 167. 1963.
- Hyponevis* Earle (non Paul.) = *Schizophyllum*.
- Hypothele* Paul.; Banker (n.v.p.) = *Hydnum*.
- Irpex* Fr. (Hyd. → Pol.).—Maas G. in Proc. Ned. Akad. Wet. (C) 66: 452. 1963.—Typified by *I. lacteus*, cf. Donk in *Taxon* 5: 100. 1956.
- Irpicochaete* J. Rick in Ann. mycol. 38: 58. 1940.—Nomen dubium.
- Jaapia* Bres. (Con.).—Nannf. & John Erikss. in *Svensk bot. Tidskr.* 47: 183. 1953.
- †*Karstenia* Britz. = *Tomentella*, fide Donk in *Taxon* 6: 91. 1957.
- Kavinia* Pilát (Go.).—John Erikss. in *Svensk bot. Tidskr.* 48: 197. 1954 (*Clavaria himantia*, *C. bourdotii*); M. P. Christ. in *Dansk bot. Ark.* 19: 330. 1960.
- †*Kneiffia* Fr. (Cor.). = *Hyphoderma*.
- Kneiffiella* P. Karst. (Th.).—Donk, Rev. nierderl. Homob.—Aph. 2: 25. 1933; Bourd. & G., *Hym. France* 472. 1928 (*Tomentellina*); M. P. Christ. in *Dansk bot. Ark.* 19: 300. 1960 (*Tomentellina*); Svrček in *Sydowia* 14: 239. 1960 (*Tomentellina*).
- †*Kneiffiella* P. Henn. = *Kneiffia* = *Hyphoderma*.
- †*Kneiffiella* Underw. = *Kneiffia* = *Hyphoderma*.

- Koleroga* Donk in *Fungus* **28**: 35. 1958 (Cor.).
- Kordyanella* Höhn., *vide* D. P. Rog. in *Mycologia* **49**: 902. 1957, a species of Deuteromycetes.
- Lachnella* Fr. (Cy. → Agaricales).—Donk *apud* Sing. in *Lilloa* **22**: 343. 1951; in *Persoonia* **1**: 97. 1959; D. Reid in *Kew Bull.* **15**: 266. 1961; in *Persoonia* **3**: 105. 1964.
- Lachnocladium* Lév. (nom. cons. prop.) (Hym.).—Corner, *Monogr. Clav.* **83**, 416. 1950.
- Laeticorticium* Donk in *Fungus* **26**: 16. 1956 (Cor.).—John Erikss. in *Symb. bot. upsal.* **16** (1): 73. 1958.
- Langloisula* Ell. & Ev. (nom. conf.), cf. D. P. Rog. & Jacks. in *Farlowia* **1**: 292. 1943 & Donk in *Taxon* **6**: 82. 1957 = *Vararia* (Cor.) + Deuteromycete.
- †*Laschia* Jungh. ≡ *Junghuhnia* Corda (Pol.).—Not referable to *Hymenogramme* Mont. & Berk.
- †*Laschia* Fr. sensu Pat. = *Campanella*.
- Laudatea* Johow = *Dictyonema*, *vide* Hariot in *Bull. Soc. mycol. France* **7**: 40. 1891.
- Laurilia* Pouz. in *Česká Mykol.* **13**: 14. 1959 (St.).—John Erikss. in *Symb. bot. upsal.* **16** (1): 128. 1958 (*Stereum sulcatum*); R. Davids. & al. in *Mycologia* **52**: 262 (*S. taxodii*), 272 (*S. sulcatum*). 1961; Aoshima & al. in *Mycologia* **53**: 145. 1962 (*S. taxodii*). — *Stereum taxodii* may be generically different.
- Laxitextum* Lentz (He.).—John Erikss. in *Symb. bot. upsal.* **16** (1): 129. 1958; Boid. in *Bull. Jard. bot. Brux.* **30**: 70. 1960; Lentz in *Sydowia* **14**: 123. 1960.
- Leaia* Banker = *Gloiodon*.
- Lentaria* Corner, *Monogr. Clav.* **94**, 437. 1950 (Go.).—Type group only.
- Lentinellus* P. Karst. (Au.).—Kühner in *Botaniste* **17**: 99. 1926 (*Lentinellus* Fayod); Sing., *Agar.*, 2nd Ed., 299. 1962.
- †*Lentinellus* Fayod ≡ *Lentinellus* P. Karst.
- Lenzitopsis* Malenç & Bertault in *Bull. Soc. mycol. France* **79**: 75. 1963 (Th.).
- Leptochaete* Lév. (nom. rejic. prop.) ≡ *Hymenochaete*.
- Leptodon* Quéf. = *Steccherinum*.
- Leptoglossum* P. Karst. (Ca., Cy. → Agaricales).—Sing., *Agar.*, 2nd Ed., 273. 1962.
- Leptotus* P. Karst. = *Leptoglossum*.
- Leucogyrophana* Pouz. in *Česká Mykol.* **12**: 32, 35. 1958 = *Serpula*.
- Libellus* Lloyd = *Hymenogloea*.
- Licentia* Pilát = *Lopharia*.
- Lindtneria* Pilát (Th. → Pol.).—L. Hansen in *Bot. Tidsskr.* **55**: 277. 1960.
- Lloydella* Bres. = *Lopharia*.
- Lloydellopsis* Pouz. = *Amylostereum* Boid.
- †*Lomatia* (Fr.) P. Karst. = *Cytidia*.
- Lomatina* P. Karst. ≡ *Lomatia* = *Cytidia*.
- Lopharia* Kalchbr. & McOw. (St.).—Talbot in *Bothalia* **6**: 339. 1954; Boid. in *Bull. Soc. linn. Lyon* **28**: 206. 1959; Maas G. in *Proc. Ned. Akad. Wet (C)* **66**: 456. 1963 (in obs.).

*Lyomyces* P. Karst. 1881 = *Hyphoderma*.

†*Lyomyces* P. Karst. 1882 = *Laeticorticium*.

*Maireina* (Pilát) W. Cooke = *Cyphellopsis*, *vide* Donk in *Persoonia* 2: 345. 1962.

*Malacodermum* (Fr.) Léon March.—Nomen dubium, cf. Donk in *Taxon* 6: 84. 1957.

*Malacodon* Bataille in *Bull. Soc. mycol. France* 39: 203. 1923.—Nomen dubium.

*Manina* Banker = *Hericum* Pers. per S. F. Gray.

*Manuripia* Sing. in *Sydowia* 14: 273. 1960 (Agaricales).—Sing., Agar., 2nd Ed., 409. 1962. Hymenophore smooth.

*Martella* Endl. = *Hericum* Pers. per S. F. Gray, *vide* Donk in *Taxon* 5: 103. 1956.

†*Martella* Adans. ex O.K. = *Hericum* Pers. per S. F. Gray, *vide* Donk in *Taxon* 5: 102. 1956.

*Masseola* O.K. (perhaps correct name for) = *Sparassis*.

*Matruchozia* Boul. (Cl. → Deuteromycetes).—Presumably non-basidiomycetous.

*Medusina* Chev. = *Hericum* Pers. per S. F. Gray.

*Membranicium* John Erikss. in *Symb. bot. upsal.* 16 (1): 115. 1958; M. P. Christ. in *Dansk bot. Ark.* 19: 180. 1960; (n.v.p.) = *Phanerochaete*, *vide* Donk in *Persoonia* 2: 223. 1962.

*Merisma* Pers. per S. F. Gray = *Thelephora*.

*Merismodes* Earle (Ca., Cy. → Agaricales).—D. Reid in *Persoonia* 3: 113. 1964.

*Merulioporia* Bond. & Sing. = *Merulius*, *vide* Donk in *Persoonia* 2: 227. 1962.

*Meruliopsis* Bond. apud Parmasto = *Merulioporia* Bond. & Sing. = *Merulius*.

*Merulioporia* Murrill; W. Cooke in *Mycologia* 49: 222. 1957 = *Serpula*, *vide* Donk in *Bull. bot. Gdns, Buitenz.* III 17: 474. 1948.

*Merulius* Fr. (Cor.).—Bourd. & G., *Hym. France* 344. 1928.

*Merulius* [Haller] St.-Am. = *Cantharellus*.

*Mniopetalum* Donk & Sing. apud Donk in *Persoonia* 2: 332. 1962 (Cy. → Agaricales) = *Leptoglossum*?

*Muciporus* Juel (nom. conf.), *vide* Juel in *Ark. Bot.* (III) 14 (1): 6. 1916 = a resupinate polypore ("Polyporus" *corticola* Fr.) overgrown by a species of *Tulasnella* (Cor.).

*Mucronella* Fr. (Cl.).—Corner, *Monogr., Clav.* 95, 451. 1959.

†*Mucronia* Fr. = *Mucronella*.

*Mycoacia* Donk (Cor.).—Bourd. & G., *Hym. France* 414. 1928 (*Acia*).

*Mycobonia* Pat. (nom. cons.) (St.).—G. W. Mart. in *Mycologia* 31: 247. 1939 (*M. flava*); Sing., Agar., 2nd Ed., 160. 1962.

*Mycodendron* Mass. in *J. Bot., Lond.* 29: 1. 1891.—Nomen dubium.

*Mycoleptodon* Pat. = *Steccherinum*.

*Mycoleptodonoides* Nikol. (residual Hyd.).—Maas G. in *Persoonia* 1: 409. 1961; 2: 392. 1962.

*Mycorrhaphium* Maas G. in *Persoonia* 2: 394. 1962 (residual Hyd.).

*Myxomycidium* Mass. (Cl.).—Linder in *Mycologia* 26: 332. 1934; G. W. Mart. in *Mycologia* 30: 435. 1938 (*M. flavum*); Y. Kobay. in *Nagaoa* 4: 46. 1954 (*M. yakusimense*); in *J. Jap. Bot.* 38: 363. 1963; R. Heim in *Rev. Mycol.* 25: 38. 1960.

*Neokneiffia* Sacc. = *Kneiffia* = *Hyphoderma*.



- †*Nevrophyllum* Pat. apud Doass. & Pat. = *Gomphus*.  
 †*Nodularia* Peck = *Aleurodiscus*.  
*Nyctalis* Fr. (Ca. → Agaricales).  
*Odontia* Pers. per S. F. Gray (nom. rejic. prop.) = *Caldesiella*.  
 †*Odontia* Fr. = *Steccherinum*. — Suggested for continued use as the name of a 'residual' genus of unplaced resupinate 'hydnum' (Cor.).  
*Odontina* Pat. = *Steccherinum*, *vide* Donk in *Taxon* 5: 107. 1956.  
*Odontiochaete* J. Rick in *Ann. mycol.* 38: 60. 1940.—Nomen dubium.  
*Oliveonia* Donk in *Fungus* 28: 20. 1958 (Cor.).—L. Olive in *Amer. J. Bot.* 44: 432. 1957 (*Heteromyces*).  
*Ordonia* Racib. = *Septobasidium* (Septobasidiales).  
*Oxydantia* L. W. Mill. = *Sarcodontia*.  
*Pachysterigma* J.-Olsen apud Bref. = *Tulasnella*.  
*Palaecephala* Sing. (Agaricales).—Dennis & Reid in *Kew Bull.* 11: 292. 1957 (*Marasmius cymatelloides*); Sing., *Agar.*, 2nd Ed., 409. 1962. Hymenophore smooth.  
*Parapterulicium* Corner in *Ann. bot., Lond.* II 16: 285. 1952.  
*Paulliticortium* John Erikss. (Cor.).—Liberta in *Brittonia* 14: 219. 1962.  
*Pellicularia* Cooke (nom. conf.), *vide* Donk in *Reinwardtia* 2: 425. 1954 = *Koleroga* (Cor.) + non-basidiomycetous Deuteromycete.  
*Pellicularia* Cooke sensu D. P. Rog. = *Koleroga*, *Botryobasidium*, &c.  
*Pellidiscus* Donk in *Persoonia* 1: 89. 1959 (Cy. → Agaricales).—Sing., *Agar.*, 2nd Ed., 668. 1962; D. Reid in *Persoonia* 3: 135. 1964.  
*Peniophora* Cooke (Cor.).—John Erikss. in *Symb. bot. upsal.* 10 (5): 76 pp. 1950 (*Peniophora* sect. *Coloratae*); Donk in *Fungus* 27: 15. 1957; Boid in *Bull. Soc. mycol. France* 74: 436. 1959 & *Rev. Mycol.* 26: 153. 1961 (species with 'dendrophyses').  
*Peniophorella* P. Karst. (nom. conf.), *vide* Donk in *Persoonia* 2: 220. 1962 = *Hyphoderma* (Cor.) + foreign, non-basidiomycetous spores.  
*Peniophorina* Höhn. ("Th." → Deuteromycetes?), *vide* Donk in *Reinwardtia* 1: 216. 1951, not a Basidiomycete.  
†*Perona* Pers. (Agaricales).—Nomen dubium. Cf. Donk in *Beih. Nova Hedw.* 5: 217. 1962; Sing., *Agar.*, 2nd Ed., 416, 799. 1962. Hymenophore smooth. — Presumably preoccupied by *Peronia* F. de la Roche (Marantaceae), but this is not yet generally accepted.  
†*Perona* [Pers. sensu] Fr. = *Caripia*.  
*Persooniana* Britz. (Hyd. → Pol.).—Nomen dubium.  
*Phacorrhiza* Pers. = *Typhula*.  
*Phaeoaphelaria* Corner in *Ann. Bot., Lond.* II 17: 357. 1853 (Cl.).  
†*Phaeocarpus* Pat. ≡ *Cymbella* ≡ *Chromocyphella*.  
*Phaeoclavulina* W. Brinkm. = *Ramaria*.  
*Phaeocyphella* Pat. ≡ *Cymbella* ≡ *Chromocyphella*.  
†*Phaeocyphella* Speg. = *Chromocyphella*, *vide* Sing., *Agar.*, 2nd Ed., 669. 1962.  
*Phaeocyphellopsis* W. Cooke = *Merismodes*, *vide* D. Reid in *Persoonia* 3: 110, 113. 1964.

- Phaeoglabrotricha* W. Cooke = *Pellidiscus*, *vide* D. Reid in *Persoonia* **3**: 136. 1964 (for *Cyphella sessilis* Burt, the type species).
- Phaeodepas* D. Reid in *Kew Bull.* **15**: 273. 1961 (Cy.).
- Phaeodon* J. Schroet. = *Hydnellum*, *vide* Donk in *Taxon* **12**: 155. 1963.
- Phaeophlebia* W. Cooke in *Mycologia* **48**: 401. 1956 (Pu.) = *Punctularia*, *vide* Talbot in *Bothalia* **7**: 142. 1958.
- Phaeoporotheleum* (W. Cooke) W. Cooke in *Beih. Sydowia* **4**: 129. 1961 (Cy.).
- Phaeopterula* (P. Henn.) Sacc. & D. Sacc. = *Pterula*.
- Phaeoradulum* Pat. in *Bull. Soc. mycol. France* **16**: 178. 1900; *Ess. tax. Hym.* 69. 1900 (Con. ?).—*Incertae sedis*.
- Phaeoschizophyllum* W. Cooke in *Mycologia* **53**: 594. 1962 = *Schizophyllum*.
- Phaeosolenia* Speg. (Cy. → Agaricales).—Donk in *Persoonia* **2**: 344. 1962; Sing., *Agar.*, 2nd Ed., 667. 1962; D. Reid in *Kew Bull.* **17**: 299. 1963.
- Phanerochaete* P. Karst. (Cor.).—Donk in *Persoonia* **2**: 223. 1962.
- Phellodon* P. Karst. (Ba.).—Coker & Beers, *Stip. Hydn.* 21. 1951; Maas G. in *Fungus* **28**: 48. 1958; in *Persoonia* **2**: 399. 1962.
- Phlebia* Fr. (Cor.).—Donk in *Fungus* **27**: 8. 1957; John Erikss. in *Symb. bot. upsal.* **16** (1): 90. 1958.
- Phlebiella* P. Karst.; cf. D. P. Rog. in *Mycologia* **36**: 79. 1944; (n.v.p.) = *Cristella*. Cf. Donk in *Taxon* **12**: 163. 1963.
- Phlebohora* Lév. ("Th." → Agaricales) = *Tricholoma* (Fr.) Staude; based on deformed or parasitized fruitbodies.
- Phylacteria* (Pers.) Pat. = *Thelephora*.
- Phyllocarbon* Lloyd = *Polyozellus*, *vide* Imaz. in *Nat. Sci. & Mus.* IX **10**: 3. 1938.
- Physalacria* Peck (Cl. → Agaricales).—McGuire in *Mycologia* **31**: 432. 1939 (*P. inflata*); G. E. Bak. in *Bull. Torrey bot. Cl.* **68**: 265. 1941; Corner, *Monogr. Clav.* 96, 456. 1950; in *Ann. Bot., Lond.* II **17**: 361. 1953; Sing., *Agar.*, 2nd Ed., 406. 1962.
- Pistillaria* Fr. (Cl.).—Corner, *Monogr. Clav.* 98, 472. 1950.
- Pistillina* Quéf. (Cl.).—Corner, *Monogr. Clav.* 107, 497. 1950.
- Pleurodon* Quéf. ex P. Karst. = *Auriscalpium*.
- Pleurotopsis* (P. Henn.) Earle (Cy. → Agaricales) = *Resupinatus* (Nees) ex S. F. Gray, *vide* Sing. *apud* Donk in *Beih. Nova Hedw.* **5**: 236. 1962.
- Plicatura* Peck (Cor.).—Bourd. & G., *Hym. France* 343. 1928.
- Plicaturopsis* D. Reid in *Persoonia* **3**: 150. 1964 (Sch.?).
- Podoscypha* Pat. (St.).—Boid. in *Rev. Mycol.* **24**: 205. 1959.
- Podoserpula* D. Reid in *Kew Bull.* **16**: 437. 1963 (Con.).
- Podostrombium* Kunze (n.v.p.) = *Caripia*.
- Polyozellus* Murrill (Th.).—A. H. Sm. & Morse in *Mycologia* **39**: 499, 502. 1947 (*Cantharellus* sect. *Polyozellus*); Imaz. in *Mycologia* **45**: 555. 1953.
- † *Polyozus* P. Karst. = *Tremellodendropsis*.
- Porogramme* (Pat.) Pat., *Essai tax. Hym.* 63. 1900 (Cor.).
- Porolaschia* Pat. = *Favolaschia*, *vide* Sing. in *Lloydia* **8**: 195. 1945.

- Porostereum* Pilát = *Lopharia*, *fide* Boid. in Bull. Soc. linn. Lyon **28**: 207. 1959.
- Porothelium* (Fr. per Fr.) Fr. ≡ *Stromatoscypha*.
- Prilleuxia* Sacc. & P. Syd. ≡ *Karstenia* = *Tomentella*.
- Prototremella* Pat. = *Tulasnella*.
- Pseudasterodon* J. Rick in Iheringia (Bot.) **5**: 169. 1959 (n.v.p.)—Nomen dubium.
- Pseudocraterellus* Corner in Beih. Sydowia **1**: 268. 1957 (Ca.).
- Pseudodasyscypha* Velen., Nov. mycol. **1**: 167. 1939 = ? *Cyphellopsis*, *fide* Donk in Persoonia **2**: 345. 1962.
- Pseudohydnum* P. Karst. (Tremellaceae).
- †*Pseudohydnum* J. Rick = *Hydnodon*.
- Pseudofistulina* O. & K. Fidalgo in Mycologia **54**: 344. 1963 (Fi.).
- Pseudotomentella* Svrček; Svrček in Sydowia **14**: 172. 1960 = *Tomentella*.
- Pseudotremellodendron* D. Reid in Kew Bull. **11**: 535. 1957 (Cl. → Tremellaceae).
- Pseudotyphula* Corner in Ann. Bot., Lond. II **17**: 361, 366. 1953 (Cl.).
- Pterula* Fr. (Cl.).—Corner, Monogr. Clav. 109, 118, 501. 1950; in Ann. Bot., Lond. II **16**: 531. 1952.
- Pterulicium* Corner, Monogr. Clav. 122, 536. 1950 (Cl.).
- Ptychella* Roze & Boud. (Agaricales) = *Agrocybe* Fayod, abnormal fruitbodies with folded hymenium.
- Punctularia* Pat. apud Pat. & Lagerh. (Pu.).—Talbot in Bothalia **6**: 25. 1951; **7**: 140. 1958.
- Pycnodon* Underw. ≡ *Kneiffia* = *Hyphoderma*.
- Radulochaete* J. Rick in Ann. mycol. **38**: 58. 1940.—Nomen dubium.
- Radulomyces* M. P. Christ. in Dansk bot. Ark. **19**: 230. 1960, in part. (Cor.).—*Corticium* Pers. per S. F. Gray (residual genus).
- Radulum* Fr. (Hyd. → Ascomycetes). Cf. Petrak in Sydowia **9**: 409. 1955 (*Xenotype aterrima*); Donk in Taxon **5**: 109. 1956.
- Ramaria* S. F. Gray (nom. rejic. prop.) = *Clavulinopsis*.
- Ramaria* (Fr.) Bon. (nom. cons. prop.) (Go.).—Donk, Rev. niederl. Homob.-Aph. **2**: 103. 1933; Corner, Monogr. Clav. 124, 542. 1950; Corner & Thind in Trans. Brit. mycol. Soc. **44**: 233. 1961.
- Ramarcium* John Erikss. in Svensk bot. Tidskr. **48**: 189. 1954 (Go.).
- Ramariopsis* (Donk) Corner, Monogr. Clav. 144, 636. 1950 (Cl.).
- Repetobasidium* John Erikss. in Symb. bot. upsal. **16** (1): 67. 1958 (Cor.).
- Rhipidium* Wallr. (nom. rejic.) = *Schizophyllum*. Cf. Donk in Beih. Nova Hedw. **5**: 261. 1962.
- Rhipidonema* Mattirollo in Nuovo G. bot. ital. **13**: 259. 1881 (Di.).—Metzner in Ber. dtsh. bot. Ges. **52**: 232. 1934 (*R. crustaceum*).
- Rhipidonematomyces* Ciferri & Tomaselli in Atti Ist. bot. Univ. Lab. critt. Pavia V **10**: 294. 1954 = *Rhipidonema*.
- Rhizonema* Thwait. in Engl. Bot., Suppl., **4**: pl. 2954. 1849 = *Dictyonema*, *fide* Bornet in Ann. Sci. nat. (Bot.) V **17**: 82. 1873.
- Rhodoarrhenia* Sing., Agar., 2nd Ed., 803. 1962 (n.v.p.) (Cy.).

- Rhodocyphella* W. Cooke = *Stigmatolemma*, *vide* Donk in *Persoonia* 2: 337. 1962.  
*Ricinophora* Pers. = *Phlebia*.  
*Rimbachia* Pat. (Ca., Cy. → Agaricales).—Sing., Agar., 2nd Ed., 404. 1962.  
*Sarcodon* Quéf. ex P. Karst. (Th.).—Coker & Beers, *Stip. Hydn.* 36. 1951; Maas G. in *Fungus* 26: 45. 1956; in *Persoonia* 2: 401. 1962.  
*Sarcodontia* S. Schulz. (Cor.).—Kotlaba in *Česká Mycol.* 7: 117. 1953 (*Sarcodontia crocea* [= *S. setosa*]).  
*Sarcopodium* Ehrenb. per Brogn.—Deuteromycetes.  
*Scaphophorum* Ehrenb. per Wallr. ≡ *Schizophyllum*.  
*Schizonia* Pers. ≡ *Schizophyllum*.  
*Schizophyllum* Fr. per Fr. (Sch.).—Essig in *Univ. Calif. Publ. Bot.* 7: 447. 1922; Linder in *Amer. J. Bot.* 20: 552. 1933; W. Cooke in *Mycologia* 53: 575. 1962.  
*Sclerodon* P. Karst. ≡ *Gloiodon*.  
*Scleromitra* Corda = *Pistillaria*.  
*Scopuloides* (Mass.) Höhn. & Litsch. = *Phanerochaete*, *vide* Donk in *Persoonia* 2: 223. 1962.  
*Scyphopilus* P. Karst. = *Thelephora*.  
*Scytinopogon* Sing. (Th.).—Corner, *Monogr. Clav.* 647. 1950.  
*Scytinostroma* Donk in *Fungus* 26: 19. 1956 (Cor.).—Boid. in *Bull. Jard. bot. Brux.* 30: 283. 1960.  
*Serpula* (Pers.) per S. F. Gray (Con.).—Bourd. & G., *Hym. France* 352. 1928 (*Gyrophana*); W. Cooke in *Mycologia* 49: 201. 1957.  
*Sesia* Adans. per O.K. sensu O.K. in part = *Serpula*.  
*Sistotrema* Fr. (Cor.).—D. P. Rog. in *Mycologia* 36: 73. 1944 (resupinate species only; *Trechispora* [sensu D. P. Rog.]); Donk in *Fungus* 26: 4. 1956; M. P. Christ. in *Dansk bot. Ark.* 19: 78. 1960.  
† *Sistotrema* S. F. Gray = *Sistotrema* Fr. (typonym).  
*Sistotremastrum* John Erikss. in *Symb. bot. upsala.* 16 (1): 62. 1958 (Cor.).—M. P. Christ. in *Dansk bot. Ark.* 19: 87. 1960.  
*Skepperia* Berk. (St. ?).—Pat. in *Bull. Soc. mycol. France* 9: 1. 1893. — Cf. Sing., Agar., 2nd Ed., 805. 1962.  
*Skepperiella* Pilát (Ca. → Agaricales) = ? *Rimbachia*, *vide* Sing., Agar., 2nd Ed., 404. 805. 1962.  
† *Solenia* Pers. per Fr. ≡ *Henningsomyces*.  
*Soppitiella* Mass. = *Cristella*, *vide* Donk in *Taxon* 6: 113. 1957.  
*Sparassis* Fr. per F. (correct name perhaps *Masseola* O.K.) (Sp.).—Cotton in *Trans. Brit. mycol. Soc.* 3: 333. 1912; Buller, *Res. Fungi* 2: 188. 1922; D. Reid in *Trans. Brit. mycol. Soc.* 41: 439. 1958 (*S. simplex* & in obs.).  
*Sphaerula* Pat. = *Pistillaria*, *vide* Corner, *Monogr. Clav.* 101, 473. 1950.  
*Stecchericum* D. Reid in *Kew Bull.* 17: 270. 1963 (He.).—Maas G. in *Proc. Ned. Akad. Wet (C)* 66: 440. 1963.  
*Steccherinum* S. F. Gray (residual Hyd.).—Maas G. in *Persoonia* 2: 403. 1962; 3: 176. 1964.

- Stelligera* R. Heim = *Lachnocladium*, *vide* Corner, Monogr. Clav. 416. 1950.
- Sterbeekia* Dumort. ≡ *Craterellus*.
- Sterellum* P. Karst.; John Erikss. in Symb. bot. upsal. 16 (1): 119. 1958 = *Peniophora*, *vide* Weres. & Gibson in Can. J. Bot. 38: 857-858. 1960.
- Stereofomes* J. Rick; J. Rick in Iheringia (Bot.) 4: 85. 1959.—Nomen dubium. Cf. Donk in Taxon 12: 163. 1963 (typification).
- Stereogloeocystidium* (J. Rick) J. Rick = *Podoscypha*, *vide* Boid. in Rev. Mycol. 24: 211. 1959 (type).
- †*Stereophyllum* P. Karst. in Hedwigia 28: 190. 1889 (St.).—No correct name available.
- Stereum* Pers. per S. F. Gray (Cor.).—Boid. in Rev. Mycol. 23: 324. 1958; in Bull. Jard. bot. Brux. 30: 56. 1960; Lentz in Sydowia 14: 116. 1960.
- Stichoclavaria* Ulbr. (Cl.).—Nomen dubium. Cf. pp. 222, 253, 299.
- Stichoramaria* Ulbr. = *Clavulina*.
- Stigmatolemma* Kalchbr. (Cy. → Agaricales).—Donk in Persoonia 2: 337. 1962; Sing., Agar., 2nd Ed., 281. 1962.
- Stromatocyphella* W. Cooke (Cy.).—D. Reid in Persoonia 3: 139. 1964.
- Stromatoscypha* Donk (Sch.).—Donk in Persoonia 1: 78, 1959; D. Reid in Persoonia 3: 147. 1964.
- Suillosporium* Pouz. in Česká Mykol. 12: 31, 35. 1958 (Con.) = ? *Jaapia*.
- Sulphurina* Pilát = *Cristella*.
- Szygospora* G. W. Mart. (nom. anam.) (Cor.).—Cf. Kao in Mycologia 48: 677. 1956; Donk in Taxon 11: 101. 1962 (nomenclature).
- †*Terana* Adans. per O.K. = *Corticium* Pers. per S. F. Gray (residual genus).
- Thanatephorus* Donk (Cor.).—Donk in Fungus 28: 28. 1958.
- Thelephora* Ehrh. ex Fr. (Th.).—Burt in Ann. Missouri bot. Gdn 1: 199. 1914.
- Thelephorella* P. Karst. in Hedwigia 28: 191. 1889.—Nomen dubium.
- Thelepora* Fr. ≡ *Theleporus* Fr. (Fi. → Pol.).
- Thwaitesiella* Mass. = *Lopharia*.
- Tinctoporia* Murrill = *Porogramme*.
- Tomentella* Pat. (Th.).—Bourd. & G., Hym. France 473. 1928; M. P. Christ. in Dansk bot. Ark. 19: 248. 1960; Svrček in Sydowia 14: 187. 1960.
- †*Tomentella* J.-Olsen apud Bref. (nom. conf.), *vide* Donk in Persoonia 2: 217-220. 1962 = *Botryohypochnus* (Cor.). + non-basidiomycetous Deuteromycete.
- †*Tomentella* P. Karst. = ? *Cristella*, *vide* Donk in Taxon 6: 119. 1957; 12: 164. 1963.
- Tomentellastrum* Svrček; Svrček in Sydowia 14: 179. 1960 = *Tomentella*.
- Tomentellina* Höhn. & Litsch. = *Kneiffiella* P. Karst.
- Trabecularia* Bon. = *Merulius*, *vide* Donk in Fungus 28: 14. 1958.
- Trechispora* P. Karst. = *Cristella*, poriid species, *vide* Donk in Fungus 26: 7-8. 1926 & in Persoonia 1: 288. 1960.
- †*Trechispora* P. Karst. sensu D. P. Rog. & Jacks.; D. P. Rog. in Mycologia 36: 73. 1944 = *Sistotrema* Fr., *vide* Donk in Fungus 26: 4, 7. 1956.
- Tremellodendropsis* (Corner) D. A. Crawford. (Cl. → Tremellaceae).—Corner, Monogr., Clav. 192. 1950 (*Aphelaria tuberosa*).

- Tremellodon* (Pers.) Fr. = *Pseudohydnum* P. Karst.  
 †*Trichocarpus* P. Karst. = *Amylostereum*.  
*Trogia* Fr. (Ca. → Agaricales).—Sing., Agar., 2nd Ed., 306. 1962; in part (exclusive of type) = *Plicatura*, *Plicaturopsis*.  
*Trombetta* Adans. per O.K. = *Craterellus*.  
*Tubulicrinis* Donk in *Fungus* 26: 13. 1956 (Cor.).—John Erikss. in *Symb. bot. upsal.* 16 (1): 79. 1958; Weres. in *Can. J. Bot.* 39: 1453. 1961 (*Peniophora* sect. *Tubuliferae*), in part.  
*Tulasnella* J. Schroet. (Cor.).—D. P. Rog. in *Ann. mycol.* 31: 183. 1933; L. Olive in *Mycologia* 49: 671. 1957.  
*Tumidapexus* D. A. Crawf. in *Trans. roy. Soc. New Zeal.* 82: 626. 1954 (Cl.).—An *Clavulinopsis* ?  
*Turbinellus* Earle = *Gomphus*.  
*Tylocladon* Banker ≡ *Radulum*. Cf. Donk in *Taxon* 12: 155. 1963.  
 †*Tylospasma* Donk ≡ *Tylospora*.  
*Tylospora* Donk (Cor.).—Donk in *Fungus* 27: 28. 1957 (*Tylospasma*); John Erikss. in *Symb. bot. upsal.* 16 (1): 116. 1958 (*Tylospasma*); M. P. Christ. in *Dansk bot. Ark.* 19: 170. 1960 (*Tylospasma*).  
*Typhula* (Pers.) per Fr. (Cl.).—Corner, *Monogr. Clav.* 144, 655. 1950.  
*Tyrodon* P. Karst. = *Hydnum*.  
*Uthatabasidium* Donk (Cor.).—Donk in *Fungus* 28: 21. 1958; John Erikss. in *Symb. bot. upsal.* 16 (1): 58. 1958; M. P. Christ. in *Dansk bot. Ark.* 19: 48. 1959.  
*Van-Romburghia* Holterm. ex Sacc. & P. Syd. (Agaricales).—Boed. in *Sydowia* 5: 213. 1951, but cf. Sing., Agar., 2nd Ed., 808. 1962 (= *Marasmius*?).  
*Vararia* P. Karst. (Hym.).—Donk in *Meded. Ned. mycol. Ver.* 18-20: 191. 1931; in *Fungus* 26: 11. 1956; Bourd. & G., *Hym. France* 394. 1928 (*Asterostromella*); Corner in *Trans. Brit. Mycol. Soc.* 31: 244 *fs.* 8, 9. 1948 (*Asterostromella* sp.); John Erikss. in *Svensk bot. Tidskr.* 48: 194. 1954 (spores).  
*Veluticeps* (Cooke) Pat. (Cor.).—Burt in *Ann. Missouri bot. Gdn* 6: 260. 1920 (*V. berkeleyi*).  
*Vuilleminia* R. Maire in *Bull. Soc. mycol. France* 18 (Suppl.): 81. 1902 (Cor.).—Bourd. & G., *Hym. France* 338. 1928.  
*Wainiocora* Tomaselli in *Arch. bot.*, Forli 26: 105. 1950 = (presumably) *Dictyonema*.  
*Waitea* Warcup & Talb. in *Trans. Brit. mycol. Soc.* 45: 403. 1962 (Cor.).  
*Wiesnerina* Höhn. (Cy.).—Corner in *Trans. Brit. mycol. Soc.* 44: 230. 1961.  
*Woldmaria* W. Cooke in *Beih. Sydowia* 4: 29. 1961 (Cy.).  
*Xenasma* Donk in *Fungus* 27: 25. 1957 (Cor.).—Liberta in *Mycologia* 52: 884. 1962.  
*Xenopus* Penz. & Sacc.; Penz. & Sacc.,  *Ic. Fung. javan.* 98. 1904; (nom. anam.?).—Nomen dubium. — *Fide* Hughes in *Can. J. Bot.* 36: 824. 1958 “=Basidiomyces.”  
 †*Xerocarpus* P. Karst. = *Phanerochaete*, *fide* Donk in *Persoonia* 2: 223. 1962.  
*Xylobolus* P. Karst.; Boid. in *Rev. Mycol.* 23: 333. 1958; Lentz in *Sydowia* 14: 118. 1960 = *Stereum*.

- Xylodon* (Pers.) per S. F. Gray.—Nomen dubium, *vide* Donk in *Taxon* **12**: 156. 1963.  
*Xylomyzon* Pers. = *Serpula*.  
*Xylophagus* Link per Murrill = *Serpula*.  
*Zygodesmus* Corda (nom. anam. ?) (Cor.).—Cf. Donk in *Taxon* **11**: 103. 1962.

## REFERENCES

The following titles have been cited by their dates printed in italics. Many references will be found in the synonymy throughout this paper, as well as appended to the individual generic names in the "Alphabetical enumeration of genera".

- BANDONI, R. J. (1957) in *Mycologia* **49**: 250-255 2 fs.  
 BARY, A. H. DE (1884), *Vergl. Morph. Phys. Pilze*.  
 BIGGS, R. (1938) in *Mycologia* **30**.  
 BOIDIN, J. (1951 a) in C.R. Acad. Sci., Paris **233**: 1667-1669.  
 — (1951b) in *Bull. Soc. Nat. Oyonnax* **5**: 72-79.  
 — (1958a) in *Bull. Soc. linn. Lyon* **28**.  
 — (1958b), *Essai biotax. Hydnes résup. Cort. Thèse, Lyon. (Rev. Mycol., Mém. Hors-série 6)*.  
 BONDARTSEV, A. S. (1953), [Russian title]. (Bracket Fungi Europ. Part U.S.S.R. & Caucasus).  
 BONDARTSEV, A. S. & R. SINGER (1941) in *Ann. mycol.* **39**: 43-65.  
 — & — (1943) in *Sovetsk. Bot.* **1943** (1): 29-43. — Known to me through an unpublished English translation made under the supervision of Dr. W. B. Cooke.  
 BOURDOT, H. & A. GALZIN (1928), *Hymén. France. "1927"*.  
 BREFELD, O. (1888), *Unters. Mykol.* **8**.  
 BULLER, A. H. R. (1922), *Researches on Fungi* **2**.  
 — (1924), *Researches on Fungi* **3**.  
 COKER, W. C. (1927) in *J. Mitchell sci. Soc.* **43**.  
 COLEMAN, L. C. (1927) in *Bot. Gaz.* **83**: 48-60 pl. 5.  
 COOKE, W. B. (1961) in *Beih. Sydowia* **4**.  
 CORNER, E. H. J. (1932a) in *Ann. Bot., Lond.* **41**: 71-111 17 fs., pl. 5.  
 — (1932b) in *Trans. Brit. mycol. Soc.* **17**: 51-81 13 fs.  
 — (1932c) in *Gdms' Bull., Straits Sett.* **5**: 317-350 8 fs., (1) pl.  
 — (1950), *Monogr. Clavaria & all. Genera. (Ann. Bot. Mem. 1)*.  
 — (1948) in *Trans. Brit. mycol. Soc.* **31**.  
 — (1953) in *Phytomorphology* **3**: 152-167 13 fs.  
 — (1957) in *Beih. Sydowia* **1**: 266-276 7 fs.  
 CORNER, E. H. J. & K. S. THIND (1961) in *Trans. Brit. mycol. Soc.* **44**: 233-238 1 f.  
 COTTON, A. D. (1912) in *Trans. Brit. mycol. Soc.* **3**: 333-339.  
 CUNNINGHAM, G. H. (1947) in *New Zeal. J. Sci.* **28**: 238-251 10 fs. "1946".  
 — (1954) in *Trans. Brit. mycol. Soc.* **37**.  
 — (1955) in *Trans. roy. Soc. New Zeal.* **82**.  
 DOGUET, G. (1962) in C.R. Acad. Sci., Paris **254**: 4336-4338 12 fs.  
 — (1963) in *Bull. Soc. mycol. France* **78**: 283-290 2 fs.  
 DONK, M. A. (1931) in *Meded. Neder. mycol. Ver.* **18-20**.  
 — (1933), *Revis. niederl. Homob.-Aph. 2. Proefschr., Utrecht (& Meded. bot. Mus. Herb. Utrecht No. 9, & Meded. Nederl. mycol. Ver. 22)*.  
 — (1948) in *Bull. bot. Gdms, Buitenz. III* **17**.  
 — (1954) in *Bothalia* **6**: 301-302.

- DONK, M. A. (1956a) in *Reinwardtia* **3**: 363-379.  
 — (1956b) in *Fungus* **26**.  
 — (1957) in *Fungus* **27**.  
 — (1958) in *Fungus* **28**: 16-36.  
 — (1962) in *Persoonia* **2**.  
 DOTY, M. S. (1948) in *Bull. Chicago Acad. Sci.* **8**.  
 — (1950) in *Lloydia* **13**.  
 ERIKSSON, JOHN (1950) in *Symb. bot. upsal.* **10** (5).  
 — (1954) in *Svensk bot. Tidskr.* **48**: 188-198 2 fs.  
 — (1958) in *Symb. bot. upsal.* **16** (1).  
 FAYOD, V. (1889) in *Ann. Sci. nat. (Bot.)* **VII** **9**: 181-411 pls. 6, 7.  
 FRIES, E. M. (1874), *Hym. europ.*  
 FURTADO, J. S. (1962) in *Rickia* **1**: 227-241 22 fs.  
 GÄUMANN, E. (1926), *Vergl. Morph. Pilze*.  
 GRASSI, M. M. (1950) in *Lilloa* **24**.  
 GRIPENBERG, J. (1960) in *Tetrahedron* **10**: 135-143 2 fs.  
 HANSEN, L. (1958) in *Bot. Tidskr.* **54**: 333-352 9 fs.  
 HEGNAUER, R. (1962), *Chemotax. Pfl.* **1**.  
 HEIM, R. (1939) in *Rev. Mycol.*  
 — (1954) in *Rev. Mycol.* **19**.  
 — (1960) in *Rev. Mycol.* **25**.  
 — (1962) in *Rev. Mycol.* **27**: 199-212 pls. 11-15.  
 HEINEMANN, P. (1961) in *Sydowia* **15**: 200-203.  
 HÖHNEL, F. X. R. VON & V. LITSCHAUER (1907) in *S.B. Akad. Wien (Math.-nat. Kl. I)* **116**.  
 IMAZEKI, R. (1943) in *Bull. Tokyo Sci. Mus. No. 6*.  
 — (1953) in *Mycologia* **45**: 555-561.  
 IMAZEKI, R. & S. TOKI (1954) in *Bull. Govt For. Exp. Sta., Tokyo No. 67*.  
 JOSSERAND, M. (1952), *Descr. Champ. sup. (Encycl. mycol.)* **21**.  
 JUEL, H. O. (1898) in *Jb. wiss. Bot.* **32**: 361-388 pl. 4.  
 — (1916) in *Nova Acta Soc. Sci. upsal.* **IV** **4** (6).  
 KILLERMANN, S. (1928) in *Nat. PflFam., 2. Aufl.*, **6**: 99-283 fs. 81-157, 5 Vollb.  
 KOBAYASI, Y. (1954) in *Nagaoa* **4**.  
 KÖGL, F., H. ERXLIEBEN & L. JÄNECKE (1930) in *Lieb. Ann. Chem.* **482**: 105-119.  
 KOTLABA, F. & Z. POUZAR (1963), *Prelim. Results Staining Spores Homobas. Cotton Blue*.  
 Mimeographed summary distributed at the Third European Mycological Congress,  
 Glasgow; & in *Fedde's Repert.* **69**. 1964.  
 KREISEL, H. (1961) in *Z. Pilzk.* **26**: 44-47. "1960".  
 KÜHNER, R. (1926) in *Botaniste* **17**.  
 — (1929) in *Bull. Soc. mycol. France* **44**: 331-335 pl. 20.  
 — (1947) in *C.R. Acad. Sci., Paris* **224**: 1068-1069.  
 — (1950a) in *C.R. Acad. Sci., Paris* **230**: 1606-1608.  
 — (1963) *apud Kühner & al* in *Bull. Soc. mycol. France* **78**: 255-259 fs. 1-3. "1962".  
 KÜHNER, R. & H. ROMAGNESI (1953), *Fl. anal. Champ. sup.*  
 LEMKE, P. A. (1964) in *Canad. J. Bot.* **42**: 213-282 23 fs.  
 LENTZ, P. L. (1964) in *Bot. Rev.* **20**: 135-199.  
 — (1957) in *Mycologia* **49**: 534-544 21 fs.



- LINDER, D. H. (1934) in *Mycologia* **26**: 332-343 5 fs., pl. 39.  
— (1940) in *Mycologia* **32**.  
LLOYD, C. G. (1925), *Mycol. Notes* **7**.  
LOCQUIN, M. (1957) in *Bull. Jard. bot. Brux.* **27**: 560-562.  
LOHWAG, H. (1941), *Anat. Asco- u. Basidiomyc.* In *Handb. PflAnat.*, II Abt., 3. Teilb. c: Eumyceten **6**.  
LOHWAG, H. & L. FOLLNER (1936) in *Ann. mycol.* **34**: 456-464 5 fs.  
LOTSY, J. P. (1907), *Vorträge bot. Stammesgesch.* **1**.  
LOWY, B. (1954) in *Bull. Torrey bot. Cl.* **81**.  
MAAS GEESTERANUS, R. A. (1962) in *Persoonia* **2**: 377-405 65 fs.  
— (1963) in *Proc. Ned. Akad. Wet. (C)* **66**: 426-436 17 fs., 437-446 18 fs., 447-457 13 fs.  
MAIRE, R. (1902), *Rech. cytol. taxon. Basid.* Thèse, Paris [*& in Bull. Soc. mycol. France* **18** (Suppl.)].  
MALENÇON, G. (1959) in *Bull. Soc. mycol. France* **74**: 423-435 5 fs. "1958".  
MARTIN, G. W. (1938) in *Mycologia* **30**.  
— (1957) in *Brittonia* **9**.  
MATTIROLO, O. (1881) in *Nuovo G. bot. ital.* **13**.  
MELZER, V. & J. ZVARA (1928) in *Bull. Soc. mycol. France* **44**.  
MÖLLER, A. (1893) in *Flora* **77**: 254-278.  
NANNFELDT, J. A. & J. ERIKSSON (1953) in *Svensk bot. Tidskr.* **47**: 177-189 2 fs.  
NOBLES, M. K. (1958a) in *Canad. J. Bot.* **36**.  
— (1958b) in *Canad. J. Bot.* **36**.  
OLIVE, L. S. (1954) in *Mycologia* **46**.  
— (1957) in *Amer. J. Bot.* **44**: 449-435.  
OVEREEM, C. VAN (1923) in *Bull. Jard. bot. Buitenz. III* **5**: 254-280 f. 4.  
— (1924) in *Icon. Fung. malay.* Heft 7.  
— (1925) in *Bull. Jard. bot. Buitenz. III* **7**: 434-436.  
OVERHOLTS, L. O. (1953), *Polypor. U.S., Alaska, & Canada* (Univ. Michigan Stud., Sci. Ser. **19**).  
PATOULLARD, N. (1890) in *Bull. Soc. mycol. France* **6**: xix-xxi.  
— (1900), *Essai taxon. Hymen.* Thèse, Paris.  
PENANGIER, N. (1961) in *Trav. Lab. «La Jaysinia»* **2**: 57-71 3 fs.  
PILÁT, A. (1942), *Polyporaceae.* In *Atl. Champ. Eur.* **3**: 1936-42.  
REID, D. A. (1956) in *Kew Bull.* [**10**].  
— (1958) in *Trans. Brit. mycol. Soc.* **41**.  
— (1963) in *Kew Bull.* **17**.  
ROGERS, D. P. (1933) in *Ann. mycol.* **31**.  
— (1944) in *Mycologia* **36**.  
— (1947) in *Mycologia* **39**: 556-564 1 f.  
ROMAGNESI, H. (1939) in *Rev. Mycol.* **4**.  
— (1944) in *Rev. Mycol.* **9** (Suppl.): 4-21 12 fs.  
— (1953) in *Bull. Soc. Nat. Oyonnax* **7**: 111-112.  
ROMELL, L. (1901) in *Bih. svenska VetAkad. Handl. (III)* **26** (16).  
SINGER, R. (1945) in *Lloydia* **8**: 170-230.  
— (1951), *Agaricales.* In *Lilloa* **22**. "1949".  
— (1959) in *Ark. Bot., Stockh.* II **66**.  
— (1962), *Agaricales*, 2nd Ed.  
SINGER, R. & I. J. GAMUNDI (1963) in *Taxon* **12**.

- TALBOT, P. H. B. (1954) in *Bothalia* **6**: 249–299 20 fs.  
— (1958) in *Bothalia* **7**.  
TEIXEIRA, A. R. (1956), Método Estudio Hifas Carpóph. Fungos polip.  
— (1958) in *Mycologia* **60**: 671–676 7 fs.  
— (1961) in *Mycologia* **52**: 30–39 14 fs. "1960".  
— (1962) in *Biol. Rev.* **37**: 51–81 2 fs.  
TOMASELLI, R. (1949) in *Arch. Bot., Forli.* **25**.  
— (1950) in *Arch. Bot., Forli.* **26**: 19 pp. 5 fs. (reprint).  
WELLS, K. (1962) in *Mycologia* **63**.  
WHITE, J. H. (1919) in *Trans. roy. Canad. Inst.* **12**.

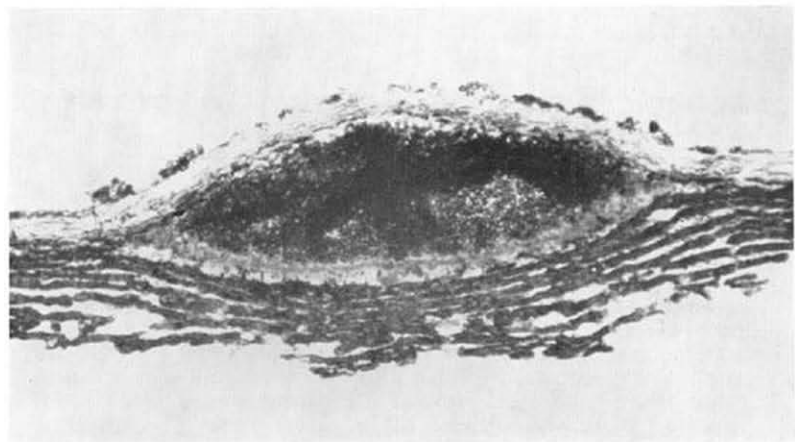


Fig. 1

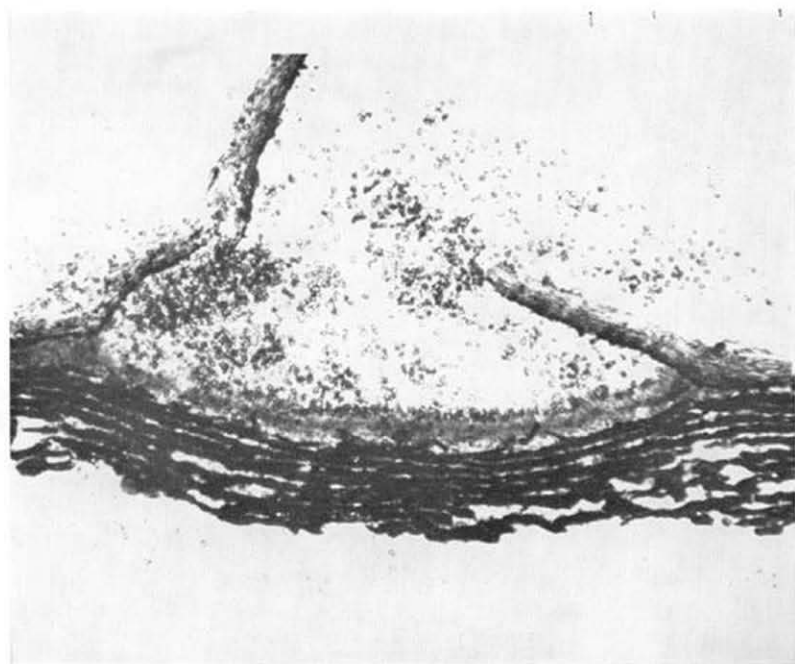


Fig. 2