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HYPHAL STRUCTURES IN HYDNUMS

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(With 65 Text-figures)

In this paper descriptions are given of the hyphal structure in the hydnaceous genera *Climacodon* P. Karst., *Creolophus* P. Karst., *Donkia* Pilát, *Hydnellum* P. Karst., *Mycoleptodonoides* Nikol., *Mycorrhaphium* Maas G. (which is introduced as a new genus), *Phellodon* P. Karst., *Sarcodon* P. Karst., and *Steccherinum* S. F. Gray.

The following new combinations are proposed: *Hydnellum piperatum* (Coker) Maas G., *Mycorrhaphium adustum* (Schw.) Maas G., *M. pusillum* (Brot. ex Fr.) Maas G., and *Steccherinum murashkinskyi* (Burt) Maas G.

Since the studies by E. J. H. Corner (1932) on the hyphal systems in Polyporaceae, various authors all over the world have followed his lead. They have mainly concerned themselves with the same group. Among the few authors to include the hyphal structure in their specific descriptions of hydnaceous fungi are Cunningham (1958), Ragab (1953), and Reid (1955, and subsequent papers), but no attempt has thus far been made to give a more complete characterization of the hydnaceous genera by describing the hyphae of their type species. The necessity and importance of the anatomical structure for the correct understanding of a genus becomes at once apparent when one considers *Steccherinum* as it was conceived by Banker (1912) and extended by subsequent authors: Miller (1935), Miller & Boyle (1943), and Coker & Beers (1951). *Steccherinum* was well on the way to become a depository of species that, on account of their spore-characters and the colour of the context, could not readily be placed elsewhere. Also, the apparent difficulty experienced by some authors sharply to delimit *Hydnellum* and *Sarcodon* disappears as soon as the hyphal system in both genera is taken into account.

Thus, the purpose of the present paper is to describe as fully as possible within the limits determined by material in dried condition, the hyphal structure in a number of genera, thereby indicating those differential characters which were formerly overlooked.

The genera treated have been chosen at random, and no effort is as yet made to arrive at any kind of classification. It is more likely that, with the spines as the sole character in common, the connection of many of the hydnaceous genera will have to be sought not within the 'Hydnaceae' but, irrespective of hymenial configuration, with groups now widely separated.

Similar descriptions are in preparation for the remaining hydnaceous genera.

A great debt of gratitude is due to the Directors of the Herbarium of the University of California (Berkeley), of the Herbarium of the University of North Carolina (Chapel Hill), of the New York Botanical Garden (New York), of the "Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie" (Paris), and of the Botanical Department of the National Museum (Prague) for the loan of collections; and to Dr T. L. Nikolajeva, Leningrad, for the generous gift of a part of the type of *Mycoleptodonoides vassiljevae*.

CLIMACODON P. Karst.—Figs. 1–9

Climacodon P. Karst. *in* Rev. mycol. **3**/No. 9: 20. 1 Jan. 1881 & *in* Medd. Soc. F. Fl. fenn. **6**: 15. 1881. — Type species: *Hydnum septentrionale* Fr.

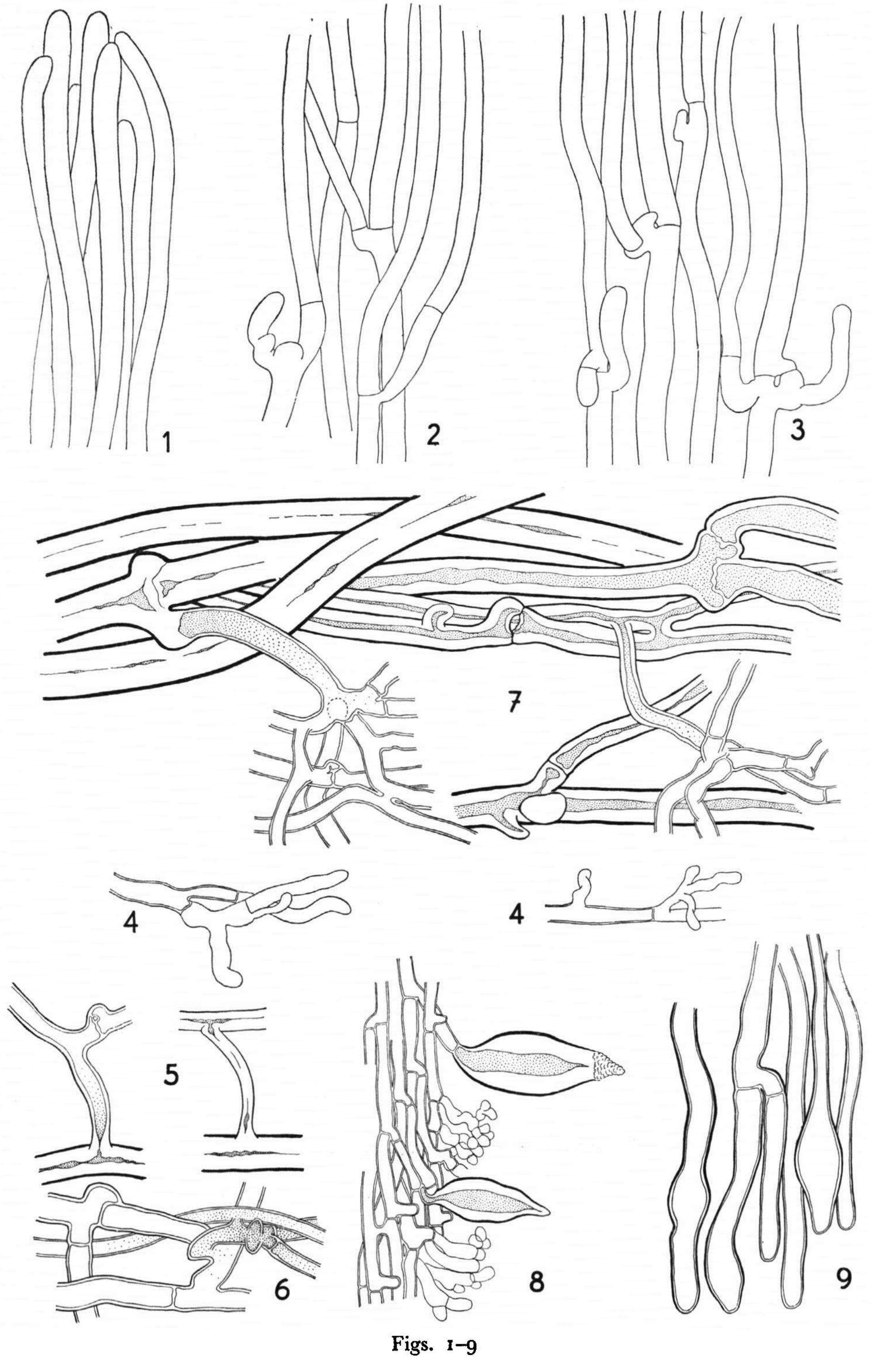
Context tough and fibrous throughout, zoned (at times indistinctly in the dried material), white, consisting of generative hyphae united into bundles, and 'bridge hyphae' connecting them. Generative hyphae not inflating, with clamp-connections in the older stages only, becoming very thick-walled with age. Clamp-connections also lacking in the hyphae of the spines and at the base of the basidia. Cystidia of subhymenial origin, fusiform, thick-walled, often encrusted at the pointed tip.

MATERIAL EXAMINED: *Climacodon septentrionalis* (Fr.) P. Karst. (CANADA, Quebec, Taylor Lake, Gatineau Park; L 959.16-253. — CZECHOSLOVAKIA, several collections; PRC).

The margin in a young specimen of *Climacodon septentrionalis* is strigose-hairy. The hairs consist of tapering bundles of hyphae, the hyphae of each bundle being tightly coherent. The hyphae at the tip of a bundle are straight to somewhat flexuous, 4.5–6.3 μ wide, very thin-walled, with the cell-wall less than 0.5 μ, and filled with an oily matter (Fig. 1). The terminal cells of these hyphae constituting the axis of the bundle are fairly long, the septum separating them from the next cell often occurring at distances of 200–250 μ from the tip of the hyphae. The peripheral hyphae of the bundle do not reach its apex, and usually have much shorter terminal cells, measuring 90–150 μ. The first cross-walls are invariably devoid of clamp-connections, as is illustrated in Fig. 2, which shows the situation at about 170 μ distance from the apex of a bundle. Clamp-connections make their first appearance

EXPLANATION OF FIGURES 1–9

Figs. 1–9. *Climacodon septentrionalis* (Fr.) P. Karst. — 1. Generative hyphae from the tip of a hair at the margin of the pileus. — 2. The same, taken about 170 μ farther down the hair, showing the first appearance of septa. — 3. The same, at a distance of 200–250 μ from the tip of the hair, with clamp-connections at the septa, and side-branches developing from the clamps. — 4. Detail of the apical part of two hyphae from the periphery of a hyphal bundle in a hair, showing the origin of lateral excrescences. — 5. Lateral excrescences with much thickened cell-walls in older tissue, forming a bridge between two adjacent hyphae. — 6. Lateral developing into an intricate knot through ramification and anastomosis. — 7. Detail of the context, showing some thick-walled hyphae of two adjacent hyphal bundles, and two much-branched laterals in the intervening interstice. — 8. Detail of a spine, illustrating the hyphae which toward the side give rise to both subhymenial tissue and cystidia. — 9. Generative hyphae near the margin on the underside of the pileus, with the apical portion fusiformly swollen, which makes them resemble cystidia (all figures × 700).



Figs. 1–9

still farther away from the tips of the hyphae, sometimes, as in the case of axial hyphae, as far as 450 μ, but usually at distances of 200–250 μ (Fig. 3). A peculiarity is that several of the clamps give rise to side-branches. The numerous side-branches, the coherence of the hyphae, and the occasional anastomoses (the latter not illustrated) certainly combine to make it difficult even to tear apart the hairs.

The hairs gradually pass into the context, and the bundles can be followed rearward for several millimetres. When followed in the direction of the base of the pileus, these bundles are seen to diverge and converge alternately, in this way assuming an undulating course. The interstices between the bundles at first grow in size with increasing distance from the margin, but then become smaller again owing to the gradual expansion of the bundles, until an area is reached which is completely made up of a solid mass of bundles. Beyond this area, viz. farther toward the base of the pileus, the interstices appear anew until they, too, are interrupted by another solid area. The alternating sequence of comparatively wide-meshed and compact areas is repeated a great many times throughout the entire length of the pileus, which in a radial section is macroscopically visible as a transverse zonation of the flesh, although often rather indistinctly so in the dried material. In the more marked cases, the zonation is mainly indicated by the compact areas showing as darker curved lines convex toward the margin.

The hyphae, which are of one kind—generative hyphae—, gradually widen with increasing distance from the margin, ultimately reaching a width of 10–11 μ and even twice as much at the septa, but they do not inflate. Simultaneously the cell-walls become thicker, those of the hyphae in the axis of the bundles even obliterating the lumina.

In the hairs mentioned before, the peripheral hyphae of the bundles develop lateral excrescences which may remain simple, but more often tend in their turn to produce side-branches (Fig. 4). Either type of laterals sooner or later fuse with some adjacent hypha, forming a bridge (Fig. 5, which is a detail from much older tissue). They may be called 'bridge hyphae' in accordance with Teixeira (1961: 38). The older the tissue the more pronounced the tendency in the laterals of forming dense knots of side-branches (Fig. 6) in which join through anastomosis side-branches of other laterals. This results in extremely intricate clusters of hyphae which fill the interstices (Fig. 7, showing the less complicated examples). Although the hyphae have the same function as interweaving hyphae (Corner, 1932b: 318 and 1950: fig. 8) they probably cannot be identified with these on account of their different appearance.

The hyphae in the spines are of the same kind as the generative hyphae of the context, but resemble more especially those in the younger stage in that they lack clamp-connections. The hyphae in the axis of a spine are 3.6–7.2 μ wide and often have their lumen completely obliterated, while the peripheral hyphae are narrower, 2.7–4.5 μ wide, with moderately thick to very thin cell-walls. From the side-branches produced by these peripheral hyphae arise both the subhymenial cells and the cystidia (Fig. 8). The body of the latter is more or less fusiform, 27–49 ×

10–14 μ, sometimes long-stalked, often mucronate, with the tip smooth or encrusted, and usually very thick-walled, with the cell-walls 1.5–5 μ thick. The subhymenial cells as well as the basidia lack clamp-connections.

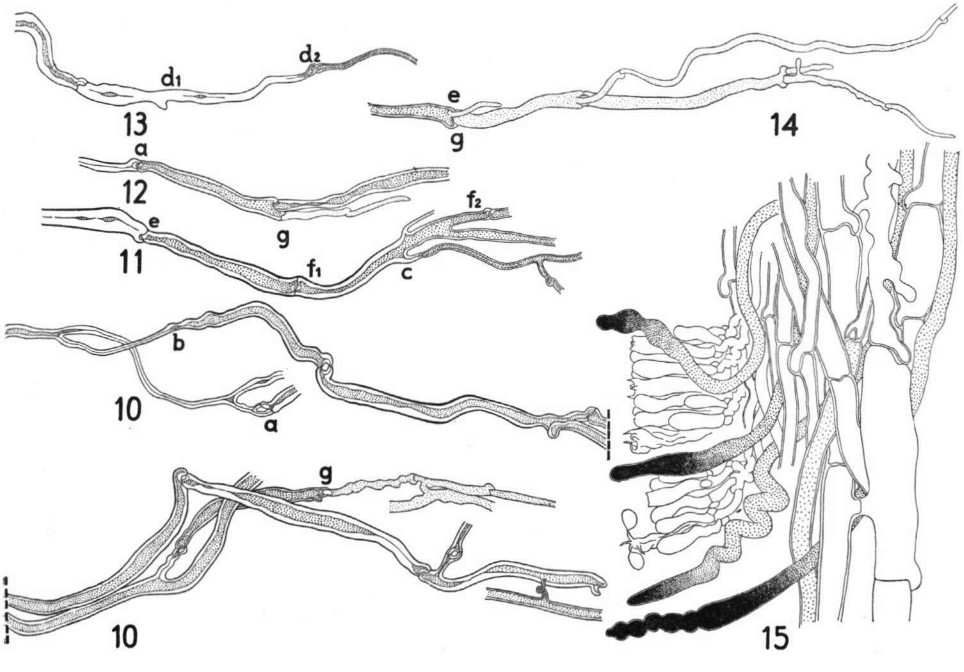
Peculiar hyphae were found close to the margin on the underside of the pileus (Fig. 9) in Fungi exs. suec. No. 251 (PRC). Here, several of the generative hyphae appeared fusiformly swollen at the apex (8–10.5 μ) and even moderately thick-walled, in some respects forming a transition to the cystidia.

CREOLOPHUS P. Karst.—Figs. 10–15

Creolophus P. Karst. *in* Medd. Soc. F. Fl. fenn. 5: 41. 1879. — Type species: *Hydnum corrugatum* Fr.

Context soft, spongy, not zoned, white, consisting of generative hyphae. Hyphae with clamp-connections, inflating, becoming thick-walled. Tramal hyphae of the spines similar to the generative hyphae but remaining thin-walled. Basidia with clamp-connections. Gloeocystidia constituting the distal ends of tramal hyphae, thin-walled, filled with oily matter.

MATERIAL EXAMINED: *Creolophus cirrhatus* (Pers. ex Fr.) P. Karst. (CZECHOSLOVAKIA, several collections in PRC).



Figs. 10–15. *Creolophus cirrhatus* (Pers. ex Fr.) P. Karst. — 10–14. Various generative hyphae; for explanation, see text (× 200). — 15. Detail of a spine, showing tramal hyphae, hymenium, and gloeocystidia, the latter with the contents dotted for greater clarity (× 700).

In a medial section of a young pileus of *Creolophus cirrhatus*, the hyphae at the very margin appear mainly radiately arranged and parallel, except on the surface of the pileus, where occasional free ends of the hyphae are seen to project into the air. While the superficial hyphae are fairly loosely interwoven (which makes the surface appear felted), those deeper down are firmly coherent and practically without intervening spaces. They resist all attempts to being teased apart and can rarely be traced rearward for more than 100 μ uninterruptedly.

A short way back from the margin—a distance which is not a fixed one and probably dependent on the age of the pileus, but which does not exceed 1 mm—a change in the context can be noticed. There is still the thin superficial layer of loosely interwoven hyphae which gradually pass downward into a dense layer of agglutinated parallel hyphae, but from the underside of this second layer hyphae are seen to curve down toward the lower surface of the pileus, either solitary or joined into strands. The farther away from the margin, the more apparent the differentiation of the context. Sooner or later the superficial hyphae collapse, becoming firmly glued to the underlying layer of compacted hyphae. This layer, which toward the base of the pileus may reach a width of 80–120 μ, tends to become cartilaginous and is set off against the remainder of the context as a dark shining line. Concurrently with the collapse of the superficial hyphae, the surface of the pileus becomes glabrous or, at the most, innately fibrillose. The hyphae in the context underneath the cartilaginous layer are no longer radially arranged, nor do they keep together in closely coherent parallel bundles. The hyphae, singly or in bundles, begin to diverge rearward, whilst their course becomes increasingly tortuous, with side-branches running in all directions. This process results in the fairly sudden appearance of meshes which with increasing distance from the margin rapidly grow in size and number. Consequently, the context becomes at once very much loosened and thickened; it retains its homogeneous spongy texture throughout the entire fruit-body, without a trace of zonation.

The hyphae at the margin of the pileus are narrow, 1–4.5 μ wide, and thin-walled. Side-branches and anastomoses are frequent and clamp-connections occur at all septa. Inflation of the cells soon takes place and at the same time the cell-walls begin to thicken. At a distance of about 500 μ from the margin, many of the hyphae have become inflated, some reaching a diameter of 10 μ, while their cell-walls are thickened to 1 μ or somewhat more. However, neither the inflation of the cells, nor the thickening of the cell-walls is a uniform process. A hypha traced back from its distal end toward its origin may show a succession of wide and narrow cells, and some of the proximal cells may have thinner walls than a distal cell. In the same hypha, a narrow cell may be followed by a wide one (Fig. 10a, 12a), or the cell itself inflates to twice or thrice its width (Fig. 10b). On the other hand, wide hyphae may produce narrow branches (Fig. 11c), or taper to narrow threads (Fig. 13 d_1–d_2). The widest hyphae may reach a diameter of 14 μ, with the cell-walls up to 4 μ thick. The walls thicken from one cell to the next (Fig. 11e, 14e) or even in the same cell from the distal end to the proximal end (Fig. 13d_2–d_1, 11f_2–f_1), but the reverse is by no means uncommon. Thin-walled hyphae (Fig. 10g, 12g, 14g) springing from thick-walled cells are obviously younger shoots in an otherwise old tissue and are of common occurrence throughout the fruit-body. Their course is often strongly undulating and some of their constituent cells are found to grow to amazing lengths, one of the longest measuring up to over 700 μ, with the distal end torn off. Although no thick-walled hyphae of that size have been found, there is no reason to believe that these very long thin-walled hyphae belong to a special kind. They grow in the same direction, their growth is unlimited, they are septate and possess clamps, which proves them to be basically the same as the thick-walled hyphae.

The hyphae in the spines agree with the generative hyphae, but they are all thin-walled and the transition from very narrow to very much inflated cells toward the axis of the spine is much more abrupt (Fig. 15). The widest inflated cells may reach a diameter of 14 μ. Clamp-connections are numerous in the hyphae and always present at the base of the basidia. Especially toward the tip of the spine there are numerous slender gloeocystidia protruding beyond the hymenium. They have their origin far back in the axis of the spine and represent the distal ends of tramal hyphae. The apical part of the gloeocystidia, which may reach a width of 4.5–5.5 μ, gradually tapers to a point or is fusiformly swollen. Not infrequently the apex is distinctly torulose. These gloeocystidia are very sparsely septate, and in one case not a single septum was found over a distance of 270 μ, which was as far as the gloeocystidium could be traced back. The oily or resinous contents appears more concentrated toward the apex which in consequence becomes more intensely coloured by Congo red.

Since the time of Karsten, *Creolophus* was not accepted as a separate genus, until it was recently reintroduced by Donk (1962: 231). Of the type species, *Hydnum corrugatum*, the most recent description is the one published by Cejp (1928: 101; 1930: 321), but in view of the fact that this author found the spores to be non-amyloid, the correctness of the identification is open to questioning.

Banker (1906: 135), who did not know *H. corrugatum*, referred the specimens thus reported from various localities in the United States to *Hydnum pulcherrimum* or *H. septentrionale*. Later on (1913: 293), he associated *Hydnum corrugatum* with *H. septentrionale* on account of the similarity of form, colour, and substance, placing both in the genus *Creolophus*.

Whatever *Hydnum corrugatum* may look like, there is no doubt as to the identity of *Creolophus cirrhatus*, and both Karsten's unmistakable description and figure (1899: 144, pl. 7 fig. 100) of that species make it clear what genus this author had in mind.

The most recent transfer was made by Nikolajeva (1950: 343; 1961: 222), who placed *Creolophus cirrhatus* under *Hericium* on the grounds that microscopically the species is hardly distinguishable from *Hericium coralloides* (l.c. 332). This author moreover supposed it permissible to regard the meshes in the context of *C. cirrhatus* as homologous with the spaces separating the branches in *Hericium corralloides*, at the same time pointing out that there exist forms of the latter whereby the branches are contracted and most of the intervening spaces obliterated.

Although these arguments have their merits, more weight should be attributed to the fact that, as related by Donk, the fruit-body in *Creolophus* is dorsiventrally flattened and its context non-amyloid.

Both Bourdot & Galzin (1914: 278; 1928: 443) and Pilát (1934: 314, fig.) mentioned the occurrence of 'paraphysoid filaments' among the basidia bearing microconidia, but whereas the French authors found the conidia arranged in torulose chains, Pilát's figure more or less clearly depicts the conidia in a terminal position. In a study on the conidial production in *Hericium*, Nikolajeva (1956: figs. 4, 5) distinguished between conidia produced in chains (inside a gloeocystidium), and such as develop at the tip of a special hypha, calling them micro- and macroschizospores respectively. From this it becomes apparent that Bourdot & Galzin would have found the former type and Pilát the second. In a later paper Nikolajeva (1958: 73) stated to have found both types in the present species, adding that the development of the conidia chiefly accompanies the mature basidia. This may be the reason that no macroconidia were found in the material examined, since, with a different goal in view, the region mainly near the tip of the spines was investigated. Nor was any observation made to confirm that in the specimens used for the present investigation the contents of the gloeocystidia are liberated in the form of microconidia.

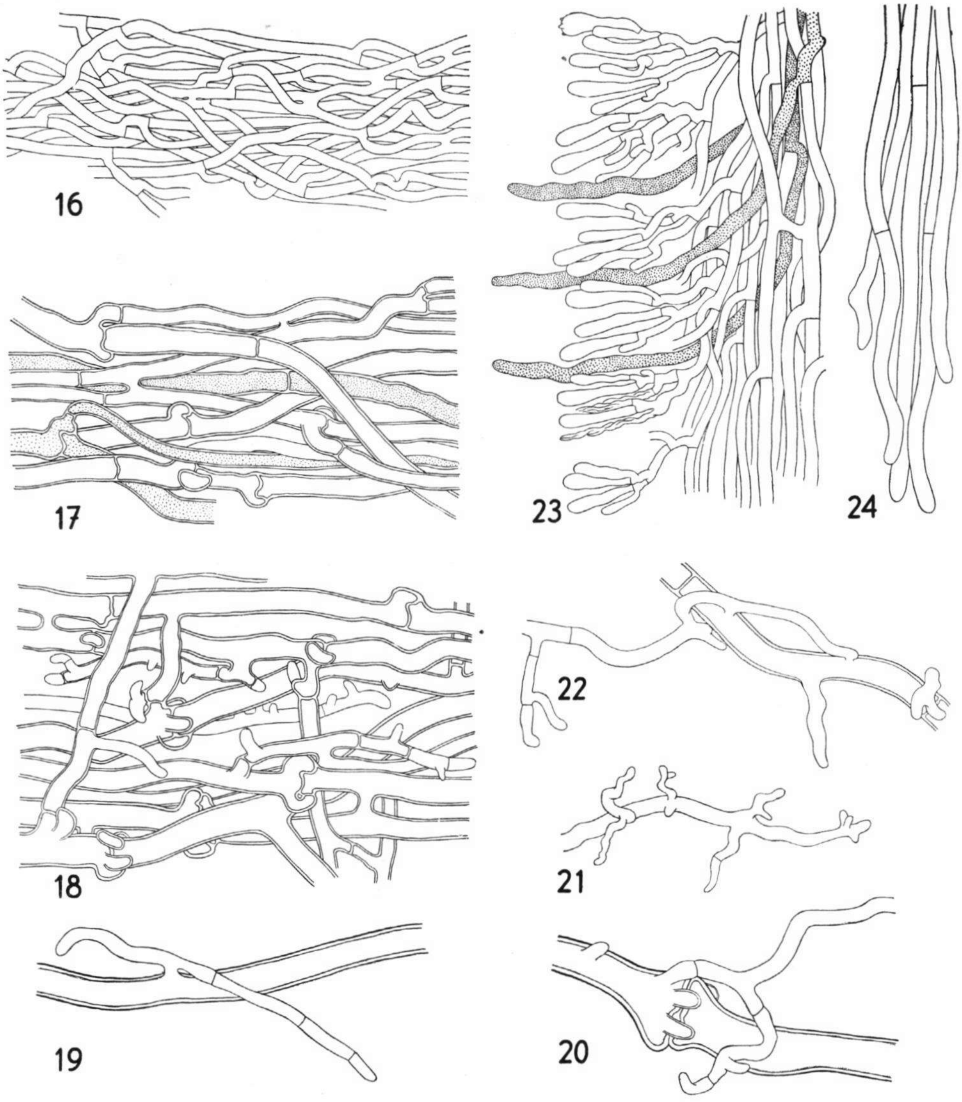
DONKIA Pilát—Figs. 16–24

Donkia Pilát *in* Bull. Soc. mycol. France **52**: 328. 1936. — Type species: *Hydnum pulcherrimum* Berk. & Curt.

Context fairly soft to tough, stringy, zoned in the thicker parts, white (when fresh), consisting of generative hyphae which become increasingly mixed with interweaving hyphae toward the older parts of the pileus. Generative hyphae near the margin of the pileus very thin-walled and lacking clamp-connections, not inflating. Farther away from the margin the hyphae become moderately thick-walled or may even become solid. Clamp-connections appear at some distance from the margin, at first one per septum, then two on opposite sides of a septum, finally in whorls of three to four on the widest hyphae. Tramal hyphae of the spines similar to the hyphae of the youngest parts of the pileus, i.e. without clamp-connections. Basidia lacking clamps. Gloeocystidia numerous.

MATERIAL EXAMINED: *Donkia pulcherrima* (Berk. & Curt.) Pilát (FIJI ISLANDS, Viti Levu, Tamavua-Sawani road; UC 275810. — U.S.A., Florida, Alachua County, Gainesville, Sanchez Hammock; UC 669605. — U.S.A., Louisiana, Baton Rouge; L 957.173–261).

The pileus of a dried specimen of *Donkia pulcherrima* shows a matted upper surface with an embedded or raised network of rather coarse anastomosing fibrils which have a somewhat cartilaginous appearance. Under the microscope it is only just possible to discern that both the outermost layer and the margin are made up of agglutinated and collapsed hyphae from which oozed quantities of an oily substance. It is farther down in the context and at some distance from the margin that the separate hyphae can be made out. These hyphae (Fig. 16, drawn after the



Figs. 16–24. *Donkia pulcherrima* (Berk. & Curt.) Pilát. — 16. Generative hyphae of the context at a distance of about 300 μ from the margin and near the lower surface; margin to the right. — 17. Similar hyphae about 800 μ distant from the margin and near the upper surface of the pileus, showing the presence of clamp-connections. — 18. Similar hyphae about 2.5 mm away from the margin, showing (i) clamp-connections in varying numbers per septum, (ii) lateral excrescences, and (iii) 'bridge-hyphae'. — 19. Divaricating side-branch, about to develop into an interweaving hypha. — 20–22. Various interweaving hyphae. — 23. Tramal hyphae near the axis of a spine, giving rise to gloeocystidia (dotted for greater clarity), and developing the hymenium toward the side of the spine. — 24. Gloeocystidia at the tip of a spine (all figures × 700).

situation at a distance of about 300 μ from the margin and near the lower surface) are of one kind (generative hyphae), 2.2–3.6 μ wide, very thin-walled, with the cell-walls less than 0.5 μ thick, tightly interwoven, flexuous, much branched, with frequent anastomoses, septate, without clamp-connections, and most of them, if not all, filled with an oily substance. Farther back from the margin, the hyphae slowly increase in width and begin to unite into bundles. At some 500 μ away from the margin the first clamp-connections begin to make their appearance, and they become more numerous with increasing distance from the margin (Fig. 17, at about 800 μ from the margin and near the upper surface). The clamps do not occur at all septa, and there is only one clamp per septum. In this part of the pileus the width of the hyphae ranges from 3–5.4 μ, with the cell-walls about 0.5 μ thick. All hyphae are arranged in a strictly longitudinal direction, which holds for the more loosely interwoven hyphae as well as for those of the bundles which by now are clearly defined. Macroscopically (and even seen with a hand-lens) the context in this part of the pileus looks fairly uniform, but farther back a gradual change takes place in that the context appears made up of an arachnoid tissue traversed by anastomosing longitudinal strings. The larger and heavier the pileus, the greater the proportion of the strings in the context.

To return to the microscopical investigation of the context: at a distance of some 2.5 mm from the margin several changes in the hyphae can be noticed (Fig. 18). First, the hyphae are still wider, ranging from 3–10 μ, with the cell-walls 0.5–1.5 μ thick. Secondly, at many of their septa the wider hyphae possess two opposite clamp-connections, which produces a most characteristic picture indeed. However, several others do not stop at that number and develop whorls of three or even four clamps plus a bud. This bud grows out into a branch which, running cross-wise for a short distance, fuses head-on with some adjacent hypha. At irregular intervals on the sides of the hyphae excrescences appear which, too, grow out into side-branches. These may develop at right angles from the parent hypha, or follow the longitudinal direction, or again divaricate, one branch pushing forward and the other backward (see also Fig. 19). These side-branches are notable for their frequent lateral excrescences and the lack of clamp-connections. With increasing distance from the margin—perhaps, more correctly, with increasing thickness of the pileus—both the side-branches arising from just beneath a septum and those springing from the sides of the main hyphae become increasingly longer and more tortuous. They wind their way in every direction (Figs. 20–22), branch in every direction, attach themselves to other hyphae, forming anastomoses, and thus prove themselves to be interweaving hyphae.

The greatest width to which the hyphae have been found to grow is 10–11 μ, whilst their walls as a rule are of moderate thickness, viz. 1–1.8 μ. Occasionally, however, some hyphae have somewhat thicker cell-walls and in one particular case a hypha measuring 7 μ was found to have its lumen completely obliterated (collection from Gainsville). This find is of particular importance as it allows the material to be considered the bridge connecting two extremes: on the one hand the collection from Baton Rouge which has the hyphae thin-walled to moderately thick-walled, on the other the collection from Viti Levu in which already close behind the margin many of the hyphae are so thick-walled as to be practically solid.

Fruit-bodies with a thin pileus appear devoid of any zonation of the context, but in thick-fleshed fruit-bodies there are numerous colour-zones, both vaguely and sharply defined. These zones are caused not by changes in the hyphal structure but by more or less regularly recurring variations in the quantities of the oily matter exuded.

The transition from the generative hyphae of the older parts of the pileus to the tramal hyphae of the spines is abrupt and rather surprising in that at one stroke interweaving hyphae, thickened cell-walls, and clamp-connections are left behind. The tramal hyphae (Fig. 23) are almost identical with the generative hyphae of the youngest parts of the pileus, differing only in the much longer intervals between two septa. The hyphae are all filled with an oily substance and very thin-walled. The widest hyphae, up to 3.6 μ, occur in the axis of a spine. The hyphae become gradually narrower toward its sides, where they develop the basidia which also lack clamps. Certain side-branches, which have their origin near the axis, curve outward and form gloeocystidia. These become increasingly numerous toward the tip of the spine. The tip consists solely of 2.7–3.6 μ wide gloeocystidia (Fig. 24).

A peculiarity of *Donkia pulcherrima* is the sticky sap which in the dried material fills practically every hypha with a brownish oily substance, rendering it exceedingly difficult to study the microscopical structure.

From the appearance of such hyphae as have been illustrated in Figures 5–7, it has been concluded that they are interweaving hyphae. It is clear, however, that this term becomes less and less appropriate the shorter these hyphae grow. Short hyphae connecting two generative hyphae might be called 'bridge hyphae' (Teixeira, 1961: 38), but the gradual transition from one kind to the other sufficiently demonstrates in certain cases the futility of a fixed term.

Miller (1935: 361) and Miller & Boyle (1943: 51) described the hyphae as having "fewer clamp connections in the spines," but in the material cited above they have been shown to be definitely without clamps.

Pilát (1934: 316, fig.) seems to have been the first to observe the presence of gloeocystidia in the species under discussion, but his figure is rather vague with regard to their origin. Later authors (Miller & Boyle and Coker & Beers) did not even mention the gloeocystidia.

Quite recently, Nikolajeva (1961: 194) transferred *Donkia pulcherrima* to the genus *Climacodon*. Although it is true that both genera have several features in common (such as the fibrous construction of the context, the occurrence of 'bridge hyphae', the remarkable absence of clamp-connections in the youngest hyphae and in the spines) one need only compare more attentively their hyphae, clamp-connections, and the origin of the (gloeo-)cystidia, at the same time bearing in mind that the former genus is characterized by its sticky sap, to realize that *Donkia* and *Climacodon* are widely different genera.

HYDNELLUM P. Karst.—Figs. 25–31

Hydnellum P. Karst. *in* Medd. Soc. F. Fl. fenn. 5: 41. 1879. — Type species: *Hydnum suaveolens* Scop. ex Fr.

Context tough to somewhat fleshy, zoned, pale to variously coloured, consisting of generative hyphae. Hyphae with or without clamp-connections, rarely inflating, thin-walled to thick-walled. Tramal hyphae of the spines similar to the generative hyphae but remaining thin-walled. Concurrently with the presence or absence of clamp-connections in the generative hyphae, the tramal hyphae and the basidia possess or lack clamps. Cystidia or gloeocystidia lacking.

MATERIAL EXAMINED: *Hydnellum suaveolens* (Scop. ex Fr.) P. Karst. (AUSTRIA, Tirol, Seefeld; L 960.260-997. — CZECHOSLOVAKIA, Mt. Brdy near Dobříš; L 955. 132-057. — SWITZERLAND, Neuchâtel, Val de Travers; L 961.54-877); also *Hydnellum velutinum* (Fr.) P. Karst. var. *scrobiculatum* (Fr. ex Secr.) Maas G. (NETHERLANDS, Baarn; L 956.066-066), and *Hydnellum compactum* (Pers. ex Fr.) P. Karst. (GERMANY, Saar, Mettlach; L 953.112-378).

The surface of the pileus in a young specimen of *Hydnellum suaveolens* is plushy, but becomes matted to glabrous toward the centre and with age. Very probably the margin, too, is plushy when young, but this could not be verified from lack of suitable material. It certainly is in other species. The entire pileus consists of one kind of hyphae, the generative hyphae, and those at the surface are seen to project into the air more or less parallel to each other and at right angles to the surface (Fig. 25). They are 2.7–5.4 μ wide, thin-walled, with the cell-walls less than 0.5 μ to up to 0.9 μ, occasionally branched, septate, and with clamp-connections at all septa. The hyphae are filled with a substance (pale and with the appearance of oil in the present species, but much darker and more like resin in such coloured species as of the *Hydnellum velutinum* complex) which appears most concentrated, and hence is more intensely coloured by Congo red, at the tips. Also, the contents darkens with age. Some 80 μ below the apices of the erect hyphae, others are seen lying prostrate with their tips pointing in the direction of the margin of the pileus. It would seem that these hyphae, representing the ultimate level of a previous growth-period, have collapsed and have subsequently been left behind by the advancing hyphae of a new growth. The prostrate hyphae form a transverse zone in the flesh, and the number of hyphae, or in other words the thickness of the zone, presumably depends on the climatic conditions which cause the hyphae to collaps. An extreme case in which the hyphae not only have collapsed but become firmly agglutinated is shown in Fig. 26 which depicts a zone about 650 μ below the surface. This particular zone showed as a very dark line in the context, the colour being probably also caused by the darkened matter in the hyphae. A further example of the very tortuous course of the hyphae and their much darkened contents in a zone has been taken from *Hydnellum velutinum* var. *scrobiculatum* (Fig. 27) which shows the hyphae to have retained their normal width.

In older tissues (Fig. 28), at a distance of about 2 mm from the margin in this particular case, the generative hyphae have gradually widened to 3.5–5.5 μ, with the cell-walls in the main about 1 μ thick. At various points narrow hyphae, 2–4 μ wide and with very thin cell-walls which are hardly coloured by Congo red, can be seen to branch off from the generative hyphae. These hyphae develop blunt outgrowths with which they attach themselves to adjoining generative hyphae, several of which remain firmly entwined by them as far as they can be traced. Especially the occasional side-branches at their base make the narrow hyphae resemble interweaving hyphae which, however, they are not because of their longitudinal and unlimited growth. These narrow hyphae appear to be nothing but young shoots which are constantly being formed throughout the older tissues of the pileus. The older the context, the more kinked the shoots (Fig. 29, showing the situation near the centre of the pileus) and the thicker the cell-walls in general. In the widest hyphae (up to 7.2 μ), the cell-walls may be as thick as 2 μ, whilst some of the narrower hyphae are in places almost solid.

The hyphae in the spines do not differ from the generative hyphae except that in general they are somewhat narrower, measuring 2.7–4.5 μ, the widest being situated in the axis of a spine, with the cell-walls 0.5–0.9 μ (Fig. 30). Branching and anastomosing are frequent, and clamp-connections occur at all septa as well as at the base of the basidia. Cystidia and gloeocystidia are absent.

While it is true that the hyphae in *Hydnellum suaveolens*, like in most other species of this genus, have predominantly parallel walls, inflated hyphae are not entirely lacking. Portions of the hyphae containing resinous matter (e.g. in *Hydnellum diabolus*, and see also Fig. 27) may be considerably swollen, and inflated hyphae are very common indeed in *Hydnellum compactum* (Fig. 31), which explains the fleshy nature of its context. Here, the generative hyphae (which ordinarily are 3.5–5 μ wide near the margin) or portions of them may be seen to become inflated up to 7–12.5 μ farther toward the centre of the pileus.

The fleshy context places *Hydnellum compactum* in a position very near the genus *Sarcodon*, and indeed Quélet once called the species *Sarcodon acer* (Quél.) Quél. The important distinguishing character, however, determining this species as a *Hydnellum*, is the zonation of the context as described above for *H. suaveolens*. If Harrison and Coker had recognized the value of this feature, they certainly would not have experienced any difficulty in distinguishing *Hydnellum* from *Sarcodon*. The former (1961: 25) stated that "it is difficult to draw a sharp line between the two genera . . . under all conditions of growth.", while the latter (1951: 36) found *Sarcodon* "not consistently distinct from *Hydnellum*, the more fleshy species of that genus obscuring a sharp definition." As far as can be judged from the descriptions and figures all the Hydnellums described in Coker & Beers's monograph are true members of the genus, but *Sarcodon piperatus* is not a *Sarcodon*. Examination of the type and some additional material (Nos. 10683, 10687) clearly revealed the zonation of the flesh, which is also readily visible in the photograph (Coker & Beers, 1951: pl. 24). Accordingly, the following recombination is proposed: **Hydnellum piperatum** (Coker) Maas G., *comb. nov.* [*Sarcodon piperatus* Coker *in* J. Elisha Mitchell sci. Soc. **55**: 373, pl. 34. 1939 (basionym). — *Hydnum piperatum* (Coker) Pouz. *in* Česká Mykol. **10**: 68. 1956; not *Hydnum piperatum* (Banker) Sacc. & Trott. *in* Sacc., Syll. Fung. **21**: 373. 1912].

From Coker's description and figures it would at first sight seem that *Hydnellum piperatum* is very near *H. compactum*, but even in the dried material a good many differences can be found which are summarized in the following table.

HYDNELLUM COMPACTUM	HYDNELLUM PIPERATUM
Pileus plano-convex or depressed over a wide area, with the margin plane to ascending.	Pileus often with a rather narrow central depression or with a navel which in mature specimens is in marked contrast with the drooping margin.
Surface of pileus without radiately arranged striations or ridges; not concentrically zoned.	Surface of pileus with radiating striations, fibers, or ridges; near the margin with more or less obscure concentrical zones.
Colour of pileus becoming darker with age, with bistre or olivaceous tints.	Pileus not turning bistre or olivaceous with age.
Stipe gradually flaring upwards into pileus.	Stipe abruptly joining the pileus.
Odour (when fresh) of watermelon (*Citrullus vulgaris* Schrad.), cucumber, French beans, or meal.	Odour "very faint, suggesting some desinfectant or rarely fenugreek." (Coker & Beers, 1951: 42).
Taste instantly acrid, later on bitter and astringent.	Taste "strongly peppery" (Coker & Beers, l.c.).
Spores 5–6 μ diam. (Donk), 5–7 × 5–6 μ (Bourdot & Galzin).	Spores 4.2–5.5 μ diam. (Coker & Beers).

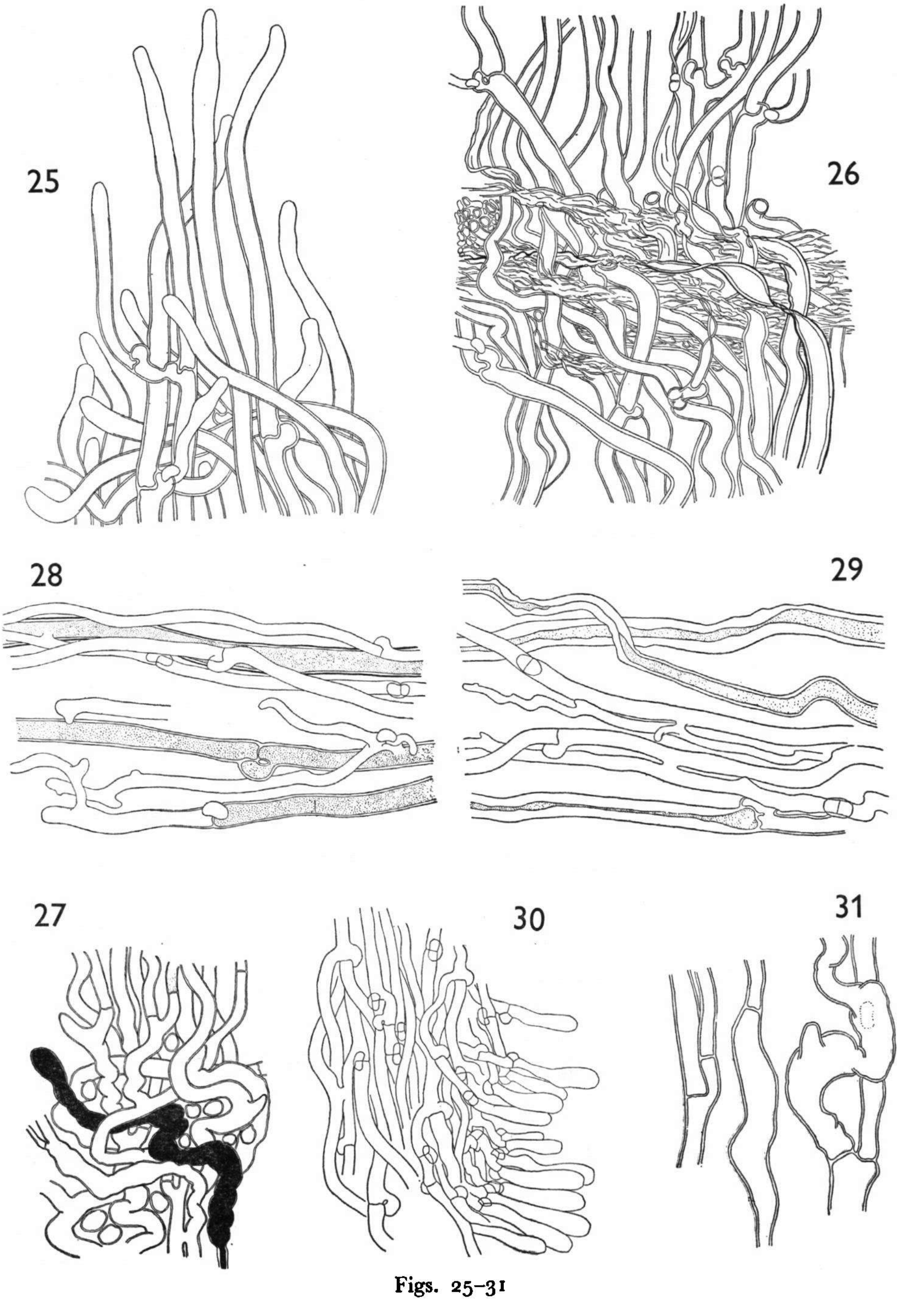
Sarcodon stereosarcinon Wehm. is another example of a species which is marked by the zonation of the context, but in this case the species is a true *Sarcodon*. The zones have their origin not in the deflection of hyphae (as they would in *Hydnellum*), but in the sudden termination of a number of hyphae which, whilst remaining parallel and strictly aligned in a radial direction, are somewhat swollen at their tips and filled to capacity with an oily matter. In some cases large quantities of a brownisch matter have accumulated in between the hyphae, which causes the zones to appear as very dark lines.

EXPLANATION OF FIGURES 25–31

Figs. 25, 26, 28–30. *Hydnellum suaveolens* (Scop. ex Fr.) P. Karst. — 25. Hyphae of the surface of the pileus, some of which project into the air, while others are deflected in the direction of the margin to form a transverse zone. — 26. Transverse zone in the context about 650 μ below the surface of the pileus, consisting of shrivelled hyphae. — 28. Detail of the context at a distance of about 2 mm from the margin (to the left) showing the younger shoots: their origin, their attachment to other hyphae, and their tendency of entwining older hyphae. — 29. Detail of the context near the centre of the pileus showing older generative hyphae with thickened cell-walls, and the kinked contours of the shoots. — 30. Tramal hyphae of a spine giving rise to the hymenium (all figures × 700).

Fig. 27. *Hydnellum velutinum* (Fr.) P. Karst. var. *scrobiculatum* (Fr. ex Secr.) Maas G. — Detail of a transverse zone in the context to show the very tortuous course of the hyphae while retaining their normal width (× 700).

Fig. 31. *Hydnellum compactum* (Pers. ex Fr.) P. Karst. — Fragments of parallel-sided and inflated generative hyphae (× 700).



Figs. 25–31

Some comments need here be made in connection with Ragab's paper. This author very justly remarked (1953: 942) that "Any student who has devoted considerable attention to taxonomic study of the Hydnaceae will recognize that little or no attention has been given to the character of the hyphal elements in delimiting genera and species." In his zeal, however, Ragab slightly overshot. Any student who has devoted considerable attention to taxonomic study of the Hydnaceae will recognize that *Phellodon* is a perfectly sound genus which should on no account be united with *Hydnellum*, even if it were true that their hyphal structures are alike. For it would be illogical to maintain that a single character—the similarity of the hyphal structures—should have more weight than the unvarying combination of three other and unrelated features such as spore-colour, spore-ornamentation, and odour. However, the hyphae in both genera are not completely similar. The cell-walls in *Hydnellum* gradually thicken with age, becoming 1–2 μ thick and sometimes even obliterating the lumina of the hyphae. In *Phellodon*, on the contrary, there is not a single species known to have the cell-walls thicker than 0.5 μ in any part of its fruit-body.

MYCOLEPTODONOIDES Nikol.—Figs. 32–34

Mycoleptodonoides Nikol. *in* Bot. Mater. (Not. syst. Sect. cryptog. Inst. bot. Acad. Sci. USSR) **8**: 117. 1952. — Type species: *Mycoleptodonoides vassiljevae* Nikol.

Context rigid, not zoned, pallid, consisting of generative hyphae which are thin-walled only near the margin and the surface of the pileus. The hyphae are branched, with frequent anastomoses, septate, with clamp-connections at all septa, and throughout the greater part of the context very thick-walled or practically without a lumen. In the lower portion of the pileus the generative hyphae become much swollen and very tortuous, and produce much narrower side-branches which connect the hyphae through anastomosis. Tramal hyphae of the spines very thick-walled in the axis, thinner walled toward the sides, branched, anastomosing, with clamp-connections at all septa. Basidia with clamps. Cystidia and gloeocystidia lacking.

MATERIAL EXAMINED: *Mycoleptodonoides vassiljevae* Nikol. (U.S.S.R., "reservatum suputinicum", part of type; L 961.54-850).

The entire pileus is made up of generative hyphae which near the margin, as is apparent from a medial section, mainly run in a radial direction (Fig. 32, showing the situation 100 μ behind the margin). The hyphae are very closely packed (much more so than shown in the figure), much branched, anastomosing, septate, with clamp-connections at all septa, 2.7–5.4 μ wide and very thick-walled or with hardly any lumen at all. Toward the margin (which in the material available could not be studied because the hyphae remained a solid collapsed mass) the hyphae tend to become narrower and thinner walled. The same holds for the hyphae on the surface which are equally hard to distinguish since they are embedded in an amorphous matter.

Farther away from the margin the hyphae gradually increase in width, maintaining much the same radial arrangement, but those deeper down in the context undergo a marked change. They become very tortuous indeed, widen enormously, up to 32 μ, with the cell-walls thickening at the same rate, and assume the oddest shapes (Fig. 33). Another peculiarity is to be found in the narrow hyphae, 2–4 μ in diameter, which branch off from the thickened hyphae at various places. Some are short and winding, others considerably longer and straight, but although it is not exactly known where the latter go or how they terminate, it is suggested that the short and long hyphae do not represent two different kinds. Their function in any case seems essentially the same: connecting one hypha to another, thus strengthening the tissue. Because of their very thick cell-walls and the unlimited growth of the longer hyphae, these side-branches can be identified neither with interweaving hyphae, nor with binding hyphae. Probably they are nothing else but shoots of the generative hyphae, and the occurrence of thicker but otherwise similar (probably older) side-branches seem to strengthen this supposition.

In the spines (Fig. 34) the axis is made up of agglutinated hyphae, 4.5–7.2 μ in diameter and either very thick-walled or practically without lumen. Their course is undulating and they branch and anastomose frequently; clamp-connections are found at all septa. Toward the sides of the spines the thick-walled hyphae are gradually replaced by hyphae with thinner cell-walls, and these eventually give rise to the very wide subhymenial tissue, up to 60–70 μ, which consists of very closely packed and extremely tortuous hyphae, 2–3 μ wide and with the cell-walls less than 0.5 μ thick. The basidia possess clamp-connections. Cystidia and gloeocystidia are absent.

32 33 34

Figs. 32–34. *Mycoleptodonoides vassiljevae* Nikol. (part of type). — 32. Generative hyphae of the context 100 μ behind the margin of the pileus; margin to the left. — 33. Generative hyphae farther away from the margin and the upper surface. — 34. Tramal hyphae about 500 μ away from the base of a spine, very thick-walled in the axis of the spine, becoming thinner walled toward its side, and finally producing the very thin-walled hymenial elements (Figs. 32 and 34, × 700; Fig. 33, × 200).

It will be observed that in the generic description given on an earlier occasion (Maas Geesteranus, 1961: 409) the context was described as fleshy. This term, which suggested itself on account of the presence of inflating, thin-walled hyphae in the context of *M. aitchisonii*, needs reconsideration in view of the very different situation in *M. vassiljevae*. Since very thick-walled generative hyphae do occur in the type material of *Hydnum aitchisonii*, only with less frequency, that species is still considered congeneric with *Mycoleptodonoides vassiljevae*. However, this makes it necessary in the generic description to replace the word "fleshy" by "more or less fleshy to rigid". The description can be further emended by the definite statement that (i) the hyphae in the pileus and the spines have clamp-connections at all septa, and (ii) the basidia possess clamps at their base.

Like in *Mycoleptodonoides aitchisonii* the hyphae in *M. vassiljevae* may become enormously swollen, but it remains to be seen whether the term 'inflating hyphae' should be equally stretched to include such hyphae as are practically solid from the thickening of their walls.

In contrast with the view expressed previously (1961: 411), *Mycoleptodonoides* and *Hydnum* are no longer regarded as related genera. Whereas the former is characterized by the glabrous surface of the pileus composed of agglutinated hyphae and the thickening of the cell-walls of many of the hyphae in the older tissues, the latter shows a tomentose surface of the pileus, whilst all the hyphae remain thin-walled.

Mycorrhaphium Maas G., *gen. nov.*[1]—Figs. 35–52

Hoc a genere *Steccherinum* S. F. Gray, a quo disiungitur, notis carnis aculeorumque differt. Caro e hyphis unae speciei admodum formata, aculei tametsi hyphis biformibus instructi gloeocystidiis carentes. *Mycoleptodonoides* Nikol. pileo glabro, hyphis pilei partis inferioris immodice turgentibus earumque parietibus pariter incrassatis, atque aculeorum hyphis omnibus aequalibus longe distat. — Typus generis: *Hydnum adustum* Schw.

Differing from *Steccherinum* S. F. Gray in the monomitic context of the pileus and, although the spines do possess skeletal hyphae, in the lack of cystidia. Easily distinguishable from *Mycoleptodonoides* Nikol. in that (i) the pileus in the latter is glabrous, (ii) its hyphae in the lower part of the pileus are very much swollen, while their cell-walls are proportionally thickened, and (iii) the spines lack skeletals. The zonation of the surface of the pileus (and of the context near the margin) may well prove to be a further character by which *Mycorrhaphium* can be distinguished from *Mycoleptodonoides*. — Type species: *Hydnum adustum* Schw.

MATERIAL EXAMINED: **Mycorrhaphium adustum** (Schw.) Maas G., *comb. nov.* [*Hydnum adustum* Schw. *in* Schr. naturf. Ges. Leipzig **1**: 103, pl. 2 figs. 7–9. 1822 (basionym). — *Steccherinum adustum* (Schw.) Banker *in* Mem. Torrey bot. Cl. **12**: 132. 1906. — *Mycoleptodonoides adusta* (Schw.) Nikol. *in* Bot. Mater. (Not. syst. Sect. cryptog. Inst. bot. Acad. Sci. USSR) **8**: 120, figs. 2, 3, pl. 44. 1952] (U.S.A., North Carolina, Hendersonville; UC 669567. — U.S.A., Tennessee, near Knoxville; L 960.340-064. — U.S.A., Baton Rouge; L 959.140-804).

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[1] ETYMOLOGY: ἥ μύκης, fungus; τό ράφιον, small needle, which refers to the small, straight, needle-like spines.

Context tough, anoderm, indistinctly zoned (probably only zoned near the margin), white, consisting of generative hyphae. Hyphae not inflating, much branched, often anastomosing, septate, with or without clamp-connections, thin-walled, becoming moderately thick-walled. Trama of the spines dimitic (for exceptions, see detailed description), consisting of generative as well as skeletal hyphae. Basidia with or without clamp-connections. Cystidia or gloeocystidia lacking. Spores almost cylindrical to ellipsoid, smooth, colourless, non-amyloid.

The greater part of the surface of the pileus in *Mycorrhaphium adustum* is minutely velutinous, becoming finely woolly-strigose toward the centre, and showing one to several zones of a matted or glabrescent surface near the margin. Seen under the microscope, the velutinous parts appear made up of a single kind of hyphae, the generative hyphae. These run mainly in radial direction but have their tips curved upward, ending freely into the air, as do the side-branches. In Figure 35, drawn after a section of the pileus about 1 mm distant from the margin, the hyphae are 2–4.5 μ wide. They are very thin-walled, the cell-wall less than 0.5 μ thick, frequently branched, and septate. They possess clamp-connections which, however, do not appear to occur at all septa, a phenomenon also known to occur in Polyporaceae and amply discussed by Teixeira (1962: 62). The free-ending tips of the hyphae retain much the same width all over the surface of the pileus, but tend to cohere into tufts (which are responsible for the strigose appearance in the centre of the pileus), and become thicker walled, with the cell-walls 0.5–0.9 μ (Fig. 36). In the glabrescent zones (e.g. in Fig. 37 which shows the situation at 500 μ distant from the margin) the distal ends of most of the superficial hyphae are deflected in the direction of the margin, lying flush with the surface. Incidentally, one of the hyphae is shown partially filled with resinous matter.

The context is entirely made up of generative hyphae which differ from the superficial hyphae only in that they very gradually increase in width in the older tissues, become somewhat thicker walled, and are more frequently connected by anastomosis. Hyphae of the context 15 mm distant from the margin may be found to measure 4–6.3 μ in width, with the cell-walls up to 1 μ thick.

Throughout the greater part of the pileus the context is uniform, with the hyphae running in several directions, but with a slight predominance of a radial arrangement. Near the margin, however, and convex toward it several faint zones can be seen to interrupt this radial alignment. The zones consist of bundles of more closely cohering hyphae which all converge into an arc (Fig. 38, from a region 270 μ below the surface and 1000 μ behind the margin). The narrower hyphae beyond the arc obviously developed during a renewed growth of what at the time constituted the margin.

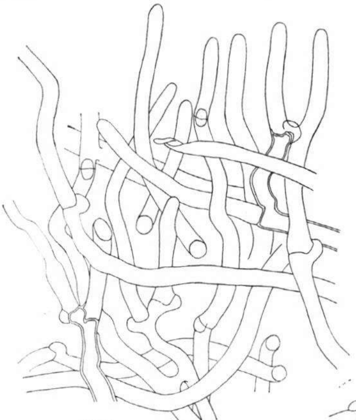
The trama of the spines is usually very much different from the context of the pileus in that it consists of both generative and skeletal hyphae. Such cases as in UC 669567 in which the same specimen possesses spines full of skeletals and others completely without any may perhaps be considered exceptional. The origin of the skeletals seems equally subject to some variation. Most skeletals arise in the basal portion of the spine, either as a side-branch or as the distal end of a generative hypha (Fig. 39), but some have their origin deeper in the context of the pileus. They constitute the main body of the axis of a spine but are to an increasing extent substituted by generative hyphae toward the periphery. Running down the length of a spine, in a somewhat undulating course, the skeletals gradually increase in width, up to 4.5–6.3(–7.2) μ, and become steadily thicker walled (Fig. 40, drawn after the situation about half way down the spine). Farther toward the tip of the spine the skeletals taper to 3–4.5 μ in width and their cell-walls at the very apex become less than 0.5 μ thick. They do not curve sideways to form cystidia. At their distal ends the skeletal hyphae are filled with a fluid which causes the spines in the fresh state to turn black when bruised, and to become covered at their tips with blackish crystals in dried specimens. Quite a number of the skeletals appear septate at their apices, with the septa convex toward the apex and sometimes numbering as many as eleven, and becoming thinner the farther away from the apex (Fig. 41).

The tramal hyphae in the spines (Fig. 40) run of necessity more parallel and their septa are spaced at shorter intervals, but otherwise they are not different from the generative hyphae in the context of the pileus. They are 2.7–4.5 μ wide and the peripheral hyphae tend to have somewhat thicker walls than those nearer the axis of the spine. Especially the terminal cells may have the cell-walls 0.5–1 μ thick. These terminal cells end below or at the level of the subhymenial tissue in the middle part of the spine, but close to its tip (at 125 μ distance from the tip in the case examined, Fig. 42), where there is no trace of a subhymenium, they curve outward, projecting freely into the air. They differ from true gloeocystidia in that they are septate and lack resinous contents. It should be noted that the generative hyphae do not reach as far as the skeletals, ending about 60 μ short of the apices of the latter (Fig. 41). The basidia possess clamp-connections.

In connection with the occurrence of septa in the apical portion of the skeletal hyphae in the spines, it may be pointed out that Corner (1932a: 73, fig.1a) described a similar septation in the skeletals of *Polystictus xanthopus*, whilst Boidin (1958a: 335, Fig. 2B) found it in the acanthophyses of *Stereum annosum*. Shortly afterwards Boidin (1958b: 49) used the name 'cloisons de retrait' for cross-walls which in

EXPLANATION OF FIGURES 35–42

Figs. 35–42. *Mycorrhaphium adustum* (Schw.) Maas G. — 35. Velutinous surface of the pileus, about 1 mm distant from the margin which is to the left; tips of the hyphae projecting freely into the air. — 36. Finely strigose surface at the base of the pileus, with the hyphae cohering into tufts. — 37. Glabrescent surface of the pileus, showing most of the hyphae deflected in the direction of the margin which is 500 μ distant. — 38. Transverse zone in the context, 270 μ below the upper surface, and 1000 μ behind the margin. Zone convex toward the margin which is to the left. — 39. Origin of skeletal hyphae in the base of a spine. — 40. Detail half way down the spine, showing skeletal and generative hyphae, the latter forming the subhymenial tissue toward the side of the spine. — 41. Skeletals from the tip of a spine, showing the 'cloisons de retrait' in some of them, and some generative hyphae which do not reach as far as the skeletal hyphae. — 42. Detail of the side of a spine 125 μ back from its apex, showing some skeletals and generative hyphae, the tips of the latter curving sideways (all figures × 700).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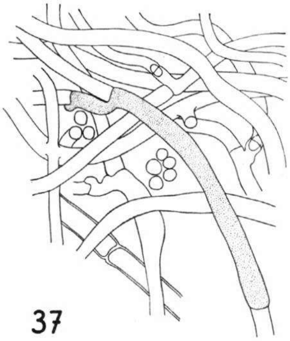
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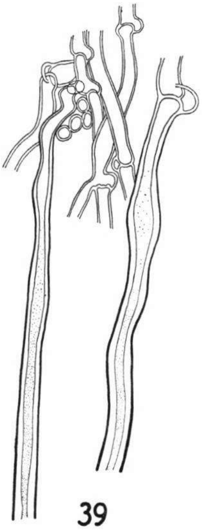
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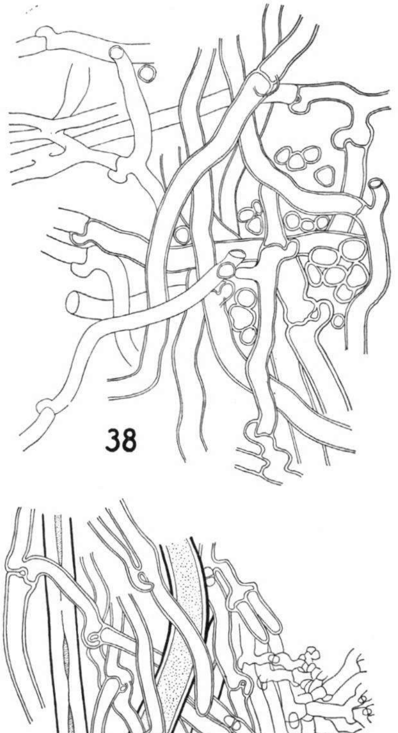
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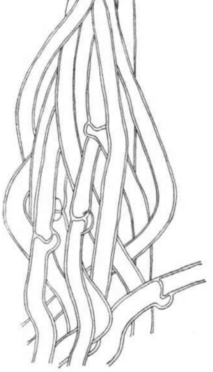
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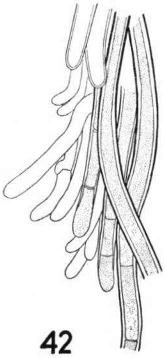
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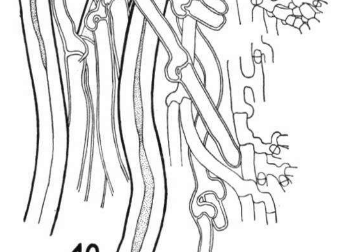
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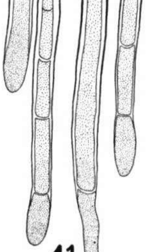
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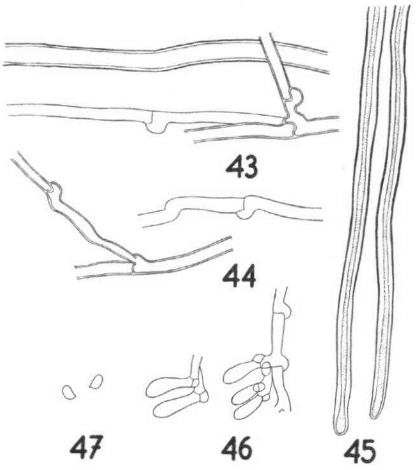
Figs. 35–42

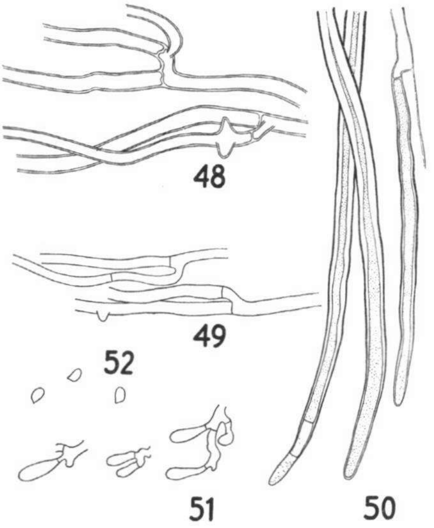
general separate the living contents in hyphae from the dead portions, and which apparently also occur in species of various corticiaceous genera like *Corticium*, *Vuilleminia*, and (1961: Fig. 4, 5) *Peniophora*.

A second species of the present genus is **Mycorrhaphium pusillum** (Brot. ex Fr.) Maas G., *comb. nov.* [*Hydnum pusillum* Brot., Fl. lusit. **2**: 470. 1804; *ex* Fr., Syst. mycol. **1**: 407. 1821 (basionym). — *Leptodon pusillus* (Brot. ex Fr.) Quél., Ench. Fung. 192. 1886; Fl. mycol. 441. 1888. — *Steccherinum pusillum* (Brot. ex Fr.) Banker *in* Mycologia **4**: 313. 1912. — *Pleurodon pusillus* (Brot. ex Fr.) Bourd. & Galz. *in* Bull. Soc. mycol. France **30**: 275. 1914; Hym. France 439. 1928. — *Mycoleptodon pusillus* (Brot. ex Fr.) Bourd. *in* Bull. Soc. mycol. France **48**: 220. 1932].

Banker, who studied material at Uppsala marked "*Hydnum pusillum* Brot.", came to the conclusion that it was identical with, and an earlier name for, his *Steccherinum adustulum*.

Bourdot & Galzin, on the other hand, believed (1914, 1928) that perhaps Fries's *Hydnum luteolum* was not distinct from *H. pusillum*. Afterwards, after having seen further





Figs. 43–47. *Steccherinum adustulum* Banker (type). — 43. Generative hyphae from the surface of the pileus, 1.8–4.0 μ wide, with the cell-walls < 0.5–0.9 μ thick. — 44. Tramal hyphae of a spine, 2.2–2.7 μ wide, with the cell-walls < 0.5–0.5 μ thick. — 45. Skeletal hyphae at the tip of a spine, 2.2–3.1 μ wide, gradually widening to 3.6 μ (at a distance of 270 μ), with the cell-walls up to 1.5–1.8 μ thick. — 46. Basidia with clamp-connections at their base. — 47. Spores, non-amyloid, 3.1 × 1.9 μ (all figures × 700).

Figs. 48–52. *Mycoleptodon luteolus* (Fr.) Bourd./*M. pusillus* (Brot. ex Fr.) Bourd. (from Herb. Bourdot). — 48. Generative hyphae from the context of the pileus, 2.2–4.5 μ wide, with the cell-walls < 0.5–0.9 μ thick. — 49. Tramal hyphae of a spine, 2.2–3.1 μ wide, with the cell-walls c. 0.5 μ thick. — 50. Skeletal hyphae at the tip of a spine, 2.2–2.7 μ wide, gradually widening to 3.6 μ (farther back), with the cell-walls up to 1.8 μ thick. — 51. Basidia without clamp-connections. — 52. Spores, non-amyloid, 2.8–3.1 × 1.9 μ (Figs. 48–51: Herb. Bourdot No. 4189; Fig. 52: Herb. Bourdot No. 41410; all figures × 700).

collections, Bourdot (1932) became convinced that both names referred to one and the same species.

Examination of both Banker's type specimen of *Steccherinum adustulum* (U.S.A., New York, Mohawk, summer [18]90, Mrs. W. C. Lobenstine; NY) and Bourdot's material of *Mycoleptodon luteolus/pusillus* (FRANCE, bois de Séganges, près Moulins, août 1888, *H. B[ourdot]*, Herb. Bourdot 4189; Forêt de Bagnolet, 23 VIII 1927, *F. Rémy*, Herb. Bourdot 41410; PC) showed that with the exception of a single character the former is identical with the latter. The one difference, as illustrated in Figures 43–47 and 48–52, is that the American material possesses clamp-connections, which are absent from the European material. Ten further collections from NY, and two more from France (Montbéliard, Bois de Thür, 3 Aug. 1956, *H. S. C. Huijsman*; L 956.110-617. — Lougres (Doubs), 28 Sept. 1956, *Mrs. L. Huijsman*; L 956.147-373) confirm the fact that the presence of clamps is as constant a feature in the specimens of *Mycorrhaphium pusillum* of North America as is the absence in those of Europe. It would seem that the specimens of both continents belong to two constant races of the same species.

No mention has been made with regard to the number of spores per basidium in either North American or European literature. It proved unexpectedly difficult to ascertain this number from the dried material, the best result being obtained in Bourdot's material from Bagnolet, which gave a faint indication of the basidia producing four sterigmata.

A third collection in Bourdot's herbarium under the name of *Mycoleptodon luteolus* (Franois, près Besançon, X 1928, *P. Cretin*, Herb. Bourdot 42301; PC) contains some resupinate specimens with the upper margin reflexed. These agree in all respects, excepting the clamps, with the resupinate specimens in several of Banker's collections.

Miller (1935: 364) and Miller & Boyle (1943: 53) reported the hyphae of *Steccherinum pusillum* to be thick-walled and without clamp-connections. This, in the American race, is correct only for the skeletal hyphae in the spines.

The fungus described by Benzoni (1933: 10) under *Hydnum pusillum* does not represent this species, as the spores were said to measure 5 × 4 μ, while the fruit-bodies were collected from dead stems of *Pteris aquilina*.

PHELLODON P. Karst.—Fig. 53–55

Phellodon P. Karst. *in* Rev. mycol. 3/No. 9: 19. 1 Jan. 1881 & *in* Medd. Soc. F. Fl. fenn 6: 15. 1881. — Type species: *Hydnum nigrum* Fr. ex Fr.

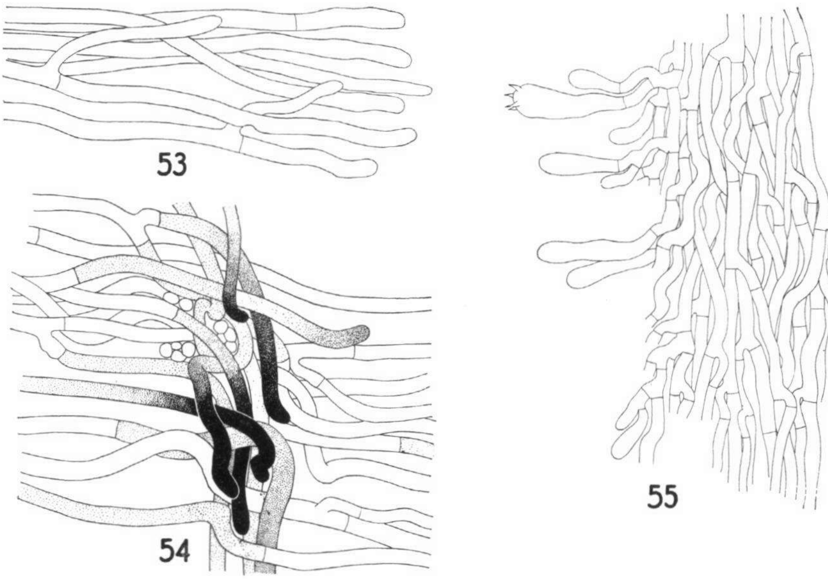
Context firm (with a hard core in some species), zoned, coloured, consisting of generative hyphae. Hyphae not inflating, always thin-walled, without clamp-connections. Tramal hyphae of the spines similar, somewhat narrower, lacking clamp-connections. Basidia without clamps. Cystidia or gloeocystidia absent.

MATERIAL EXAMINED: *Phellodon niger* (Fr. ex Fr.) P. Karst. (CZECHOSLOVAKIA, South Bohemia, Šalmanovice; L 960.216-709. — SWEDEN, Gotland, Othem, Klints; L 960.260-867).

The entire surface of the pileus, which in young specimens of *Phellodon niger* is finely plushy, consists of erect hyphae of a single kind, the generative hyphae. These project into the air more or less parallel to each other and at right angles to the surface (Fig. 53, which has been taken from the very margin). The hyphae are 2.3–3.6 μ wide, very thin-walled, with the cell-walls less than 0.5 μ thick, sparingly branched, septate, without anastomoses or clamp-connections, and filled with an oily matter. Like in *Hydnellum,* the tips of the hyphae deflect after some time, forming a transverse zone which appears nearly black on account of the rapidly darkened contents (Fig. 54). The thickness and density of the zone as well as its distance from the surface vary a great deal.

No matter how far back into the interior of the fruit-body the hyphae are retraced, they retain much the same width, which varies from 2.7 to 4.5 μ, and they never have the cell-walls thicker than 0.5 μ. The hyphae are firmly coherent, much more so than in *Hydnellum,* which makes it hard to be certain whether or not there are anastomoses. If there are, these are extremely rare, which makes it probable that the coherence of the hyphae alone is responsible for the firmness of the tissue.

The hyphae in the spines (Fig. 55) are in general somewhat narrower than the hyphae of the pileus, being 2.2–3.6 μ in diameter, and the septa are spaced at shorter intervals. Side-branches are frequent, anastomoses and clamp-connections



Figs. 53–55. *Phellodon niger* (Fr. ex Fr.) P. Karst. — 53. Generative hyphae from the margin of the pileus. — 54. Generative hyphae at some distance from margin (which is to the right), deflected to form a transverse zone; darkened contents adding to mark the zone. — 55. Detail of a spine, showing tramal hyphae and hymenium (all figures × 700).

are absent. Toward the sides of the spine the side-branches develop the basidia which also lack clamps. There are neither gloeocystidia nor cystidia.

SARCODON P. Karst.—Figs. 56–60

Sarcodon P. Karst. *in* Rev. mycol. 3/No. 9: 20. 1 Jan. 1881 & *in* Medd. Soc. F. Fl. fenn. 6: 16. 1881. — Type species: *Hydnum imbricatum* L. ex Fr.

Context soft, fleshy, not zoned,[1] white or coloured, consisting of generative hyphae only. Hyphae inflating, thin-walled to moderately thick-walled, with or without clamp-connections. Spines with tramal hyphae similar to the generative hyphae. Basidia with or without clamp-connections, which coincides with the presence or absence of the latter in the context. Cystidia and gloeocystidia lacking.

MATERIAL EXAMINED: *Sarcodon laevigatus* (Sw. ex Fr.) P. Karst. (FRANCE, Belfort; L 956.110-779); for details also *S. fuligineo-violaceus* (Kalchbr. apud Fr.) Pat. (NETHERLANDS, Nunspeet; L 960.318-845); *S. imbricatus* (L. ex Fr.) P. Karst. (FRANCE, Martignat; L 952.199-125), and *S. scabrosus* (Fr.) P. Karst. (NETHERLANDS, Ulvenhout; L 951.255-224).

The surface of the pileus in mature specimens of *Sarcodon laevigatus* is usually found to be smooth and glabrous, under circumstances becoming areolate or scaly, but in young specimens it is finely velutinous, which character is best retained in the growing margin.

The velutinous margin is composed entirely of closely packed generative hyphae which project at right angles to the surface (Fig. 56). They are 2.7–4.5 μ wide, thin-walled, filled with an oily matter, and possess clamp-connections at all septa. Occasional side-branches arise from some of the hyphae, while processes, developing from the sides of others, touch adjacent hyphae, thus initiating anastomoses. Both side-branches and anastomoses become more frequent in older parts of the pileus (Fig. 57, showing the situation 200 μ farther down the velutinous covering), the side-branches often arising from clamp-connections.

Farther toward the centre of the pileus, the surface changes from velutinous to radiately fibrillose, then becomes glabrous. The explanation is that farther away from the margin increasingly longer portions of the hyphae bend down radially. At first, that is just behind the margin, the individual hyphae are still clearly distinguishable (Fig. 58), but with age, which means farther away from the margin, the cells shrivel and their walls gelatinize and become agglutinated, thus forming a firm and shining pellicle. In the course of the development of the fruit-body this pellicle ruptures into areoles or scales. It is not known whether in the scaly species, such as *Sarcodon imbricatus* and *S. scabrosus*, the pileus in the youngest stages is velutinous, too, as such stages were not available.

The context, which is devoid of any zonation, seems at first sight to be made up of two different kinds of hyphae; one kind composed of very narrow cells, the other of very wide cells. It appears, however, that rearward the narrow hyphae gradually widen into the inflated ones, whilst in their turn the latter can again be seen to arise from narrow-celled hyphae. This succession of narrow (3–5 μ wide)

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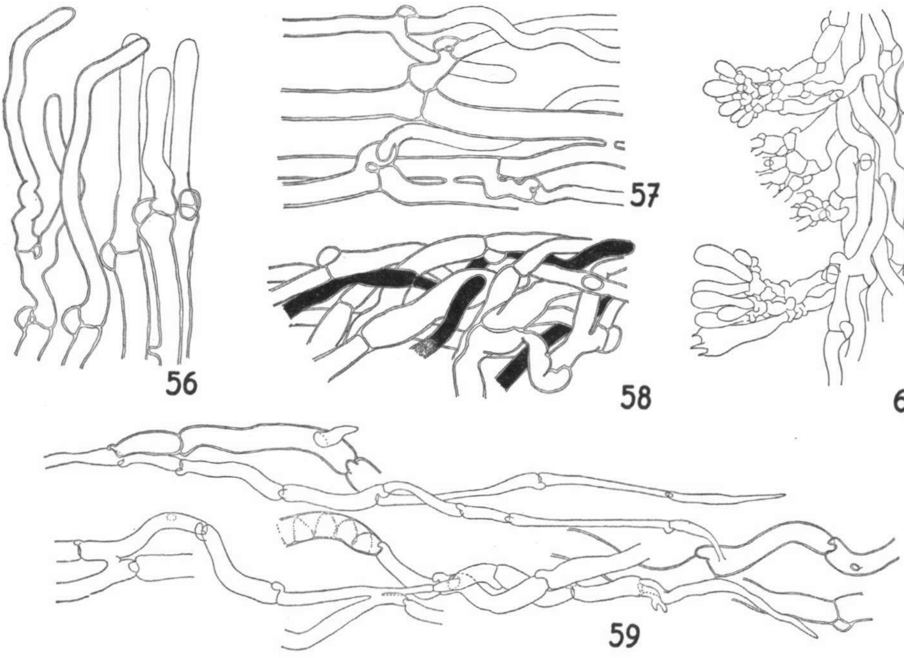
[1] However, see remark on *Sarcodon stereosarcinon*, p. 390.

and inflated (up to 14 μ wide) generative hyphae is illustrated in Fig. 59 (drawn after the situation at a distance of 25 mm from the margin, and 5 mm below the surface). It is of interest to note that even in older tissues of the pileus the hyphae continue to produce actively growing shoots which wedge themselves between the surrounding hyphae. Frequently, some part of the terminal cell of the shoot attaches itself to an adjacent hypha, thus initiating anastomosis, but in rare cases it is the tip of the cell which has become fused.

The cell-walls, which are less than 0.5 μ thick in the narrow hyphae, become somewhat thickened in the inflated hyphae, and may reach a thickness of 1 μ in those found in the base of the spines on the underside of the pileus.

A feature worth mentioning is that in some of the inflated cells the cell-wall on the inside seems reinforced by a spiral rib.

In the axis of the spines hyphae with the cells inflated up to 10 μ and with somewhat thickened cell-walls constitute an important element, but their number rapidly diminishes toward the sides and the tip of the spines. At the periphery of the spines



Figs. 56–60. *Sarcodon laevigatus* (Sw. ex Fr.) P. Karst. — 56. Generative hyphae from the velutinous margin of the pileus. — 57. The same 200 μ farther down the velutinous covering (figure turned 90° round to the right). — 58. Generative hyphae behind the growing margin, deflected radially to form the pellicle. — 59. Detail of the context, showing the succession of narrow and inflated cells in the hyphae; 25 mm behind the margin of the pileus, 5 mm below the upper surface. — 60. Detail of a spine, with tramal hyphae and hymenium (Fig. 59, × 200; all others × 700).

thin-walled hyphae 2.7–6 μ wide prevail, and from these numerous side-branches curve outward to form the hymenium (Fig. 60). There are neither gloeocystidia nor cystidia. Species which possess clamp-connections in the context (*S. imbricatus*, *S. laevigatus*), also have them in the trama of the spines and at the base of the basidia. If there are no clamps in the context (*S. fuligineo-violaceus*, *S. scabrosus*), they are also absent from the trama of the spines and the basidia.

STECCHERINUM S. F. Gray—Figs. 61–65

Steccherinum S. F. Gray, Nat. Arrang. Brit. Pl. **1**: 597, 651. 1821. — Type species: *Hydnum ochraceum* Pers.

Context pliable, tough, not 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, aseptate. Trama of the spines dimitic. Basidia with clamp-connections. The tramal cystidia formed by the swollen ends of skeletals curving outward, thick-walled, encrusted.

MATERIAL EXAMINED: *Steccherinum ochraceum* (Pers. ex Fr.) S. F. Gray (NETHERLANDS, 's-Graveland; L 958.319-049).

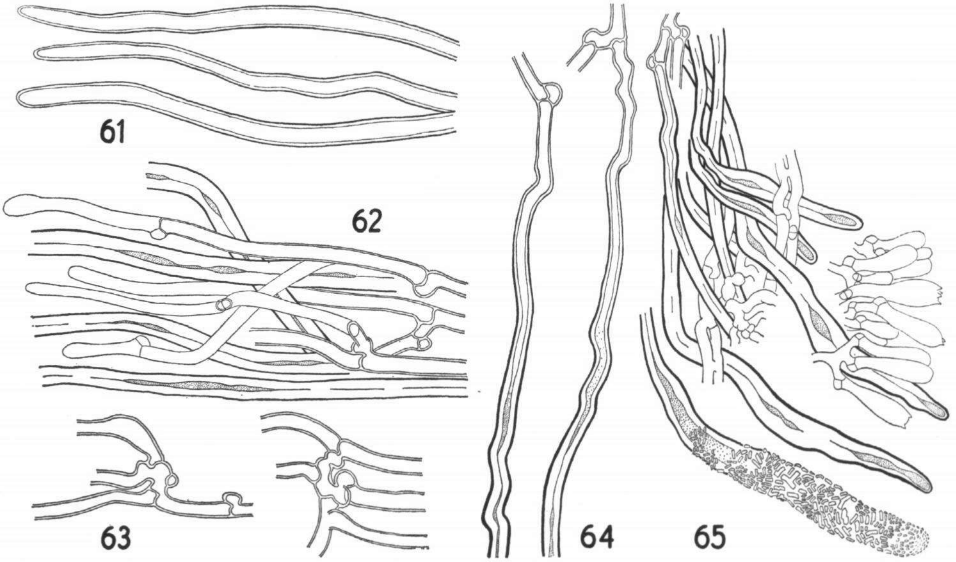
In a young specimen of *Steccherinum ochraceum* the margin of the pileus is minutely plushy and, seen under the microscope, appears to consist of fairly rigid hyphae. These hyphae, which have rounded or slightly pointed tips (Fig. 61), are 3.6–4.5 μ wide at their apices and retain much the same diameter when traced back over a distance of 200 or 300 μ. Their cell-walls, however, gradually thicken rearward. At the apex the cell-walls are about 0.5 μ thick, 100 μ farther back they measure 0.9–1.3 μ, and still 100 μ farther back 1.8–2.2 μ, so that in places the lumina are obliterated. Further characters of these hyphae are the lack of side-branches and septa, their somewhat undulating course, and longitudinal growth. These criteria determine the hyphae as skeletal hyphae. They are found without interruption throughout the entire pileus, which explains the lack of zones in the context. Seen under a low magnification, the context seems made up solely of skeletals, and only under a higher magnification can a second type of hyphae be detected. These hyphae, the generative hyphae, do not reach the extreme margin, but end about 200 μ short of the apices of the skeletals. (Fig. 62). (The strigose to tomentose upper surface of the pileus is likewise formed of these two kinds of hyphae, but here the generative hyphae end at almost the same height as the skeletals.) The generative hyphae are 2–3.6 μ wide at the tip, septate, with clamp-connections at all septa, and extremely thin-walled, with the cell-wall less than 0.5 μ at the apex. Side-branches do occur, rather sparingly at first, but with increasing frequency toward the base of the pileus. A side-branch often originates from a clamp and a second side-branch may arise in its turn from a clamp of the first branch. The knot resulting from this process becomes progressively intricate the more side-branches come into play, and the tangle becomes inextricable when anastomoses with adjoining hyphae are established. Figure 63 shows some simple cases. Obviously, these knots are largely responsible for the resistance of the context to tearing.

Occasionally, hyphae may be found intermediate between generative and skeletal hyphae in that they are extremely long and thick-walled, but possess one or two septa with clamp-connections close to their origin.

At a distance of 600–700 μ from the margin some of the skeletals are seen to originate from a generative hypha, either simply as a terminal continuation or, more frequently, as a side-branch (Fig. 64). It is quite possible that there exist even longer skeletals.

The trama of the spines consists of the same two kinds of hyphae, generative hyphae and skeletals, and here, too, the latter form the bulk. The tip of a spine is entirely formed of skeletal hyphae which are similar to those of the extreme margin of the pileus, except that at their apices some of them have one to several thin cross-walls, the 'cloisons de retrait' of Boidin (see also under *Mycorrhaphium*).

Farther away from the tip of a spine several of the more peripheral skeletals are seen to curve outward, forming the tramal cystidia. The deflected portions are more or less fusiformly swollen, up to 7–10 μ wide, and heavily encrusted (Fig. 65).



Figs. 61–65. *Steccherinum ochraceum* (Pers. ex Fr.) S. F. Gray. — 61. Skeletal hyphae from the extreme margin of the pileus. — 62. Detail of the context 200 μ behind the margin, showing thick-walled skeletals, and thin-walled generative hyphae, the latter with clamp-connections. — 63. Fragments of generative hyphae, forming anastomoses and developing side-branches from the clamps. — 64. The origin of two skeletal hyphae 600–700 μ behind the margin, arising from generative hyphae; skeletals in the spines develop in exactly the same manner. — 65. Detail of a spine, showing skeletals and generative hyphae. The former deflecting sideways and developing into encrusted tramal cystidia; the latter giving rise to the hymenium (all figures × 700).

In the figure some of the cystidia are depicted without their coating of crystals to show their true form.

The generative hyphae showing among the skeletals are thin-walled and possess clamp-connections, but differ from the generative hyphae of the pileus in that anastomoses are much more frequent, while septa occur at much shorter intervals. Toward the sides of a spine the generative hyphae give rise to the subhymenial tissue and the basidia, the former with clamp-connections at all septa, the latter at their bases (Fig. 65).

Apart from the type, the following were examined and recognized as true species of the present genus: *Steccherinum fimbriatum* (Pers. ex Fr.) John Erikss. (Netherlands, 's-Gravenzande, Staelduinen; herb. M. A. Donk); *Steccherinum laeticolor* (Berk. & Curt.) Banker (U.S.A., Iowa, Yellow River, Postville; herb. M. A. Donk); *Steccherinum litschaueri* (Bourd. & Galz.) John Erikss. (according to the description by the original authors); **Steccherinum murashkinskyi** (Burt) Maas G., *comb. nov.* (basionym: *Hydnum murashkinskyi* Burt *in* Ann. Missouri bot. Gdn **18**: 477. 1931; Siberia, Distr. Tara; herb. M. A. Donk); *Steccherinum rhois* (Schw.) Banker (U.S.A., Pennsylvania, West Brownsville; UC 525476); and *Steccherinum setulosum* (Berk. & Curt.) Miller (U.S.A., Iowa, Wellman; herb. M. A. Donk).

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