

SUPPLEMENTARY NOTES ON BASIDIOCARP ONTOGENY IN AGARICS

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Basidiocarp ontogeny is described and illustrated of eight species of agarics, viz. *Hygrophoropsis aurantiaca*, *Hygrophorus pudorinus*, *Tricholoma populinum*, *T. ustaloides*, *T. vaccinum*, *Marasmiellus candidus*, *Marasmius wynnei*, and *Panellus mitis*

In many cases it still is not clear to what extent ontogenetic structures of basidiocarps of agarics can be used as taxonomic characteristics. Earlier (Reijnders, 1963) we published a table with data on the development of the basidiocarp of 232 species of Agaricales. Although the data of some of these species were still incomplete, a number of regularities or conformities between allied species became nevertheless apparent from the table. The difficulty of the application of these data in systematics is that, in most cases, they are known of too few species. For instance, it is not known if a special structure is correlative with other features and consequently is characteristic of a certain group; in other words, the limits of the different structures are insufficiently known.

Although veils in mature basidiocarps are only remnants of primordial structures and thus can be studied better and more completely in the primordium, one can determine their presence or absence with routine methods in all species of a monographically treated group. The development of the veils in the primordium is only to be studied by time-absorbing technics and is known in only a few cases. That counts even more for another aspect of basidiocarp development: the succession of the internal differentiation of stem, cap and gills.

When only a limited amount of data are available one is easily inclined to generalize; the application of ontogenesis in mycological taxonomy indeed bristles with such often unwarranted generalisations.

Yet in a completely elaborated taxonomy the characteristics of ontogenesis will have to play their rightfull part. It has already often been said that in a taxonomy reflecting natural affinities, all characteristics have to be weighed by their importance. So we are still intent on extending our investigations on ontogenetic structures in agarics as far as they are perceptible by the light-microscope (a limiting factor is often the difficulty to collect primordia of the desired species). In the following notes we present the results of our studies of another eight species.

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Hygrophoropsis aurantiaca (Wulf.: Fr.) Maire

1. Here we are concerned with a pure stipitocarpous species. The first stages of the developing basidiocarp consist of long very slender stems, even up to 1–2 cm high.

Fig. 1 shows the microphoto of a top of such a stem; width approximately 345 μm . In general the hyphae are parallel, but not strictly so; they are divided into short, binucleate cells of a rather varying width (2–7.5 μm).

2. The cap comes into being because hyphae at the top of the stem change direction and bend outward. Consequently the upper part widens and a chromophilous rim develops in which the radial hyphae run parallel. At the same time the hyphae in the centre of the stem do not grow straight upwards anymore but begin to intertwine and the cells are becoming wider (up to 10 μm ; those in the section of the cap have an average width of $\pm 6.5 \mu\text{m}$; in the stem only 3–5 μm). Fig. 3 shows a median section of a cap at that stage. At the underside of the cap and decurrent on the stipe the formation of anastomosing veins has already started by now. These veins are lined with a hymenial palisade (width of the elements $\pm 5 \mu\text{m}$) in which already numerous slender basidia (diam. $\pm 7 \mu\text{m}$) with mature spores are present. This palisade continues over about 1 mm downwards along the stipe (Fig. 5) and then changes into a more irregular covering with strongly branched hyphae, often with club-shaped extremities (diam. $\pm 6.5 \mu\text{m}$) (Fig. 6). On the surface of the cap we already find some differentiation, viz. a layer (50–60 μm thick) in which the hyphae are closely interwoven and in which many ramifications take place. The hyphal tips tend to turn outwards and make the surface more or less felty; sometimes they form a loose palisade.

3. A tangential section shows clearly that gill-folds are joined by anastomoses (Fig. 2; width of the section of the cap $\pm 3.5 \text{ mm}$). The descriptions of the gill-trama by Kühner (1980: 652), by Singer (1975: 688) and by Corner (1966: 134) are rather different, although all three authors recognize a mediostratum, which has a loose texture and outer layers consisting of hyphae or cells with mucilaginous walls, densely packed together. Singer distinguishes in these outer layers a hymenopodium and a subhymenium but he adds that the latter is only slightly differentiated from the former. Apart from the fact that in our opinion the term 'hymenopode' is rather questionable in such cases, we were unable to detect any differentiation in the outer layers, which have mainly a cellular structure with some short scattered hyphae and a width of 20 μm (also according to Corner). With respect to the mediostratum: Kühner observes in cross-sections a wedge-like structure, with the sharp angle pointing towards the edge of the gill, consisting of loosely interwoven hyphae like in the trama of the cap ('aérifère comme la chair piléique'). Though he did not observe divergent hyphae he quotes Singer's mentioning of such hyphae in the hymenopodium ('but this divergence is inconstant and not persistent').

When we follow the formation of the gills from the beginning (Fig. 4) we must conclude that the folding-activity is exclusively brought about by inflation of the narrow cells of the subhymenium and the hymenial palisade. In this manner arise the shallow

folds near the margin of the cap. There is neither in the beginning nor afterwards any pushing done by the hyphae of the mediostratum: some hyphae of the pileal trama are simply taken along with the folds; they may ramify and increase in number to a certain extent and show a somewhat divergent or axillary arrangement, but the construction remains so loose that there are finally only a few hyphae which traverse the space between the lateral strata. Corner mentions that the trama becomes: 'hollow and mucilaginous' (Fig. 11). Kühner was struck by the fact that the lamellae of *Hygrophoropsis* easily split along the medial plane. This is not caused by the divergent trama with a mediostratum of strictly parallel hyphae as in *Limacium*, but by the almost empty space between the lateral layers.

It must be stressed that the hymenophoral trama of *Hygrophoropsis* is quite different from the divergent (or somewhat bilateral) trama of the Boletaceae and the Paxillaceae, etc. The relation of *Hygrophoropsis* with the latter family has been thought to be proved by the presence of a pulvinic-acid derivate, but can by no means be based on the structure of the gill-trama, which is more similar to that of *Cantharellus*.

Hygrophorus pudorinus (Fr.) Fr.

At present it is general practice to divide Fries' large genus *Hygrophorus* into different genera. In the first place the three sections, into which Fries divided this genus, have been raised to the rank of genus. *Limacium* is one of them, now bearing again the name *Hygrophorus* (s.str.). This genus is specially characterized by the permanently divergent gill-trama and the usually viscous covering of stem and cap. As to the development, a certain amount of species of this genus have been examined with few differences between them (see Reijnders 1963: 146). To this we should like to add some more observations.

1. *Hygrophorus pudorinus* is a species with large basidiocarps. The primordia show a stipitocarpous development. Soon a ring-shaped edge growing outward originates at a short distance below the top of the primordial stem. This is the beginning of the cap. The youngest stage represented (Fig. 7) has a diameter of 4.2 mm where it is widest. In this median section one can see the edge of the cap turning downward and inward. Lamellae are already present as well: shallow folds with divergent trama. The tissues of stem and cap differ already considerably but the demarcation is not clear. In the stem-part the hyphae are more or less parallel. They are not yet strongly inflated (diameter in the base up to 10 μm , higher up in the stem 6 μm on an average). The hyphae in the pileus are intricate; their width is on the whole somewhat larger (diam. up to 11 μm). This is also the case above the lamellae. Parallel hyphae are rather restricted to the edge of the cap.

At the outside of the stem, especially in the upper part, one finds thin hyphae (diam. $\pm 3 \mu\text{m}$) which are more or less interwoven, but underneath the edge of the cap they form bundles which are directed outwards and here this layer is widest ($\pm 250 \mu\text{m}$).

Fig. 8 shows the edge of the cap in a younger stage (largest width 1.8 μm) than in the above-described median section. Over the pileipellis, composed of closely jointed hyphae, there is in addition a fluff of entangled short hyphae.

Fig. 9 shows the margin of the cap at a later stage (diam. of the primordium here 7.7 mm). The outwards turning hyphae along the surface of the stem are here to be found over a greater length (the stem has become longer) but the layer is less broad (110 μm). The walls of these hyphae, which more or less form a palisade, have already become mucous at an early stage. Fig. 10 represents the stem-surface further downwards in the stage of 7.7 mm width.

At the stage of which we have represented the median section (diam. 4.2 mm, Fig. 7) the fluff on the cap has disappeared and the cap is completely closed in by a thick mucous layer ($\pm 250 \mu\text{m}$). Just as in the other species of *Hygrophorus* examined the strong development of mucous appears first on the cap. One might consider the hyphae that grow outwards from the stem and the fluff on the cap as a veil but then as an emanated veil. There is hardly a connection between the hyphae on the edge of the cap and those along the stem, even at an early stage. So the species is rather gymnocarpous than mix-angiocarpous.

***Tricholoma populinum* J. Lange, *T. ustaloides* Romagn.,
and *T. vaccinum* (Pers.: Fr.) Kumm.**

In a former publication (Reijnders, 1963: 59–63, 162–169) we described the development of some species of the genus *Tricholoma*. It is remarkable that all these species show a primary angiocarpy, though mostly in a very rudimentary form.

Most of these species are monovelangiocarpous but some are weakly paravelangiocarpous, i.e. the universal veil is lacking completely. The paravelangiocarpy in those species is however quite weak, as the hyphae of the hymenophore in the initial stage are hardly internal and are enveloped by only a few hyphae (as in *Tricholomopsis rutilans*; see Reijnders, 1963: pl. 17).

We are able now to add some more species of *Tricholoma* to the list of those that have been examined so far. Since the development of these species is very much alike, we describe them together. We shall observe the same order as in the title above.

1. The youngest stage consists of a small column which is widest in *Tricholoma populinum* (diam. in the centre respectively about 755 μm , 690 μm and 380 μm). It consists of protenchymatic hyphae, which are interwoven in the entire primordium of *T. populinum*, but in the other two species only in the lower half (Fig. 12, Fig. 17, Fig. 23). In the last two species the hyphae in the upper half run more longitudinally. The universal veil is clearest in *T. ustaloides*, where it consists of slightly wider hyphae (diam. 1.5–3.5 μm) which are interwoven or directed outwards. In *T. vaccinum* the universal veil is hardly showing and consists of a few loose hyphae. These are also found in *T. populinum* but then at the outside of a dark-coloured zone, consisting of hyphae which deviate in colour, parallel to the surface (diam. 15–20 μm). The loose hyphae on the outside are by no means present everywhere along the surface (diam. of this layer at most 30 μm); they are either pushed off or possibly have been removed artificially during the preparation of the mounts.

2. We now have to pay attention to the origin of the margin of the cap and the hymenophore. In the present three species these develop underneath the universal veil (Fig. 14, width at the hymenophore 504 μm ; Fig. 18, width 380 μm ; Fig. 24, width also 380 μm). The primordium of *T. populinum* remains widest and shortest, the other primordia are very slender. The universal veil in *T. ustaloides* remains the strongest developed one. To demonstrate that the first palisade-hyphae of the hymenophore really develop internally (although they are covered by only a very thin layer of other hyphae), we add a few photos of details of *T. ustaloides* (Fig. 19; diam. of the primordium 440 μm) and of *T. vaccinum* (Fig. 25; diam. 706 μm).

3. The next stage is slightly more developed. Here the universal veil is already reduced to remnants at the margin of the cap, which probably will disappear in later stages (Fig. 13, diam. at the hymenophore 135 μm ; Fig. 20, diam. 755 μm ; Fig. 26, diam. 690 μm). The hyphae in the stem in *T. populinum* (of which only one side of the median section has been photographed) are still rather strongly interwoven, while, in the other species they are longitudinal. In *T. populinum* they are also rather strongly widened: diam. in the stem up to 10 μm and in the trama of the cap up to 6.5 μm , or even up to 8 μm . In the other *Tricholoma*'s in the base of the stem, in the top of the stem and in the trama of the cap respectively diam. up to 6.5 and 13 μm , up to 5 and 9.5 μm , and up to 3 and 7 μm .

4. In later stages not much is to be perceived of the veil any more. Fig. 15 (diam. at the level of the margin of the cap 4 mm) shows an older primordium of *T. populinum*. The short, wide shape has been retained so far. Over the cap of this species a lively growth of new hyphae has developed, to be seen on the photograph as a strongly chromophilous layer (diam. \pm 95 μm). In this layer we observe — as always, when in a plectenchyma new hyphae develop — the twisted hyphae of the hyphal knots, here present in abundance. The outward growing hyphae already have strongly mucous walls (width of this layer up to 130 μm , Fig. 16). The dark particles on the surface of the cap in the photograph for the greater part are fragments of dirt sticking to the cap. We may assume that the weak rests of the veil, barely visible any more, have been pushed away and have disappeared as a result of the strongly growing layer under it.

It is notable that in *T. populinum* the development of the hymenophoral palisade is relative late.

We also photographed the margin of the cap of the median section of *T. ustaloides* (Fig. 21; diam. of this stage 2.3 mm). Here one can see that the hymenophoral palisade runs down the apex of the stem; lower down the universal veil (width 50–100 μm) covers the entire stipe and consists of hyphae that are somewhat interwoven. The transition from the hymenophoral palisade to the veil is rather gradual.

It is interesting to compare the veil of *T. ustaloides* with that of *T. ustale* (Fr. ex Fr.) Kumm., of which we examined the development before (Reijnders 1963: 59). Romagnesi (1954: 157) distinguished *T. ustaloides* from *T. ustale* by a few characteristics, one of which is the stronger development of the veil in the former species. We were able to compare older primordia of the two species of about the same size. Pl. 16 fig. 6 in our

publication of 1963 shows the margin of the cap of a primordium of *T. ustale* with a width of 2.5 mm. When we compare the median section of this primordium with one of a similar primordium of *T. ustaloides* (Fig. 20) we are indeed struck by the different widths of the veil along the stipe (in *T. ustale* 30–70 μm). There is also a difference in structure; in *T. ustale* the hyphae of the veil, which gradually merge into the cortex of the stem, run parallel; at the surface there are only very loose hyphae directed outwards.

Marasmiellus candidus (Bolt.) Sing.

1. We reproduce photomicrographs of median sections of a number of successive stages of this species, starting with a primordium of which the largest width is 271 μm and the height 240 μm (Fig. 22). Very often the basidiocarps of this species develop in lenticels of small twigs, which then are filled with intertwining mycelial hyphae (height e.g. $\pm 90 \mu\text{m}$).

The section shows two chromophilous spots, to the right and the left of the axis, where a dense ramification of the generative hyphae takes place. These ramifications will turn downwards to form the hymenophore, which develops internally as the dark spots are surrounded by ordinary protenchyma. A universal veil, however, is not differentiated. Some strongly coloured hyphae, scattered in the tissue, may belong to a parasitic or saprophytic mould; at later stages they are lacking.

2. Fig. 27 shows a section of a stage of a similar size (greatest width 240 μm , height 195 μm), but here the whole primordium has been depicted. The hyphae in the stem already show a longitudinal direction but in the pileus they are interwoven. The veil is restricted to the sides of the stem.

3. The lipsanenchyma is thin and sparse but still clearly present in the next stage (Fig. 28; largest width 385 μm , height 390 μm). The hyphae in the stem are a little wider (diam. up to 3 μm), but the hyphae in the trama of the cap and also the chromophilous hyphae of the hymenophore, running downwards in a curve, are thin (diam. $\pm 1.5 \mu\text{m}$). There is now, over the cap, a layer (width $\pm 25 \mu\text{m}$) in which the interwoven hyphae are somewhat wider (diam. up to 3 μm).

4. A tangential section (Fig. 31; width of the section 330 μm) shows that the palisade of hyphae of the hymenophore is not interrupted and that the extreme tips of the hyphae are on the same level. This is quite normal in Agaricales and different in only a few groups.

5. In a rather more developed stage (Fig. 29; width 605 μm , height 630 μm) the lipsanenchyma has almost disappeared and exists only of a few loose hyphae. The diameter of the longitudinal hyphae of the stem is up to 5 μm . Here the separate upper layer of the cap, as well as the demarcation between stem and trama of the cap, show up more clearly.

6. The gills develop through folding as in most of the Agaricales. The hymenophoral trama is divergent at first, as usual. We photographed the young folds of the gills of a section of which the largest width was $695\ \mu\text{m}$ (Fig. 32; the height of the fold at the right is $95\ \mu\text{m}$). Also in a later stage, when the gills are slightly higher, the trama remains divergent or — as so often happens — it shows a more or less regular structure. The gills, however, do not become very high. It is known that in mature sporocarps they anastomose and form a kind of network of veins. The hyphae of the hymenophoral trama remain thin.

7. In a following stage the stem starts lengthening (Fig. 30; diam. of the cap $1010\ \mu\text{m}$, height $1640\ \mu\text{m}$). The cells of the hyphae of the stem show a strong inflation (diam. up to $11\ \mu\text{m}$), while the diameter of those in the trama of the cap only attains $5\ \mu\text{m}$.

8. In most cases the cap will later develop one-sidedly and consequently the stem will become excentric or even lateral. This can already be observed at a stage in which the cap has a width of $\pm 2\ \text{mm}$ (Fig. 33). Here again we are dealing with a species where the primordia are radially symmetric but where the cap may develop excentrically depending on how the basidiocarp is situated on the wood (compare Reijnders, 1963: pl. 12, fig. 1–5, *Pleurotus dryinus*, pl. 13, fig. 1–3, *Pl. ostreatus*, etc.).

The demarcation between the trama of the cap and the trama of the stem is very clear here and lies considerably higher than the level of the hymenophore so that the trama of the cap is thin. The covering of the cap is little differentiated in this species (diam. of the hyphae of the trama of the cap, also in the upper part, up to $6.5\ \mu\text{m}$). The cells in the stem can reach a width of $\pm 10\ \mu\text{m}$, which is not particularly much.

Summarizing it can be said that *Marasmiellus candidus* is paravelangiocarpous. The youngest primordia are relatively short and remain so for some time. When the hyphae of the stem become longitudinally arranged, the hyphae of the cap remain interwoven. This species is at least pileostipitocarpous and because of the relatively early development of the hymenophore it could even be considered isocarpous.

Marasmius wynnei Berk. & Br.

1. The youngest stages of this species have the shape of subglobular to ellipsoid bodies with a smooth outline. We represent sections of two of them. In the first the hyphae in the lower part show already a longitudinal arrangement (Fig. 34; largest width $500\ \mu\text{m}$, length $\pm 655\ \mu\text{m}$), while the hyphae in the future cap trama form a plectenchyma (diam. of the hyphae in the stem up to $5\ \mu\text{m}$, in the cap $2\text{--}3\ \mu\text{m}$). Already the pileipellis consists of club-shaped elements (diam. up to $8\ \mu\text{m}$). The second section depicted is somewhat smaller (Fig. 35; width $365\ \mu\text{m}$, length $575\ \mu\text{m}$), but shows a little more differentiation; the parallel hyphae in the lowest part of the stem are up to $7\ \mu\text{m}$ wide, those of the trama of the cap up to $6\ \mu\text{m}$. In this section we can see a fissure developing underneath the future margin of the cap, probably as a result of tensions caused by irregular growth. In this fissure the tissue is torn and some hyphae are crushed. The slowly

downwards and inwards curving margin of the cap has a tendency to press firmly against the stem. The fissure has a depth of 95 to 110 μm .

2. In a slightly more differentiated stage the outer primordial tissue that was originally covering the developing margin of the cap, has been torn loose and as a result of further growth of the stem is now situated a little below the margin of the cap (Fig. 36; largest width 530 μm , length 705 μm). The tendency of the margin of the cap to press against the stem is very clear here; this margin consists of bundles of generative hyphae ramifying strongly (diam. 1–2 μm) and running in a downward direction. A detail of the margin of the cap at this stage we present stronger enlarged (Fig. 37).

3. We photographed still another median section of a primordium demonstrating the typical development of this species (Fig. 39; width 730 μm , height 1090 μm). The curved margin of the cap presses firmly against the stem. The demarcation between the trama of the cap and the parallel hyphae of the stem has become very clear now. At a short distance below the margin of the cap are the remnants of the torn outer primordial tissue in the shape of a ring-like rim round the stem. Although the hyphae of this stage have not become much wider, the club-shaped elements of the pileipellis have reached a diameter of 10 μm .

4. The margin of the cap of a broader primordium is shown separately and higher magnified (Fig. 43; width of the primordium 975 μm , height 895 μm). Here the tissue that is pushed aside still lies against the margin of the cap. It is notable that hyphae are still passing from the margin of the cap into this strip of tissue.

5. Finally a median section of a somewhat older primordium (Fig. 38; width of the cap 945 μm , height 1555 μm) is depicted. The now strictly parallel hyphae of the stem have not yet widened much (diam. up to 6 μm). The demarcation between the trama of stem and cap is very abrupt since the thin hyphae of the cap often have a direction perpendicular to that of the hyphae of the stem. The trama of the pileus consists of two parts: a central loose tissue of thin hyphae (diam. 2–4 μm), about 110 μm high, is surrounded by a compact plectenchyma in which the hyphae usually are a little wider (diam. up to 6 μm) and in which there are many club-shaped terminal cells (diam. up to 7 μm). The pileipellis consists of a compact tissue of cells with, at the outside, many palisade-like elements. The margin of the cap is still pressed against the stem, which shows at that spot a ring of inflated hyphae (diam. 10 μm). It is clear that the unevenness of the stem, still present in mature basidiocarps, is caused by fragments of the primordial cortex of the stem and the margin of cap. When we call this a veil, it is a very rudimentary one.

Marasmius wynnei is paravelangiocarps since in the early stages the palisade of hymenophoral hyphae develops more inward, between other elements. The primordium is robust and at first short. Since the plectenchyma of the trama of the pileus, the margin of the cap, and the stem differentiate more or less simultaneously we consider this species pileostipitocarps. A comparison with the fairly related *Marasmius rotula* (Scop.: Fr.) Fr. is given in the concluding paragraph.

Panellus mitis (Pers.: Fr.) Sing.

1. Young primordia of this species have an oblong form; the length can be very different. Our photo (Fig. 40) shows a median section which is 410 μm thick and 865 μm long. Usually these primordia are already more or less flat so that the width is larger than the thickness. The body consists of flexuous, mainly parallel hyphae which are 3 μm wide in the base and 1–2 μm in the top where they have more protoplasm and thinner walls. The top of the primordium is turned down and shows a strong growth. Already at this stage the primordium is, up to about half the length, enveloped by a mucous layer. This mucous layer develops first at the base of the primordium. On the outside of this layer is a covering of loose hyphae which have not become mucous (diam. 2–3 μm). This felty layer is only $\pm 10 \mu\text{m}$ wide, but is still present in mature basidiocarps.

2. The next stage (Fig. 41) has a length of 1.7 mm and is 960 μm thick. In principal there are no changes, but a thick mucous layer (diam. 190–260 μm) now envelops almost the whole primordium, with the exception of the tip which keeps growing continually. Although the hyphae gather little width they get a thicker wall in the lower part of the primordium and therefore are stained more highly. The presence of thick-walled hyphae (but no skeletal) is a generic characteristic of *Panellus*.

3. Figs. 42 represents the distal extremity of a stage with a length of 3–4 mm and a largest thickness of 1.5 mm. We can see here that, at the underside of the curved zone of growth, a hymenial palisade has started to develop; its elements are still thin (diam. up to 3 μm). Folds of the lamellae are already developing; in this practically median section one of them has been cut. At this stage in a large part of the primordium the hyphae are somewhat wider (diam. up to 7 μm), however without being subject to strong inflation.

4. Finally a few photos of a young fungus (Fig. 45; length 6.3 mm, thickness 2.2 mm). At this stage the young specimen is already divided into a stem-shaped part, and a flat or shell-shaped part. The edges of this second part are curved downwards, not only at the apex, but also at the sides. Lamellae originate only at the underside of the shell-shaped part. The mucous layer still envelops almost the whole primordium and thus is also to be found on the outside of the inflexed margin. This explains why, in a not quite median section, a part of this mucous layer seems to cover the part with the hymenophore (Fig. 44). In this section the shell-shaped part with the hymenophore is 770 μm long. The hyphae of the stem have hardly widened (diam. up to 8 μm).

From these observations it appears that *Panellus mitis* is stipitocarpous and gymnocarpous as earlier mentioned by Singer (1975: 340).

A short comparison with *Tectella patellaris* (Fr.) Murr. will be given in the concluding chapter.

CONCLUSIONS

1. The development of *Hygrophoropsis aurantiaca* shows the primitive character of this species; stipitocarp, and the simple origin of the cap from outward-curving apical

hyphae. We have treated the origin of the trama of the gills at some length. The folding of the hymenium is caused by the multiplying and inflating hymenial elements and not by tramal hyphae growing downwards from the underside of the trama of the cap. In this respect *Hygrophoropsis* is pronouncedly cantharelloid.

2. The development of *Hygrophorus pudorinus* is comparable to that of other species of *Hygrophorus* s. str. (see Reijnders, 1963: 146). In all cases there is an emanated universal veil which becomes mucous, to begin with on the cap. Consequently these species are mixangiocarpous or, when, like in this species, the veil is only very slightly developed, they are practically gymnocarpous.

3. The development of the three species of *Tricholoma* which have been examined here, also fits in well with the pattern already determined for *Tricholoma* (Reijnders, 1963: 162). In general these species are monovelangiocarpous with a rather weakly developed universal veil, which is, however, clearly visible in most cases. There is no clear lipsanenchyma. In *Tricholoma focale* (Fr.) Ricken (see Reijnders, 1952: pl. 7, fig. 2–6) however there is no veil over the cap; that species is paravelangiocarpous. We already examined *Tricholoma ustale* (Fr. ex Fr.) Kumm. (Reijnders, 1963: 59, 162). Comparing *Tricholoma ustaloides*, described in the paper, with the previous species, we observe a stronger development of the universal veil in the last one, which agrees with Romagnesi's observations when describing *T. ustaloides* as a new species. Generally these species are stipitocarpous; however the exceptionally robust form of the primordium of *T. populinum* is striking.

4. It stands to reason that the development of *Marasmius wynnei* is compared with that of *Marasmius rotula* (Scop. ex Fr.) Fr. (see Kühner, 1980: 607; Reijnders, 1963: 64, 150) and that of *Marasmiellus candidus* with that of *Marasmiellus ramealis* (Bull.: Fr.) Fr. (Reijnders, 1963: 68, 150). But there also is reason to compare these four species with each other for they show remarkable similarity in the most important criteria of the ontogeny among themselves and with the related genus *Micromphale* (*M. perforans* (Hoffm.: Fr.) S.F. Gray; see Reijnders, 1963: 69, 150, pl. 23). They all are pileostipitocarpous and paravelangiocarpous.

There is some difference between the sections of the youngest stages of *Marasmius rotula* represented by Kühner (l.c.) (1980: fig. 174) and ours (1963: pl. 21). The fact is that in Kühner's illustrations the tissue at the side of the stem, which we would call lipsanenchyma, is much stronger developed; in the youngest stage even so strongly, that Kühner talks about a 'bourrelet' and thinks of 'endocarp'. We do not believe, however, that this tissue ever was closed at the upper side and that it ever enveloped the whole primordium. In our figures this 'bourrelet' is indeed visible (1963: pl. 20 fig. 6, pl. 21 fig. 2); it apparently develops in the same way as the rings of *M. wynnei*. In *M. rotula* the margin of the cap is also pressed against the stem.

Apart from the amyloidity one may wonder if the structural differences, which are the basis of the distinction of the genera *Marasmius*, *Marasmiellus*, and *Micromphale*, are sufficient to justify this distinction, where on the other hand there is such a remarkable conformity in the development of the basidiocarps. It is well known that in *Copri-*

mus the structural differences are greater (see among others Reijnders, 1979) and that one still has not succeeded in splitting up this genus in a satisfactory way. Especially in cases like the marasmiod fungi it would be of great value to know the development of more species. See also Kühner's observations on marasmiod fungi (1980: 735–763).

5. *Panellus mitis* has been studied in order to be able to compare the development of this species with that of *Tectella patellaris* (Fr.) Murr. We had the good luck to obtain primordia in all stages of the latter from the South of France. The results of our observations on the development of this rare and important species have recently been published (Reijnders, 1983).

There are certainly a number of resemblances between *Panellus mitis* and *Tectella* such as the character of the tramal hyphae (thick-walled, without strong inflation), the presence of the enveloping mucous layer and in the form and size of the spores. But the development is very different: in *Panellus mitis* stipitocarpous and gymnocarpous, from the beginning a continuous growth; in *Tectella* at least isocarpous and bivelangiocarpous with a primordium that remains short for a certain time, with a hymenium developing deeply internally, and with a veil that covers the hymenophore for a long time. Further observations are to be found in the above mentioned publication.

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REFERENCES

- CORNER, E.J.H. (1966). A monograph of cantharelloid Fungi. In Ann. Bot. Mém. 2.
KÜHNER, R. (1980). Les hyménomycètes agaricoïdes In Bull. Soc. linn. Lyon 49 (Num. spéc.).
REIJNDERS, A.F.M. (1952). Recherches sur le développement des carpophores dans les *Agaricales*. In Verhand. K. Nederl. Akad. Wetensch., afd. Natuurk., II 48 (4).
— (1963). Les problèmes du développement des carpophores des *Agaricales* Den Haag.
— (1979). Developmental anatomy of *Coprinus*. In Persoonia 10: 383–424.
— (1983). Le développement de *Tectella patellaris* (Fr.) Murr. et la nature des basidiocarpes cupuliformes. In Bull. Soc. mycol. France 99: 109–126.
ROMAGNESI, H. (1954). Compléments à la "Flore analytique". III. Espèces nouvelles, critiques ou rares, In Bull. Soc. Natur. d'Oyonnax 8: 73–167.
SINGER, R. (1975). The *Agaricales* in modern taxonomy, 3rd Ed. Vaduz.

EXPLANATION OF THE FIGURES

Figs. 1–6. *Hygrophoropsis aurantiaca*. — 1. Tip of youngest stage $\times 172$. — 2. Tangential section of cap and gills $\times 20$. — 3. Median section; older stage $\times 10$. — 4. Trama of young gill-fold $\times 223$. — 5. Palisade on upper part of stem $\times 203$. — 6. Surface of stem below palisade $\times 225$.

Figs. 7–10. *Hygrophorus pudorinus*. — 7. Rather young stage; median section $\times 10$. — 8. Margin of cap; young stage $\times 86$. — 9. Surface of stem and margin of cap of rather advanced stage $\times 86$. — 10. Surface of lower part of stem $\times 86$.

Fig. 11. *Hygrophoropsis aurantiaca*; longitudinal section of trama of older gill $\times 330$.

Figs. 12–16. *Tricholoma populinum*. — 12. Young stage $\times 86$. — 13. Margin of cap of somewhat older stage $\times 220$. — 14. Origin of margin of pileus in rather young stage $\times 105$. — 15. Upper part of older primordium $\times 20$. — 16. Gelatinized surface layer of cap of older stage $\times 220$.

Fig. 17. *Tricholoma ustaloides*; young stage with veil $\times 56$.

Figs. 18–21. *Tricholoma ustaloides*. — 18. Somewhat older stage $\times 70$. — 19. Origin of margin of cap in young stage $\times 340$. — 20. Somewhat more advanced stage $\times 56$. — 21. Margin of cap of more advanced stage $\times 170$.

Fig. 22. *Marasmiellus candidus*; origin of hymenophore in very young stage $\times 347$.

Figs. 23–26. *Tricholoma vaccinum*. — 23. Very young stage $\times 59$. — 24. Somewhat older stage with margin of cap $\times 72$. — 25. Margin of cap of more advanced stage $\times 226$. — 26. Upper part of primordium of more advanced stage $\times 71$.

Figs. 27–28. *Marasmiellus candidus*. — 27. Young stage $\times 213$. — 28. Rather young stage with veil $\times 138$.

Figs. 29–33. *Marasmiellus candidus*. — 29. Rather young stage (veil cast off) $\times 86$. — 30. Somewhat more advanced stage with last fragments of veil $\times 43$. — 31. Tangential section of a rather young stage $\times 213$. — 32. Young gill-fold $\times 259$. — 33. More advanced stage with beginning of one-sided development of cap $\times 35$.

Figs. 34. *Marasmius wynnei*; very young stage without differentiation $\times 86$.

Figs. 35–39. *Marasmius wynnei*. — 35. Very young stage with differentiation of margin of cap $\times 136$. — 36. Young stage (note rib below margin of cap) $\times 86$. — 37. Detail of preceding section $\times 345$. — 38. More advanced stage with two zones in trama of cap $\times 55$. — 39. Intermediate stage with margin of cap pressed against stem $\times 57$.

Figs. 40–42, 44–45. *Panellus mitis*. — 40. Very young stage (gelatinized coating reaching up to half-way) $\times 86$. — 41. Young stage with gelatinized layer enveloping whole primordium $\times 43$. — 42. Distal part of somewhat older stage $\times 86$. — 44. Advanced stage with hymenium at distal end $\times 87$. — 45. Median section of advanced stage $\times 12$.

Fig. 43. *Marasmius wynnei*; detail of margin of pileus and rib below margin $\times 340$.















