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THE DEVELOPMENT OF THE FRUIT-BODY OF MARASMIUS CORNELII (AGARICALES) AND OF A NEW SPECIES OF MARASMIUS SECT. GLOIOCEPHALA

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The gymnocarpic development of the very small and gill-less fruit-body of *Marasmius cornelii* is directed by intrinsic factors until the lengthening stem becomes geotropic. The primordium is covered from a very early stage by a hymenioderm of clavate encrusted cells with a few lanceolate pileocystidia; the smooth clavate cells are a later development from the marginal growth of the pileus. The intercalary formation of the stem separates the pileus from the basal disc which acts as a turgid cushion supporting the stem round its insititious base. The hymenium is microscopically collariate. The Malayan *M. poculiformis* spec. nov. develops in the same way but lacks the basal disc to the stem which lengthens by secondary septation of its hyphae.

When studying recently my collections of Malesian *Marasmius*, I came upon my drawings of a species of sect. *Gloiocephala* (Mass.) Jansen & Noordeloos (Noordeloos, 1981), here described as *M. poculiformis* spec. nov. I was returned to a much earlier study which I had made of the species now known as *M. cornelii* Laessøe & Noordel. (Noordeloos, 1987). In 1927 I had studied it in great detail under the mistaken name of *M. menieri* Boud., and it seems helpful to publish my account along with the original illustrations. They reveal the precision with which the agaric properties of *Marasmius* are inherited in a very reduced state and without any evident means of direction. The general features of the mature fruit-body have been illustrated by Bas (1961) and by Laessøe & Noordeloos (l.c.). My account can be compared with the similar development of *M. rotula* investigated by Kühner (1933) and the microphotographs of *Marasmiellus candidus* and *Marasmius wynnei* given by Reijnders (1983). He calls the development paravelangiocarpic but, for me, it is gymnocarpic.

Development of the fruit-body

The fruit-bodies, with mature pileus up to 6 mm wide and stem up to 10 × 0.8 mm, develop from the outer surfaces of the dead leaf-sheaths of *Cladium mariscus* (Cyperaceae), which are retained upright round the massive rosettes of this sedge; occasionally the fruit-bodies may form in the horizontal cut edges of the dead leaf.

The first indication of the fruit-body is a minute mass, 80–120 × 70–100 µm, of contiguously interwoven, thin-walled and clamped hyphae 2–4 µm wide, situated a few cell-

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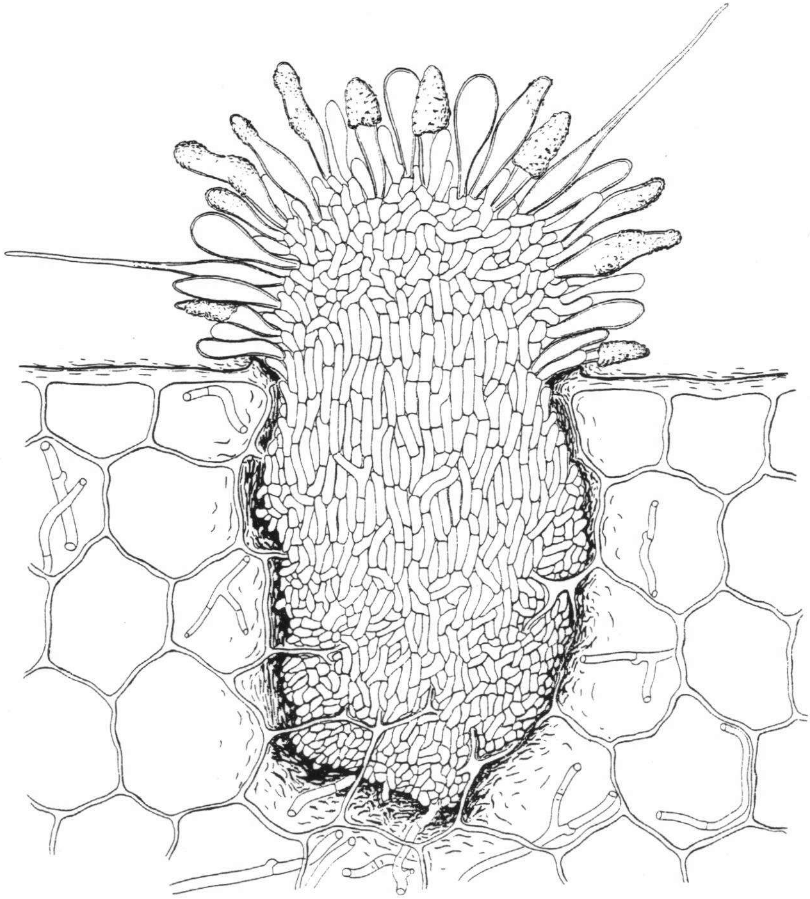

Fig. 1. *Marasmius cornelii.*—The primordial knob on the sedge-leaf, × 500.

layers below the surface of the leaf-sheath. This dense knot of hyphae becomes the plug or insititious base which holds the fruit-body in position. Then, the hyphae on the outer and, perhaps, more illuminated side of the knot grow into line as a minute primordial shaft to make the beginning of the stem. It bursts the dead epidermis of the leaf-sheath and proceeds to form a minute knob which is the hemispherical primordium c. 150 × 130 μm. There is no further apical growth of this primordium but the end-cells of all the superficial hyphae transform into rather thick-walled and encrusted, more or less clavate cells 20–30 × 6–12 μm; a few lengthen into a filiform process and take the form and size of the ventricoso-filiform pileocystidia of the mature pileus. All these end-cells proceed to lobe subterminally and develop more clavate and ventricose cells which cover the whole surface, but these additional clavate cells are more regular in form and not encrusted. They make eventually the mature hymenioderm in which the original encrusted cells become widely scattered and easily overlooked in

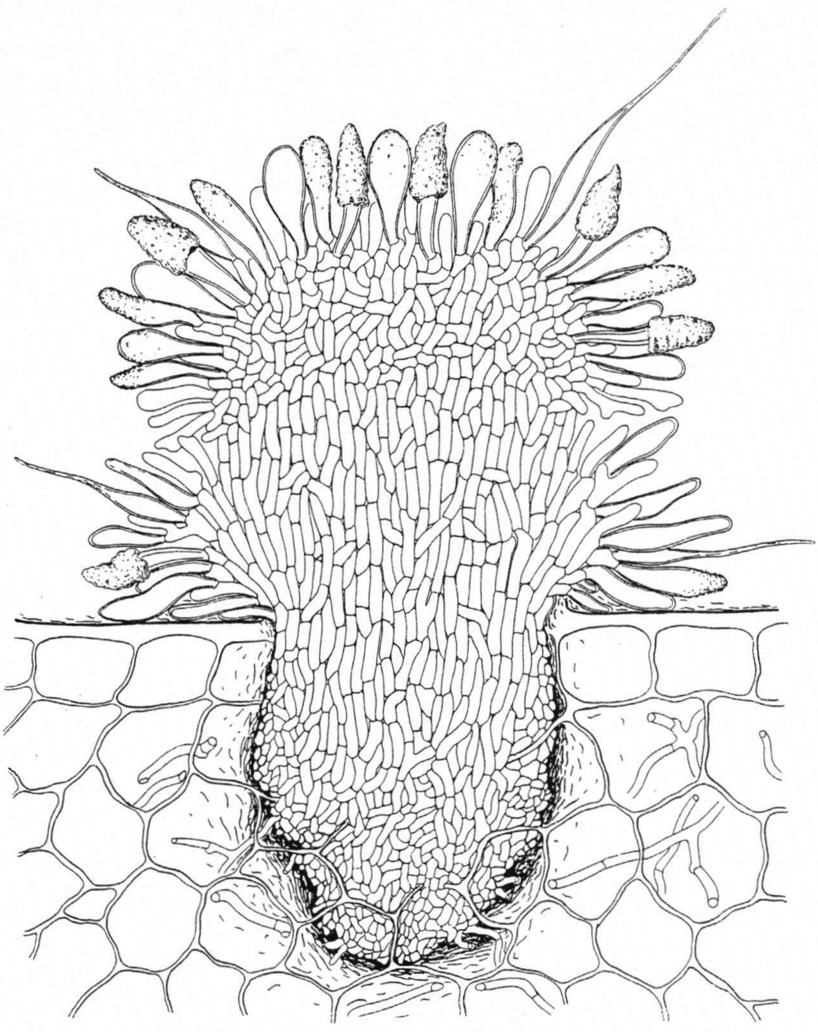

Fig. 2. *Marasmius cornelii.*—The primordium as the stem begins to separate the pileus from the basal disc, × 500.

the central part of the pileus. At the same time, the narrow hyphae of the internal tissue are multiplying by branching and their cells begin to lengthen (Fig. 1).

The next stage in development is revealed by a slight groove which encircles the primordium transversely and divides it into a proximal half, which becomes the basal disc of the stem, and a distal half which becomes the pileus. The groove is caused, evidently, by the incipient elongation of the stem-region (Fig. 2). The internal tissue continues to straighten and enlarge its cells and to fill any gap that might appear with hyphal branches.

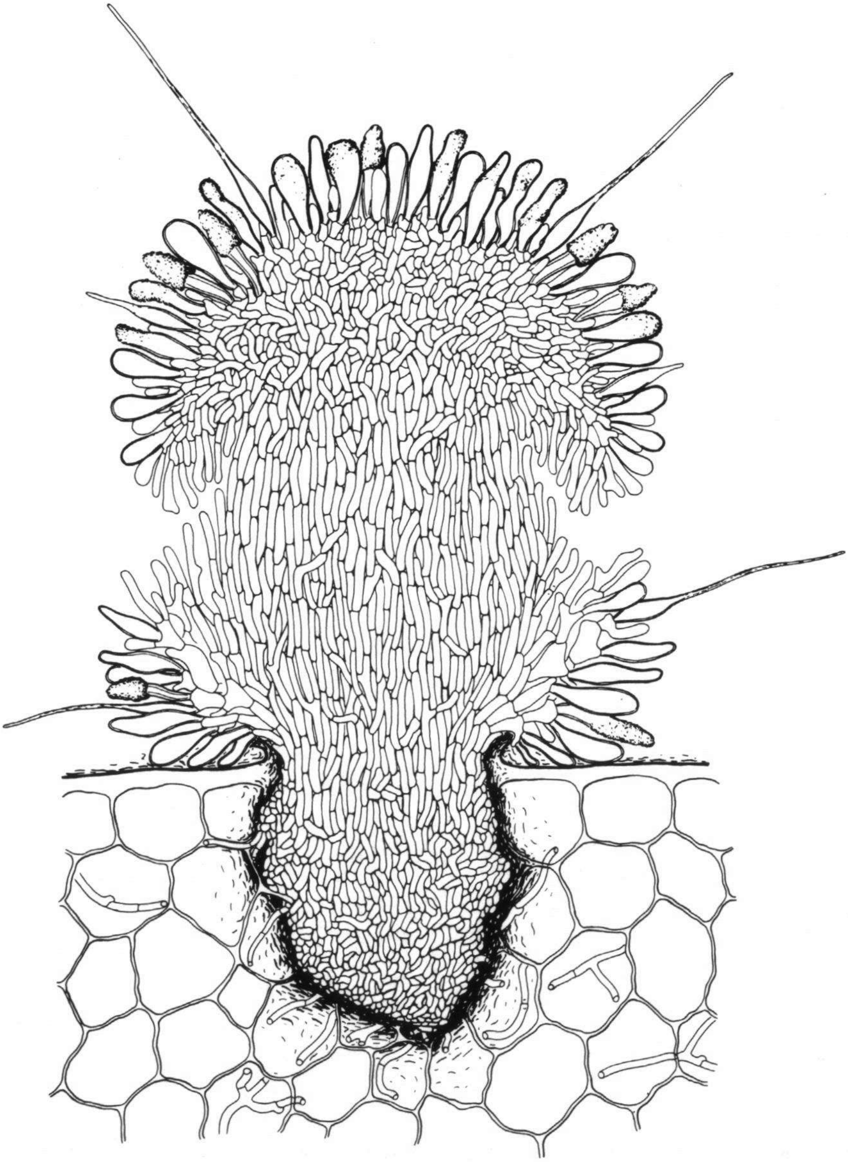

Fig. 3. *Marasmius cornelii.*—The primordium with marginal growth of the pileus beginning and hyphae beginning to grow up the stem from the basal disc, × 500.

A later stage (Fig. 3), c. 250 × 200 μm, shows clearly the four parts of the fruit-body, namely the plug, the basal disc, the stem and the pileus. Marginal growth has begun round the periphery of the pileus and the disc, and hyphae have begun to grow up the outside of the stem from its junction with the disc. The subterminal cells of the disc have begun to enlarge, unlike those over the pileus; thus, from a very early stage, the projecting and commonly horizontal young fruit-body has a secure and resilient base. In other respects, the disc and incipient pileus are similar, opposing each other and more or less parallel with the support, not orientated geotropically but, possibly, subject to different illumination.

Marginal growth

Enlargement of the pileus continues with intercalary growth in the original and, now, central palisade of clavate cells and by marginal growth which produces both the hymenium on the side towards the stem and new palisade tissue on the outer side. Marginal growth is first directed towards the basal disc but soon becomes transverse as the hymenium forms. Lateral hyphae on the side next to the stem lengthen for a few cells when their terminal cells become the first basidia. Abundant intercalation of basidia, sympodially from the subterminal cells, forces the margin of the pileus outwards; it never becomes incurved either by the lateral pressure of the palisade or by any inflation of the inner hyphae. At this narrow margin there is a precise distinction. Hyphal ends on the side away from the substratum become palisade cells or ventricose pileocystidia while those on the side towards the substratum become basidia;

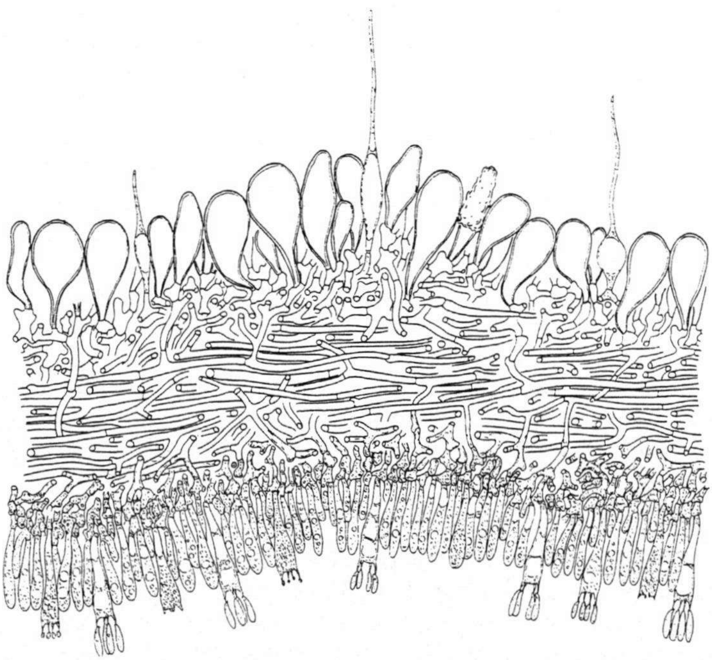

Fig. 4. *Marasmius cornelii.*—The limb of the mature pileus in radial section, × 500.

their separation is merely the width of two or three hyphae and at this very narrow periphery the hyphal ends extend and proliferate. It seemed that few of these ongoing hyphal ends continue for more than two or three cells before they become deflected into the palisade or the hymenium and that a lateral from them continues the marginal growth. A radial section of the mature pileus (Fig. 4) gives the impression of having been constructed by marginal hyphae with continuous monopodial growth; their cells have lengthened without inflation but it seems that they are the outcome of sympodial growth.

The hyphae in the flesh of the mature pileus become subgelatinous. The subhymenium, 5–10 μm thick and composed of interwoven hyphae, is much denser than the corresponding layer on the upper side of the pileus because fewer of the wider clavate cells are intercalated than basidia. The young basidia are subacerose, as general in *Marasmius*.

Stem

The cells of the stem-region continue to inflate, mostly up to 10 μm wide but some up to 20 μm, and their cells lengthen up to 170 μm with broad septa. They form a wide cylinder of longitudinal and contiguous hyphae except for a narrow central strand of rather loose and uninflated hyphae. This motor tissue which projects the pileus evidently becomes negatively geotropic in the distal part of the stem and curves the pileus into the horizontal position. Sometimes the apical curvature in pilei which have been projected horizontally or obliquely is so strong that it rotates the pileus on to the upper side of the stem and its weight seems to cause the distal part of the stem to sag (Fig. 5); along this line of contact and pressure, the hymenium fails to develop and, likewise, the caulocystidia.

The hymenium is not in any degree decurrent on the stem; a slight ring of shortly descending and uninflated sterile hyphae separates it from the stem-apex and is, in fact, a trace of the collar of such species as *M. rotula*.

The caulocystidia arise from the outer uninflated hyphae of the stem, many of which have grown up from the base of the primordial stem and with shorter cells, 20–50 μm long, have not contributed to the motor tissue. The process is acropetal; the caulocystidia are best developed near the base of the stem and become progressively fewer and smaller distally; at the stem-apex they are lacking or reduced to mere bulges.

In the case of the Malesian *M. poculiformis* there is some secondary septation in the cells at the stem-apex and this, with its added cell-extension, may achieve the geotropic curvature (Fig. 7). Such septation may have escaped my notice in the early study of *M. cornelii*.

Since the hyphae are contiguous in the cylindrical stem, how many there are can be reckoned from the average hyphal width and their number as seen in a median longitudinal section of the stem. I concluded that there were c. 300 in the primordial stem and c. 1000 in the mature stem.

Basal disc

This slight cushion reaches 300–800 μm wide. It has the structure of the surface of the pileus except that the cells of the hypodermal tissue inflate 10–25 μm wide without much elongation (Fig. 6). The walls of the compact hyphae which connect as a strand with the plug, thicken rather strongly and form a taut cable which holds the fruit-body against the basal cushion. These hyphae have somewhat elongate cells but are not sarcodimitic.

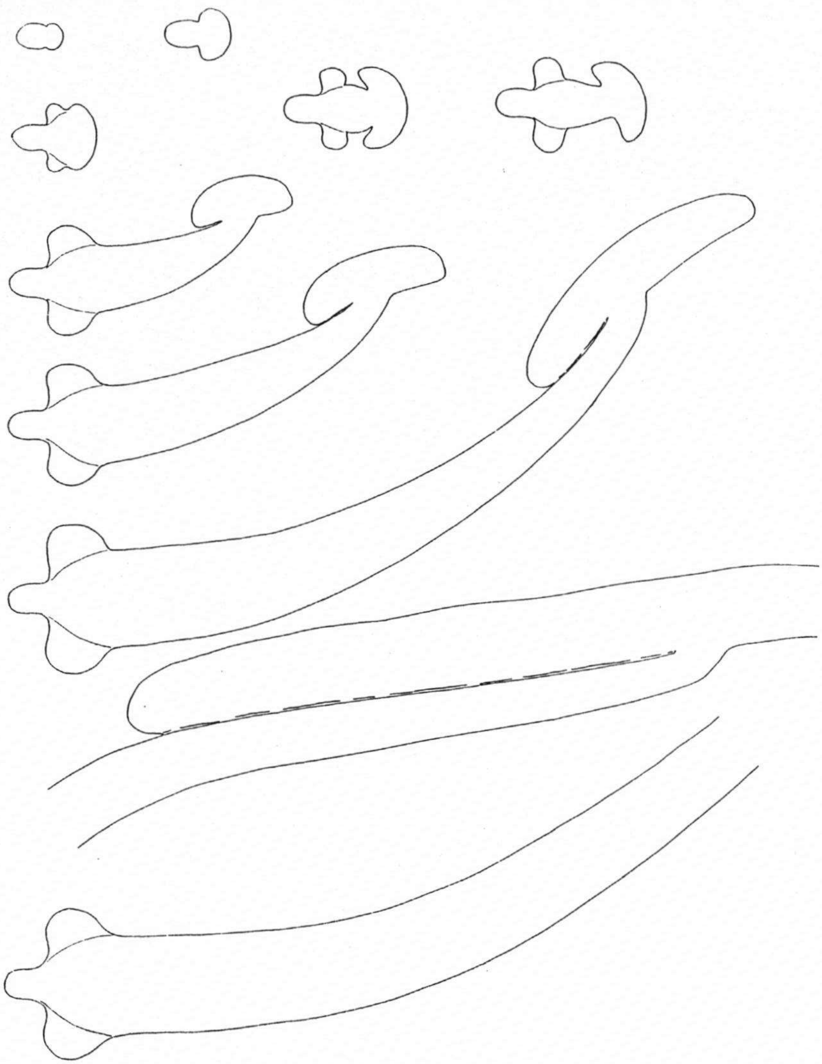

Fig. 5. *Marasmius cornelii.*—Developing fruit-bodies in longitudinal section, showing the pileus lying on the stem, × 50.

Veil

Usually there is no sign of a veil but in one primordium the superficial hyphae of the stem grew over the incipient hymenium and shortly over the margin of the pileus 1 mm wide, giving the appearance of a slight veil.

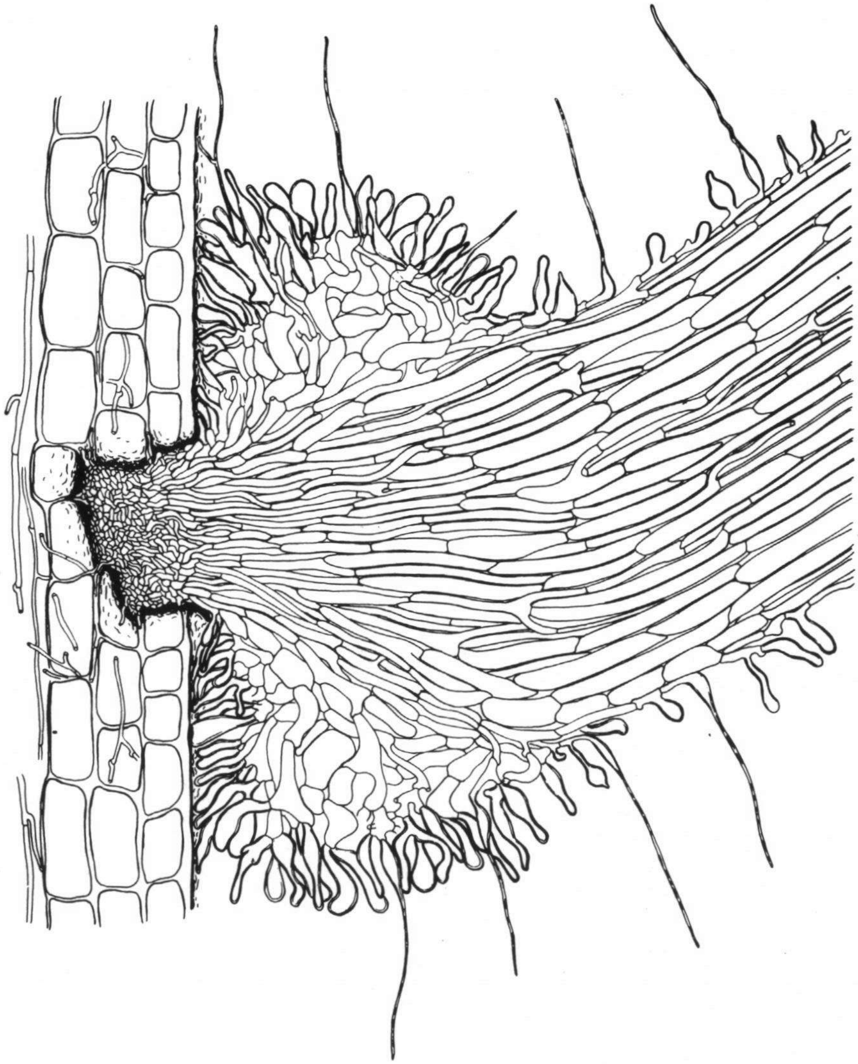

Fig. 6. *Marasmius cornelii.*— The mature basal disc in longitudinal section, × 250.

Duration and decay of the fruit-body

The fruit-bodies, according to their size, take 7–10 days to develop from the first visible primordium. Elongation of the stem takes 2–3 days after which the fruit-body persists for 5–21 days at 20°C, provided that the atmosphere is more or less saturated; dried fruit-bodies do not recover. Sporing begins when the pileus is merely 0.8–1 mm wide, before the stem is fully elongated, and may thus continue for 3–4 weeks. In the more or less saturated atmosphere there is much guttation from the ventricose-filiform cystidia on stem and pileus; presumably, much water passes along the stem and the guttation helps to keep the immediate atmosphere saturated. Eventually, the effete hymenium disintegrates and is dissolved by bacteria whereon the palisade layer, still turgid on the pileus, causes it to curl in upon the stem which collapses.

CYTOLOGY

All cells of the fruit-body are at first binucleate. The elongated cells of the stem and some of the clavate cells on the pileus become multinucleate. Nuclear fusion occurs in the proximal third of the basidium and meiosis transversely in the distal third. The spores are uninucleate. The chromosomes were too small to be counted.

Marasmius poculiformis Corner, *spec. nov.*—Fig. 7

Pileus 1–5 mm latus, convexus subacutus dein concavus cyathiformis vel infundibuliformis, laevis vel in centro leniter ruguloso-reticulatus, sparsim puberulus sed marginem versus ciliatus, albus dein cremeicolor subtranslucidus. Stipes 4–15 × 0.1–0.35 mm, centralis capilliformis corneus, basi abrupto insititio, brunneolus albipuberulus, apice glabro albo, dein e basi fuscescens. Lamellae nullae, hymenio laevi vel prope stipitem vix plicato-reticulato, albo dein cremeo. Caro 100–150 μm crassa. Odor nullus.

Sporae 9–12 × 3–4 μm, albae laeves fusiformes aguttatae. Basidia 22–34 × 6–8 μm, basidiolis subacerosis; sterigmata 2–4, 3–5 μm longa. Cystidia nulla. Caulocystidia -90 × 1.5–2.5 μm ad basim, filiformia simplicia vel raro ramis brevibus 1–2, ad apices 0.5–1 μm latos attenuata, tenuitunicata sed basim stipitis versus tunicis subincrassatis flavibrunneis, laevia. Superficies pilei cellulis subglobosis vel clavatis 20–60 × 7–55 μm laevibus, tunicis hyalinis vel flavibrunneis subincrassatis obtecta, etiam cellulis clavatis 7–15 μm latis tunicis 1–2 μm crassis aliquando brunneo-incrustatis dispersis. Pileocystidia 60–120 × 10–18 μm, marginem pilei versus -350 × 12–20 μm, ventricoso-fusiformia, ad apices 1.5–2.5 μm latos obtusos vel subacutos attenuata, hyalina raro ad basim tunicis brunneolis. Hyphae in pileo 1.5–3 μm latae, fibulatae, tunicis submucilaginosis; in stipite 8–20 μm latae, cellulis 30–350 μm longis, apicem stipitis versus ordine secundo septatae; ad stipitis superficiem 2–5 μm latae, tunicis brunneis -1.5 μm incrassatis, agglutinatae.

Ad ramulos corticesque emortuos foliaque dejecta gregarius in silva. Peninsula Malayana vulgaris.

Typus in herb. Corner, Singapore Botanical Garden, *E.J.H. Corner s.n.*, 19 Feb. 1935, etiam 27 July 1940.

This is near to *Gloiocephala albocapitata* (Petch) Singer of Ceylon (Pegler, 1986), but *Marasmius poculiformis* has no gills at all, much larger clavate cells on the pileus and no wide thick-walled cystidia. I cannot equate it with any of the species of *Discocyphella* to which Singer (1952) refers. In general form, the fruit-body resembles that of *Trogia aphylla* (Corner, 1966).

The fruit-body develops in the same way as in *Marasmius cornelii* except that no disc forms at the base of the stem and there is a considerable amount of secondary septation of the hyphae in the stem-apex. The primordial pileus is covered with a palisade of small clavate cells with thickened brown walls, among which there are a few pileocystidia. When marginal growth of the pileus is established, the larger and thin-walled clavate cells are copiously intercalated and the original small ones become widely dispersed, even concealed, as happens in various species of *Marasmius*. The slight hymenial collar is tightly pressed round the stem-

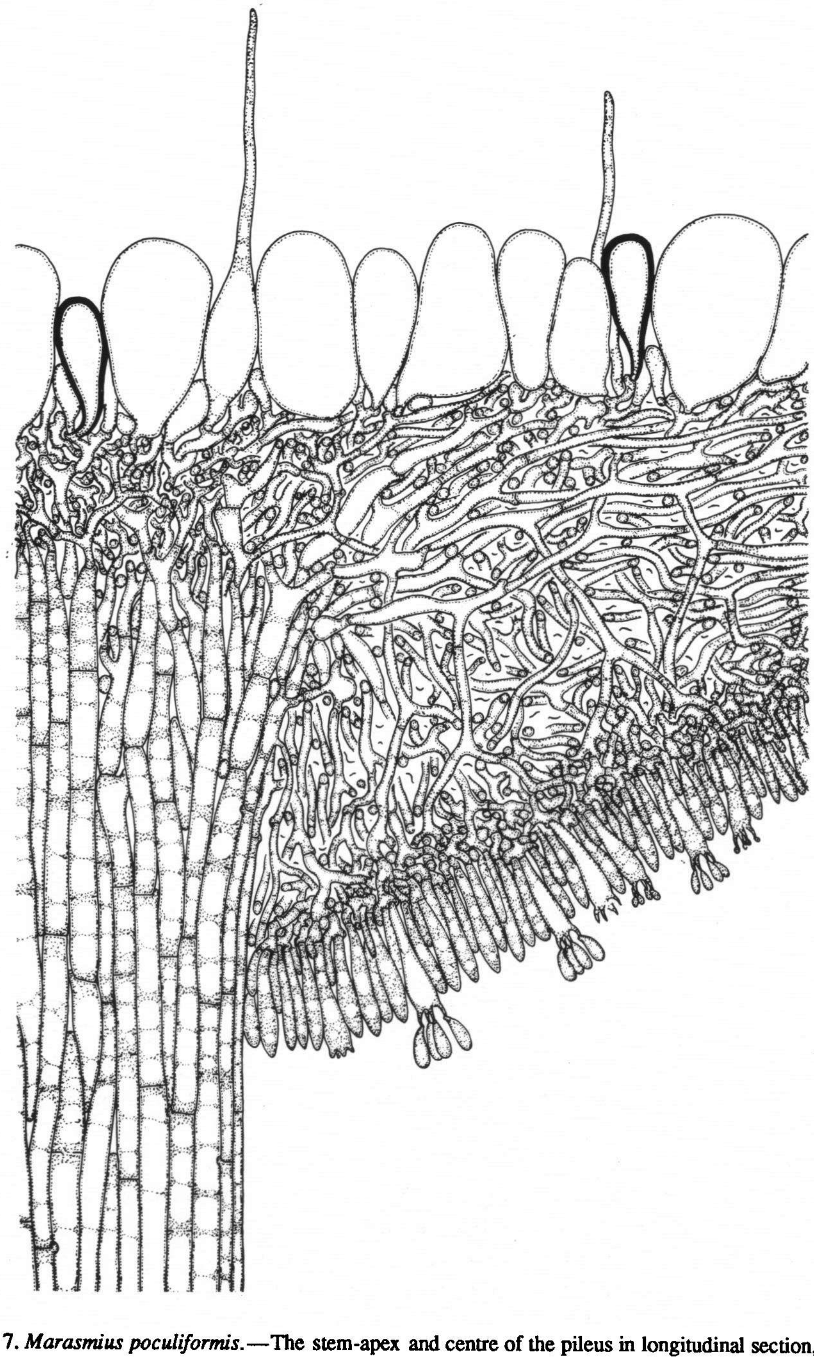

Fig. 7. *Marasmius poculiformis*.—The stem-apex and centre of the pileus in longitudinal section, × 500.

apex and in the expanded fruit-body is recognisable only on sectioning the pileus when it can be seen that the flesh between the stem-apex and the palisade of the pileus is 70–120 μm thick and the depth of the collar is 150–250 μm. As often is the case among tropical *Marasmius*, the fruit-body does not begin to spore until it is nearly fully grown.

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