A *FOMES* WITH TWO SYSTEMS OF HYPHAE

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(With 13 Text-figures)

Of the five systems of hyphae in the fruit body of *Polystictus xanthopus*[*] only the skeletal, binding and generative systems are characteristic; they are the result of division of labour in the common arrangement in which all the hyphae having the same structure and function belong to one system. For, of the other two, that of the mycelium must occur in all, and a skeletal system implies a mediate, though it vary in extent as the transition from generative to skeletal hyphae is gradual or abrupt. It is convenient for comparison to say thus that such a fruit body is composed of three systems of hyphae, or that it is *trimitic* (μίτος, a thread of the warp). Similarly the species of *Fomes* which I have now examined, has but two systems (*dimitic*) and in this respect is at a lower level of evolution; it has skeletal and generative hyphae essentially as in *P. xanthopus*, but a binding system is not differentiated.

The dimitic construction seems to be general in the section of *Fomes* with brown woody flesh, and I have observed it in *F. rimosus*, *F. pectinatus*, *F. senex*, *F. setulosus*, *F. lamaensis* and *F. pachyphlöeus*. The trimitic construction is characteristic of the coriaceous species of *Polystictus* and, perhaps, of the corky and felted fruit bodies of *Trametes*, *Hexagonia* and *Daedalea*, but no classification is discriminating enough for a definite statement, and both kinds, in addition to the ordinary *monomitic* construction, are to be met with in *Polyporus*.

The species described in this paper has been fruiting for the past two years on a log in the Singapore Botanic Gardens, and the opportunity of investigating the structure and biology of a *Fomes* with such abundant material close at hand was not to be missed. But I find it must be described as new. It is very like *F. senex* and *Polyporus gilvus* but it has distinctive microscopic features, which will be considered at length at the end of the paper along with the related species. It does not appear to be common in Malaya though widespread in the lowland forest.

In the text-figures, the indurated yellow-brown walls of the hyphae, so characteristic of this section of *Fomes*, have been drawn as thick black lines, and by this means the skeletal hyphae are easily distinguishable from the generative. Where the lumen of a skeletal

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hypha has disappeared through the thickening of the wall, the hypha has been drawn naturally as a black rod.

To investigate the hyphal system in dried herbarium material the best method is to mount the sections in dilute potash (5 per cent.). The thin-walled hyphae, which have collapsed in the drying, are swollen out to their natural size and the thick-walled yellow-brown elements are rendered more conspicuous by turning to a very dark colour.

Fomes levigatus, n.sp.

Pileus *sessilis*, basim versus saepe angustatus sed raro substipitatus, *applanatus*, vix ascendens, dimidiatus, plerumque postice breviter resupinato-effusus, rigidus, antice subvelutinus dein *levigatus*, *impolitus aut subnitidus*, in *senectute postice subtuberculatus*, vix sulcatus, *haud zonatus*, raro subzonatus, *laete castaneo-brunneus demum umbrinus*, siccus cinnamomeo-umbrinus, usque 7·5 cm. radio, 13·5 cm. latus: *margine* obtuso raro subacuto, velutino, *laete aureo-fulvo.*

Substantia paullum crassa, lignosa, vix suberosa, *saturo fusco-ferruginea*, sicca dura et cinnamomeo-brunnea, postice 2–9·5 mm. crassa, 5 mm. de margine 1–4 mm. crassa: *crusta superficiali* tenui, *coriacea*, *fusca*, nec nigra nec carbonacea, demum usque 800 μ crassa, praedita.

Tubuli *breves*, *fusco-ferruginei*, postice 2–2·5 mm. longi, 5 mm. de margine 0·3–0·5 mm. longi: *poris minutis*, rotundis, velutinosis, *fusco-ferrugineis*, 65–95 μ latis, dissepimentis 30–75 μ crassis.

Sporae *albae*, ellipsoideae, unilateraliter applanatae, leves, tenuiter tunicatae, intus gutta una parvula 0·5 μ lata praeditae, 3·5–4 × 2·5 μ.

Basidia subcylindrica, tenuiter tunicata, intus vacuolata, 9–11 × 3–4 μ: sterigmatis 4, 1·5–2 μ longis.

Cystidia vix numerosa, parva, subventricosa aut subcylindrica, hyalina, tenuiter tunicata, intus vacuolata, apicibus attenuatis acutis filiformibus saepe setis connitentibus, 16–25 μ longa, 2–3·5 μ lata, apicibus 1 μ latis.

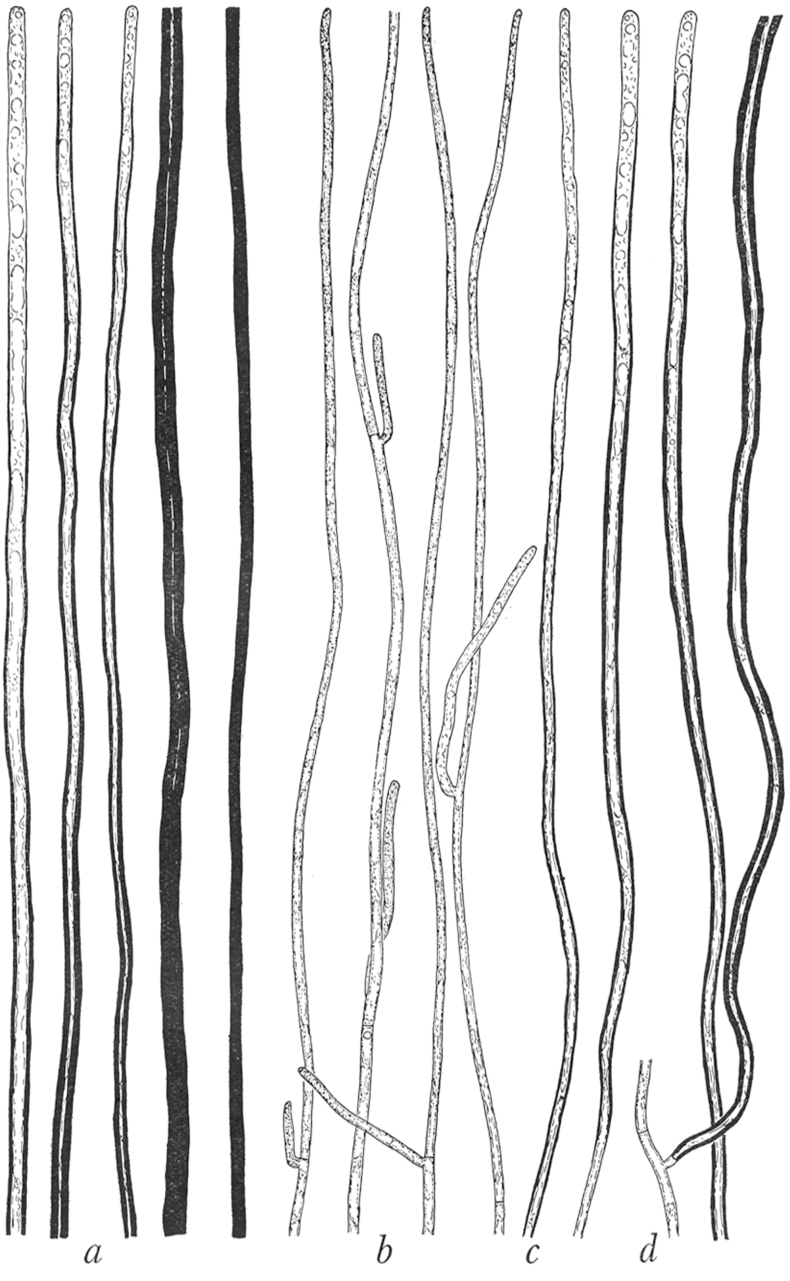
Setae numerosae, conicae, subventricosae, crasse tunicatae, fusco-ferrugineae, apicibus pallidis vel hyalinis acutis rectis, 13–26 × 5–7 μ.

Hyphae skeletales *crasse tunicatae*, *aseptatae*, *haud ramosae*, parietibus laete ferrugineis 1–2 μ crassis praeditae, luminibus plus minus occlusis, 3–5 μ latae.

Hab. ad truncos emortuos, pileis imbricatis saepe lateraliter conjunctis, Malaya (Singapore, Johore, Penang, Perlis).

Singapore Field No. 23709, from the Botanic Gardens, is the type collection. Sing. F. No. 5619, det. C. G. Lloyd as *Polyporus carneo-fulvus* Berk., belongs to this species.

The colour of the fresh pileus is a rich burnt umber becoming dark umber when old and cinnamon-bay when dry: the flesh is dark rich ferruginous: the pores and tubes are dark date-brown.



Text-fig. 1. *F. levigatus*. *a*, skeletal hyphae; *b*, generative hyphae; *c*, a mediate hypha; *d*, three skeletal hyphae at their origin from mediate and generative hyphae. × 500.

SYSTEMS OF HYPHAE

Skeletal hyphae: 3–5 μ wide, cylindric, *unbranched*, *aseptate*, often flexuous, sometimes curled or kinked, rarely with short spine-like projections (up to 10 μ long), *radiating* though often oblique, with smooth *dark yellow-brown walls*, 1–2 μ thick, and narrow lumen becoming linear or occluded in old parts: growing apices pale yellowish or colourless, cylindric, rounded, obtuse, thin-walled, not tapering (Text-fig. 1 *a*).

The walls of the skeletal hyphae stiffen about 10–25 μ behind the apex, and at 30–50 μ back the wall is about 0·5 μ thick, whence it gradually thickens, and at 100–200 μ back it is about 1 μ thick. The walls are often slightly and irregularly wavy owing to unequal thickening. The contents of the hyphae at the apex appear very viscous, smeary colloidal, with numerous small vacuoles.

Generative hyphae: 1·5–3 μ wide, cylindric, *branched*, *septate without clamps*, with thin colourless walls or more usually with the walls firm, very slightly thickened, pale yellow or brownish and often slightly wavy as those of the skeletal hyphae: radiating or interwoven, sparingly or frequently branched, the branches often growing parallel with the parent hypha for some distance: apices obtuse, thin-walled, colourless, full of dense protoplasm rather more fluid than in the skeletal hyphae: septa at intervals of 25–300 μ, mostly 50–180 μ, but very variable: H-connections frequent (Text-figs. 1 *b*; 2 *c*, *d*).

The walls of the generative hyphae remain thin for some distance behind the apex and first begin to stiffen about 100–200 μ back. In the old parts of the flesh, especially just above the tubes, the walls may become as much as 1 μ thick.

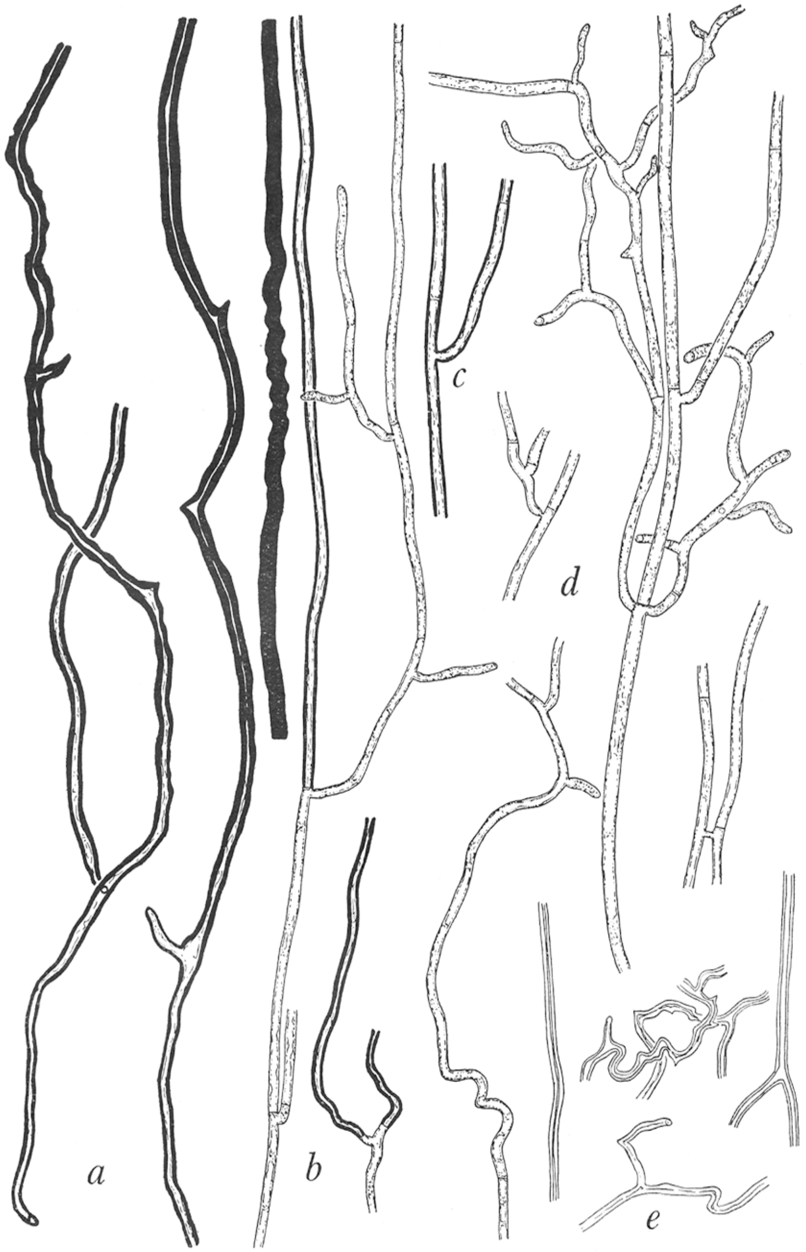
Mediate hyphae: 2·5–3·5 μ wide, cylindric, rarely branched, rarely septate, radiating or oblique, often flexuous or kinked, with pale yellow-brown walls *ca.* 0·5 μ thick (Text-figs. 1 *c*; 2 *a*).

The apices are similar to those of the generative hyphae, but the wall begins to stiffen and colour up at 35–100 μ from the apex.

Mycelial hyphae: 1–2 μ wide, very fine, branched, septate, without clamps, straight or flexuous, often subnodular, with thin colourless hyaline walls, sometimes slightly thickened and yellowish in the old hyphae.

Stuffing hyphae: 1·5–2·5 μ wide, *narrow*, rather sparingly branched, *aseptate*, with thin nearly colourless or more or less strongly thickened and pale yellowish walls, sometimes nearly solid, often flexuous, nodular or kinked but mostly stiffly straight (Text-fig. 2 *e*).

These hyphae occur only in the old tubes the effete portions of which they fill in with a pale yellow wadding. They are derived partly from the generative hyphae of the dissepiments, but mostly, it seems, from the mycelium. In many species of *Fomes* and *Ganoderma*



Text-fig. 2. *F. levigatus*. *a*, mediate hyphae; *b*, mediate hyphae at their origin from generative hyphae; *c*, a thick-walled generative hypha from the oldest tissue of the pileus; *d*, thin-walled generative hyphae from near the margin; *e*, stuffing hyphae. × 500.

the mycelial hyphae grow into the old flesh from the base of the fruit body and cause a partial or complete autolysis of the original tissue, the hyphal walls being eroded in the same way as in the starved fruit bodies of *P. xanthopus*, and eventually they form fairly conspicuous white or yellowish strands and penetrate into the tubes. In *F. levigatus* the strands are poorly developed and there is little autolysis: the mycelial hyphae are not characteristic and it is impossible to trace them individually through the tissue.

INTERRELATIONS OF THE HYPHAE

The origin of the skeletal hyphae from the generative hyphae can be observed directly in this species, since the transitional region is short, and need not be inferred as in *P. xanthopus*. The generative hyphae lose the power of septation, become rather thick-walled and stop branching. They thus become mediate hyphae. Their apices then enlarge slightly and the wall thickens more strongly and they become skeletal hyphae. The transition may be effected in as short a distance as 50 μ, when the skeletal hyphae practically arise directly from the generative hyphae, as in Text-fig. 1 *d*, but more frequently in a distance of 100–300 μ, as in Text-fig. 2 *a*, *b*. Sometimes it seems that the mediate hyphae may grow for several millimetres before becoming skeletal elements, and possibly some persist indefinitely in this state. Similarly it appears that the transition from generative to mediate hyphae may be delayed because elements with the appearance of narrow, distantly septate mediate hyphae may occasionally be seen.

The skeletal hyphae always arise at the growing margin of the bracket. Though I searched carefully, I found no evidence that laterals of the generative hyphae in the mature flesh ever became mediate or skeletal elements in the manner of origin of binding hyphae.

The skeletal hyphae of the dissepiments also arise from the generative hyphae, but apparently without mediate elements. However, it is difficult to trace their origin owing to the very intricate growth of the hyphae in that part of the flesh which overlays the tubes.

THE STRUCTURE OF THE MATURE TISSUES

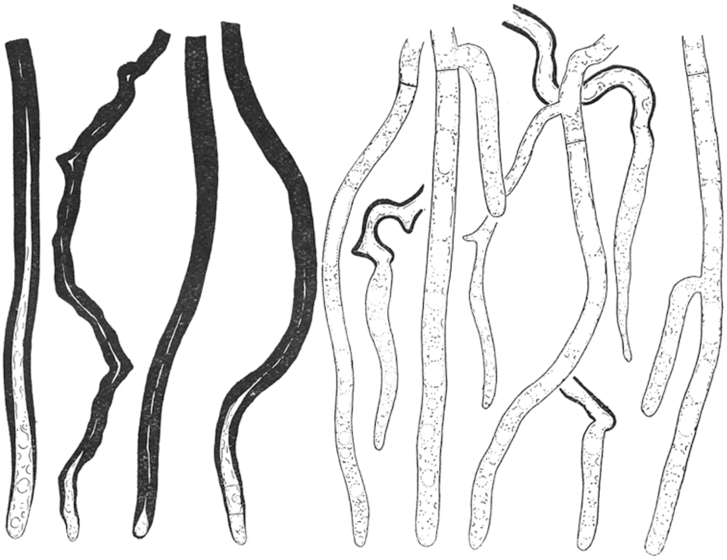
The mature flesh is composed of fairly closely interwoven skeletal and generative hyphae. Their direction is chiefly radial but many pass transversely, or obliquely, to the upper and lower surfaces, or even occasionally backward, so the texture is felted rather than fibrillar. Immediately above the tubes the tissue is denser on account of the profuse branching of the generative hyphae which takes place in this region near the margin of the pileus.

On the upper side of the pileus there is a thin crust which is often scarcely visible to the naked eye, though its presence might be guessed from the peculiar dull, smooth appearance of the surface. It is about 20–30 μ thick at a distance of 1–2 cm. from the margin, and at the base of the pileus it may be as much as 800 μ thick. It is composed of very intricately and irregularly interwoven, contiguous generative hyphae with slightly thickened pale yellowish or brownish, agglutinated walls without air-spaces between them. The ends of the skeletal hyphae project shortly—up to 30 μ—into the crust, and here and there embedded in the thicker parts are short flexuous skeletal hyphae up to 200 μ long, orientated more or less vertically, and scattered singly or in small groups. The walls of the generative hyphae never become dark brown or carbonaceous, so that the crust is rather soft and leathery and not of the hard, black, stony consistency which is usual in *Fomes*.

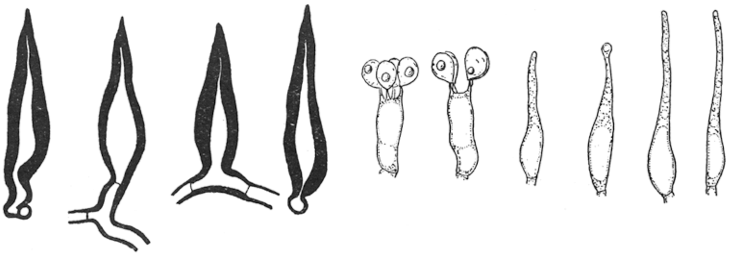
Text-fig. 3. *F. levigatus*. The crust on the upper side of the pileus about 1 cm. from the margin. × 500.

The dissepiments are composed of compact skeletal hyphae with longitudinal and interwoven generative hyphae among them. At the ends of the dissepiments the hyphal apices form a regular palisade and are not turned aside as in *P. xanthopus*. The skeletal hyphae of the dissepiments differ in some minor points from those of the flesh. They are narrower, being 2–3 μ wide, more or less strongly flexuous, frequently kinked and nodular, and their walls thicken nearer to the apex. Thus, in newly formed dissepiments up to 200 μ long, the walls begin to thicken about 10 μ from the apex and are completely thickened with the lumen linear or wholly occluded at 50–100 μ back: in older dissepiments of slower growth the walls begin to thicken at 2–8 μ from the apex and are fully thickened at 10–30 μ back: while in some specimens, in which growth has probably ceased, however, even the apex itself is slightly thick-walled. A few of these hyphae also have 1–3 septa at the apex, but they are soon re-absorbed, as in

P. xanthopus (cf. Text-fig. 4). The narrowness and dense arrangement of these nearly solid, dark yellow-brown skeletal hyphae not only cause the colour of the tubes to be considerably deeper than that of the flesh, but make them harder and woodier. The generative hyphae are affected in a similar manner. At the base of the dissepiments, where they descend from the flesh, the generative hyphae may have their walls so much thickened that the lumen is nearly obliterated, and being interwoven and subnodular they thus have incipiently the character of binding hyphae.



Text-fig. 4. *F. levigatus*. Skeletal hyphae from the ends of the dissepiments and generative hyphae from the pore field. × 1000.



Text-fig. 5. *F. levigatus*. Setae, basidia and cystidia. × 1000.

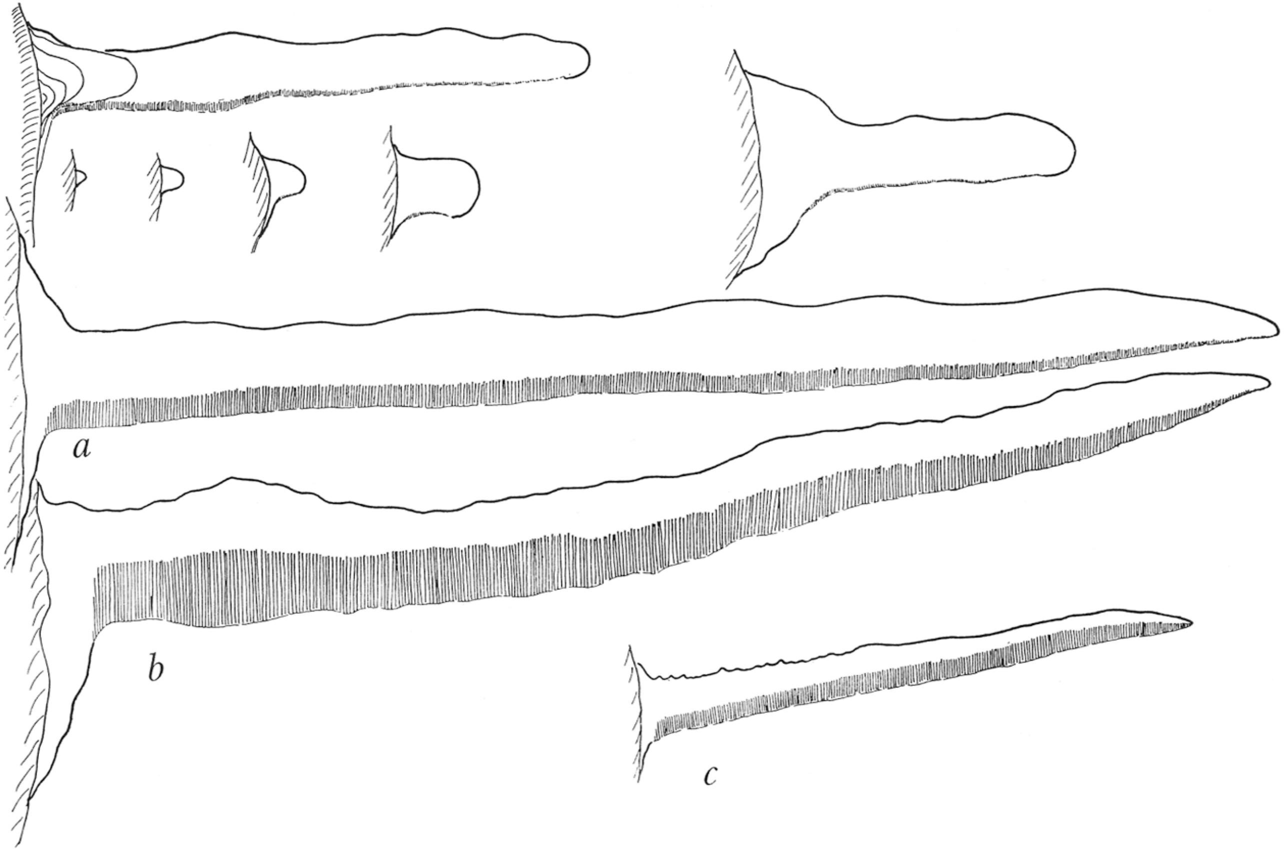
The hymenium is continuous over the dissepiments down to a distance of 30–100 μ from the pores. The subhymenium is very slightly developed, 1–2 hyphae thick, and consists of colourless, thin-walled generative hyphae, 1–2·5 μ wide: it is best developed over the upper ends of the tubes. The setae arise at the ends of thick-walled generative hyphae, while the true cystidia arise as the basidia from thin-walled, colourless generative hyphae.

Basidia begin to mature almost as soon as the downgrowth of the dissepiments has started, but in the longer tubes the hymenium is fertile only for a distance of ½–1 mm. from the pores. The upper parts, as already described, are filled in by the stuffing hyphae, and the old basidia, instead of collapsing and disappearing, develop slightly thickened, pale yellowish walls and become cemented together to form a pavement-like layer: the hymenium thus persists long after it is functionless. The same can be seen also in many other species of *Fomes.*

THE DEVELOPMENT OF THE FRUIT BODY

As in *P. xanthopus* the primordium first appears as a small fleck on the wood and rapidly enlarges into a hemispherical body, 1–6 mm. high. It is a bright tawny yellow and is composed of skeletal and generative hyphae which grow out in all directions at the surface so that the tissue is felted. The outgrowth soon slackens on the upper and lower sides but continues vigorously in the intermediate band-like region, and the primordium spreads out as a semicircular bracket (Text-fig. 6). The direction of marginal growth is horizontal or very slightly ascending, in which case the tubes, on growing vertically, appear to be inclined backward a little and their axes make an acute angle with the radius of the bracket. As marginal growth proceeds, the sides of the bracket are pressed firmly against the wood and may become attached to it by a small amount of secondary mycelium. At the base of the bracket the tissue thickens slowly for some time and often the lower margin on the under side spreads out as a thin sterile sheet, or resupinate "foot," for a distance of 10–15 mm., and possibly continues to spread very slowly throughout the life of the fruit body. By these means the bracket acquires a greater purchase on the support, which in *P. xanthopus* is provided by the discoid expansion at the base of the stem. On the other hand the flesh of the limb scarcely thickens at all behind the margin, but remains remarkably even until it tapers off rapidly on cessation of growth.

The tubes may develop when the bracket is barely 2 mm. in radius or not until it has reached 10 mm., according to the size of the primordium. The downgrowth of the dissepiments proceeds very slowly for several weeks after their inception in the pore field, and a common pore level is thus attained only in the proximal half of the bracket.



Text-fig. 6. Stages in the development of the fruit body of *F. levigatus* in radial section: *a*, a mature fruit body; *b*, a fruit body of *F. senex* in the first season; *c*, a fruit body of *Polyporus gilvus* var. *licnoides*. × 2.

The margin of the bracket, when fresh, is lurid golden yellow and rather coarsely velutinate. It consists of the radiating ends of skeletal, mediate and generative hyphae which are drawn up compactly to an even front. But as apical growth slackens in the hyphae situated near the upper and lower surfaces, their distal portions are pushed aside by the new branches formed in the middle region, and on cessation of growth many of them become curved or hooked, crozier fashion, at the ends. Shortly behind the margin, also, the generative hyphae give off numerous laterals many of which become mediate and skeletal hyphae, and these grow through the tissue radially or obliquely, as best they may between the preformed elements, and reach the margin or the upper or lower surfaces. It thus comes about that these surfaces, just behind the margin, consist of hyphal ends which project outward in any direction and give the coarsely velutinate appearance. Then, through the activity of the generative system, the crust develops on the upper side and the tubes on the lower side.

THE DEVELOPMENT OF THE CRUST

On the upper side, at 2–3 mm. from the margin, after the general outgrowth has stopped, thin-walled colourless hyphal processes, 1·5–3 μ wide, arise from the generative hyphae which lie near the surface, and they grow between the ends of the skeletal and mediate hyphae. Either they apply themselves directly round the ends of these thick-walled elements and by lobing and branching very irregularly weave them into the compact tissue of the crust, or they grow straight beyond the general level for a distance of 20–30 μ before they are deflected and begin to interweave, in which case a delicate canopy is at first formed, and subsequently, by the ingrowth of branches and lobes, the tissue is built back to the flesh and incorporates the ends of the thick-walled elements. The walls of these hyaline hyphae then thicken and agglutinate by squeezing out or absorbing the air between them, and a crust is formed which has the appearance already described (cf. Text-fig. 3).

In some fruit bodies the crust thickens no further. Usually it continues in the same manner. Either short hyphal processes continually grow out for distances up to 20 μ and then branch, lobe and unite with each other, thus gradually extending the crust: or, as appears to happen in spells of very wet weather which follow on a dry week or two, the processes grow out for a distance of 60–70 μ in a loose palisade or in groups, giving a fine bloom to the surface, and then form another layer of crust as before, only it rarely happens here that the new layer is built back completely to the old, and a crust, thickened in this manner, shows in section the agglutinated plectenchyma with groups or strips of vertical generative hyphae loosely arranged within it. The small tubercles on the upper side of old fruit bodies also arise by such local excrescence, and probably at such times the generative hyphae produce the skeletal hyphae which may occasionally be found in the old crusts.

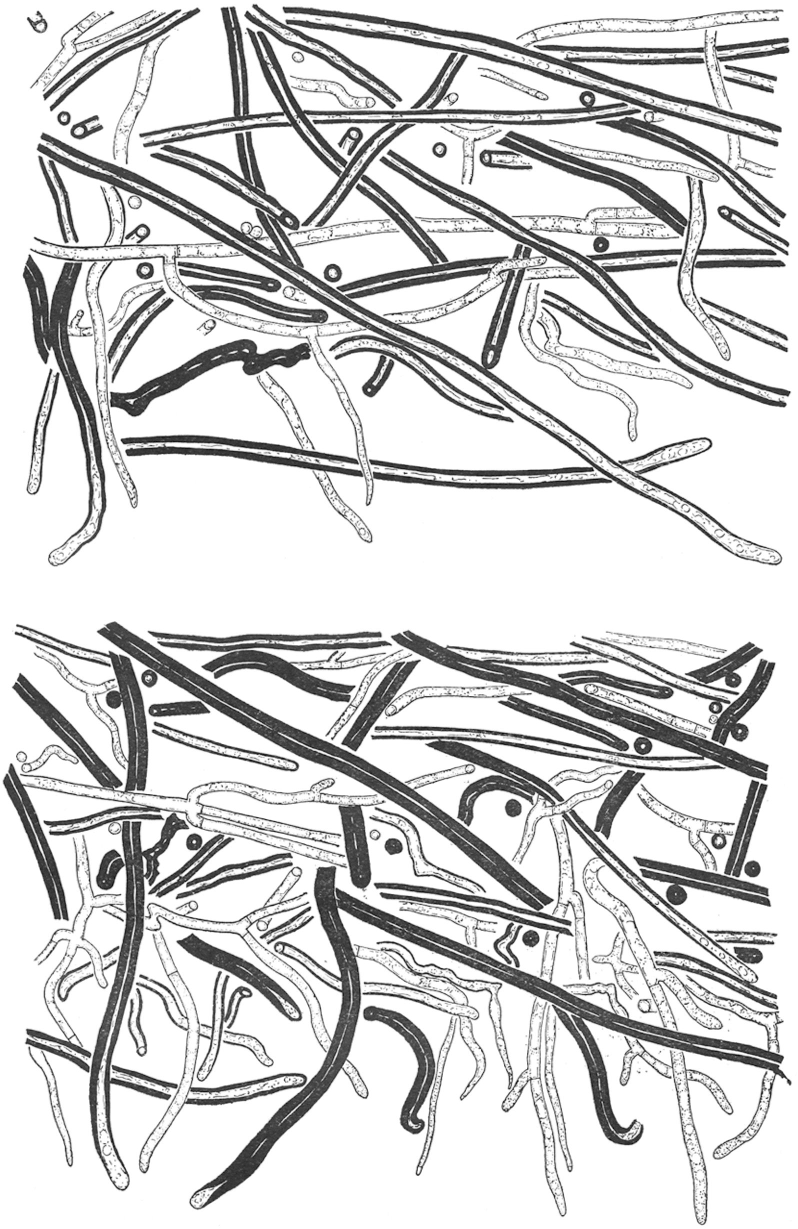
THE DEVELOPMENT OF THE TUBES

The skeletal and mediate hyphae on the lower side of the margin appear to grow out for a longer time than those on the upper side, and on cessation of growth they are not arrested so definitely at a common level. The posterior border of the coarsely velutinate margin passes on the lower side into a very finely velutinate, narrow, dark brown zone, which is the pore field, and at the posterior border of this zone, in turn, at 1·5–2 mm. from the margin, the dissepiments begin to develop. The compactness of the pore field, which is only about 500 μ wide, is due to the great amount of branching among the generative hyphae in the lower layer of the flesh and the outgrowth of these laterals at the surface: it is already dark brown like the mature pores, because many of these laterals have begun to develop into the skeletal hyphae of the dissepiments and to acquire the thick, dark yellow-brown walls. The superficial appearance of the pore field is essentially the same as in *P. xanthopus*.

I have explored in great detail the very complicated behaviour of the hyphae in the pore field and have reconstructed from sections and teased-out fragments six stages in the development of a dissepiment. The drawings are as faithful as possible though some liberty has been taken in representing the longer hyphae as if they lie in one plane, whereas in reality they wander to and fro and one must focus up and down in the section to follow them even for short distances: but a facsimile would be but a meaningless display of chips.

The first three stages are taken from sections of corresponding parts of the flesh and they show how the pore field develops by a downgrowth of hyphae from the lowest layer of the flesh. The last three stages are taken from the extreme surface and they show the special outgrowth of the dissepiment. A corresponding level in all six stages can be obtained by drawing a horizontal line through the tips of the stout skeletal hyphae which project from the flesh: thus, to combine the last stage with the first, the base of the dissepiment in the lower figure of Text-fig. 9 should be placed on a line joining the two lowest tips of the skeletal hyphae in the upper figure of Text-fig. 7, and this level corresponds with that reached by the excrescent skeletal hyphae in the coarsely velutinate under side of the margin immediately anterior to the pore field: it is the limit to which the flesh is built out on the under side.

In the first stage (Text-fig. 7, upper figure), taken about 900 μ from the margin, the skeletal hyphae have almost stopped growing, and



Text-fig. 7. *F. levigatus*. For explanation see text. × 500.

as yet there are few laterals from the generative hyphae: so the tissue is loose and the surface coarsely velutinate.

In the second stage (Text-fig. 7, lower figure), at *ca.* 1300 μ from the margin, the projecting skeletal hyphae have definitely stopped growing and their apices are becoming thick-walled. The main generative hyphae have produced many laterals which are interweaving or growing downwards with their ends projecting freely, and some of them are already developing into narrow skeletal hyphae. The tissue is becoming felted and finely velutinate in surface view.

The third stage (Text-fig. 8, upper figure), at *ca.* 1600 μ from the margin, represents the middle of the pore field. Very numerous laterals of the generative hyphae have grown down and brought the general level of the flesh to that of tips of the skeletal hyphae, which have thus been incorporated in the tissue. Many of the laterals remain thin-walled, but in others the walls have become more or less indurated and yellowish brown and yet others have become narrow skeletal hyphae. Some have grown nearly vertically downward and point fairly straight from the surface, but the majority, and especially the narrow skeletals, are more or less interwoven having grown in any direction except back again into the flesh. Such lack of direction must mean that the hyphal tips are not yet definitely geotropic.

The fourth stage (Text-fig. 8, lower figure), at *ca.* 2000 μ from the margin, shows the very beginning of a dissepiment. In the middle of the section the excrescent hyphae are crowded, projecting slightly beyond the general surface, and their direction of growth is more distinctly downward. This configuration means that in a certain region the production of narrow skeletal hyphae has been increased, that both the narrow skeletal and the generative hyphae of the same region have been stimulated to further outgrowth and that they are becoming positively geotropic. It is the first sign of the operation of the force in the pore field which creates the dissepiments (and incidentally the tubes).

In the fifth stage (Text-fig. 9, upper figure), at *ca.* 2500 μ from the margin, the dissepiment is clearly defined. It is a short column, about 60 μ long, of downgrowing narrow skeletal and generative hyphae. In the intervals between the dissepiments, over the blind upper ends of the tubes, the hymenium has developed and some basidia have even ripened spores. In these parts the downgrowth of the thin-walled generative hyphae is arrested; the terminal cell enlarges into a basidium or a cystidium, then laterals from the subterminal cells build up the hymenium in the usual manner by further sympodial branching, and the subterminal cells of the hyphae form the subhymenium.

Finally, in the sixth stage, at *ca.* 3500 μ from the margin, the dissepiment is about 120 μ long and the hymenium has begun to develop over the sides. It is constructed in the same way as in *P. xanthopus* by the downward creep of the subhymenial hyphae and from laterals of the generative hyphae in the dissepiment itself. Many of the generative hyphae at the base of the dissepiment and in the flesh immediately above have become thick-walled and rather intricately interwoven, even irregularly lobed, and in thus assuming to a small

Text-fig. 8. *F. levigatus*. For explanation see text. × 500.

extent the appearance and function of the binding hyphae of *P. xanthopus* they help to strengthen the layer of flesh above the tubes. The setae are formed at the ends of these thick-walled generative hyphae where they reach the surface, never while embedded in the tissue: the ends, which are thin-walled for a short distance, swell into the

Text-fig. 9. *F. levigatus*. For explanation see text. × 500.

conical or ventricose shape and when full-sized the wall thickens and becomes yellow-brown from the base to the apex which, however, usually remains colourless: setae may also be formed on short diverticula and they then appear forked at the base.

To summarise: there are three kinds of hyphal end in the pore field. First, there are the wide, blunt, yellow-brown ends of the skeletal and mediate hyphae the walls of which thicken rapidly behind the apex: they are the ends of the hyphae from the margin of the bracket which have dropped behind on the lower side and have stopped growing; so they project in any direction but mostly obliquely forward, in the direction of marginal growth, and they are often curved. Secondly there are the narrow ends of the laterals of the main generative hyphae; they have grown from the lower layer of the flesh and are colourless and thin-walled, $1{\cdot}5$–$3\,\mu$ wide, and cylindric or tapering. Thirdly there are the narrow ends of the skeletal hyphae of the dissepiments; they are colourless or yellow-brown, 2–$3\,\mu$ wide, cylindric or tapering, and their walls thicken shortly behind the apex. But, as is to be expected in this developing region, there are many other hyphae of character intermediate between the generative and skeletal hyphae, being generative hyphae in the process of becoming the skeletals of the dissepiments, and by confusing the identification of each kind they make impossible an exact analysis of the behaviour of the different elements. Moreover there are irregularities in the deportment of the generative hyphae; for some of them stop growing and their walls thicken up to the apex, and then delicate, colourless processes are frequently extruded which grow on as ordinary generative hyphae and apparently contribute to the hymenium (cf. Text-fig. 4).

The three kinds of hyphal end appear in fairly definite sequence. Immediately behind the margin there are only the skeletal and mediate hyphae of the flesh with a few generative hyphae. A little further back the thin-walled laterals of the generative hyphae are most abundant. In the pore field the skeletal hyphae of the dissepiments begin to appear and, as their production is increased along the lines of the dissepiments, they come to outnumber the rest. Nor is it till the dissepiments have been localised that their skeletals become definitely geotropic.

It is clear, therefore, that the dissepiments are formed by a special outgrowth of hyphae along certain paths, as was concluded in *P. xanthopus*, and not merely by the arrest of the general outgrowth in the pore field over certain areas which correspond with the tubes, although this process must certainly take place in the formation of the hymenium between the dissepiments. A new factor must be introduced, as a force in the pore field, to account for the localised increase in production of skeletal hyphae and for their geotropism.

THE BIOLOGY OF THE FRUIT BODY

In July, 1930, I removed all the fruit bodies from the log on which they had been growing and let the surface dry out to ensure the development of a fresh crop on subsequent wetting. Three weeks later I had the log removed to a shady place and watered twice daily, at 8 a.m. and 1 p.m., except in rainy weather; the conditions were made as favourable as possible for the continuous growth of the fruit bodies yet without an excess of moisture. By the beginning of September the primordia began to appear as specks on the wood and four were marked down with pins to measure their rate of growth. In nine days they had become small semicircular brackets, 10 mm. in radius, and marginal growth continued uninterruptedly for the next five months by which time they had reached their full size of 7–7·3 cm. in radius and 13–13·6 cm. in width, *i.e.* the greatest length taken at right angles to the radius. The rate of growth was too slow to measure accurately the daily increment, and the following figures are derived from weekly measurements on the four fruit bodies, all of which gave nearly identical results: and to judge from several others which came up about the same time, I have no doubt that they give a fair indication.

Size of pileus	Average rate of radial growth
0–10 mm. in radius	*ca.* 1 mm. per 24 hours.
10–32 mm. ,,	*ca.* 0·6 mm. ,,
32–53 mm. ,,	*ca.* 0·4 mm. ,,
53–62 mm. ,,	*ca.* 0·35 mm. ,,
62–70 mm. ,,	*ca.* 0·3 mm. ,,

The rate of growth gradually declined and by the beginning of February, 1931, it had ceased. But the brackets remained fresh and continued to form spores until the middle of April. Small tufts of hyphae then began to grow from the edges of the dissepiments and to cover the pores with a thin felt which thickened irregularly in small tubercular patches, as if a new layer of tubes was to be formed. However the fruit bodies have persisted in this state until the time of writing at the end of August. The arrest of growth must be due to internal causes, since the fruit bodies were never allowed to dry up or become too wet and there was no rotting: and the temperature followed the same daily fluctuation throughout, from 75 to 85° F., probably, in this shaded place.

A few basidia develop sterigmata as soon as the pores are delimited and the spores are matured and shed shortly afterward. Thus the young brackets begin to spore when only 2–10 mm. in radius, and the whole period of sporing in the four fruit bodies was about seven months. From December to the end of March a thin spore cloud could be seen issuing from the under side of the brackets and I have little doubt that they spored incessantly day and night.

It appears that marginal growth is intermittent and proceeds in small bursts. Some fruit bodies have broad shallow sulcations on the upper surface, which probably correspond with spells of wet weather, the margin narrowing as growth is delayed by low humidity of the air. But there are also narrow, alternating, light and dark zones in the flesh, which are slightly convex toward the margin and stretch as arcs from the upper side to the base of the tubes. In the dark zones the skeletal hyphae appear more abundant as they are closer together, and the distance from one dark zone to the next, 0·3–1 mm., corresponds with the daily increment of marginal growth. The skeletal hyphae may be produced at a definite stage in the twenty-four hours, during the night perhaps when the humidity of the air is highest, when a dark zone will be formed: and during the rest of the twenty-four hours the hyphae in growing radially separate from each other and cause the less dense, lighter zones. The phenomenon occurs in many species of *Fomes*.

Detached fruit bodies cannot withstand desiccation even for a few days. On several occasions I dried fruit bodies in the laboratory for four or five days, ten days, twenty days and thirty days, but on soaking out again they merely grew very mouldy and no basidia were found on microscopic examination. If dried off while still attached to the substratum, however, they may perhaps form a new layer of tubes, though I have not seen any specimens with this *Fomes* character.

Discussion

A comparison between *Fomes levigatus* and *Polystictus xanthopus* is instructive, because each represents a common form of polyporoid fruit body. Some further points of construction which the study of *F. levigatus* has disclosed must also be considered.

The fruit body of all polypores must begin development as a small hemispherical primordium, and on the limitations imposed on the radial growth of this body depends the adult form. In some species with massive fruit bodies, as *F. robustus* or *P. betulinus*, the initial radial growth continues for a long time to form a large primordial knob or tubercle before the form factors come into play; mostly the radial growth is interrupted after a few days. In *P. xanthopus* the outgrowth is restricted at such an early stage over the whole surface except on the distal side where the growing-point of the primordial shaft is delimited. In *F. levigatus* the outgrowth is similarly restricted but on the upper and lower sides only, and it continues in the intermediate strip or hoop as the growing margin of the pileus. The growing-point of the primordium in *P. xanthopus* is positively phototropic and becomes diageotropic at a later stage after the formation of the pileus. In *F. levigatus* the growing margin is diageotropic from the first and apparently never phototropic. Consequently the hemispherical primordium of *P. xanthopus* grows towards the source of light of optimum intensity as a cylindrical shaft and that of *F. levigatus* spreads out centrifugally in an equipotential plane in the gravitational field. In each it seems that the hyphae on emergence from the wood are insensitive to external stimuli and firstly, therefore, construct a hemispherical body of interwoven hyphae. On becoming phototropic or geotropic they come into alignment to form the characteristic growing regions, and by deflecting the food supply to their own ends the outgrowth from the rest of the surface is slowed down, and the specific form is gradually assumed.

The direction of marginal growth in *F. levigatus* may be exactly diageotropic at right angles to the force of gravity or slightly ascending. The degree of diageotropism varies considerably in different species but is fairly constant for any one. Some, as *F. lignosus* or *P. giganteus*, have the fruit body strongly ascending and others, as *P. amorphus*, are descending, although this feature is better displayed in some of the bracket forms of *Hydnum*.

As regards the details of the geotropic mechanism much can be learned from the manner of growth of the hyphae. From their straight course and from the fact that they form the bulk of the tissue and lead the marginal growth, it is natural to conclude that the skeletal hyphae are the sensitive elements. But whether the main generative hyphae, which grow radially in the flesh, are also geotropic cannot be decided by mere inspection, for they may follow simply the path of least resistance: the possibility is precluded, however, from their laterals which wander about. Now the set of any portion of a skeletal hypha depends solely on the direction of the apex when it traversed the region in which that portion of the hypha was laid down, because there is no motor mechanism and the walls thicken rigidly close to the apex. The geotropic mechanism must therefore reside in the apices of the hyphae. I have looked very carefully without being able to detect anything so gross as a granule, so that it must depend on microphysical forces. In *P. xanthopus* it is very precise, and the skeletal hyphae in the flesh are strictly longitudinal, but in the flesh of *F. levigatus* they are inclined to be sinuous and in the dissepiments they show most striking irregularities. As can be seen from Text-figs. 4 and 9, it is the exception rather than the rule for the skeletal hyphae to grow straight; they may deviate as much as 50° from the vertical and then gradually or abruptly return to a mean course. Yet the tubes are perpendicular. One must suppose that the mechanism is imperfectly developed here and that the set of the limb and the dissepiments is merely an average result obtained by employing a large number of hyphae. In this, perhaps, is the explanation of the unnecessary thickness of flesh and apparent waste of substance in the fruit body of *F. levigatus*: with straight growth, and a rigid crust, a platform firm enough for the suspension of the tubes would be provided by a quarter the thickness.

Unquestionably the fruit body of *P. xanthopus* is the more highly evolved. There is greater division of labour among the hyphae; they are better organised; and the sterile tissue of the pileus is very much reduced, possibly to the minimum. *F. levigatus* has an advantage in the absence of a stem—which is scarcely necessary for the elevation of the hymenophore in an epixylous fruit body and merely delays the beginning of sporing—and, may be, in the longer tubes, but there is little to choose in this connection. The hymenium is fertile only in the lower part of the tubes in *F. levigatus*, the effective length being at most nine or ten times greater than in *P. xanthopus* (the diameter being the same in both), and the continuous production of spores is extravagantly obtained by continuously extending the hymenium through the downgrowth of the tubes. In *P. xanthopus*, the sterile tissue of the dissepiments is also reduced; the downgrowth is soon arrested, and the area of the hymenium is increased no further, but sporing continues from all parts until the decay of the fruit body through the efficient means of intercalary growth and interpolation of new basidia. Moreover the fruit body will revive after desiccation which is fatal to that of *F. levigatus*. One might boldly declare, indeed, that the *Polystictus* type is one of the most elaborate and refined of fruit bodies in the Polyporaceae.

The structural dorsiventrality of the pileus in *F. levigatus* is brought about by the generative system. If no crust or tubes were developed, both upper and lower surfaces would have the same structure. In any case the skeletal stroma, formed by marginal growth, is isobilateral, and the generative hyphae, which are equally distributed throughout, give rise at each surface, just behind the margin, to similar excrescent branches. A physiological distinction then appears. The force which generates the dissepiments is limited to the lower side, and it is only on this side that the generative hyphae, on cessation of growth, produce basidia. There is not the least sign of any such partition of outgrowth on the upper side, and the generative hyphae form the crust independently of geotropic stimuli. But the nature of this force is yet incomprehensible: it must be connected with the geotropic sensitiveness of the hyphae and it must also act at a distance, since the hyphal tips, which are not contiguous, act in unison.

Lastly, there is a point in the construction of the tubes which was overlooked in *P. xanthopus*, but is more evident in *F. levigatus* as the dissepiments are longer and thicker. The hyphal ends are arranged at the edges of the dissepiments to form growing regions similar to that at the margin of the pileus, and the growth of the hyphae on the outside of these growing regions similarly slows down and they get left behind on the walls of the tubes. As the dissepiments remain of constant thickness, the generative hyphae must produce just sufficient new skeletal elements to replace those lost from the growing regions in this manner, or the dissepiments would grow thicker or thinner, with an irregular outline in longitudinal section, and the effectiveness of the tubes in increasing the hymenial area without interfering with the free dispersal of the spores would be much impaired. The point reveals again the remarkable precision in the minute organisation of these filamentous plants.

RELATED SPECIES

The fruit bodies of the following species are constructed on exactly similar lines to that of *F. levigatus.* They differ specifically in the characters of the spores, the setae, the upper surface of the pileus, the crust, the skeletal hyphae and in the thickness of the flesh and tubes: they differ, that is, as one would expect, in the properties of the hyphal wall, in the modification of the hyphal ends on cessation of growth, in the behaviour and manner of branching of the hyphae and in the factors governing the relative development of the tissues. These are seldom recorded in specific descriptions; reliance is had rather on macroscopic characters, which are but secondary effects of the minute construction with little or no mycological significance. Differences in colour and texture are determined by the characters of the crust and the hyphal systems; the microscopic structure of the upper surface decides whether it will be smooth, matt, velutinate, tomentose, laccate, and so forth. Such descriptive terms would serve if they really indicated definite microscopic characters, but in referring only to the gross appearance they are too vague. A matt surface, for instance, may be caused by the crowding of the ends of the skeletal hyphae at a common level, by the development of an irregular crust by the generative hyphae, or merely by the excretion of granular and crystalline matter: a woody or corky texture may be due to the abundance of oblique and transverse skeletal hyphae, or to the presence of a binding system as well, or even to a single system of hyphae with thickened walls and compact arrangement. And should such fundamental differences reach a macroscopic level they can be expressed only very inadequately in degrees of woodiness, heaviness, roughness or hardness most difficult to appreciate. Hence it is almost impossible to identify a polypore with certainty from the customary descriptions; a thorough microscopic examination will so often disclose constant peculiar details in otherwise similar fungi that the type material must be re-examined to decide the issue. The published descriptions of all the following apply equally well to *F. levigatus*, so that, in the absence of type material, I can merely set forth in a preliminary manner the results of microscopic examination of the authentically named specimens in the Singapore herbarium, and trust that they will be checked over in time by reference to the types.

The Polyporaceae are acknowledged among the most perplexing fungi to identify. The reason is surely because their detailed study has scarcely begun: only by carrying the microscope to all points can one try out the limitations of a morphological classification.

Fomes senex (Nees et Mont.) Fr.

Material:

Sing. F. No. 5387. Singapore, det. C. G. Lloyd.
Sing. F. No. 5867. Singapore, det. C. G. Lloyd.
Sing. F. No. 5853. Johore, det. C. G. Lloyd.
Sing. F. No. 8390. Singapore, det. C. G. Lloyd.

This species differs from *F. levigatus* in the following points:

(1) At the upper surface of the pileus the skeletal hyphae are arranged in a fairly regular pile with their ends free or only slightly agglutinated and projecting perpendicularly or obliquely forward. There is no crust, or only a thin (5–10 μ), structureless, hyaline, interrupted layer above the pile (Text-fig. 10).

(2) The skeletal hyphae are light yellow, rather narrower, (2–3·5 μ wide, rarely 4 μ), and those of the dissepiments are very much straighter.

(3) The flesh is relatively thinner (1–5 mm. thick at the base of the pileus, though up to 12 mm. thick if there is a basal pad, and 0·5–2 mm. at 5 mm. from the margin), and the tubes in fruit bodies of the first season are much longer (up to 6 mm. long at the base) (Text-fig. 6).

(4) The spores have a large median or basal gutta, 2–2·5 μ wide (Text-fig. 11). Such a difference appears trivial though it is constant nevertheless.

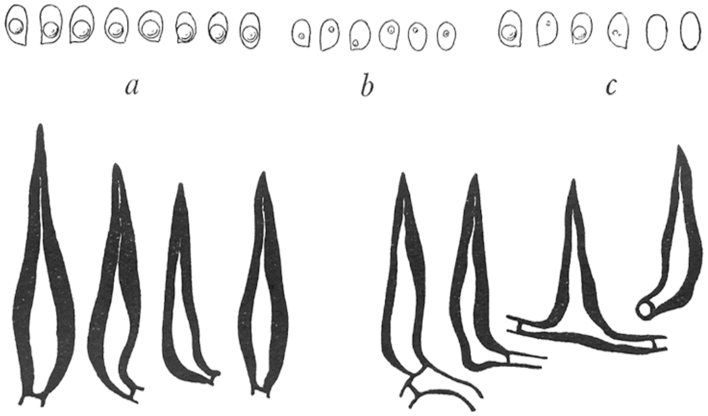
(5) The setae are rather larger, 18–30 × 5–7 μ, rarely up to 36 × 7–8 μ (Text-fig. 11).

(6) The cystidia are very sparse.

Moreover, the fruit body is very variable in shape and grows to a large size. Typically it is bracket-shaped, but it is often widely effuso-reflexed and occasionally wholly resupinate like a *Poria*, and it may be perennial, the tubes developing up to 6 cm. long in indistinct layers 1–3 mm. thick. The largest Malayan specimen as yet discovered measures 27·5 cm. in radius and 45 cm. wide. It is also very common, perhaps the commonest *Fomes* in the country, and occurs at all altitudes up to 6000 ft.

To the naked eye fruit bodies of *F. senex* are distinguished by a roughish or velutinate, dull and narrowly sulcate upper surface, the thinner and much paler, cinnamon-tawny or tawny-ochraceous flesh and the longer tubes. A comparison of specimens of both species side by side enables one to separate those of *F. levigatus* at a glance by the smooth, unpolished surface and the deep brown flesh.

Text-fig. 10. A part of the upper surface of the fruit body of *F. senex* taken near the base. × 500.



Text-fig. 11. *a*, spores and setae of *F. senex*; *b*, spores of *F. levigatus*; *c*, spores and setae of *Polyporus gilvus* var. *licnoides*. × 1000.

Concerning the colour of the spores there appears some misunderstanding. Lloyd says that they are yellow-brown and are rather scanty and often absent from herbarium specimens. I have obtained spore prints from fruit bodies of several different collections and they are always pure white: the fresh spores are colourless, 3·5–5 × 2·5–3 μ, and shaped as in *F. levigatus*. On the other hand, old spores lying in the tubes in these fruit bodies had pale yellow walls and some of the basidia in the effete portions of the tubes had contracted into small subglobose bodies, 3–5 μ wide, with thick yellow-brown walls remarkably like the spores of *F. rimosus*. The fruit bodies were identical with the authentically named material, wherefore it must be concluded that *F. senex* has white spores.

Although a crust does not develop on the upper surface, there is a slight outgrowth of generative hyphae just behind the margin similar to that in *F. levigatus*. The colourless processes from the generative hyphae may project up to 12 μ and be so numerous and lobed as to form a loose covering over the surface about 5 mm. from the margin, but as they do not become thick-walled they soon wither away and leave the ends of the skeletal hyphae free or slightly agglutinated in their structureless remains, in which foreign spores and bacteria may then begin to grow.

I have tested their ability to resist desiccation on several occasions, but the fruit bodies are no better equipped than those of *F. levigatus* and survive not even a few days.

On the form of the setae two varieties can be distinguished as follows:

var. *hamatus* var.nov. Text-fig. 12.

Setis majoribus, apicibus plerumque curvatis vel hamatis, 26–35 × 5–8·5 μ.

Loc. Pahang, 6000 ft.: Pahang, 4000 ft. (parasitic at the base of a large tree): Negri Sembilan, 2300 ft.: Penang, sea-level, Sing. F. No. 5597: Singapore, 400 ft., Sing. F. No. 5098.

While most of the setae are characteristically hooked, some are merely flexuous and a few are of the straight conical kind. I have examined some hundred fruit bodies of typical *F. senex*, however, and have not seen one which had such strongly curved setae.

The specimens from Pahang were very large, thick *Fomes* forms; those from Negri Sembilan were medium sized; those from Singapore were small and polyporoid; and that from Penang was small and effuso-reflexed.

var. *bulbosetosus* var.nov. Text-fig. 12.

Setis multo majoribus, valde ventricosis, apicibus plerumque hamatis, 20–40 × 7–15 μ.

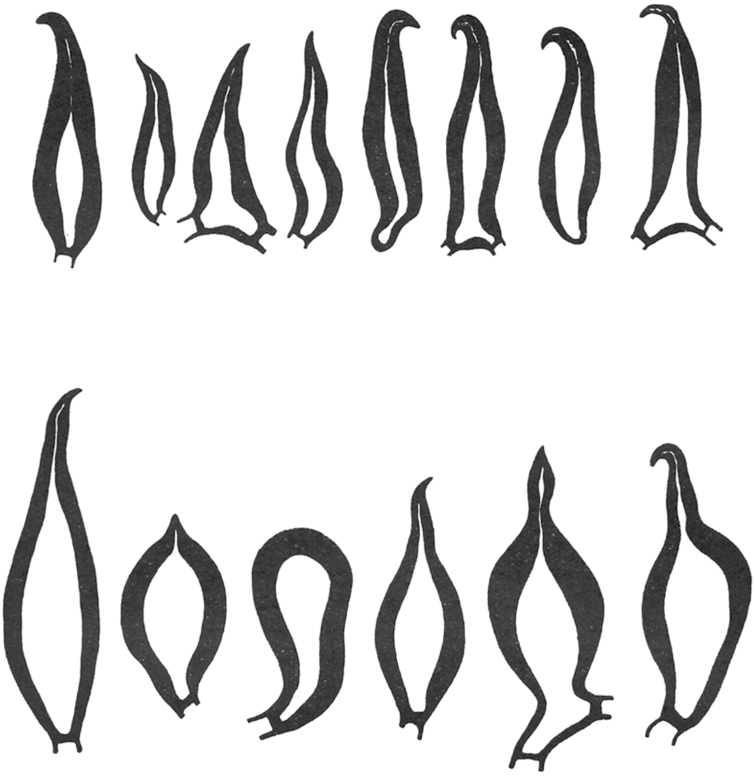
Loc. Endau River, Johore, Sing. F. No. 24875.

This variety is founded on a single collection of typical medium-sized fruit bodies with one or two layers of tubes, made by the Director of the Singapore Botanic Gardens. The setae are, however, most characteristic and very few of the ordinary kind occur.

Fomes zelandicus Cke.

Cunningham has described this species in detail from New Zealand (*Trans. N.Z. Instit.* LVIII (1927), 213).

It is a question whether it is not *F. senex*. Specimens sent abroad for determination were referred to that species, but as Lloyd had ascribed coloured spores to *F. senex* and those of the New Zealand specimens were white, Cunningham retained Cooke's name for them.



Text-fig. 12. Setae of *F. senex* var. *hamatus* above and of var. *bulbosetosus* below. × 1000.

His description of *F. zelandicus* applies so exactly to the Malayan specimens also that they are surely the same species, though I have not examined material of the former. As I have just shown, the yellow-brown colour of spores in *F. senex* is probably a post-mortem effect and they are colourless when fresh. Alternatively, *F. senex* is another species with truly coloured spores, as the type came from Chili and the Malayan and New Zealand specimens are wrongly referred to it. It will be necessary to re-examine the type.

Fomes velutinosus Hutchings, Lloyd, *Syn. Fom.* 1915, 260.

Material:

Sing. F. No. 8786. Pahang, det. C. G. Lloyd.

Lloyd (Letter 48, note 110) says that this species differs from *F. senex* in the much smoother surface which often has a banded effect (as in *Polyporus gilvus* var. *licnoides*), the softer, well-developed context and, especially, in the strongly velutinate, deeper coloured pores. He says that it may be the *Polyporus* form of *F. senex* since all the specimens have only one layer of tubes, and later (Letter 66, note 642) calls it *Polyporus velutinosus*. The diagnostic characters suggest *F. levigatus*, but Sing. F. No. 8786 is typical of *F. senex* in the first season with a single layer of tubes. It seems therefore that *F. velutinosus* is synonymous with *F. senex*. Every *Fomes* is a *Polyporus* at the outset, and dark velutinate pores are characteristic of the growing dissepiments of *F. senex* as of most other brown species.

Text-fig. 13. Setae of *F. extensus*. × 1000.

Fomes extensus Lév.

Material:

Sing. F. No. 10890. Johore, det. C. G. Lloyd.
Sing. F. No. 18665. Borneo, det. E. M. Wakefield.

Except for slight differences in shape the specimens in these two collections are identical. The species can be distinguished readily from *F. senex*, to which it is closely allied, by the following points:

(1) There is a hard black crust, 300–500 μ thick, just beneath the upper surface of the pileus. The ends of the skeletal hyphae project freely for a distance of 100–400 μ beyond the crust in a close pile.

(2) The setae are stouter with very thick dark brown walls, 20–35 × 6–10 μ (Text-fig. 13).

(3) Possibly the flesh is thicker (7–11 mm. thick at the base, 3–4·5 mm. at 5 mm. from the margin).

Macroscopically it can be distinguished from *F. senex* and *F. levigatus* by the hard, rigid, finely villose surface. It is superficially very like *F. lamaensis*.

The crust is formed, as in *F. levigatus*, from branches of the generative hyphae which interweave among the skeletals but beneath the surface, and they acquire thick, dark brown, resinaceous or carbonaceous walls on becoming agglutinated. Before the crust develops the structure of the upper surface is the same as in *F. senex*. It is noteworthy that occasionally fruit bodies of *F. senex* have a very thin, black, crustaceous line, 50 μ thick, near the base of the pileus, about 1 mm. below the surface, and composed of similar resinaceous generative hyphae.

I did not find spores, but Bresadola gives them as subglobose, yellow-brown, 3–4 μ (*Ann. Myc.* XIV (1916), 236): but conceivably the fresh spores are white also. The skeletal hyphae are narrow, 2–3·5 μ wide, seldom 4 μ.

The species is evidently rare in Malaya and Lloyd mentions having seen besides Sing. F. No. 10890 only the type collection from Guadeloupe.

Polyporus gilvus (Fr.) Schw.

Material:

No. 5831, ex herb. J. Weir, Indiana, N. Am., det. J. Weir.

This species can readily be told from the foregoing by the hyphal organisation which is advanced but little beyond the monomitic state. The generative hyphae are very abundant and conspicuous and form the greater part of the flesh; they have the same characters as in *F. levigatus* but are more inclined to be thick-walled (0·5–1 μ thick). The skeletal hyphae, which are 3–6 μ wide, rarely 7 μ, are distinctly in the minority, and, while being unbranched with thickened, light golden yellow walls (0·5–2 μ thick), they retain a *wide septate lumen*: only occasionally in the oldest tissue at the base of the fruit body the lumen is reduced to a line. The septa are spaced 25–180 μ apart and frequently are slightly convex forwards. Mediate hyphae are hardly recognisable. The hyphae are mostly radial and loosely arranged: consequently the flesh has a light fibrillose texture, scarcely woody, and a bright tawny yellow colour: and owing to their wide lumen most of the hyphae collapse on drying.

On the other hand the skeletal hyphae of the dissepiments are well differentiated with the same characters as in *F. levigatus* and the tubes have the same compact structure.

A crust also develops on the upper side of the pileus in the same way as in *F. levigatus*; it may reach 60 μ thick at the base of the pileus, though usually it is 10–20 μ thick, and there is no regular pile such as in *F. senex*. The upper surface appears therefore smoothed over with a dull finish.

The small, granular, substrigose or subtuberculate excrescences near the base of the pileus, which are conspicuous in the variety

Hookeri (= *P. Hookeri* Berk.) are formed by the outgrowth of narrow skeletal hyphae having the same characters as those of the dissepiments: they arise evidently in the same manner, from branches of the generative hyphae at the surface, and grow out irregularly, intertwining with others, and are covered by the crust on cessation of growth: sometimes they do not penetrate the original crust which is therefore just raised in small bulges. The excrescences are without order, scattered or crowded, unlike the dissepiments, and they do not begin to develop until the margin has advanced a distance of 1–2 cm. Nevertheless it is interesting to find a comparable behaviour in the generative hyphae on both sides of the pileus, for it is well known that when a branch or log bearing polyporaceous fruit bodies is turned upside down tubes will then develop from the original upper side.

Typical specimens of *P. gilvus* have not been found in Malaya, all the collections being referred to the following variety.

var. *licnoides* (Mont.) Lloyd.

Material:

Sing. F. No. 5136. Singapore, det. C. G. Lloyd.
Sing. F. No. 8460. Pahang, det. C. G. Lloyd.
(*Fungi Malay*, C. F. Baker, No. 384, det. N. Patouillard is *F. senex.*)
(Sing. F. No. 5098, det. C. G. Lloyd is *F. senex.*)

This variety is distinguished by the thin flesh (1–4·5 mm. thick at the base of the pileus, 0·3–0·5 mm. at 5 mm. from the margin), the shorter tubes (1–2·5 mm. long at the base, 0·5–1·5 mm. at 5 mm. from the margin), the reddish brown zones on the pileus and the fact that it occurs only in tropical or subtropical countries, while *P. gilvus* extends to the temperate regions. Microscopically it is identical with *P. gilvus*, though the crust is but very slightly developed. It seems not uncommon in Malaya. The spores, basidia and setae are exactly as in *F. senex* only the setae are a trifle narrower (4–6 μ wide), and the gutta in the spore varies much in size (0·5–2 μ) and may even be absent; the cystidia are as numerous as in *F. levigatus.*

var. *scruposus* (Fr.) (= *P. scruposus* Fr.).

Material:

Sing. F. No. 5772. Singapore, det. C. G. Lloyd.

These specimens have the same shape and hyphal characters as *P. gilvus*, but the structure of the upper surface is decidedly different. It is like that of *F. senex* only the skeletal hyphae project freely to a much greater distance in more or less discrete fascicles to give a strigoso-fibrillose (neither tuberculate nor granular) appearance: nor is there a crust. The fascicles are formed by the main skeletal hyphae of the flesh which continue to grow out though they fall behind the margin, and not, as in *P. gilvus*, in a secondary manner from superficial generative hyphae. So, if this collection be correctly named, the superficial outgrowths of var. *scruposus* differ in origin from those of var. *Hookeri*, and the former bears the same relation to *P. gilvus* in this respect as *F. senex* does to *F. levigatus*: it may prove specifically distinct.

Polyporus carneofulvus Berk.

Material:

Sing. F. No. 5619. Penang, det. C. G. Lloyd.

This collection is *F. levigatus*. *P. carneofulvus* is stated to be a synonym or merely a variety of *P. gilvus*, and if so should have the same hyphal characters: those of Sing. F. No. 5619, however, are identical with *F. levigatus*. The problem thus arises whether Lloyd was correct in this determination, in which case *F. levigatus* becomes a synonym of *P. carneofulvus* and *P. carneofulvus* a distinct species: but reference must be made to the type.

Polyporus biogilvus Lloyd.

Material:

Sing. F. No. 5092. Singapore, det. C. G. Lloyd.
Sing. F. No. 23720. Singapore, det. E. M. Wakefield.

Lloyd described this species from an African collection and remarked that it differed from *Polyporus gilvus* in context, absence of setae and spores (*Myc. Notes*, LXII (1920), 943). On the label of Sing. F. No. 5092 he wrote: "It is *gilvus* without setae."

Both collections are of the same species. The fruit bodies are trimitic with conspicuous binding hyphae, like *P. xanthopus*, but I have not been able to determine exactly the nature of the generative system. The skeletal hyphae have mostly a wide lumen with but slightly thickened walls.

The species is not nearly related to *P. gilvus*, however much alike superficially. As Miss Wakefield remarked on the label of Sing. F. No. 23720, "it is better as *Polystictus*."

The following species may also belong to the *gilvus* alliance, but there is no material of them in the Singapore herbarium: *Polyporus chrysellus* Bres., *P. intactilis* Lloyd, *P. multisetosus* Lloyd, *P. pseudogilvus* Lloyd, *P. Ramosii* Lloyd, and *P. subgilvus* Bres. Lloyd also describes as *Fomes gilvus* some indurated, perennial specimens from several tropical countries, and implies that they are merely perennial forms of *P. gilvus*. That they have a hard consistency throws doubt on the suggestion, since the flesh of *P. gilvus* is essentially light and fibrillosely woody on account of the peculiar hyphal characters: indurated flesh probably means abundant very thick-walled skeletal hyphae and such forms must belong rather to *F. senex* or *F. levigatus*. As already mentioned, both Patouillard and Lloyd mistook specimens of *F. senex* for *P. gilvus* or its varieties.

SUMMARY

The structure, development and biology of the fruit body of *Fomes levigatus* n.sp. are described, with a specific diagnosis.

The fruit body is a diageotropic bracket composed of aseptate, unbranched, thick-walled, skeletal hyphae and septate, branched and thin-walled generative hyphae; binding hyphae are absent; the generative hyphae are not clamped.

The development of the dissepiments from the generative system is described in detail. The skeletal hyphae of the dissepiments do not become positively geotropic till some time after their origin in the pore field.

Radial growth of the bracket is slow with an initial rate of about 1 mm. per 24 hours gradually falling off to zero. In the fruit bodies studied, marginal growth continued for five months: sporing began when the primordia were 2–10 mm. in radius and lasted for seven months. Basidia begin to mature almost immediately after the pores are delimited but only the lower parts of the tubes, for ½–1 mm. from the pores, are fertile in matured fruit bodies: the upper parts are lined with effete hymenium and stuffed with hyphae derived from the mycelium. Continuous sporing is obtained by the continuous development of new hymenium through the downgrowth of the dissepiments.

The fruit bodies cannot survive desiccation. Perennial specimens have not been collected.

Comparison is made with the fruit body of *Polystictus xanthopus*. The *Polystictus* type is considered the more highly evolved on account of the greater division of labour among the hyphae, the more precise organisation, the continuance of sporing by means of persistent intercalary growth of the hymenium (thus dispensing with long tubes), and the ability to resist desiccation.

The distinctive characters of related species, especially of *F. senex*, *F. extensus*, and *Polyporus gilvus*, are enumerated. They have the same systems of hyphae as *F. levigatus*, but the skeletal hyphae in the flesh of *P. gilvus* are poorly differentiated, retaining a wide, septate lumen, and are much less numerous than the generative hyphae. *Polyporus biogilvus* is not nearly related, having three systems of hyphae like *P. xanthopus*.

Fomes velutinosus and *F. zelandicus* are considered synonyms of *F. senex*.

Two new varieties of *F. senex* are proposed on the form of the setae, namely var. *hamatus* and var. *bulbosetosus*.

The terms *dimitic* and *trimitic* are proposed for fruit bodies composed of two and three systems of hyphae; *monomitic* for those of one system.