Micromorphology of the lower Hymenomycetes.

By

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To classify the lower Hymenomycetes, not often distinguished by their shape, colour or hymenial configuration, mycologists eventually turned to the microscope to seek more exact diagnostic characters. As far as the circumscription and identification of species is concerned, microscopy has revealed many useful characters. But the other ideal of taxonomy, namely a natural classification, is still far from realisation as the significance of facts already observed has only partially been evaluated.

This paper is an attempt to review with illustrations the morphology of the microscopic organs found in the lower Hymenomycetes, special attention being given to the basidium. For amplification examples are cited from other groups of fungi as well. Some standard of terminology has been aimed at, particularly with regard to the basidium. The conclusions reached are that Linder's terminology for the basidium is unacceptable as it over-simplifies this organ, while Neuhoff's terminology is based on homologies which are unacceptable. Moreover, Neuhoff's terminology is flexible and in many instances would vary according to the subclass in which a particular fungus is classified. We believe, with Donk, that the place or stage of karyogamy, and the place or stage of meiosis, are fundamentals which should be used in formulating a terminology for basidia.

The new term **protosterigma** coined by Dr. M. A. Donk, is published here for the first time with its originator's generous permission. The term is explained in a note on sterigmata in general provided by Dr. Donk, which should be read in conjunction with this paper.

Morphology, Cytology and Terminology of Basidia.

(NOTE.—In reading this section, reference should be made to Fig. 1 for terminology and to Fig. 2 for cytology).

In the simpler Hymenomycetes, basidial characters are most important for the recognition of genera and higher ranks, and studies of basidial types have led to a better understanding of basic relationships on which to build a more natural classification (Juel, 1898; Maire, 1902; Neuhoff, 1924; Gäumann, 1928; Donk, 1931; Rogers, 1934; Martin, 1938; Linder, 1940; Heim, 1948, 1949). Rogers (1944) summarised the position in stating that classification is implicitly an embodiment of an hypothesis concerning phyletic relation and that arising from this there are two views of reliable indications of relationship in the Hymenomycetes, viz. (1) that hymenial configuration is a reliable indication of kinship and (2) that the basidium and associated characters are reliable indications of kinship, and that hymenial variations are comparatively recent and trivial. There seems no doubt that the second view is the more acceptable one. Increasing use of the microscope has demonstrated affinities which were long unsuspected.

One of the most significant steps in the study of Basidiomycetes was the recognition of the homo- and heterobasidial subclasses by Patouillard (1900), and the resultant attention given to basidial morphology. Since then, many new facts have been observed about the morphology and cytology of the various types of basidia, but there is still much controversy in their interpretation, and particularly in the terminology applied to the different parts of basidia.
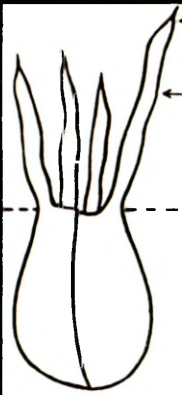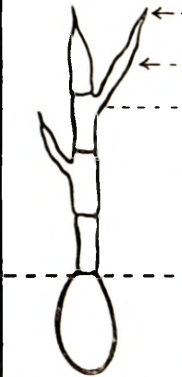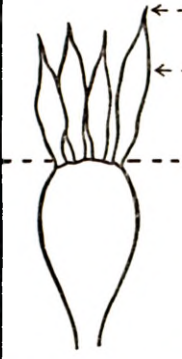
	LINDER	NEUHOFF & ROGERS	DONK
TREMELLA	STERIGMA	←STERIGMA---→ EPIBASIDIUM	←SPICULUM---- PROTO--STERIGMA } STERIGMA
	BASIDIUM	HYPOBASIDIUM (4-CELLED)	METABASIDIUM (REPLACING PROBASIDIUM)
SEPTOBASIDIUM	STERIGMA		SPICULUM--- PROTO--STERIGMA } STERIGMA
	BASIDIUM	EPIBASIDIUM (4-CELLED)	METABASIDIUM
	PROBASIDIUM	PROBASIDIUM REPLACED BY HYPOBASIDIUM	PROBASIDIUM
TULASNELLA	STERIGMA	←STERIGMA----→ EPIBASIDIUM	←SPICULUM--- PROTO--STERIGMA } STERIGMA
	BASIDIUM	HYPOBASIDIUM	METABASIDIUM (REPLACING PROBASIDIUM)

FIG. 1.—Three mature heterobasidial types, **Tremella, Septobasidium** and **Tulasnella,** drawn diagrammatically to indicate the terminologies used by Linder, Neuhoff (as elaborated by Rogers), and Donk.

In any science terminology is necessary to define objects unambiguously. For objects such as basidia, which are composed of a number of different parts, it is necessary that only those parts which are entirely homologous (and not merely similar, or analagous) should receive the same name. By homologous is meant " fundamentally corresponding in value or relationship with one another ". For such structures to be homologous they must develop in the same way, serve the same function, have the same relation to a fundamental type, or have the same relative position (Shorter Oxford
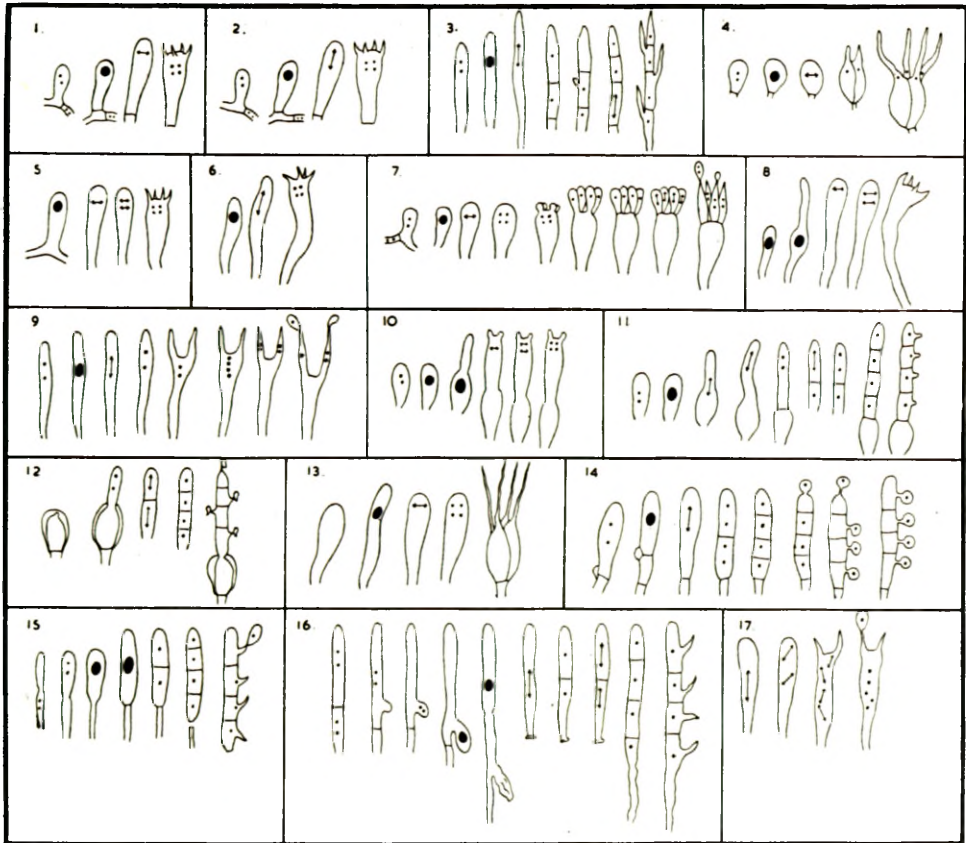

FIG. 2.—Diagrammatic representation of cytological changes in several types of homo- and hetero-basidia. Details reconstructed from information or illustrations by authors cited below:—

1. Karyogamy followed by chiastic meiosis. 2. Karyogamy followed by stichic meiosis. 3. **Auricularia** (Maire, 1902). 4. **Sebacina** (Whelden, 1935 b). 5. Agaricaceae, **Hygrophorus** (Maire, 1902). 6. **Cantharellus** (Maire, 1902). 7. **Tulasnella** (Rogers, 1932). 8. **Vuilleminia** (Maire, 1902). 9. **Guepinia** (**Dacryopinax spathularia**) (Bodman, 1938). 10. **Brachybasidium** (Gäumann, 1922 a). 11. **Jola** (Gäumann, 1922 b). 12. Uredinales (Linder, 1940). 13. **Hyaloria** (Martin, 1937). 14. **Phleogena** (Shear & Dodge, 1925). 15. **Mycogloea** (Olive, 1950). 16. **Helicogloea** (Baker, 1936). 17. **Clavaria** (Maire, 1902). Note that there may be minor variations in different species of the genera cited, but that the course of events has been generalised. Note too that the spindle orientation is variable in some species, and also the plane of septation.

English Dictionary, 1933). Terminologies have been proposed or clarified by three recent exponents of various hypotheses, namely Neuhoff (1924) and his followers, especially Rogers (1934) and Martin (1938), secondly Donk (1931) and thirdly Linder (1940). These terminologies are illustrated diagrammatically in Fig. 1. Of these, Rogers's contribution has perhaps received the most support; but the time has come to re-examine all three in an attempt at revaluation and clarification.

In the older descriptions of Basidiomycetes there was little differentiation in terminology of the various parts of the basidia. The whole organ was known (as it is now) as the basidium. Sterigmata and probasidia were recognised as parts of the basidium. The term probasidium originated with van Tieghem (1893) to denote the basal vesicles of the basidia of rusts and smuts, i.e. the teleutospores and chlamydospores of these groups respectively; but it was later rightly extended by Donk to include all primary basidial cells in the same stage of development, and particularly the more or less resistant or persistent vesicles in a similar position on the basidia of the Auriculariaceae. The term sterigma was applied to such spore-bearing structures as those found in the normal clavate homobasidium, as well as to tubular extensions of the primary basidial cell found in Heterobasidiomycetes. One cannot accept Boedijn's (1937) contention that the primary basidial cell and its tubular extensions (e.g. in *Helicogloea*) are separate organs; they are each part of a single organ, the basidium.

The first consideration is whether an extended terminology is essential or whether we may be content, as Linder (1940) was, to return to the simple terminology of probasidium, sterigma, and basidium. The bone of Linder's thesis is phylogenetic, namely that the septate basidium and germination of the basidiospores by repetition are primitive characters. To quote, " The basidium, once established, is essentially the same throughout the class, but has undergone simplification as a result of loss of septation. Also it has in higher forms taken over the functions of the probasidium and become the locus of both caryogamy and meiosis. Because of the essential unity in structure and function of this organ, the relevant terminology can be greatly reduced and a return made to the simple descriptive terms which were in vogue previously ".

Although phylogeny has been called " the playground of imaginative theorists ", there is a phyletic implication in all plant classification. It is likely that the simplification or reduction in the basidium, which Linder suggests, has been the course of evolution of these fungi, and not as Neuhoff (1924) suggested that heterobasidial types are derivative from homobasidial types. Martin (1938) agrees that the clavate basidium with four sterigmata at the apex of the gonotocont is a reduced, and not a primitive, type. He also observes that reduction is carried still further in the Gasteromycetes, whose sterigmata may be eliminated. Rogers (1934, 1947) comments at some length on this reduction in the Gasteromycetes, in whose homobasidia there is degenerative variability with loss of function. Their sterigmata, no longer serving as spore-projectors, are either grotesquely long and tenuous, or progressively short and obsolescent.

Let us now examine Linder's simple terminology and see how adequate it is in homologising and defining the different parts of heterobasidia (See also Figs. 1 and 2).

(1) PROBASIDIUM.—The term used by van Tieghem (1893) in the connotation given above, was extended by Donk (1931) to include all basidia in the stage between the formation of the primary basidial cell until the time that it forms protuberant extensions which bear the spores directly or indirectly. This is undoubtedly " that part or stage in which karyogamy occurs " (Donk, 1931). Such a definition homologises such diverse structures as: the basal sac of *Helicogloea*; the young, undivided cell of *Tremella*, which later becomes four-celled; the persistent or resistant basal vesicles of some Auriculariaceae, e.g. *Septobasidium*; the young basidium of the Dacryomycetaceae before forking; and the young, clavate basidium of the higher Hymenomycetes before production of sterigmata. Whether these cells are narrow or inflated, thickwalled and resistant or thinwalled and evanescent, does not alter the basic fact of their homology. The point is that these cells bear the same relation to one another in time of appearance

in cytological function for karyogamy, and in development to give rise to further structures designed for spore formation and liberation. Variations such as sclerotic walls are surely insignificant except as biological or ecological adaptations.

For Linder (1940) to limit the term probasidium to the precursor of the young basidium in rusts, smuts and Auriculariaceae is to ignore the potentialities of essentially the same type of cell in other Basidiomycetes.

In some basidia (see Fig. 2) both karyogamy and later meiosis take place in the primary basidial cell which we have here termed the probasidium. In others, karyogamy and meiosis are separated in place, as well as in time of occurrence. Rogers (1934) expresses the view, concerning ancestral types, that if both these events took place in the primary cell (hypobasidium), four nuclei were available to thrust out the four extensions of the wall which he terms epibasidia (e.g. in basidial types such as *Tremella* and *Tulasnella*). On the other hand, if meiosis were delayed and took place in an extension of the hypobasidium, there was only one nucleus to thrust at the wall, and thus only one extension (epibasidium) would be formed (e.g. in basidial types such as *Helicogloea* and other Auriculariaceae). Although it has been shown by Whelden (1935 a, p. 52) and also by Bodman (1938) that the epibasidia of some heterobasidio-mycetes may sometimes be initiated before meiosis of the fusion nucleus, Rogers' explanation given above would certainly appear to be a good one connecting morphological and cytological development in heterobasidia, at least in ancestral types. But can this be used, as by Rogers, to homologise the epibasidium of *Tremella* with that of *Auricularia*? If so, can it ignore the fact that the sterigmata of the clavate homobasidium are produced in the same way as the epibasidia of *Tremella*, yet receive a different name? We think it cannot. On the above explanation Rogers (1934) states that there are two fundamental phyletic tendencies among Basidiomycetes (a) those which have epibasidial meiosis and (b) those with hypobasidial meiosis; but he adds that Donk's distinction between the part or stage of karyogamy (probasidium) and the part or stage in which meiosis occurs (metabasidium) introduces a false complexity. If, however, the phyletic tendencies and the morphological differentiation depend upon the place of meiosis, is this not a fundamental character which should be used in formulating a terminology?

To put the argument another way: Baker (1936) has stated, " If karyogamy and meiosis both take place in the hypobasidium, several epibasidia result; if meiosis is delayed and takes place in an extension of the hypobasidium there can be only one epibasidium ". Again we do not question the correctness of this statement, but only its interpretation for the purposes of a terminology. All that is implicit in this statement forms the crux of the differences between the terminology of Neuhoff and followers, and Donk. From Rogers' and Baker's statements above, the conclusion must inevitably be that the form of the mature basidium is conditioned by the time and place of meiosis, and not that the time and place of meiosis are conditioned by the form of the mature basidium. Yet Rogers accepts the second alternative by basing his terminology on the morphology of the mature basidium, and rejects Donk's terminology which is based on developmental morphology arising from cytological change.

Now, is it possible to homologise the epibasidia of the *Tremella* and *Auricularia* types? Emphatically no! Taking in order the criteria of homology as defined previously, we shall see how the two views clash, and which view best meets the case.

(A) *To be homologous the structures must develop in the same way.*

The epibasidia of *Tremella* and *Auricularia* both develop supposedly in response to the thrust of nuclei and protoplasm upon the wall of the young basidial cell in which karyogamy has occurred; but in *Tremella* the nucleus first divides so that there are four daughter nuclei available to thrust out four extensions. In *Auricularia* the whole protoplast and its single nucleus thrusts out a single extension and the nucleus then

divides. In *Tremella* the epibasidia bear spores directly upon their narrowed apices. In *Auricularia* the epibasidium divides into four cells, and in each cell a nucleus is present to thrust out from the epibasidial segments, terminal or lateral extensions on whose narrowed apices the spores are borne. The development of the epibasidia is certainly not the same in both cases.

(B) *To be homologous the structures must serve the same function.*

The epibasidia of *Tremella* merely serve to carry the nuclei to the spores, and if necessary they may extend so that the spores are produced in the open. The epibasidium of *Auricularia* serves as the place of meiosis, then from its cells are produced the extensions which are necessary for nuclear migration to the spores. These extensions are capable of elongation to meet the ecological need; not so the epibasidium itself which remains fairly constant in length. Surely it is the extensions which are homologous with the epibasidia of *Tremella*. It is naturally realised that extension of part or the whole of the basidium is only one aspect of the variability of heterobasidiomycetes. For example, in *Vuilleminia* it is the metabasidia which extend to enable the spores to be produced at the surface. Taken alone, the functional aspect of extending epibasidia is perhaps not important in homologising these structures, but in conjunction with other facts, particularly morphological, it seems to have a bearing on the subject.

(C) *The structures must have the same relation to a fundamental type.*

Here there is a phyletic implication, which may be largely speculative in fungi, but nevertheless cannot be ignored as it is the basis of our ideas on classification. We therefore agree with Rogers that Basidiomycetes show two distinct phyletic tendencies (*a*) those with epibasidial meiosis and (*b*) those with hypobasidial meiosis. This only serves to strengthen the argument that on account of the different places of meiosis in *Tremella* and *Auricularia* their epibasidia cannot be homologised.

(D) *The structures must have the same relative position.*

In *Tremella* and *Auricularia*, the structures which are called epibasidia are both borne as extensions of the cell in which karyogamy takes place. However, the sterigmata of clavate homobasidia are formed as extensions of a cell in which karyogamy takes place in exactly the same way as in *Tremella* by upthrust of four daughter nuclei. On this view the sterigmata must be homologues of the *Tremella* epibasidia, which Rogers does not accept. In *Auricularia* although the epibasidium is borne as an extension of the cell in which karyogamy takes place, it is not another homologue because meiosis has not yet occurred. It is the terminal or lateral extensions of the epibasidial segments in *Auricularia* which have the same relative position as the epibasidia of *Tremella* and the sterigmata of higher Basidiomycetes.

Neuhoff's terminology does not stand the tests of homology, which have been defined here in most inclusive terms.

(2) BASIDIUM.—Linder (1940) defines a basidium as " that organ which is in part the homologue of the ascus, and which following karyogamy and meiosis bears the basidiospores either directly or through the interpolation of the sterigmata ".

It must be accepted, as previously stated, that the *whole* organ including any basal vesicle or cell, any septate or non-septate extensions, and any spicules on which the basidiospores are borne, must be included in the term basidium. This inclusive sense of the term may be what Linder intended, but actually his definitions limit the term to the part of the basidium left after subtracting probasidia and sterigmata. If this interpretation is correct, then obviously Linder's simplification does not suffice. For descriptive taxonomy alone it would cause unwarranted circumlocution and confusion. The whole mature organ must be called the basidium, and other names sought for its parts. It appears difficult to settle upon terms which convey these distinctions satisfactorily. Neuhoff's epibasidium implies the same as Linder that the spore-bearing

tubules are something " upon the basidium " and not a part of the basidium itself—
though this interpretation is not qualified by its application. Donk's term metabasidium
may be translated as something which is " the conclusion of the basidium ", although
the metabasidium is also only part of the whole basidium. The original meaning of
the term probasidium was " that which comes before the basidium ", but now as an
antithesis to metabasidium it may be interpreted as " the first stage of the basidium ".

(3) STERIGMATA.—Linder (1940) applies this term to " that structure which arises
from the basidium and bears the basidiospores." He continues, " The restriction of
the sterigmata to apply only to that portion of the spore-bearing filament which is very
slender and through which the nucleus squeezes in its passage to the spore, not only
leads to confusion but is illogical."

It has been put forward that there are two criteria of a true sterigma:—

(a) Neuhoff (1924) gives the cytological criterion that the nucleus in passing through
a true sterigma to a spore, becomes elongated and assumes the staining properties
of chromosome-material. All Neuhoff's followers have accepted this as the
criterion of a sterigma. Quite obviously the nucleus must elongate to squeeze
through a narrow passage, but it has been argued that the spatial relation is
inconsequential because in many species the nucleus has been observed to
elongate and change its staining properties before it actually reaches the narrow
passage. This is taken to indicate that the area approaching the passage is
distinguished in some way other than narrowness from the remainder of the
tubular appendage, and should be named differently. Early attenuation of
the nucleus was observed in *Helicogloea* (Baker, 1936), *Exidia* (Whelden,
1935 a) and *Tremella* (Whelden, 1934), and may be accepted as fact. If, as
in *Helicogloea*, elongation of the nucleus is initiated in the epibasidial segments
well before the nucleus approaches the narrow passage, or if elongation occurs
at a variable distance from the passage, what are to be regarded as the
morphological limits of the " true sterigma "? Where is the point where one
may say, " Here the epibasidium ends, and here the sterigma begins?" There
are a few exceptions, e.g. *Xenolachne* (Rogers, 1947) where there is a fairly
sharp distinction on account of the grossly attenuated, long sterigma, and also
in *Tulasnella tulasnei* (Rogers, 1932, pp. 95–96) where the sterigmata elongate
greatly as an adaptation to the presence of a gelatinous matrix round the
basidia. Even in these it is possible that the nucleus might elongate at a variable
distance from the morphological " sterigma ". It is obviously impossible to
set the limits of the " true sterigma " without a cytological investigation of
each and every basidium in development, and even then it may be found that
this point is variable in a single species, or even in different basidia of the same
specimen. Further, may not the change in staining reaction be due simply
to the physical fact of elongation, so that the nuclear components are spread
out and of necessity become coloured differently from an opaque and compact
body? Such an effect is frequently seen in staining blood smears, where the
staining reaction of the nuclei of various types of cells depends to an extent
upon the thinness of the smear.

(b) Buller's (1922, p. 31) criterion of a sterigma is functional and not cytological,
viz. that a sterigma is an organ for bearing and forcibly discharging the spore.
True, forcible discharge is not universal. There are gymnocarpous Basidio-
mycetes in which forcible discharge is either impossible or of no advantage to
the fungus, and in these the sterigmata have lost their function, becoming
reduced to very short attachments or alternatively becoming disproportionately
long and filamentous. In either of these instances the attachment of the spore
is delicate and enhances the possibility of its being set free by fracture. In
other words this reduction or distortion is an adaptation to loss of function,

and must strengthen the opinion that the functional criterion of a sterigma is important. Rogers (1947) has given a clear account of such basidia, terming them apobasidia with the definition of an apobasidium as " a basidium whose basidiospores are not apiculate, nor borne obliquely on the sterigmata, nor forcibly discharged ".

Further to the functional aspect, it has been argued that the epibasidium is an adaptation to ensure that the migrating nucleus shall be transported through varying depths of jelly in gelatinous Heterobasidiomycetes to the surface, where a true sterigma may be formed in the open to serve its function of discharging the spore freely and with the greatest possible chance of subsequent dispersal. We do not question that this process occurs, but only that it serves further to distinguish the parts called epibasidia and sterigmata by Neuhoff. Considering the whole organ as designed to bear and liberate the spores under the best possible conditions, why, from the fact that part of it is capable of elongation to meet the environmental conditions, should that part be held a separate entity? And further, it is true that in some instances [e.g. in *Tulasnella tulasnei* (Rogers, 1932)] the other part, namely the narrow terminal pedicel or " true sterigma " of Neuhoff, is also capable of extension when embedded in a gelatinous matrix. Baker's work (1936) on *Helicogloea* shows that if the epibasidia are immersed each cell may develop a tubular extension as an adaptation to the immersed condition, but protruding epibasidia form " sterigmata " directly without the need for tubular extensions. In this case, are the lateral extensions and the sterigmata to be held apart, or are they merely variations of a single organ? Surely the second alternative! Again, in *Vuilleminia* the whole basidium may elongate according to the depth at which it is embedded in a semi-gelatinous matrix. Variation in length to meet the environmental conditions is certainly not solely an attribute of epibasidia. It occurs in epibasidia, and in sterigmata (both sensu Neuhoff) and also in metabasidia (sensu Donk). Variation, as Rogers (1934) justly observes, is one of the hall-marks of Heterobasidiomycetes, and is largely a response to the ecological conditions and especially to the water factor. One comes to the conclusion that the whole tubular appendage is a single entity in which the nucleus migrates to the apex, elongates on approaching, but at no fixed distance from the narrow passage with change in staining properties, and enters the spore which is finally discharged. Conditional upon the type of basidium and the depth at which it is embedded, the basal part or sometimes the narrower apical part of the spore-bearing organ, or even the whole basidium, may elongate to ensure that the spore is formed and receives its nucleus in the air, so that it may be freely liberated for dispersal.

From the foregoing we can agree with Donk (1931) and Linder (1940) to call the whole tubular spore-bearing appendage a sterigma. But there is still the somewhat exceptional case of *Tulasnella* to consider. In the development of the *Tulasnella* basidium there are two divergences from the usual state in most hererobasidia, namely that the " epibasidia " are cut off by basal septa, and that the first post-meiotic mitosis takes place in the " epibasidia ".

The ovoid form of the *Tulasnella* epibasidium is suggestive of a spore; this fact has lead to its being considered as a sessile basidiospore which germinates in place to form a conidium. Heim (1949) has suggested that the basidia of *Tulasnella* are similar to teratological basidia of certain Homobasidiomycetes, in which the basidium produces a prolongation terminating in a sporoid body, the latter liable in turn to produce a conidium. Heim terms this prolongation (epibasidium sensu Neuhoff) a hemibasidiospore, and its terminal " spore " a basidioconidium, which can produce secondary conidia. He suggests that the whole structure composed of hemibasidiospore and basidioconidium, corresponds to a sessile basidiospore produced incompletely by an

accelerated sporogenetic rhythm. This is essentially a more modern version of Juel's (1897) interpretation of the *Tulasnella* basidium as one bearing sessile basidiospores germinating in place to give secondary spores or conidia. Rogers (1932) summarised Juel's points for this interpretation and provided convincing counter-arguments to show that Juel's points are, on the whole, not antagonistic to Neuhoff's conception of this basidium. Donk (1931, p. 115) has also dismissed Juel's interpretation mainly on the grounds of similarity in the basidia of *Tulasnella* and *Botryobasidium* (*Pellicularia*). This would perhaps be more correct if the similarities offered were as between *Tulasnella* and *Ceratobasidium* (some species of which were formerly placed in *Botryobasidium*).

In *Tulasnella* (Rogers, 1932) following karyogamy and two meiotic divisions of the fusion nucleus, the epibasidia are formed and are then cut off by a basal septum from the rest of the basidium. In the epibasidia there follows the first post-meiotic mitosis, after which one of the daughter nuclei migrates to the apical sporoid body. Rogers (1932, p. 100) states, " Mitosis within the appendage is not the impossible behaviour of an extension of the basidium that it would be for a sterigma." This statement should at least be qualified by the definition accepted for a sterigma, for both epibasidia (sensu Rogers) and sterigmata (in our sense) *are* extensions of the basidial cell. Certainly the " sterigma " of Rogers (i.e. Donk's spiculum) would be too confined a space in which to expect mitosis. But is it correct to say that this mitosis within the tubular organ really distinguishes this organ from homology with similar organs which apparently only serve for migration of the nucleus and spore-bearing? If it is held that they are not homologous solely on this account, then equally well these tubes cannot all be called epibasidia, nor sterigmata. On the other hand, if they *are* homologous then they may be called either sterigmata or epibasidia according to choice of terminology. Taken alone, the first post-meiotic mitosis within the tubes of *Tulasnella* cannot serve as an argument for not calling these organs sterigmata.

Martin (1938) observes that the place of meiosis should not be regarded as a fundamental basidial character as it may take place within the limits of the original cell (pro- or hypobasidium) or within extensions of the cell wall (epibasidium). He considers it a secondary character, conditioned at least in some instances by the nature of the zeugite. If we took up this premise then it would be illogical to regard either Donk's probasidium (the place of karyogamy) or his metabasidium (the place of meiosis) as fundamental. But we have already observed that the two fundamental phyletic tendencies in Basidiomycetes are indicated by epibasidial meiosis and hypobasidial meiosis, and that the morphological differentiation of the basidium is connected with the place or stage of meiosis. That being so, this is most surely a fundamental basidial character, which governs the final form of the basidium. The possibility that meiosis may take place in one of two set places and thus be bound up with the production of either one or several extensions of the primary basidial wall, points to this feature as fundamental. But on the contrary the place of the first post-meiotic mitosis cannot be considered fundamental, for it does not alter the established pattern of morphological change. In Hymenomycetes it may occur either in the metabasidium, or in the sterigmata (our sense) or in the spores, and is not bound to a fixed site. In *Tulasnella* (Rogers, 1932, p. 103) all three possibilities seem to occur. In the basidia with more than four sterigmata the first post-meiotic division is likely to occur in the metabasidium; in some species it is known to occur in the sterigmata; and in a few other species it is unknown either in the metabasidium or in the sterigmata, hence likely in the spores. But note that in all these instances the general pattern of the *Tulasnella* basidium is unchanged. In several other genera the first post-meiotic mitosis occurs in the spores (cfr. Maire, 1902). As this mitosis may occur in the metabasidia or in the spores, there is no reason why it should not be expected in an intermediate organ, the sterigma, especially if the last passes through an accumulative phase in which it achieves a certain degree of independence from the rest of the basidium, and if it is spacious enough to permit nuclear division to occur.

In the Clavulinaceae (Gäumann, 1928, p. 532) the mature basidia contain eight nuclei as a result of a triple division of the diploid nucleus, the number of sterigmata is variable, the spores each contain one nucleus, and a variable number of nuclei degenerate within the body of the basidium. The position regarding the third division of the fusion nucleus within the basidium is much the same in the Cantharellaceae (Gäumann, 1928, pp. 533–534). Also in a species of *Kordyana* (Gäumann, 1928, p. 530) the basidia may be the seat of extra (abnormal for the species) divisions under certain weather conditions, producing extra nuclei for which extra sterigmata are formed.

The foregoing arguments, it is hoped, serve to show that the occurrence of the first post-meiotic mitosis within the spore-bearing organ is not a valid argument for not calling this organ a sterigma in *Tulasnella*. Now, what about the basal septation of these organs in *Tulasnella*? There seems no *a priori* reason why a sterigma on receiving its protoplast and nucleus, should not become inflated and separated from its parent cell by a septum, particularly if this represents an accumulative phase in which the nucleus is about to divide. The fact is, however, that apart from *Tulasnella* and certain irregular cases recorded in *Ceratobasidium* and in some Dacryomycetaceae (Rogers, 1934, p. 170; Rogers, 1935, p. 4), septa are not known at the base of the sterigmata. It is part of the Neuhoff school of thought that epibasidia may be characterised by production of septa; it is not commonly a way of characterising a sterigma, although it could be argued that just as a spore may become septate, so also could a sterigma without justifying a change of name. The standpoint we adhere to is that this is merely another aspect of the variability of heterobasidia particularly in a primitive type coming near to its Ascomycete ancestors.

There is a good deal of agreement between many workers (cfr. Rogers, 1932, 1934; Gäumann, 1928; Heim, 1949) that the spore-bearing organ of *Tulasnella*-type may have originated from a type of Ascomycete showing ascospores thrusting out the wall of the ascus and germinating exogenously by a conidium. On this hypothesis Rogers (1934, p. 168) suggests that " the *Tulasnella* basidium, as highly organised as any existing type, is phylogenetically closest of existent types to the antecedent ascus ", and further that the epibasidia are essentially homologous with ascospores. The same explanation may be given for the origin of the sterigma, and is accepted as that here; or it may also be given as the origin of the sporoid hemibasidiospore of Heim's interpretation. Allowing now for the primitive nature of the *Tulasnella* type of basidium, or of its immediate ancestors in which the process of exogenous spore formation may be only lightly established, what is more likely than that there should be variations in this process? And what variation is more likely than one involving the degree of independence of the ascospore (or the derivative " epibasidium ") from its parent cell, i.e. the formation of septa?

The close affinity of *Ceratobasidium* (Rogers, 1935, p. 4; Martin, 1948, p. 114) with *Tulasnella* makes possible either the derivation of the former from the latter type of basidium, with loss of septation, or suggests an independent derivation of *Ceratobasidium* from an Ascomycete type, in this case no septa appearing at the base of the sterigmata. The fact that there are occasionally adventitious septa in *Ceratobasidium* (Rogers, 1935) is highly suggestive that this process was once a normal occurrence in a related type which has now been lost. Alternatively it may argue the derivation of the *Tulasnella* type of basidium from that of *Ceratobasidium*. Whichever way about, it shows that the septation is variable as would be expected in a primitive type. From types such as *Ceratobasidium sterigmaticum*, with two inflated sterigmata, (Rogers, 1935, 7, fig. 4) could be derived the Dacryomycete basidium which is known to produce occasional adventitious septa (Rogers, 1934, p. 170) in the sterigmata, while *Pellicularia flavescens* with inflated cornute sterigmata and repetitive spores (Rogers, 1935; Rogers, 1943, p. 105) provides a link between *Ceratobasidium* and other *Pellicularia* species and hence to the Corticiaceae. From the inflated and septate sterigma to the filamentous and non-septate sterigma there are a series of known types which

indicate the possible phylogenetic changes, and simultaneously there has been a change from variability in these features to stability. In essentials the sterigma has remained the same throughout, an organ for the migration of the nucleus to the spore and one which bears and discharges the spore.

If the sterigmata are called epibasidia in *Tulasnella* and *Ceratobasidium*, but sterigmata in *Pellicularia* (which includes species such as *P. flavescens* with sterigmata no different from the *Ceratobasidium* epibasidia) one is bound to establish a special family Ceratobasidiaceae (Martin, 1948, p. 114). If all these structures are sterigmata, and they undoubtedly are all homologous, such families are at least suspect.

From the foregoing we accept the tubular sporebearing structure(s) *in toto* as a sterigma. Donk has differentiated the apex of the sterigma by the term spiculum (coined by Tulasne, 1853) and the lower part of the sterigma by the term protosterigma (coined by Donk, and used here for the first time in publication with his kind permission). This differentiation in the terminology of the parts of the sterigma is best understood by referring to Dr. Donk's own " Note on Sterigmata in General ". (See p. 301).

This interpretation of the sterigma may not be accepted by followers of Neuhoff's terminology. But again consider the case of an auricularious basidium like that figured for *Septobasidium* in Figs. 1 and 3. Here the part which we call a sterigma is entirely homologous with the same extensions in a *Tremella* basidium. To us they are both sterigmata. To Neuhoff those structures in *Tremella* are four one-celled epibasidia (or " not separate cells, but extensions of the hypobasidial segments "—Martin, 1938). But in the auricularious basidium, organs having the same morphology, function and cytology are either known as sterigmata (if they are short consequent upon being produced on emergent basidia) or as unnamed lateral extensions of each cell of the four-celled epibasidium (if they are elongated consequent upon being formed on deeply immersed basidia). In the latter instance Donk has ironically suggested (in Litt.) that it would be logical to call them epiepibasidia! It cannot be controverted that the Neuhoff School homologises the four epibasidia (sterigmata in our view) of *Tremella*, with the single four-celled epibasidium *and* its lateral extensions or sterigmata of the auricularious basidium. The point is that the sterigmata, in our sense, of the auricularious basidium are regarded as part or extensions of the epibasidium by Neuhoff, but as the whole epibasidium in tremellaceous basidia. To equate the part (in *Tremella*) with the whole (in *Auricularia*) is preposterous, and on this contention alone it is impossible to accept Neuhoff's terms epi- and hypo-basidium.

On the other hand, the four-celled parts of the *Auricularia* and *Tremella* basidia are entirely homologous and should receive the same name. Both develop from a probasidium in which karyogamy occurs. In both meiosis takes place, followed by septation (differing only in the plane of septation) and production of a sterigmatic outgrowth from each cell. That the plane of septation is different is of little importance, as is shown by the fact that in various Tremellaceae marked variation in the plane of septation may occur (Whelden, 1935 c).

Now, having rejected Neuhoff's and Linder's terminologies can we accept Donk's? We have already accepted his probasidium, and sterigma composed of protosterigma and spiculum; there remains to consider his metabasidium, for whose acceptance some arguments have already been given. The definition of a metabasidium as that part or stage of the basidium in which meiosis occurs, is a cytological one. It may be held that a definition based on cytology is impracticable in routine work on morphology and taxonomy, and thus an undesirable, even though fundamentally true, definition. It may be held that Neuhoff's terms are simpler to apply, that the swollen basal part of the basidium is the hypo-basidium and that everything above that is the epibasidium, except the spore-bearing spicules, which are true sterigmata. In practice Donk's terminology is no more difficult to apply: a probasidium, whether as a resistant or merely as a primary basidial cell can be recognised at once; so can the sterigmata or

tubular spore-bearing filaments; what is left is the metabasidium, which in some cases quite obviously replaces the primary cell.

Now consider the basidia of *Phleogena faginea* (Shear & Dodge, 1925) and *Mycogloea carnosa* (Olive, 1950), both illustrated in Fig. 3. In *Phleogena* there is a basidial stipe bearing a cell in which successively karyogamy, meiosis, transverse septation and production of lateral spore-bearing filaments occur. In Neuhoff's terminology, the whole basidium here must be an epibasidium, but this epibasidium is not a structure seated " upon a basidium " or even upon a hypobasidium. It is instead simply seated upon a basidial stipe, i.e. a basidium-bearing hypha. Donk's terminology, however, accounts for a probasidium replaced by a (four-celled) metabasidium each cell of which bears a sterigma and spore. It appears to the writer that the developmental connotation in Donk's terminology is important, and that it is insufficient to define a basidium only on its mature morphology.

Or again, in *Mycogloea*, there is a basidial stipe bearing a cell which is similarly changed from a probasidium to a metabasidium with sterigmata. Again Neuhoff's terminology is quite inadequate as it allows only for the epibasidium.

Further interesting basidial types, which put terminology to the test of constancy to the same principles, are those in which the basidia are somewhat intermediate between other well-known basidial types such as characterise different families or even sub-classes. Their intermediate nature allows actual or potential disagreement on their taxonomic position. Is the terminology applied to one and the same part of the basidium to change according to the family or sub-class in which the fungus is classified? A good example is *Patouillardina (Atractobasidium)*, illustrated in Fig. 3, 10. The author of this genus did not describe it adequately or quite correctly (Bresadola, 1906 and 1920, p. 52), but appeared to place it in the Auriculariaceae. Martin (1935, 1939, 1945) has classified it in the Tremellaceae on account of the " regular perpendicular alignment of the second basidial septa with reference to the first septum ", but also noted that the basidia are somewhat intermediate between those of these two families. Thus Martin would consider that the basidium is composed of one four-celled hypobasidium, each cell bearing an epibasidium. Suppose now a good reason were found for allying *Patouillardina* with the Auriculariaceae; the basidium would still be exactly the same but the terminology would be reversed. The basidium would then be composed of a four-celled epibasidium, each cell of which bears an extension. In Donk's terminology, no matter which classification is accepted, the names of the parts of the basidium remain constant, i.e. in *Patouillardina* there is a probasidium which develops into a four-celled metabasidium, each cell bearing a sterigma.

Another example is *Peniophora heterobasidioides* (Rogers, 1935, p. 30–31). This has affinities with both homo- and heterobasidiomycetes, but is classified as homobasidial with sterigmata and repetitive spores. If the sterigmata had been a little more swollen, can we not suppose that they would have been called epibasidia and the fungus classed as a heterobasidiomycete?

The genus *Ceratobasidium* is placed as a heterobasidiomycete with a primitive type of holobasidium (Rogers, 1935, p. 4; cfr. Martin, 1948). This assignation is probably correct, as indicated by the germination of the basidiospores by repetition. But suppose the point were controversial and it could be held that these were homobasidia. If they are heterobasidia, Rogers' terminology provides for a hypobasidium surmounted by a number of stout epibasidia. If they were homobasidial, the same basidia would be said to consist of basidia with four sterigmata. Donk's terminology for both homo- and heterobasidia of this type is inflexible. For him the basidia of *Ceratobasidium* consist of a metabasidium and four sterigmata, no matter which sub-class is to receive the genus.

Similar arguments apply also to the basidia of *Pellicularia* (*Botryobasidium*), which has already been touched on. Rogers (1935, 1943) classes some species of *Pellicularia* (e.g. *P. flavescens*) as homobasidial, with sterigmate basidia; yet these species have stout, cornute sterigmata no different from those of *Ceratobasidium*, which Rogers classes as heterobasidial, with hypo- and epibasidia. *Ceratobasidium* also links with *Tulasnella* through such species as *C. anceps* in which the epibasidia are not cut off by a basal septum.

To what Extent are Morphology and Cytology linked?

From the examples given above in various connections it is obvious that the probable sites of karyogamy and meiosis can be inferred from the mature morphology of the basidium, given the basic knowledge we already have of the cytology of a number of basidial types. The place of the first post-meiotic mitosis, variations in the plane of formation of the septa, and the plane of the mitotic spindles cannot generally be inferred. One might suppose that generally in a broad ovate or clavate basidium there would be sufficient space for the mitotic spindle to lie horizontally (i.e. chiastic division). This does not always happen, for in such basidia stichic division, with the spindle placed longitudinally, sometimes takes place. Also in a narrow, cylindrical basidium the spindle might be supposed to lie longitudinally, but again this is not constant. The orientation of the spindle is not even to be correlated with the class of the basidium, for stichic and chiastic types may occur in either homo- or heterobasidiomycetes. Examples of such variations in spindle orientation may be seen by reference to Fig. 2.

The plane of the spindle may not even be constant in a single species (e.g. in *Helicogloea lagerheimi*, Baker, 1936; *Sebacina globospora*, Whelden, 1935 c). It is not impossible that this might be due to sectioning technique, but it might just as well be due to natural variation. Despite this, there is probably not one species sufficiently investigated in this regard that cannot be definitely classed as either chiastic or stichic, especially if in deciding this character one restricts oneself to the first division, which has the longest spindle, and neglects the following ones. In many cases cytology helps to underline differences in basidial shape which would otherwise be underrated or even overlooked, or are difficult to express in terms of basidial morphology (cfr. *Clavulina*, stichic and *Clavaria*, chiastic). However, where the character of spindle orientation has been used as a primary basidial character (Juel, 1898; Maire, 1902; Gäumann, 1928) it has resulted in a quite unnatural grouping of genera. Its use in such instances has been properly censured by Rogers (1934) and Lohwag (1937). Its best use is as a secondary character for the separation of small groups, and certainly not as a primary one for the linking of large groups.

Size and Shape of Basidia.

In the higher Hymenomycetes the hymenium is compact and resists lateral expansion of the basidia, with the result that they tend to be clavate or cylindrical. In simpler forms, which are often gelatinous or composed of loosely arranged tissues with an irregular or discontinuous hymenium, the basidia can expand laterally and assume many different shapes. Several of these types are illustrated in Fig. 3, which exemplifies the strange shapes encountered particularly among heterobasidia. A more complete collection of illustrations is not possible here, owing to the difficulty of obtaining suitable material for drawing, or in obtaining permission to reproduce published illustrations.

Basidia may arise singly at the apices of subhymenial hyphae, or in botryose clusters which are perhaps best seen in the genus *Pellicularia*. Basidia ranging in size from $3 \times 7 \mu$ (*Corticium galzini*) to $25 \times 210 \mu$ (*Aleurodiscus amorphus*) have been noted by the writer. To see basidia clearly, crush preparations of very thin sections mounted in 5 per cent potassium hydroxide solution to which a very small drop of 1 per cent aqueous phloxine has been added (Martin, 1934) have been found very satisfactory.
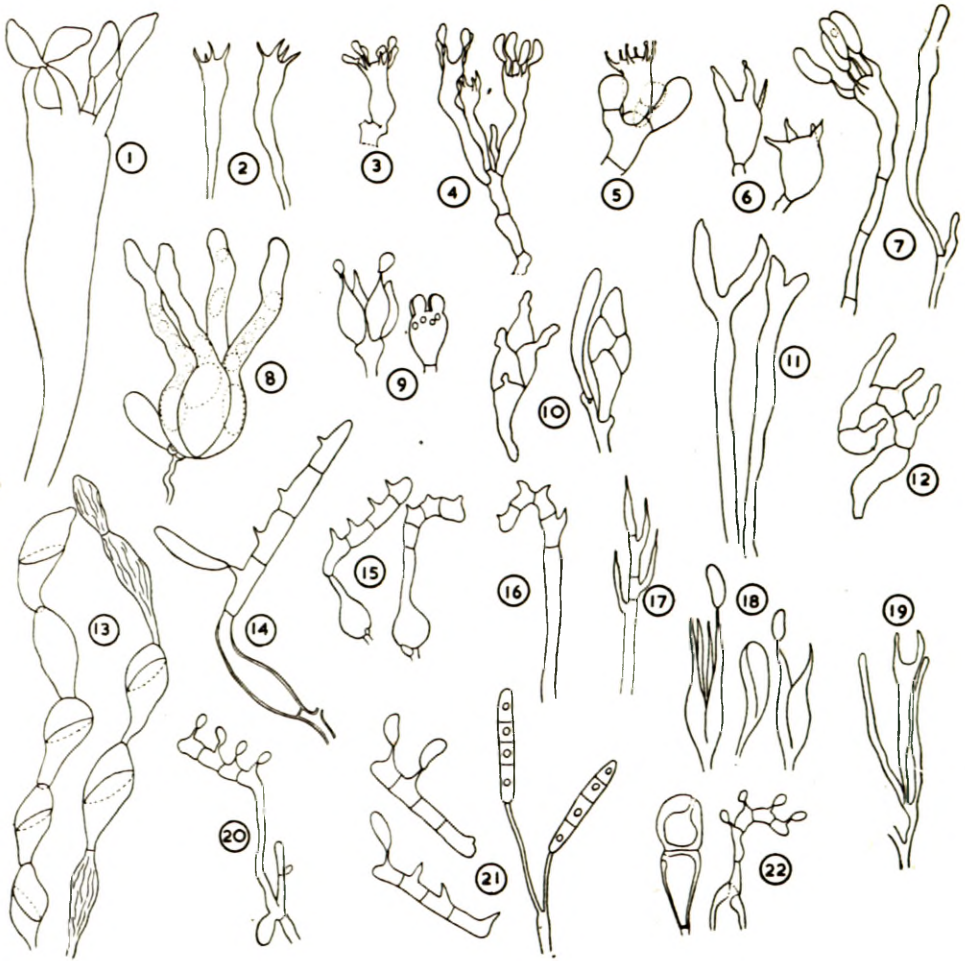
FIG. 3.—A selection of basidial types:—

1. **Aleurodiscus** sp. 2. **Craterellus sinuosus.** 3. **Trechispora raduloides** (after Rogers, 1944). 4. **Galzinia cymosa** (after Rogers, 1944). 5. **Botryobasidium coronatum** (= **Pellicularia pruinata**; after Rogers, 1934). 6. **Ceratobasidium fibrillosum** (after Martin, 1948). 7. **Vuilleminia comedens.** 8. **Sebacina megaspora** (after Martin, 1936). 9. **Tulasnella violacea** (after Rogers, 1934). 10. **Patouillardina cinerea** (after Martin, 1935, as **Attractobasidium corticioides.** 11. **Femsjonia luteoalba.** 12. **Neotyphula guianensis** (after Martin, 1948). 13. **Sirobasidium brefeldianum** (after Coker, 1920). 14. **Septobasidium burtii** (after Couch, 1938) 15. **Cystobasidium sebaceum** (after Martin, 1939). 16. **Helicobasidium purpureum.** 17. **Auricularia** sp. 18. **Eichleriella** (the two figs. to the right after Bourdot & Galzin, 1928; the one to the left, **E. incarnata,** after Bresadola, 1903). 19. **Dacryomyces deliquescens.** 20. **Helicogloea lagerheimi** (=**Saccoblastia sebacea**; after Wakefield & Pearson, 1923). 21. **Mycogloea carnosa** (after Olive, 1950). 22. **Puccinia caricis** (after Grove, 1913).

Summary of Terminology for Basidia Accepted here.

Basidium.—That organ of the Basidiomycetes which is partly the homologue of the ascus, and which following karyogamy and meiosis bears the basidiospores either directly or on extensions of the gonotocont wall, the sterigmata. The term is taken to include the probasidia, metabasidia and sterigmata as parts of the whole basidium.

Probasidium.—That part or stage of the basidium in which karyogamy occurs, i.e. the primary basidial cell. Included also in this term are the teleutospores of Rusts, the chlamydospores of Smuts, and the more or less persistent or resistant cells in the same stage of development in the Auriculariaceae. The term is intended to denote the " first stage of the basidium " rather than " that which precedes the basidium ".

Metabasidium.—That part or stage of the basidium in which meiosis of the diploid nucleus occurs. In many basidia it obviously replaces the probasidium. The term is intended to denote the final stage of the basidium as an antithesis to the first stage, or probasidium.

Sterigma.—That part of the basidium which comes between the metabasidium and the basidiospores, or the elongations of the metabasidium through which the nuclei migrate to the spores which are borne terminally. The sterigma is composed of a basal, filamentous or inflated part called the protosterigma, and an apical point called the spiculum on which the spore is borne. (See also pp. 301–302).

Holobasidium.—An unseptate basidium. It is most common in homobasidiomycetes, but is sometimes encountered among heterobasidiomycetes, e.g. in *Ceratobasidium* and Dacryomycetaceae.

Phragmobasidium.—A basidium which is divided by septa. The metabasidium is divided into a number of cells (usually four) by cruciate or parallel septa after meiosis, or in some instances the sterigmata are separated from the metabasidium by basal septa. The term is the antithesis of a holobasidium.

Heterobasidium.—A basidium of the Heterobasidiomycetes.

Homobasidium.—A basidium of the Homobasidiomycetes.

Heterobasidiomycete.—A basidiomycete in which there is a phragmobasidium, or if the basidia are holobasidia then the sterigmata are differentiated as stout, subulate or cornute structures associated with basidiospores which germinate by repetition. The definition of a Heterobasidiomycete based on the presence of an epibasidium is inherently unsound because, as we hope to have shown, the epibasidium itself is not defined in such a way as to represent a constant entity. Among holobasidia such as found in *Dacryomyces* or *Ceratobasidium* the " epibasidium " is recognised in practice as a swollen, stout sterigma associated with other characters such as spore repetition, or elongation of tne sterigma to meet the environmental conditions, which give the clue to the heterobasidiomyceteous nature of the fungus. The concept of an epibasidium is quite unnecessary for the definition of a Dacryomycete basidium.

Homobasidiomycete.—A Basidiomycete other than a Heterobasidiomycete. The group is characterised by basidia which are not septate, do not possess stout, swollen sterigmata, and which produce basidiospores which germinate directly to form a mycelium.

Texture.

Although the character of texture is a complex of several properties, and eludes precise definition, it has sometimes been used successfully in the taxonomy of the resupinate Hymenomycetes, for example by Bourdot & Galzin (1928) in the genera *Corticium* and *Peniophora*. Texture is a physical character, but may be modified by chemical changes. This occurs in matrices which become gelatinous, mucilaginous

or ceraceous, or which have mineral matter deposited in the tissues. In the higher Hymenomycetes, especially those which are coriaceous, suberose or ligneous, the consistency of the pileus and cuticle may be correlated with the type of hyphae and their direction in a particular plane (Ames, 1913, p. 220; Lohwag, 1940). In resupinate Hymenomycetes the texture depends mostly on the compactness of the hymenium in relation to that of the intermediate and basal layers, but it is also influenced by the thickness, and particularly the moistness of the fungus.

The texture may vary with the age of the fungus, and also with the relative rates of tangential and radial growth. Thus the margin of a fungus often differs in texture from the older parts, owing to a difference in compactness of growth. *Duportella tristicula* when young, is velutinate owing to the presence at the surface of numerous upright hyphae; later the hymenium forms above these hyphae and the fungus becomes membranous or coriaceous, with a rather waxy hymenium. Similarly, purely superficial modifications of texture may occur in the genera *Peniophora* and *Hymenochaete* by late production of cystidia and setae respectively. These often impart a glitter to the surface, and feel scabrid if they are sufficiently robust.

The texture may be modified by chemical change. *Ceraceous* fungi appear waxy. The tissues are usually compacted by a waxy substance which may obliterate the hyphae or render them indistinct, giving the impression of degeneration. The wax often forms an obstructive emulsion in alkaline mounts of sections. Gloeocystidia filled with oily globules can also give the fungus a ceraceous appearance. This state, where the waxy or oily substance is intracellular, contrasts with the commoner one where it invests the outside of the cells. The latter condition is particularly common in the genera *Acia* and *Phlebia*, but is by no means confined to those genera.

The hyphae of *gelatinous* species (Fig. **4**, 1) often appear filamentous, only the lumen showing distinctly with stains like phloxine. Gelatinised hyphae are best stained with iodine or with ammoniacal aqueous methylene blue (Nannfeldt, 1947, p. 332), which reveals that the hyphae are frequently loosely intertexed but held together by a gelatinous substance. This has the power of imbibing water, in contrast with non-gelatinous matrices which absorb water by capillarity (Buller, 1922, p. 157). The gelatinous modification is characteristic of the majority of common Heterobasidiomycetes, where it would seem to be an ecological adaptation for securing quick imbibition and retention of water. It may also be regarded as the author of the heterobasidium, which requires a spacious hymenium for its development.

Mucilaginous species have much the same construction as gelatinous ones, but differ in having a matrix of thinner, slimy consistency.

A *corneous* texture usually results from the loss of water from tissues which were previously ceraceous, gelatinous or mucilaginous. This is exemplified in the genera *Tremella* and *Auricularia*, and in such species as *Peniophora gigantea*.

For taxonomic work on the lower Hymenomycetes, the types of texture described below are important:—

(1) *Membranous* (Fig. **4**, 5).—The hymenium is a compact palisade but not otherwise sharply differentiated from the subhymenial and deeper tissues, which are usually also fairly compact. The fructification may be adnate, separable, or held to the substratum by superficial intrusive hyphae. This group contains most of the species with thick, moist hymenophores.

(2) *Pellicular* (Fig. **4**, 4).—The hymenium is sharply differentiated as a thin crust lying above loosely arranged inferior tissues. The hymenium is continuous and compact at maturity, but at times may be discontinuous in patches thus appearing minutely poroid under the lens. Pellicular species are generally rather thin and
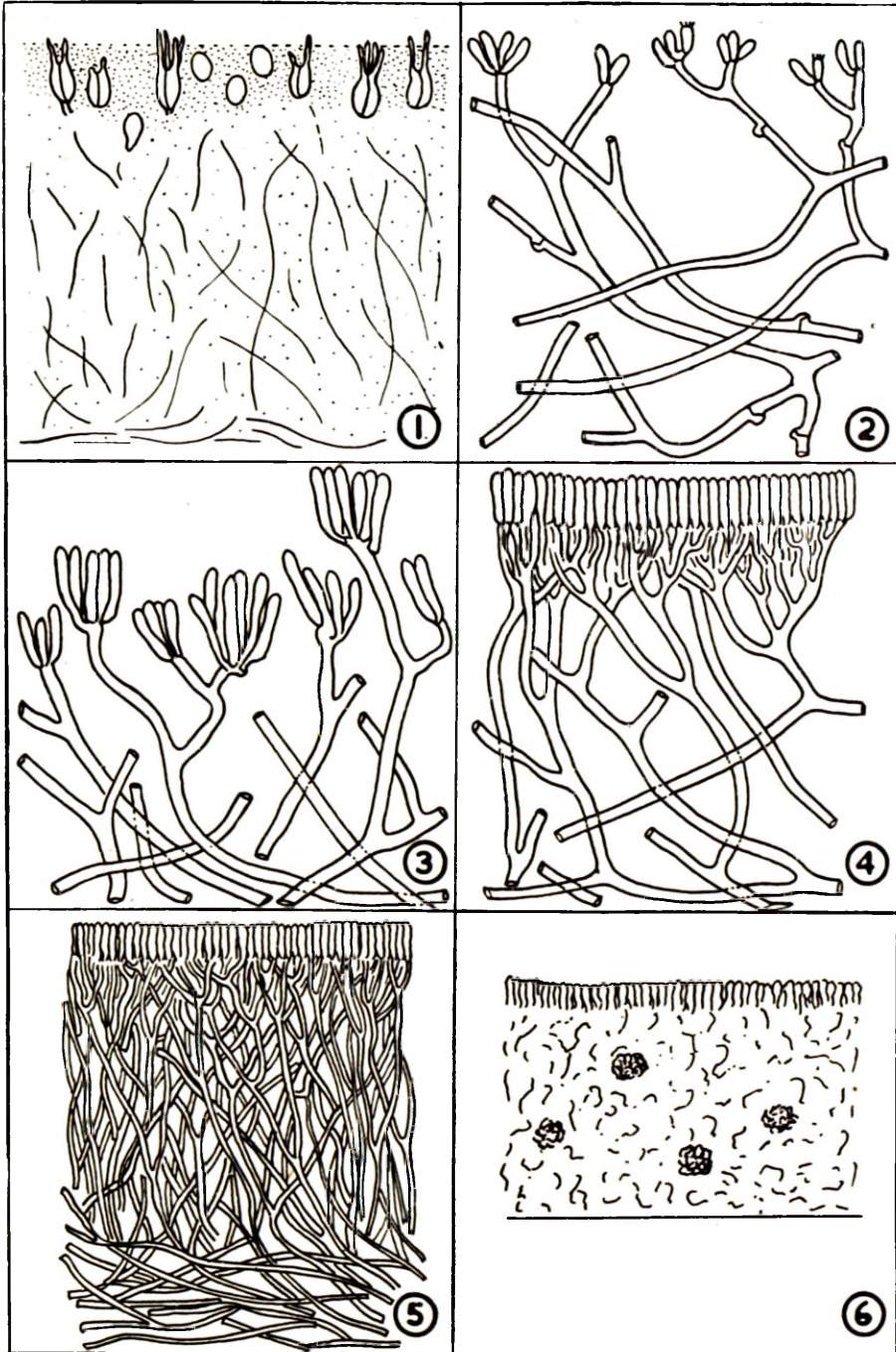
FIG. 4.—Diagrams of sections of fructifications of resupinate Hymenomycetes illustrating the arrangement of tissues in the following textural types:—

1. Gelatinous. 2. Arachnoid. 3. Byssoid. 4. Pellicular. 5. Membranous. 6. Crustose.

dry; the open nature of the tissues is doubtless responsible for quick drying out. The hyphae are usually very distinct. Most of these species are separable from the substratum by snapping of the basal tissues under tension.

(3) *Byssoid or Floccose* (Fig. **4**, 3).—Here there are no compact tissues, even the hymenium being irregular, discontinuous, and often staged at different levels. A fairly thick, tufted or woolly structure results, in which the hyphae are loosely arranged throughout. The hyphae are easily detached from the substratum by breaking under tension.

(4) *Arachnoid* (Fig. **4**, 2).—This type of texture is common in the young stages of growth but may persist into maturity, and then the hymenial elements are quite scattered and discontinuous. The hyphae are usually delicate (though not in the genus *Pellicularia*), and more or less adpressed to the substratum in an openwork structure reminiscent of cobwebs. When the elements of the fungus are so dry and discontinuous as to appear scurfy or mealy, then the terms *furfuraceous* or *farinaceous* are applicable; in a finer and more powdery state the structure may be termed *pruinose* or *pulverulent*.

(5) *Crustose or Arid* (Fig. **4**, 6).—Certain resupinate fungi are thin, dry, and compact througout their tissues, and lack a distinct cortex. They are conveniently termed crustose. Usually they are adnate; frequently they are charged with mineral matter (e.g. *Aleurodiscus acerinus*). But it is more common for fungi to be *arescent*, that is becoming crustose only on drying, a character well shown in the section Coloratae (Bourdot & Galzin, 1928) of the genus *Peniophora*.

The successful use of texture as a taxonomic character is much limited by the difficulty in defining the types of texture unambiguously. With this in mind, Table 1 has been prepared so that the usage adopted by the writer may be checked by direct reference to material of several species differing in texture.

Margin.

The type of margin depends typically on the compactness of the hyphae composing it, and the direction in which they are intertwined. It may readily be observed that as a resupinate fructification grows, new hyphae and young hymenial elements are differentiated behind the radially expanding periphery. Radial growth generally precedes the tangential growth which is responsible for knitting the hyphae together into a firm fructification. It is thus probable that the presence or absence of marginal hyphal strands depends largely upon the relative rates of radial and tangential growth. The marginal character is fairly constant, and useful in taxonomy. The more important types of margin (illustrated in Fig. 5) are fibrillose, fimbriate, arachnoid (byssoid), villose or pubescent, farinaceous, and pruinose.

Hyphae may be aggregated into thick mycelial strands which sometimes meander over the surface of the fructification or extend beyond the margin [e.g. the cords of hyphae found in *Coniophora arida*, and especially in the section Radicatae (Bourdot & Galzin, 1928) of the genus *Peniophora*]. Certain of the lower Hymenomycetes also develop rhizomorphs (e.g. *Asterostroma rhizomorpha, Septobasidium bagliettoanum, Helicobasidium compactum*). Absence of suitable material has precluded a study of these, but it would be interesting to know how far these thick mycelial cords approach the degree of differentiation of tissues seen in the rhizomorphs of some Agaricaceae [e.g. *Armillaria mellea*, where conducting vessels and hyphae are enclosed in a protective sclerotic rind; *Marasmius* species which form the rhizomorphs known as " horse-hair blights " (Petch, 1915)].

TABLE 1.

SOME SPECIES OF FUNGI WITH THEIR CHARACTERISTIC TEXTURE (MARKED O). THE PRINCIPAL TEXTURE MAY BE MODIFIED BY CHEMICAL OR PHYSICAL CHANGE TO OTHER TEXTURES (MARKED X).

Species of fungus.	Texture, or modifications of the principal texture.								
	Membranous.	Pellicular.	Byssoid.	Arachnoid.	Crustose or Arescent.	Corneous.	Gelatinous.	Ceraceous.	Mucilaginous.
Peniophora									
aspera (= *setigera*)..........	O	—	X	—	—	—	—	—	—
byssoidea....................	—	O	X	—	—	—	—	—	—
cinerea.....................	X	—	—	—	O	—	—	X	—
gigantea....................	O	—	—	—	—	O	—	—	—
proxima....................	O	—	—	—	—	—	—	X	—
pubera......................	O	—	—	—	—	—	—	—	—
velutina.....................	O	—	—	—	—	—	—	—	—
Corticium									
albostramineum..............	O	—	X	—	—	—	—	—	—
arachnoideum................	—	O	—	X	—	—	—	—	—
atrovirens...................	—	—	O	—	—	—	—	—	—
comedens...................	X	—	—	—	—	—	O	—	—
confluens...................	O	—	—	—	—	—	—	O	—
galzini.....................	—	O	—	X	—	—	—	—	—
laeve.......................	O	—	—	—	—	—	—	O	—
polygonium..................	O	—	—	—	—	—	—	O	—
Coniophora									
arida......................	—	O	—	—	—	—	—	—	—
puteana.....................	O	—	—	—	—	—	—	—	—
Tulasnella violea................	—	—	—	—	O	—	—	—	—
Exidia thuretiana...............	O	—	—	—	—	O	X	—	—
Sebacina fugacissima............	—	—	—	—	—	—	—	—	O

Sclerotia.

Sclerotia are stromatic aggregations of hyphae, sometimes as big as a mustard seed, with a compact rind and a mass of pseudoparenchyma within. They occur especially among some of the parasitic species of lower Hymenomycetes, which are pellicular or pruinose and liable to dry out, e.g. *Pellicularia filamentosa* (Rogers, 1943) and *Ceratobasidium anceps* (sub *Corticium*, Gregor, 1932). Probably owing to their hard rinds these sclerotia are able to withstand dry conditions. When present they are an aid to specific diagnosis, but they are not invariably found in any one species.

Relation of hyphae to the substratum.

In his studies of the Thelephoraceae, Burt (1925, 1926) stressed the character of separability of the fungus from the substratum. The writer has examined the reasons why some fungi adhere firmly to the substratum, while others are easily separable. The property of adherence is not entirely an attribute of the fungus, but also derives from the nature of the substratum, and is thus not constant for the same species of fungus. The conclusion is that this character should not be stressed in taxonomy, though it is very interesting biologically. The following are some of the reasons for this conclusion:—

(1) Species which are usually separable, may be adnate or separable in small pieces only, when growing on rough bark into the interstices of which the hyphae may penetrate and there form a compact mass.

(2) Separation may be achieved either by snapping of the basal hyphae under tension, or by carrying away small pieces of the substratum. The character is thus dependent on the relative tensile strengths of the hyphae and the substratum, and in turn upon the state of decomposition of the substratum.

(3) To some extent separability depends upon the composition of the basal tissues of a fungus, which will distrupt more easily if they are loosely interwoven even though such hyphae may be attached to the substratum by numerous intrusive hyphae spread over their entire under surface. There are indeed few resupinate fungi (e.g. *Aleurodiscus amorphus* and *A. disciformis*) which radiate from their primordium without putting down an extensive system of intrusive hyphae into the substratum.
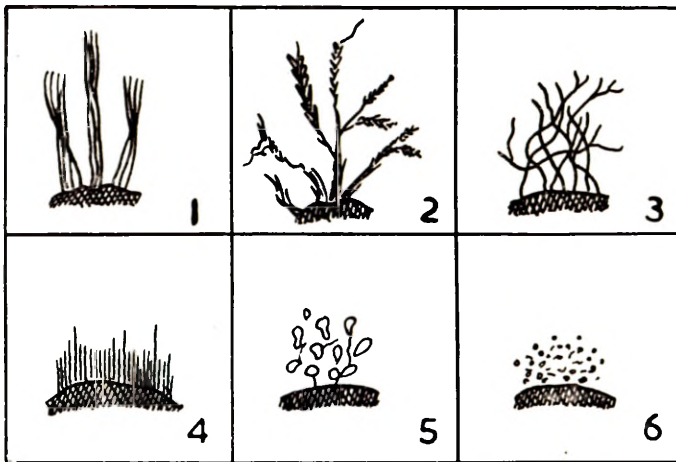

FIG. 5.—Diagrams illustrating terms used in describing margins of lower Hymenomycetes:—
1. Fibrillose. 2. Fimbriate. 3. Arachnoid or Byssoid. 4. Villose or pubescent. 5. Farinaceous. 6. Pruinose.

The question of separability is closely linked with the way in which a resupinate fungus develops from its primordium. One may imagine a fallen twig becoming infected by a fungus. The sequence of events after infection must frequently be as follows:—

The hyphae first ramify through the subcortical layers of the twig then emerge through cracks or lenticels to produce hymenophores. This is supported by the observation that the wood is frequently permeated by hyphae, and that the primordia of the fructifications develop usually above lenticels or cracks in a hard substratum, such situations being paths of little resistance to emergent hyphae. That these hyphae are emergent is deduced from the simultaneous appearance of several primordia which later coalesce (e.g. in *Peniophora cinerea*, *P. quercina*, *P. aurantiaca*); for it is improbable, knowing the low germination rate of basidiospores in nature (Buller, 1909), that the tufts of mycelium at these foci are each the product of separate spores which have lodged in lenticels or cracks, achieved simultaneous germination, and sent down hyphae into the substratum. In some other species, e.g. the *Aleurodiscus* spp. mentioned above, there is often only one primordium and consequently only one deep-seated mass of hyphae concerned in the nutrition of the hymenophore. Sectioning of many fructifications which appear to have arisen from only one primordium and then spread radially, will often reveal that the hyphae lying behind the growing edge may penetrate into the body of the substratum. This effect of secondary penetration by the hyphae is sometimes concerned in giving rise to the adnate condition of resupinate fungi. From a biological point of view, the adnate condition may be supposed to confer an advantage on the fungus by assuring a supply of nutrients and moisture from a wider area of the substratum, and by protecting the fungus from easy dislodgment.

New concepts in studying micromorphology.

Corner (1947, 1948a) has broken new ground in the study of micromorphology of the Basidiomycetes by introducing mathematical expressions derived from careful measurements of a great number of basidiospores, basidia and cystidia. These expressions appear to be of general application. They relate the length and width of these organs, and the volume and spore number of the basidia and basidiospores.

The ratio D/d (where D is the length, and d the width of the basidiospore) expresses the shape of the spore. This ratio plotted against D gives a locus which is called a "sporograph". Corner shows that a locus, and not a point determined by the average range of D and d, is necessary in studying the size and shape of basidiospores, i.e. that a developmental analysis is necessary to understand the adult structure. For example, in certain *Clavaria* species the sporograph clearly relates $5\cdot5 \mu$, subglobose spores with 10–17μ cylindric-fusiform spores. It shows that "giant spores" may not be freaks, but in certain species are spores of the same kind as normal ones only produced on basidia of greater volume than usual. It shows that spores of different kinds may have the same size and shape under certain circumstances. It also shows that in some species at least, micro- and macro-spores are inherently different kinds of spores.

Corner also derived the more general expression $D = d(a + bD)$, where a and b are constants for the species. The values for a and b define different loci for different kinds of spores. A similar relationship holds for basidia, viz. $l = w(a + bl)$, where l is the length of the basidium, w is its width, and a and b are constants for the species. This curve is termed a "basidiograph". The same expression holds for certain types of cystidia which were studied, and Corner proved that some types of cystidia were sterile, precocious and overgrown basidia.

Further studies (Corner, 1948a) on the basidium show that it may be regarded as a self-charged ampoule, containing dense protoplasm which is injected into the basidiospores by enlargement of a basal vacuole acting as a plunger. He established
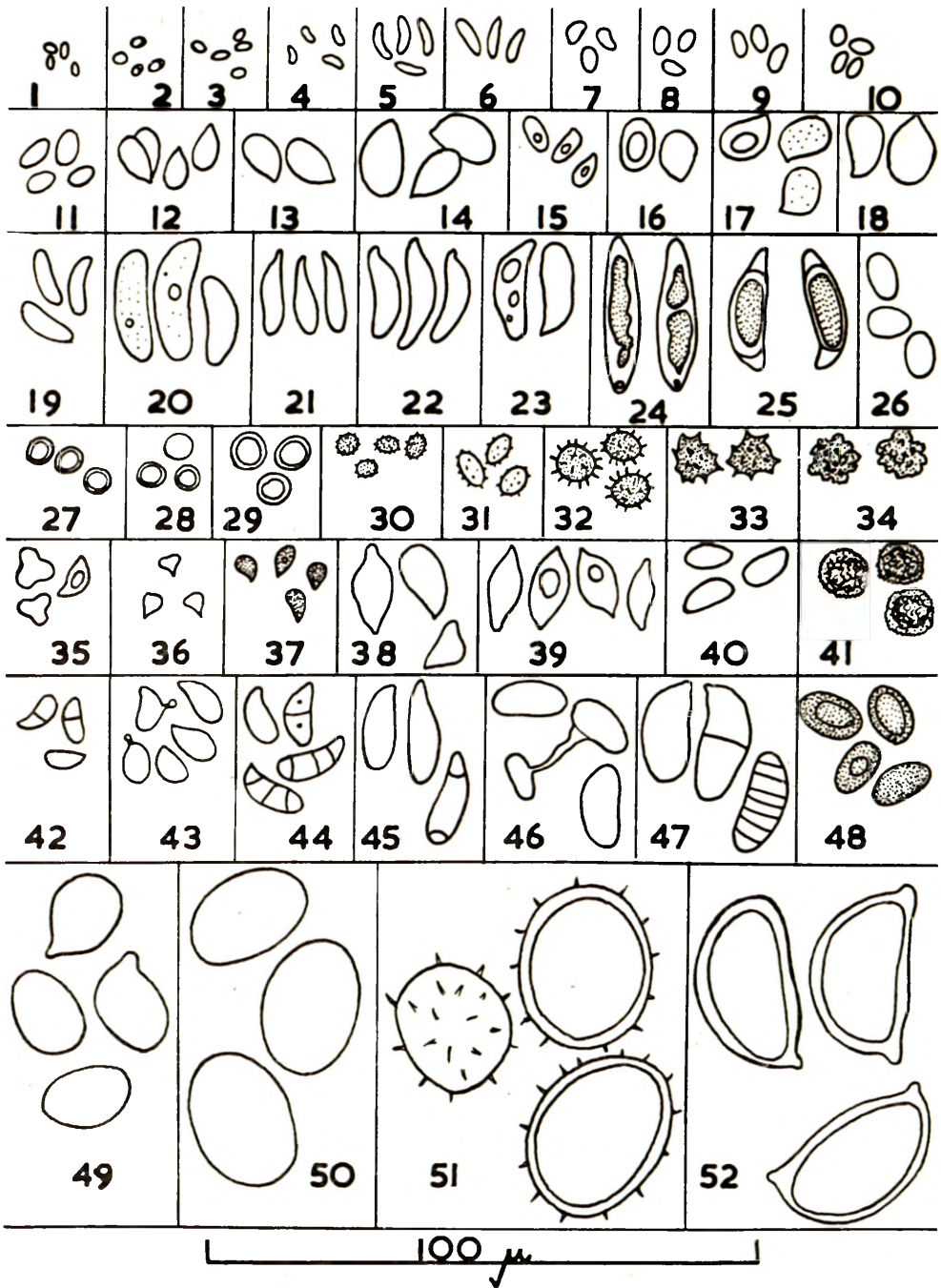
Fig. 6.—A selection of basidiospores:—

1. **Corticium galzini.** 2. **Corticium microsporum.** 3. **Peniophora byssoidea.** 4. **Poria viridans.** 5. **Peniophora subalutacea.** 6. **Cytidia flocculenta.** 7. **Corticium tulasnelloideum.** 8. **Corticium lacteum.** 9. **Corticium niveocremeum.** 10. **Cor-**

the mathematical expression $V - A = nv$, where V is the volume of the basidium, A is the volume of the initial vacuole, v is the volume of the spore, and n is the spore number.

Mathematical expressions such as these are essential for an analysis of the development of these organs, and may be used very successfully to determine whether certain morphologically dissimilar organs are actually homologous. This new concept in the study of micromorphology has been applied with striking success by Corner to a few carefully studied species.

Basidiospores.

The basidiospores are borne singly at the apex of each sterigma, or they are rarely sessile in some Gasteromycetes. There are usually two to four sterigmata per basidium, but some species have a corona of 6–8 or more, which is particularly characteristic of the Urnigera section (Bourdot & Galzin, 1928) of the genus *Corticium*, that is the genus *Trechispora* Karst emend. Rogers (Rogers, 1944).

A selection of basidiospores is illustrated in Fig. 6. In shape they may be subglobose, ovate, oblong, cylindrical, elliptical, navicular, reniform, allantoid, cordate or pyramidical. They frequently have one side depressed and their shape may be modified by an apiculus. They may be hyaline or coloured a light brown, yellowish-brown, sepia, or less commonly brightly coloured in a mass, such colours usually being rosy, violaceous or blue-green. Often the spores are guttulate. Chlamydospores may be developed in the basidiospores of *Jaapia argillacea* (Fig. 7, 4). These are lightly coloured, and form in such a way that the ends of the basidiospore are distinct and colourless, thus this structure has sometimes been regarded as a guttulate basidiospore. Rogers (1935, pp. 29–30) disposes of that interpretation effectively. The majority of spores are smoothwalled, but in some species they are minutely sculptured, or in others bear large spines, warts or reticulations. Sculpturing is frequently accompanied by a slight thickening of the spore wall and also by coloration. Taken alone, sculpturing and coloration are not good generic characters, though they have often been misused as such. Miss Wakefield (1935) cites several examples of this misuse.

The range of spore size is large. To quote the two examples used in connection with basidia, *Corticium galzini* has spores measuring $1 \cdot 5 – 2 \cdot 5 \times 3 – 4 \cdot 5 \ \mu$, while those of *Aleurodiscus amorphus* measure about $22 \cdot 5 \times 29 \cdot 5 \ \mu$ excluding the spiny outgrowths. The spores of the latter species give an amyloid reaction, turning blue in the presence of Melzer's chloral-iodine solution. This reaction is given by many species and is a useful aid in diagnosis.

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ticium centrifugum. 11. **Corticium calceum.** 12. **Corticium laeve.** 13. **Corticium salmonicolor.** 14. **Cyphella alboviolascens.** 15. **Cyphella punctiformis.** 16. **Corticium karstenii.** 17. **Corticium confluens.** 18. **Corticium laetum.** 19. **Corticium polygonium.** 20. **Vuilleminia comedens.** 21. **Corticium aurora.** 22. **Septobasidium bogoriense.** 23. **Auricularia auricula-judae.** 24. **Epithele typhae.** 25. **Jaapia argillacea** (after Wakefield & Pearson, 1920). 26. **Cyphella pelargonii.** 27. **Ecchyna faginea.** 28. **Corticium vellereum.** 29. **Corticium albostramineum.** 30. **Tomentella echinospora.** 31. **Corticium polyporoideum.** 32–34. **Tomentella** spp. 35. **Corticium trigonospermum** (after Wakefield & Pearson, 1913). 36. **Pistillaria cardiospora.** 37. **Hypochnella violacea.** 38. **Pellicularia flavescens.** 39. **Cyphella** sp. near **C. citrispora.** 40. **Merulius lacrymans.** 41. **Phaeocyphella galeata.** 42. **Dacryopinax spathularia.** 43. **Platygloea effusa.** 44. **Dacryomyces deliquescens.** 45. **Helicobasidium compactum.** 46. **Eichleriella spinulosa.** 47. **Femsjonia luteoalba.** 48. **Coniophora arida.** 49. **Aleurodiscus aurantius.** 50. **Aleurodiscus oakesii.** 51. **Aleurodiscus amorphus.** 52. **Aleurodiscus mirabilis.** With the exception of Nos. 7, 24, 25, 35, the spores are all drawn to the scale shown.

The spores of homobasidiomycetes germinate directly to give a mycelium, and are never septate. Those of heterobasidiomycetes may become septate (Fig. **6,** 44, 47) and germinate by putting out a small process termed a secondary sterigma, from which arise in series one or more secondary spores (Fig. **6,** 43, 46) which later give rise to the mycelium. This sequence of events was called " germination par renovation " by Patouillard. It is perhaps best translated as " germination by repetition " (Rogers, 1933, p. 183) but has also been known as " renovation " (Donk, 1931, in translation). The secondary spores are the same shape as the original basidiospore, but smaller. In *Exobasidium* and *Dacryomyces*, sessile secondary spores, or conidia, are formed by gemmation from the sides of the basidiospore, either singly or in chains. This process should not be confused with germination by repetition.

Donk's term ballistospore is sometimes used to designate " those spores of Basidio-mycetes which are actively projected at maturity according to the specific mechanism studied and amply described by Buller in his *Researches on Fungi*. Ballistospores are found in Basidiomycetes with exposed hymenia, Uredinales, Tilletiaceae and Sporo-bolomycetaceae (comprising the genus *Tilletiopsis*) " (Derx, 1948, p. 468, translated; see also Nyland, 1949).

Chlamydospores.

Though they are uncommon in the lower Hymenomycetes, chlamydospores are present in some species and should not be overlooked. They may be defined as large, asexual, resting spores, characterised by a thick, refractile wall and dense lipid contents. They occur in a terminal or intercalary position on the hyphae. The spore wall may be smooth or variously sculptured.

Chlamydospores are found in cultures of many wood-rotting Basidiomycetes, e.g. *Trametes serialis* group (Fig. 7, 3). Good examples may also be seen in the genus *Nyctalis*, one of the parasitic Agaricaceae. In *N. parasitica* the chlamydospores are smooth, and occur in the subhymenium (Fig. 7, 2). In *N. asterophora* they are stellate and occur in the tissue of the upper part of the pileus (Fig. 7, 1). This interesting genus has been well investigated by Buller (1924), Thompson (1936) and Ingold (1940).

In *Sebacina epigaea* (see McGuire, 1941, Pl. 2, figs. 18–19) the basidiospores may be transformed into resting spores resembling the chlamydospores of *N. asterophora*. In *Corticium laetum* intercalary chlamydospores are sometimes found.
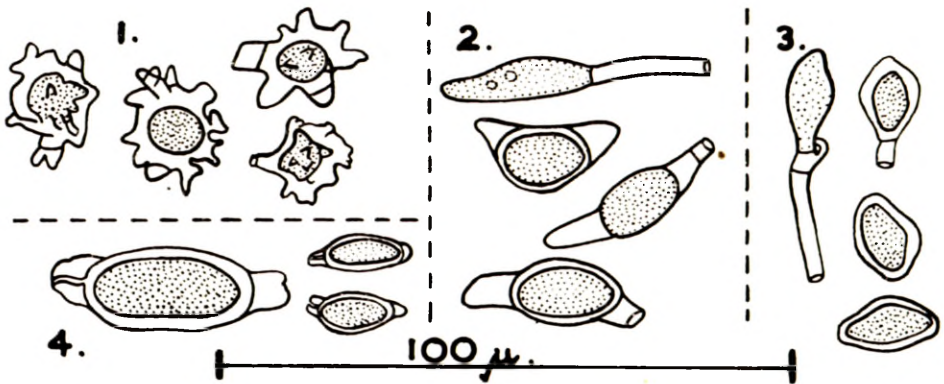

Fig. 7.—Chlamydospores:—

1. **Nyctalis asterophora.** 2. **Nyctalis parasitica.** 3. in culture of **Trametes serialis** group. 4. basidiospores of **Jaapia argillacea** with internal chlamydospores, the left-hand spore diagrammatic and not drawn to scale shown.

The basidiospores of *Jaapia argillacea* (Fig. **7**, 4) may develop to contain a large, thickwalled, yellowish chlamydospore separated from the poles of the basidiospore by septa. Accounts of these structures have been given by Wakefield & Pearson (1920) and by Rogers (1935, Pl. iii, fig. 14).

Hyphae.

The hyphae of the lower Hymenomycetes may be hyaline or coloured, thick- or thin-walled, with or without clamp connections, loosely or compactly arranged, with frequent or infrequent septa, and a variable degree of branching. Hyphae tend to branch most just beneath the hymenium. The hyphae range in width from a minimum of about $1 \cdot 5 \mu$ in some species to a maximum of 12–18–(29) μ in species of the genus *Pellicularia*, e.g. *P. pruinata* (Bres.) Rogers ex Linder. The walls of gelatinised hyphae do not show distinctly except by special staining, and normally one sees only their filamentous, refractile lumen. The gelatinised walls may be stained with strongly ammoniacal methylene blue (Nannfeldt, 1947).

The colour of the hyphae appears to be significantly related to other structural characters, particularly to the development of setae and asterosetae (see p. 291).

Recently great strides have been made in classifying the types of hyphae encountered in the Polyporaceae (Corner, 1932 a; Corner, 1932 b; Cunningham, 1946). It has been shown that a similar classification may be applied to the hyphae of the Thelephoraceae (Banerjee, 1942). Corner (1932 a) defined four types of hyphae, viz. *generative, skeletal, binding* and *mediate* hyphae. In a second paper (1932 b) he defined the systems into which these types could be combined, namely *monomitic, dimitic* and *trimitic* systems, to form tissues. Cunningham (1946) extended this work and standardised the technique for examining hyphae. Largely on this basis, Cunningham (1947–1950) has classified and described the polypores of New Zealand.

Hyphal types.

(1) Generative hyphae (Fig. **8**, 1, 2): These are branched, thin-walled, septate, hyaline or coloured, with or without clamp connections, usually staining readily, and varying in width from about $1 \cdot 5$–10 μ.

(2) Skeletal Hyphae (Fig. **8**, 3, 4): These are of two general types, which Cunningham distinguishes as " bovista " and " long " types. The bovista type has a main axis 3–10 μ in width, with several lateral branches which may in turn branch and taper. They are usually aseptate, and may be hyaline or coloured. The long type lacks the complexity of the bovista, and is slender, 3–7 μ in diameter, septate or aseptate, branched or typically unbranched, usually thick- but sometimes thin-walled, hyaline or coloured and loosely interwoven.

(3) Binding hyphae (Fig. **8**, 5): These also occur in the bovista and long forms. They are aseptate, interweaving, branched or sparingly branched, and thickwalled. As their name suggests they serve to consolidate the hyphae into firm tissues.

(4) Mediate hyphae: For practical purposes these need not be recognised. They are intermediate between generative and skeletal, and generative and binding hyphae, forming the transition from one to another of these types.

So far as the writer has been able to ascertain, " bovista " types of hyphae have not yet been found in the Thelephoraceae, though well known in the Polyporaceae. The " long " type of skeletal hypha is readily distinguished; not so the " long " binding hypha.
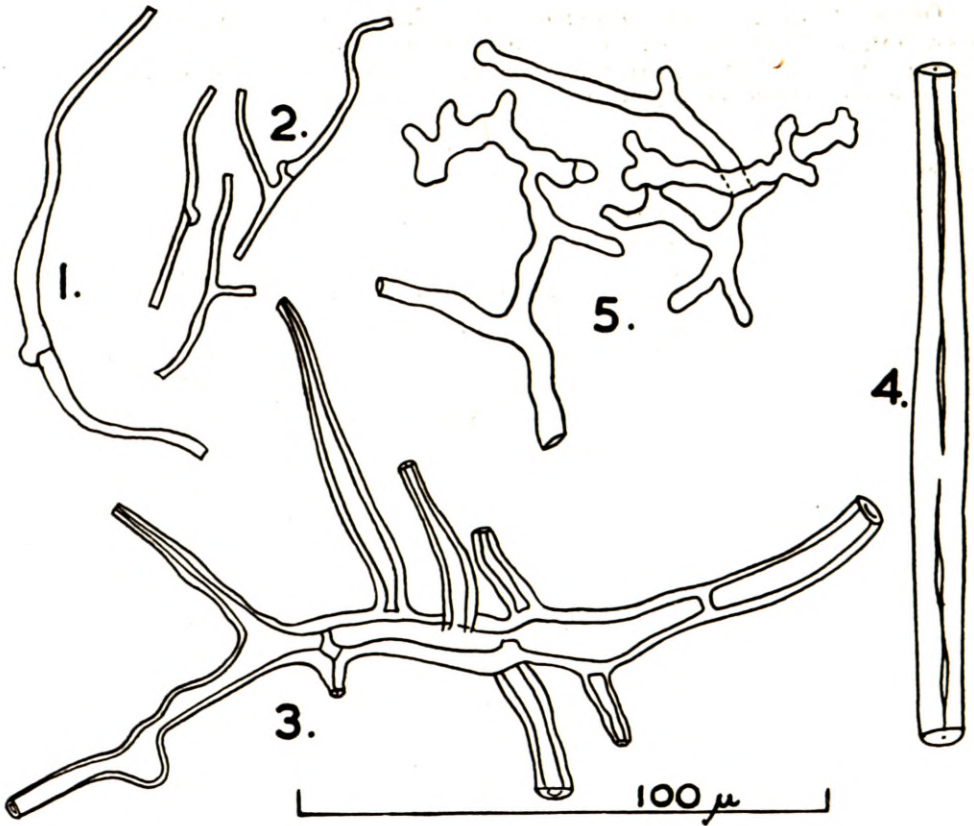
Fig. 8.—Hyphal types:— *A*

1. Generative hyphae from **Polyporus angolensis.** 2. Generative hyphae from **Trametes serpens.** 3. Skeletal hyphae of the " bovista " type from **Polyporus sulphureus.** 4. Skeletal hyphae of the " long " type from **Polystictus pinsitus.** 5. Binding hyphae of the " bovista " type from **Polystictus pinsitus.**

Hyphal systems.

(1) Monomitic: In this system there are only generative hyphae.
(2) Dimitic: The system is composed of generative and skeletal hyphae.
(3) Trimitic: Three hyphal types, generative, skeletal and binding hyphae, are present.

Cunningham (1946) has made several useful generalisations which help in deciding the kind of hyphal system present in a specimen. Thus: If all the hyphae are of one kind, or all possess clamp connections, the system is monomitic; if clamps are present in species with coloured hyphae of more than one type, the system is trimitic; clamps are absent from species with coloured hyphae and a dimitic system; clamps are usually present in the generative hyphae of hyaline dimitic systems. Cunningham has shown that the presence or absence of clamps is significantly connected with the hyphal types and systems.

Some clamp connections are illustrated in Fig. **8,** 1, 2 and Fig. **9.** The cytology of clamp connection formation is reviewed by Rogers (1936), where it is shown that clamps may be concerned in basidial proliferation as well as in a reproductive function

in the hyphae where they serve to " increase indefinitely the number of dikaryotic cells from which may be formed gonotoconts ". Rogers also shows that the clamp is a homologue of the crozier of Ascomycetes, and gives evidence of the derivation of Basidiomycetes from Ascomycetes.
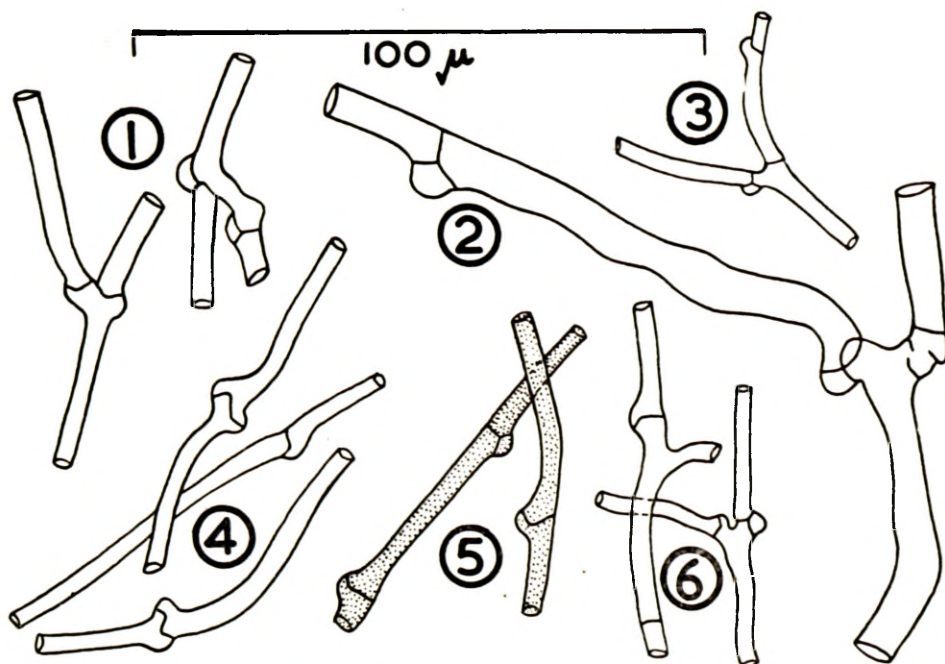

FIG. 9.—Clamp connections in:—
1. **Stereum schomburgkii.** 2. **Pellicularia subcoronata.** 3. **Odontia arguta.** 4. **Corticium armeniacum.** 5. **Stereum bicolor.** 6. **Corticium gloeosporum.**

Hyphal pegs.

These are erect, wartlike, papillate, tubercular or spiny structures projecting from the hymenium and often big enough to see with the naked eye. They are composed of sterile hyphae arising in coherent fascicles from the subhymenial or deeper tramal tissue. The thelephoroid forms bearing hyphal pegs might mistakenly be classed in the Hydnaceae without checking that the pegs are sterile.

The term " hyphal peg " has been commonly applied only to the Polyporaceae, in which group the sterile tufts of hyphae project into the lumen of the tubes (Fig. **10**, 1). Overholts (1929) commented that hyphal pegs were never found in the genera *Fomes*, *Daedalea* and *Lenzites*, nor in species with brown context, nor in the soft, white species of *Polyporus*, nor in true species of *Poria*. He found that they were common in *Polystictus*, were present in some species of *Favolus*, and in *Trametes serpens*, and were very large in the genus *Mycobonia*. A common South African species, *Trametes meyenii*, bears abundant hyphal pegs in most collections. Bose (1944) noted that hyphal pegs, common in certain species at high altitudes, may be scarce or absent in the same species at low altitudes.

As was done by Rogers (1935, p. 25) and Banerjee (1942), it seems desirable to extend the term " hyphal pegs " to include the strictly comparable structures found not only in the Polypores but also in the Thelephoraceae. In the latter group they have

been variously known as " sterile emergences " (Patouillard), " emergent fascicles of hyphae " (Burt, 1919), or " cystidiform synnemata " (Langeron, 1945). As a synnema implies a fructification it should be avoided as a term for these sterile aggregations of hyphae.

Sometimes the presence of hyphal pegs has been the basis for splitting off new genera (e.g. *Dendrothele* separated from *Aleurodiscus*: cfr. Rogers, 1935, p. 25); at other times they are regarded only as useful confirmatory specific characters. Generic distinctions involving hyphal pegs have been based on their hyphal composition and upon their arrangement either as discrete spines or, extending the conception, as confluent into sterile linear ridges or shallow poroid networks. To illustrate the use of hyphal pegs in taxonomy some of the series which are apparent are set out in key form below, but in doing so no close affinity of genera is implied:—

A.—Hyphal pegs discrete.
    1. Pegs formed of coloured hyphae. Fructification dimidiate or sessile, but   *Veluticeps.*
    not resupinate
    2. Pegs formed of colourless hyphae.
        (A) Basidia tremelloid; texture sometimes subgelatinous.........   *Heterochaete.*
        (B) Basidia claviform.
            (a) Pegs composed of delicate, much branched and inter-   *Dendrothele*
            woven dendrophytic hyphae, which are also present in the   (Fig. **10**, 3).
            hymenium.
            (b) Pegs composed of delicate ordinary hyphae, little
            branched or slightly forked, and arranged more or less
            parallelly.
                (x) Fructifications resupinate, lacking a well devel-   *Epithele*
                oped intermediate layer between substratum and   (Fig. **10**, 2).
                hymenium
                (y) Fructifications pileate, sessile or shortly stipitate,   *Mycobonia.*
                or if resupinate then having a broad intermediate
                layer
B.—Hyphal pegs united linearly..   *Grammothele*
                                                     (see below).
C.—Hyphal pegs united to form shallow networks........................   *Hymenogramme* and
                                                     Porogramme (see
                                                     below).
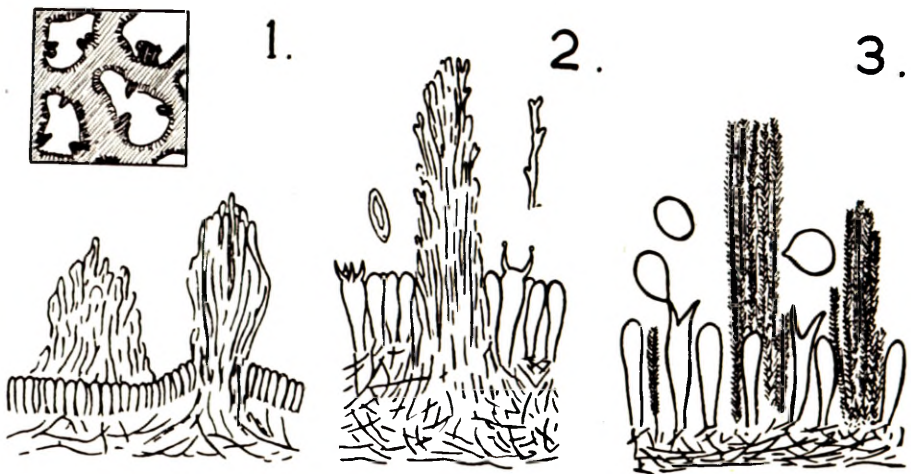

Fig. 10.—Hyphal pegs from:—
    1. **Trametes meyenii,** inset showing a cross section of the pores. 2. **Epithele typhae.** 3. **Dendrothele** (after Höhnel & Litschauer, 1907). All diagrammatic.

Veluticeps was regarded as a synonym of *Hymenochaete* by Killerman (fide Ainsworth & Bisby, 1945), but is used by Burt (1919, p. 259) in the sense given above, and is distinguished by him from *Mycobonia* by its coloured pegs. Malencon's (1939) description and illustrations of *Veluticeps heimii* show clearly that it is structurally quite distinct from *Hymenochaete*, a fact which Patouillard (1894) correctly observed.

One may imagine hyphal pegs to be united laterally so that sterile ridges, or pores surrounded by sterile walls, are formed over the surface of the hymenium. Two genera, which when mature have a hymenium covered with small, sterile, poroid ridges, are *Hymenogramme* and *Porogramme*. Patouillard (1899) states that *Porogramme* differs from *Hymenogramme* in having pores which are isodiametric instead of elongated as in the latter. They are genera which are insufficiently known to pass further comment on their structure. Lloyd (1923, p. 1232) has suggested that *Hymenogramme* should be united with *Grammothele*.

The genus *Grammothele*, though still imperfectly understood, requires comment. The hymenium is covered with ridges which are sometimes quite regular and linearly arranged, though not necessarily continuous (e.g. in *G. liniata* and *G. polygramma*), or sometimes more tubercular and irregular (e.g. in *G. mappa*, *G. pseudomappa* and *G. cineracea*). Through these ridges there project erect sheaves of hyphae surrounded and capped by large aggregations of minerals which cause a distinct glitter. These hyphae are very dilutely coloured and roughly parallelly arranged, not branched, and together with their sheaf of minerals form a type of hyphal peg resembling a very large cystidium at first sight (Fig. **16, 12**). In *G. cineracea* these sheaves are branched and the branchlets terminate in mineral caps. The hyphal pegs in *G. mappa* are more often immersed than emergent.

The genus *Gloiothele* (Bresadola, 1920), founded on *Poria lamellosa* P. Henn., may be defined as a *Grammothele* possessing gloeocystidia. The conformation of the hymenium resembles that of *Heterochaete*, but there are holobasidia and a crystal incrustation of the hyphal pegs as found in *Grammothele*.

Ampoule hyphae.

In some lower Hymenomycetes, e.g. *Grandinia farinacea* and species placed by Bourdot & Galzin (1928) in the section Humicola of the genus *Corticium*, a number of hyphae become swollen into shapes resembling ampoules (Fig. **11**). These are not always easy to find, and appear to be less obvious in material which is not fresh. Ampoules are generally associated with clamp connections, which here and there become much enlarged as the hyphae on one or both sides of the clamps become inflated and bulbous. When ampoules develop on both sides of a clamp, they meet obliquely in the middle. Sometimes the ampoule is viewed from a position where no sign of a clamp is present (Fig. **11, 3**). Such structures seen alone might be confused with intercalary vesicles in the sense used elsewhere in this paper.
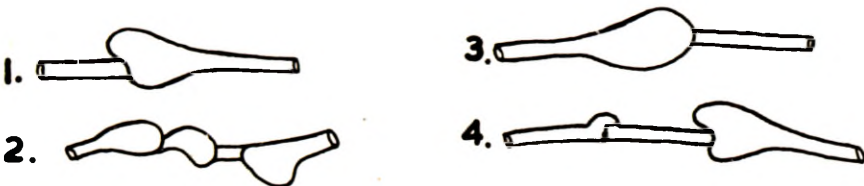

FIG. 11.—Ampoule hyphae drawn diagrammatically from:—
1–3. **Corticium confine. 4. Corticium fastidiosum.**

The species of *Corticium* grouped in the section Humicola are not related solely by the possession of ampoule hyphae. They have other characters in common which suggests that the grouping is a natural one, e.g. a rather pellicular or farinaceous hymenium bearing veinlike mycelial strands or granules, and spores which are usually sculptured.

Conducting hyphae.

In many Hymenomycetes the context contains, in addition to the usual hyphal systems, a network of special hyphae with dense contents, which are known as conducting or laticiferous hyphae. In their best-developed form they are seen to be of indeterminate length, much branched, anastomosing, of wide diameter, relatively thinwalled, at first non-septate and coenocytic but later becoming sparsely septate. The dense sap may be hyaline, milky or brightly coloured, and in some species changes colour on exposure to light and air. Such hyphae are reminiscent of the latex tubes of higher plants. Their contents stain easily with Melzer's chloral-iodine, or with phloxine. In some species the sap is coagulated by alcohol (especially in Agarics). Such conductors may be up to 24 μ in diameter. They are characteristic of the genus *Lactarius* (Fig. 12, 2), and are present in some species of *Mycena* and *Collybia*, and in some polypores, e.g. *Polyporus sulphureus* (Fig. 12, 1). Heim (1936) has studied the conducting systems of several Agaric species and gives excellent illustrations of them.

Little appears to be known about the composition of the sap of conducting hyphae. This would probably be a clue to their function, which is generally supposed to be the conduction of nutrient emulsions. Conductors are present in the rhizomorph of *Armillaria mellea* and if their function is nutritive it might explain in part the success of rhizomorphs in penetrating far into unfavourable situations, this action being assisted
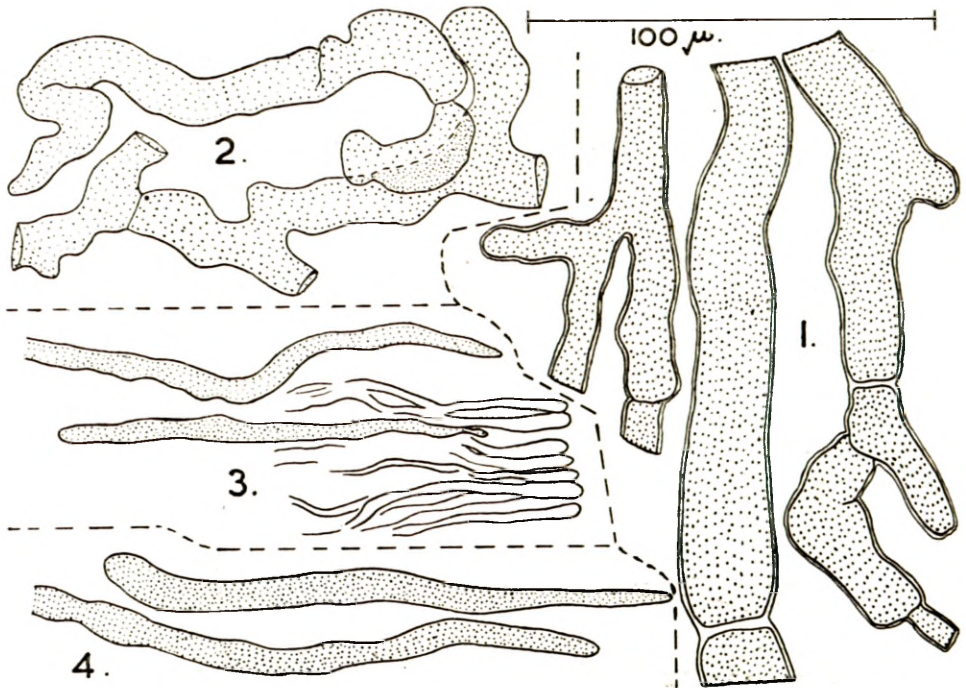

FIG. 12.—Conducting vessels of:—

1. **Polyporus sulphureus.** 2. **Lactarius deliciosus.** 3. **Stereum spadiceum.** 4. **Corticium lactescens.**

by their sclerotic rind. Confirmation of this supposition is given by Findlay's (1951) account of nutrients being transported distances of up to thirty feet along the rhizomorphs of *Armillaria mellea*.

Conducting hyphae as described above are distinguished from gloeocystidia by the fact that the latter are unbranched and limited in length. In *Hydnum erinaceum*, long yellowish conductors in the tissues of the spines curve out into the hymenium and their appear like gloeocystidia. The distinction between conductors and gloeocystidia is not so obvious in another type of conducting hypha found in several species of *Stereum* (Fig. **12,** 3) which exude reddish juice on being bruised, and in *Corticium lactescens* (Fig. **12,** 4), which exudes a milky juice when fresh. Here the conductors are comparatively narrow (4–9 μ diam. in *Stereum spadiceum*), apparently unbranched or very sparsely branched and relatively limited in length. Their connection with any extensive network of conductors is obscure, if in evidence at all. In fact it is usual to say that *C. lactescens* has gloeocystidia, though Miss Wakefield (1935) has pointed out that these are the terminations of a system of conducting hyphae. Perhaps, then, the best criterion of a conductor is that its contents exude when it is broken across and are often brightly coloured, added to the fact that the contents are very dense and that the conductors are long and indeterminate in length.

Vesicles.

Vesicles are pyriform or subglobose, hyaline, thinwalled swellings, usually borne terminally but occasionally in an intercalary position on the context hyphae. In section they may appear devoid of contents, or filled with a homogeneous, or globular or granular, matter which stains deeply with phloxine. They occur typically in the trama, and are conspicuous objects when numerous or large. They are figured in this situation by Overholts (1929) and Burt (1920), pp. 125–134, figs. 13–16) for certain species of *Stereum*. The vesicles seen in *Stereum murraii* (Fig. **13,** 2) and *S. purpureum* (Fig. **13,** 1) illustrate typically what is meant by this term. Miss Wakefield (1911) described the vesicles found in *Grandinia mucida*.

Structures similar to vesicles, but smaller, may be found with some difficulty in the pore tissues of certain polypores, e.g. *Polyporus subiculoides* (Fig. **13,** 3) and a species of *Poria* near *P. mucida* (Fig. **13,** 4). These are immersed in the subhymenium and are probably better referred to as cystidia than vesicles. They are comparable with the cystidia of *Odontia bicolor* (Fig. **16,** 13), which, however, have a crystalline crown.

To the writer there is little doubt that vesicles are a form of gloeocystidium, judging not only from their position in the fructification but also from their general morphology: there is also the observation that in *Stereum murraii* they are seen intergrading from the typical pyriform shape of vesicles to the typical elongated shape of gloeocystidia, with simultaneous change of their contents from homogeneous to granular or globular. The gloeocystidium of *Corticium polygonium* (Fig. **17,** 13) may equally well be considered as a vesicle with dense, granular contents. In *Stereum murraii* at least, it would seem that vesicles devoid of contents have simply lost their contents in the sectioning and mounting treatment. If the organs are short, swollen, and without very dense contents the tendency is to call them vesicles; if elongated they may be called gloeocystidia.

Three types of structure which might be confused with vesicles are worth mentioning. Firstly the short, dumpy basidia of species of *Amauroderma* (Fig. **13,** 5–6) may easily be mistaken for vesicles or gloeocystidia in crush mounts if sterigmata are absent. Secondly in some species (e.g. *Stereum hirsutum*) when surface scrapings of the hymenium are made for mounting, one often cuts transversely across the underlying hyphae, obtaining a structure which appears like a refractile, thickwalled globose cell in optical section (Fig. **13,** 8). It is well to emphasise that vesicles are thinwalled and larger.

Thirdly, some species (e.g. *Daedalea biennis*) have conidia embedded in the tissues (Fig. **13**, 7). These are small, subglobose or ovate, and appear thickwalled owing to the presence of a large, dilutely coloured guttule. They arise from very delicate hyphae which are seldom seen, but whose presence may be inferred from fragments still attached to the conidia making them appear apiculate.

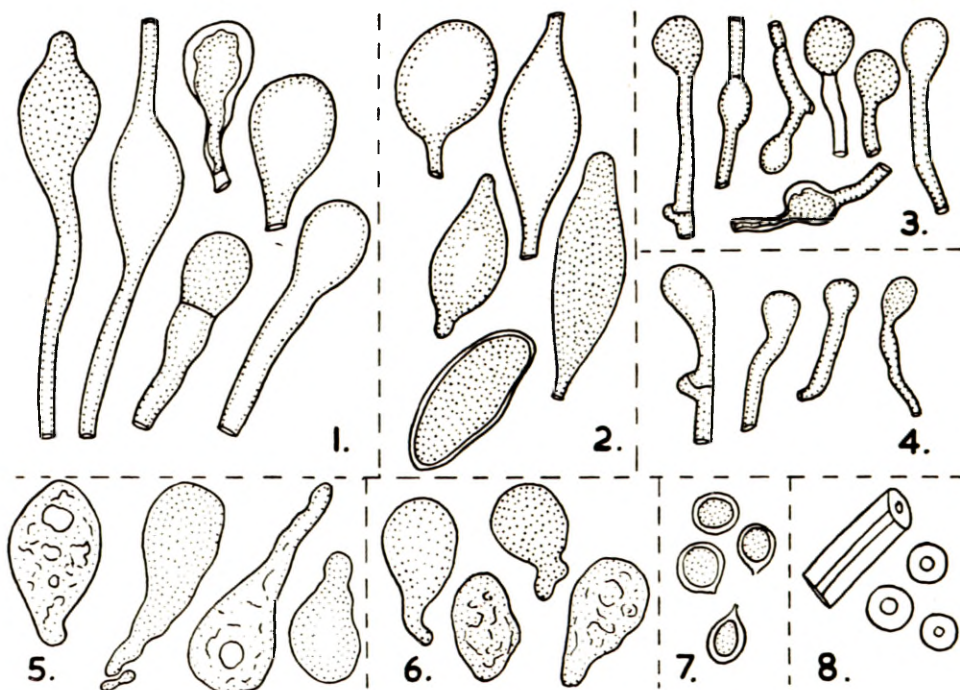In a compact trama empty spaces are sometimes left when vesicles collapse.

FIG. 13.—Vesicles and structures resembling them:—

1. Tramal vesicles in **Stereum purpureum.** 2. Tramal vesicles in **Stereum murraii,** showing variation towards gloeocystidia. 3. Hymenial cystidia in **Polyporus subiculoides.** 4. Hymenial cystidia in **Poria** sp. nr. **P. mucida.** 5–6. Immature basidia of **Amauroderma** spp. 7. Conidia embedded in the subhymenial tissue of **Daedalea biennis.** 8. Cross section of thickwalled hyphae from **Stereum hirsutum** and part of a hypha to show their origin.

Coscinoids.

This term was given by Singer (1947, pp. 155–157) to the hyphae in a peculiar type of conducting system in *Paxillus lateritius*, on the basis of which he erected a new genus, *Linderomyces*, to accommodate this species.

Coscinoids are long, filamentous, brown, aseptate, non-clamped hyphae, with a pitted sieve-like surface and a sponge-like interior. The surface perforations are the orifices of a system of meandering tunnels of the same diameter as the orifices, and separated by a wall substance coloured deep brown. The whole structure is sponge-like and thus distinct from all other types of conducting system. When found in the hymenium, these structures were referred to by Singer as " coscinocystidia ". Fragments of coscinoids are illustrated in Fig. **14.**
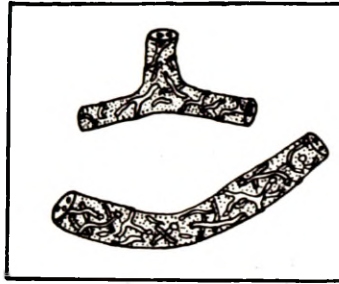
Fɪɢ. 14.—Fragments of coscinoids drawn semidiagrammatically from the type of **Paxillus lateritius** in Kew Herbarium.

Paraphysoid structures.

A number of sterile accessory hymenial structures are often grouped for convenience under the general name of *paraphyses*, though they are a heterogeneous collection and probably not homologous with the paraphyses found in Ascomycetes, to which group the term is sometimes restricted. For that reason the various types are sometimes distinguished as *pseudoparaphyses* and subdivided according to their form, but the terminology has been used in somewhat different senses by different authors.

In many of the Agaricaceae and in some of the Thelephoraceae there are hymenial cells which separate and support the basidia in such a way that the efficiency of basidiospore projection is increased. Langeron (1945, p. 323) terms these cells *pseudoparaphyses* or *basidioles*, and considers that they are merely aborted basidia. Miss Wakefield (1935) noted that in species showing differentiation of tissues resulting from a compact growth form, it is possible that some of the terminal cells of the hyphae remain permanently sterile and serve only to space out the basidia. Such sterile cells may acquire a distinctive form and be known as paraphyses; if they are indistinguishable from immature basidia they may be known as basidioles. It is possible that by mathematical analysis in the manner of Corner (1947; 1948 a) proof may be obtained whether these cells termed basidioles might have assumed the function of basidia or not. On the other hand there are sterile interbasidial cells which differ entirely from those just mentioned, and which are conspicuous enough to be classified and to be used as specific characters in taxonomy. Miss Wakefield (1935) observes that the distinction between paraphyses and cystidia is not always very clear, and that in practice the more or less elongated, filiform structures are liable to be called paraphyses and the stouter bodies cystidia. The distinction at present is one of form rather than of development or function. At present the emphasis must be on morphology alone, for our knowledge of the function and development of all such structures is almost negligable. Certain elements grouped here as *paraphysoid structures* are allied to basidia, cystidia, gloeocystidia or hyphae in morphology, but may likely bear no close relationship to any of these.

The various forms grouped as paraphysoid structures in the Hymenomycetes (excluding Agaricaceae) will be considered now, following the usage proposed by Pilát (1926) with slight modification. We shall endeavour to point out where this differs from the usage of other authors, so that some uniformity may result.

(1) *Simple paraphysoids* (Fig. **15, A**).—These are colourless, cylindrical or filiform, elongated, unbranched, rarely septate, smooth, thinwalled, straight, flexuous or spirally twisted elements which are prominent in the hymenium. In form there is often little to distinguish them from hyphae or immature basidia or cystidioles. It may be that their form can change in a manner analogous to that described by Bose (1940), who observed that different moisture conditions could convert regular basidia of some
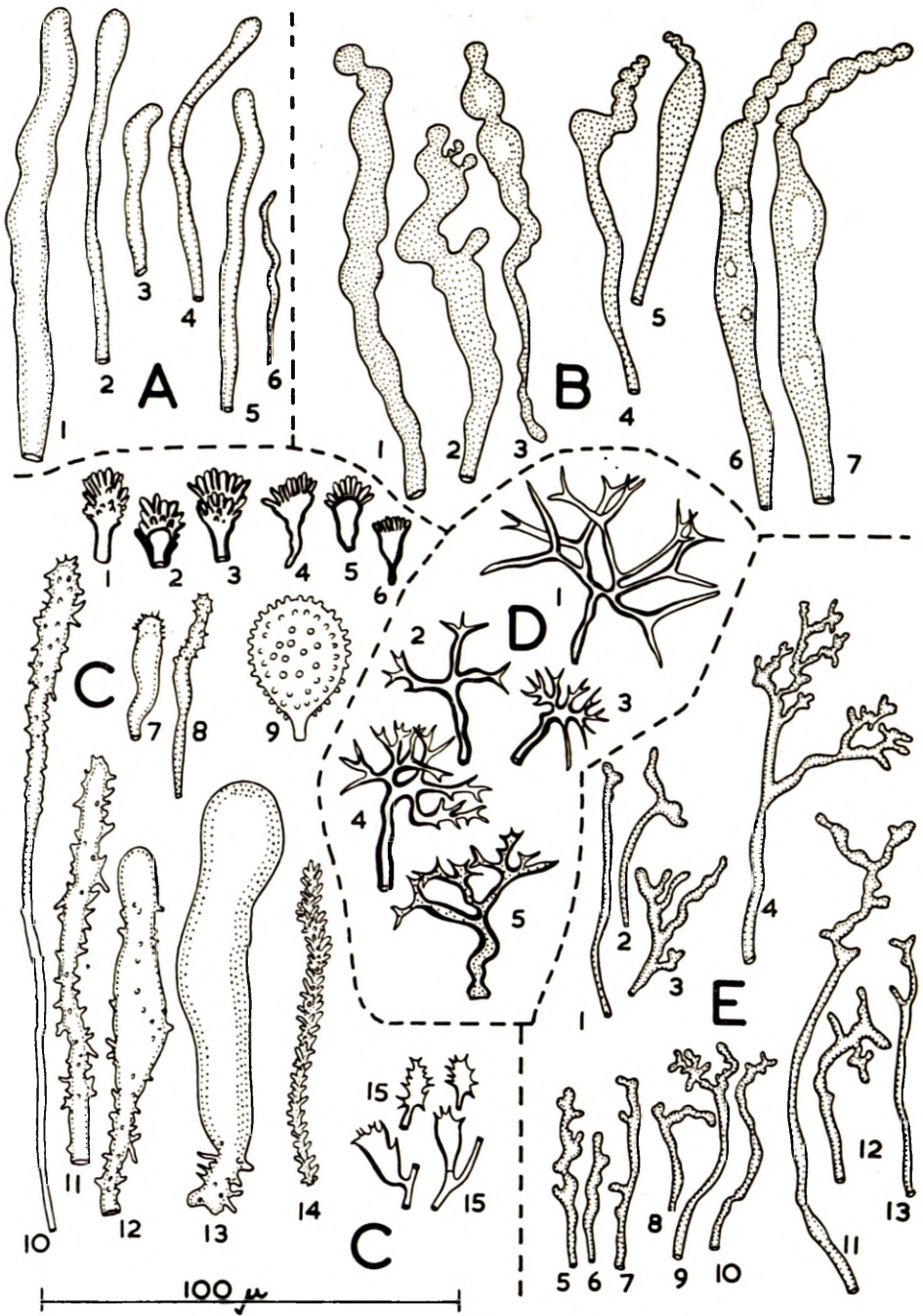
FIG. 15.—Paraphyses and paraphysoid structures:—

Group A.—simple paraphyses from 1. **Aleurodiscus mirabilis.** 2. **Aleurodiscus amorphus**. 3. **Aleurodiscus** sp. 4. **Aleurodiscus amorphus** (after Burt, 1918). 5. **Aleurodiscus oakesii** (after Burt, 1918). 6. **Corticium confluens.** **Group B.**—

polypores into hyphal elongations, and *vice versa*. The distinction between simple paraphysoids and dendrophyses in such species as *Corticium roseum* Pers. and *Corticium confluens* (Fig. **15, A,** 6 and **15, E,** 13) is merely one of degree of branching. In these species there is no fundamental difference, and their simple paraphysoids and dendrophyses are only different stages in development of the same type of organ.

Simple paraphysoids were included as paraphyses by Pilát (1926), and by Höhnel & Litschauer (1907); they were distinguished as flexuous or spirally twisted paraphyses by Burt (1918); in some senses they were termed pseudoparaphyses or basidioles by by Langeron (1945).

(2) *Pseudophyses* (Fig. **15, B**).—These structures are thinwalled, not septate, hyaline, unbranched or occasionally forking slightly (Fig. **15, B,** 2), somewhat clavate and constricted especially near the apex into a number of bead-like parts. The cells are homogeneous and stain deeply with phloxine. They would appear to be a form of gloeocystidium, and the term used by Bourdot & Galzin (1928), *torulose gloeocystidia,* is probably far more accurate than their description as a form of paraphysis.

Pilát (1926), Höhnel & Litschauer (1907), Singer (1945), Langeron (1945) and Wakefield (1945) all termed these structures pseudophyses. Burt (1918) and Overholts (1929) called them moniliform paraphyses. De Bary (1887) described them as " narrowly filiform hairs often constricted like a rosary ".

(3) *Acanthophyses* (Fig. **15, C**).—Pilát (1926) introduced this term for the peculiar form of dendrophysis which is clavate or cylindrical and decorated with a number of short, pin-like outgrowths chiefly near the apex. He specified also that this term included Burt's (1918) " bottle-brush paraphyses ", such as are common in many species of *Stereum* and *Aleurodiscus.*

We have here extended the circumscription of this term to include an assortment of paraphysoid structures all characterised by bearing short, pin-like outgrowths, but probably differing widely in origin and function. For example, Singer (1945) compared the " dendrophyses " of *Favolaschia* (cfr. Fig. **15, C,** 9) with the " cellules en brosse " of some Agaricaceae, and found that they belonged to different types. In a wide sense, however, both might be included as acanthophyses following the conception given here. In *Favolaschia* these cells occur both on the sterile surface of the pileus and in the hymenium; in Agarics they are on the upper surface of the cap only. *Cellules en brosse* have also been termed " digitate cystidia " (Corner, 1948 b, p. 243). While observing the somewhat similar morphology of *cellules en brosse*, which might be considered as acanthophyses with swollen bases, and other acanthophyses, it is felt that the former term is useful in its application to the Agaricaceae, since these cells do not occur in the hymenium.

Pseudophyses from : 1–3. **Aleurodiscus amorphus.** 4–5. **Aleurodiscus aurantius.** 6–7. **Aleurodiscus oakesii; Group C.**—Acanthophyses and related structures. 1–3. " cellules en brosse " from **Marasmius (Androsaceus) epiphylloides** (after Conrad & Maublanc, 1924–1933). 4–6. " cellules en brosse " from **Marasmius** sp. 7–8. Acanthophyses from **Aleurodiscus oakesii.** 9. from **Favolaschia pezizoidea** (after Singer, 1945). 10–13. from **Aleurodiscus mirabilis.** 14. from **Aleurodiscus farlowii** (after Burt, 1918). 15. A group of four " cockroach cells " from **Aleurodiscus weirii** (after Burt, 1918): **Group D.**—Dichophyses from 1. **Asterostromella investiens.** 2–5. **Asterostromella** sp.: **Group E.**—Dendrophyses from 1–3. **Aleurodiscus oakesii.** 4–7. **Aleurodiscus** sp. 8–10. **Aleurodiscus aurantius.** 11–12. **Aleurodiscus amorphus.** 13. **Corticium confluens.** All drawn to scale shown except Nos. **A,** 4, 5; **C.** 1–3, 9, 14, 15.

In the sense used here acanthophyses are hyaline cells with hyaline or occasionally dilutely coloured pin-like processes. They occur in the hymenium. They may have thickish walls and be cylindrical or clavate, resembling some forms of cystidia (Fig. 15, C, 10–12), or thinwalled with a few basal processes (Fig. 15, C, 13) and in this case may be modified basidia. In some species (Fig. 15, C, 14) they possibly represent a modified hypha.

Pilát (1926) appears to have restricted the term acanthophysis to the bottle-brush type of paraphysis, or to forms very similar to it. This usage is followed by Overholts (1929) and Wakefield (1935). Höhnel & Litschauer (1907) and Langeron (1945) grouped such forms as dendrophyses, and in part Singer (1945) did the same, e.g. in *Favolaschia*. Included in our conception of acanthophyses are elements which Bresadola named " cystidia corniculato-pinnata ", and those which Burt (1918) described as paraphyses with aculeate prongs, bottle-brush paraphyses, and cockroach-shaped paraphyses " (Fig. 15, C, 15).

(4) *Dichophyses* (Fig. 15, D).—This term was introduced by Pilát (1926) for a special form of dendrophysis distinguished by its more or less regular dichotomous branching. They are clearly seen in species of *Asterostromella*, also in *Stereum albobadium*, " *Stereum ayresii* " (" *S. midas* "), and in the genus *Dichostereum* Pilát or *Vararia* Karst.

Dichophyses are undoubtedly a form of hypha having rather thick walls, narrow lumina and subulate apices to the dichotomous branches. They are usually coloured and may occur in the hymenium or in the tramal tissues, or both. Only in the hymenium should they be considered for convenience as a type of paraphysis. Corner (1948 b, f. 8) shows clearly the origin of dichophyses in *Asterostromella* sp. as lateral branches of generative hyphae. Bourdot & Galzin (1928) emphasised their hyphal nature, referring to them as " corne de cerf " (deer-antlers), or dichotomous-divaricate or dendroid-branched hyphae. Höhnel & Litschauer (1907) described them as " tree-like, branched cystidia ". Burt (1918) included them under the category of " granule-bearing para-physes ". Wakefield (1935) mentioned Pilat's usage.

(5) *Dendrophyses* (Fig. 15, E).—These are thinwalled, usually colourless, vaguely and irregularly but not dichotomously branched hyphae, which occur intermingled with other hymenial elements. Pilát (1926) restricted the term to paraphyses of tree-like form with irregular branching. Höhnel & Litschauer (1907) did not distinguish between these and acanthophyses, naming both dendrophyses. Wakefield (1935) followed Pilát's usage. Overholts (1929) termed those with short lateral branches " antler paraphyses ", though this description is usually reserved for dichophyses. Burt (1918) shows both dendrophyses and dichophyses under forms classed as " granule-bearing paraphyses ".

Dendrophyses occur in many species of *Aleurodiscus* (Fig. 15, E, 1–12), in some of *Sebacina* (e.g. *S. sublilacina*), and in various species of *Corticium*, especially the section Aleurodiscoidea of Bourdot & Galzin (1928), e.g. *Corticium roseum*. In *C. roseum* and *Corticium confluens* simple paraphysoids are found as well, and these differ from the dendrophyses only in being unbranched and presumably in a younger state (cfr. Figs. 15, A, 6 and 15, E, 13).

Cystidioles.

A cystidiole is defined by Ainsworth & Bisby (1945) as " a sterile structure in the hymenium, at the same level as the basidia, wider than a paraphysis, thin walled and little differentiated ". They are usually inconspicuous, colourless, subulate or fusoid, often with a sharply pointed apex, thinwalled, sometimes finely encrusted, or smooth, sometimes projecting a short distance above the basidia. Usually they have no septa, but in *Corticium gloeosporum* an occasional subapical septum may be found. In *Stereum purpureum* cystidioles seem to appear under wet conditions, giving rise to the

form once known as *S. rugosiusculum*. There has been some doubt whether the corticioid forms bearing cystidioles should be classified under *Corticium* or under *Peniophora*. Thus on account of the cystidioles *C. sambuci* is sometimes classed as a *Peniophora*, while in *Peniophora cremea* the cystidioles are large and could well be called cystidia.

Among the species of resupinate Hymenomycetes bearing cystidioles are the following: *Corticium laeve, C. sambuci, C. ochraceofulvum, C. gloeosporum* (Fig. **16,** 39), *Stereum purpureum, Peniophora cremea, P. sanguinea, Acia subceracea, Odontia crustosa* (Fig. **16,** 34), *O. knysnana* (Fig. **16,** 35) and *Hypochnella violacea*.

Cystidia.

These are a rather heterogeneous assemblage of sterile bodies commonly occurring in representatives of the Agaricaceae, Polyporaceae, the genus *Peniophora*, and in certain species of the genera *Stereum, Odontia, Mycoleptodon, Cladoderris* and *Duportella*, to mention some of the better known. It is improbable that the so-called cystidia of all these groups are homologous, for they differ considerably in form, origin and probably in function. More information is urgently needed on these points, but for the time they are all discussed under the general category of cystidia. Many more studies such as those of Corner (1947) are needed, where it was shown that the cystidia of some species of *Clavaria* and *Oedemansiella* conform to the same mathematical equations as their basidia and are to be regarded as sterile, mostly precocious, overgrown basidia.

Certain generic segregates have been based on the presence of cystidia. For example *Peniophora* was segragated from other corticioid fungi originally on account of its "metuloids", but since then has included forms with very different cystidia; *Lloydella* was erected to include species of *Stereum* with metuloids; *Kneiffia* was ill-defined but its type species, *K. setigera* (= *Peniophora aspera*) has characteristic cystidia; *Heterochaetella* was segregated from *Sebacina* on account of its cystidia, and *Coniophorella* from *Coniophora* on the same grounds.

In the Agaricaceae, where the term "cystidium" originated with Montagne and was taken up by Leveille, the cystidia are sterile, hyaline, unicellular, ovoid cylindrial or clavate, blunt or pointed, smooth or ornamented or encrusted, originating as the terminal cells of branched hyphae and projecting from the hymenium. Buller (1924, pp. 52–53) classified them according to their position on the fructification, thus: *Pilocystidia* on the surface of the pileus; *Cheilocystidia* on the edge of the gills; *Pleurocystidia* on the sides of the gills; *Caulocystidia* on the stipe; *Dematocystidia* on the cuticle. Langeron (1945, p. 325, fig. 278) classifies the principal types of pleurocystidia giving examples of fungi in which they occur. There are five types, including those with spinous, barbed, crowned, and hooked apices, and those which have an encrustation resembling a muff round the middle of the cystidium. Langeron also noted a dimorphism in the cheilocystidia found on the large and small gills of some Agarics. The supposed functions of the cystidia in Agrics have been debated in various works, but it is difficult to ascertain the original source of some of these ideas. Cystidia have been thought to function as excretory hydathodes (Knoll) 1912. De Bary (1887) mentions that cystidia are often covered with slime, but observes that this condition is common in fungus cells rich in cell sap. Levine (1913, p. 161) considered that the cystidia in Boleti were modified basidia with a glandular function, excreting mucilage from their whole surface. Cystidia are also thought to have a mechanical value in maintaining the rigidity of the gills, in spacing adjacent gills apart, or in loosening appressed lamellae from the stipe. In the lower Hymenomycetes the pointed, encrusted "metuloids" were suggested to have a protective function against small animals feeding on the hymenium.

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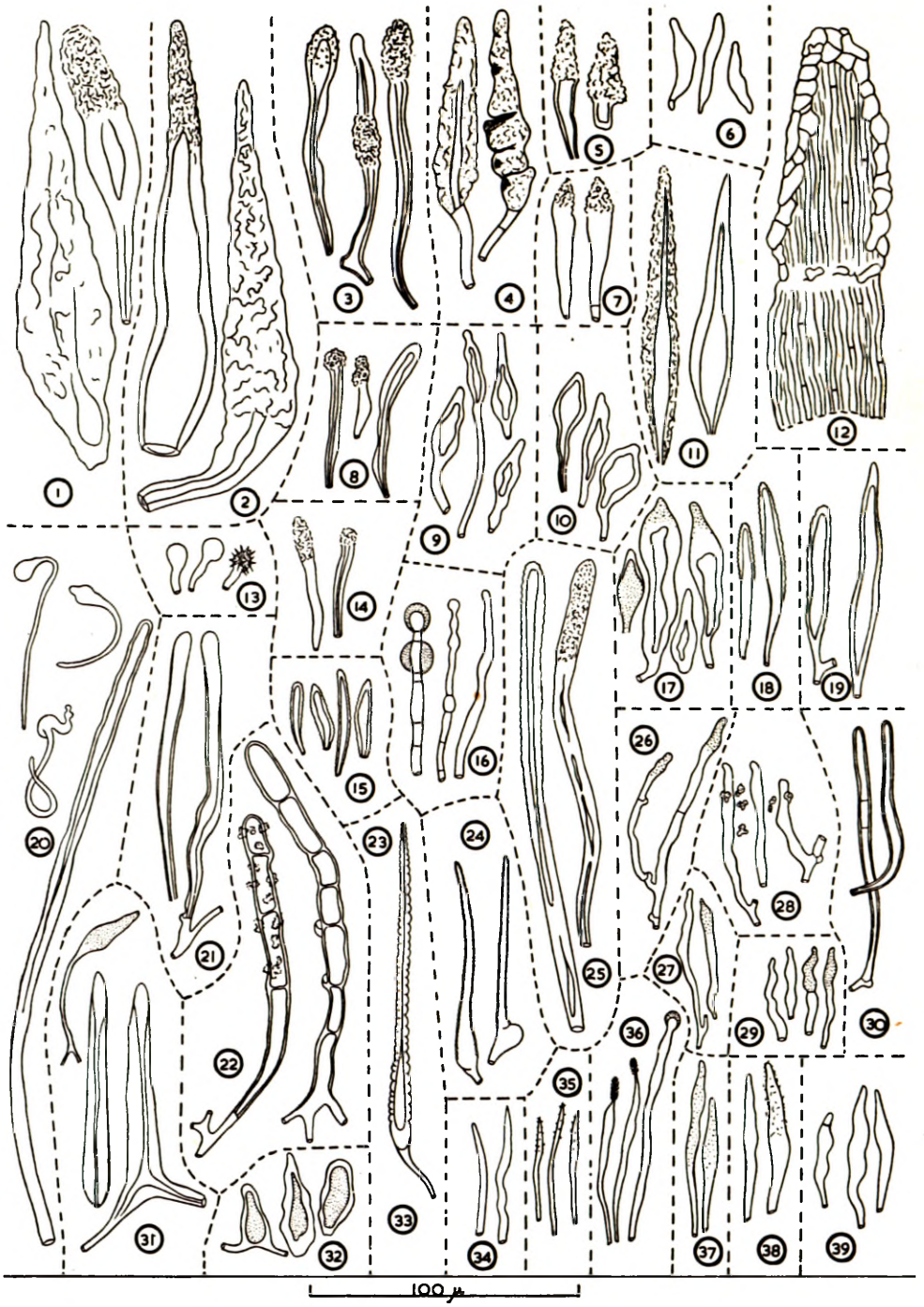
This study is more concerned with the cystidia of the lower Hymenomycetes (See Fig. 16), which again are very heterogeneous even in a single genus such as *Peniophora*. Thus it is impossible to give a general description of them. They may be conical or cylindrical in shape, or sometimes narrow and flexuous. The walls are sometimes characteristically thick and encrusted on the outside, but there are many species which have smooth, thinwalled cystidia. Some species, e.g. *Peniophora proxima* (Fig. 16, 15) have cystidia with finely sculptured walls. The lumen is usually narrow towards the apex, but in *Peniophora* section Tubuliferae (Bourdot & Galzin, 1928) the lumen is very narrow at the base and expands towards the apex of the cystidium. Incrustation of the walls may take the form of very fine amorphous, to large crystalline, deposits of mineral matter. In *Odontia bicolor* (Fig. 16, 13) the incrustation is in the form of druses of crystals, while in *Odontia arguta* (Fig. 16, 36) and *Peniophora pallidula* (Fig. 16, 16) the cystidia bear droplets of brownish resin. The small capitate cystidia of *Odontia bicolor* are similar in shape to those of *Polystictus subiculoides*, and resemble small vesicles except for their occurrence in the hymenium. Cystidia are usually hyaline, but if dilutely coloured then the colour resides in their walls and not in their contents. The contents are seldom well differentiated. In *Peniophora* section Gloeocystidiales (Bourdot & Galzin, 1928) the cystidia are smooth and thinwalled and have a fine, dense, granular content like that of gloeocystidia, but they originate in the basal part of the trama and project far beyond the hymenium, which according to Bourdot & Galzin distinguishes them from gloeocystidia. The distinction is not particularly clear.

The type of cystidium termed a " metuloid " by Cooke, is thickwalled, heavily encrusted and usually conical (e.g. Fig. 16, 1, 2, 4, 7, 17). They are sharply differentiated from the hyphae from which they rise. The smooth cystidia of *Peniophora* section Tubuliferae have a lumen which expands at the apex; they arise from the basal tissues and often have a forked base, and possess the curious property of dissolving in Potassium hydroxide solution so that only the shrunken cell contents are left behind. Examples are *Peniophora glebulosa*, *P. subalutacea*, and similar cystidia found in *Stereum karstenii* (Fig. 16, 31, 21, and 20 respectively). Septation is not usual in cystidia, but is very well seen in *Peniophora aspera* (Fig. 16, 22), *Coniophorella olivacea* and *Peniophora tomentella* (Fig. 16, 30). In the first species the cystidia also show occasional clamp connections.

The place of origin is probably important in classifying the types of cystidia encountered among the lower Hymenomycetes. Some cystidia are little modified from the hyphae from which they arise, e.g. *Peniophora tomentella* (Fig. 16, 30)

FIG. 16.—Cystidia and Cystidioles: **Cystidia** from the following species:—

1. **Stereum cinerascens.** 2. **Lopharia mirabilis.** 3. **Poria eupora.** 4. **Peniophora roumeguerii.** 5. **Peniophora pelliculosa.** 6. **Grammothele pseudomappa.** 7. **Duportella tristicula.** 8. **Poria obducens.** 9. **Cladoderris australica.** 10. **Cladoderris infundibuliformis.** 11. **Peniophora pubera.** 12. Hyphal peg from **Grammothele mappa** (type) resembling a cystidium. 13. **Odontia bicolor.** 14. **Daedalea quercina.** 15. **Peniophora proxima.** 16. **Peniophora pallidula.** 17. **Stereum involutum.** 18. **Peniophora laevis** forma **P. affinis.** 19. **Peniophora velutina.** 20. **Stereum karstenii** in acid and alkaline mounts. 21. **Peniophora subalutacea.** 22. **Peniophora aspera** (= **P. setigera**). 23. **Peniophora aegerita.** 24. **Peniophora longispora.** 25. **Irpex dregeanus.** 26. **Peniophora byssoidea.** 27. **Sebacina** sp. 28. **Odontia papillosa.** 29. **Sebacina sublilacina.** 30. **Peniophora tomentella.** 31. **Peniophora glebulosa.** 32. **Peniophora cinerea.** 33. **Peniophora aegerita.** Cystidioles from the following species: 34. **Odontia crustosa.** 35. **Odontia knysnana.** 36. **Odontia arguta.** 37. **Stereum purpureum.** 38. **Peniophora cremea.** 39. **Corticium gloeosporum.** All are drawn to the scale shown except Nos. 16, 23, 24, 31, 33.

P. byssoidea (Fig. **16**, 26) and *Stereum umbrinum* (Fig. **19**, 11–13). Others, especially the metuloid type, are sharply differentiated from the hyphae. Many cystidia originate from the base of the trama, e.g. *Peniophora glebulosa* (Fig. **16**, 31), *P. subalutacea* (Fig. **16**, 21) and *Stereum karstenii* (Fig. **16**, 20). Especially in the Coloratae section of *Peniophora* (Bourdot & Galzin, 1928) the cystidia are arranged in stages throughout the trama, e.g. *P. proxima* (Fig. **16**, 15) and *P. roumeguerii* (Fig. **16**, 4). Still other cystidia arise in the hymenium or at least in the upper half of the trama, e.g. *Peniophora gigantea*, *P. longispora* (Fig. **16**, 24), *P. byssoidea*, *P. pallidula*, and *P. pubera* (Fig. **16**, 26, 16 and 11 respectively.

Illustrated in Fig. **16**, 12 is the form of hyphal peg found in the trama of *Grammothele mappa*. At first it might be thought to be a large cystidium, but more careful observation reveals the core of erect sheaves of brownish hyphae capped by a heavy mineral incrustation (see also under Hyphal Pegs, p. 277).

Gloeocystidia.

In Fig. **17** are shown a number of bodies found in species of many genera and all classed as gloeocystidia. These are sterile organs mainly distinguished by their thin walls, dense and deeply staining contents, lack of sculpturing and incrustation, and their position in the tissues of the fungus. The contents may be hyaline or lightly coloured, yellow to brownish; they are highly refractile, homogeneous or granular or globular, in the last instance usually of an oily nature. Commonly they arise from hyphae situated in the subhymenium or deeper tissues and may be completely embedded, or extend as far as the level of the basidia; only in a few species are they found projecting above the hymenium. Their walls are colourless. Any colour they may possess is located in the cell contents.

Gloeocystidia stain deeply with phloxine or eosin in pctassium hydroxide mounts, and ones which are normally coloured take on a deeper, brownish colour with iodine solutions. Singer (1945) recommends the use of brilliant cresyl blue for differential staining of the contents and walls of gloeocystidia; with this stain the contents turn blue, while the walls are stained lilac.

In shape, gloeocystidia may be narrow, flexuous and subcylindrial, or wider and clavate, or uncommonly (e.g. *Corticium polygonium*, Fig. **17**, 13) inflated and ovoid or pyriform. They are not branched. Septation is very rare but is known to occur in the gloeocystidia of *Duportella tristicula* (Fig. **17**, 15), where a single subapical septum is sometimes seen. Many species show pseudoseptation of the gloeocystidia when mounted in glycerine, which causes the contents to contract (Overholts, 1929). The walls are normally smooth and not encrusted with mineral matter. However, in *Corticium pallidum* (Fig. **17**, 12) the gloeocystidia are capped with a brownish resinous substance which is soluble in hot lactic acid but not in alkali (Höhnel & Litschauer, 1907).

Despite the distinguishing features outlined above, gloeocystidia may be confused with other organs in a few specific cases. Some examples are now given:—

(1) In the genus *Aleurodiscus* the basidia are very large and stain deeply, thus immature basidia may be taken for gloeocystidia in crush mounts where the hymenial elements are displaced. Basidia of *Amauroderma* may also be taken for gloeocystidia or vesicles (see p. 279 and Fig. **13**, 5–6).

(2) The conducting hyphae of the bleeding species of *Stereum*, and of *Corticium lactescens*, do not form an obvious network, and their terminations may be thought to be gloeocystidia. Conductors exude their contents readily, whereas the contents of gloeocystidia usually cohere fairly well. In *Hydnum erinaceum* there are " gloeocystidia " in the spines which connect with an extensive system of conducting hyphae. They are part of one system and should not be differentiated.
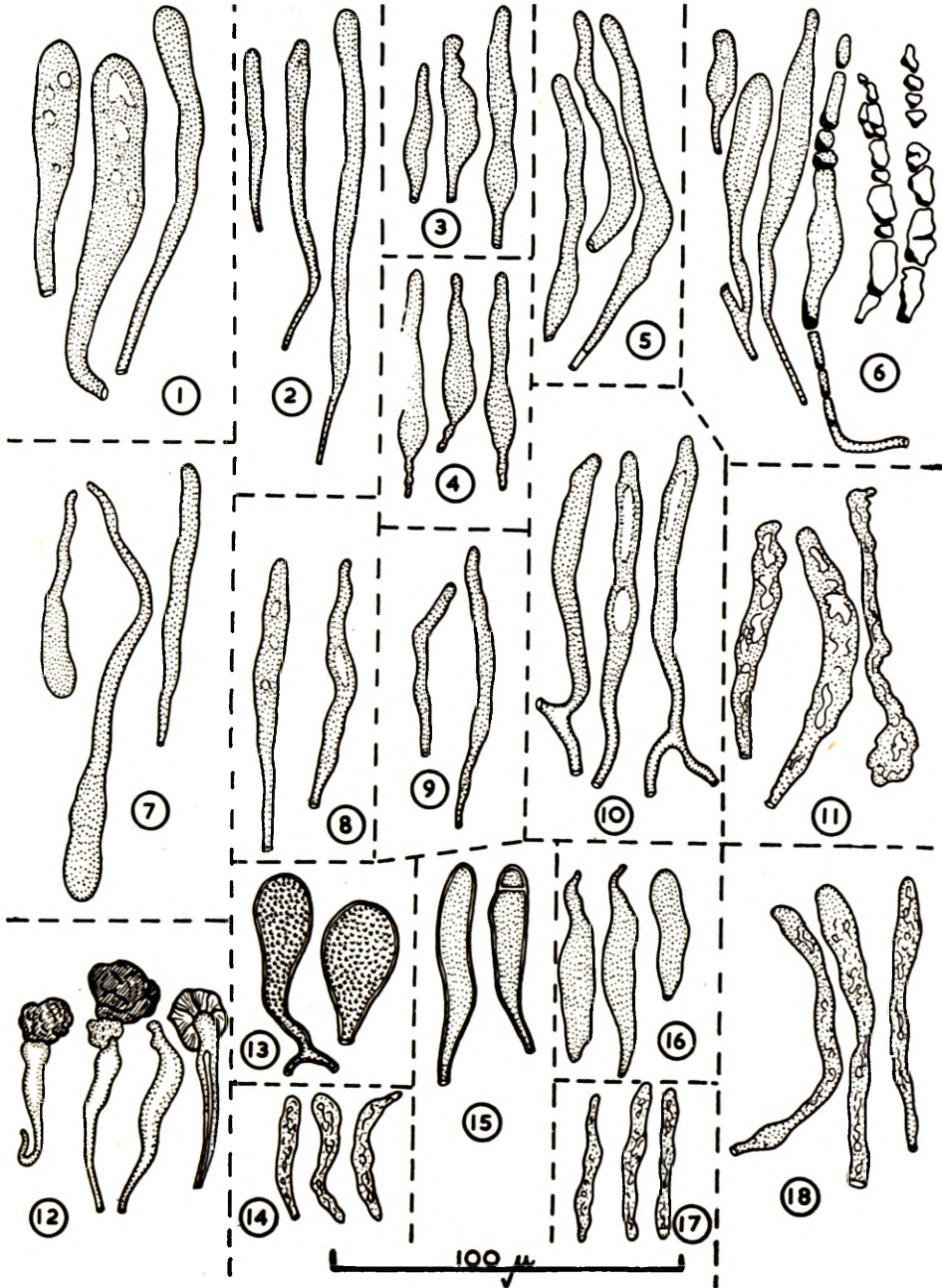
FIG. 17.—Gloeocystidia from the following species:—
1. Stereum diaphanum. 2. Stereum duriusculum. 3. Stereum affine. 4. Stereum involutum. 5. Stereum thozetii. 6. Stereum bicolor. 7. Corticium praetermissum (= Peniophora tenuis). 8. Corticium roseocremeum. 9. Corticium coroniferum. 10. Corticium albostramineum. 11. Corticium luteocystidiatum. 12. Corticium pallidum. 13. Corticium polygonium. 14. Bourdotia cinerella var. trachyspora. 15. Duportella tristicula. 16. Asterostroma cervicolor. 17. Bourdotia eyrei. 18. Seismosarca sp. All drawn with camera lucida, but scale varying.

(3) Certain species of *Peniophora* (e.g. *P. sphaerospora, P. tenuis*) with non-encrusted, thinwalled cystidia which project above the hymenium, have frequently been classed as *Corticium* as there is some doubt whether these organs are cystidia or gloeocystidia. The tendency nowadays is to place these under *Peniophora,* for example Rogers & Jackson (1943) refer *Corticium praetermissum* (Fig. **17,** 7) to *Peniophora* under the species *P. tenuis.* Again in *Stereum diaphanum* it is difficult to decide whether these organs are cystidia or gloeocystidia; they may be embedded or project above the hymenium.

(4) Some cystidia, when mounted in alkali, have their encrustation dissolved away, and but for their position and thick walls may be confused with gloeocystidia. Numerous illustrations of this condition are to be found in Fig. **16,** e.g. 6, 9, 10, 11, 17.

(5) The vesicles in some species resemble gloeocystidia. See note on p. 279.

(6) The pseudophyses (moniliform paraphyses) of species of *Aleurodiscus* are probably best considered as a form of gloeocystidium. See note on p. 283.

(7) In *Stereum bicolor, Peniophora incarnata,* and some other species of *Peniophora* in the section Coloratae (Bourdot & Galzin, 1928) there appears to be a distinct intergrading of form between gloeocystidia and cystidia. This is well shown in *S. bicolor* (Fig. **17,** 6). In most species where cystidia and gloeocystidia occur together, the two kinds of organ are distinct at all times. This bears on the origin of these organs, which will be considered now.

As gloeocystidia are probably not all homologous organs no generalisation is possible regarding their origin and funtion, and these aspects have only been studied in a very few species. In the species just mentioned, there is a difinite intergrading from gloeocystidia to cystidia. Massee (1887) concluded that cystidia were the terminal growing points of laticiferous vessels, and that the young ones contained a hyaline, dense protoplasm which was later replaced by a finely granular substance which eventually escaped through an apical pore to nourish the spores. A very common idea was that gloeocystidia exude at the apex and become changed into encrusted cystidia in species such as *P. incarnata.* Present observations on *Stereum bicolor* (Fig. **17,** 6) suggest that the whole wall of the gloeocystidium dissolves and that the contents, now very dense and coherent, remain as a highly refractile body which resembles a fragmented and encrusted cystidium. Whelden (1936) carefully studied the cystidia and gloeocystidia of *Peniophora livida* and concluded that the cystidia originated in the same way as basidia from the apex of an hymenial hypha, while the gloeocystidia arose laterally from hyphae near the substratum. In this fungus these organs were always entirely distinct from one another. Mention has already been made of Corner's work on the origin of cystidia on some species of *Clavaria* and *Oedemansiella* (see p. 285).

Nothing definite is known of the function of gloeocystidia, but it is likely that they are concerned in nutrition. Overholts (1929) suggested that they might have a protective function if their contents were unpalatable to animals.

Gloeocystidia are uncommon among higher Hymenomycetes, but are widespread among the genera of the lower Hymenomycetes. For example, they are found in many species of the genera *Aleurodiscus, Stereum, Corticium, Sebacina,* and *Asterostromella.* They form the so-called " colour cells " found in the genus *Favolaschia* (Singer, 1945). Their presence is the reason for splitting off new genera from old, e.g.

Gloeocystidiellum from *Corticium*, *Gloeopeniophora* from *Peniophora*, *Bourdotia* from *Sebacina*, *Seismosarca* from *Exidia*, and *Gloeotulasnella* from *Tulasnella*. This practice is now ceasing, and at the most the presence of gloeocystidia is given subgeneric significance.

Setae.

Setae may be defined as sterile, rigid, dark-coloured, thick-walled, spine-like organs, usually having a more or less pointed apex, and possessing the property of darkening in alkali. Burt (1918, p. 302) drew attention to this chemical reaction as a fundamental way of distinguishing setae from similar structures such as elongated coloured cystidia (e.g. in *Stereum umbrinum*). Setae are yellowish- or reddish-brown in colour, and the pigment is located mainly in the walls. The lumen is usually narrow.

Simple, unbranched setae vary in size and shape, and in the character of their apices. Such variations are usually only of minor specific significance, for on the whole their appearance is fairly uniform. Compound setae are not common; they may assume bizarre shapes, but may be analysed as composed of a main axis united to branches which individually do not differ much from forms encountered among simple setae.

In different species, setae may be abundant or rare, emergent from the hymenium or embedded deeply, or found upon the cuticular surface.

Cunningham (1946) has studied the origin of setae in some species of polypores. They usually develop below the hymenium and project beyond the basidia. Cunningham states that they arise from skeletal hyphae in species with a dimitic hyphal system, and from generative hyphae in species with a monomitic system; they are absent from species with a trimitic system. However, as Corner (1932 b, p. 59) showed that the setae of *Fomes laevigatus*, a species with a dimitic system, arose from generative hyphae perhaps no generalisation is yet possible. With most setae it is extremely difficult to trace the type of hypha from which they arise.

Regarding the function of setae nothing definite is known, but it has been speculated that they may provide rigidity to the fructification and protect the tissues from damage by small animals. Overholts (1929) mentioned these speculations, but added that the function is probably far more fundamental. Considering that small animals provide a useful alternative to anemochory or water dispersal of spores of many resupinate Basidiomycetes (Talbot, 1952), the writer is inclined to minimise any protective function ascribed to setae, cystidia or gloeocystidia.

As with most other conspicuous organs, setae have been used in the erection of new genera, e.g. *Hymenochaete* Lév. and *Mucronoporus* Ell. & Everh. They are common in *Phellinus* Quél. and *Xanthochrous* Pat., are found in many species of *Poria*, and were estimated by Overholts (1929) to occur in 5–10 per cent of species of *Fomes* and *Polyporus*.

Of themselves, setae would not appear to have any generic significance. They are, however, associated with other characters which occur in a series of fungi at present classed in many different genera and families, and which seem to constitute a natural series. Donk (1933) refers to this series as the Hymenochaetoideae, a sub-family of the Aphyllophoraceae, while Corner (1948 b) calls it the Xanthochroic series. As Corner (1948 b, p. 235) expresses it, " These Xanthochroic fungi are distinguishable not so much by the *Hymenochaete* setae, which are absent from many of them, as by the character of their hyphae. The absence of clamp connections, the lack of inflation of the cells of the fruit body, and the ochraceous or brown colour of the hyphal walls, which darkens to ferruginous or date brown with alkali, distinguish these fungi ".

FIG. 18.—Setae:—

1. Uncinate (hamate) seta from **Poria uncinata** (after Cunningham, 1946).
2. Ventricose seta from **Polyporus tabacinus** (after Cunningham, 1946). 3. Compound seta of **Polyporus grammocephalus** (after Cunningham, 1946). 4. Subulate seta (after Lowe, 1942). 5. Ventricose seta (after Lowe, 1942). 6. Setae from the hymenium of **Polyporus gilvus**. 7. from **Polyporus radiatus**. 8. from **Hymenochaete fasciculata** (type). 9. from **Poria contigua**. 10. from **Hymenochaete nigricans**.

This, and similar trends in classification are among the most significant to have arisen recently. The Friesian classification was based on macroscopic characters. Later with Patouillard (1900) came the first and greatest attempt to utilise microscopic characters in taxonomy, but the trend was then to give too much prominence to them, with the result that many genera became defined by single microscopic characters. The present tendency is to bring into their right perspective the wealth of microscopic characters which are already known, and through this to reveal a series of affinities which cut right across the classical groups. A more natural classification will result from this type of work, but only when more species have been scrutinised and more is known of the function of their microscopic organs.

For the diagnosis of species, some of the differences seen in setae are the following:—

(1) Size. Cunningham (1946) mentions a size range of 10–160 μ long and 6–12 μ wide.

(2) Shape. Subulate (Fig. **18**, 4), ventricose (Fig. **18**, 2, 5), conical and elongated (Fig. **18**, 8, 9) shapes are common.

(3) Colour.

(4) Apex. The apex is often sharply pointed, but sometimes blunt. It may be hamate or uncinate (Fig. **18**, 1).

(5) Position of the setae in the hymenium, trama or cuticle, and their relative abundance.

(6) The type of hypha from which the setae arise.

(7) Branching. Simple, or compound setae (Fig. **18**, 13).

Setoid structures.

In certain species of resupinate Hymenomycetes and polypores, structures are found which resemble setae except that they are much more elongated and may differ in their origin. They are usually more cylindrical, of comparatively great length, and not limited in size and shape as is a well defined seta. This is because they are apparently only modified thickwalled skeletal hyphae. The lumen is usually very narrow, sometimes expanding a trifle towards the apex, which itself is frequently wider than the rest of the hypha. The apex may be minutely sculptured as in *Stereum schomburgkii* and *Duportella tristicula* (Fig. **19**, 8–10). In other species the wall is quite smooth, e.g. in *Polyporus ochroporus* and *P. patouillardi* (Fig. **19**, 14–17). In all these species the setoid structures darken slightly in alkali while the rest of the trama shows an even darker reaction. Similar structures occur in *P. tabacinus* (fide Cunningham, 1946). In some collections of *Stereum hirsutum* some of the hyphae though only very faintly coloured, have thick walls and a lumen which expands near the inflated apex in a way similar to that found in the species just mentioned. Pilát (in Hedwigia, Vol. 70) records some collections of *S. hirsutum* of this type. These structures are included here for comparison, but they do not darken in alkali and are not setoid structures. In *Stereum umbrinum* there are mineral-encrusted organs which are usually called cystidia (Fig. **19**, 11–13) but which are frequently smooth-walled and might then be considered as setoid structures. They too are only modified skeletal hyphae and sometimes give a faint colour reaction with alkali.

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11. from **Polyporus carneofulvus** (type). 12. from **Polyporus ochroporus** (cotype). 13. Compound cuticular setae from **Polyporus cuticularis**. 14. **Favolus megaloporus.** 15. **Polyporus dryadeus.** All except Nos. 1–5 drawn to the scale shown.

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17

100 μ

A form of setoid structure differing from those already mentioned is found in the pore walls of *Polyporus dictyopus*. These terminate some of the hyphae. They take the form of a blunt, irregular axis with irregular, narrower lateral outgrowths. The axis is brown and darkens in alkali; the lateral outgrowths are paler and often almost hyaline at their apices (Fig. **19,** 1-7).

Asterosetae.

In the genera *Asterostroma, Asterodon,* and in some species of *Lachnocladium* there occur brown, stellate organs composed of several rays, each like a seta, radiating from a common centre which is sometimes expanded into a distinct boss. They terminate some of the laterals of generative hyphae, which, in *Asterodon*, also give rise to skeletal hyphae independently, and to extrahymenial setae and hymenial setae (Corner, 1948 b). The largest asterosetae occur towards the base of the fructification; they diminish progressively in size as the hymenium is approached. The rays of the asterosetae may be simple or branched in the same fructification. When they are branched, the organ is still regular in shape, and stellate. Asterosetae are related to ordinary setae in composition and basic structure, and may be regarded as a special form of compound seta. They darken in alkali and the species bearing them also show other indications of belonging to the Xanthochroic series, or Hymenochaetoideae.

Corner's work (1948 b) on the morphology and development of *Asterodon ferruginosus* is especially interesting in relating the shape and direction of the asterosetae to the forces controlling the growth and form of the fructification. Thus, in the resupinate part of the fructification there are evidently no form factors in operation and stellate setae are developed (Fig. **20,** 6). In the hymenium the setae become simple, or those parts of the setae lying in the subhymenium become shortly substellate (Fig. **20,** 7). In the spines, where a positive geogropism is in action, the setae lying in the context tissue are elongated downwards (Fig. **20,** 8-10), while those near the hymenium where the factor responsible for lateral production of basidia is in operation, become drawn out into lateral branches simulating ordinary hymenial setae (Fig. **20,** 10). As Corner expresses it, " The shape of the setae and the direction of the skeletal hypha express the action of the form-factors of the fruit body ". This most significant work in interrelating these forms of setae provides a reason for the bewildering shapes which setae may assume.

Mineral inclusions.

Very little is known about the chemical composition of the minerals which so commonly occur in the trama, or encrust the hyphae and other organs of fungi. Calcium oxalate is a common mineral found in the form of octahedra, acicular crystals or irregular nodules or granules; in fact most mineral substances found in fungi were once assumed to be calcium oxalate without further inquiry. Recent investigations into the metabolic products of fungi have shown that a vast number of organic compounds may be isolated from growing fungi and then crystallised.

Added to the mineral forms mentioned above, it is also common to find small mineral platelets, druses of crystals (e.g. in the trama and crowning the cystidia of *Odontia bicolor*), and large irregular concretions (e.g. in the trama of *Grammothele*

FIG 19.—Setoid structures:—
1-7. Hyphal terminations in the pore walls of **Polyporus dictyopus.** 8-9. Hyphal terminations in the hymenium of **Stereum schomburgkii.** 10. Hyphal terminations in the hymenium of **Duportella tristicula.** 11-13. Modified skeletal hyphae (cystidia) of **Stereum umbrinum.** 14-15. Setoid hyphae of **Polyporus ochroporus** (cotype). 16-17. Setoid hyphae from the pore tissue of **Polyporus patouillardii** (short examples).
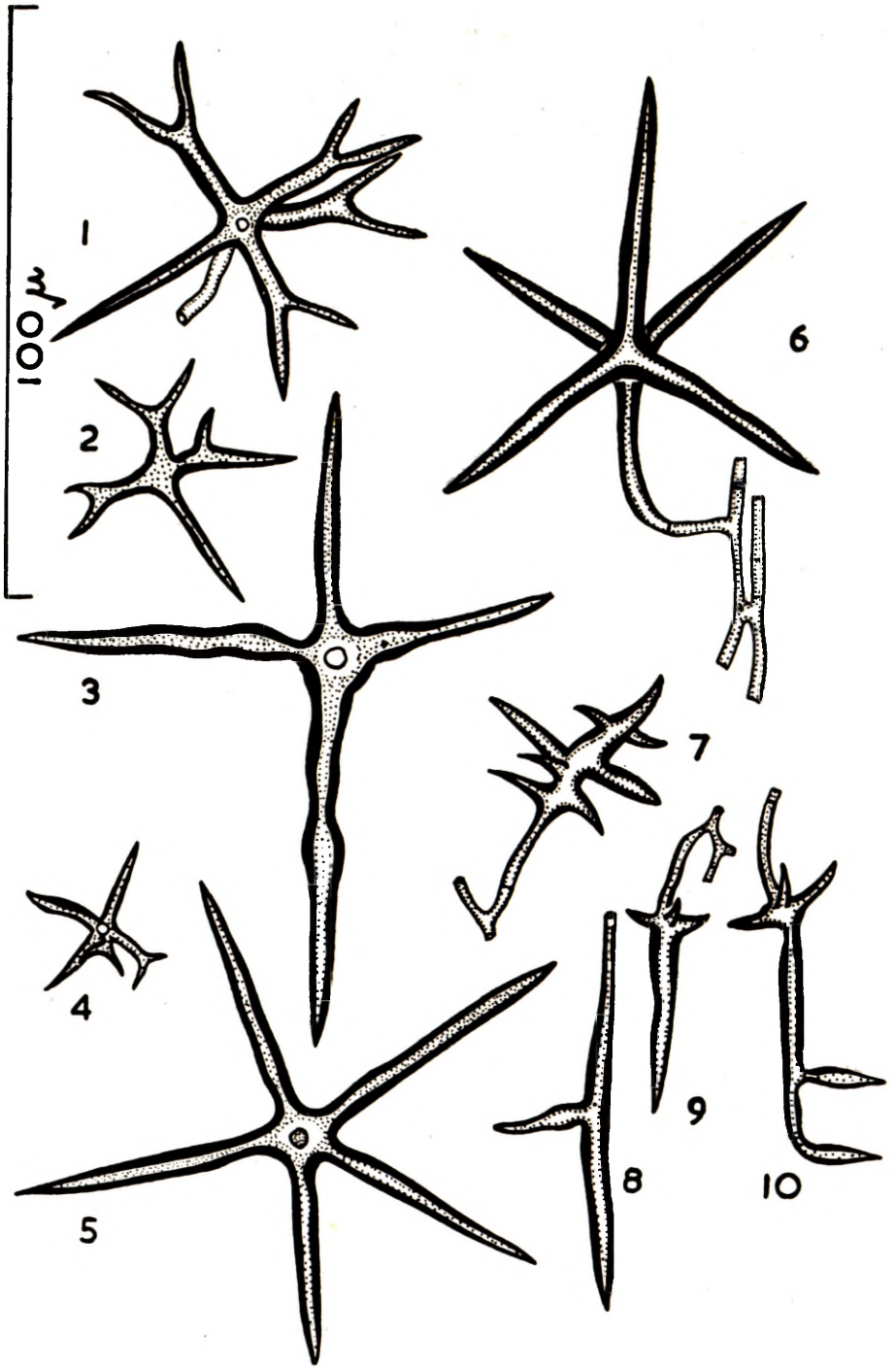
spp.). Incrustation of the cystidia is particularly common in the genus *Peniophora*, and in species of *Stereum* which were at one time segregated as the genus *Lloydella* Incrusted hyphae also occur in many species and are then an aid to specific diagnoses (e.g. in *Peniophora filamentosa* and *Polyporus rutilans* and *Coniophora betulae*). In *P. filamentosa* and *P. rutilans*, which but for the difference in hymenial configuration are identical, the crystals are rapidly soluble in potassium hydroxide solution and react to give a vinous colour. Some mineral inclusions are soluble in alkali, others in acid solutions, thus it is desirable to make mounts in more than one medium. Occasionally the mineral incrustation has its own bright colour which colours the whole fungus; more often the minerals are colourless or light yellowish and at the most impart a glitter to the surface of the fungus.

Large airspaces which are frequently observed in sections of fungi may be due to the former presence of mineral inclusions. These are sometimes torn out during sectioning as the razor comes up against the hard obstruction, or they may sometimes have been leached out prior to collection. It is possible that during its growth the fungus produces minerals in solution, which, with the advent of dry conditions, become deposited in the tissues as large concretions. On subsequent leaching of the trama these may be redissoved and thus leave an airspace.

FIG. 20.—Asterosetae:—

1–5. from **Asterostroma cervicolor.** 6–10. from **Asterodon ferruginosus** (after Corner, 1948 b). 6. Stellate setae in the resupinate part of the fructification. 7. substellate setae near the subhymenium. 8–10. Setae in the tissues of the spines and emerging laterally into the hymenium on the spines (simple, forked or substellate setae). Nos. 1–5, only, drawn to scale shown.

Cambridge University Press: W. B. Grove, "The British Rust Fungi" (1913) 14, Fig. 16 a and b.

Department of Scientific and Industrial Research, New Zealand: G. H. Cunningham in N.Z. Journ. of Science & Technology 28 (1946) Figs. 7, 8, 9.

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