Taxonomy of Stereum and Allied Genera.

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With Plate XXI.

In the United States all taxonomical studies of *Stereum* during the past forty years have been based on the classical and conservative work of Burt (1920). So influential was Burt's treatment of *Stereum* that it prevailed throughout much of the world, although this influence was counteracted in Europe to a considerable degree by the more incisive treatise of Bourdot and Galzin (1928). Somewhat earlier, Karsten (1889) was an advocate of grouping species in small homogeneous groups that presumably showed natural relationships relatively lacking in the comprehensive genera of Fries (1874), Massee (1889, 1890), and Burt. Several years ago (1955), I discussed the genus *Stereum* in the upper Mississippi valley [1]). Although striving to retain, at least in general circumscription, the generic definition of Burt, I realized then that this was difficult for some species and impossible for others. Three genera were separated from *Stereum* in that paper, but the general treatment was rather conservative and based largely on macroscopic and gross microscopic characteristics. Recently, some authors have been more perspicaceous in dissecting the genus and attempting to eliminate species not obviously congeneric with *S. hirsutum* (Willd. ex Fr.) S. F. Gray, the type species. As a basis for an attempt to assess the validity of these activities, it seems advisable to characterize the group of species that includes the pertinent aspects of the genus.

Stereum.

In *S. hirsutum* and obviously related species the basidiocarp is normally effused-reflexed or distinctly pileate, often dimidiate or laterally sessile. The texture is usually tough-leathery or almost woody, but in the latter instance the basidiocarp is usually flexible. Because of the generally parallel arrangement of thick-walled context hyphae, the basidiocarp may be split rather easily, starting from any

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[1]) Attention should be called to the fact that specimens cited in that paper as having been obtained from the Commonwealth Mycological Institute, Kew, were actually obtained from the Royal Botanic Gardens at Kew. Thus IMI, in each instance where cited in that paper, refers to a specimen borrowed from the Royal Botanic Gardens.

point around the periphery and cleaving in a line toward the basal attachment point or toward the center of basidiocarps that have a growing margin of 360 degrees. On the contrary, the basidiocarp is exceedingly tough and resistant to being pulled apart across the direction of hyphal orientation. Usually the hymenial surface is smooth and dry and the superior surface tomentose.

When a vertical section of the basidiocarp is observed, the tomentum is seen to arise usually from a zone of densely aggregated hyphae that form the superior surface and have a golden-yellow to reddish-brown color in mass. The central context is usually broad and hyaline to pale yellowish. It is bordered by a hymenial region where the basidia develop. The hyphae are of two general kinds. Many are relatively thin-walled, branched and septate. These are generative (see Corner, 1932 a, b). Others are thick-walled, unbranched or perhaps branched very infrequently and characteristically non-septate; whether they fit within the precise definition of the term in every instance or not these are either skeletal hyphae or at least hyphae of very similar nature. Thus the hyphal system is at least usually and perhaps always dimitic. A more definite statement must depend on corroboration of the nature of the thick-walled hyphae in some species. The generative hyphae do not have any conspicuously unidirectional orientation except as they become directed into the basidial fascicles at the base of the hymenium, but the thick-walled hyphae are more or less longitudinally parallel in the context and curve into the hymenium on one side as pseudocystidia (Fig. 1, C) and extend from the superior surface on the other side to form the tomentum.

In the hymenium, in addition to thick-walled pseudocystidia and 4-sterigmate basidia, there may be thin-walled basidioles. Some of the basidioles are beset with a few aculeate protuberances at or near their tips (Fig. 1, C). The spores are typically cylindrical, smooth, hyaline, and amyloid; each has two nuclei (Boidin, 1950). Clamp-connections seem to be absent from hyphae of well-developed basidiocarps; possibly a study of very young basidiocarps would reveal clamps on the generative hyphae. In culture several species have been shown to form clamp-connections, and some may even have more than one clamp formed at many of the septa (see Boidin, 1950; Lentz, 1955, p. 47).

Species having the characteristics just described seem to form a homogeneous group which may be thought of as the natural genus *Stereum*. Cultures of several of these species have been studied in relation to their oxidase reactions on gallic and tannic acid media (Davidson, Campbell and Blaisdell, 1938; Boidin, 1951 b) and in all instances have been found to produce a positive reaction. All woodinhabiting species of *Stereum sensu stricto* seem to cause white rots of their substrata. Among the species that belong in *Stereum,* some of the most familiar are *S. hirsutum,* the type species; *S. complicatum* (Fr.) Fr.; *S. gausapatum* (Fr.) Fr.; *S. ochraceo-flavum* (Schw.) Ell.; *S. ostrea* (Blume & Nees ex Fr.) Fr. (including *S. fasciatum* (Schw.) Fr. and *S. lobatum* (Kunze ex Fr.) Fr.); *S. rugosum* (Pers. ex Fr.) Fr.; *S. sanguinolentum* (Alb. & Schw. ex Fr.) Fr.; *S. striatum* (Fr.) Fr.; and *S. vellereum* Berk.

Xylobolus.

In addition to species sharing the characteristics of the preceding group, many other species have historically been included in *Stereum* but differ in some ways from the typical group. Several of these form another homogeneous group which, following Karsten (1881), some authors have referred to the genus *Xylobolus* Karst. Whether *Xylobolus* is an autonomous genus or a subgenus of *Stereum* is not yet established. Boidin (1958) and Pouzar (1959) regard *Xylobolus* as a distinct genus that includes *X. frustulatus* (Pers. ex Fr.) Boidin as the type. Closely related species are *X. annosus* (Berk. &. Br.) Boidin, *X. princeps* (Jungh.) Boidin, *X. subpileatus* (Berk. & Curt.) Boidin, and several other species, some of which are listed by Boidin. I feel that *Xylobolus* may be closely enough related to *Stereum* to be conveniently treated as a subgenus until more conclusive evidence of unrelatedness is produced, but it also may be treated as a separate genus if its close relationship with *Stereum* is kept in mind.

The basidiocarps of some species of *Xylobolus* are very similar in form to those of *Stereum,* although generally somewhat more sturdy. However, *X. frustulatus* has basidiocarps formed as tuberculiform frustules, and those of *X. annosus* appear as thick, broad sheets on the substratum. The horizontally parallel arrangement of thick-walled hyphae is not always obvious in basidiocarps of this group; nevertheless the developmental pattern is fundamentally the same as in the typical species of *Stereum,* even though obscured by the formation of a thickened stratum of vertical development. The hyphal system is dimitic, with some of the skeletal hyphae appearing in the hymenium as pseudocystidia. As in *Stereum,* clamp-connections are apparently absent from the basidiocarp. Aculeate protuberances may appear on almost any hyphal endings in the hymenium, possibly excepting the fertile basidia. The most scantily beset of these elements may resemble the aculeate-tipped basidioles found in some species of *Stereum,* but the more profuse development of protuberances results in the formation of acanthophyses. Some species of *Xylobolus* have encrusted cystidia, often with aculeate protuberances under the encrustation. These protuberances may also appear farther toward the base of the cystidium than the encrustation extends. Similar hyphal endings may have aculeate protuberances but lack encrusting matter. Thus, *Xylobolus* may have acanthophyses, cystidia, pseudocystidia, encrusted acanthophyses, acanthophysoid encrusted cystidia, and perhaps other hyphal forms. Of the characteristics thus far enumerated, these are the only ones tending to deviate much from those of *Stereum,* and even these have some less exaggerated counterparts in *Stereum.* In culture (Davidson, Campbell, and Blaisdell, 1938; Boidin, 1951 b), *X. frustulatus* and *X. subpileatus* differ from species of *Stereum* by their negative oxidase reaction on gallic and tannic acid media. Although the decay they cause in woody substrata is white, it is a very much specialized and characteristic white pocket rot instead of the diffuse white rot characteristic of *Stererum.*

Peniophora sect. **Coloratae.**

Peniophora cinerea (Fr.) Cke. and related species of *Peniophora* sect. *Coloratae* do not seem to be at all closely related to *Stereum,* certainly not to *Stereum sensu stricto.* By definition, *Peniophora* has traditionally been regarded as including only resupinate species, while *Stereum* has included only reflexed or pileate species. But in the corticioid and stereoid fungi, the macroscopic form of the basidiocarp is now assigned a role of only secondary importance. Thus, Eriksson (1950) was able to assign both *Stereum versiforme* Berk. & Curt. and *Cryptochaete polygonia* (Pers. ex Fr.) Karst. to *Peniophora* sect. *Coloratae* on the basis of anatomical and microchemical aspect while minimizing the significance of basidiocarp growth habit.

In my previous paper on *Stereum* (1955), I was not able to give strong support to the validity of including *S. versiforme* in *Stereum* but nevertheless did include it in that genus as a matter of convenience. In the arrangement of that paper, *S. versiforme* was grouped with *S. erumpens* Burt and *S. albobadium* (Schw. ex Fr.) Fr. Both species are very closely related to *S. versiforme* and must be treated as congeneric with it. In expressing this belief, I have already been preceded by Eriksson (1950), with respect to *S. albobadium,* and by Boidin (1959 a). Eriksson (1958) more recently expressed some hesitancy about including these species directly in the *Coloratae* and suggested that they may constitute a closely related satellite genus. I believe these species may be more closely related to *P. cinerea* than *X. frustulatus* is to *S. hirsutum* but that the various species of the group are perhaps not quite so homogeneous as the various species of *Xylobolus;* therefore these and related species may be placed directly in *Peniophora.*

S. albobadium[2]), *P. erumpens* (Burt.) Boidin, and *P. versiformis* (Berk. & Curt.) Bourd. & Galz. may be delineated as follows: Although often resupinate, the basidiocarp has a definite tendency to become slightly or at times markedly reflexed. The hymenial surface is usually grayish to brownish and tends to have an obscurely and minutely velutinous aspect. The hyphae of the context are septate and have clamp-connections; many are brown. In and near the hymenium, especially, are numerous brownish dendrophyses or occasionally only noteworthy colored hymenial hyphal tips. All three species have encrusted cystidia, 4-sterigmate basidia, and spores which are curved-cylindrical to allantoid, smooth, and non-amyloid. According to Boidin (1959 a), the spores of *P. versiformis* are uninucleate.

Some authors (Boidin, 1959 a; Eriksson, 1950, 1958) place considerable emphasis on the deposition of a red spore print as a generic characteristic in *Peniophora* sensu stricto (the *Coloratae*). The difficulty of applying this criterion will be emphasized later when *Cryptochaete polygonia* is discussed. In the meantime, it may be noted that Boidin (1959 a) reported that the spores of *P. versiformis* are pale orange in mass and therefore fulfill the conditions necessary for referring this species to *Peniophora.* Spore print color of *S. albobadium* and *P. erumpens* apparently is not known, and I believe it to be relatively unimportant if the other characteristics of the three species are as similar as they seem to be. In *Stereum,* for example, most of the species have white spore prints. The fact that *S. complicatum* may produce an orange print on occasion certainly does not indicate that it is unrelated to the other species. The same statement may also be made concerning the spore print color and the presence or absence of gloeocystidia in *S. albobadium* and *P. erumpens.* By use of the sulfo-aldehyde reaction, Boidin (1951 a, 1959 a) was able to demonstrate the presence of gloeocystidia in some species that previously were thought to lack such elements. He found, for example, that gloeocystidia are formed in *P. versiformis* and especially in *P. versiformis* forma *carbonicola,* and suggested that they may be present in *S. albobadium* and *P. erumpens.* From the multitude of hyphal tendencies and aberrations in these species, it is very difficult to characterize each modification. Boidin and others have shown that certain chemical reactions, cytological relationships, and hyphal modifications are shared characteristics of apparently closely related species, but there is an almost infinite variety of modifications of every kind and degree in the corticioid fungi; thus, it would not be too difficult to show that many apparently unrelated species also have various

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2) It does not seem desirable to make new combinations in the present paper.

characteristics in common. The presence of gloeocystidia in *P. versiformis* and the possibility of their absence from *S. albobadium,* conversely, may not actually be very significant in the determination of relationships.

As mentioned in an earlier paragraph, Eriksson (1950) included *Cryptochaete polygonia* in *Peniophora* sect. *Coloratae.* This was rather unusual treatment in some respects because this species deviates from the traditional concept of *Peniophora* by having the capability of forming slightly reflexed basidiocarps and also by lacking cystidia (although having gloeocystidia). Eriksson recognized the unique aspects of this species and placed it in a distinct group of sect. *Coloratae* characterized by the absence of cystidia and the presence of gloeocystidia and hyaline dendrophyses. Although *P. polygonia* was thus unique among the *Coloratae,* it is in fact very much like two species formerly placed in *Stereum.* The relationships among these species are very interesting and perhaps instructive as to the difficulty of establishing conclusive taxonomic criteria.

In 1889, Karsten published two new genera of significance with reference to the classification of the *Coloratae.* One was *Sterellum,* with only the type species *S. pini* (Schleicher ex Fr.) Karst. The other was *Cryptochaete,* with the two species *C. rufa* (Fr.) Karst. and *C. polygonia* (Pers. ex Fr.) Karst. Because *C. rufa* was the first species considered in Karsten's genus, I (1955) originally selected it as the lectotype. As mentioned at that time, *C. polygonia* was placed by Pilát (1926) in *Aleurodiscus* as the only species in subgenus *Cryptochaete.* He did not account for *C. rufa,* which presumably still fitted into Karsten's definition of *Cryptochaete.* That *C. polygonia* should become the type of the genus *Cryptochaete* by being placed in the genus *Aleurodiscus* as the only species of the subgenus *Cryptochaete* seems somewhat debatable. However, according to Donk (1957), that is what happens. As described by Karsten, *Sterellum* included only species without cystidia. Unfortunately even the type species of *Sterellum* does have cystidia and, in addition, also gloeocystidia. *Cryptochaete,* on the contrary, was said to have cystidia, although the elements that Karsten described are now called gloeocystidia. *C. polygonia* does not seem to have encrusted cystidia, and those of *C. rufa* apparently had never been noted before my study of this species (1955). As illustrated by Eriksson (1958) they closely resemble the encrusted cystidia of *S. pini.* Thus, neither *Sterellum* nor *Cryptochaete* was originally described with complete accuracy. As previously mentioned, Eriksson (1950) transferred *C. polygonia* to *Peniophora* sect. *Coloratae.* Later (1958), he transferred *C. rufa* to *Sterellum* where it appears to be closely related to *S. pini.*

At this point some speculation must arise concerning the relationship of *P. polygonia* to *S. pini* and *S. rufum.* The spores of *Peniophora* sect. *Coloratae* are reputed to be red in mass. Eriksson (1950) noted that *P. polygonia* is typical in that respect, as it has a light-red spore print. According to Eriksson (1958), the species of *Sterellum* are quite distinct in this respect. These are said to have white spore prints. Boidin (1951 a, 1959 a) stated that the gloeocystidia of *P. polygonia,* like those of other *Coloratae,* are strongly sulfo-aldehyde positive. He (1958) then said that *Stereum pini* has all the characters of *Peniophora* sensu stricto, including reddish spores (previously noted by Eriksson as white) and sulfo-aldehyde positive gloeocystidia. Thus the gloeocystidia of *P. polygonia* and *S. pini* are alike in being sulfo-aldehyde positive, and in this respect *S. pini* can be said to resemble *Peniophora* sect. *Coloratae.* If, as Boidin said, the spores of *S. pini* are red in mass, this is still another item of similarity to *P. polygonia* and the *Coloratae.* Actually, this may not be of any considerable importance. When all the similarities of *P. polygonia* and *S. pini* are considered, little doubt can remain that they are closely related.

If *S. pini* and *S. rufum* are included in a single genus, probably *P. polygonia* should be placed in the same genus. This may be *Sterellum,* but the preferable course may be to include these species in *Peniophora* sect. *Coloratae* as exhibiting rather extreme examples of some characteristics noted in other *Coloratae.* Recently Boidin (1959 a) transferred *S. rufum* to *Peniophora* as *P. rufa* (Fr.) Boidin, thus uniting it with other species of *Coloratae.* The basidiocarps of the small group of species with which it is most closely allied have a distinct tendency to be erumpent-tuberculiform, although this tendency is really very pronounced only in *P. rufa. P. pini* (Schleicher ex Fr.) Boidin (1956) and *P. polygonia* become effused and often slightly reflexed at the margin. The hymenial surface is brightly colored in a reddish or vinaceous hue and may be somewhat pruinose. The hyphae of these species are branched, form clamp-connections, and are especially distinctive because so many of them have thick gelatinous-appearing walls. This gelatinous condition may be a modification associated with the development of these fungi in the xerophytic environment afforded by dead twigs and branches. If so, why have not the other *Coloratae* developed similary? As previously mentioned, all three species have gloeocystidia. In addition, *P. polygonia* has hyaline dendrophyses and both *P. pini* and *P. rufa* have encrusted cystidia. The spores are curved-cylindrical, smooth, and non-amyloid.

Laxitextum.

It now becomes necessary to enter into a meticulous examination of a varied group of species many of which may be placed in separate genera. Some of these species were studied by Pouzar (1959) and assigned as types of the six new genera which he described. Boidin (1959b) reviewed Pouzar's work and at least tentatively accepted some of its implications. In his paper Boidin mentioned the difficulties that result from splitting genera so much that the resulting multiplicity of small units creates taxonomic clutter. But as the criteria upon which each genus is based are both multiplied and refined, the difficulty of finding any considerable number of species that agree in all or most respects with these criteria is also increased. A case in point is my genus *Laxitextum* (1955). This was a segregate from *Stereum,* a segregation which was necessary but which perhaps was not pursued quite to its ultimate realization. As a result, *Laxitextum* has now been reduced to include only the type species, *L. bicolor* (Pers. ex Fr.) Lentz (see Boidin 1958; Eriksson, 1958).

The basidiocarp of *L. bicolor* is effused-reflexed to distinctly pileate, with a conspicuous contrast between the brown superior surface and the whitish hymenial surface. The hyphal system is monomitic and the hyphae branch and extend in all directions in the context. Those constituting the brown spongy layer are very loosely arranged, as seen in a vertical section through the basidiocarp. All hyphae have clamp-connections. Slender gloeocystidia originate in the subhymenial area and extend into the hymenium. When mounted in potassium hydroxide solution, the spores are hyaline and smooth. In Melzer's reagent they are amyloid and have a tendency to be slightly rough, although apparently not quite so prominently as illustrated by Boidin (1958). The spores are uninucleate (Boidin, 1950). *L. bicolor* causes a white rot of woody substrata.

Laeticorticium.

In 1956, Donk published *Laeticorticium,* a new genus with *L. roseum* (Pers. ex Fr.) Donk as the type. If one is willing to depart from the rigidity with which the term "resupinate" has traditionally been applied in the corticioid fungi, then perhaps Boidin (1959 a) may be followed in referring *Laxitextum roseo-carneum* (Schw.) Lentz to *Laeticorticium* as *L. roseo-carneum* (Schw.) Boidin. *L. roseo-carneum* is often, but not always, entirely resupinate. The hyphal system is monomitic. The hyphae have numerous clamp-connections and branch freely throughout the loose-textured context. In the hymenium, the hyphae are profusely short-branched, appearing as dendrophyses but with clamp-connections even near the hyphal tips. Because they are septate and have clamp-connections throughout, I (1955) called them "pseudodendrophyses". The spores are broadly ellipsoidal and somewhat flattened along the sides, smooth, hyaline, and non-amyloid. A moderate sense of uneasiness experienced when I examined Boidin's illustration of pseudodendrophyses (1959 a, fig. 12) in this species caused me to examine the specimen which he illustrated. The pseudodendrophyses are accurately drawn, but the striking appearance is caused by the fact that they tend to be somewhat collapsed and disintegrating near the tips. This may be a condition that one would often find, but not one most advantageously revealing the form of these elements when they are in the best stage of development.

Lopharia.

The other species that I placed in *Laxitextum* was *L. crassum* (Lév.) Lentz. This is the species that Burt (1920) called *Stereum umbrinum* Berk. & Curt. Cunningham (1956 a) included this species in *Lopharia* as *L. vinosa* (Berk.) Cunn. In choosing *vinosa* as the specific epithet, Cunningham ignored the fact that *Thelephora crassa* was originally published not in 1846, as he cited it, but in 1844, as I had previously (1955) stated. Further, the original publication of *vinosa* by Berkeley (1845) was not as *Thelephora vinosa,* but as *Corticium vinosum.* Boidin (1959 a) renamed *L. vinosa* as *L. crassa* (Lév.) Boidin. According to Cunningham, *Stereum papyrinum* Mont. also belongs in *Lopharia.* I agree that *S. papyrinum* should be included in whatever genus *L. crassa* is placed.

To determine whether *Lopharia* is a good genus and whether *L. crassa* may be placed there, the history of the genus must be reviewed. *Lopharia* was originally established by Kalchbrenner and MacOwan (Kalchbrenner, 1881) with *L. lirellosa* the single species described. Recently Talbot (1954 b) reported *L. lirellosa* to be synonymous with *Stereum cinerascens* (Schw.) Mass. Cunningham (1956 a) included both *L. lirellosa* and *S. cinerascens* as synonyms of *Lopharia cinerascens* (Schw.) Cunn. In 1892, Massee described the genus *Thwaitesiella* with *T. mirabilis* (Berk. & Br.) Mass. as the type species. Both Talbot and Cunningham considered this to be a synonym of *L.* (or *S.*) *cinerascens.* In addition, Donk (1957) listed *Licentia* Pilát as a synonym of *Lopharia.* Boidin (1959 b) placed *L. lirellosa* in synonymy with *L. mirabilis,* which has precedence because it was originally described, as a species of *Radulum,* in 1873. According to Boidin, *L. cinerascens* is distinct from *L. mirabilis* and should be treated as a separate species of *Lopharia.*

Among the species heretofore included in *Stereum* by many authors are some characterized by the possession of cystidia. For these, Bresadola (1901) devised the genus *Lloydella,* in which he included *L. cinerascens* (Schw.) Bres. *(Stereum cinerascens), L. striata* (Schrad.) Bres. (*S. abietinum*), *L. chailletii* (Pers.) Bres. (*S. chailletii*), *L. spadicea* (Pers.) Bres. (*S. spadiceum* Quel. non Fr.), *L. spadicea* var. *venosa* (Quél.) Bres., *L. bicolor* (Pers.) Bres. (*S. bicolor* or *S. fuscum*), *L. membranacea* (Fr.) Bres. (evidently *S. papyrinum*), *L. papyrina* (Mont.) Bres. (*S. papyrinum*), and *L. ferrea* (Berk. & Curt.) Bres. (*S. ferreum*). Cunningham (1956 a) included *Lloydella* as a synonym of *Lopharia.* Pouzar (1959) stated that to revive *Lloydella* in the broad sense of Höhnel and Litschauer (1908) would be inconvenient because the species included are not phylogenetically related. That statement is undoubtedly true. The only real concern is whether the same may be true of *Lopharia.*

Cunningham (1956 a) emended *Lopharia* to include species having an essentially *Stereum*-like habit but possessing "the microstructure of *Peniophora,* including typical crystal-coated cystidia of the pedicellate section". Included in the genus, according to Cunningham, are species having either a monomitic or a dimitic hyphal system but with generative hyphae lacking clamp-connections. The context is said to be composed of a basal layer of parallel hyphae, with an intermediate layer of ascending hyphae. Of course this form of hyphal arrangement is similar to that of *Stereum* and was one of the reasons I previously included *L. cinerascens* in *Stereum.* Talbot (1954 b) also cited the same reason for including this species in *Stereum.* This hyphal arrangement is scarcely apparent in *L. crassa,* although the latter species shares the effused-reflexed basidiocarp habit with *L. cinerascens.* Cunningham stated that *L. cinerascens* is dimitic and *L. crassa* (as *L. vinosa*) monomitic. However, Talbot (1954 a) wrote that *L. crassa* (as *S. umbrinum*) is dimitic. According to Boidin (1959 b), *L. crassa* has generative hyphae lacking clamp-connections and brownish skeletal hyphae ending in the subhymenium or hymenium as pseudocystidia.

Hyphal relationships should not be dealt with in a dogmatic manner. The terminology used to refer to different kinds of hyphae may provide a convenient means of characterizing the appearance, origin, and perhaps the function of various hyphae forming the basidiocarp. But embracing the implications of these terms too rigidly may result in the development of artificial taxonomic concepts. Generative hyphae are usually branched, septate, often with clamp-connections, and ultimately capable of producing basidia. Skeletal hyphae originate from septate hyphae at a very early stage in the morphological development of the basidiocarp and apparently serve as the thick-walled, unbranched, usually non-septate skeletal framework during the construction of the basidiocarp. If some hyphae develop very early as thick-walled elements but then resume apical growth as thin-walled septate hyphae, the thick-walled portions may not be called skeletal hyphae. In addition, thick-walled, unbranched hyphae may develop as Pouzar (1959) said those of *Stereum gausapatum* and *S. sanguinolentum* do, i. e., with their origins in the region not very far beneath the hymenium rather than in the undifferentiated growing region of the basidiocarp. Pouzar did not consider these to be skeletal hyphae even though some may actually extend for a considerable distance through the context. If they are not skeletal hyphae, are they different from skeletal hyphae in any absolute sense or only relatively? A recent article by Boidin (1959b) includes a discussion of hyphal-system definitions; his view seems to be similar to but more extreme than that which I present. In relation to cystidia and pseudocystidia he wrote that one does not differ essentially from the other except in the length of the stalk, both types originating from generative hyphae. This may also be said of the origin of skeletal hyphae, but the concept of the various hyphal series nevertheless remains useful if not applied too rigidly.

In utilizing hyphal characteristics as taxonomic criteria, consideration should be given to elements that do not exactly coincide with definitions but which approach them very closely. Thus, to return to *L. crassa,* the pedicels of the cystidia (Fig. 1, A) may be skeletal hyphae, as Talbot and Boidin believe, or may not be, as Cunningham implied. The distinction does not seem to be extremely important except as a matter of definition. Essentially the same kind of thick-walled, non-branching, non-septate hyphae occur in both *L. crassa* and *L. cinerascens.* The two species also resemble each other in having smooth, hyaline, non-amyloid spores. However, the hyphal arrangement of *L. crassa* is not horizontally parallel, as in *L. cinerascens*; thus the texture of the two species is dissimilar. In addition, the basidia and spores of *L. cinerascens* are approximately twice those of *L. crassa* in length and width. These differences may not seem important, but the total aspect is of two entirely dissimilar fungi. Therefore, I believe that *L. crassa* should not be included in *Lopharia* and that *Lopharia* may be in need of even further redefining to restrict it to species clearly congeneric with *L. cinerascens* and with *L. mirabilis* if, as Boidin said, that species is distinct from *L. cinerascens.*

Lopharia cinerascens is remarkably similar to the common species of *Stereum* in its morphology. Only the production of encrusted cystidia marks it as unusual. The basidiocarp is effused-reflexed. In section, it looks very much like *S. hirsutum*, except for the cystidia. The superior surface is a dense, colored, differentiated layer from which the tomentum arises. The context has an arrangement similar to that of *S. hirsutum* and is formed of both generative and skeletal hyphae. However, the spores and basidia are considerably larger than those of most species of *Stereum*; the hymenium includes encrusted cystidia (though the importance of these as a generic character may not always be very great); and the spores are non-amyloid. While none of these characteristics would be very important separately, together they seem to indicate that *L. cinerascens* may not be very closely related to *S. hirsutum*. *Lloydella* has been rejected by nearly all mycologists as based on an artificial concept. Therefore *Lopharia* cannot be accepted merely as a substitute for *Lloydella*. Boidin (1959 b) redefined *Lopharia* to include species with or without clamp-connections, resupinate, with cystidia, and having non-amyloid spores. The emended genus is still somewhat heterogeneous and apparently not a great improvement over *Lloydella*.

Chondrostereum.

Most of the remaining *Stereum*-like species to be discussed in this paper were previously considered by Pouzar (1959) and made the types of new genera. His concept solves some problems but creates others. If one is unwilling to define *Stereum* on gross morphological characteristics, there is no place to stop short of being very meticulous concerning differentiating characters. For example, having removed *L. crassa* from *Lopharia*, we may wish to ally it with *Stereum chailletii* (Pers. ex Fr.) Fr., which has a somewhat similar aspect. If so, we find that the two differ in their oxidase reaction, in spore amyloidal reaction, and in presence or absence of clamp-connections in the basidiocarp. Thus a genus embracing these two species may not be very homogeneous except in superficial aspect. The same may be said in relation to *Stereum purpureum* (Pers. ex Fr.) Fr. and *S. hirsutum*. *S. purpureum* is very much like *S. hirsutum* in general habit and in producing a relatively strong oxidase reaction on gallic and tannic acid media and a white rot of woody substrata. According to Pouzar (1959) *S. purpureum* is dimitic, but Boidin (1959 b) denied this. Thus *S. purpureum* apparently differs from *S. hirsutum* by having a distinctly waxy hymenium, by forming vesicles in the subhymenium and adjoining context, by having a monomitic hyphal system with hyphae bearing numerous clamp-connections (Boidin, 1959 b), and by having non-amyloid spores that are uninucleate (Boidin, 1958). Pouzar (1959) placed *S. purpureum* in a distinct genus as *Chondrostereum purpureum* (Pers. ex Fr.) Pouzar.

Phaeophlebia.

Another species having a cartilaginous aspect somewhat resembling that of *C. purpureum* was discussed recently by Cunningham (1956 b). This species, which he called *Stereum strigoso-zonatum* (Schw.) Cunn., is the same as *Phaeophlebia strigoso-zonata* (Schw.) W. B. Cke. (1956). In almost all respects, *P. strigoso-zonata* deviates from the usual characteristics of *Stereum*; so it appears to be somewhat out of place even in a broadly conceived genus *Stereum*. In addition to having a cartilaginous texture, *P. strigoso-zonata* is monomitic, with clamp-connections even on the tomental hyphae, with dendrophyses, and with non-amyloid spores. Some tropical species now referred to *Stereum* tend to have a cartilaginous texture or waxy hymenium. Further study is needed to show the true relationship among the various species. In the meantime, Cooke's treatment of *P. strigoso-zonata* may be followed.

Cystostereum.

Stereum murraii Berk. & Curt. resembles *C. purpureum* somewhat in several microscopic details. Both produce vesicles in the context, form clamp-connections, and have non-amyloid spores. In all of these aspects they differ from *S. hirsutum*. Although *C. purpureum* and *S. murraii* share many characteristics, they do not really give an impression of being more closely related to each other than either is to *S. hirsutum*. If, as Boidin (1959 b) intimated, *C. purpureum* has a monomitic hyphal system, it differs in that respect from *S. murraii*, which is dimitic. Pouzar (1959) made *Cystostereum murraii* (Berk. & Curt.) Pouzar the type and only species in a new genus.

Columnocystis.

A few species remain to be discussed. Although having the general form of *Stereum*, most of them differ enough from that genus to be removed without undue regret. *S. abietinum* (Pers. ex Fr.) Fr., for example, produces only a very weak or negative oxidase reaction on gallic acid medium (Boidin, 1951 b) and causes a brown rot of woody substrata. According to Pouzar (1959) this species is dimitic. It is characterized by relatively thick-walled cylindrical cystidia produced from generative hyphae with clamp-connections (Fig. 1, D). The spores are non-amyloid. Pouzar placed this species in a new genus as *Columnocystis abietina* (Pers. ex Fr.) Pouzar together with *C. carpatica* (Pilát) Pouzar and *C. ambigua* (Pk.) Pouzar. According to Boidin (1959 b), *C. ambigua* does not have clamp-connections, so the original generic diagnosis must be emended to remove the words "nodoso-septatis".

Amylostereum.

Another new genus erected by Pouzar is *Lloydellopsis*. The type is *L. chailletii* (Pers. ex Fr.) Pouzar, formerly known as *Stereum* *chailletii* (Pers. ex Fr.) Fr. This species is like *Stereum* in having amyloid spores, as well as in having a strongly positive oxidase reaction on gallic acid medium (Boidin, 1951 b). It differs in forming encrusted cystidia (Fig. 1, E) in having clamp-connections in the basidiocarp, and in having uninucleate spores (Boidin, 1950). If *S. chailletii* is accepted as the type of a new genus, then *Lloydellopsis* must be regarded as a synonym of *Amylostereum* Boidin (1958), which was based on the same type species.

Other Taxa.

Stereum radiatum Pk. is another species that resembles *C. abietina* and *A. chailletii* in having an effused-reflexed *Stereum*-like habit. The distinctively rusty-brown hymenial surface is minutely velvety in appearance, because it is beset with innumerable slender cystidioles (Fig. 1, B). *S. radiatum* has non-amyloid spores which are usually hyaline but may have a very pale brownish tinge. This species should be excluded from *Stereum,* but I cannot say where it belongs.

In 1959, Davidson, Toole, and Campbell published a note on a disease of bald cypress (*Taxodium distichum* (L.) Rich.). Although this disease reduces the quality of cypress lumber, it may be of some commercial benefit because of the aesthetic appeal of the infected wood which is known as "pecky cypress". The disease is apparently caused by a species of *Stereum* which has been found to resemble *S. sulcatum* Burt to a remarkable degree. During the study of this fungus, two specimens of the same species were found already on file in the National Fungus Collections. Each had been identified as *S. sulcatum.* One specimen is from Florida and was identified by H. S. Jackson; the other is from Louisiana and was identified by E. A. Burt. This fungus is to be described as a new species in an article written by Davidson and co-authors (1960, tentative). In the meantime, it may serve as an interesting example to illustrate the difficulties involved in the taxonomy of this group.

The new species will be published as a *Stereum.* It resembles *S. hirsutum* in having a reflexed to pileate basidiocarp, a smooth hymenial surface, and a tomentum arising from the superior surface. It has a *Stereum*-like appearance in vertical section, a dimitic hyphal system, and amyloid spores. In its macroscopic appearance it differs from *S. sulcatum* only in one somewhat nebulous aspect, i. e., the hymenial surface is bright in *S. sulcatum* and somewhat grayish in *S.* sp. Both species have dimitic hyphal systems and encrusted cystidia. The amyloid spores of the two species are of similar or practically identical shape and slightly asperulate; they differ only slightly in size. However, *S. sulcatum* has a strongly positive oxidase reaction, whereas the reaction of *S.* sp. is weak or negative. *S. sul-*

catum produces conidia on oedocephaloid conidiophores in culture, but *S.* sp. produces only chlamydospores. *S.* sp. has skeletal hyphae of the context strikingly well-developed and lying in a generally parallel arrangement much like those of *S. hirsutum*; in *S. sulcatum* the skeletal hyphae are rather weak and are twisted and pulled in every direction by abundant and often thick-walled branching generative hyphae. The tomentum of *S.* sp. consists of skeletal hyphae, but the tomentum of *S. sulcatum* consists of generative hyphae with clamp-connections.

In characterizing his new genus, *Laurilia,* which includes *L. sulcata* (Burt) Pouzar as the only species, Pouzar (1959) stated that it "is characterized by the superficial tomental layer, here very scanty, which is composed of nodose hyphae — therefore generative, not skeletal — which is a unique feature among the dimitic amylosporous sterea". The pecky cypress fungus is a species which resembles *S. sulcatum* so closely that consideration may very well be given as to whether one species may have developed from the other. Yet, according to the definition given by Pouzar, they do not even belong in the same genus. The spores, basidia, and cystidia of these species differ slightly in size but not in any other respect. Both have dimitic hyphal systems, but the arrangement of hyphae in the basidiocarps is not identical. In the oxidase reaction, the one known respect (except for possession of cystidia) in which *S.* sp. deviates from the *S. hirsutum* pattern, *S. sulcatum* corresponds to that pattern. *S. sulcatum* may be regarded as a species of *Laurilia,* if one so desires, and *S.* sp. placed in *Stereum* or perhaps even in some other genus. But even yet it cannot be said which characters are really fundamental, and which only appear to be, in the taxonomic criteria applied to these and other stereoid fungi.

Provisional Key.

At present, any key to segregates from *Stereum* must be regarded as tentative. Adequate key characteristics will not be available until additional study has resulted in more thorough knowledge of many species. I have previously discussed the controversy about the nature of hyphal systems in several species. According to Pouzar (1959), the cystidia of *Amylostereum chailletii* arise from skeletal hyphae, but I previously stated (1955) and now reaffirm that at least some cystidia of that species have basal clamp-connections. Thus, without further study, I can neither accept nor deny the statement that he hyphal system of *A. chailletii* is dimitic and cannot use this as a key characteristic. In addition to problems of a similar nature that may be solved by further observation, there are those arising from the difficulty of determining whether characteristics used as generic criteria are fundamental. If, for example, the generic description of

Laurilia can validly be emended to include *Stereum* sp., previously discussed, then *Laurilia* may be distinguished from *Stereum* sensu stricto by its possession of encrusted cystidia and asperulate basidiospores. Still other difficulties arise from the fact that some species seem isolated from any recognized organization of species. An example is *"Stereum" radiatum,* which is omitted from the following key to the genera previously discussed but which may be characterized as a species by its possession of distinctive cystidioles.

1. Spores amyloid 2
1. Spores non-amyloid 6
2. Basidiocarp often becoming woody; mycelium causing a white pocket rot of substrata; oxidase reaction negative on gallic acid agar . . . . *Xylobolus*
2. Basidiocarp usually remaining flexible or soft; mycelium causing a diffuse rot; oxidase reaction positive 3
3. Superior surface of basidiocarp not differentiated as a conspicuous cuticular layer; basidiocarp lacking cystidia; hyphal system monomitic; context hyphae loosely organized . . . . *Laxitextum*
3. Superior surface usually at least somewhat differentiated as a cuticular layer; basidiocarp having cystidia and or hyphal system dimitic; context hyphae more or less compactly grouped 4
4. Cystidia having brown and rough or encrusted walls . . . . *Amylostereum*
4. Basidiocarp lacking cystidia, or cystidia having pale walls if present 5
5. Skeletal hyphae of the context longitudinally parallel . . *Stereum*
5. Skeletal hyphae of the context interwoven . . . . *Laurilia*
6. Basidiocarp cartilaginous, or hymenium waxy-cartilaginous . . . 7
6. Basidiocarp not cartilaginous; hymenium dry and chalky to powdery or velvety 8
7. Hymenium even; spores hyaline . . . . *Chondrostereum*
7. Hymenium warted and folded; spores becoming somewhat colored . . . . *Phaeophlebia*
8. Basidiocarp lacking accessory structures such as cystidia, cystidioles, gloeocystidia, vesicles, and pseudocystidia; context loose-textured; hyphae having clamp-connections . . . . *Laeticorticium*
8. Basidiocarp having one or more kinds of accessory structures; context dense-textured or more uncommonly loose-textured; hyphae either having or lacking clamp-connections 9
9. Cystidia brown, thick-walled, and cylindrical, originating from generative hyphae; mycelium causing a brown rot; oxidase reaction weak or negative . . . . *Columnocystis*
9. Cystidia differing from the kind previously described; mycelium causing a white rot; oxidase reaction typically positive 10
10. Basidiocarp having pedicellate cystidia; hyphae lacking clamp-connections 11
10. Basidiocarp either having or lacking cystidia; at least some hyphae having clamp-connections 12
11. Context hyphae densely and longitudinally parallel . . . *Lopharia*

11. Context hyphae usually somewhat loosely arranged and lacking any conspicuously unidirectional orientation . . . . *"Stereum" crassum* group
12. Basidiocarp having cystidia and (or) gloeocystidia; spores curved-cylindrical to allantoid . . . *Peniophora* sect. *Coloratae*
12. Basidiocarp having gloeocystidia and vesicular bodies, lacking cystidia; spores subcylindrical to ovoid . . . . *Cystostereum*

Conclusion

The taxonomic study of corticioid and stereoid fungi has been stimulated during recent years by increased use of genetics, cytology, physiology, histochemistry, and micromorphology as tools for determining relationships. This has resulted in the recognition of many similarities among species previously regarded as belonging in different genera or families and of many differences among species heretofore regarded as forming homogeneous groups. Doubt may exist as to whether all these differences are really basic, but some, at least, seem important. As a result of applying recently devised criteria, many genera have been redefined to form presumably natural groups with unrelated species excluded. An example is the limitation of *Stereum* to include only those species obviously related to *S. hirsutum.* Another is the segregation of *S. frustulatum* and related species as *Xylobolus,* either as a distinct genus or as a well-defined subgenus of *Stereum.* A third example is the establishment of species of *Peniophora* related to *P. cinerea* (Fr.) Cke. as the only ones properly referred to *Peniophora* sensu stricto. Recent work has resulted in the recognition that species such as *Corticium polygonium, Stereum rufum, S. pini, S. versiforme, S. erumpens, S. albobadium* and various others properly belong in *Peniophora* sect. *Coloratae,* and many have already been transferred.

The withdrawal of misfit species from natural genera requires, as a corollary, that something be done with the extracted species. A considerable number of cystidiate species have been placed in *Lopharia.* As now defined, *Lopharia* seems to consist of heterogeneous elements and is scarcely more natural than either *Lloydella* or *Stereum sensu lato.* Consistency can be attained only by restricting *Lopharia* to species clearly congeneric with *L. cinerascens* and *L. mirabilis,* if the latter is distinct from the former. Such restriction requires the removal of *L. crassa (Stereum umbrinum)* and related species such as *L. papyrina (Stereum papyrinum)* from *Lopharia.* Various mycologists have indicated that *S. umbrinum (Laxitextum crassum)* does not belong in *Laxitextum;* therefore some other niche must be found for that and related species, but it should not be joined with *Lopharia cinerascens.* Boidin (1959 a) transferred *Laxitextum roseo-carneum* to *Laeticorticium,* thereby leaving only *L. bicolor,* the type species, in *Laxitextum.*

Knowledge and techniques have developed enough to permit removal of various other species from *Stereum*, if one wishes to make that genus homogeneous rather than merely comprehensive. But after all of the previously mentioned species have been resituated, most of the others seem isolated from any existing genera. *Stereum radiatum* is a very unusual species obviously much more distantly related to *S. hirsutum* than most of the preceding species. At present no satisfactory disposition of *S. radiatum* can be suggested. Five other species constitute the types of genera erected by Pouzar (1959). *Stereum abietinum* is the type of *Columnocystis; S. chailletii* of *Lloydellopsis*, which must become a synonym of *Amylostereum* Boidin; *S. sulcatum* of *Laurilia; S. murraii* of *Cystostereum; S. purpureum* of *Chondrostereum*. As previously noted, once the genus *Stereum* is depicted on any basis more critical than growth habit and general hyphal configuration, there is no possibility of being conservative in making taxonomic definitions. Pouzar, Boidin, and others are following logic to its only possible conclusion in segregating *Stereum*-like species. However, the incomplete system resulting from the various monotypic genera will still induce many mycologists to be rather conservative as to the taxonomy of *Stereum*. Probably future work will show that these fragmentary genera may include additional species or that the species now assigned to them may be referred to still other genera.

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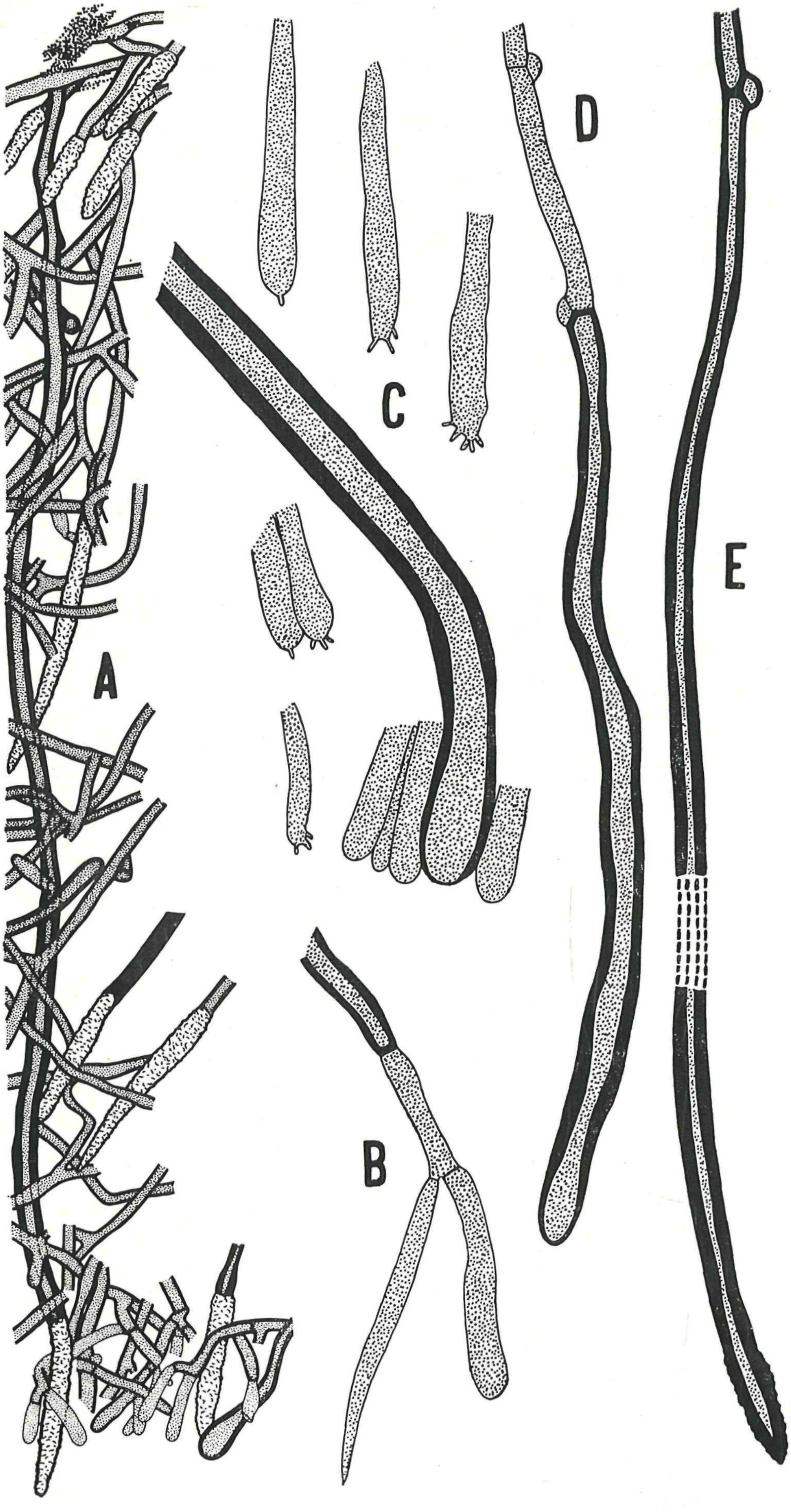
A
B
C
D
E

Explanation of Figure.

Fig. 1. Camera lucida drawings: A — "*Lopharia*" *crassa*, showing thick-walled, non-septate cystidium that has originated from the vicinity of the substratum and grown beyond the hymenial surface; B — *Stereum radiatum*, showing thin-walled basidium, cystidiole, and subtending cell that have formed at the end of a thick-walled, septate hypha; C — *Stereum ostrea*, showing thick-walled pseudocystidial apex of a skeletal hypha and smooth- and aculeate-tipped basidioles; D — *Columnocystis abietina*, showing thick-walled cystidium that has originated from a thin-walled, clamped generative hypha; E — *Amylostereum chailletii*, showing thick-walled cystidium that has originated from a moderately thick-walled, clamped generative hypha. A, × 370; B—E, × 1065.

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