community with so many eastern and southern species, makes it worthy of particular mention.

Specimens of *Scleria reticularis* on which this report is based are deposited in the Hanes Herbarium at Western Michigan University (WMU) and in the University of Michigan Herbarium (MICH): Allegan County, Clyde Township, Crooked Lake, T2N, R15W, NW1/4 section 36, *Pierce 1811*, 13 Sept. 1970; *Pierce & Pippen 1834*, 17 Aug. 1971.

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DIMORPHISM IN COLLYBIA RACEMOSA

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The large, branched "coremia" of *Sclerostilbum septentrionale*, a hyphomycete described by Povah (1932), were found by its author springing from sclerotia among dead leaves on Isle Royale, Michigan. Povah suggested that it might be the asexual (or conidial) state of an ascomycete, possibly a

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species of *Xylaria*. During a survey of the conidial states of Basidiomycetes, upon which we are currently engaged, one of us (RW) found a suggestion by Singer (1951 *et seq.*) linking *Collybia racemosa* and *Sclerostilbum*. Singer, as shown by Donk (1962), relied on observations made by Lütjeharms (1934), who apparently appreciated the relationship between the two genera. Singer, however, was unsure whether the *Sclerostilbum* coremia represented conidial fructifications or early stages in basidiocarp development. Kendrick & Carmichael (1973) missed this connection in their compilation of hyphomycete genera, and there is no description elsewhere in the literature of how the mitospores of *C. racemosa* are formed.

From an examination of Povah's text and diagnosis, supported by a fragment of the type collection (MICH–Figs. 1D, 2E-I), it was possible to make a comparison with material of *C. racemosa* from Britain (*Orton 1137*) and from continental Europe (*Orton 37*), both in herb E (Figs. 1A-C, 2B-D). The collections were virtually identical in all respects but one–Povah's material had no apical cap or pileus and, therefore, no basidial hymenium. Slight differences in conidium size among the three collections were not considered significant.

Lange (1936) illustrated "headless" specimens of *C. racemosa* (just like those figured by Povah) alongside illustrations showing a fungus with all the features of a basidiomycete classifiable in the Agaricales. Lange indicated that the cap (pileus) may sometimes fail to develop; he noted that the side branches possess small "pilei," and implied that these too might remain undeveloped.

Rea (1922) incorrectly considered the branches to be simple capitate hairs with oblong, hyaline, glutinous heads.

One of us (RW) has recently examined material of *Collybia racemosa* (in K). In a packet accessioned by Crossland, about 1912, was a note from Crossland to Thwaites, who had made the collection:

> Taking the branches only into consideration apart from the central pileus the fungus would be placed in the genus *Stilbum* (hyphomycetes); the branches bear conidia at their tips, oblong-elliptic, 2 guttulate, 8-12 X 3-3.5 μm, straight or slightly incurved.
>
> The branches undoubtedly belong to the *Collybia* stem. Don't see how they can be parasitic upon it.

Crossland was clearly the first to recognize, or at any rate to express an opinion on, the unity of the conidial and the basidial states of *C. racemosa*.

It is now clear that the large "coremium" mentioned by Povah (1932) is the stalk or stipe of the agaric and that only the small side branches can be regarded as true coremia.

C. racemosa is placed in *Collybia* section *Collybia* (=*Cirrhatae* Singer) along with *C. cirrhata* (Schum. *ex*. Fr.) Kummer, *C. cookei* (Bres.) Arnold, and *C. tuberosa* (Bull. *ex* Fr.) Kumm., all of which are widely distributed in north-temperate countries, are much commoner than *C. racemosa**, and have been extensively studied by Arnold (1935).

Agarics of section *Collybia* are very frequently associated with decaying fungi, usually other agarics, but sometimes members of the Aphyllophorales.

*The agaric figured by Brefeld (1889) as *C. racemosa* is certainly *C. tuberosa*, and his *C. tuberosa* is probably *C. cookei*.

related to *Squamanita*, also possesses smooth conidia (Watling, 1974). The mitospores in *Squamanita* and *Dissoderma* are considered to be chlamydospores because the end-product is thick-walled.

Singer (1970) erected the genus *Arthrosporella* for a tricholomataceous agaric in which the conidial state is formed on a clavarioid fruit body to which the form-generic name *Nothoclavulina* has been assigned. In some individuals the apex of the clavarioid conidial fructification later differentiates into a pileus with accompanying hymenium. The genus is related to *Gerronema* and *Armillaria* (*Armillariella sensu* Singer). No definite indication is given of the mode of conidiogenesis in this fungus, but the name *Arthrosporella*, Singer's designation of the conidial fructifications as "arthrosporocarps," and the fact that some of the conidia are septate suggest that they form in true thallic-arthric manner by the fragmentation of hyphae at septa. Clamp connections are not present, and the individual conidia are reported to be uninucleate, but it is possible for dikaryotic hyphae to produce monokaryotic conidia, as in *Flammulina velutipes.*

Similar chains of conidia are found in *Ptychogaster*; these, like those already mentioned in *Pleurotus dryinus* and *Squamanita*, become thick-walled at maturity and are usually regarded as chlamydospores. Species of *Ptychogaster* are genetically connected to polypores, particularly of the genus *Tyromyces.* One of us (RW) has shown that *Phaeotrametes decipiens* (Berk.) Wright, in addition to forming basidiospores in tubes, has, on the basidiome, cup-shaped depressions lined with hyphal tips producing conidia. Conidiogenesis is similar to that in *Collybia racemosa,* though here again the mitospores of the polypore ultimately become thick-walled and distinctly pigmented chlamydospores and are not formed on coremia.

Among Arnaud's obscure genera, all unfortunately invalidly published, one finds the form-genus *Osteomorpha* (Arnaud, 1952), named from the resemblance its conidia bear to (wrist) bones. Arnaud's illustration clearly shows a closely-septate, dikaryotic hypha with a clamp connection at almost every septum. The bizarre, irregular shape of the free conidia (which would be extremely mystifying if they were to be found without the accompanying hyphae) reveals that they have been derived from the disarticulation of the hyphae across the clamp. Arnaud's illustration is reproduced here (Fig. 2J) for comparison with the cellular detail of conidiogenesis in *C. racemosa.* It is extremely unfortunate that we have no information concerning the nature of the basidiomycete whose conidial state this is.

It is interesting to speculate concerning the part played by the arthroconidia described above. Those found in the field are dikaryotic and are always formed on structures which have a much longer existence than a normal basidiome: the stipe of *C. racemosa* or the pseudosclerotial stipe-base in *Squamanita.* Species of *Pleurotus* possess woody or leathery, tough basidiomes uncommon in other agaric genera. Arthroconidia formed on specialised structures appear to be a feature of various genera within the Tricholomataceae, and if parallels can be drawn with laboratory experiments in other genera, these coremia may be even the site of a parasexual cycle.

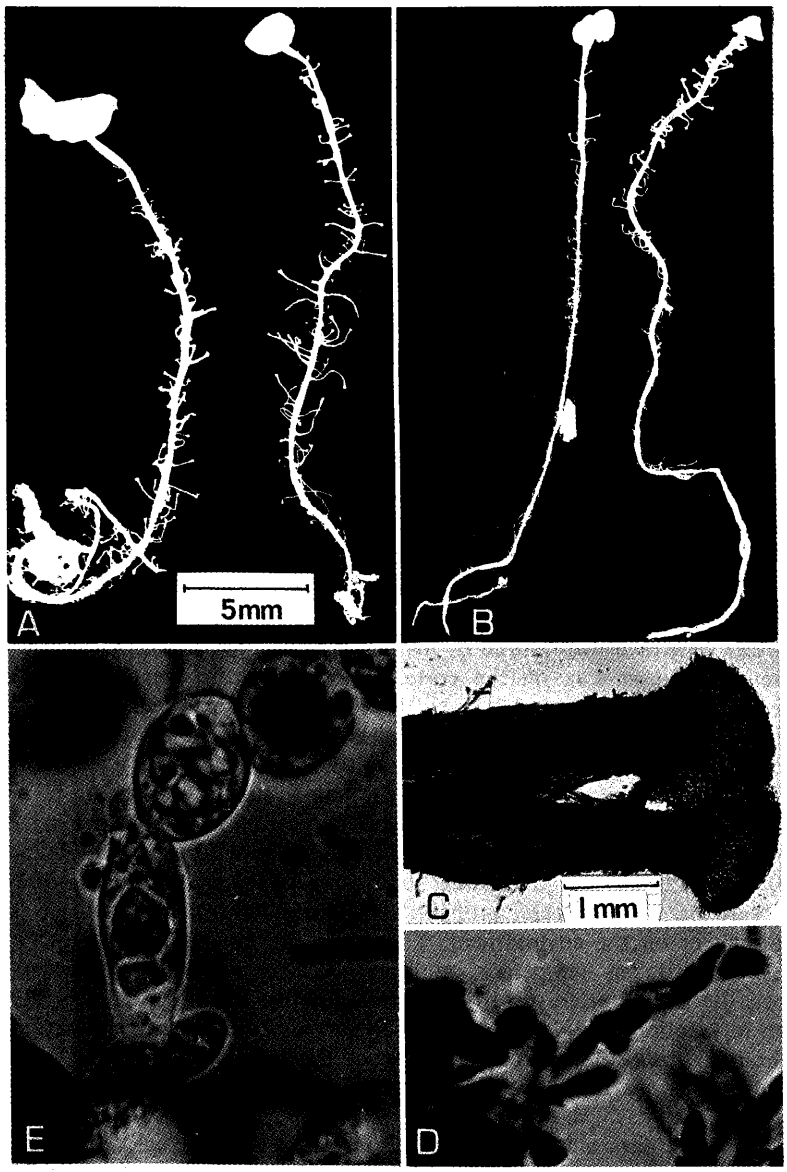

Fig. 1.A-B. Silhouettes of *Collybia racemosa* (A. Belleme, Normandy, *Orton 37*; B. Clapham Wood, Yorkshire, *Orton 1137*). C. Two coremia of *Sclerostilbum septentrionale* from B. D. Part of a coremium of *S. septentrionale* squashed to show a chain of conidia with subtending clamp connections. E. Chain of chlamydospores with clamp connections in vegetative culture of *Pleurotus dryinus (Watling 11639)*.

of the coremium stalk are much more sparsely septate than those in the fertile head. Some of the superficial hyphae along the side of the stalk also give rise to narrow conidiogenous hyphae. At maturity, the hyphae in the crown of the coremium cease apical growth and disarticulate across the clamps, the resulting conidia retaining the remnant of the clamp-connection as a basal and/or apical hook which may subsequently be obliterated by further swelling. Conidia apparently mature basipetally while remaining together in a linear series. They are clearly thallic-arthric conidia, as described by Hughes (1953, 1971) and Kendrick (1971a,b).

Arnold (1935) successfully obtained fruiting in pure culture, on fungal material or extract, of the three species she studied. She observed "oidia" in all three, but only on the haploid hyphae. In *C. racemosa,* haploids and diploids have not been studied, but all the basidiomes examined show clamp-connections, strongly suggesting that the dikaryon is present. Arnold recorded that the species she studied were heterothallic; *C. racemosa* probably exhibits the same pattern. Arnold gave no description of the "oidia" in sect. *Collybia,* but these would probably be similar to those of *Flammulina velutipes* (Curt. *ex* Fr.) Karsten and should be considered thallic-arthric conidia (arthroconidia).

A similar pattern of conidiogenesis to that described above for *C. racemosa*–the thallic-arthric mode–is found in the genus *Pleurotus. P. cystidiosus* O. K. Miller in culture forms coremioid structures, both on the vegetative mycelium and distributed over the maturing basidiomes. Kaufert (1935) described this fungus under the name *P. corticatus* Fr. [=*P. dryinus* (Pers. *ex* Fr.) Kumm.] and demonstrated the presence of both monokaryotic and dikaryotic coremia. Miller (1969) demonstrated the differences between Kaufert's isolate and the typical *P. dryinus,* which, though producing similar arthroconidia, does not form them on coremia (see below).

While the coremia of *C. racemosa* have dark stalks and pallid conidial heads, those of *P. cystidiosus* have white stalks and black heads which contrast vividly with the white stipe of the *Pleurotus* basidiome and so resemble the hyphomycete *Antromycopsis* Pat. & Tr., with which Jong & Peng (1975) and more recently Pollack & Miller (1976) have considered it to be connected. Singer (1975) considered these structures to be chlamydosporocarps, but the arthroconidia produced are not thick-walled. We do not know whether the thallic-arthric propagules of *P. cystidiosus* or *C. racemosa* act as spermatia.

Similar chains of thallic-arthric mitospores are produced by *Pleurotus dryinus*, but there they are not formed on coremia, and individual cells become swollen, pigmented and thick-walled–recognizably chlamydosporic (Fig. 1E). The nuclear behaviour of *P. dryinus* has been followed by Semerdzieva (1965). In *Squamanita* (Bas, 1965), hyphae covering the protocarpic bulbs form conidia, but here the growth of the hyphal tip gives rise to a sympodial arc of conidia. These conidia are well-differentiated and may be either smooth, in *S. odorata* (Cool) Imbach, or ornamented, in *S. pearsonii* Bas. *Dissoderma paradoxa* (Smith & Singer) Singer, very closely

C. cirrhata is sometimes found where there is no evidence of the prior existence of a dead fungus. One of us (RW) has found *C. racemosa* growing in humus, but Rea (1922) and Smith (1937) recorded this species as occurring on decaying fungi.

Rea, following Quélet, described the spores of *C. racemosa* as oval and ornamented; this suggests that the ammoniogenous agaric, *Tephrocybe tesquorum* (Fr.) Moser, may in part have been confused with *C. racemosa.* Certainly *Tephrocybe* is similar in structure and general facies (although it lacks the small branches on the stipe), and it has been found on dead agarics (RW).

All species of section *Collybia* except *C. cirrhata* produce sclerotia: that of *C. cookei* is yellow to ochraceous; that of *C. tuberosa* is a dark red-brown and often resembles an apple-seed; that of *C. racemosa* is roundish and black (Fig. 2E).

Arnold induced the formation of sclerotia in cultures of *C. cookei* and *C. tuberosa* and in fact obtained mature fruit bodies from them. The sclerotia of *Coprinus sclerotiger* Watl. will germinate readily if kept in damp sand, but those of *Collybia cookei* (Bres.) Arnold studied (*Watling 17c*) remained sterile. We know little about the factors which break the dormancy of *C. racemosa* sclerotia, but we do know that the natural fruiting period is during the autumn.

The basidiome of *C. racemosa* develops directly from a sclerotium, first forming a long, dark stipe with a pale, obtuse tip resembling an erect, negatively geotropic rhizomorph of *Armillaria mellea* (Vahl. *ex* Fr.) Kumm. At apparently random areas in the cortex along the entire length of the stipe small branches push out, and in a fully elongated stipe such branches may number several score. These small branches may themselves branch, and every branch terminates in a pale, slightly swollen head which produces chains of conidia. At maturity, the apex of the main stipe swells, and a pileus differentiates, apparently in gymnocarpous fashion (Fig. 2A). This is certainly in keeping with the development of the closely related *C. tuberosa* (Reijnders, 1933). The ultimate length of the stipe on which a mature pileus develops appears to be very variable, probably depending on the size of the original sclerotium, or on the environment. This is like the phenomenon found in an unnamed Australian temperate rainforest *Mycena*, whose stipe may wind through the leaf litter for up to half a metre before forming a pileus. All four species of section *Collybia* normally form a very thin-fleshed, rather small, membranous, pale-coloured pileus. Three of the species have a finely pruinose stipe: *C. racemosa* is unique in its possession of coremioid structures arising from the stipe.

The tiny, dark side-branches of *C. racemosa* (the asexual fructifications, of a type often called synnemata or coremia) are composed of parallel, aggregated, broad hyphae with hard, glassy, fairly brittle, little-pigmented walls, and disorganized cytoplasm containing amorphous dark-coloured material. Where the coremium stalk expands into the crescent-shaped fertile head, the hyphae become thin-walled and slightly swollen, and their contents have a strong affinity for cotton blue. All hyphae are clamped, though those

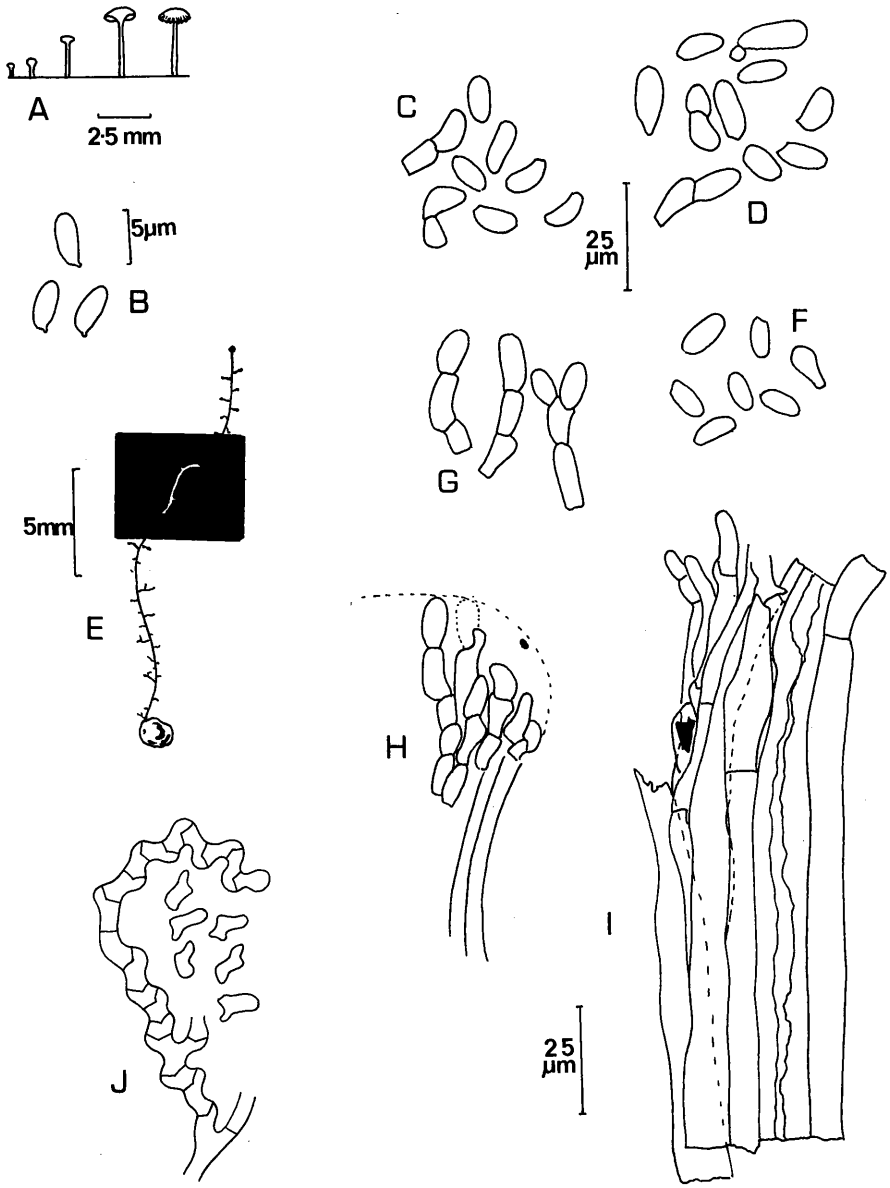

Fig. 2.A. Gymnocarpic development of *Collybia racemosa.* B. Basidiospores from *Collybia racemosa (Orton 1137).* C-D. Arthroconidia of the *Sclerostilbum* state of *Collybia racemosa.* C from *Orton 37;* D from *Orton 1137.* E. Reconstruction of *Sclerostilbum septentrionale* with silhouette of part of the type inserted. F-I. From the type of *Sclerostilbum septentrionale* F, dissociated arthroconidia; G, arthroconidial chains in isolation; H, arthroconidal chains in coremial head; I, hyphae on cortex of coremial stipe giving rise to arthroconidia. J. *Osteomorpha fragilis* redrawn from Arnaud.