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FOSSIL FUNGI FROM AMERICAN PENNSYLVANIAN COAL BALLS[1]

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ABSTRACT

The current status of knowledge regarding fossil fungi from American Pennsylvanian coal balls is discussed under the following general headings: 1) Phycomycetes, 2) Ascomycetes, 3) Basidiomycetes, 4) fungal sclerotia, 5) mycorrhizal fungi, and 6) "fleshy fungi." *Protoascon missouriensis* is redescribed as a possible Phycomycete. *Sporocarpon, Mycocarpon,* and *Dubiocarpon* are suggested as having closest relationships to the Ascomycetes. Possible reasons for the difficult taxonomy of Middle Pennsylvanian coal ball fungi are presented.

INTRODUCTION

In the approximately half century since the beginning of investigations of the fossil plants found in American coal balls of Pennsylvanian age there have been scarcely more than a half dozen publications devoted to the fungal remains found associated with the rich flora of vascular plants. The sparsity of specific fungal investigations over the years has been due not so much to lack of occurrence of fungal remains as to the absence of material possessing even a minimum of diagnostic taxonomic characters. Most fungal remains, as exposed in coal ball peel thin sections, consist of sterile fragments of septate and nonseptate hyphae, or scattered small, spherical, smooth-walled "spores" offering little, if any, describable features.

In spite of these difficulties, a sufficient quantity (if not quality) of material has accumulated to permit the following generalization regarding the kinds of fungi present in the coal ball flora. These seem to fall into the following general categories: 1) nonseptate hyphae and possible reproductive parts comparable to the Phycomycetes, 2) septate hyphae and reproductive parts (including the various multicellular spherical bodies variously described as *Sporocarpon, Mycocarpon,* and *Dubiocarpon*) that seem comparable to the Ascomycetes, 3) septate hyphae and reproductive parts comparable to the Basidiomycetes, 4) fungal sclerotia, 5) mycorrhizal fungi associated with *Amyelon* and other roots and rhizomes, and 6) fragments of a possible saprophytic "fleshy" fungus.

In the following pages evidence for the presence of the categories enumerated above is described and discussed.

CATEGORIES OF FUNGI

PHYCOMYCETES

The most obvious vegetative character of the Phycomycetes is the usual nonseptate nature of their hyphae. Andrews and Lenz (1943) found that the majority of the hyphae occurring in the cortex of their fossil fern rhizome were nonseptate and they attributed the few septate hyphae to

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different species. Abundant nonseptate hyphae (Pl. 3, fig. *4*) were found some years ago by me in the secondary xylem ray cells of a *Calamites* stem from Berryville, Illinois. These hyphae were only 4 microns in width, but profusely branched and very commonly filled entire ray cells.

Another specimen that I am now inclined to view as a possible Phycomycete is *Protoascon missouriensis* (Batra, *et al.,* 1964), which, as the generic epithet indicates, was initially attributed by the senior author to the Ascomycetes. However, I have now carefully reexamined all of the type material and have found the following discrepancies in the original description:

1) The so-called perithecium (fruiting body) consists only of a terminal vesicular swelling of the hypha with a thickened, rugose outer wall and a smooth-walled terminal pore. In other words, it is only a single cell separated from the vesicular base by a thin septum and differing from it only in the thickened ornamentation of its outer cell wall. It cannot, accordingly, in any sense be compared to an Ascomycete perithecium.

The evidence for the unicellular nature of this structure is quite clear and is illustrated in Plates 1 and 2. In the hundreds of specimens present in our peel series there are many in which the terminal "fruiting body" is much smaller and obviously less mature than those that are full size. In these (Pl. 2, fig. *4*) it can be seen that the "fruiting body" wall is only slightly thickened with the early deposit of the outer wall ridges. On the other hand, others (Pl. 1, fig. *2*; Pl. 2, fig. *1,3*) show mature stages where the outer cell wall has been partially lost as frequently happens in coal ball spore preservation (Baxter, 1967). Plate 2, figure 2 shows a mature fruiting body with its thickened outer wall and the smooth-walled terminal pore previously referred to as an "ostiole."

2) The hyphae are nonseptate; the only septations being those at the base of the whorled "appendages" and the cross wall separating the terminal cell from its basal vesicle (Pl. 1, fig. *4*; Pl. 2, fig. *1*). The "septate mycelium" originally reported by Dr. Batra appears to have been based on numerous detached "appendages." No other hyphae have been found.

In contrast to this lack of ascomycete characters, a number of features now seem most comparable to the Phycomycetes. The terminal cell of the hypha, surrounded by the whorl of septate appendages, is similar in some ways to the oogonia and surrounding antheridia of certain species of the Saprolegnioles. The genus *Apodachlya* (of the same order) shows a similar swollen hyphal base, while certain genera of the Peronosporales are characterized by having terminal oogonia that develop spined and other types of thickened walls (Fitzpatrick, 1930). The comparison of the terminal vesicle (previously interpreted as a perithecium) to an oogonium is enhanced by the frequent penetration of its terminal pore by the tips of the surrounding antheridial-like hyphae (Pl. 1, fig. *2,4*; Pl. 2, fig. *7*) and the formation of a possible oospore at the apex of the oogonium (Pl. 1, fig. *3*).

An additional feature, unreported in the original description, is the relationship of the fungus to its surrounding matrix of coal ball vascular plants. As shown in Plate 1, figure 1, the fungal remains all lie within the confines of the megaspore membrane of a poorly preserved specimen of *Nucellangium glabrum.* This was also clearly shown (but not commented on) in figure 1 of the original description (Batra, *et al.,* 1964). No remnants of the female gametophyte tissue are still present, but it seems reasonable to assume that this was the host tissue of the fungus. The very poor preservation of the seed integuments, compared to the excellent preservation of the fungus, also suggests that the seed may have been submerged in water of the surrounding swamp and that the fungus was a saprophytic aquatic form comparable to the Saprolegniales.

The concept of an aquatic environment is supported by the fungal specimens (Pl. 3, fig. *1*) in which a *Conostoma* seed also has its entire area of the female gametophyte tissue replaced by what appear to be spherical fungal spores. A closer examination, however, shows that the "spores" may be interpreted as "swarmsporangia" of the order Chytridiales of the Phycomycetes, a primarily aquatic group. In Plate 3, figure 2 one of these possible swarmsporangia from the *Conostoma* seed is shown at greater enlargement. It can now be seen to have an apparent exit tube and a possible developing zoosporangial protoplast. Oliver (1903) points out that many of the European Carboniferous seeds such as *Stephanospermum* and *Conostoma* had clusters of spherical, thin walled "vesicles" that he felt resembled chytrid swarmsporangia occupying their nucellus area. There is also the possibility, of course, that the so-called "exit tube" is actually the tip of a hypha bearing a terminal vesicle or oogonium. In either case, at least, the fungi would appear to be attributable to the Phycomycetes.

Among the most frequent fungal-like remains in American Middle Pennsylvanian coal balls are smooth-walled spherical "spores" averaging 360 microns in diameter. These often occur in clusters of up to 40 to 50 in poorly preserved cortical tissues of cordaitean roots and other degraded plant material (Pl. 3, fig. *3*), but are rarely found in assemblages of well-preserved plants. No hyphae have ever been found in association with them and their own complete lack of distinctive features has discouraged any attempts at taxonomic placement. However, it seems possible that these also may represent primitive chytrid swarmsporangia. While no exit tubes have been observed on them and they are of unusually large size, their frequent occurrence in "sorus" clusters along with the complete lack of associated mycelium suggests a chytridean relationship. Again the extreme degradation of the plant tissues in which they usually occur suggests a prolonged immersion in water and the possible aquatic, saprophytic nature of the fungus.

ASCOMYCETES

With the removal of *Protoascon missouriensis* as a possible ascomycete, the specimens seemingly most comparable to this class are the assemblages of small, spherical fruiting bodies variously described as *Sporocarpon, Dubiocarpon,* and *Mycocarpon* (Hutchinson, 1955; Baxter, 1960; Davis & Leisman, 1962). While the generic names themselves indicate the frustration of the authors in their morphological interpretation and taxonomic assignment, this assemblage of enigmatic structures still represents a diverse and widely distributed complex during the Pennsylvanian period. Davis and Leisman (1962) favor their interpretation as fungi, pointing out that the parenchyma nature of *Sporocarpon* is duplicated in tissues of certain ascomycete cleistothecia. Cooke (1969) illustrates perithecia of *Chaetomium erraticum* that show a definite resemblance to the spherical bodies of some specimens of *Mycocarpon* and *Dubiocarpon*. His figures 7 and 8, with their radiating perithecial hairs, are suggestive in many respects of Davis and Leisman's (1962) figure 16 of *Dubiocarpon elegans* with its radially arranged "spines."

While one can make a case for the resemblance of the multicellular spheres of *Sporocarpon, Mycocarpon,* and *Dubiocarpon* to ascomycete perithecia or cleistothecia it is considerably more difficult to compare the contents of these spherical bodies. The true ascomycete fruiting bodies have one or more ascus hyphae projecting into the perithecium or cleistothecium center, each containing a number of ascospores. The fossil spheres of *Sporocarpon, Dubiocarpon,* and *Mycocarpon,* however, usually contain only one or two noncellular concentric membranes seemingly unattached to the cells of the outer sphere (Pl. 4, fig. *1,3*).

It was of interest, therefore, in the course of this study, to find a specimen of *Dubiocarpon elegans* that seems to show a large sac-shaped ascus projecting inward from the sphere wall (Pl. 4, fig. *2*). The dimensions of this specimen are: sphere, not including spines, 730 microns; ascus, 450 microns; enclosed "spore," 300 microns. The coal ball material in which the above specimen was found consisted of poorly preserved *Amyelon* roots in association with over 40 specimens of the *Dubiocarpon* spheres, but lacking any fungal vegetative hyphae or mycelium. Plate 4, figure 1, shows a specimen from a New Calhoun, Illinois, coal ball that is tentatively assigned to *Mycocarpon ornatus* Davis and Leisman. It is distinctive in that the projecting, raylike hyphae have an outer covering of dense hairy projections forming a feltlike covering 50 to 90 microns thick. The specimen measures 630 microns in diameter with a central cavity 420 microns in diameter containing a concentric layer of poorly preserved hyphae surrounding a cuticle-like membrane. Another specimen of this same species has been found in a Lancashire, England, coal ball, which, with the type material being from the Bevier coal of Arma, Kansas, illustrates the widespread occurrence of these forms.

Sporocarpon cellulosum (Pl. 4, fig. *15*) was originally described by Williamson (1878) from Lancashire, England, coal balls and since reported from Kansas (Baxter, 1960). The specimen measures 450 microns total diameter and contains a cuticular-like central sphere. Its parenchyma-like cells are characteristically rectangular and tangentially elongated with thickened radial walls.

BASIDIOMYCETES

The almost sole evidence for the class Basidiomycetes in the coal ball fossil flora consists of the report of Dennis (1970) on septate hyphae with clamp connections and chlamydospores, which he named *Palalancistrus martinii* and compared to the extant *Panus tigrinus*. It is of interest to note that Dennis' fungus specimen was found growing in the wood of the same coenopterid fern genus, *Zygopteris illinoiensis*, from which Andrews and Lenz (1943) described their "mycorrhizal" hyphae. In the case of Andrews and Lenz's specimen, it was noted that the majority of the hyphae were nonseptate, although there were occasional hyphae with cross walls, which led the authors to assume that more than one species of fungus was present.

FUNGAL SCLEROTIA

Rothwell (1972) has described *Palaeosclerotium pusillum* from Middle Pennsylvanian coal balls from the Sahara Mine, Williamson County, Illinois. These sclerotia are oval to spherical in shape, measuring about 0.77 to 1.20 mm in diameter, and consist of a central medulla of branched, septate hyphae surrounded by a "cortex" and outer rind of pseudoparenchyma cells, the outer rind cells being smaller and thicker-walled than the cortex. Their relationships were thought to be with the Basidiomycetes.

MYCORRHIZAL FUNGI

The mycorrhizal nature of hyphae occurring in rhizomes and roots of coal ball vascular plants has been implied by numerous authors for both American and European coal balls (Andrews & Lenz, 1943; Osborne, 1909; Lignier, 1911; Halket, 1930). Cridland (1962), on the other hand, disputes the mycorrhizal nature of many of these fungi (particularly those occurring on *Cordaites* roots) on the following bases: 1) low percentage of hyphae infection, 2) similar hyphae in the surrounding plant debris, 3) overall degradation and decay of most cordaitean roots containing the hyphae, 4) presence of both nonseptate and septate hyphae in the roots, although in a mycorrhizal relationship one would expect just one species of fungus to occur. Cridland considered that the hyphae were probably saprophytic or parasitic in nature.

On the basis of my own experience, I am inclined to agree with Cridland that the mycorrhizal nature of the fungi is open to question. This opinion is based primarily on a confirmation of Cridland's point 3 of the correlation of fungal hyphae occurrence with degraded and poorly preserved host tissues. In my observation of thousands of specimens of *Amyelon* roots over a period of over 25 years of investigating coal ball plants, I have never found any hyphae in the tissues of the well-preserved specimens. This is certainly in contrast to what one would expect if the hyphae were a naturally occurring component of the living root.

"FLESHY" ? FUNGI

Large epiphytic parasitic fungi as well as fleshy saprophytic forms have not previously been reported for the coal ball fossil flora. If the environment was, as suspected, a brackish or freshwater coastal swamp, the absence of terrestrial saprophytic fungi is perhaps not surprising. However, one would still expect some occurrence of parasitic wood-destroying fungi and the growth of fleshy fruiting bodies as well as the inter- and intracellular endophytic hyphae.

What may possibly be a portion of such a fleshy form is shown in Plate 4, figure 4. This specimen consists of an irregular fragment (5.0 mm $\times$ 2.0 mm) of homogeneous mycelium made up of branched, septate hyphae measuring 20 microns in width. The mycelium was much denser on one side of the fragment, possibly representing cortical zonation. The mycelium fragment was isolated in the coal ball matrix and not associated with any host tissue.

DISCUSSION

While the present study is concerned primarily with the Pennsylvanian fungi found in association with the vascular plant flora of Mid-American coal balls, it seems relevant at least to mention for purposes of comparison the classical study made by Kidston and Lang (1921) on the fungi associated with the primitive vascular plants of the Lower Devonian Rhynie Chert. Part V of their series of publications on the Rhynie plants was devoted exclusively to a description of the fungal hyphae, which were apparently numerous and diverse. Many of the variations in form were referred to just by number (of which there were 15), but in addition they recognized and described six different species of *Palaeomyces.*

It may be of significance that, even with the above diversity, Kidston and Lang considered all of them to have closest relationship probably with the Phycomycetes. The hyphae were branched and nonseptate with frequent terminal or intercalary "vesicles." *Palaeomyces asteroxyli* (which was found in the cortex of *Asteroxylon*) was described and illustrated as having terminal vesicles (oogonia?) similar to our Plate 2, figure 2. Kidston and Lang (1921) also state in their summary, ". . . many of the fungi were living as saprophytes and are associated with the decay of the tissues in which they were found."

Possibly one of the most puzzling aspects of coal ball fungi is their relative rarity. Certainly, they do not seem to occur in anywhere near the abundance they did in the Rhynie Chert flora. The problem is further compounded by the unusual structure of such forms as *Sporocarpon, Mycocarpon,* and *Dubiocarpon,* which, while showing certain resemblances to fruiting bodies of the Ascomycetes, defy confident assignment due to the absence of clearly defined asci and the usual presence of cuticle-like spheres in their central cavity.

Protoascon, which at first seemed to be a definite ascomycete, must now be regarded to be of uncertain status although possibly closer to the Phycomycetes than any other group. Indeed, with the possible exception of the apparently clearcut characters of Dennis' (1970) basidiomycete hyphae, showing clamp connections, it is doubtful that we can be very certain of the true relationships of any of these Middle Pennsylvanian fungi. Perhaps this in itself is of significance. Since the great majority of extant fungi have a present saprophytic or parasitic relationship to plant and animal groups which *were not even present* 300 million years ago in the coal-age swamps, and since the evolution of such living fungi had to wait on the prior evolution of their hosts, it seems reasonable to assume that the relationships of upper Paleozoic fungi may be no closer to living forms (if as close) as the vascular plants of that period are to the living flora.

It also is suggested that the semiaquatic swamp habitat of the coal ball vascular plants (which is well supported by the nearly constant presence of aerenchyma cortex in their roots) would have been conducive to a dominance of primitive aquatic, saprophytic fungi, possibly precursors of present members of the Chytridiales and Saprolegniales.

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EXPLANATION OF PLATES

PLATE 1

Protoascon missouriensis.

FIGURE

1. Fragments of fruiting bodies and appendages lying within the megaspore membrane of a *Nucellagium glabrum* ovule, ×133. [*M,* megaspore membrane.]
2. Terminal vesicle (oogonium?) surrounded by appendages (antheridia?), several of which are apparently penetrating the apical pore, ×400. Note smooth, thin wall of terminal vesicle.
3. Vesicular swollen base with terminal, thick-walled cell (oogonium?) containing a possible oospore at apical end, ×400.
4. Structures as in figure *2* but from a different specimen, ×400. Note apparent penetration of apical pore by surrounding antheridia-like appendages.

PLATE 2

Protoascon missouriensis.

FIGURE

1. Median-longitudinal section through swollen vesiculate base bearing appendages and the terminal oogonium-like cell, ×400. Note wall dividing terminal cell from base, also rugose thickening of outer wall of terminal cell.
2. Oblique, side view of terminal cell and surrounding appendages, ×400. Cell wall covered with thick, rugose ridges except for apical pore area which shows partially broken, thin inner wall.
3. Side view of fruiting body in which thickened outer cell wall has flaked off to expose thin inner wall comparable to surrounding hyphae, ×400. Note apparent penetration of terminal pore by antheridial-like appendages.
4. Small, immature specimen, showing beginning of outer wall thickening of terminal oogonium-like cell, ×400.

PLATE 3

Conostoma sp.

FIGURE

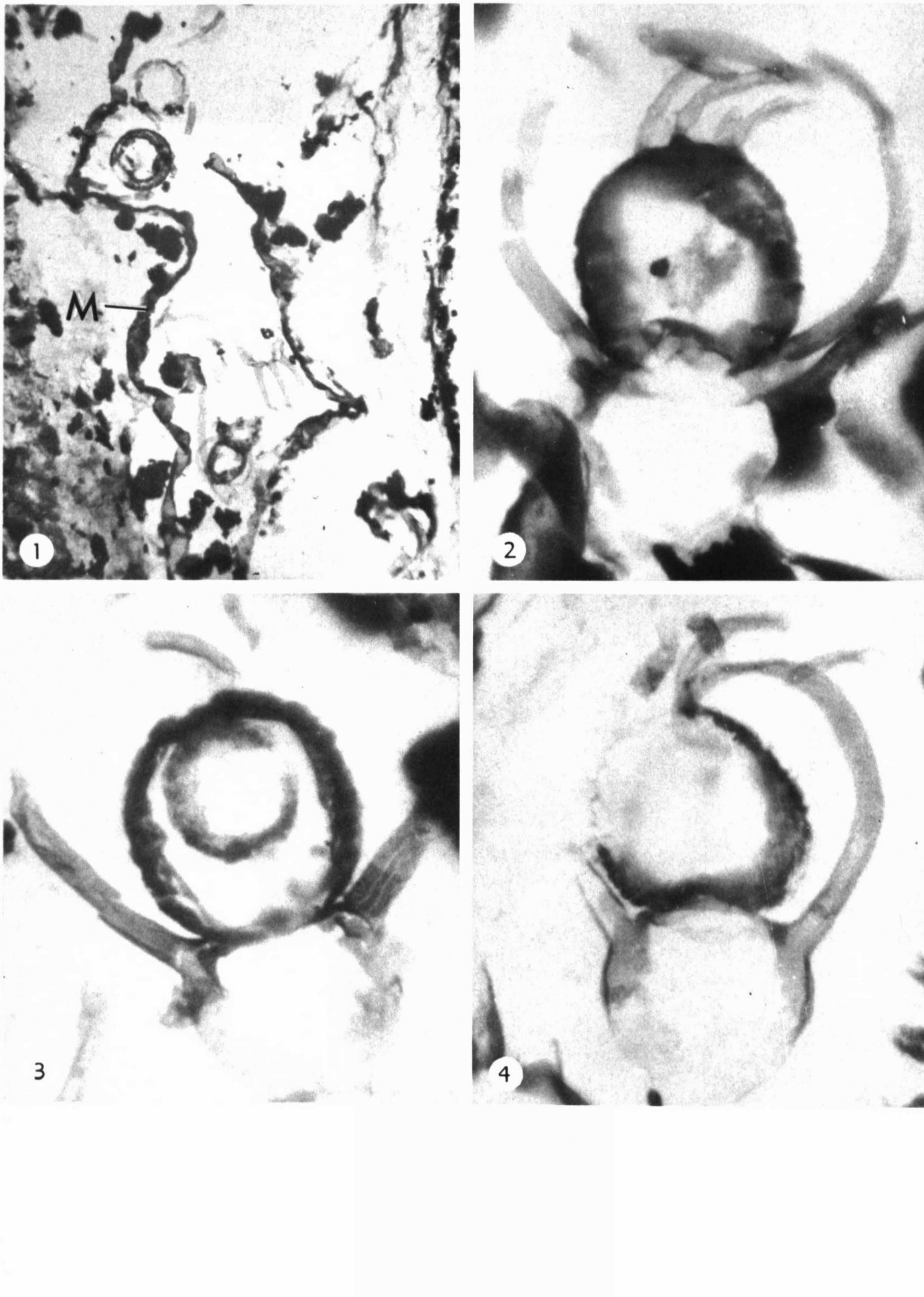
1. Specimen with central gametophyte tissue replaced by a mass of possible chytrid swarmsporangia or phycomycete oogonia, ×25.
2. Higher magnification of one of the fungal spheres from the seed at the left, ×400. Note protruding hypha (exit tube?).
3. Potion of "soral" cluster of smooth, thin-walled fungal "spores" (swarmsporangia?) in decayed *Amyelon* cortex, ×40.
4. Nonseptate branched hyphae in ray cell of secondary xylem of a *Calamites* stem, ×380.

PLATE 4

Mycocarpon ornatus (1); Dubiocarpon elegans (2); Sporocarpon cellulosum (3).

FIGURE

1. *Mycocarpon ornatus;* central cavity containing several cuticle-like spheres, ×96. Radiating hyphae are covered with dense felt-like covering of fine hairs.
2. *Dubiocarpon elegans;* sphere of radially arranged hyphae with projecting broken spines, ×75. Note attachment of ascus-like cell on right side of inner sphere.
3. *Sporocarpon cellulosum;* multicellular wall around central cavity consists of rectangular pseudo-parenchyma cells with cuticle-like sphere inside cavity, ×220.
4. Portion of mycelium of possible fleshy fungus showing branched, septate hyphae, ×100.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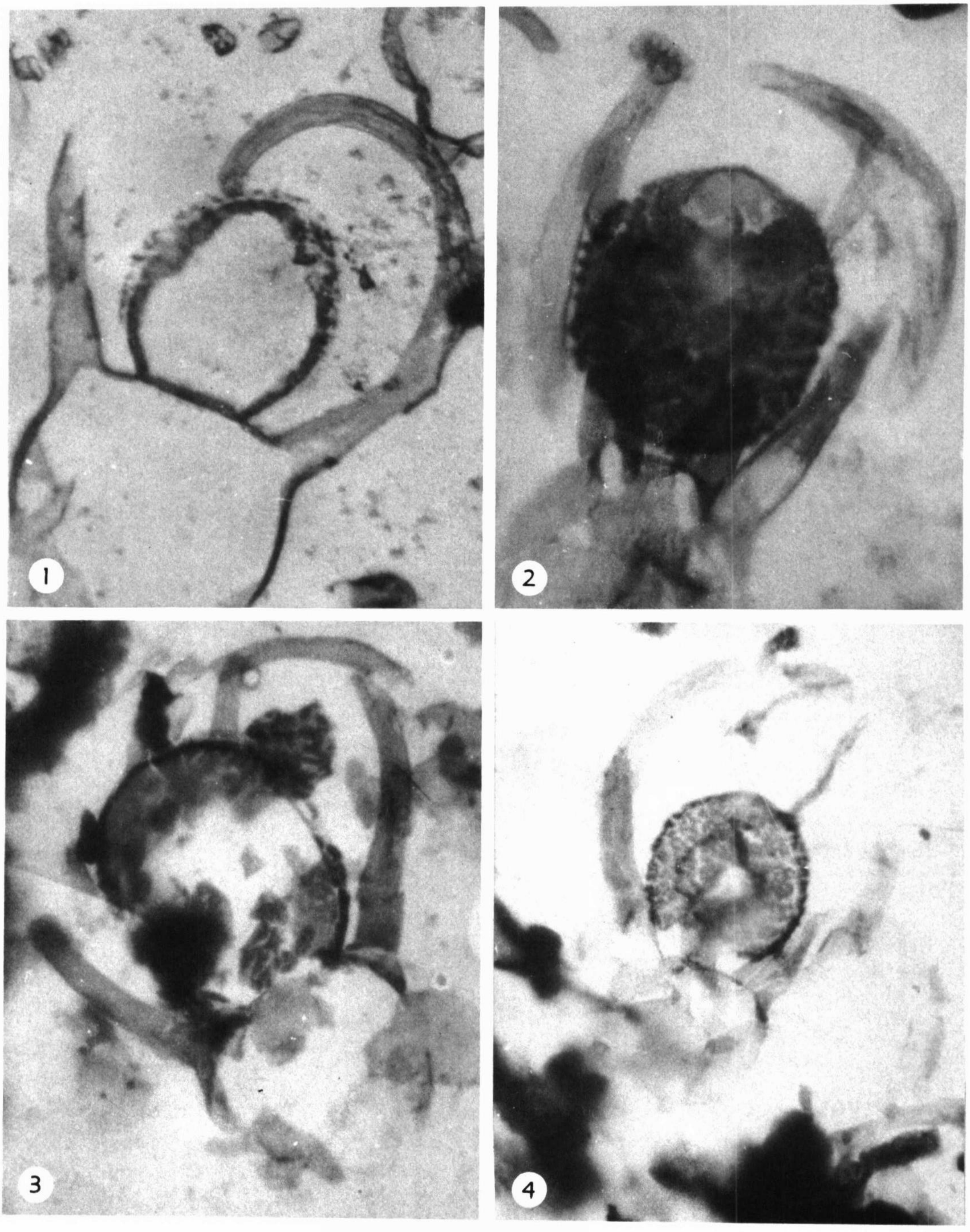
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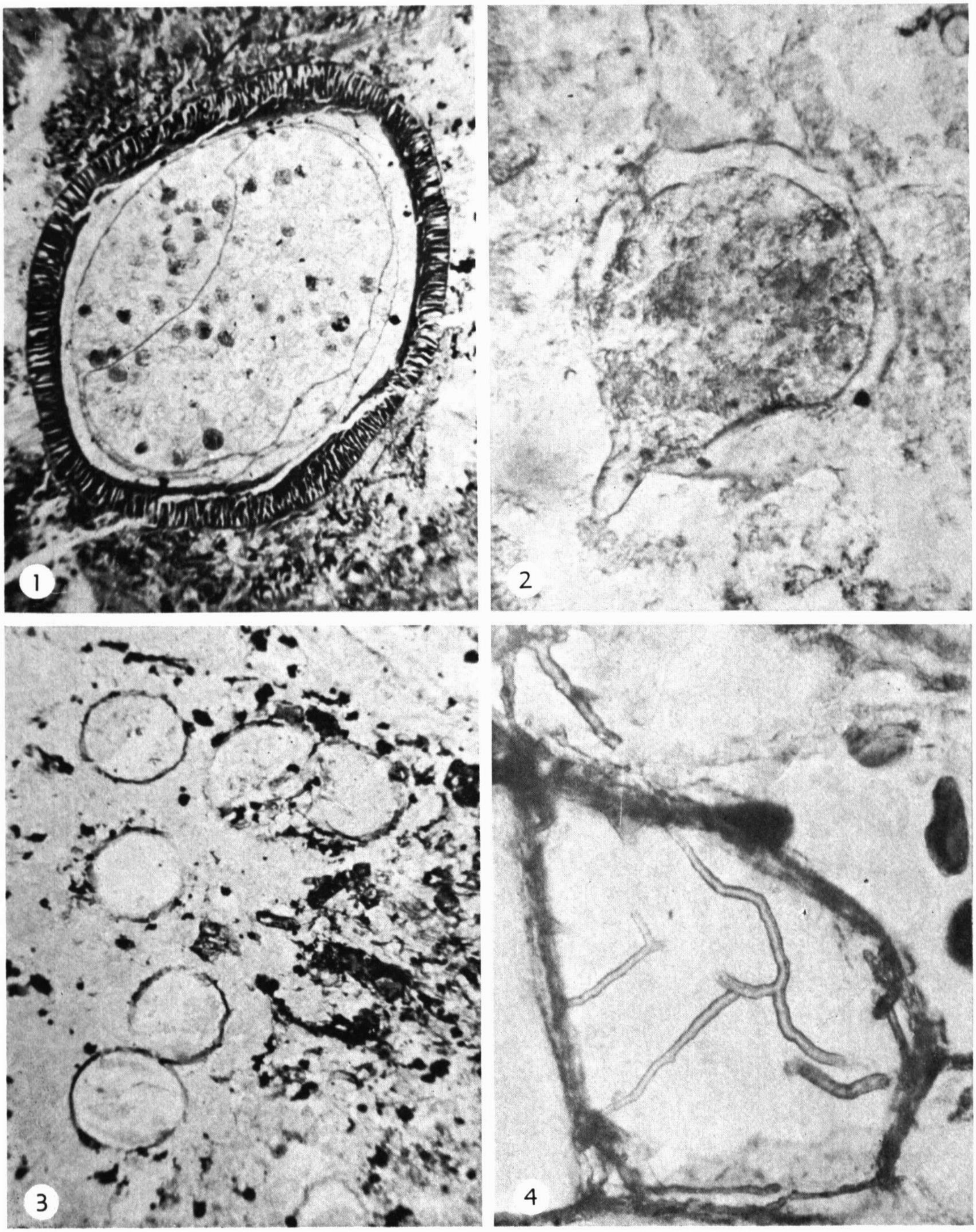
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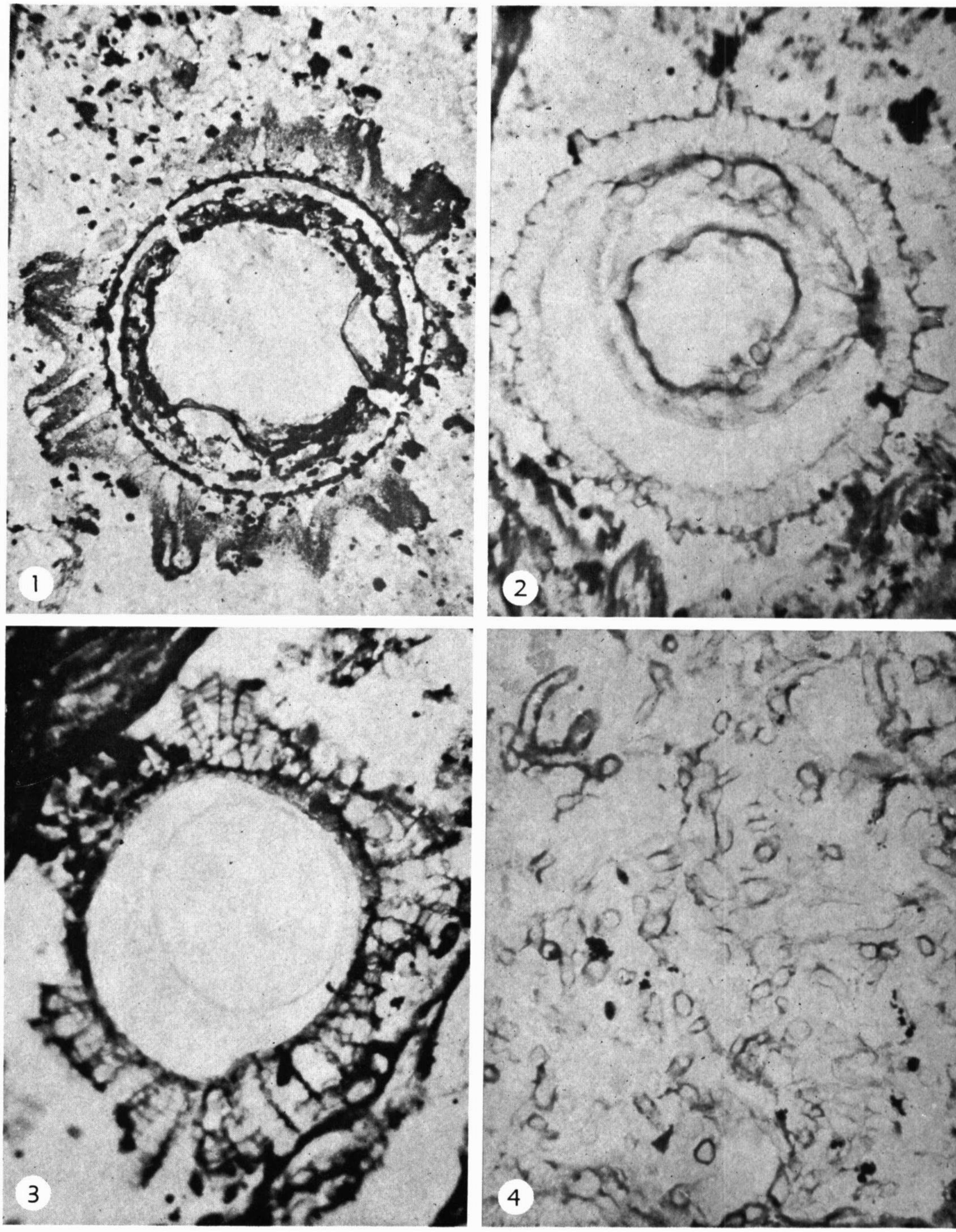
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