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EPIPHYLLOUS FUNGI FROM EOCENE DEPOSITS IN WESTERN TENNESSEE, U.S.A.

BY

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With 26 Plates and 1 table in the text

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* Cost of the plates was partially defrayed by the Department of Biology, Yale University.

Introduction

Numerous incidental reports of various forms of fungi and fungus-like forms have been made since early in the nineteenth century. Fungi are recorded from Precambrian (TYLER & BARGHOORN, 1954) to modern times and members of the Myxomycetes, Phycomycetes, Ascomycetes, Basidiomycetes, and Deuteromycetes (classification according to G. W. MARTIN's "Key to the families of fungi" in AINSWORTH & BISBY, 1950) are all reported in the fossil record by the end of the Paleozoic (PIA, 1927). Many of the early fossil fungi and nearly all of the more recents forms (Mesozoic and Cenozoic) have been identified with specific modern genera. Since the classification of modern fungi is based upon sexual reproduction and developmental morphology the isolated mycelium, fruiting body, or spore, typical of most of the reports of fossil fungi, is very tenuous evidence upon which to base the identification of fungi in the fossil record to a specific modern genus, family, or order.

Since the relationships drawn between fossil and modern fungi are often questionable and since all the modern classes of fungi are reported to be in existence by the end of the Paleozoic with little evidence concerning their evolution available, the fossil record offers almost no aid in discovering the evolutionary development of modern fungi. As A. C. SEWARD (1933) wrote:

Among the numerous examples of fungi described and illustrated in accounts of Palaeozoic, Mesozoic, and Tertiary floras there are very few which make any appeal to the student of evolution. Dark spots on the surface of fossil leaves bearing a superficial resemblance to the spore-producing fructifications of existing fungi are fairly common, and in some instances they are well enough preserved to be compared with modern genera; but the great majority have no botanical value. One thing is clear: from the Devonian period onwards and even from a more remote age there were parasitic and saprophytic fungi—fungi thriving on living hosts or deriving food from dead tissues—which so far as we can tell differed in no essential respects from living representatives of the class.

Most of the previous reports of epiphyllous fossil fungi have been made in studies dealing specifically with the microfossil or megafossil flora of a particular age and area. In this paper these scattered reports, as well as the few studies dealing solely with epiphyllous fossil fungi, are considered in order to provide a basis as complete as possible for understanding both the forms of epiphyllous fossil fungi previously recorded and the new forms described here. The fungi described in this study were found upon well-preserved leaves from lower Eocene deposits in western Tennessee, U.S.A., and are all relatable to either the Ascomycetes or Deuteromycetes.

By critical examination of cuticular preparations of nearly 500 leaves, excellently preserved specimens of several forms of fungi were found. These fungi are so well preserved that many can be positively related to modern genera and in some cases the life cycles of the fossil forms can be completed. In one such case more complete material of the fossil form was found than is known for the corresponding modern genus.

An attempt has been made in this study to relate isolated parts — mycelia, ascocarps, pycnidia, and spores — to the fungi to which they belong. Some of the fungi presented in this paper are new to the fossil record while others extend the range, both geographically and geologically, of previously-known fossil fungi. This study is presented, not as a final or complete report of epiphyllous fungi present during the Eocene, but as a record of those forms which have been found to this time. It is hoped that this work will stimulate further paleomycological studies which will add to our presently incomplete record of epiphyllous fungi.

History

As a result of the investigations of UNGER (1848) and GOEPPERT (1836, 1841—1846) of Tertiary leaf compressions, 13 species and 4 genera of epiphyllous fossil fungi were recognized by 1849 when F. UNGER compiled *Genera et Species Plantarum Fossilium* which was published in 1850. As these and other paleobotanists continued their study of leaf compressions additional reports of epiphyllous fossil fungi were made. MESCHINELLI (1892, 1898) listed and illustrated most of the fossil fungi reported up to that time. While UNGER in 1850 listed only 2 species of *Sphaerites*, 2 species of *Hysterites*, and 8 species of *Xylomites*, by 1892 MESCHINELLI listed 100 species of *Sphaerites*, 16 species of *Hysterites*, and 56 species of *Xylomites*. Of such reports of epiphyllous fossil fungi A. C. SEWARD (1898) wrote: "In the literature on fossil plants there are numerous recorded species of fungi founded on dark coloured spots and blotches on the impression of a leaf. Most of such records are worthless; the external features being usually too imperfect to allow an accurate identification." Despite the numerous reports of such evidences of fungi in the fossil record very little could be done to relate with certainty the spots or thickenings found on leaf compressions to modern forms of fungi. Concerning this problem E. W. BERRY (1916) wrote:

> The presence of spots of different shapes on the leaves of fossil plants is exceedingly common, and a very large number of so-called species of fossil leaf-spot fungi have been described by ETTINGSHAUSEN, HEER, SAPORTA, and others. These species are referred for the most part to the genera *Sphaeria, Phacidium, Dothidia, Depazea, Sclerotia, Hysteria, Rhytisma, Xylomites*, and the like. A large list of such forms was published by MESCHINELLI in 1892. All these determinations are based entirely on superficial similarities between the fossil and some modern leaf-spot fungus, of which there are thousands of species, most of them distinguishable only by their methods of reproduction or the morphology of their reproductive parts.
>
> The identification of these fossil forms obviously rests on a very insecure foundation, especially when it is recalled that scale insects and a great variety of insect galls would resemble epiphyllous fungi when preserved on impressions of fossil leaves. Nevertheless large numbers of undoubted fungi are preserved in this manner and it is the legitimate duty of the paleobotanist to describe and illustrate them.

In spite of the superficiality and uncertainty of the identification of species of fossil leaf-spot fungi, there was little else an early paleobotanist could do but describe a fungus-like spot on a leaf compression and assign it to one of the already-proposed artificial fossil leaf-spot genera. However in this century improved paleobotanical techniques for clearing fossil leaves and macerating sediments have made more detailed and meaningful reports of epiphyllous fossil fungi possible. ENGELHARDT and KINKELIN (1908), COLANI (1920), KRÄUSEL (1920, 1929, 1961), EDWARDS (1922), BRADLEY (1929, 1931), POTONIÉ (1934, 1951), THIERGART (1937), KÖCK (1939), KIRCHHEIMER (1942), ROSENDAHL (1943), COOKSON (1947), GODWIN and ANDREW (1951), LESCHICK (1952), POPOV (1956, 1959, 1962), CHITALEY (1957), MACKO (1958), NEUY-STOLTZ (1958), RAO (1958), SOHMA (1958,) ALTEHENGER (1959), FRANTZ (1959), KEDVES (1959), SIMONCSICS (1959), DEÁK (1960), DILCHER (1963), PETERS (1963), and THIERGART, FRANTZ, and RAUKOPF (1963) have all described and illustrated cellular fruiting bodies, mycelia and / or spores of epiphyllous fossil fungi. However because characters used in the identification of modern epiphyllous fungi are often undeterminable in the isolated fragments of fossil fungi, it is still difficult, even though modern techniqnes are used, to identify even well-preserved fossil forms precisely.

As more work is done to fit together the often isolated parts of the life cycles of forms of fossil fungi, and as more reports are published on the modern fungi to which such fossil forms are related, more critical and precise studies of epiphyllous fossil fungi will be possible.

Most of the reports of epiphyllous fossil fungi from the more recent publications (since about 1920) are the result of detailed pollen analysis of sediments or of cuticular analysis of fossil leaves. The types of paleobotanical techniques used to prepare material for pollen analysis and cuticular analysis are well suited for the study of epiphyllous fossil fungi; thus as more work is done in these fields well-preserved epiphyllous fungi will be reported from other ages in the geologic record and additional areas of the world.

In addition to the published reports mentioned above, fossil epiphyllous fungi have been found in late Tertiary Hawaiian peats and subantarctic peats (L. CRANWELL SMITH, personal correspondence), early Tertiary sediments of Alaska (V. PAGE, personal correspondence), Miocene lignites of South India (RAMANUJAM, 1963; RAMANUJAM and RAMACHÁR, 1963), Miocene-Pliocene sediments of central Alaska (E. LEOPOLD, personal correspondence), Quaternary sediments of the eastern United States and Canada (E. LEOPOLD, L. R. WILSON, personal correspondence), and in numerous other sediments whose ages and locations were not recorded (J. SCHOPF. L. NOREM, personal correspondence).

Location and Stratigraphy

All of the material used in this investigation was collected from the Lawrence clay pit of the Spinks Clay Co., Paris, Tennessee. The Lawrence clay pit is located 4 miles northwest of Henry, Tennessee at 36° 13′ 22″ N. Lat. by 88°29′05″ W. Long. and can be easily located on the Henry Quadrangle, Tennessee, topographic map (U. S. Geological Survey, 1955). The pit was dug in order to mine a large deposit of clay which extends for several acres and consists of numerous layers of clay. The fossil plant material is most abundant and best preserved in a thick band of g r e y clay which was being actively mined from the pit at the time of collection. This grey clay lies just below a 10—20 foot thick layer of light brown and banded red and pink colored clay.

E. W. BERRY (1916, 1930) described a large number of leaf compressions which he and others collected from clay deposits in Tennessee, Mississippi, and Alabama, and which he considered to be from the Wilcox formation (lower Eocene). He mentions two areas in Henry county, Tennessee from which he collected fossil leaves. One is the well-known locality at Puryear, Tennessee about which BERRY (1916) wrote: "This is the most remarkable leaf-bearing clay that I have ever seen at any geologic horizon." The other is a small deposit 1 mile southwest of Henry, Tennessee from which only a few leaves were collected. In 1924 BERRY described from the same area several fossil leaves from the Claiborne formation of middle Eocene age. However in recent years the correctness of the formations to which BERRY (1916, 1924, 1941) assigned the plant fossils which he described and consequently the age he ascribed to these fossils have been open to serious doubt.

F. S. MacNeil (personal correspondence), a stratigrapher with the U. S. Geological Survey who has mapped large sections of Tennessee, Mississippi, and Alabama, wrote: "I did find that Berry's stratigraphic assignment of most of his important plant localities . . . was incorrect. His large 'Wilcox flora' is mostly Claiborne, as are some of the famous localities in Tennessee, including Puryear. As a field guide, and as a rule of thumb, the Wilcox is sombre, mainly olive and gray. The Claiborne is white to pink to red. The Claiborne progressively overlaps the Wilcox to the north. Where the Wilcox passes from Alabama into Mississippi it is about 800 feet thick. It thins, by overlap, at the outcrop to the north so that in Tennessee less than 100 feet of Wilcox remains." Thus the clays in the Lawrence clay pit appear to he from two distinct formations: 1) the overlying light brown to pink to red clays are Claiborne formation (middle Eocene) and 2) the underlying dark grey clays are Wilcox formation (lower Eocene). All of the material discussed in this paper is lower Eocene in age since it was collected from the underlying grey clays of the Wilcox formation.

Methods

Fragments of wood, fruits, seeds, and leaves were abundant in the grey clay in which the fossil plant material used in this investigation was preserved. The leaves were compressed with cuticular material still preserved. Most of the leaves were typical of compression material and were very delicate, cracking and curling upon drying. Some of the leaves however were so well preserved that they could be lifted from the surfaces of the broken pieces of clay and stored in envelopes. The selective preservation of these leaves is probably due to the resistant nature of their tissues. All of the fossil fungi described in this study were epiphytic upon these exceptionally well-preserved leaves.

In many of these fossil leaves the mesophyll cells and the vascular tissne were still intact (Pl. 24, fig. 186). The fine venation of these leaves could be examined and photographed when their transparency was enhanced by wetting them with xylene (Pl. 24, fig. 183—186). Photographs of several of the fossil leaves were taken while they were temporarily mounted in xylene. The leaves were then dried and stored for future reference. Small squares were later cut from these photographed leaves, cleared, and mounted for cuticular analysis. These squares were placed in a 5 % KOH solution until clear (1—4) days, washed in distilled water, dehydrated in a series of alcohols (50 %, 95 %, and 100 %), placed in xylene, and then mounted in H.S.R. (Harleco synthetic resin). The squares were cut along the margin of the leaf; thus the upper and lower cuticle of each leaf were held together by the marginal cells throughout the above process. Before mounting this material all of the remaining mesophyll was carefully removed and the cuticles were separated so that the exterior surfaces of the leaf were mounted up.

Using this method, a photograph of the fossil leaf showing its fine venation and a sample of the leaf's cuticle with associated epiphyllous fungi could be examined critically for each type of fossil leaf which had heen peeled from the surface of the clay (Pl. 24, figs. 187, 188). In addition several hundred fragments of well-preserved leaves were also cleared and mounted, using the technique described above, and then identified by comparison with the cuticle of the photographed reference fossil leaves. In order to insure the success of this method of relating the fragments of the fossil leaves examined to well-known fossil types from the same beds, extreme care was taken to always mount a specimen of both the upper and lower cuticle on each slide and to mount them with the outer surface of the leaf up. This permitted a critical examination not only of the guard cells, accessory cells, cuticular striations, trichomes, and associated glands but also of the epiphytes.

These well-preserved leaves could also be compared with angiosperm leaves found by other paleohotanists in other deposits and also with modern leaf material. On this basis the host leaves of the fungi described in this investigation were identified.

Host Leaves

The fossil leaves examined for epiphyllous fungi represent only a very small and select part of the total population of leaves present in the early Eocene sediments of western Tennessee from which they were collected. As noted above only well-preserved leaves which could be removed from the clay intact were used.

Two genera of host plants, *Sapindus* (Sapindaceae) and *Chrysobalanus* (Rosaceae), are recognized. The hosts were related to the genera *Sapindus* and *Chrysobalanus* on the basis of their gross similarities to fossil forms previously described and illustrated from Eocene deposits in western Tennessee by BERRY (1916) and their similarities to modern forms of these genera based on both their gross appearance and the fine structure of their cuticle.

One cuticular fragment of an unidentified angiosperm leaf, upon which *?Parasterina* was found (Pl. 10, fig. 82), was also used in this study.

Pl. 24, figs. 183—185 are examples of various leaves of *Sapindus* upon which epiphyllous fungi were found. The leaf illustrated in Pl. 24, fig. 184 is similar to the fossil leaves described as *S. knowltoni* BERRY, the leaf in Pl. 24, fig. 183 is similar to *S. formosus* BERRY, and the leaf in Pl. 24, fig. 185 is similar to *S. eoligniticus* BERRY (BERRY, 1916).

In discussing *S. knowltoni*, BERRY (1916) wrote:

> It resembles several of the Wilcox species, however, especially *Sapindus formosus* BERRY and *Sapindus eoligniticus* BERRY, both of which are slightly smaller and neither has such a long and stout petiolule. Both of these species are also more coriaceous and have thinner, more regular secondaries, and the areolation is more immersed.
>
> Among existing species of *Sapindus* the present form can scarcely be distinguished from *Sapindus marginatus* WILLDENOW, a small coastal tree of the Florida peninsula.

Little concerning anatomical features of the leaves of the genus *Sapindus* is mentioned in METCALFE and CHALK's *Anatomy of the Dicotyledons* (1950). To determine more about their anatomy, a modern reference collection of the cuticles of 13 genera of the Sapindaceae including 7 species of *Sapindus* was prepared and examined. Upon comparison with the modern cuticular preparations the fossil material was found to be similar to the modern material of *Sapindus* and unlike any of the other modern genera of the Sapindaceae examined.

In most of the modern species of *Sapindus* examined glandular cells were common (Pl. 25, fig. 190). They are uniseriate and terminate in an oval head of several cells. The glandular cells are not situated perpendicularly to the surface of the leaf but lie horizontally to the surface and frequently have subtending "pockets" in the epidermis associated with them. The glandular cells in the fossil leaves of *Sapindus* examined are short, uniseriate, and when complete frequently terminate with a single large bulbous cell (Pl. 24, fig. 188). The glandular cells lie horizontally to the surface of the leaves; however there are no subtending "pockets" associated with them.

The stomata are much more crowded in the modern species of *Sapindus* (Pl. 25, fig. 190) than in the fossil material examined (Pl. 24, fig. 188). The guard cells of both the modern and fossil forms are surrounded by 5 to 8 accessory cells. The accessory cells, guard cells, and stomata are similar in both the modern and fossil forms of *Sapindus* examined. Cuticular striations found in several of the modern forms of *Sapindus* (Pl. 25, fig. 189) are similar to those observed in the fossil material (Pl. 24, fig. 187).

Of the seven modern species of *Sapindus* examined, the cuticular characters of *S. marginatus* are most similar to the fossil material of *Sapindus* examined in this study.

One leaf upon which abundant epiphyllous fungi were found is not Sapindaceous. The entire leaf was not collected, however the emarginate apex, the middle section, the venation, and the entire margins of the leaf are similar to modern and fossil forms of *Bumelia* (Sapotaceae) and *Chrysobalanus* (Rosaceae) (Pl. 24, fig. 182). Cuticular preparations of modern species of *Bumelia* and *Chrysobalanus* were compared with the cuticle of this host leaf (Pl. 25, figs. 191, 192). The ranunculaceons arrangement of the accessory cells in modern species of *Bumelia* is not at all like that found in the fossil host leaf while the rubiaceous arrangement of the accessory cells in the modern genus *Chrysobalanus* is very similar (Pl. 25, figs. 193, 194). This fossil

leaf is similar to the modern somewhat coriaceous species *C. icaco,* which occurs in Florida and the West Indies.

Berry (1916) described the fossil leaf *C. inaequalis* from Puryear, Tennessee, a location near the deposits from which the material for this investigation was collected. He considered *C. inaequalis* similar to but more elongate than and perhaps ancestral to the modern *C. icaco*. The host leaf considered here does not appear to have been elongate and is more similar to the modern *C. icaco* than to the fossil material of *C. inaequalis*. Since a complete study of the cuticular characters of the fossil and modern species of *Chrysobalanus* has not been made, the fossil host leaf is simply referred to in this investigation as *Chrysobalanus* sp.

Description and Discussion of New Forms

Order: Erysiphales

Family: Meliolaceae

Meliola Fries, 1825

Meliola anfracta sp. nov.
Pl. 1, figs. 1—4; Pl. 2, figs. 5—8

2- 11. 52-- (Beeli formula as revised by Hansford, 1961)

Description: Colonies 1—3 mm in diameter, subdense to dense, generally branch alternately (may branch oppositely) at acute angles (30—40°). Hyphal cells 4—9 μ wide x 14—37 μ long. Lateral walls of hyphae sinuous; often the hyphae appear undulating. Capitate hyphopodia 10—15μ wide x 14—28μ long, generally alternate, occasionally unilateral, rarely opposite, may spread straight out from the hyphae but usually stalk cells noticeably bent disposing the hyphopodia distally. Stalk cells 5—11 μ wide x 4—11 μ long, generally cylindrical with straight or undulating lateral walls, rarely cuneate. Head cells 10—15 μ wide x 10—17 μ long, rarely entire or angular, most often lobate. Mycelial setae 3—6 μ wide x 300 μ long, absent to moderately abundant, scattered, arise directly from hyphal cells and arch upward, straight to slightly curved, apex not seen. Spores 20 μ wide x 50 μ long, slightly bent, psilate, 3-septate (4-celled), may produce hyphae from any or all of the 4 cells, 2 central cells largest, 2 smaller end cells have rounded ends. No mucronate hyphopodia or perithecia found. Found only on upper piedermis of *Sapindus* sp. Syntypes: slide L.f. 96 [1]).

Discussion: Several fragmentary specimens but only a few well-preserved colonies were found (Pl. 1, figs. 1, 2). All the specimens were limited to the upper epidermis of *Sapindus* sp. The mycelia of *Meliola anfracta* branch frequently and the hyphae often intertwine producing a subdense to dense colony (Pl. 2, figs. 5, 7).

Various forms of microthyriaceous fungi were found growing in close association with *M. anfracta* (Pl. 1, fig. 4). Both Stevens (1918) and Hansford (1946) report parasitism of modern melioliaceous forms by other fungi. The close association of *M. anfracta* and microthyriaceous forms in the fossil material may represent such a form of parasitism, although no proof of actual parasitism is evident in the material examined. Both *M. anfracta* and the microthyriaceous forms seem to have flourished in this close association.

The 2-celled capitate hyphopodia of *Meliola anfracta* (Pl. 1, fig. 3) are generally antrorse and the head cells are variously lobed. They are the anchoring and parasitic organs of the hyphae. Haustorial processes of *M. anfracta* are no longer preserved; only remnants of their parasitic action exist. In modern forms of

[1]) All type slides are deposited in the paleobotanical collections of the Peabody Natural History Museum, Yale University, New Haven, Connecticut.

Meliola haustoria develop from each of the head cells of the capitate hyphopodia and penetrate the cuticle and outer cell walls of the epidermis of the host leaf (HANSFORD, 1961). In *M. anfracta* the hyphopodial head cells are closely adpressed to the surface of the host leaf. Each head cell has a pore in its lower surface which is in direct association with a pore in the upper epidermis of the host leaf (Pl. 2, figs. 5, 6). The pore in the leaf is surrounded by a thickened ring produced by the leaf in reaction to the invasion of the haustorium. The pores are 1—2 μ in diameter which must have been the diameter of the haustorial processes penetrating the surface of the host leaf; in modern forms the haustoria are 1—1.5 μ in diameter (HANSFORD, 1961). Only rarely did more than one haustorium penetrate an individual epidermal cell.

Mycelial setae are absent to moderately abundant in colonies on various leaves. When present the setae are regularly scattered along the length of the hyphae. They are produced near the distal end of the hyphal cells and bend upward away from the surface of the leaf (Pl. 2, fig. 7). No complete mycelial setae were found so the maximum length, presence or absence of branching, and nature of the apex are not known. In all the material examined no mucronate hyphopodia or perithecia were found.

Spores of *M. anfracta* may persist in the center of the colony. One such persistent spore (Pl. 2, fig. 8) had germinated and produced the colony seen in Pl. 1, fig. 2. It is difficult to determine the exact nature of the germination of this spore since the colony which it produced is well developed. However all 4 of the individual cells of the spore had germinated and contributed hyphae to the colony.

Meliola anfracta is superficially similar to the modern forms *Meliola nidulans* (SCHW.) COOKE, parasitic on the Cornaceae of North America; *M. missleana* WINT., parasitic on the Ericaceae of Europe; and *M. cuscutae* HANSF., parasitic on Convolvulaceae. The known modern forms of Meliolaceae usually occur on a limited number of host plants; therefore HANSFORD (1961) lists the modern forms by host plant only. No modern form of *Meliola* that is parasitic on members of the Sapindaceae is in any way similar to the fossil form *M. anfracta*. Because of the difference of its host family and the differences in the general appearance and the habitat of its colonies, *M. anfracta* is placed in a new species.

Meliola spinksii sp. nov.

Pl. 2, figs. 9—11; Pl. 3, figs. 12—14

3-- 3. 42-- (BEELI formula as revised by HANSFORD, 1961)

D e s c r i p t i o n : Only young colonies found; mature colonies probably thin. Hyphae straight, branch oppositely to alternately at right angles. Hyphal cells 5—9 μ wide x 14—50 μ long, produce capitate hyphopodia laterally at the distal ends of the cells. Capitate hyphopodia 5—10 μ wide x 10—18 μ long, opposite or occasionally unilateral, generally antrorse. Stalk cells 4—9 μ wide x 2—5 μ long, somewhat cuneate to cylindrical. Head cells 5—10 μ wide x 8—13 μ long, entire, oblong to ovoid. Mucronate hyphopodia 5—7 μ wide x 11—18 μ long, taper gradually, opposite. Spores 12—15 μ wide x 37—43 μ long, 4-septate (5-celled), psilate, linearly arranged, middle cell often largest, end cells rounded, hyphae originate from any or all of the 5 cells. Found only on the lower epidermis of *Chrysobalanus* sp. Syntypes: slide L. f. 87.

D i s c u s s i o n : Colonies and germinating spores are scattered randomly over the lower surface of the host leaf, *Chrysobalanus* sp. All the colonies arose from single spores and appear to be in early stages of development. Hyphae branch oppositely or unilaterally at right angles (Pl. 3, fig. 15). In these young colonies branching is sparse and the hyphae are very straight and seldom intertwine (Pl. 3, figs. 13, 14). This suggests that the mature colonies would be very thin. No parasitic forms of fungi were found intimately associated with *Meliola spinksii*.

Capitate hyphopodia project straight out or slightly antrorsely from the hyphae (Pl. 3, figs. 15—17). The stalk cells are somewhat cuneate in the antrorse hyphopodia, but in all cases their width is greater than their length (Pl. 3, fig. 16). An incomplete septation is often evident between the stalk cell and its associated head cell (Pl. 3, fig. 16). The head cells are hemispherical to oblong and entire. They are closely adpressed

to the lower epidermal cells and pores are present in the surface in contact with the leaf cuticle (Pl. 2, fig. 10; Pl. 3, figs. 15, 16). These pores correspond to those described for modern forms of *Meliola* (HANSFORD, 1961) through which haustorial processes pass and infect the associated epidermal cells. However no corresponding pores or thickened infected areas were found in the host leaf of *M. spinksii*. HANSFORD (1961) also notes that in germination a single cell of a spore of the modern Meliolaceae produces an initial capitate hyphopodium which in turn produces a haustorial process. This haustorium penetrates the epidermis of the leaf and if it is not the proper host leaf all further germination of the cells of the spore is arrested. Thus, although the colonies of *M. spinksii* appear to be much younger than those of *Meliola anfracta*, it is doubtful that *M. spinksii* could have developed even to a young colonial stage unless some parasitic haustoria had penetrated the epidermal cells of the host leaf. The absence of haustorial pores in the host leaf must be due to either lack of preservation or absence of a thickened area around the pore, such as was seen in *M. anfracta*.

Mucronate hyphopodia (Pl. 3, fig. 17) are present in *M. spinksii* and generally occur oppositely. They are intermixed with capitate hyphopodia on the same hypha. The mucronate hyphopodia are single celled and taper gradually to a rounded tip which bends away from the surface of the leaf. Similar mucronate hyphopodia are commonly found in modern forms of *Meliola* (HANSFORD, 1961).

The presence or absence of mycelial setae is a character used to distinguish the modern genus *Meliola* from several other modern genera in the Meliolaceae. However several modern species of *Meliola* have a very limited production of mycelial setae; setae may be present only around the base of the perithecia or absent entirely on some of the colonies (HANSFORD, 1961). No mycelial setae were present on any of the young colonies of *M. spinksii* observed; however mycelial setae in several modern species are often localized around perithecia and perithecia were not yet developed by the young colonies of *M. spinksii*. Since the spores and hyphopodia of *M. spinksii* suggest an affinity with *Meliola*, it was placed in the genus *Meliola* despite the absence of setae.

The 5-celled spores of *M. spinksii* were found both in initial stages of germination (Pl. 2, figs. 9—11) and attached to young colonies which they had produced (Pl. 3, figs. 12—14). In early stages of germination one or two initial 2-celled capitate hyphopodia are produced from a single cell of the spore. The initial hyphopodium is usually produced from either a terminal cell or one of the cells adjacent to the terminal cells. Modern forms of the Meliolaceae (HANSFORD, 1961) with opposite hyphopodia also often produce one or sometimes two initial capitate hyphopodia upon germination. After the initial hyphopodia are produced the spore produces hyphae from any or all of the cells.

Meliola spinksii is named for the Spinks Clay Company which generously aided in the collection of much of the material described in this paper.

There are only two previous reports of *Meliola* or material similar to *Meliola* in the fossil record. COLANI (1920) reported some material epiphyllous upon *Taxus* leaves from Tertiary deposits in Indochina. He called it a "thallophyte", a term he used for several uncertain algal and fungal remains found, and thought it might be referable to the Dematiaceae, a family of Imperfect Fungi. Close examination of his illustrations reveals that the "thallophyte" has 2-celled, lobed hyphopodia and sinuate hyphae similar to those of *Meliola anfracta* as shown in Pl. 2, figs. 5 and 7. However not enough is known about it to justify a generic designation.

KÖCK in 1939 described several fossils from the Eocene brown coals of Germany including some material of *Meliola* sp. In his paper he illustrated several colonies, hyphae, capitate hyphopodia, and spores, some of which are similar to *M. anfracta*. However the colonies appear to be smaller (.5—1.5 mm in diameter) and less dense than those of *M. anfracta* and the spore size (9 μ wide x 28 μ long) is smaller. The host plants are unnamed. In his *Meliola* sp. KÖCK also included some 5-celled spores (10 μ wide x 34 μ long) and hyphae bearing mucronate hyphopodia which superficially resemble *M. spinksii*. However since the material KÖCK found is incompletely described, no critical comparisons can be made between the German and American material and therefore no more than a generic relationship can be drawn between meliolas of the German and North American Eocene at this time.

Modern forms of Meliolaceae are widely distributed throughout the warm regions of the world (HANS-

FORD, 1961). In the Americas they are distributed from the southern United States to Chile but reach their maximnm development in the tropics.

STEVENS (1925) noted in his report on Hawaiian fungi that members of the Meliolaceae are parasitic upon the native flora of the island but not upon the introdnced forms. From this he concludes: "This relationship of the meliolas to the ancient floras of the islands clearly points to their long, even very ancient, association with these hosts or their progenitors." The wide distribution of the Meliolaceae to Germany, Indochina, and the United States by Eocene times also suggests an early association of this family with angiosperm hosts. The material found in this investigation indicates that this relationship was a specific one; *M. anfracta* was found only upon the upper epidermis of the leaves of *Sapindus* sp. and *M. spinskii* was found only upon the lower epidermis of *Chrysobalanus* sp.

Having found microthyriaceous forms of the same species parasitic on Meliolaceae in two widely-separated island areas, Puerto Rico and Hawaii, STEVENS (1925) theorized that this parasitic relationship was also an ancient one. The microthyriaceous forms found intimately associated with *Meliola anfracta* appear to subtantiate STEVENS's theory.

Order: Microthyriales

Family: Microthyriaceae

Young forms (germlings) of microthyriaceous fungi

Pl. 4, figs. 18—36

Previously Reported as:

1916, *Pediastrum* sp., DAVIS, Proc. Natl. Acad. Sci. U. S., v. 2, p. 116.
1920, *Phyllites* sp., COLANI, Bull. Serv. géolog. de l'Indochine, v. 8, p. 444, fig. 47.
1922, *Phragmothyrites eocaenica*, EDWARDS, Trans. Brit. Mycol. Soc., v. 8, p. 67–68, pl. 8, figs. 5—6.
1931, *Coelastrum?* sp. cf. *C. verrucosum* REINSCH, BRADLEY, U S. Geol. Survey Prof. Paper 168, p. 43, pl. 21, fig. 5.
1939, *Phycopeltis* sp., KÖCK, Nova Acta Acad. Leop. Carol., v. 6, p. 344, table 39, figs. 1—7, table 40, fig. 3, table 41, fig. 2, table 44, fig. 13.
1942, *Phycopeltis microthyrioides*, KIRCHHEIMER, Botanisches Archiv, v. 44, p. 179, fig. 6.

Hundreds of young spore-like stages of microthyriaceous fuugi were observed in this study. It is difficult to discuss these immature forms separately from mature forms of fungi with which they have affinities; rather complete developmental stages from spore-like forms to mature forms have been observed. But since these spore-like forms are identical in their early stages of development, even though they later develop into various forms of mature fungi, they are best dealt with as a separate group. Because they represent the early stages of development of several genera and species of microthyriaceous fungi they are not given a generic name but are termed germlings of microthyriaceous fungi. These germlings were found on all areas of both the upper and lower epidermis of *Sapindus* sp. (Pl. 4, fig. 35) but were more abundant on the upper epidermis.

In its initial and simplest stage the germling is a disc-shaped, spore-like body with a psilate wall (Pl. 4, fig. 18). As this disc-shaped body develops the germling wall appears to invaginate at several places (Pl. 4, figs. 19—21). These "invaginations" are formed by the differential outgrowth of the margin of the germling; they are actually marginal areas which thickened and ceased to grow outwards while adjacent marginal areas continued to grow. As the germling continues to mature these thickened marginal areas become the sites at which radial walls develop and grow inward from the edge of the germling (Pl. 4, figs. 22—24). Thickenings or knobs often appear at the advancing edges of these walls due to the lateral and terminal folding under of the "invaginations" there (Pl. 4, figs. 33—34). As the first-formed "invaginations" continue towards the center of the germling, secondary "invaginations" often form. The germling then ap-

pears to be a round or elongated disc, generally 10—15 μ but ranging from 6-22 μ in diameter, with numerous centripetally-developing walls. At this stage a light area surrounded by a dark ring appears in the center of the germling, caused by a thickened raised ring on the lower surface of the germling. This ring penetrates the cuticle of the host leaf, effectively anchoring the germling to its host as illustrated in the cross section of a germling, Pl. 4, fig. 36. There is no evidence to indicate if a haustorium develops from the germling or if there is any actual parasitic action of the germling upon its host leaf.

As the radial walls continue to develop they meet and fuse, cutting the germling into numerous segments (Pl. 4, figs. 27—29). At the same time the central hyaline area disappears and cross walls are formed within each of the segments forming a multicellular plate of cells. The resulting cells are randomly orientated, angled and somewhat isodiametric except for the marginal cells which are elongate and form a radiating row of cells around the central cells (Pl. 4, figs. 30, 31). During the "cell-forming" process the germlings grow to nearly twice their original size producing young stromata 15—25 μ in diameter.

None of the developmental stages (Pl. 4, figs. 18—29) can be identified any further than to say they have affinities with some form of microthyriaceous fungus. Pl. 4, fig. 30 is the youngest recognizable form of *Callimothallus pertusus* and Pl. 4, fig. 31 is the youngest stroma of *Trichopeltinites fusilis* found. These new species (which are described later) have very different mature forms but develop from similar germlings in a nearly identical manner and cannot be differentiated until the young stromata are formed.

Similar young stages of microthyriaceous fungi have been found in Tertiary deposits throughout the world. They have been reported most often in palynological investigations; in some reports they have been related to algae and in others to fungi. Both DAVIS (1916) and BRADLEY (1931) considered the germling forms which they found in the oil shales of the Green River formation (middle Eocene, WILSON *et. al.*, 1959) to be algal. DAVIS related the material to *Pediastrum* sp. but BRADLEY later named the same material *Coelastrum?* sp. cf. C. *verrucosum* REINSCH. BRADLEY considered 8 closely clustered germlings to represent "a flattened and partly fragmented coenobium whose cells are more or less rounded and irregularly lobed". No other stages of development nor any mature microthyriaceous fruiting bodies were found in the Green River formation by DAVIS or BRADLEY.

COLANI (1920) illustrated small particles or corpuscles which he found adhering to the cuticle of early Tertiary angiosperm leaves from the Dong-giao formation in Indochina. He considered these peculiar objects to be possible fungi or multicellular hairs and termed them *Phyllites* sp. In figure 47, page 444, he illustrated a small lobed one-celled form of *Phyllites* sp., which is a young microthyriaceous germling. Some other forms of *Phyllites* sp. appear to be mature fruiting bodies of microthyriaceous fungi. The mature fungal forms which COLANI reports will be discussed later; no definite relationship can be established between the mature and immature microthyriaceous forms which he described.

EDWARDS (1922) described a fossil fungus, *Phragmothyrites eocaenica,* from the Eocene of Scotland. He illustrated both mature and immature (microthyriaceous germling) stages. Concerning the germlings, which he calls stigmocysts, EDWARDS states: "There is no mycelium on the surface of the leaf, but stigmocysts . . . are abundant, and all stages of growth are to be found between them and the largest of the ascostromata. The stigmocysts (unicellular capitate hyphopodia) are circular and deeply crenulate, about 10—12 μ in diameter, and the clear central spot is usually distinctly seen." These germlings appear to be definitely related to the mature forms of *Phragmothyrites eocaenica.* However it must be stressed that this relationship can be determined only indirectly by their intimate association and that the developmental series which EDWARDS reconstructed from the individual stages that he found links the young and mature forms together but does not prove their relationship. EDWARDS's suggestion, "that the name *Phragmothyrites* be used for fossil forms belonging to the Microthyriaceae, the exact position of which is uncertain, but which appear to be most closely related to *Phragmothyrium* as defined by VON HÖHNEL", shonld not be extended to the germling stages of microthyriaceous fungi. Because the germling stages are often found isolated from any mature forms or associated with numerons mature microthyriaceous forms they should be regarded simply as young forms of microthyriaceous fungi. Since the germlings can not be identified with one specific mature form, the developmental

series reconstructed by EDWARDS (1922) and later by KÖCK (1939) and KIRCHHEIMER (1942) represent only generalized developmental series and may in fact be based upon germlings of various species or genera of microthyriaceous fungi. The classification of all the germling stages simply as young forms of microthyriaceous fungi heeds A. C. SEWARD's advice (1898) to refrain "from converting a possibility into an apparently recognised fact by the application of definite generic and specific names".

Isolated microthyriaceous germlings have also been described from palynological investigations of Eocene deposits of the Geisel valley (POTONIÉ, 1934), from Oligocene brown coal deposits of the Rheinland (POTONIÉ and VENITZ, 1934), and from Pliocene sediments of central Europe (ALTEHENGER, 1959). They were found in macerations for analysis of microfossils and were identified as *Phragmothyrites eocaenicus.*

KÖCK (1939) discussed numerous stages of young forms of microthyriaceous fungi from Eocene brown coals in the Geisel valley of Germany, illustrating developmental stages from spore-like cells to mature trichopeltoid stromata. He identified this material as *Phycopeltis* sp., an alga in the Trentepohliaceae. The proper designation of the mature forms of this material as *Trichopeltinites* sp. is discussed under that generic heading in this report. A developmental series from microthyriaceous germlings to mature *Trichopeltinites* stromata reconstructed from material in this study is similar to the developmental series KÖCK reconstructed in his report.

In 1942 KIRCHHEIMER published a report of *Phycopeltis microthyrioides* from the Oligocene brown coal deposits in Germany in which he illustrated and described a complete developmental sequence from young germlings to mature "thalli". KIRCHHEIMER not only considered the material he described to be *Phycopeltis* but attempted to relate all of the above mentioned reports of microthyriaceous germlings to the genus *Phycopeltis* as well. However the material KIRCHHEIMER described is not in fact *Phycopeltis* but is relatable to the Microthyriaceae. The mature stromata which he described are considered later in the discussion of *Callimothallus pertusus,* for which a similar developmental sequence has been found.

FRANTZ (1959) described and illustrated some microthyriaceous germlings which he considered referable to young forms of Microthyriaceae from Miocene brown coal deposits of Lohsa/Niederlausitz in Germany. KEDVES (1959) and SIMONCSICS (1959) both described microthyriaceous germlings *(Phycopeltis* sp.) found in their palynological investigations of Miocene deposits in Hungary.

ARNAUD (1918) illustrated several ways in which mature stromata may develop in the modern Microthyriales. Three of the types of development illustrated produce crenulate spore-like cells similar to the microthyriaceous germlings found in the fossil record.

1) *Rhipidocarpon javanicum* (PAT.) TH., (plate XI, pp. 119—121): crenulate germlings produced immediately upon germination of 2-celled ascospores. These germlings then develop into mature stromata.

2) *Prillieuxina winteriana* (PAZCHKE) ARNAUD, (plate XXIX, pp. 162—163): non-hyphopodiate hyphae produce smooth, round cells which crenulate and proliferate to form matnre stromata.

3) *Maublancia myrtacearum* ARNAUD, (plate XXVIII, pp. 158—159): hyphopodiate hyphae, hyphopodia crenulate, produce young stromata by cellular proliferation and continue radial development producing mature stromata.

MILLARDET (1870) illustrated developmental stages of *Phycopeltis epiphyton* MILLARDET which are superficially similar to microthyriaceous germlings; however they are nearly twice as large as any modern or fossil microthyriaceous germlings. The crenulate stage in *P. epiphyton* is $15 - 30\,\mu$ in diameter and the young thalli measure $35 - 50\,\mu$ in diameter. The size and nature of the cells of the thalli of *Phycopeltis* sp. are quite different from those found in the stromata of the microthyriaceous fungi. Individual cells of stromata of *Trichopeltinites fusilis* and *Callimothallus pertusus* are considerably smaller than those found in thalli of modern forms of *Phycopeltis.* A very distinct color difference exists between modern algal material of *Phycopeltis* sp. and associated epiphytic material (microthyriaceous fungi). The fungi, germlings included, appear brown to red-yellow brown to dark brown while the algae are very light in color to almost transparent. The same brown hues which characterize modern micro-

thyriaceous fungi and germlings are characteristic of the fossil microthyriaceous germlings found in this investigation. KIRCHHEIMER (1942) reports the same brown to red-brown hues in the material he described as *Phycopeltis microthyrioides*. Color is usually a very uncertain distinguishing character when dealing with fossil plants. However, in this case, the modern material (dead material found on dried leaves from herbarium sheets) and fossil material (dead material found on exceptionally well-preserved fossil leaves) are so similar that this color differentiation is a considerable factor in concluding that these spore-like crenulate cells are not algal but have their affinities with microthyriaceous fungi.

Confusion of adult stromata and germling stages of fungal forms with *Phycopeltis* is not limited to fossil forms. SANTESSON (1944) has noted that a modern form "*Phycopeltis nigra*" which was originally described by JENNINGS (1896) was misidentified and is in fact an epiphyllous fungus. SANTESSON concludes that this form is a species of *Trichopeltis*, very probably *T. reptans*.

A. CHAVES BATISTA (personal correspondence) and F. UECKER (personal correspondence), mycologists, have both agreed that fossil microthyriaceous germlings found in this investigation are indeed fungal and relatable to various forms in the Microthyriales. R. THOMPSON (personal correspondence), a phycologist presently monographing the genus *Phycopeltis*, stated that these germlings are not referable to *Phycopeltis* sp. but appear to be fungal in nature.

Therefore the spore-like cells and developmental stages found in this study and the previous published reports of such material are all referred to as germlings of microthyriaceous fungi and are considered to be in synonymy. In the fossil record microthyriaceous germlings range stratigraphically from the lower-middle Eocene to the present and geographically have been reported from Asia (lower Tertiary), Europe (Eocene, Oligocene, Miocene), and North America (Eocene). Today the Microthyriaceae have a world-wide tropical distribution.

Subfamily: Microthyrieae

Callimothallus gen. nov.

Congeneric Form:
1942, *Phycopeltis microthyrioides* KIRCHHEIMER, Botanisches Archiv, v. 44, p. 177, 201, figs. 1—5, 7, 8.

Description: No free hyphae. Stroma round, radiate, astomate, no central dehiscence, individual cells may possess single pore. Spores undetermined.

Discussion: *Callimothallus* was observed upon many of the leaves of *Sapindus* sp. investigated. Over one hundred stromata and numerous developmental stages were examined in detail. *Callimothallus* is similar to the astomate immature forms of *Microthyriolum* SPEGAZZINI described by STEVENS and RYAN (1939) as "No free mycelium, ascomata round, astomate, glabrous, stellate, dehiscent, spores 2-celled, hyaline, pseudoparaphyses few". *Microthyriolum* differs from the closely related and much more common genus *Microthyrium* by one character; it is astomate with stellate dehiscence. In the many fossil forms of *Callimothallus* which were carefully examined, forms ranging from 50—250 μ in diameter, many of which appear to be mature, no stellate dehiscence was found. In fact *Callimothallus* lacks any central dehiscence and is characterized by numerous pores. Therefore the new genus *Callimothallus* was established for these fossil forms despite their similarity to immature forms of *Microthyriolum*.

Generitype: *C. pertusus* sp. nov.

Callimothallus pertusus sp. nov.

Pl. 5, figs. 37—42; Pl. 6, figs. 43—46; Pl. 7, figs. 47—55

Description: Stroma round, often somewhat lobed, astomate, multiporous, entire to crenate margins, lack free hyphae. Stroma 30—250 μ in diameter, consist of radiating rows of cells which increase in num-

ber as the diameter of the stroma increases. Center of the stroma consists of irregularly angled, often isodiametric cells 3—5 μ in diameter. Central cells often much darker than the rest of the stroma, may proliferate to form a mound of several cells "humped up" in the center. Radiating rows of cells extend outward from central cells. Individual cells in radiating rows 2—8 μ wide x 3—12 μ long, rectangular, often slightly wedge-shaped. Most cells of the stroma have a small pore, 1—2 μ in diameter, in upper surface of the cell. Pores slightly elevated, may be randomly placed, generally limited to extreme proximal end of the cell. No spores found. Host leaves *Sapindus* sp., most frequently occur on upper surface, occasionally on lower surface. Syntypes: slides L.f. 32 and L.f. 186.

Discussion: The mature stromata of *Callimothallus pertusus* develop from single-celled spores; their development has already been described and discussed in detail (see microthyriaceous germlings) (Pl. 4, figs. 18—30). The young stromata can generally be identified as *C. pertusus* when they are 25—30 μ in diameter (Pl. 4, fig. 30; Pl. 7, fig. 54). At this young stage the stromata are compact, round, radiate and consist of 35—45 cells. Abont 20—25 of the centralmost cells already have small pores in their external walls. Stromata 50—100 μ in diameter were the most frequent fonnd in this investigation (Pl. 5, figs. 37, 38) but some as large as 250 μ in diameter were observed (Pl. 5, fig. 40). As the stromata grow larger they often becoue somewhat lobed.

The young stromata increase in size by growth of the marginal cells. In *Callimothallus pertusus* all of the marginal cells usually grow actively to form more or less round stromata. However Pl. 7, fig. 55 shows one stroma in which the marginal growth was erratic resulting in an asymmetric shape. The marginal cells elongate and widen and, as this growth continues, one (Pl. 6, fig. 44) to several (Pl. 6, fig. 41) "invaginations" form. These "invaginations" may split the cell lengthwise (Pl. 6, fig. 44) or may stop at a newly-formed cross wall (Pl. 6, fig. 44) in the marginal cell. Both cross walls and longitudinal walls are formed only within the marginal cells and all the new rows of cells and individual cells that are added to the stromata as they increase in diameter are produced by the marginal cells. The margins of most of the stromata examined appear more or less entire (Pl. 6, fig. 39, 42; Pl. 7, fig. 45) but a few stromata have very fimbriate margins resulting from the large number of longitudinal invaginating walls in the marginal cells (Pl. 6, figs. 41, 44).

It is impossible to determine with certainty the function of the numerous pores which occnr in the stromata of this fossil material. However their detailed development may be observed in the stromata from newly-formed pores in the marginal area to old and open pores in the central area (Pl. 6, figs. 41, 42). The pores originate as raised areas, usually near the centralmost cross wall of the cell, which open to form a simple pore, 1—2 μ in diameter, in each cell. Nothing has been observed inside the cells in which the pores are developing nor are there any spores associated with the pores externally. Since there is no evidence of any other means of dehiscence, it is very possible that the pores were functional in the release of some type of spores. Stevens (1925) made no mention of any possible function of the "secondary ostioles" which he described for *Microthyriella hibisci* except that which is implied in his term "secondary ostiole". *Microthyriella rickii*, also described by Stevens (1925), lacks on ostiole; the whole surface of the stroma fragments to release its spores. The entire stroma of *Callimothallus pertusus* also may have functioned in the release of spores, however not by fragmentation but by the release of spores from individual cells.

In some of the stromata observed a few (1—6) cells in the center of the stromata proliferated (Pl. 6, figs. 44—46). Such proliferations were observed in medium-size stromata 60—90 μ in diameter. The cells produced mound up in the center of the stromata, are thick walled, and are generally slightly angular or round, 6—10 μ in diameter. A few such clusters of cells were also observed on the surface of the host leaves where they appear to have begun to form small *C. pertusus* stromata (Pl. 7, figs. 50—53). These free clusters of cells, often composed of less than 12 cells, have several porate cells, are very similar to the groups of cells formed in the center of some of the stromata, and may be a form of vegetative propagation.

There is no evidence of parasitism of the host leaves by the germling stages (see microthyriaceous germlings) or by adult stromata. Pl. 7, fig. 48 shows in cross section the close association which existed between a

stroma and leaf cuticle. However there is no erosion or penetration of the cuticle or epidermal cells which are in immediate contact with the stromata (Pl. 7, figs. 47—49).

Callimothallus is the only genus in the Microthyriaceae which is multiporate; the only report of such pores in modern fungal material was made by STEVENS (1925) for *Microthyriella* (Micropeltaceae) for which he described "secondary ostioles". Similar pores have also been described for mature forms of an alga, *Phycopeltis epiphyton* MILLARDET (1870). KIRCHHEIMER (1942) described some epiphyllous fossil "thalli" from Oligocene brown coal beds in Germany which are very similar to *C. pertusus.* However, on the basis of the similarity of the porate condition and the general similarities of the developmental stages and adult thalli of the modern forms of *Phycopeltis* and the fossil material he found, KIRCHHEIMER named the fossil material *Phycopeltis microthyrioides.* The fact that the two principal diagnostic features of his material, complete lack of any central means of dehiscence and the presence of a single pore on the upper surface near the proximal end of nearly every cell of the stromata except the marginal cells, have not been found in modern Microthyriaceae also influenced him to identify the material he fonnd as an alga instead of a fungus. Since there is no modern genus in the Microthyriaceae to which this fossil form, which is congeneric with *Callimothallus,* can be related and since the algal genus *Phycopeltis* has many superficially similar characters, it seemed quite reasonable to assume this fossil material to be algal (KIRCHHEIMER, 1942; DILCHER, 1962). However a critical examination of both the developmental and mature stages of *Phycopeltis* sp. and several forms of microthyriaceous fungi casts grave doubts on this assumption.

As discussed earlier, the germlings found associated with and related to *Callimothallus pertusus* and other microthyriaceous forms do not appear to have any relation to the alga *Phycopeltis.* These germlings have only a superficial similarity to the young forms of *Phycopeltis* and differ in color and in the size and natnre of the cells.

Thalli of *Phycopeltis* consist of a few large cells(e. g. 15 cells in a thallus 30 μ in diameter, 96 cells in a thallus 135 μ in diameter), while the stromata of *Callimothallus* consist of numerous small cells (e. g. 40 cells in a stroma 30 μ in diameter, 155 cells in a stroma 75 μ in diameter). In the material illustrated by MILLARDET (1870) and later by PRINTZ (1939) for *Phycopeltis epiphyton* only a few cells of the thalli (4—5 central cells in a thallus of 96 cells) actually are porate; in *Callimothallus* many more of the cells (110 in a stroma of 155 cells) are porate. The color difference noted between the microthyriaceous germlings and the developmental stages of *Phycopeltis* (transparent nature of the *Phycopeltis* material vs. the red-yellow brown, to dark brown color of the germlings) is even more evident in the mature stages of these two forms.

Finally no enlarged gametangial cells, characteristic of *Phycopeltis,* or evidence of their presence has been observed in the material *(Callimothallus)* found in this investigation. KIRCHHEIMER (1942) identified certain marginal and "thalloidal" holes in his material as areas which were at one time gametangial cells. He felt that the gametangial cell walls were not preserved because of their delicate nature. However in modern *Phycopeltis* material found upon dried herbarium specimens the gametangia are intact and preserve as well as the rest of the thallus. It also seems improbable that the rest of the somewhat fragile fossil stroma would be so well preserved when not even a trace of the gametangial cell wall persists.

I suggest that the "gametangial holes" found on the margins and in the stromata of KIRCHHEIMER's material are in fact areas where the stromata were in the process of or had already grown around a cylindrical trichome of the host leaf (KIRCHHEIMER did not describe or identify the host leaves upon which his stromata were found). STEVENS (1925) illustrated just such a circular hole, formed by growth around a cylindrical trichome, in a stroma of *Trichopeltis reptans.* The theory that the "gametangial holes" described hy KIRCHHEIMER are actually the result of the stroma growing around a cylindrical trichome explains several characters of the "gametangia" of *Phycopeltis microthyrioides* which are not found in modern *Phycopeltis:* 1) the "gametangia" are always very circular while the other stroma cells are rectangular; 2) the "gametangia" occur with no relation to the other stroma cells and actually cause the adjacent cells to bend around them; 3) the "gametangia" occur scattered randomly throughout the stroma which contains only 1, 2 or 3 such "gametangial

holes" (modern forms of *Phycopeltis* produce many more gametangia per thallus); 4) the "gametangia" always occur marginally at first and are then incorporated into the stroma as it continues its growth past the point where the "gametangial holes" were formed; and 5) the European specimens contain "gametangia" while the congeneric specimens found in the United States (which occur on host leaves which have no trichomes) have none.

For the above reasons it can be concluded that *Phycopeltis microthyrioides* KIRCHHEIMER is not algal but fungal and is congeneric with *Callimothallus*.

ink, 1974, p. 82 and 83 for discussion

Microthallites gen. nov.

Description: Stroma radiate, more or less round, lacks free hyphae, ostiolate or non-ostiolate. Spores unknown.

Discussion: The genus *Microthallites* is estahlished here for fungal forms in the subfamily Microthyrieae which can not be precisely compared with or related to the modern or fossil genera known for this subfamily because incomplete material is available. COOKSON (1947) established the genus *Microthyriacites* (Microthyriaceae incertae sedis) for fungal forms for which neither the presence or absence of free hyphae nor the ascospores are known. This genus is very useful for classifyng the poorly preserved and isolated fruiting bodies often found in palynological investigations. The two species placed in the genus *Microthallites* in this study, however, definitely lack free hyphae and so cannot be placed in the genus *Microthyriacites,* but neither can they be related to known genera in the subfamily Microthyrieae until more complete specimens are found. Therefore they are placed together in the artificial genus *Microthallites* even though they may later be found to represent two separate genera when more complete specimens are discovered.

Growth of the stromata of this genus probably is similar to that already described for *Callimothallus pertusus.* Their growth seems to be determinate while they are still small (25—60 μ in diameter).

Generitype: *M. lutosus* sp. nov.

Microthallites lutosus sp. nov.

Pl. 10, figs. 83—85

Description: Stroma 25—40 μ in diameter, radiate, more or less circular, non-ostiolate, lacks free hyphae, margins irregular, more or less fimbriate. Stroma consists of radiating rows of cells, 1.5—5 μ wide x 2—7 μ long, square to slightly rectangular, dichotomizing. Subtending layer evident, consisting of elongate cells, 1.5—3.5 μ wide x 10—15 μ long, dichotomizing 2—3 times marginally. A single thick-walled cell, 3—5 μ in diameter, present centrally on the upper surface of the stroma. No spores found. Found on the upper epidermis of *Sapindus* sp. Syntypes: slides L.f. 210 and L.f. 221.

Discussion: Only a few isolated forms were found. All the stromata are small (25—40 μ in diameter) with a small thick-walled cell in the center where an ostiole might be expected to develop (Pl. 10, figs. 83, 84). The centrally-located thick-walled cell may form a cover or lid over the area of the immature stroma which would probably form the ostiole in a mature stroma. A hyphal fragment was found associated with one stroma; however no proof of connection between the two could be established. Free hyphae are either truly lacking in this form or are evanescent and not preserved in this fossil material.

A subtending layer is very prominent in this form and consists of dichotomously branching, elongated, non-septate cells (Pl. 10, fig. 85). The relationship between this subtending layer (lower surface of the stroma) and the upper surface of the stroma is difficult to determine. The basic dichotomies of the two layers are nearly identical except that those of the lower surface are more deeply incised and lack cross walls. These two "layers" are distinguishable as separate layers in high (Pl. 10, fig. 84) and low (Pl. 10, fig. 85) focus but not as layers actually separated from one another by cell walls. This same type of pseudolayering is present in the microthyriaceous germlings which are forming "invaginations" from their margins (Pl. 4, figs. 33, 34); the invaginating wall always advances further on the lower surface of the germling than the upper surface.

Microthallites spinulatus sp. nov.

Pl. 12, figs. 92, 95—96

Description: Stroma 40—60 μ in diameter, radiate, more or less round, ostiolate, margin entire with echinate projections extending out from the base, lacks free hyphae. Stroma consists of two distinct layers, a bottom layer of dichotomizing radial hyphae, 2—2.5 μ wide x 5—12 μ long with 2 to 3 dichotomies, and a top layer of radiating rows of elongate cells, 2—5 μ wide x 6—10 μ long. Ostioles central, not surrounded by any specialized cells. Margins of ostioles appear lobed because of radiating cells surrounding them. Found on lower surface of *Chrysobalanus* sp. Syntypes: slide L.f. 87.

Discussion: Only a few specimens were found. The most characteristic features of *Microthallites spinulatus* are the basal echinations on the margin of the stroma and the central ostioles which lack encircling specialized cells (Pl. 12, fig. 96). The simple ostiole appears to result from the dissolution of the central cells of the stroma. The inner margins of the radiating rows of cells are left, producing a border of scallops around the ostiole. In this form, as in *Microthallites lutosus* (Pl. 10, figs. 84, 85), the stroma has two layers, one at a low plane of focus, and another at a high plane of focus (Pl. 12, figs. 95, 96).

Numerous flattened radiate stromata lacking free hyphae which appear to belong to the subfamily Microthyrieae have been reported from the fossil record. Most of these reports are of stromata found in samples of sediments examined for pollen and spores and therefore isolated from their host leaves. It cannot be definitely determined whether the lack of free hyphae is real or due to the isolation of the stromata from their host leaves; however in all cases the margins of the fruiting bodies appear entire and lack any evidence of free hyphae.

Stromata of this subfamily in which no ostioles are evident have been reported from the Eocene of England (Edwards, 1922), the Pliocene of Germany (Leschik, 1951), the Oligocene-Miocene of Germany (Frantz, 1959), and bauxite deposits of Hungary (Deák, 1960). These may represent immature forms or may be non-ostiolate stromata.

Ostiolate stromata, very similar to the modern genus *Microthyrium* or closely related genera, have been found in the Tertiary of Indochina (Colani, 1920), the Oligocene-Miocene of Germany (Thiergart, 1937), the Pleistocene of Minnesota (Rosendahl, 1943), the Oligocene of New South Wales (Cookson, 1947), the Pleistocene and post Pleistocene of England (Godwin and Andrew, 1951), the Pliocene of Germany (Leschik, 1951; Altehenger, 1959), the Miocene of Upper Silesia (Macko, 1958), and Meso-Cenozoic sediments of Siberia (Popov, 1962).

Microthyrium is one of the most common and widespread genera of modern Microthyrieae. As is apparent from the above list, *Microthyrium* and/or closely related genera were also widespread by Miocene-Oligocene times and seem to have been relatively abundant in many Tertiary sediments.

Subfamily: Asterineae

Asterina Léveillé, 1845

Asterina eocenica sp. nov.

Pl. 7, fig. 56; Pl. 8, figs. 57—68

Description: Fruiting body round, radiate, consists of prosenchymatous cells; small fruiting body 35—45 μ in diameter, large fruiting body 100—225 μ in diameter. Central cells of fruiting body isodiametric, 5—7 μ in diameter. Elongate marginal cells bifurcate frequently, 3—4 μ wide x 3.5—7 μ long in small fruiting body, 2.5—3.5 μ wide x 7.5—12.5 μ long in large fruiting body. Fruiting body astomate, splits open

radially at maturity, exposing radially arranged ascospores within the large fruiting body. Spores 2-celled, echinate, 9—14 μ wide x 20—28 μ long. The two cells of the spores unequal in size. the larger 9—14 μ wide x 12—15 μ long and the smaller 8—12 μ wide x 10—13 μ long. Typical germination of spores occurs from the free end of the smaller cell of the spore. Spores may persist in attachment to the young hyphae produced. Hyphae typically straight, usually branch alternately or unilaterally, may branch oppositely, hyphal cells 3—5 μ wide x 6—32 μ long. Single-celled hyphopodia produced at more or less regular intervals along the length of the hyphae, often near the distal end of the hyphal cells. Hyphopodia generally alternate, may be unilateral, single-celled, elongate and attenuate at apex, 3—5 μ wide x 9—14 μ long at base tapering to about half this width near tip. No haustorial pores present in hyphopodia; no indication of infection of host leaf. Found on lower surface of *Chrysobalanus* sp. Syntypes: slide L.f. 87.

Discussion: *Asterina eocenica* is a very completely preserved form; the ascospores, hyphae, ascocarps, pycnidia, and their developmental stages were all found. Upon germination the 2-celled ascospores produce very distinctive hyphae characterized by elongate, slightly tapering, sessile, single-celled hyphopodia with obtuse apexes (Pl. 7, fig. 56; Pl. 8, fig. 57). These hyphae spread loosely over a large area of the lower epidermis of the host leaf, *Chrysobalanus* sp. They generally branch oppositely and occasionally branches intertwine and anastomose with other branches (Pl. 8, figs. 58, 63). In Pl. 8, fig. 58 a definite connection between two anastomosing branches is illustrated; this connection could have permitted exchange of cytoplasmic and nuclear material. It could not be determined from the material available if the anastomosing hyphae were from a single colony or from two separate colonies.

The fruiting bodies may originate from medial hyphal cells (Pl. 8, fig. 59) or from terminal cells of short lateral branches (Pl. 8, fig. 60). In both cases an initial cell divides to form a group of cells between the leaf surface and the hyphae (Pl. 8, fig. 61). The cells in this group then grow radially and as the diameter of the fruiting body increases the marginal cells bifurcate and the number of radiating rows of cells increases (Pl. 8, figs. 62, 64). Thus a compact disk with a crenate margin results. As the fruiting body matures the center arches away from the surface of the leaf while the margin continues to adhere to it (Pl. 8, figs. 63, 65). No well-defined ostioles are present. At maturity radial fissures develop in the fruiting bodies (Pl. 8, figs. 63, 65) and groups of cells often break away from the center allowing spores to escape (Pl. 8, figs. 66—68).

Two distinct groups of fruiting bodies may be distinguished on the basis of size. In one group, in which no spores have been found, the maximum diameter ranges from 35—45 μ; in the other group, in which ascospores have been found, the maximum diameter ranges from 100—225 μ. Although no spores (picnidiospores) were found associated with the smaller fruiting bodies, several of them had begun to split open indicating maturity (Pl. 8, fig. 63). Doidge (1920) stated that "The pycnidia *(Asterostomella)* in the genus *Asterina* are usually identical in form with the thyriothecia, but they are smaller; these were often mistaken by the earlier workers for thyriothecia, and described as such". It is possible that the small fruiting bodies are simply developmental stages of the ascocarps. However there are no intermediate-size fruiting bodies between the 35—45 μ diameter group and the 100—225 μ diameter group. Therefore both the smaller colonies and the larger colonies are probably near maturity. The diminutive fruiting bodies are probably pycnidia, as are most of the diminutive fruiting bodies of mature colonies of modern *Asterina*.

Asterina nodosaria sp. nov.

Pl. 9, figs. 69—75

Description: No mature fruiting bodies present; only hyphae, setae, and seta bases known. Hyphae spread over upper surface of the host leaf, producing opposite or unilateral branches with frequent node-like or enlarged cells 7 μ wide x 12—20 μ long with thickened lateral walls. Hyphal cells 3—5 μ wide x 7—27 μ long. Very young developmental stages of fruiting bodies preserved, produced by node-like cells of the hyphae. Lateral walls of this cell fold outward producing a thin crenulated disk. Setae rarely preserved, 4 μ wide (tapering slightly towards apex) x 15—20 μ long, attached to fimbriate, thickened bases, 5—10 μ in

diameter. When setae are missing, seta bases have conspicuous pores, 3—6 μ in diameter, in center. Seta bases occur singly or clustered in a group. No spores found. Host leaf *Sapindus* sp. Syntypes: slides L.f. 45 and L.f. 195.

Discussion: Small, dark, fimbriate porate structures are often associated with *Asterina nodosaria* (Pl. 9, figs. 70, 72, 73). After close examination of many such structures a few setae were found attached to them. These seta bases have no evident attachment to the hyphae (Pl. 9, fig. 73). However they are always closely associated with this nodular type of hyphae and probably are produced by evanescent hyphae. The bases are generally not closely associated with one another but occasionally have been found clumped together in small groups (Pl. 9, fig. 70). They develop from small irregular cells (Pl. 9, fig. 72). A young hase forms a dark central area, then a seta, and finally after the seta has broken away a fimbriate cell with a central pore, the seta base, remains (Pl. 9, fig. 73). Only rarely are setae found still attached.

This fossil form of *Asterina* is similar to *Asterolibertia couepiae* (P. Henn.) Arnaud described by Arnaud (1918) and later put in synonomy with *Asterina* as *Asterina couepiae* Henn. by Clements and Shear (1931). The most striking feature of *A. nodosaria* and *A. couepiae* is that their hyphopodia are merely thick-walled bulges in the hyphal cells (Pl. 9, fig. 71). The overall appearance and habitat of the hyphae of the modern form and the fossil form are very similar. The hyphae spread loosely over the upper surface of the host leaf and branch oppositely or occasionally unilaterally at a 40—50° angle to the parent hyphae (Pl. 9, fig. 69). Branches may intertwine with each other but only occasionally anastomose (Pl. 9, fig. 71). However no evidence of haustoria was found either in the hyphae or subtending leaf of *A. nodosaria,* while in *A. couepiae* haustoria originate from many of the node-like cells. The fruiting bodies of the modern form arise from the node-like cells (hyphopodia) just as they do in the fossil form (Pl. 9, figs. 74, 75). Since mature fruiting bodies are not known for the fossil form and since the setae and seta bases common in the fossil material are not present in *A. couepiae,* a new species is established for the fossil material.

Asterina nodulosa, described by Spegazzini (1889), now in synonymy with *Asterina inaequalis* Mont., according to Stevens and Ryan (1939), is also similar to *A. nodosaria.* The material Spegazzini described lacked hyphopodia and the hyphae were characterized by nodnlar thickenings. However no setae or seta bases are mentioned in the description of this modern form.

Parasterina Theissen and Sydow, 1917

? Parasterina plectopelta sp. nov.

Pl. 10, figs. 76—82

Description: No fruiting bodies or spores known; only hyphopodiate hyphae found. Hyphae branch and anastomose irregularly forming a loose to more or less dense network over the upper and lower surface of the host leaf. Hyphal cells 3—5 μ wide x 6—28 μ long. Sessile hyphopodia 6—12 μ wide x 8—13 μ long, ovate, borne singly or in pairs on the hyphae. Hyphopodia irregularly spaced along the hyphae, may be unilaterally or oppositely arranged. Small areas of dense irregular cellular proliferation frequently associated with the hyphae. Found on *Sapindus* sp. and unidentified cuticular fragment. Syntypes: slides L.f. 195, L.f. 201, and L.f. 211.

Discussion: This form is placed in the genus *Parasterina* on the basis of its mycelia and hyphopodia. Because the fruiting bodies and spores are unknown its affinities cannot be determined with certainty. The mycelium is however similar to the mycelium of *Parasterina implicata* Doidge, a modern form from South Africa that is parasitic upon *Sideroxylon.* Doidge (1920) described the mycelium of *P. implicata* as "branching irregularly and anastomosing freely to form a network of entangled hyphae, tips of branches often club-shaped, . . . hyphopodia sessile, not very numerous, . . . ovate or obliquely flattened". Hyphae of *?Parasterina plectopelta* branch randomly, anastomose and intertwine readily, and may cover the epidermis of the host leaf with either a loose (Pl. 10, figs. 76, 77) or very dense network of hyphae (Pl. 10, figs. 79, 81).

Hyphopodia of *?P. plectopelta* are also very similar to those described for *P. implicata;* they are sessile, ovate, and not very numerous (Pl. 10, figs. 77, 78). Occasionally two hyphopodia may arise side by side from the same place on the hypha (Pl. 10, fig. 78), but usually they occur singly (Pl. 10, fig. 77). Hyphopodia may arise from any given hyphal cell. There is no evidence of the presence of haustoria either in the hyphopodia or the leaf epidermis.

Small groups of irregularly shaped cells which are sometimes found scattered among the anastomosing hyphae of this species vary in size (25—85 μ in diameter) and character but very rarely appear organized into a fruiting body-like structure (Pl. 10, figs. 80, 81). Pl. 10, fig. 82 illustrates one proliferation which has grown around several hairs and is somewhat more compact than most. The hairs later broke away from the leaf leaving hair bases on the leaf surface and holes in the proliferated mass of hyphae. Therefore these pores or holes should not be considered to be ostioles.

The irregular cellular proliferations are somewhat similar to the young fruiting bodies produced by the Micropeltaceae. However since no mature fruiting bodies or spores were found and since it is impossible to determine if the cellular proliferations actually are very immature fruiting bodies this material is tentatively classified as *?Parasterina* on the basis of the similarity of its mycelia and hyphopodia to the modern species *Parasterina implicata.*

Asterothyrites Cookson, 1947

Asterothyrites tennesseensis sp. nov.

Pl. 12, fig. 97

Description: Stroma 130 μ in diameter, more or less round, consists of radiating rows of cells. Margins more or less entire, slightly irregular. Free hyphae attached marginally, poorly preserved; hyphal cells 1.5—3 μ wide x 10—25 μ long, sinuous. Stroma cells 2.5—5.5 μ wide x 2.5—8 μ long, dichotomize marginally forming additional rows of cells, cell walls sinuous. Central part of stroma slightly raised, individual cells shorter and cell walls thicker than those of marginal cells. No spores known. Presence or absence of ostiole undetermined since much of the central area of the stroma is not preserved. Found on the upper surface of *Sapindus* sp. Holotype: slide L.f. 32.

Discussion: All that is known of this form is a flat radiate stroma with which free hyphae are associated; the ostiolate condition and spores are unknown (Pl. 12, fig. 97). Thus this form fits Cookson's generic description (1947) of *Asterothyrites,* a genus for round radiate stroma of the subfamily Asterineae in the Microthyriaceae: "Mycelium superficial, persistent. Ascoma round, flat, radiate. Ascospores unknown." The genus name *Asterothyrites* does not imply any generic affinities with the modern genus *Asterina,* only that they are in the same subfamily. *Asterothyrites tennesseensis* is probably not relatable to the modern genus *Asterina.*

The center of the stroma is slightly arched away from the surface of the host leaf suggesting that it might be a mature fruiting body since in many of the Microthyriaceae the central portions of the fruiting bodies arch away from the surface of the host leaf as they begin to mature. However, unlike the other microthyriaceous fruiting bodies described in this study, the cell walls of the stroma of *A. tennesseensis* are very noticeably sinuate (Pl. 12, fig. 97) and the individual cells are square to rectangular but not elongate. The central cells of the stroma (Pl. 12, fig. 97) may be missing due to a dehiscence mechanism or to lack of preservation or to a combination of both factors. Any judgement concerning the nature or existence of an ostiole is precluded by the absence of the center of the stroma. Therefore no affinities with modern forms, other than subfamily, can be drawn at this time.

Modern forms in the subfamily Asterineae have been reported from subtropical and tropical areas around the world. A large number of the forms that have been described are from South America (Doidge, 1920) as

are many of the genera of the Microthyriaceae. However this may reflect the fact that more extensive work has been done and more collections have been made in the tropical areas of the Americas than elsewhere in the world.

Cookson (1947) described several fossil fungi belonging to the subfamily Asterineae. She established two new genera for the fossil forms of Asterineae she found: 1) *Asterothyrites:* "Mycelium superficial, persistent. Ascomata round, flat, radiate. Ascospores unknown." 2) *Euthythyrites:* "Mycelium superficial; ascomata linear, radiate, characters of spores unknown." All the material which she found in this subfamily was epiphytic upon leaves of *Oleinites willissi* of ?Oligocene-Miocene age from Australia. The genera that Cookson established for incompletely known fossil forms are used in this investigation where applicable; however whenever possible modern genera are used.

This study represents the only published report of the genus *Asterina* in the fossil record and of any member of the subfamily Asterineae in the fossil record of the Americas. The subfamily Asterineae must have had an early association with the angiosperm floras since it was widely distributed (Americas-Australia) by ?Oligocene-Miocene times.

Subfamily: Trichopelteae

Trichopeltinites Cookson, 1947

Congeneric Forms:

1939, *Phycopeltis* sp., Köck, Nova Acta Acad. Leop.-Carol., n. s., v. 6, p. 343, table 39, figs. 8—11, table 40, figs. 1—6, table 41, fig. 1, table 44, fig. 14.

1942, *Phycopeltis koeckii*, Kirchheimer, Botanisches Archiv, v. 44, p. 201.

Trichopeltinites fusilis sp. nov.

Pl. 11, figs. 86—89; Pl. 12, figs. 90—94

Description: Stroma extremely variable in size and shape, 30—500 μ in diameter, circular to tongue shaped with irregularly lobed margins. Stroma most common on upper epidermis, one cell thick, free hyphae may be present. Hyphae closely adpressed together and to the surface of the host leaf forming radiate and linear stromata. Rows of hyphae originate from a central area in a stroma and grow out in all directions, dichotomizing and forming arms or lobes of various shapes and sizes. Cells near central area of stroma generally isodiametric, 3—8 μ in diameter, angular, lack any specific orientation. Cells elsewhere in stroma square to elongate, 2—4 μ wide x 8—25 μ long, frequently dichotomize increasing the radiating rows of cells. Upper surface of stroma slightly granulose. Matnre stroma characterized by ascomata which are local, round, thickened areas 25—50 μ in diameter, located centrally within the lobes or main body of the stroma. One to several fruiting bodies present in a single stroma. At maturity the thickened cells located over the ascomata arch away from the surface of the host leaf and split apart. Eventually they break away from the stroma leaving holes which then indicate the positions of former ascomata. Small fruiting body 25—40 μ in diameter, develops central irregular openings 5—7 μ in diameter at maturity, is associated with and/or connected to large stroma by evanescent hyphae, appears to be diminutive fertile stroma. Seta bases 4—5 μ in diameter, rarely present, dark, thickened points, may be surrounded by rosette of mycelial cells. No spores found. Host plants various species of *Sapindus*. Syntypes: slides L.f. 37, L.f. 61, L.f. 206, and L.f. 217.

Discussion: *Trichopeltinites fusilis* is one of the forms of fungi most commonly found in this study. Several mature stromata were found (Pl. 11, figs. 86—89) which display very clearly the characteristic features of the Trichopelteae, viz. the covers of the ascomata appear as local thickenings of the vegetative mycelium and the mycelium is either radial or formed of sterile laterally-united parallel hyphae (Bessey, 1950). Also a great many developmental stages (Pl. 4, figs. 18—29) and immature forms (Pl. 4, fig. 31; Pl. 12, fig. 93) were found

which have the same characteristic features as the vegetative mycelium of the mature forms. Several of these immature sterile stromata have been included in this species. When these young sterile stromata are included, the range of size variation of stromata increases considerably; some of the young stromata may be 30—50 μ in diameter while the largest mature stromata may measure 450—500 μ in diameter.

Since all stages of development of this form were fonnd in intimate association with inature stromata, a complete developmental series of spores, small germlings, young stromata, and immature sterile stromata could be reconstructed. However, it must be kept in mind that the young developmental stages can only be considered as possible links in the reconstruction of the development of this form since they are identical to those of related fungi and thus can not be identified in isolation from mature stromata. For the same reason they cannot be assigned a generic or specific name. No previously established generic or specific affinities should be assigned to any isolated young stages of development of plant fossils when they may be related to more than one adult fossil plant form.

Stromata of this species occur almost exclusively on the upper epidermis and usually are randomly spread over the leaf's surface. Young stromata are often circular and the first stage of growth after the germling stage produces cells marginally on all sides of the stroma. As the stromata continue to develop the marginal cells in some areas may cease to divide while others continue to produce new cells, thus forming lobes. Lobes radiating in several directions may be found in mature stromata (Pl. 11, figs. 86—89). Loosely arranged cells may extend from the margins of the less actively growing portions of a stroma (Pl. 11, fig. 86); these cells may produce new lobes or separate stromata. The actively growing margins of the stromata, however, are always compact and lack any irregularly arranged cells. The stromata are a single cell thick.

Cells produced by the growing margin of an older stroma are generally rectangular, commonly measuring about 2.5 μ wide x 16 μ long. Cells in or near the original centers of the stromata are generally isodiametric, appear very angular, and lack any specific orientation. As the marginal cells elongate and widen tbey divide periclinally by lateral walls and anticlinally by walls which "invaginate" from the outer margin of the cell (Pl. 11, fig. 88; Pl. 12, fig. 93). Tbese walls either completely or partially divide the marginal cells anticlinally allowing new rows of cells to be formed as the diameter of a stroma or width of a lobe increases.

Marginal cells most frequently form well-defined margins and the stromata generally have few or no associated free hyphae. However some of the stromata have areas from which free hyphae are produced. Thus a compact stroma of *T. fusilis* may have associated with it and/or connected to it free hyphae wbich may in turn form loosely organized sterile or fertile stromata (Pl. 11, fig. 87; Pl. 12, figs. 90, 91). Therefore free hyphae and loosely organized stromata in addition to various immature stages are known for *Trichopeltinites fusilis*.

The free hyphae are a single cell wide and somewhat evanescent (Pl. 12, figs. 90, 91). No spores nor any form of germination contributing to the formation of the free hyphae were found. Some of the small stromata connected to free hyphae appear to function completely as fruiting bodies and lack any extensive vegetative growth (Pl. 12, fig. 91). The entire diminutive stroma mounds up at maturity and the central cells disintegrate forming openings in the upper surface (Pl. 12, fig. 90). Thus *T. fusilis* may assume very diverse appearances depending upon the nature of its growth or the stage of its development.

No evidence of direct parasitism of the host leaves was observed.

Trichopeltinites fusilis is very similar to an epiphyllous form described by Köck (1939) from Eocene brown coal deposits in Germany which he considered to be *Phycopeltis*, a green alga, on the basis of gross morphologic similarities. After considering material similar to that described by Köck it was first thought that *T. fusilis* was indeed algal in its affinities (Dilcher, 1962). However, upon closer examination of some material of modern *Phycopeltis*, the general aspect of modern *Phycopeltis* was found to be quite different from both *T. fusilis* and Köck's *Phycopeltis* sp. The overall size and shape of the thalli of modern *Phycopeltis* and the fossil material are not similar and the cells of modern *Phycopeltis* are straight walled, each

cell being clearly evident, and the entire thallus is light to almost hyaline. Cell walls of *T. fusilis* and Köck's *Phycopeltis* sp. are somewhat sinuous and appear much darker than those of modern *Phycopeltis*. They are in fact very similar to some modern epiphyllous fungi with respect to the color and nature of their cells. Also the cells of the fungal material are narrower and longer than the thallus cells typically found in modern *Phycopeltis;* individual cells of the modern material of *Phycopeltis* examined are 4—8 μ wide x 8—15 μ long while those of *T. fusilis* and Köck's *Phycopeltis* sp. are 2—4 μ wide x 10—20 μ long.

In addition to the above evidence the presence of ascomata in the mature stromata rather conclusively shows that the fossil forms described here are not relatable to algae but are relatable to fungal forms in the Trichopelteae.

A. Chaves Batista, a Brazilian mycologist who is familiar with a great many tropical epiphyllous fungi, and R. Thompson, a phycologist who is presently monographing the genus *Phycopeltis*, have both stated in personal correspondence, after having examined photographs of the fossil material in question, that *T. fusilis* is unquestionably fungal. E. Müller (personal correspondence) who has recently re-examined some of Köck's material from the Geisel valley is of the opinion that the material Köck (1939) described as *Phycopeltis* sp. is also fungal rather than algal in its affinities.

Since Köck first published his report of the occurrence of *Phycopeltis* sp. in 1939, several later papers have perpetuated his error. Kirchheimer (1942), Potonié (1951), Mägdefrau (1956), Kedves (1959), Krumbiegle (1959), Simoncsics (1959), Zappler (1960), Dilcher (1962), and Sinott and Wilson (1963) have all illustrated or discussed this or similar fossil material (developmental stages or adult forms) calling them *Phycopeltis*. All of these reports of *Phycopeltis* are actually reports of microthyriaceous fungi and as yet no valid reports of fossil material of the alga *Phycopeltis* exist.

Cookson (1947) established the genus *Trichopeltinites* for some fossil material she described which belongs in the Trichopelteae but for which the ascospores are unknown. Since ascospores are unknown for the material described here it is also assigned to the genus *Trichopeltinites*. *Trichopeltinites fusilis* is similar to the fossil material *Trichopeltinites pulcher* Cookson and to the modern forms *Trichopeltis reptans* Spegazzini and *Trichothallus hawaiiensis* Stevens. A few stromata of *Trichopeltinites fusilis* had thickened round seta bases (no setae were found) similar to those produced by the setae of *Trichothallus hawaiiensis*. However these bases were not common and the majority of the stromata lacked bases and were more similar to the fertile non-setate *Trichopeltis reptans*.

Trichopeltina Theissen, 1914b

Trichopeltina exporrecta sp. nov.

Pl. 12, figs. 98—99; Pl. 13, figs. 100—103

Description: Stroma small, sterile, associated with conspicuous free hyphae. Stroma 30—75 μ wide x 42—140 μ long, consist of rectangular to elongate cells 1.5—4 μ wide x 3.5—10 μ long united laterally, dichotomizing marginally, or a sheet of randomly orientated irregularly shaped cells 2—4 μ wide x 3—8 μ long. Stroma margins entire to lobed. Setae sometimes present, 2 μ tapering to 1.5 μ wide x 25 μ long. Free hyphae attached to stromata, more or less sinuous, anastomose freely over the upper and lower surfaces of the host leaf. Hyphal cells 1.5—4 μ wide x 5—30 μ long. Two-celled (1-septate) germinating spores attached to free hyphae. Spores 3.5—5 μ wide x 12—17 μ long, germinate terminally or laterally. Host leaf *Sapindus* sp. Syntypes: slides L.f. 8 and L.f. 189.

Discussion: Only linear and radiate sterile stromata, free hyphae, and germinating spores are known for this fossil form. It unquestionably belongs in the Trichopelteae because its stroma consists of a radiate, prosenchymatous membrane. However it is unusual in that it has a considerable number of sterile free hyphae which are not organized into typical membranes but extend loosely and anastomose freely over the surface of the host leaf. These free hyphae frequently follow the lateral walls of the epidermal cells of

the host leaf (Pl. 13, figs. 100, 103). This habit is not unique to this species but was also observed in some of the forms of Micropeltaceae and several fragments of unidentifiable fungi found in this study. Some of the stromata consist of randomly associated hyphal cells which have proliferated in an unorganized fashion from the free hyphae (Pl. 12, figs. 98, 99). The stromata may prodnce setae (Pl. 12, fig. 98).

This fossil material was placed in the genus *Trichopeltina* (CLEMENTS and SHEAR, 1931) on the basis of the 2-celled (1-septate) hyaline germinating spores which were found still attached to the free hyphae they produced (Pl. 13, figs. 101, 102). This form does not appear to develop from a germling stage as does *Trichopeltinites fusilis*, but the stromata develop by the proliferation of the free hyphae into a prosenchymatous membrane. No fertile areas were found in the young stromata observed. No direct evidence of parasitism upon the host leaves of *Sapindus* sp. was found.

Pelicothallos gen. nov.

Description: Stroma lobed, setose, composed of laterally confluent radiate hyphae. Stroma may be ostiolate and/or may produce stalked conidiophores. Conidiospores round, hyaline; ascospores unknown.

Discussion: The genus *Pelicothallos* was established for this fossil form because no similar modern genus has been recorded. The stromata, composed of radiate and confluent rows of rectangular cells, are definitely referable to the Trichopelteae and appear to be closely allied with the fossil and modern forms of the genus *Trichopeltis*. The stromata are conspicuously setose (Pl. 14, figs. 110, 112, 113) and the means for both asexual and sexual reproduction may be present on one stroma. Thickened, specialized circular ostioles (Pl. 14, fig. 111) occur in *Pelicothallos*. There are no apparent fertile areas surrounding the ostioles as has been described for many modern and fossil forms of Trichopelteae (STEVENS, 1925).

Generitype: *P. villosus* sp. nov.

Pelicothallos villosus sp. nov.

Pl. 14, figs. 109—114

Description: Lobed irregularly shaped stroma 250—1400 μ long, lobes generally 50—150 μ wide x 300—400 μ long. Stroma consists of radiating, laterally united, elongate cells, 6—12 μ wide x 16—43 μ long, dichotomizing marginally. Lateral cell walls sinuous. Surface of stroma generally rugose or granular. Radiate nature of stroma most evident in lobes and margins; radiating cells often become obscure in the central portion and main body of the stroma. Sterile setae common on all stromata observed, 10 μ tapering to 2 μ wide x 100—250 μ long, blunt apices. Conidiophores 10 μ tapering to 7 μ wide x 50—180 μ long, present on large stromata, terminated by large spore-bearing heads 30—50 μ in diameter. Conidiospores round, single-celled, 16 μ in diameter, borne on specialized structures (sterigmata). Stroma polyostiolate; ostioles 10—15 μ in diameter, round, present in central area of stroma, surrounded by a ring of small cells. The ring of cells, 20—30 μ in diameter, 5—12 μ thick, composed of numerous small cells mounded up above the surface of the stroma. No spores present within the ostioles. No free hypbae associated with the stromata. Found on upper epidermis of *Chrysobalanus* sp. Syntypes: slide L.f. 87.

Discussion: Only a few stromata of *Pelicothallos villosus* were found in this investigation. Those found are easily identified by the setose nature of the stroma (Pl. 14, figs. 110, 112) and the granulose nature of the surface of the sinuous elongate cells (Pl. 14, fig. 113). The stroma is always irregularly lobed (Pl. 14, figs. 109, 112) and may bear conidiophores (Pl. 14, figs. 114, 115) and/or ostioles (Pl. 14, fig. 111). The ostioles are located in the center of the stroma and are quite different from the dark fertile areas of *Trichopeltinites*. No organized stroma cells are evident aronnd the ostioles or in the entire central areas of the large stromata observed. This may be the result of the sloughing off of the cells or the cells may be obscured by a gelatinous deposit secreted by the stroma. Such a secretion might produce, upon drying, the granular nature characteristic of the younger cells which may be easily observed near the margin of the stroma.

The stroma produces numerous setae (Pl. 14, figs. 112, 113) and may also produce conidiophores (Pl. 14, figs. 114—116). The conidiophores are not abundant. They consist of an elongated multicellular stalk with a terminal enlarged head. Several sterigmata (Pl. 14, fig. 116) are present on each head and each sterigma bears a single round conidiospore (Pl. 14, fig. 115). Germination of these conidiospores was not observed nor were any ascospores found in or near any of the ostioles.

Pelicothallos villosus is superficially similar to *Merismella* (Leptostromaceae). The stromata of *Merismella* consist of radiate sterile hyphae which produce setae and conidiophores. However it is non-ostiolate and the conidiophores produce several long septate conidia which break into 1-celled fragments. In these two respects the fossil form *P. villosus* differs from the imperfect form *Merismella.*

Stromata bearing both conidiophores and ostioles, as found in *P. villosus,* have not been previously reported in the Microthyriaceae. The attachment of the conidiophores to the stromata was very carefully checked and the conidiophores do arise directly from the marginal areas and lobes of the ostiolate stromata. The ostioles are located centrally in the stromata. Because both the perfect stage (ostioles) and the imperfect stage (conidiophores) are present in this fossil form it is placed in the Ascomycetes rather than the Deuteromycetes.

There is no direct evidence of parasitism of the host leaf *Chrysobalanus* sp. by *Pelicothallos villosus;* however the epidermal cells underlying the stromata often have thickened lateral walls (Pl. 14, fig. 109).

Brefeldiellites gen. nov.

Description: Hyphae produce a large, rounded, mostly confluent membrane which is radiately prosenchymatous, fan shaped with marginal fertile areas or ascomata conspicuous. Central ascoma cells break away as a dehiscence mechanism. Spores unknown.

Discussion: Cookson (1947) notes that no fossil forms have ever been recorded that belong to *Brefeldiella* or closely related genera. Upon a careful search of the literature no references to any fossil forms of this group were found. Thus this is the first report of this group in the fossil record. This fossil form is similar to the modern genus *Brefeldiella* but can not be placed in it because the spores are not known. Therefore the genus *Brefeldiellites* was established for forms similar to the modern genus *Brefeldiella* for which spores are unknown.

Generitype: *B. fructiflabella* sp. nov.

Brefeldiellites fructiflabella sp. nov.

Pl. 13, figs. 104—107

Description: Radiate stroma composed of radiating rows of hyphae laterally united to each other and the upper epidermis of the host leaf. Stroma 300—675 μ in diameter, consists of cuboidal to rectangular cells 2—4 μ wide x 3—7.5 μ long which radiate out from a central area and dichotomize thereby increasing the radiating rows of hyphae marginally. Margins of colonies fimbriate. Stroma hyaline except over the ascomata. Ascomata consist of hyphal cells 3—5 μ wide x 5—14 μ long which dichotomize as they radiate out and thus increase the number of radiating rows. Ascomata formed near margins of stroma, 125—150 μ wide x 100—130 μ long, dark, arch away from the surface of the leaf at maturity, fan shaped. A ring of dense cells 20—35 μ in diameter may be present appearing to form a definite ostiole. No spores found. Host leaf *Chrysobalanus* sp. Syntypes: slide L.f. 87.

Discussion: The stroma of *Brefeldiellites fructiflabella* is round and may be slightly lobed (Pl. 13, fig. 104). However because of the hyaline nature of the stroma, often only occasional dark marginal fruiting areas are evident making this form appear to consist of isolated fan-shaped ascomata. The hyaline nature of the sterile hyphae is characteristic of this form and not the result of poor preservation or preparation of

the fossil material since associated forms of other fungi and the fertile areas of this species have been subjected to identical conditions of preservation and preparation and are not transparent.

The stroma of *Brefeldiellites fructiflabella* spreads out radially over the upper surface of the host leaf, *Chrysobalanus* sp. The central cells are square to slightly rectangular while those cells nearer the margins are rectangular to elongate (Pl. 13, fig. 106). As seen in Pl. 13, fig. 107, the cells over fertile areas dichotomize frequently, producing new rows of cells as the stroma increases in diameter.

Fertile areas are always marginal (Pl. 13, fig. 108). They are fan shaped and conspicuously arched away from the surface of the host leaf. The hyphae are dark only in the fertile areas and change abruptly to hyaline hyphae in sterile portions of the stroma (Pl. 13, figs. 104, 108). The arched hyphae of a fertile area split apart and flake back at maturity exposing a ring-like ostiole held loosely in place by hyphal tissue inside the fertile area (Pl. 13, fig. 105). As the fertile areas age the outfoldings of the hyphae break away and the central ring-like ostiole is lost (Pl. 13, fig. 107). Eventually most of the darkened hyphae break away from the surface of the host leaf (Pl. 13, fig. 104). A marginal crescent of the fertile area often remains adhering to the host leaf when little other trace of this fungus remains (Pl. 13, fig. 104).

The Trichopelteae are among the most abundant and common of all fossil fungi found in this investigation. They were found on several species of *Sapindus* leaves and also on *Chrysobalanus* sp. and were associated at least once with most of the other types of fungi described in this study. As a result of the large number of stromata of Trichopelteae which were encountered a large amount of variation (ecological and inherent) was incorporated into the four genera and species described for this subfamily.

Such variable forms as mature stromata, immature stromata, stromata with free hyphae, stromata without free hyphae, diminutive stromata, stromata with seta bases, stromata lacking seta bases, fertile stromata, and sterile stromata are all included in the one species *Trichopeltinites fusilis* since all the variant types are either connected to, associated with or gradational into each other. *Trichopeltinites fusilis* may in fact consist of more than one species, in the sense of modern mycological taxonomy, but since no clear boundaries could be established in this fossil material it was placed in a single species. The other forms of the subfamily Trichopelteae found in this investigation can be easily distinguished from *Trichopeltinites fusilis*. In *Trichopeltina exporrecta* the free hyphae are much more evident and persistent and the stromata are smaller and often consist of randomly orientated hyphal cells proliferated by the free hyphae. *Pelicothallos villosus* can be distinguished by its setose stromata and *Brefeldiellites fructiflabella* by its large round stromata consisting of sterile hyaline hyphae and conspicuous marginal ascomata.

Family: Micropeltaceae

Subfamily: Haplopeltoideae

Haplopeltis Theissen, 1914a

Haplopeltis mucoris sp. nov.
Pl. 15, fig. 117

Description: Fruiting body more or less round, 50—100 μ in diameter, not radiate, conspicuously raised above the surface of the host leaf, ostiolate. Ostioles 7—15 μ in diameter, prominent, central, round, surrounded by a ring of small (3—5 μ in diameter) cells. Fruiting body pseudoparenchymatous, cells 2—8 μ in diameter, margins not radiate, entire. No free hyphae present. No spores known. Found on the upper surface of *Chrysobalanus* sp. Syntypes: slide L.f. 87.

Discussion: Only a few fruiting bodies of *Haplopeltis mucoris* are known (Pl. 15, fig. 117). No free hyphae either above or below the epidermis are connected to the fruiting bodies. Some almost evanescent

hyphae are present around the base of these forms but no connection can be determined. There is no evidence of parasitism of the host leaf.

Fruiting bodies consist of pseudoparenchyma. Each fruiting body has one more or less round central ostiole which is encircled by a ring of small cells. This small circle of cells extends slightly above the surface of the fruiting body. The entire fruiting body mounds up away from the surface of the leaf so that when the surface of the fruiting body appears in sharp focus under the microscope the margins drop out of focus abruptly. No spores were found.

Only one modern species, *H. bakeriana* (REHM) THEISS., has been described in this genus. It was originally described as *Myiocopron bakeriana* by REHM (1913) upon branches of *Passiflora quadrangularis* from the Philippine Islands and later transferred to the genus *Haplopeltis* by THEISSEN (1914). This fossil form, *H. mucoris*, is the only record of this genus from North America. No fossil forms of this genus have been reported previously.

Microthyriella HÖHNEL, 1909

Microthyriella fungosa sp. nov.
Pl. 15, figs. 118—120

Description: Stroma 35—200 μ in diameter (one small fragment 23 μ in diameter was found), more or less round with irregular margins superficial, consists of irregularly arranged pseudoparenchymatous cells 5—12 μ in diameter. No primary ostioles present; numerons pores observed in all stromata. Pores circular to oval, 2.5—5 μ in diameter, present in many of the individual stroma cells, most often occur near margins of the cells. No free hyphae associated with the stromata. No spores found. Found on the upper epidermis of *Sapindus* sp. Syntypes: slide L.f. 77.

Discussion: *Microthyriella fungosa* fits the generic description of *Microthyriella* well; it lacks an ostiole, has no free hyphae, and consists of irregularly arranged pseudoparenchymatous cells. It is similar to *Microthyriella hibisci* STEVENS (1925). Both *M. hibisci* and *M. fungosa* differ from other species in this genus in that they have "secondary ostioles" or pores; however *M. hibisci* has both "primary" and "secondary ostioles". Most members of the Microthyriella have neither "primary ostioles" nor "secondary ostioles" (pores) but break open in an irregular fashion at maturity in order to release their spores. The numerous pores of *M. fungosa* are similar to the "secondary ostioles" of *M. hibisci*. The numerous pores present in the stromata of *M. fungosa* may or may not represent functional ostioles but they are in fact pores in the cells of the stromata; no other dehiscence mechanism was observed in any of the material of this species examined.

The stromata have irregular margins and assume an irregnlar round shape (Pl. 15, figs. 118, 120). Individual pseudoparenchymatous cells are irregularly arranged and have no superficial hyphal cells associated with them. Some subepidermal hyphae were found associated with one large stroma. But since no definite connection could be established between the two and since no subepidermal hyphae were found associated with the other stromata observed these hyphae are probably unrelated to the stroma.

Subfamily: Stomiopeltoideae

Stomiopeltis THEISSEN, 1914a

Stomiopeltis plectilis sp. nov.
Pl. 15, figs 121—124; Pl. 16, figs. 125—128

Description: Mature fruiting body 100—210 μ in diameter, more or less round, not radiate. Irregular central ostiole present. Fruiting body composed of several layers of hyphae resulting in a slightly convex overall shape. Hyphae of the fruiting body produce inordinately arranged plectenchyma of sinuous,

irregularly lobed cells. Lower layers of hyphae and marginal hyphae also plectenchymatous. Hyphal cells in the fruiting body 1.5—3 μ wide x 4—25 μ long. Margins generally not entire. Free hyphae somewhat sinuous, loosely reticulate, extending out from the margin of the fruiting body; free hyphal cells 1.5—3 μ wide x 15—30 μ long. No asci or spores found. Free hyphae and fruiting bodies limited to lower epidermis of the host leaf. Central portion of fruiting body frequently flakes away from the host leaf after maturity, leaving the marginal portion and free hyphae attached to the leaf. No evidence of parasitic action by this form on host leaf, *Sapindus* sp. Syntypes: slides L.f. 33 and L.f. 226.

Discussion: Several fruiting bodies of *Stomiopeltis plectilis* in varying stages of development were found. Young fruiting bodies are very irregular in outline (Pl. 15, fig. 123) and appear to be formed by a proliferation of cells from the free hyphae (Pl. 15, figs. 123, 124). This is similar to the manner of ascocarp formation described by LUTTRELL (1946) for *Stomiopeltis polyloculatus*. Proliferating hyphae of *S. plectilis* lack radial arrangement except occasionally along the margin (Pl. 16, fig. 125). The young fruiting bodies (Pl. 15, figs. 123, 124) are smaller, not as "well-rounded" nor completely "filled-in" as the mature forms (Pl. 15, fig. 121; Pl. 16, fig. 125), and lack ostioles. As the fruiting body matures it increases in diameter (up to 210 μ), an irregularly shaped ostiole develops centrally, and the fruiting body becomes slightly elevated above the surface of the leaf, probably as a result of the formation of the hymenium. Some post mature forms were found in which the central portions of tbe fruiting bodies had flaked away and only the marginal portions and the free hyphae remained attached to the lower epidermis of the leaf (Pl. 16, fig. 128).

Stomiopeltis citri BITANCOURT (1934) is the only modern species for which imperfect as well as perfect stages are known. In *S. citri* ascocarps are 140—200 μ in diameter and pycnidia are 80—150 μ in diameter. No ascospores or pycnidiospores have been found associated with any of the fruiting bodies of *S. plectilis*. As there is a large variation in the size of the fruiting bodies of *S. plectilis* (100—210 μ) it can not be determined whether all forms represent developmental stages of ascocarps or whether the smaller forms are pycnidia and the larger forms ascocarps. However, since the smaller fruiting bodies are flat (lack hymenial development), only loosely formed, and lack ostioles, they appear to be immature and it is more probable that they are immature ascocarps than diminutive pycnidia.

Both LUTTRELL (1946) and BATISTA (1959) used ascocarp and ascospore size as a major criterion in distinguishing the various species of *Stomiopeltis*. LUTTRELL recognized 7 species, most of which are tropical, and BATISTA included 5 additional tropical species in his monograph of the Micropeltaceae. The genus *Stomiopeltis* maintains the predominately tropical nature of the Micropeltaceae.

S. plectilis was found only on the lower epidermis of *Sapindus* sp. According to LUTTRELL (1946) *Stomiopeltis aspersa* is the only moderu species that is limited to the lower epidermis of leaves of its host plant, a species of Lauraceae from India. Other modern species may occur on the upper epidermis of the host leaves or on the stems, or may lack any specific hahitat on the host plant. Some modern species of *Stomiopeltis* have specific hosts while others are not specific to a host species, genus, or family.

There is little evidence of any parasitic action by *S. plectilis* on the host leaves either by the free hyphae or the fruiting bodies. The only type of parasitism observed was the infection (apparent entering) of a few stomata and hair bases by free hyphae. No haustorial processes or any haustorial penetration in the epidermis of the host leaf was found.

Plochmopeltidella MENDOZA in STEVENS and MANTER, 1925

Plochmopeltidella antiqua sp. nov.

Pl. 16, figs. 129—134

Description: Fruiting body 50—75 μ in diameter, more or less round, not radiate, non-ostiolate, lacks well-defined margin, may be setose. Fruiting body composed of interwoven, irregularly lobed, inordinately arranged cells, 1—2.5 μ wide x 5—15 μ long. Conspicuons free hyphae anastomose over surface

of leaf. Free hyphae sinuous, setose; hyphal cells 1.5—3 μ wide x 12—25 μ long. Setae 1.5—2.5 μ wide x 15—85$^{+}\mu$ long, multicellular (3—5 cells), usually of uniform width. Setae arise directly from free hyphae. Germinating spore 4.5 μ wide x 14 μ long, 1-septate, fusiform, constricted, psilate, attached to free hyphae. Hyphae produced from both ends of cells of the spore. Found on lower surface of *Sapindus* sp. Syntypes: slide L.f. 170.

Discussion: CLEMENTS and SHEAR (1931) put *Plochmopeltidella* in synonymy with *Chaetopeltopsis;* however BATISTA (1959) revalidated the genus *Plochmopeltidella,* differentiating it from *Chaetopeltopsis* on the basis of the absence of an ostiole and the presence of setae. Thus this fossil form was assigned to the genus *Plochmopeltidella* as described by MENDOZA (STEVENS and MANTER, 1925) and revalidated by BATISTA (1959). No ostioles or suggestion of the formation of any spore dehiscence mechanism was found in any of the material examined. Ascocarps consist of a more or less uniformly plectenchymatons network of cells (Pl. 16, figs. 129—131). Setae and seta bases are present but not abundant on the ascocarps and free hyphae (Pl. 16, figs. 129—132, 134); setae associated with the ascocarps are not as well preserved as those associated with the free hyphae. Setae are multicellular and vary considerably in length; the maximum length cannot be determined however since the longer setae are not entire (Pl. 16, fig. 134).

Often free hyphae cross over and extend out from the surface of the ascocarps forming a loose anastomosing network over the lower surface of the leaf (Pl. 16, fig. 129). The free hyphae often follow the lateral walls of the epidermal cells "outlining" many of the epidermal cells and guard cells. However only a few cases of infection through the stomata by the free hyphae were noted.

No asci were observed in the fossil material but a germinating spore was found still attached to hyphae that were confluent with the anastomosing network of free hyphae (Pl. 16, fig. 133). Since this spore is in such direct association with the free hyphae of *P. antiqua* there is little question of its affinity to that species.

Two modern species have been described in this genus, *Plochmopeltidella smilacina* MENDOZA and *P. gelsemiae* BATISTA and COSTA, both known from the tropical areas of South America. Size is the principal characteristic used by BATISTA (1959) to distinguish *P. gelsemiae* from *P. smilacina. P. antiqua* is similar in all respects to the two modern species except that it is somewhat more diminutive than the smaller of the two, *P. smilacina.* The size difference found in the ascocarps of the three species of this genus could be the result of differences in growth stages; however the differences in the sizes of the ascospores, setae, and hyphal cells do not appear to be growth stages but distinctive species characters.

Shortensis gen. nov.

Description: Colonies epicuticular. Free hyphae dichotomize frequently. Ascocarp round, consists of numerous irregularly arranged pseudoparenchymatons cells, margins sometimes radiate. Ascocarp has one central ostiole; no specialized cells surround ostiole. Pycnidium diminutive, otherwise identical to ascocarp. Ascospores 2-celled (1-septate), composed of a small hyaline cell and a large non-hyaline cell; pycnidiospores single-celled, ovate to elliptical.

Discussion: The genus *Shortensis* is established here for species of the genus *Manginula* for which perfect stages are known. Only one species, *Manginula perseae,* has heen described. The genus *Manginula* was established in 1918 by ARNAUD for a form of epiphyllous fungi about which ARNAUD wrote: " . . . le type est extrêment remarquable par les caractères de son mycélium, par sa haute différenciation, n'a pas d'analogue chez le champignons." In his study of the Asterinaceae ARNAUD examined numerous leaves from the Herbier Cryptogamique de Muséum d'Histoire naturelle de Paris. He found sterile mycelia and pycnidia on leaves of *Perseae palustris* from Green Cove, Florida, and sterile mycelia on unidentified coriaceous leaves from Puerto-Zamuro in the area of the upper Orinoco River in Venezuela which he assigned to the genus *Manginula.* The only description ARNAUD gives of the "ascostroma" is that it is light colored and subcuticular. He does not mention either asci or ascospores nor does he illustrate any perfect stage for the genus. He classified *Manginula* on the basis of the mycelial and pycnidial material he had at his disposal and in-

cluded it in the Fungi Imperfecti. AINSWORTH and EISBY (1950) included *Manginula* in the Sphaeropsidales, an order of Fungi Imperfecti that reproduce by means of conidia borne in pycnidia. CLEMENTS and SHEAR (1931) put this genus in the form family Leptostromataceae in which the pycnidia are shield-shaped or elongate and flattened. Since perfect as well as imperfect stages are known for the fossil material described here this fungal form is placed in the new genus *Shortensis* in the family Micropeltaceae (subfamily Stomiopeltoideae) in the Ascomycetes.

Generitype: *S. memorabilis* sp. nov.

Shortensis memorabilis sp. nov.

Pl. 17, figs. 135—137; Pl. 18, figs. 138—144; Pl. 19, figs. 145—151; Pl. 20, figs. 152—159; Pl. 21, figs. 160—161

Description: Epicuticular colonies 90—450 μ in diameter, may originate from germination of a 2-celled spore. Initial hyphal cell produces hyphae in two opposite directions. Hyphae dichotomize at short intervals, forming an anastomosing network. Angles of dichotomies become progressively narrower distally in the colonies. Hyphal cells 3—6 μ wide x 6—24 μ long. Lateral hyphal walls thin, slightly sinuous; end walls markedly thickened. Incomplete septations apparent in end walls. Lateral walls often disintegrate leaving persistent, conspicuous end walls. Hyphopodium-like lateral branches most often unicellular, occasionally multicellular, arise medially from hyphal cells, may be unilateral, alternate, or opposite. Evidence of haustorial penetration of the host leaf present in several of the hyphopodium-like branches. Hyphal cells occasionally parasitize host leaf directly. Reproductive multicellular lateral branches also produced by hyphal cells. Both hyphopodium-like and reproductive lateral branches consist of cells shorter and wider than the hyphal cells, 6—17 μ wide x 5—15 μ long. Fruiting body formed by irregular proliferation of cells from short reproductive lateral branch or, rarely, by a medial hyphal cell. Mature fruiting body composed of dense mass of randomly orientated hyphal cells, often hyphae radiate out in all directions from margin. At maturity the center of the fruiting body arches away from the host leaf and a distinct ostiole develops. Two types of fruiting bodies occur: 1) Large fruiting body (ascocarp) 88—150 μ in diameter in which 2-celled spores occur. Spores are 5—10 μ wide x 11—14 μ long composed of two unequal cells, a smaller hyaline cell 2.5—3.5 μ wide x 2.5—3.5 μ long and a larger brown cell 6—8 μ wide x 8—12 μ long often encircled by a conspicuous hyaline band. 2) Smaller fruiting body (pycnidium) 48—110 μ in diameter in which single-celled spores occur. Spores are 2—3 μ wide x 6—7 μ long, brown with no hyaline band evident. Found on upper and lower surface of *Sapindus* sp. and *Chrysobalanus* sp. Syntypes: slides L.f. 32, L.f. 60, L.f. 87, and L.f.240.

Discussion: *Shortensis memorabilis* is one of the most common and conspicuous fungi found in this investigation (Pl. 17, fig. 135). The colonies observed had all developed from a 2-celled spore similar to those found in many of the mature fruiting bodies (Pl. 20, fig. 158; Pl. 21, figs. 160, 161). These spores consist of two unequal cells, one small hyaline cell and a larger brown cell which often has a conspicuous hyaline band around it (Pl. 20, figs. 157—159). Upon germination a haustorial process breaks through the thin hyaline area of the larger cell of the spore (Pl. 20, fig. 158) and penetrates the surface of the host leaf. Eventually the entire "cap" of the spore above the hyaline band breaks away and a large irregular haustorium protrudes from the open end of the large cell of the spore (Pl. 21, fig. 161). The small hyaline cell of the spore develops into the initial hyphal cell which produces a terminal hypha and an obliquely disposed lateral hypha in opposite directions (Pl. 21, fig. 161). The central portion of the larger cell of the spore with its protruding haustorial process remains attached for some time and appears as an appendage to the two initial hyphae of the colony (Pl. 21, fig. 160). These hyphae branch dichotomously at irregular intervals, first forming broad-angled dichotomies and later much narrower-angled dichotomies (Pl. 17, fig. 135). The dichotomies vary from pseudodichotomies (a hyphal cell simply branches and bends at the branch) (Pl. 18, fig. 143; Pl. 21, fig. 160) to true dichotomies (two dichotomously arranged branches arise from a single hyphal cell) (Pl. 18, fig. 140; Pl. 19, fig. 145; Pl. 21, fig. 160). These two types of dichotomies are commonly found scattered throughout a single colony. *Shortensis memorabilis*, as a result of its dichotomizing hyphae, spreads

over the surface of its host leaf forming large round colonies 90—450 μ in diameter (Pl. 17, fig. 135). The numerous peripheral hyphae anastomose freely with hyphae of their own (Pl. 17, fig. 135) and adjacent colonies (Pl. 17, fig. 137).

Shortensis memorabilis is not limited to a specific fossil host plant but was found on several species of *Sapindus* and on a single species of *Chrysobalanus*. The mycelia and fruiting bodies of colonies found on *Sapindus* sp. were all similar (Pl. 17, figs. 135, 136); however the colonies observed on *Chrysobalanus* sp. were somewhat different in their general appearance (Pl. 18, fig. 138). Small colonies occur only on the lower epidermis of *Chrysobalanus* sp. and the mycelia are much less well-developed, rarely dichotomizing and anastomosing. The fruiting bodies are often somewhat lobed and very conspicuously arched away from the host leaf and the ostioles are conspicuously raised above the level of the fruiting bodies (only asexual fruiting bodies are known on this host) (Pl. 20, fig. 153). Colonies are most abundant on the upper epidermis of the host leaves of *Sapindus* sp.; however the hyphae often grow over the edge of the leaf onto the lower epidermis. A few colonies were found which had developed from germinating spores to maturity on the lower epidermis of *Sapindus* sp.

Shortensis memorabilis is often found in close association with several other microthyriaceous forms (Pl. 5, fig. 37) but no parasitic relationship appears to exist between them.

The hyphal cells are often characterized by thin lateral walls and thick conspicuous end walls (Pl. 18, figs. 138, 139, 143); the end walls of the hyphae are 2—4 times thicker than the lateral walls. Pores .25—.5 μ in diameter are easily seen in the end walls of the hyphal cells indicating that the end walls are actually incomplete septations, a characteristic of the Ascomycetes (Pl. 18, fig. 139). When the hyphae are first formed the lateral walls are extremely delicate and often the only remaining evidence of the young hyphae are the thickened end walls of the hyphal cells. In the older hyphae of the colonies both the end walls and the lateral walls become slightly thicker and the lateral walls are somewhat more persistent. The parts of the lateral wall immediately adjacent to the end walls may thicken more than the center of the lateral wall and thus characteristic — and H configurations persist for some time on the surface of the host leaf when a mycelium disintegrates (Pl. 18, fig. 139; Pl. 19, fig. 149).

Hyphopodium-like cells frequently arise at right angles from the lateral walls of the hyphae and are scattered unilaterally, alternately, or oppositely along the length of the hyphae. A hyphopodium originates as a bulge in the lateral wall of a hyphal cell (Pl. 18, fig. 140). The bulge enlarges, "pinching" in at its base to form an incomplete septation and a thickened end wall. Most hyphopodia are single-celled, although a few multicellular hyphopodiate branches were found (Pl. 18, figs. 140—144). The hyphopodia are much wider (6—17 μ) than the hyphal cells (3—6 μ). The single-celled hyphopodia are bell shaped (Pl. 18, figs. 140—142). Each is attached by a narrow (3—6 μ) incomplete septation to a lateral cell wall of the hyphae and widens to a broadly rounded, 10—17 μ wide, irregularly lobed and flattened cell. Hyphopodial cell walls are thickened near the base of the hyphopodia but taper to very thin, often poorly preserved cell walls near the broadly rounded tips of the hyphopodia.

Conspicuous pores 1—1.5 μ are present in some of the epidermal cells that are in direct contact with some of the hyphopodia (Pl. 18, fig. 141). The pores are surrounded by a thickened ring of material which appears to be of fungal origin. Unlike *Meliola*, in *Shortensis memorabilis* more than one haustorium may penetrate a single epidermal cell of the host leaf. Evidence of intercellular hyphal or haustorial processes is frequently present in the epidermal cells of the host leaf over which the hyphae and hyphopodia are closely adpressed (Pl. 18, fig. 144; Pl. 19, fig. 145). These haustorial processes proceed from the cells originally penetrated by a haustorium of a hyphopodium through the lateral epidermal cell wall to numerous other epidermal cells of the host leaf. The haustorial processes (haustorial sheaths) are located on the inner surface of the exterior wall of the epidermal cells. They are byaline, branch freely within each epidermal cell, and have sinuous lateral walls and irregular dichotomies. The intercellular haustoria vary in their general appearance and nature from cell to cell within a single host leaf. Similar evidence of haustorial processes has also been found associated with hyphae of other fossil epiphyllous fungi.

Multicellular branches consisting of wide cells, similar to the cells of the few multicellular hyphopodiate branches observed, arise at right angles to the hyphae and function in the production of fruiting bodies. Medial hyphal cells also occasionally produce fruiting bodies directly. Two types of fruiting bodies are known; the development of hoth types appears to be identical. A hyphal cell produces a short (4 –10 celled) lateral branch (Pl. 18, figs. 142, 143; Pl. 19, fig. 145). This branch then produces numerous secondary lateral branches (Pl. 19, figs. 146, 147). These secondary lateral branches grow out in all directions and may branch again. The cells in the resulting complex are wide, square to slightly rectangular, and closely appressed to one another. This sheet of cells spreads radially over the surface of the host leaf (Pl. 19, figs. 147—149). At the same time the older cells in the fruiting body undergo several successive divisions which divide the original cells into numerous (3—12) smaller angular cells (Pl. 19, figs. 150, 151). As the fruiting body matures these divisions proceed toward the margin of the radial sheet of cells. Small pores are often formed in the upper surface of the fruiting bodies near the lateral margins of the numerous newly formed angular cells (Pl. 19, figs. 150, 151). These pores are formed randomly over the surface of mature fruiting bodies; their function is not known. Also as the fruiting body matures the center arches away from the surface of the host leaf and the centralmost cells disintegrate leaving a prominent opening or ostiole (Pl. 17, fig. 136; Pl. 18, fig. 138; Pl. 19, fig. 148; Pl. 20, fig. 152). In a mature fruiting body the radiating hyphal cells also often disintegrate while the end walls persist, encircling the fruiting bodies in a very characteristic pattern (Pl. 17, fig. 135; Pl. 19, fig. 149). Frequently fruiting bodies appear to have no direct connection to any free hyphae (Pl. 17, fig. 136). This is the result of hyphal disintegration (Pl. 18, fig. 139; Pl. 19, fig. 147) which leaves the more resistant fruiting bodies isolated upon the surface of the host leaf.

The two types of fruiting bodies are distinguished by size and spore type. In one group the fruiting bodies are large, 88—150 μ in diameter, and 2-celled spores are found (Pl. 20, figs. 157—159). In the other group the fruiting bodies are smaller, 48—110 μ in diameter, and unicellular spores are found within them (Pl. 20, figs. 152—156). In several genera of the Microthyriaceae ascospores are 2 or 3 celled while pycnidiospores are unicellular; e. g. in *Asterina* the asco pores are 2 celled aud the pycnidiospores are single celled. In *Asterina* the ascocarps and pycnidia are identical except for the diminutive size of the pycnidia. Therefore it is probable that in *Shortensis memorabilis* also the larger fruiting bodies are ascocarps, the 2-celled spores are ascospores, the smaller fruiting bodies are pycnidia, and the single-celled spores are pycnidiospores.

Germination and development of a colony from these 2-celled ascospores has already been described. The ascospores are frequently oriented within the ascocarp with the larger banded cell of the spore towards the ostiole (Pl. 20, fig. 157). The number of ascospores found within an ascocarp varies from 1, when most have been released, to 50 or 60, when few have been released. The pycnidiospores are oval to nearly rectangular in outline and are oriented in chains (Pl. 20,fig. 153), end to end, within the pycnidium. A pycnidiospore produces a germinal tube near one end on the surface of the spore adjacent to the host leaf (Pl. 20, figs. 154—156). The germinal tube penetrates the surface of the host leaf but no further growth of pycnidiospores was observed.

ARNAUD's original description in 1918 of the single species *Manginula perseae* still stands as the only record of this genus except for the present report of *Shortensis memorabilis* for which both the perfect and imperfect stages are known. On the basis of the perfect stage in this fossil form, it is placed in a new genus, *Shortensis*.

The modern form *Manginula perseae* and the fossil form *Shortensis memorabilis* are similar in general habitat, in appearance, and in pycnidial and mycelial characteristics. However there are important differences between the two forms which justify a species distinction. In *M. perseae* the mycelia, hyphopodia, and pycnidia are subcuticular; in *S. memorabilis* they are epicuticular. The hyphae of *M. perseae* consist of light long cells alternating with short darker cells which give rise to "stiginopodia" (hyphopodia); this regular arrangement and color of hyphal cells was not observed in the fossil material. Pseudo- to true hyphal dichotomies are characteristic of *S. memorabilis* while ARNAUD stated that only pseudodichotomies are pres-

ent in the hyphal branching of *M. perseae*. Distinct ostioles are found in *S. memorabilis*. ARNAUD illustrated a large irregular opening in a mature pycnidium of *M. perseae*. The pycnidiospores also differ in size and banding; *M. perseae* has large (6—7 μ wide x 11—12 μ long) banded pycnidiospores while those of *S. memorabilis* are smaller (2—3 μ wide x 6—7 μ long) and are not banded.

Subfamily: Dictyopeltoidea

Dictyotopileos gen. nov.

Description: Stroma large, round to linear, polyostiolate, radiate under a reticulate covering of hyphae. Free hyphae present. Spores not positively identified.

Discussion: The genus *Dictyotopileos* is established for several stromata which appear to be parasitic upon the upper epidermis of *Chrysobalanus* sp. The large size (300—600 μ in diameter) and polyostiolate and reticulate nature of the stroma of this genus set it apart from any other genus in the Dictyopeltoideae and the entire Micropeltaceae. Free hyphae and spores were found associated with this form but cannot be positively assigned to it.

Generitype: *D. yalensis* sp. nov.

Dictyotopileos yalensis sp. nov.

Pl. 21, figs. 162—166; Pl. 22, figs. 167—171

Description: Superficial stroma may be round, lobed, 300—600 μ in diameter, or elongate, lobed, 300 μ wide x 650 μ long. Subiculum granular, sometimes appearing radiate, with reticulate cover of anastomosing hyphae, 1.5—3 μ wide x 10—35 μ long, which forms numerous ostioles. Reticulate hyphal covering may be poorly preserved or, in older stromata, missing. In disintegrated stroma, remnants of basal portion of subiculum show a radiate or fan pattern produced by the laterally united hyphae of the subiculum. Ostioles 5—10 μ in diameter surrounded by a ring, 12—18 μ in diameter, of numerous thick-walled cells 2—4 μ in diameter. Ostioles are frequently surrounded by remnants of the reticulate covering of the stroma. Free hyphae rarely persist, when present extend from margins of stroma anastomosing in an irregular fashion over the surface of the host leaf. Free hyphal cells 1.5—3 μ wide x 15—50 μ long, may radiate from margins of stroma singly or may arise from a group of thickened marginal cells. A few spores (ascospores?) 5 μ wide x 6.5 μ long, single celled, dark, eliptical, psilate, found in one ostiole. Conidiospores 5 μ wide x 11.5 μ long, 4 celled, found attached to hyphae at the margin of one stroma. Found on the upper epidermis of *Chrysobalanus* sp. Syntypes: slide L.f. 87.

Discussion: A few stages of ostiole development were observed in the different specimens of *Dictyotopileos yalensis* examined. Young ostioles are composed of a mass of thick-walled cells which completely cover the fertile areas of the stroma and are surrounded by and intimately associated with the reticulate hyphal cover of the stroma (Pl. 21, fig. 164). As the ostiole matures the central cells in these fertile areas and the hyphae are sloughed off until only a small ring of thickened cells remains (Pl. 21, fig. 165). A stroma may have from one to several fertile areas or mature ostioles (Pl. 21, fig. 162). The ostioles always occur within the central area of the stroma and are never marginal.

The subiculum or compact mycelium underlying the reticulate network is extremely granular in appearance (Pl. 21, figs. 164, 165) and a radiate cellular pattern is evident only near the margins (Pl. 21, fig. 163) or in old stromata in which only the basal remnants of the subiculum remain (Pl. 22, fig. 168). When discernable these subicular cells are radially arranged and closely appressed to one another laterally (Pl. 22, fig. 168).

Free hyphae extend out in all directions from the margins of the stromata. However in older stromata the free hyphae are often evanescent and may not be evident. In nearly all stromata observed the free hyphae extend from specific areas of the margin which contain clusters of small thick-walled cells (Pl. 22, figs

168, 169) and anastomose over the upper surface of the host leaf as it extends out from the stroma (Pl. 22, fig. 170). The nature of the hyphae may vary slightly as they grow over the surface of the leaf. As shown in Pl. 22, fig. 170 the free hyphae may be very similar to the hyphae of the reticulate cover of the stroma (Pl. 21, fig. 166) or may be somewhat more robust. No appendages are present on the hyphae nor do any haustoria appear to penetrate the surface of the host leaf from either the hyphae or the stroma. However dark infected areas in the epidermal cells are often associated with both the free hyphae (Pl. 22, fig. 170) and the stromata; these areas may result from the parasitic action of this fossil form.

A few single-celled spores were found within an ostiole of one stroma (Pl. 22, fig. 167). Since so few spores of this form were found associated with *Dictyotopileos yalensis* and since those found were present so near the opening of the ostiole, they must be regarded as possible contaminants and can be only tenuously accepted as ascospores belonging to this form. Also a few conidiospores were found associated with the stromata of *D. yalensis* (Pl. 22, fig. 171); but these 4-celled conidiospores must be seriously qnestioned. They are associated with the hyphae which form a reticulate covering over the stroma and might be an imperfect form which is simply associated with the reticulate covering. Such conidiospores are not described for any other member of this subfamily.

Order: Moniliales

Family: Tuberculariaceae

Patouillardiella Spegazzini. 1889

Patouillardiella imbricata sp. nov.

Pl. 22, figs. 171—174; Pl. 23, fig. 175

Description: Fruiting body 50—90 μ in diameter, more or less hemispherical, superficial, composed of compact mass of conidiospores. Conidiospores radiate out from center of conidial mass. Conidiospores closely packed, imbricate, 3.5—4.5 μ wide x 13—19 μ long, 1-septate (2-celled), fusoid. Hyphae and conidiophores poorly developed, inconspicuous or possibly obsolete. Found on the upper epidermis of *Chrysobalanus* sp. Syntypes: slide L.f. 87.

Discussion: Hemispherical masses of conidiospores were found on the upper surface of *Chrysobalanus* sp. These fruiting bodies consist of hundreds of conidiospores radiating out from a common center and overlapping one another like shingles of a roof (Pl. 22, figs. 172, 174). Because the spores are imbricate only the distal portion of most is exposed (Pl. 22, fig. 174; Pl. 23, fig. 175) making it difficult to establish the presence of a central compact sporodochium (compact mass of conidium-bearing hyphae) because the conidium-bearing hyphae are covered by overlapping conidia. It has not been established in *P. imbricata* whether the conidium-bearing hyphae are hidden by the imbricate conidia or if they are truly obsolete. The arrangement and attitude of the conidiospores suggest that they probably arise from short branched conidiophores. Both the Melanconiaceae and Tuberculariaceae have modern species with compact spore-bearing bodies and short or obsolete conidiophores. There is no evidence of any subtending basal stroma typical of the Melanconiaceae in this fossil material, thus it is more similar to the Tuberculariaceae which lack a basal stroma (Clements and Shear, 1931). Clements and Shear consider the Tuberculariaceae to be characterized by the evolution or reduction of the cottony conidium-bearing hyphae found in the Moniliaceae and Dematiaceae into a compact conidium-bearing mass or sporodochium. As *Patouillardiella imbricata* indicates, some of the more highly evolved and reduced forms in the Tuberculariaceae had their origins prior to or during the Eocene and have maintained themselves in this reduced condition over a considerable period of time. If the Tuberculariaceae are actually the result of an evolutionary reduction of the

Moniliaceae and Dematiaceae as CLEMENTS and SHEAR suggest, less specialized members of one of these families must have been present before Eocene times.

SACCARDO (1892) lists a single modern species of this genus, *Patouillardiella guaranitica* SPEG. F. PUIGG., which was found parasitic upon leaves of Sapindaceae in Brazil.

Family: Dematiaceae

Sporidesmium LINK, 1825[2])

Sporidesmium henryense sp. nov.
Pl. 23, figs. 176—181

Description: Hyphae superficial, straight, may branch oppositely, alternately, or unilaterally. Hyphal cells 3—6 μ wide x 20—35 μ long. Single-celled hyphopodia 6—9 μ wide x 5—10 μ long, alternate, unilateral, or opposite, located near the distal end of hyphal cells, occur at more or less regular intervals along the length of the hypha. Hyphopodia subhemispherical, rounded at apex. Prominent pores 1—1.5 μ in diameter present in lower surface of hyphopodia and incomplete septations evident in lateral walls where hyphopodia are attached. Conidiophores not abundant, arise singly, .5—1 μ wide at point of attachment on hyphae enlarging to 1.5—2 μ wide at point of attachment of conidiospores x 4—15 μ long. Conidiospores 2—3 septate, 4—6 μ wide x 11—14 μ long, dark, borne terminally on a single conidiophore. Conidiospores linearly arranged, eliptical, end rounded to more or less flat. Found on lower epidermis of *Chrysobalanus* sp. Syntypes: slide L.f. 87.

Discussion: Only a few specimens of *Sporidesmium henryense* were found (Pl. 23, figs. 176, 178). Most of the hyphae observed were devoid of conidiospores. However whenever the hyphae occured without conidiospores they could be identified by their characteristic hyphopodia. The hyphopodia have pores on the surface adjacent to the lower epidermis of the host leaf *Chrysobalanus* sp. (Pl. 23, fig. 177). Also incomplete septa are present between the hyphopodia and the hyphae and the individual cells of the hyphae (Pl. 23, fig. 177). These features are typical of the Ascomycetes, but since only conidiospores are known for this form it is placed in the Deuteromycetes.

Conidiospores are 2 to 3 septate and occur randomly along the length of the hyphae (Pl. 23, figs. 179—181). They project away from the surface of the host leaf and the hyphopodiate hyphae. There is no evidence of direct parasitism.

According to BARNETT's key to the genera of the Fungi Imperfecti (1960) this material should he placed in the genus *Clasterosporium* which has a single species *C. caricinum.* However MOORE (1958) states in discussing the *Sporidesmium* complex: "The fungus *C. caricinum* is specifically distinct on the hasis of producing hyphopodia, but on the basis of the conidia and their production the genus can only be synonymous with *Sporidesmium*, as typified by *S. atrum.*" On the basis of MOORE's study this fossil form is placed in the genus *Sporidesmium* with specific similarities to *Sporidesmium caricinum* (SCHW.) MOORE. *Sporidesmium caricinum* differs from this fossil form in several characters; *S. caricinum* has 1) irregularly shaped hyphopodia, 2) more abundant conidiospores, and 3) 3 to several celled (often 5—10 celled) conidiospores. Thus there does not appear to be a close natural relationship between this fossil form and *S. caricinum* but the basic similarities of the hyphopodiate hyphae and the conidiophores bearing an apical conidiospore link the two forms together in the genus *Sporidesmium.* This relationship may be entirely unnatural but serves as a useful taxonomic index to these forms until more is known about them.

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[2]) Spelling *Sporodesmium* frequently used (MOORE, 1958).

Parasitism

Of the numerous types of fungi described in this paper only a few species (viz. *Meliola anfracta, Meliola spinksii, Shortensis memorabilis,* and *Sporidesmium henryense)* show evidence of probable parasitic action. Haustorial pores are present in the hyphopodia of *Sporidesmium henryense* but there is no indication of infection in the host leaf. *Meliola anfracta, Meliola spinksii,* and *Shortensis memorabilis* produce hyphopodia which have haustorial pores in direct association with thickened pores in the epidermal cells of the host leaf. Remains of the characteristic haustoria of *Shortensis memorabilis* are frequently evident in the associated infected cells of the host leaf (Pl. 18, fig. 144; Pl. 19, fig. 145).

Shortensis memorabilis is the only fossil form described in this study for which a characteristic type of haustorinm was found. However various isolated evidences of infection that can not be related to any specific fungus were frequently found in the cuticular remains examined; these evidences confirm the parasitic nature of many of the fungi which infected these leaves. Frequently stomata of the host leaves are filled with hyphae as shown in Pl. 26, fig. 195. Epicuticnlar and subcuticular free hyphae or evanescent hyphae may be associated with the infected stomata. Large infected or injured areas involving the upper and lower epidermal cells and the mesophyll cells were occasionally fonnd (Pl. 26, fig. 196). The cells of the leaves, in such areas, are often small, thick walled, and irregularly shaped. They may be the result of mechanical damage to the leaf rather than the result of fungal infection, however loose hyphae are frequently found associated with them.

Persistent hanstorial sheaths were commonly found in many of the leaves examined. Various types of haustoria, probably belonging to various species of fungi, were found (Pl. 26, figs. 197—201). WOLF and WOLF (1947) note: "Haustoria vary in form among the different species of fungi, being spherical in the simplest forms and variously branched and lobulate in the most complex ones. Their size indicates conformity to that necessary to maintain a delicate nutritional balance . . . They possess a conspicuous sheath that is deposited by and is continuous with the host-cell wall, as generally believed." The fossil haustoria found in this study are very similar to forms of haustoria known for modern fungi.

Most of the fungi described in this investigation show no evidence of parasitism. LUTTRELL (1946) mentioned one such case in modern fungi; he found that the free hyphae of *Stomiopeltis polyloculatis* were entirely superficial and did not penetrate the host plant. Nevertheless he considered this fungus to be a parasite because it had no detectable means of nourishment other than the leaf upon which it was found. Since there is no way to determine whether the superficial epiphyllous fnngi described in this study derived their nourishment from the host leaf or from excretions or exudate of foreign animals or plants, they can not he considered true parasites. However it is probable that many of these fossil forms were true parasites. deriving their nourishment from the host leaf in a manner similar to *Stomiopeltis polyloculatis.*

Fossil Record of Epiphyllous Fungi

Epiphyllous fungi are not commonly found in the fossil record until the upper Cretaceous. Of the 145 genera of epiphyllous fossil fungi listed in Table 1, only 11 are pre-Cretaceous. Of these eleven, only five are genera of epiphyllous Ascomycetes *(Sphaerites, Rosellinites, Hysterites, Xylomites,* and *Excipulites).* These genera were established upon soperficial similarities between the fossil material and modern genera. SEWARD (1898) wrote of one of the genera:

> Some examples of possible Ascomycetous fungi have been recently recorded by POTONIÉ from leaves and other portions of plants of Permian age. There is a distinct superficial resemblance between the specimens he figures and the fructifications of recent Ascomycetes, but in the absence of internal structure, it would be rash to do more than suggest the probable nature of the markings he describes. For one of the fungus-like impressions POTONIÉ proposes the generic name *Rosellinites;* he compares certain irregularly shaped projections on a piece of Permian wood with the perithecia of *Rosel-*

linia, a member of the Sphaeriaceae, and describes them as *Rosellinites Beyschlagii* POT. Various other records of similar Ascomycetes-like fossils may be found in palaeobotanical literature, but it is unnecessary to examine these in detail. Unless we are able to determine the nature of the supposed fungus by microscopical methods our identifications cannot in most cases be of any great value.

No precise identifications based upon microscopic studies have been made for epiphyllous Ascomycetes from pre-Cretaceous sediments. The tenuous identifications of pre-Cretaceous epiphyllous fungi are of little botanical value and should be seriously questioned. Numerous questionable identifications have also been made from post-Cretaceous sediments, however many of the more recent reports are based upon reliable microscopic studies.

Of all the orders of epiphyllous fuugi listed in Table 1 the Microthyriales are the most reliably identified in the fossil record. All of the genera listed under this order are known from detailed microscopic studies. The oldest known microthyriaceous fungi were found in the Laramie coal (upper Cretaceous) of South Park, Colorado (L. R. WILSON, personal correspondence). Several genera similar to modern forms of the Microthyriaceae and Micropeltaceae are recorded on a variety of host leaves from widely separated areas of the world. Since the earliest reported microthyriaceous epiphyllous fungi are from the upper Cretaceous, this group probably had its origin during the early or middle Mesozoic; by Eocene times microthyriaceous fungi have a fairly modern aspect.

The evolutionary development of microthyriaceous epiphyllous fungi may have accompanied the rise and spread of the angiosperms. At present there is no evidence to indicate whether they arose as epiphytes upon the pre-angiosperm floras of the world and later adapted to angiosperm hosts or arose in direct association with the early angiosperms. Both fossil and modern forms of microthyriaceous fungi occur on gymnosperm as well as angiosperm hosts.

The fossil records of most of the other orders of epiphyllous fungi listed in Table 1 are open to serious question and reports of many of the genera should not be fully accepted until a careful re-evaluation of the original material is made. Therefore few valid conclusions concerning their origin and evolution can be reached.

There are several reports of epiphyllous fungi from the Carboniferous. A seemingly reliable Carboniferous specimen of *Urophlyctites* is the only epiphytic phycomycete reported in the fossil record. Other Carboniferous forms of epiphyllous fungi, although questionably identified, suggest the early presence of an epiphyllous habit for many fungi. This epiphyllous habit seems to have been well developed in all the classes of fungi hy the end of the Carboniferous.

There are only a few scattered reports of epiphyllous fungi from the late Cretaceous. However by the Eocene epiphyllous fungi are abundant and have a modern aspect and a world-wide distribution. This is true of the Microthyriales and the majority of the other groups of epiphyllous fuugi in existence during the Eocene. The parasitic relationship between certain species of microthyriaceous fungi and the meliolas which is widespread today was well developed in the Eocene (Pl. 1, fig. 4). These facts very strongly suggest a pre-Cenozoic origin of the major forms of epiphyllous fungi.

A few epiphyllous forms of fungi known from the Carboniferous are only rarely reported from Permian, Triassic, and Jurassic sediments. In one report of Jurassic epiphyllous fungi T. M. HARRIS (1961) wrote:

> Many Yorkshire leaves show signs of local injury in the form of a rupture in one epidermis and a considerable increase in the thickness of internal coaly matter around this rupture . . . Some of these injuries certainly occured while the leaves were alive, as there are signs of reactioo such as local cell division or cutinisation of the inner walls of surrounding cells.
>
> ... It is likely that many are caused by leaf fungi forming spores, and sometimes little sclerotia, just under the epidermis; some are probably parasites and others (where no cell reaction is visible) probably saprophytes.
>
> ... Such local injuries are to be seen on most kinds of leathery leaves, e. g. *Ctenis, Ctenozamites, Nilssoniopteris, Eretmophyllum* and *Bilsdalea*, and their frequency at Gristhorpe is about one such injury per two to three square centimeters of isolated leaf studied. . . .
>
> More satisfactory evidence of leaf fungi is provided by . . . one of a large number of similar spots on the lamina of

a pinna of *Phlebopteris polypodioides* from Gristhorpe. While this fungus is strictly unclassifiable without closer knowledge, it is closely similar to many genera of the Sphaeropsidales, the common leaf spot fungi. Such fungi are familiar in the Tertiary but have not been much observed in the Jurassic.

The scarcity of epiphyllous fungi in pre-Cretaceous sediments is probably the result of the lack of preservation of such forms in late Paleozoic and early Mesozoic sediments. They may have been somewhat less abundant, however the large number of fungal spots found by HARRIS (1961) were as abundant locally asTertiary and modern epiphyllous fungi.

If several well preserved early Mesozoic epiphyllous forms could be examined in detail much might be learned of the evolutioinary development of epiphyllous fungi. Epiphyllous fungi were present during the early Mesozoic but very little is known concerning their similarity to modern forms (based upon detailed analysis), their abundance, or their host plants.

A great increase of reports of epiphyllous fossil fungi is associated with the rise and expansion of the angiosperm floras of the world. The epiphyllous fungi, so commonly found on Tertiary angiosperm host leaves, must have filled the ecological niche which the surfaces of broad leafed plants provided as the niche itself developed. Such evolution of the epiphyllous fungi would involve continuous adjustment of their physiology and morphology to the evolutionary changes in their angiosperm hosts. Since the host-parasite relationship is rarely a fatal one there has been great opportunity for the fungi to develop a very specialized morphology and/or physiology and to continue to be successful upon the same host genus or species for millions of years.

Not enough is known of pre-Cretaceous fungi to establish the origin and migration of specific lines or taxa of epiphyllous fungi; however by the early Eocene they appear essentially as they do today. The migration of these fungi probably followed very closely the migration of the plants which served as their hosts. However many forms which had wide host tolerance undoubtedly migrated quite independently of their host plants with the aid of insects, birds. wind, etc.

Host Plants

Little is known concerning the host plants upon which epiphyllous fossil fungi have been found since many of the more recent reports are the result of palynological investigations in which the fungi are frequently identified from isolated fragments and many of the early reports, for which the host leaves were identified, are frequently of questionable affinities. The hosts which have been reported range from *Equisetum* to *Poa* and include various forms of ferns, gymnosperms, and angiosperms. However no genus or species of epiphyllous fossil fungi and its host leaves are known completely enough to permit any definite conclusion to be made concerning host specificity. On the basis of the material found in this investigation some forms (e. g. *Shortensis memorabilis)* appear to have little host specificity while others appear to be limited to certain host leaves or even to the upper or lower surface of their host leaves (e. g. *Meliola anfracta* and *Meliola spinksii*

Ecological Interpretations

Since our knowledge of the ecology of both modern and fossil epiphyllous fungi is limited, it would be unwise to base any generalized ecological conclusions upon the frequent isolated reports of one or two fragments of fossil epiphyllous fungi described from widely separated areas of the world. Such reports are best used in collaboration with other fossils (pollen, leaves, wood) found associated with them. They should be compared with modern genera and species with the realization that new forms of fungi are continually being described which extend the host and geographic ranges of many modern forms.

Although modern forms of microthyriaceous fungi are most commonly found in tropical and subtropical areas of the world, a few forms do extend into temperate regions. Similarly, although most fossil microthyriaceous fungi have been found associated with warm or subtropical vegetation, a few isolated microthyriaceous fruiting bodies have been found in Pleistocene sediments in Minnesota (ROSENDAHL, 1943), in England (GODWIN and ANDREW, 1951), and from Hudson Bay to southern Florida (L. R. WILSON, personal correspondence).

Most of the epiphyllous fungi found in the fossil record on host leaves are associated with warm temperate or subtropical vegetation. The abundant occurrence in the Eocene of Tennessee of species of *Meliola*, *Asterina*, *Stomiopeltis*, *Haplopeltis*, *Trichopeltina*, *Plochmopeltidella*, *Sporidesmium*, and *Patouillardiella* and several fossil forms which appear to be closely related to the modern genera *Trichopeltis* and *Brefeldiella*, indicates that the limiting factors (moisture, temperature, and seasonal fluctuations) of their environment must have been similar to those required for the modern species of these genera today.

Asterina, *Meliola*, and *Stomiopeltis* occur today in Georgia (HANLIN, 1963). However such genera as *Haplopeltis*, *Trichopeltina*, *Trichopeltis*, *Brefeldiella*, and *Plochmopeltidella* are limited to subtropical and tropical areas of the world. The host leaves, *Sapindus* and *Chrysobalanus*, are presently distributed in tropical, subtropical and warm temperate areas.

BERRY (1930) suggested that the flora of the Wilcox (much of which now appears to be Claiborne) is subtropical in nature. BROWN (1944) indicated the presence of a few temperate species in the Eocene floras from the southeastern United States. A consideration of the host leaves and the entire assemblage of epiphytic fungi described in this study appears to substantiate BERRY's reconstruction (1930) of a suhtropical, moist, low-lying, coastal environment for the lower Eocene of western Tennessee.

Table 1. Epiphyllous and Probable Epiphyllous Fungi Known in the Fossil Record

Explanation

This table of generic names of epiphyllous and probable epiphyllous fungi known in the fossil record is as complete as possible; however there are undoubtedly a few forms which have escaped the attention of this writer. Listed under the section "Fossil described by" are the authors who originally described each genus from the fossil record. Usually they are also the authors of the generic names, but when fossil forms are assigned to modern genera, they are simply the investigators who described the first fossil member of the genus.

Genera listed in the table represent a compilation of the known generic names of epiphyllous and probable epiphyllous fungi. Of the nearly 150 genera listed it is estimated that fewer than 100 are valid names. In several genera the spelling of the names originally proposed was changed by later investigators by adding *-ites*, thus compounding the number of names recognized for certain genera. MESCHINELLI (1892, 1898) and PIA (1927) added several new generic names to the paleomycological literature by changing the endings of existing names. Lists of fossil fungi (e. g. GRAHAM, 1962) should be interpreted with the realization that many known generic names for fungi apply to similar if not the same forms and that many questionable fossil forms have been rather tenuously identified as fungi. HOLM (1959) and KRÄUSEL (1961) recognized the confused state of the nomenclature of fossil fungi and suggested in their papers limited lists of *nomina nuda* and synonymous names of fossil fungi.

Generic names which are grouped together without indentation in the classification section of the table are in all probability synonymous, but most of them can not be placed in synonymy here since this study involves only a few of the known forms of epiphyllous fungi. Until a critical investigation is made of these other forms all of their names must be included in any listing of fossil fungi. A few names are put in syno-

nymy and these are so indicated by listing and indenting the non-valid name directly below the valid genus name.

At present the taxonomy of fungi is in a very unsettled condition. As ALEXOPOULOS (1962) noted: "Not all authors agree on this classification, but then you should begin to suspect by now that there are few points of agreement on almost any question concerning the classification of the Ascomycetes!" The classification followed in this table and paper is based for the most part upon the one presented by CLEMENTS and SHEAR (1931) and is used simply as a convenient system of presenting and organizing the data.

Many fossil species have been described for some of the genera listed in the table. Therefore the age, location, and host sections often include diverse listings for a single genus or group of genera.

Table 1. Epiphyllous and Probable Epiphyllous Fungi Known in the Fossil Record

Classification	Fossil Described By	Age	Location	Host
PHYCOMYCETES				
Protococcales				
Chytridiaceae				
Urophlyctites	MAGNUS, 1903	Up. Carboniferous	France	*Alethopteris*
ASCOMYCETES				
Perisporiales				
Erysiphaceae				
Erysiphe *Erysiphites* *Erisiphites*	SCHMALHAUSEN, 1883 MESCHINELLI, 1898 PAMPALONI, 1902	Eocene, Miocene	Sicily	*Ficus*
Uncinulites	PAMPALONI, 1902	Miocene	Sicily	—
Eurotiaceae				
Eurotium	GOEPPERT, 1853	Tertiary	Prussia	—
Perisporiaceae				
Meliola	KÖCK, 1939	Eocene	Germany, Indochina, Tennessee	*Taxus, Sapindus, Chrysobalanus* & unident. lvs.
Perisporiacites *Perisporites*	FELIX, 1894 PAMPALONI, 1902	Eocene, Miocene	Transcaucasia, Sicily	—
Sphaeriales				
Sphaeriaceae				
Caenomycetes	BERRY, 1916	Eocene-Pliocene	Brazil,Texas,Tennessee, Mississippi	*Nectandra, Sideroxylon, Sabalites, Cassia, Myrica*
Chaethomites *Chaetomites*	PAMPALONI, 1902 PIA, 1927	Miocene	Sicily	—
Didymosphaeria *Didymosphaerites*	COCKERELL, 1908 PIA, 1927	Oligocene	Colorado	*Typha*
Laestadites	MESCHINELLI, 1892	post Pliocene	Japan	—
Leptosphaerites	RICHON, 1885	Eocene	France	Monocotyledonous stems & lvs.
Linosporoidea	KELLER, 1895	Miocene	SwitzerIand	—
Palaeosordaria	SAHNI & RAO, 1943	early Tertiary	Chhindwara Dist., India	—

Classification	Fossil Described By	Age	Location	Host
Petrosphaeria	Stopes & Fujii, 1909	Up Cretaceous	Japan	outside cortical cells of *Saururopsis*
Pleosporites	Suzuki, 1910	Up. Cretaceous	Japan	*Cryptomeriopsis*
Rosellinia *Rosellinites*	Beck, 1882 Meschinelli, 1892	Oligocene, Permian	Germany	—
Sphaerites *Sphaeriopsis*	Unger, 1850 Geyler, 1887	Up. Carboniferous, Up. Cretaceous, Eocene, Oligocene, Miocene, Pliocene	Germany, Switzerland, Bohemia, Italy, France, England, Spitzbergen, Alabama, N. Mexico, Wyoming, Borneo, Java	*Abies, Amygdalus, Andromeda, Eugenia, Arachnitis, Betula, Bumelia. Carya, Cassia, Caulinites, Celastrophyllum, Cissus, Dalbergia, Daphne. Dryandroidis, Eugenia, Euonymus, Ficus, Juglans, Ilex, Laurus, Lygodium, Magnolia, Manicaria, Myrica, Phragmitis, Poacites, Populus, Quercus, Rhamnus, Rhus, Rubus, Salix, Santalus, Sapindus, Solandra, Typha, Ulmus, Viburnum, Widdringtonia*
Hypocreaceae				
Melanosporites	Pampaloni, 1902	Miocene	Sicily	—
Polystigmites	Massalongo, 1858	Miocene, Plioeene	Italy, France	—
Verrucariaceae				
Cucurbitariopsis	Beck, 1882	Oligocene	Germany	—
Dothideales				
Dothideaceae				
Dothidea	Heer, 1859	Miocene, Pliocene	Switzerland, Iceland	*Acer, Andromeda, Sterculia, Myrica, Betula. Cyperus*
Microtbyriales				
Microthyriaceae				
Microthyriaceous germlings Previously reported as immature forms of:	Frantz, 1959	Tertiary	Germany, Hnngary, England, Indochina, Colorado, Tennessee	*Sapindus, Pityophyllum,* & numerous unident. lvs.
Pediastrum	Davis, 1916			
Phyllites	Colani, 1920			
Phragmothyrites	Edwards, 1922			
Coelastrum	Bradley, 1931			
Phycopeltis	Köck, 1939			
Microthyrieae				
Callimothallus *Phycopeltis*	Dilcher Kirchheimer, 1942	Eocene, Oligocene	Tennessee, Germany	*Sapindus* & unident. lvs.
Leptothyriomyces	Kräusel, 1929	?Miocene	Sumatra	—
Microthallites	Dilcher	Eocene	Tennessee	*Sapindus*

Classification	Fossil Described By	Age	Location	Host
Microthyrium	Godwin & Andrew, 1951	Pleistocene, post Pleistocene	England	—
Notothyrites	Cookson, 1947	Oligocene, Miocene	New South Wales, Victoria	*Oleinites*
Phragmothyrites	Edwards, 1922	Eocene	Scotland	*Pityophyllum*
Phyllites	Colani, 1920	Tertiary	Indochina	—
Asterineae				
Asterina	Engelhardt & Kinkelin, 1908	Pliocene, Eocene	Germany, Tennessee. Ellesmere Island	*Ilex, Sequoia, Sapindus, Chrysobalanus*
Asterothyrites	Cookson, 1947	?Oligocene-Miocene. Eocene	Victoria, Tennessee	*Oleinites, Sapindus*
Euthythyrites	Cookson, 1947	?Oligocene-Miocene	Victoria	*Oleinites*
?Parasterina	Dilcher	Eocene	Teonessee	*Sapindus*
Trichopelteae				
Brefeldiellites	Dilcher	Eocene	Tennessee	*Chrysobalanus*
Pelicothallos	Dilcher	Eocene	Tennessee	*Chrysobalanus*
Trichopeltina	Dilcher	Eocene	Tennessee	*Sapindus*
Trichopeltinites *Phycopeltis*	Cookson, 1947 Köck. 1939	Eocene, Oligocene-Mioeene	Vietoria, Germany, Tennessee	*Oleinites, Sapindus*
Trichothyrites	Rosendahl, 1943	Pleistoeene	Minnesota	*Picea*
Incertae Sedis				
Microthyriacites	Cookson, 1947	Oligocene-Mioeene	Victoria	*Oleinites* & unident. lvs.
Microthyrites	Pampaloni, 1902	Miocene	Sieily	—
Micropeltaceae				
Dictyopeltoideae				
Dictyotopileos	Dilcher	Eocene	Tennessee	*Chrysobalanus*
Haplopeltoideae				
Haplopeltis	Dilcher	Eocene	Tennessee	*Chrysobalanus*
Mycrothyriella	Dilcher	Eocene	Tennessee	*Sapindus*
Stomiopeltoideae				
Plochmopeltidella	Dilcher	Eocene	Tennessee	*Sapindus*
Plochmopeltinites	Cookson, 1947	Oligocene	New Sonth Wales, Victoria	—
Shortensis	Dilcher	Eocene	Tennessee	*Sapindus*
Stomiopeltis	Dilcher	Eocene	Tennessee	*Sapindus*
Phacidales				
Hysteriaceae				
Hysterites *Hysterium* *Hysteriopsis*	Goeppert, 1836 Heer, 1855 Geyler, 1887	Devonian, Permian. Carboniferous, Rhaetic, Tertiary	Germany, Austria. Switzerland, Italy, Greenland, Borneo	*Neuropteris, Podozamites, Zostera, Pteridium, Acer, Salix, Sapotacites. Dammara,* conifer lvs

Classification	Fossil Described By	Age	Location	Host
Phacidiaceae				
Phacidium *Phacidiopsis* *Phacidites*	Ludwig, 1859 Geyler, 1887 Meschinelli, 1892	Cretaceous Oligocene, Pliocene, Quaternary	Germany, Bohemia, Switzerland, Italy, Borneo	*Pyrus, Eugenia, Populus, Salix, Fagus, Quercus, Buxus, Juglans, Smilax, Palaeocassia*
Xylomites *Xylomides* *Rhytisma* *Rhytismopsis* *Rhytismites* *Xyloma* *Xilomides*	Unger, 1841 Schimper, 1869 Engelhardt, 1885 Geyler, 1887 Meschinelli, 1892 Boulay, 1887 Graham, 1962	Lias, Keuper, Cretaceous, Paleocene, Eocene, Oligocene, Miocene	Germany, Austria, Switzerland, Italy, Sicily, France, England, Hungary, Bohemia, Croatia, Spitzbergen, Java, Greenland, Iceland, Equador, Alberta, Sumatra, Borneo	*Cassia, Cronus, Rhamnus, Pistacia, Rhus, Acer, Ceanothus, Santalum, Cinnamomum, Persea, Laurus, Myrica, Pisonia, Ficus, Grewia, Pterospermum, Quercus, Populus, Salix, Podocarpus, Sapindus, Fagus, Platanus, Zamites, Bumelia, Otozamites, Sagenopteris, Taenopteris, Podozamites, Phoenicopsis, Equisetum, Eucalyptus, Pseudoplatanus, Hedera, Castania*
Stictidaceae				
Stegilla	Braun, 1854	Eocene, Miocene	Switzerland, England	*Graminia, Cyperitum*
Pezizales				
Dermateaceae				
Cenangium *Cenangites*	Ludwig, 1859 Meschinelli, 1892	Tertiary	—	*Pyrus*
Mollisiaceae				
Excipulites *Excipula*	Goeppert, 1836 Schimper, 1869	Carboniferous, Cretaceous	Silesia, France, Prussia	*Hymenophyllites, Callipteris, Pecopteris, Macrostachya*
PROMYCETES				
Pucciniales				
Pucciniaceae				
Aecidites	Debey & Ettingshausen 1859	Cretaceous, Tertiary	Prussia, Bohemia	*Dryophyllum, Rhamnus, Quercus*
Puccinites *Puccinia*	Ettingshausen, 1853 Pia, 1927	Cretaceous, Eocene, Oligocene	Austria, Nebraska	—
Uromycetites *Teleutospora* *Teleutosporites* *Uromyces*	Braun, 1840 Renault, 1894 Meschinelli, 1898 Pia, 1927	Triassic, Carboniferous	Bavaria, France	*Lepidodendron* megaspore
Melampsoraceae				
Coleosporium	Pia, 1927	Quaternary	—	—
DEUTEROMYCETES				
Phomales				
Phomaceae				

Classification	Fossil Described By	Age	Location	Host
Depazea *Depazites*	Saporta, 1868 Meschinelli, 1892	Paleocene, Miocene, Pliocene	France, Germany, Italy, Greenland	*Acer, Salix, Andromeda, Cinnamomum, Ulmus, Fagus, Alnus, Juglans, Eugenia, Myrica, Smilax, Hymenophyllites*
Melanosphaerites	Gruss, 1928	Devonian	Bear Island	—
Phomites	Fritel, 1910	Paleocene	France	*Myrica*
Melaneoniales				
Melanconiaceae				
Melanconites	Pia, 1927	—	—	—
Pestalozzites	Berry, 1916	Eocene, Miocene, Oligocene	Georgia, Florida, Louisiana	*Thrinax, Sabalites*
Moniliales				
Moniliaceae				
Acremonites	Pia, 1927	Eocene	Prussia	—
Diplosporium *Diplosporites*	Renault, 1899 Pia, 1927	Oligocene	France	—
Fusidium *Fusidites*	Conwentz, 1890 Meschinelli, 1898	Tertiary	Prussia	—
Gonatobotrys *Gonatobotrytites*	Caspary, 1907 Pia, 1927	Eocene	Prussia	On flower in amber
Monilites	Pampaloni, 1902	Miocene	Sicily	—
Oidium *Oidites*	Goeppert, 1853 Meschinelli, 1892	Tertiary	Prussia	—
Ovularites	Whitford, 1916	Cretaceous	Nebraska	—
Penicillium *Penicillites*	Berkeley, 1848 Meschinelli, 1892	Eocene	Germany, Prussia	—
Penicilloides	Paul, 1938	Reinsch, Kohlenkalk	England	—
Ramularia *Ramularites*	Caspary, 1907 Pia, 1927	Eocene	Prussia	—
Dematiaceae				
Brachysporium	Wilson & Webster, 1946	Paleocene	Montana	—
Cercosporites	Salmon, 1903	Miocene	Italy	—
Dendryphium *Brachycladium* *Brachycarphium* *Brachycladites*	Berkeley, 1848 Berkeley, 1848 Berkeley, 1849 Meschinelli, 1892	Eocene	Prussia	—
Haplographites	Felix, 1894	Eocene	Transcaucasia	—
Macrosporites	Renault, 1899	Carboniferous, Miocene	Germany, France	—
Morosporium	Renault & Roche, 1898	Lias, Eocene	France	—
Sporidesmium	Dilcher	Eocene	Tennessee	*Chrysobalanus*

Classification	Fossil Described By	Age	Location	Host
Streptotrix *Streptotrichites*	Berkeley, 1848 Meschinelli, 1892	Eocene	Prussia	—
Torula *Torulites*	Caspary, 1907 Pia, 1927	Cretaceous, Eocene	Prussia	—
Tuberculariaceae				
Patouillardiella	Dilcher	Eocene	Tennessee	*Chrysobalanus*
Stilbaceae				
Stilbum *Stilbites*	Caspary, 1887 Pia, 1927	Eocene	Prussia	—
Sterile Mycelia				
Himantia	Debey & Ettingshausen, 1859	Cretaceous	Bohemia	*Dryophyllum*
Himantites *Himantitus*	Meschinelli, 1892 Graham, 1962	—	—	—
Sclerotium *Sclerotites*	Heer, 1859 Meschinelli, 1892	Paleocene, Eocene, Oligocene, Miocene	Switzerland, Italy. Germany, France, England, Greenland. Colorado	*Acer, Rhus, Laurus, Betula, Cinnamomum, Cyperus, Populus, Celastrus, Gingko, Flabellaria*
Incertae Sedis				
Dubiocarpon	Hutchinson, 1955	Carboniferous	England, Missouri, Kausas	—
Fungites	Hallier, 1865	Eocene	Germany	On lvs., flowers, & twigs
Mycocarpon	Hutchinson, 1955	Carboniferous	England, Kansas	—
Phyllerium *Phyllerites*	Heer, 1855 Meschinelli, 1892	Miocene, Tertiary	Switzerland, Prussia, Bohemia, France	*Cassia, Acer, Elaeodendron, Laurus, Myrica, Callicoma, Alnus, Platanus, Ficus*
Sporocarpon	Williamson, 1878	Carboniferous	England, Kansas	—

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Summary

Several species of well-preserved epiphyllous fungi were found on angiosperm leaves collected from lower Eocene deposits of western Tennessee. The leaves on which these fungi occur were cleared and mounted on slides so that a critical examination of the cellular structure of each of the fungi could be made. Members of the families Meliolaceae, Microthyriaceae, Micropeltaceae, Tuberculariaceae, and Dematiaceae are described and discussed. Detailed developmental growth stages and life cycles (including both asexual and sexual reproductive structures) of several of the fungi were observed enabling these forms and their isolated parts to be assigned more accurately to the modern groups to which they belong. New genera are proposed for fossil material described that can not be identified with any known modern or fossil taxa.

Many of these forms of Eocene fungi can be related to modern genera: this indicates that many modern epiphyllous fungi evolved prior to the Eocene probably in association with the evolution of their angiosperm hosts. Some of the fossil fungi are restricted to specific host leaves and/or specific microhabitats on their host leaves while others are not. The genera to which the fossil fungi found in this investigation belong presently occur mainly in the humid tropical and subtropical areas of the world. This supports ecological conclusions made previously, which were based upon megafossils, that the eastern shore of the Mississippi embayment appears to have been characterized by a humid subtropical climate during the early Eocene.

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Explanation of Plates

Plate 1

Figs. 1, 2. *Meliola anfracta*, colonies on upper epidermis of *Sapindus* sp., x 60. (L.f. 96). *
Fig. 3. *M. anfracta*, hypha and hyphopodia. x 1500. (L.f. 57).
Fig. 4. *M. anfracta*, hyphae with associated microthyriaceous germling and fungus, x 600. (L.f. 96).

Plate 2

Figs. 5, 6. *Meliola anfracta*, in two focal planes, x 600. (L.f. 96).
Fig. 5. Hyphae and hyphopodia.
Fig. 6. Surface of host leaf, *Sapindus* sp., showing haustorial pores associated with the hyphopodia.
Fig. 7. *M. anfracta*, hyphae, hyphopodia, and seta bases bending away from leaf surface, x 600. (L.f. 96).

* Number listed in parentheses at the end of a figure legend indicates the slide on which the material figured occurs. All slides and photographic negatives are deposited in the paleobotanical collections of the Peabody Museum, Yale University, New Haven, Connecticut.

Fig. 8. *M. anfracta,* seta base and germinating spore from the center of colony shown in Fig. 2, x 1500. (L.f. 96).

Figs. 9, 10. *Meliola spinksii,* in two focal planes, x 600. (L.f. 87).
Fig. 9. Spore.
Fig. 10. Two initial hyphopodia produced by a terminal cell; haustorial pore evident in one.

Fig. 11. *M. spinksii,* germinating spore with initial hyphopodium, x 600. (L.f. 87).

Plate 3

Figs. 12—14. *Meliola spinksii,* germinating spores and hyphae, x 400. (L.f. 87).

Fig. 15. *M. spinksii,* growing end of a branching hypha, x 600. (L.f. 87).

Fig. 16 *M. spinksii,* hypha showing a branch and associated hyphopodia with a haustorial pore and an incomplete septum evident, x 1500. (L.f. 87).

Fig. 17. *M. spinksii.* hypha with non-mucronate and mucronate hyphopodia, x 600. (L.f. 87).

Plate 4

Figs. 18—29. Microthyriaceous germlings, fossil. reconstructed developmental series progressing to the stromata in Figs. 30 and 31, x 1500.

Fig. 30 *Callimothallus pertusus,* young stroma, x 1500. (L.f. 32).

Fig. 31. *Trichopeltinites fusilis,* young stroma, x 1500. (L.f. 62).

Fig. 32. Microthyriaceous germlings, modern, x 1500.

Figs. 33,34. Microthyriaceous germling, fossil, in two focal planes, x 1500. (L.f. 32).
Fig. 33. Surface of germling showing lobes, surface features, and conspicuous "knobs" on advancing edge of invaginating walls.
Fig. 34 Optical cross section showing all the invaginating walls.

Fig. 35. Microthyriaceous germlings, fossil, on upper surfaceof *Sapindus* sp., x 600. (L.f. 128).

Fig. 36 Microthyriaceous germling, fossil, cross section showing anchoring ring penetrating cuticle of *Sapindus* sp., x 1500. (L.f.s. 1).

Plate 5

Fig. 37. *Callimothallus pertusus,* stromata on upper epidermis of host leaf, *Sapindus* sp., associated with hyphae of *Shortensis memorabilis,* x 170. (L.f. 32).

Fig. 38. *C. pertusus,* stromata, x 400. (L.f. 32).

Fig. 39. *C. pertusus,* stroma, x 600. (L.f. 56).

Fig. 40. *C. pertusus,* stroma, x 400. (L.f. 186).

Fig. 41. *C. pertusus,* portion of stroma showing porate cells and fimbriate margins, x 1500. (L.f. 32).

Fig. 42. *C. pertusus,* portion of stroma showing porate cells and entire margin, x 1500. (L.f. 56)

Plate 6

Figs. 43—46. *Callimothallus pertusus,* stromata showing the development of a central cluster of cells, x 1500. (L.f. 32).

Plate 7

Figs. 47, 49. *Callimothallus pertusus,* stroma and host leaf in two focal planes, x 600. (L.f. 186).
Fig. 47. Stroma.
Fig. 49. Upper epidermis of host leaf, *Sapindus* sp.

Fig. 48. *C. pertusus,* cross section of stroma and host leaf cuticle, x 600. (L.f.s. 24).

Figs. 50—53. *C. pertusus.* fragmentary and young stromata, x 1500. (L.f. 32).

Fig. 54. *C. pertusus,* young stroma, x 1500. (L.f. 32).

Fig. 55. *C. pertusus,* asymmetrical stroma with limited marginal growth, x 600. (L.f. 32).

Fig. 56. *Asterina eocenica,* germinating spore on lower epidermis of *Chrysobalanus* sp. showing echinate 2-celled spore, hyphae, and hyphopodia, x 1500. (L.f. 87).

Plate 8

Fig. 57. *Asterina eocenica,* hyphae and hyphopodia, x 600. (L.f. 87).

Fig. 58. *A. eocenica.* anastomosing hyphae, x 600. (L.f. 87).

Fig. 59. *A. eocenica,* early stage of fruiting body produced by a medial hyphal cell, x 400. (L.f. 87).

Fig. 60. *A. eocenica,* early stage of fruiting body produced by lateral hyphal branch, x 400. (L.f. 87).

Fig. 61. *A. eocenica,* optical cross section of young fruiting body and associated hypha, x 400. (L.f. 87).

Fig. 62. *A. eocenica,* young fruiting body showing abnormal marginal growth, x 600. (L.f. 87).
Fig. 63. *A. eocenica,* mature diminutive fruiting body (conidium). x 600. (L.f. 87).
Fig. 64. *A. eocenica,* young fruiting body. x 600. (L.f. 87).
Fig. 65. *A. eocenica,* mature fruiting body (ascocarp). x 400. (L.f. 87).
Figs. 66, 68. *A. eocenica,* mature ascocarps and 2-celled ascospores. x 400. (L.f. 87).
Fig. 67. *A. eocenica,* cluster of ascospores within ascocarp, x 600. (L.f. 87).

Plate 9

Fig. 69. *Asterina nodosaria,* hyphae on upper epidermis of *Sapindus* sp., x 170. (L.f. 195).
Fig. 70. *A. nodosaria,* hyphae and cluster of seta bases, x 170. (L.f. 195).
Fig. 71. *A. nodosaria,* nodular hyphae branching and intertwining, occasionally anastomosing (indicated by arrow), x 600. (L.f. 195).
Fig. 72. *A. nodosaria,* seta bases and setae. x 400. (L.f. 195).
Fig. 73. *A. nodosaria,* hyphae and associated seta bases, x 600. (L.f. 195).
Fig. 74. *A. nodosaria,* nodular cell beginning to invaginate, x 1500. (L.f. 45).
Fig. 75. *A. nodosaria,* young fruiting body and nodular cell, x 1500. (L.f. 45).

Plate 10

Fig. 76. *?Parasterina plectopelta,* loosely anastomosing hyphae on the upper epidermis of *Sapindus* sp., x 170. (L.f. 195).
Figs. 77, 78. *?P. plectopelta,* hyphopodiate hyphae, x 600. (L.f. 195).
Fig. 79. *?P. plectopelta,* densely anastomosing hyphae, x 170. (L.f. 201).
Fig. 80. *?P. plectopelta,* densely anastomosing and intertwining hyphae, x 600. (L.f. 211).
Fig. 81. *?P. plectopelta,* anastomosing and intertwining hyphae, x 400. (L.f. 201).
Fig. 82. *?P. plectopelta,* numerous holes in intertwining hyphae caused by trichomes of the host leaf, x 400. (L.f. 201).
Fig. 83. *Microthallites lutosus,* stroma, x 600. (L.f. 221).
Figs. 84, 85. *M. lutosus,* in two focal planes, x 600. (L.f. 210).
Fig. 84. Upper surface of stroma.
Fig. 85. Lower surface of stroma.

Plate 11

Figs. 86—89. *Trichopeltinites fusilis,* mature stromata containing ascomata (dark areas). Figs. 86, 88, x 400 (L.f. 61, 37); Figs. 87, 89, x 170 (L.f. 217, 206).

Plate 12

Fig. 90. *Trichopeltinites fusilis,* small fertile stroma attached by free hyphae to mature stroma containing an ascoma, x 400. (L.f. 217).
Fig. 91. *T. fusilis,* small fertile stroma, x 400. (L.f. 206).
Fig. 92. *Microthallites spinulatus,* upper surface of stroma showing ostiole. x 600. (L.f. 87).
Fig. 93. *Trichopeltinites fusilis,* young stroma, x 1500
Fig. 94. *T. fusilis,* immature stroma, x 400. (L.f. 62).
Figs. 95, 96. *Microthallites spinulatus,* in two focal planes. x 400. (L.f. 87).
Fig. 95. Upper surface of stroma.
Fig. 96. Lower surface of stroma; marginal echinations evident.
Fig. 97. *Asterothyrites tennesseensis,* stroma and free hyphae, x 600. (L.f. 32).
Fig. 98. *Trichopeltina exporrecta,* small stroma and attached seta. x 1500. (L.f. 8).
Fig. 99. *T. exporrecta,* sterile stroma. x 1500. (L.f. 8).

Plate 13

Fig. 100. *Trichopeltina exporrecta,* stroma and associated free hyphae, x 600. (L.f. 189).
Fig. 101. *T. exporrecta,* germinating 2-celled spore, x 600. (L.f. 189).
Fig. 102. *T. exporrecta,* germinating 2-celled spore, x 600. (L.f. 189).
Fig. 103. *T. exporrecta,* stroma and free hyphae, x 600. (L.f. 8).
Fig 104. *Brefeldiellites fructiflabella,* large portion of hyaline stroma containing two marginal ascomata; one ascoma lower left, the other ascoma (partially disintegrated) upper right. x 170. (L.f. 87).
Figs. 105, 108. *B. fructiflabella,* in two focal planes, x 400. (L.f. 87).
Fig. 105. Mature ascoma showing ring-like ostiole.
Fig. 108. Marginal hyaline cells of stroma.

Fig. 106. *B. fructiflabella,* hyaline cells of stroma, x 400. (L.f. 87).
Fig. 107. *B. fructiflabella*, post mature ascoma, x 400. (L.f. 87).

Plate 14

Fig. 109. *Pelicothallos villosus,* lobed stroma on upper epidermis of *Chrysobalanus* sp., x 60. (L.f. 87).
Fig. 110. *P. villosus,* margin of stroma showing plectenchymatous cells and numerous trichomes, x 170. (L.f. 87).
Fig. 111. *P. villosus,* one of the central ostioles of stroma shown in Fig. 109, x 400. (L.f. 87).
Fig. 112. *P. villosus,* small sterile stroma with numerous setae, x 170. (L.f. 87).
Fig. 113. *P. villosus,* lobe of a stroma showing plectenchymatous cells and a single sterile seta, x 400. (L.f. 87).
Fig. 114. *P. villosus,* conidiophore, x 600. (L.f. 87).
Figs. 115, 116. *P. villosus,* terminal portion of conidiophore in two focal planes, x 600. (L.f. 87).
Fig. 115. Conidiospore.
Fig. 116. Sterigma.

Plate 15

Fig. 117. *Haplopeltis mucoris,* fruiting bodies, x 400. (L.f. 87).
Fig. 118. *Microthyriella fungosa,* fruiting body, x 400. (L.f. 77).
Fig. 119. *M. fungosa,* fragmentary fruiting body, x 1500. (L.f. 77).
Fig. 120. *M. fungosa,* small fruiting body, x 600. (L.f. 77).
Fig. 121. *Stomiopeltis plectilis,* fruiting body and free hyphae on lower epidermis of *Sapindus* sp., x 400. (L.f. 33).
Fig. 122. *S. plectilis,* immature fruiting body, x 600. (L.f. 226).
Figs. 123, 124 *S. plectilis,* developmental stages of fruiting body, x 400. (L.f. 226).

Plate 16

Fig. 125. *Stomiopeltis plectilis,* mature fruiting body with central ostiole, x 400. (L.f. 226).
Fig. 126. *S. plectilis,* plectenchymatous cells of a fruiting body, x 1500. (L.f. 226).
Fig. 127. *S. plectilis,* marginal cells of a fruiting body, x 600. (L.f. 226).
Fig. 128. *S. plectilis,* remnants of an old fruiting body, x 170. (L.f. 226).
Fig. 129. *Plochmopeltidella antiqua,* fruiting body, free hyphae, and setae, x 400. (L.f. 170).
Figs. 130, 131. *P. antiqua,* young fruiting bodies with plectenchymatous hyphae, free hyphae, and setae, x 400. (L.f. 170).
Fig. 132. *P. antiqua,* free hyphae and setae, x 1500. (L.f. 170).
Fig. 133. *P. antiqua,* germinating 2-celled spore, x 1500. (L.f. 170).
Fig. 134. *P. antiqua,* free hyphae and incomplete seta, x 600. (L.f. 214).

Plate 17

Fig. 135. *Shortensis memorabilis,* mycelium and fruiting bodies of almost an entire colony, x 60. (L.f. 60).
Fig. 136. *S. memorabilis,* marginal isolated fruiting bodies of an old colony, x 60. (L.f. 60).
Fig. 137. *S. memorabilis,* anastomosing marginal hyphae from two colonies, x 170. (L.f. 60).

Plate 18

Fig. 138. *Shortensis memorabilis,* fruiting bodies on lower epidermis of *Chrysobalanus* sp., x 170. (L.f. 87).
Fig. 139. *S. memorabilis,* thickened walls and incomplete septations of disintegrating hypha, x 1500. (L.f. 32).
Fig. 140. *S. memorabilis,* hypha producing young and fully developed hypbopodia, x 600. (L.f. 32).
Fig. 141. *S. memorabilis,* hypha bearing single and many celled hyphopodia with haustorial pores, x 1500. (L.f. 32).
Fig. 142. *S. memorabilis,* hyphae bearing single and many celled hyphopodia, x 600. (L.f. 32).
Figs. 143, 144. *S. memorabilis,* in two focal planes, x 600. (L.f. 32).
Fig. 143. Dichotomizing anastomosing hypbae bearing hyphopodiate and/or reproductive branches.
Fig. 144. Haustorium-ridden epidermal cells.

Plate 19

Fig. 145. *Shortensis memorabilis,* dichotomizing hypha bearing a young reproductive branch; haustoria evident in epidermal cells, x 600. (L.f. 32).
Fig. 146. *S. memorabilis,* hypha bearing a young reproductive branch, x 600. (L.f. 32).
Fig. 147. *S. memorabilis,* hypha bearing reproductive branch and young fruiting body, x 600. (L.f. 32).

Fig. 148. *S. memorabilis,* two fruiting bodies in different stages of development and associated hyphae, x 600. (L.f. 32).
Fig. 149. *S. memorabilis,* disintegrating young fruiting body surrounded by resistant portions of proliferated hyphae, x 400. (L.f. 202).
Fig. 150. *S. memorabilis,* ostiole, numerous small pores and intercellular proliferation of cells in maturing fruiting body, x 600. (L.f. 32).
Fig. 151. *S. memorabilis,* intercellular proliferation of cells and marginal disintegration, x 1500. (L.f. 32).

Plate 20

Fig. 152. *Shortensis memorabilis,* fruiting body with numerous associated pycnidiospores, x 600. (L.f. 240).
Fig. 153. *S. memorabilis,* optical cross section of pycnidium showing pynidiospores within, x 600. (L.f. 87).
Fig. 154. *S. memorabilis,* germinating pycnidiospore, x 1500. (L.f. 87).
Figs. 155,156. *S. memorabilis,* pycnidiospores in two focal planes, x 1500. (L.f. 240).
Fig. 155. Pycnidiospores.
Fig. 156. Germinal tubes growing into surface of the host leaf.
Fig. 157. *S. memorabilis,* optical cross section of ascocarp containing ascospores (indicated by arrow), x 600. (L.f. 60).
Fig. 158. *S. memorabilis,* germinating ascospore, x 1500. (L.f. 60).
Fig. 159. *S. memorabilis,* optical cross section of ascocarp containing ascospores (indicated by arrow), x 600. (L.f. 60).

Plate 21

Fig. 160. *Shortensis memorabilis,* dichotomizing hypha produced by ascospore which is still evident, x 600. (L.f. 60).
Fig. 161. *S. memorabilis,* germinated spore, haustorium, and initial hyphal cells, x 1500. (L.f. 60)
Fig. 162. *Dictyotopileos yalensis,* stroma, x 170. (L.f. 87).
Fig. 163. *D. yalensis,* radiate marginal portion of an elongate granular stroma showing ostioles, x 170. (L.f. 87).
Fig. 164. *D. yalensis,* young ostiole and associated reticulate hyphae, x 600. (L.f. 87).
Fig. 165. *D. yalensis,* persisteot rings of cells surrounding ostioles in a mature grauular stroma, x 600. (L.f. 87).
Fig. 166. *D. yalensis,* portion of reticulate hyphal covering of stroma, x 600. (L.f. 87).

Plate 22

Fig. 167. *Dictyotopileos yalensis,* ostiole containing possible ascospores, x 600. (L.f. 87).
Fig. 168. *D. yalensis,* disintegrated stroma showing persistent hyaline subiculum and thickened marginal cells with free hyphae attached, x 400. (L.f. 87).
Fig. 169. *D. yalensis,* margin of stroma and free byphae, x 170. (L.f. 87).
Fig. 170. *D. yalensis,* hanstorium-like infected areas produced by anastomosing free hybae in the epidermal cells of *Chrysobalanus* sp , x 600. (L.f. 87).
Fig. 171. *D. yalensis,* conidiospore attached to margin of stroma, x 600. (L.f. 87).
Fig. 172,173. *Patouillardiella imbricata,* compact clusters of conidiospores, x 600. (L.f. 87).
Fig. 174. *P. imbricata,* 2-celled conidiospores in closely packed imbricate arrangement, x 1500. (L.f. 87).

Plate 23

Fig. 175. *Patouillardiella imbricata,* closely-packed, imbricate 2-celled conidiospores, x 1500. (L.f. 87).
Fig. 176. *Sporidesmium henryense,* hyphopodiate hyphae, x 400. (L.f. 87).
Fig. 177. *S. henryense,* hyphopodiate hypha with conspicuous incomplete septations and a haustorial pore, x 1500. (L.f. 87).
Fig. 178. *S. henryense,* hyphopodiate hypba, x 600. (L.f. 87).
Fig. 179. *S. henryense,* hyphopodiate hypha bearing conidiospore, x 600. (L.f. 87).
Figs. 180,181. *S. henryense,* conidiospores, x 1500. (L.f. 87).

Plate 24

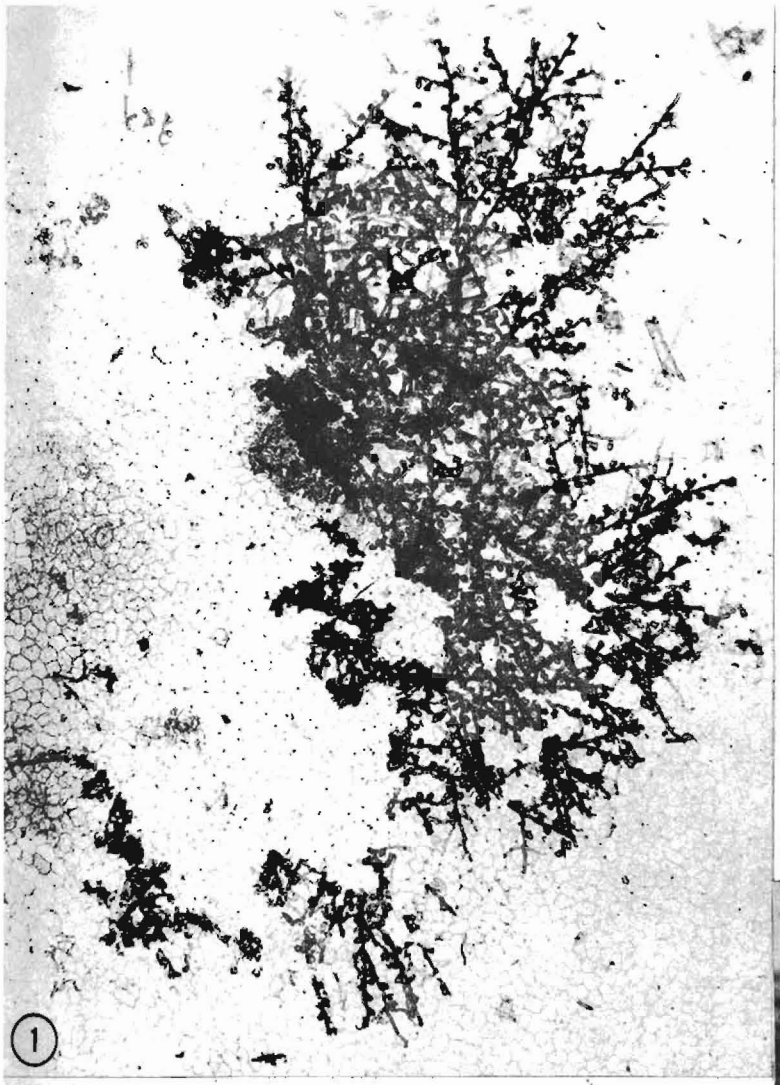
Fig. 182. *Chrysobalanus* sp., fossil leaf, x 1. (L.f. 87).
Figs. 183-185. *Sapindus* sp , fossil leaves, x 1. (L.f.c. 11, L.f.c. 9, L.f.c. 7).
Fig. 186. *Sapindus* sp., cross section of fossil leaf showing cuticle, epidermal cells, and mesophyll cells, x 400.
Fig. 187. *Sapindus* sp., cutiele of fossil leaf, upper epidermis, x 400.
Fig. 188. *Sapindus* sp., cuticle of fossil lea[illegible] ower epidermis, x 600.

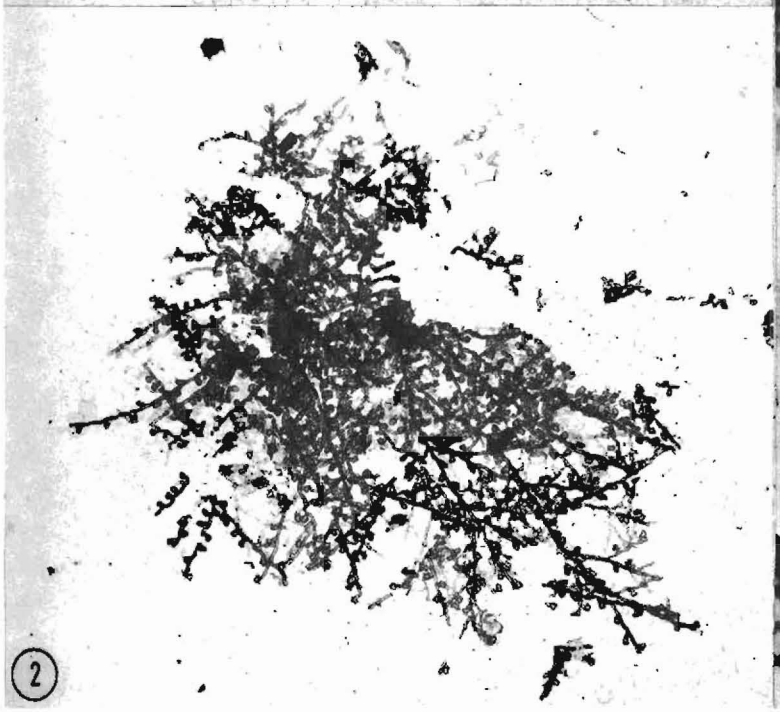
Plate 25

Fig. 189. *Sapindus marginatus*, cuticle of modern leaf, upper epidermis, x 400.
Fig. 190. *Sapindus marginatus*, cuticle of modern leaf, lower epidermis, x 600.
Fig. 191. *Chrysobalanus* sp., cuticle of fossil leaf, upper epidermis, x 400
Fig. 192. *Chrysobalanus* sp., cuticle of fossil leaf, lower epidermis, x 600.
Fig. 193. *Chrysobalanus icaco*, cuticle of modern leaf, upper epidermis, x 400
Fig. 194. *Chrysobalanus icaco*, cuticle of modern leaf, lower epidermis, x 600.

Plate 26

Fig. 195. *Sapindus* sp., cuticle of fossil leaf, lower epidermis, with infected stomata, x 170.
Fig. 196. *Sapindus* sp., cuticle of fossil leaf with injured area on lower epidermis, x 170.
Fig. 197. *Sapindus* sp., cuticle of fossil leaf, upper epidermis, haustorial penetration evident, x 400.
Figs. 198-201. *Sapindus* sp., cuticle of fossil leaf, upper epidermis with fungal haustoria. Figs. 198, 200, x 600; Figs. 199, 201, x 1500





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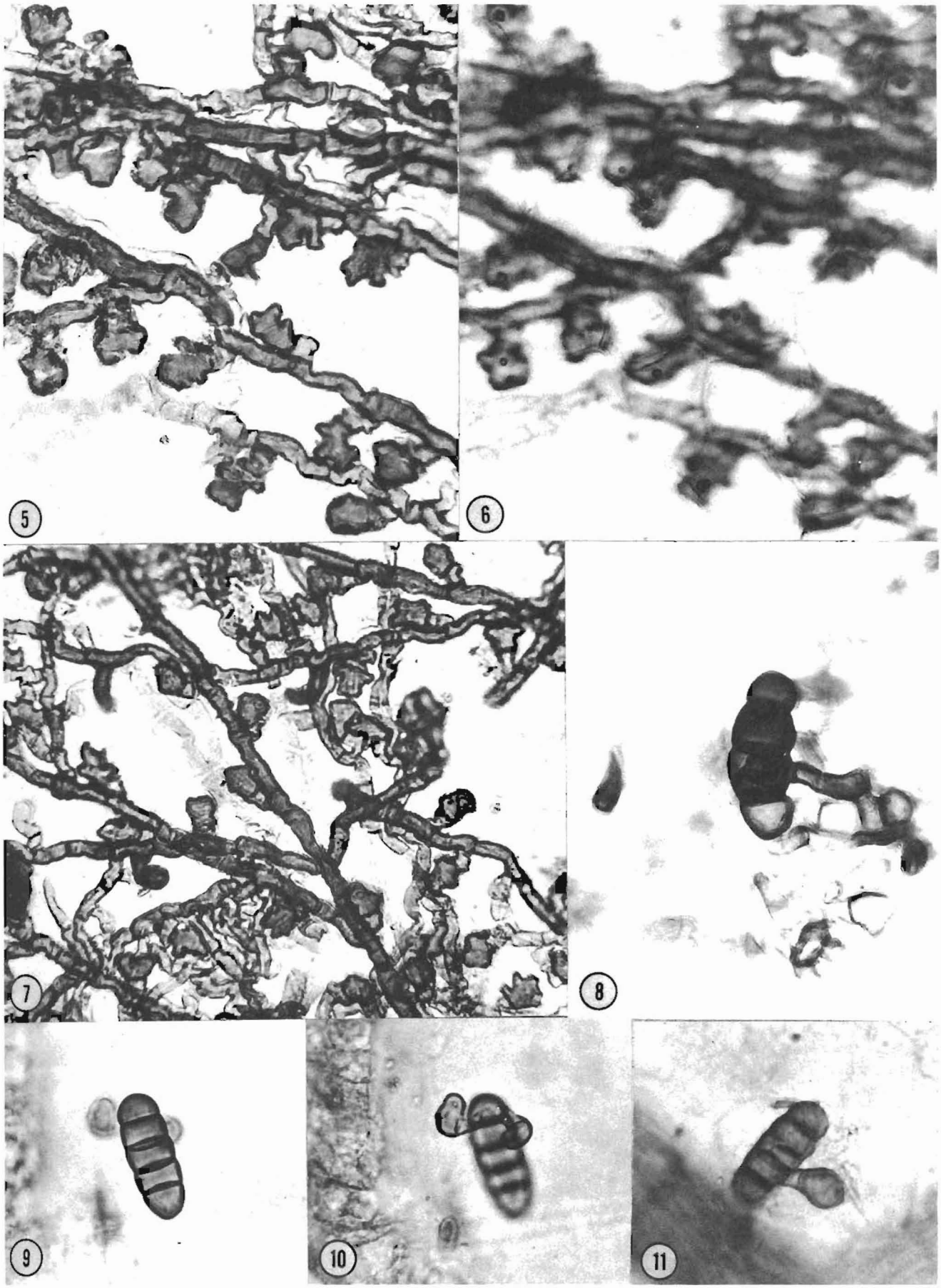

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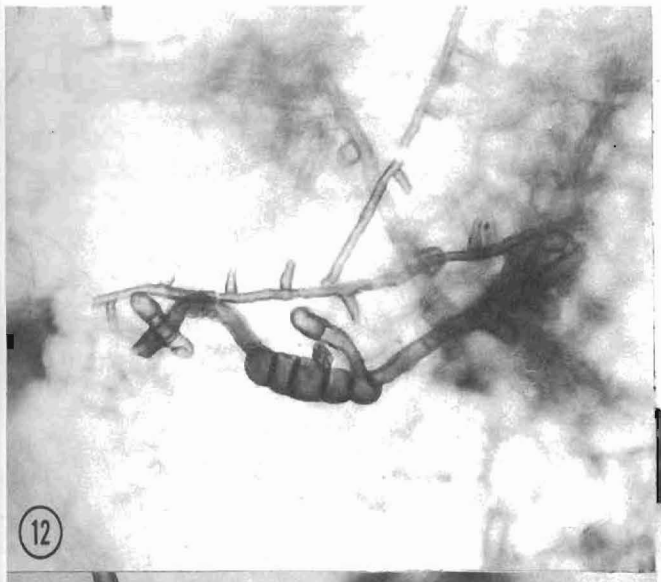

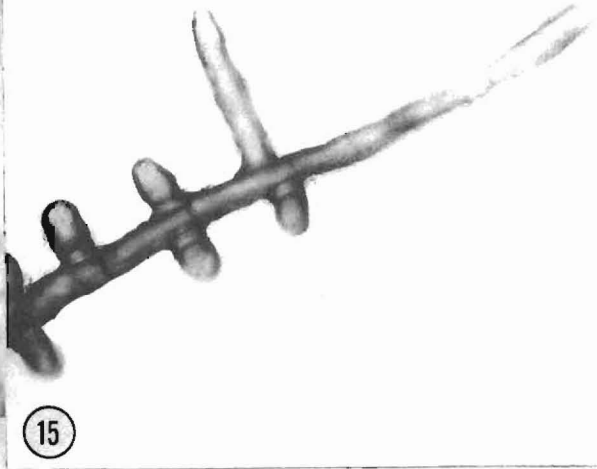

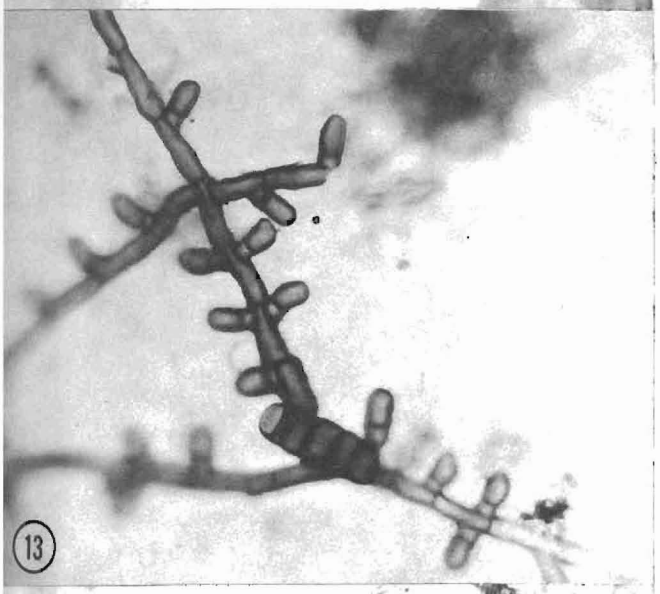

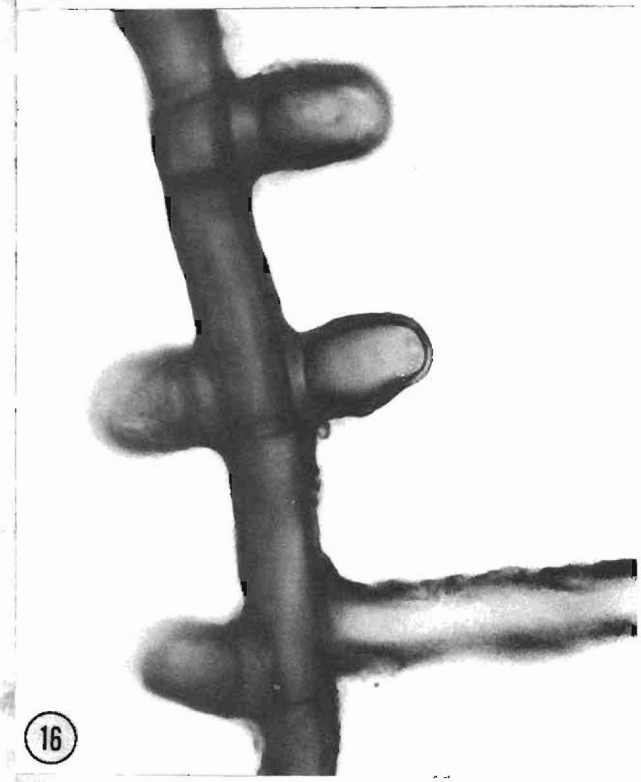

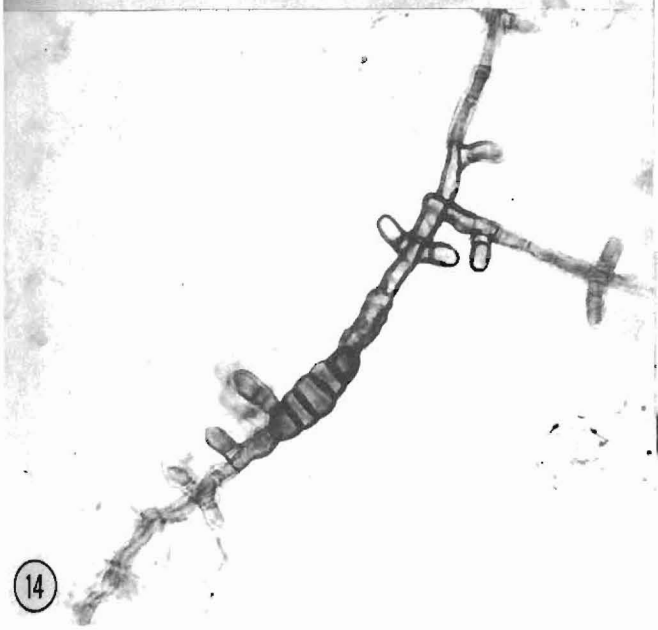

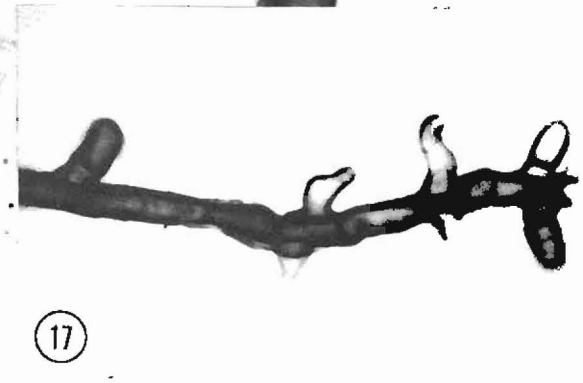

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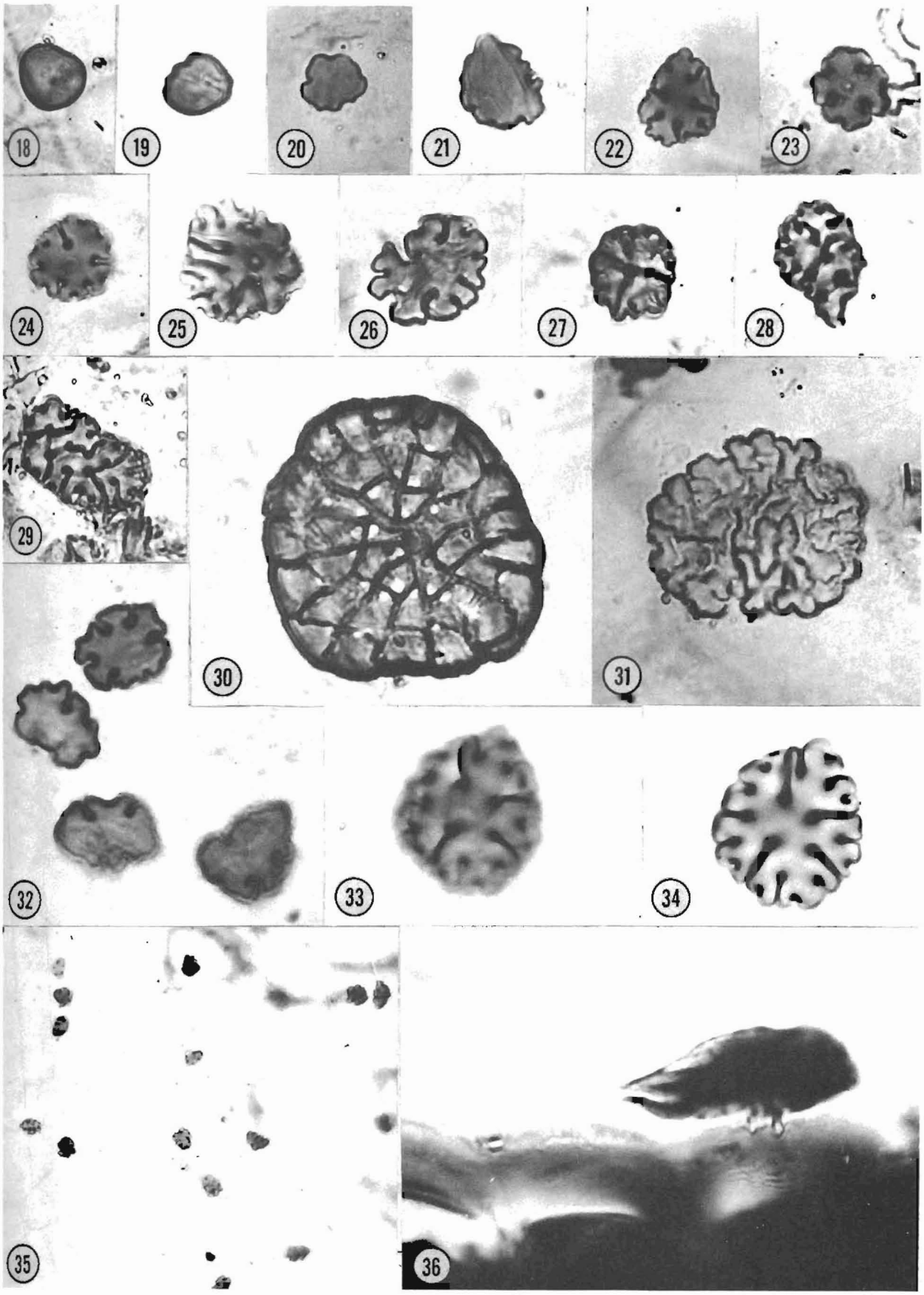

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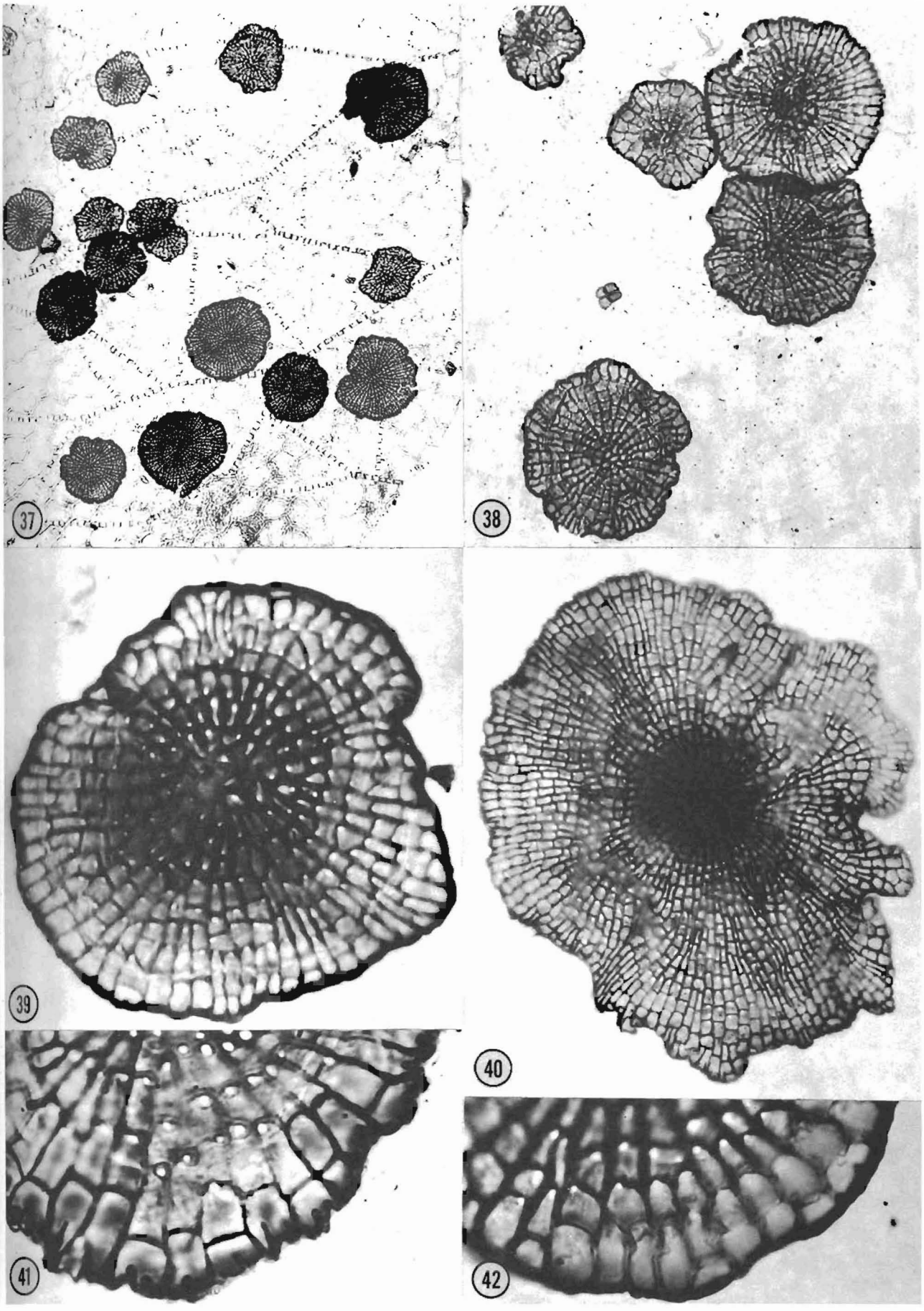

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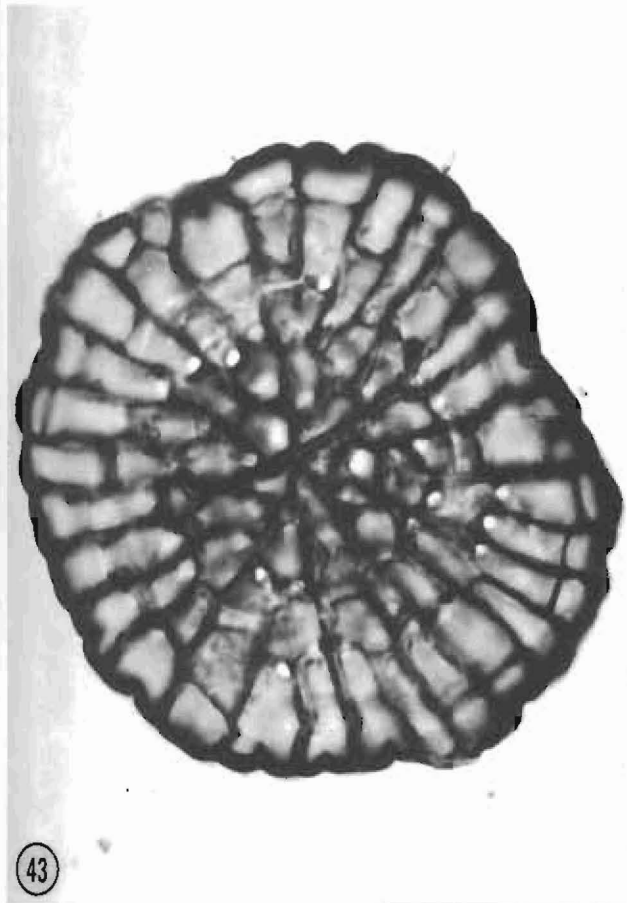

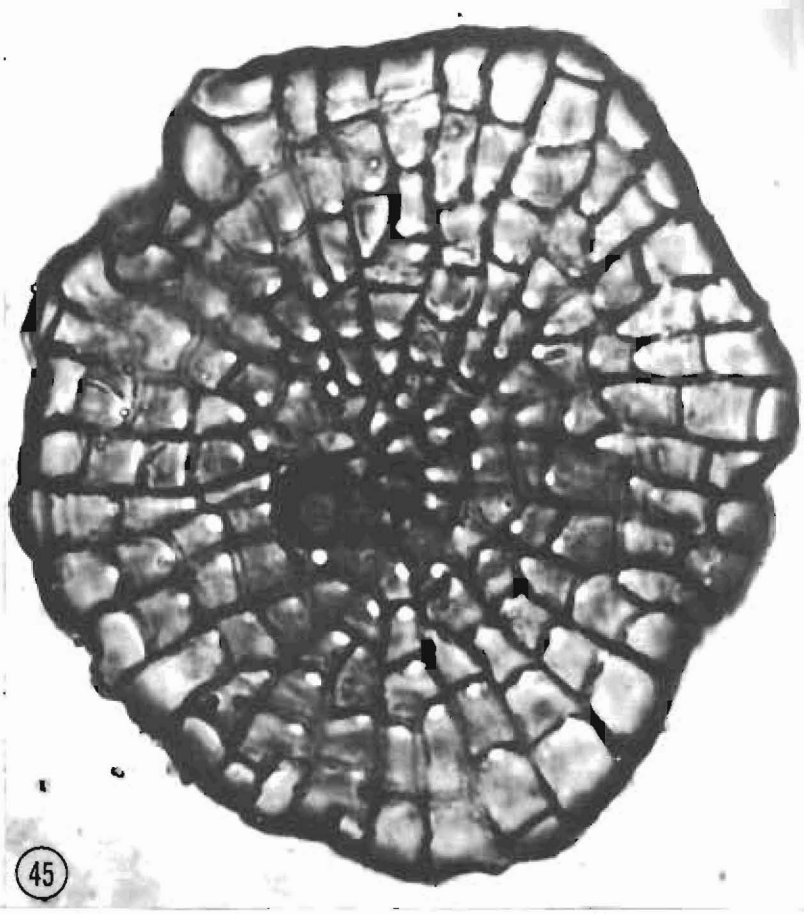

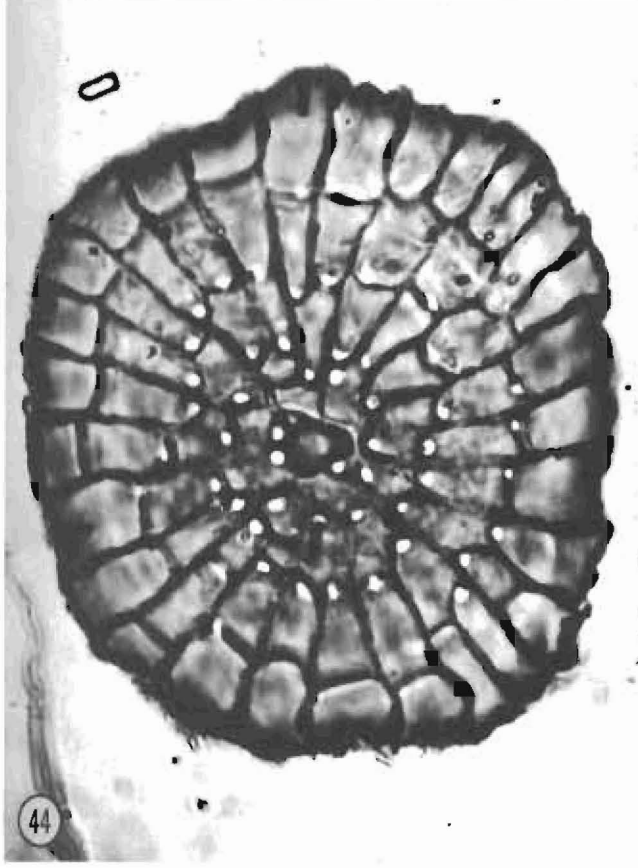

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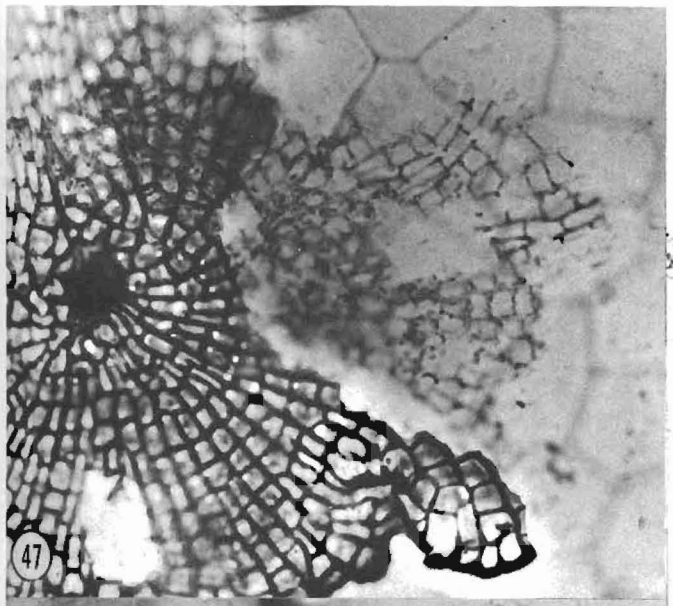

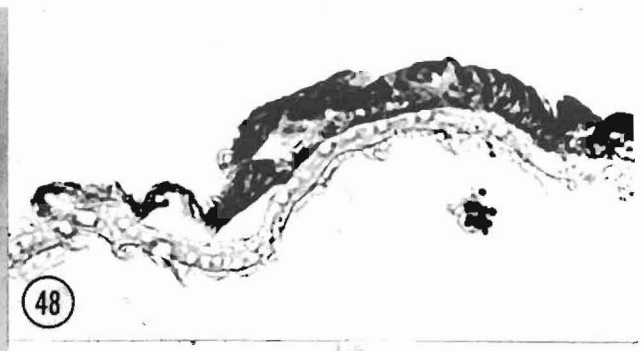

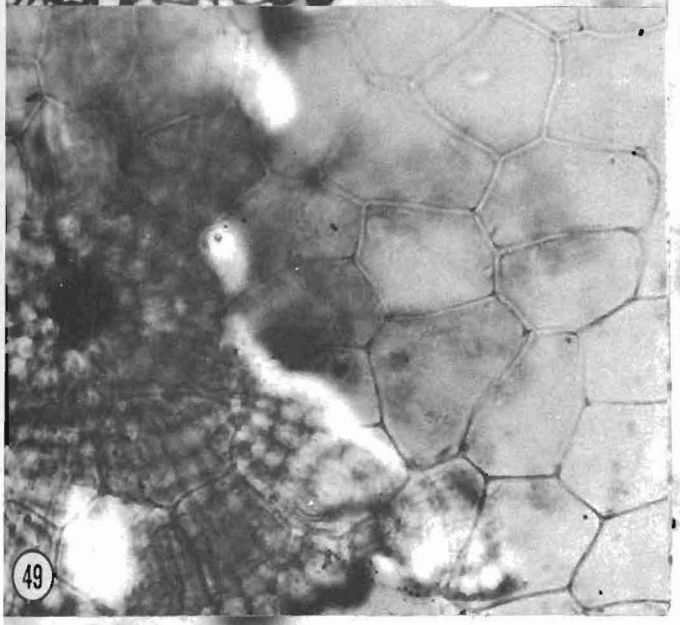

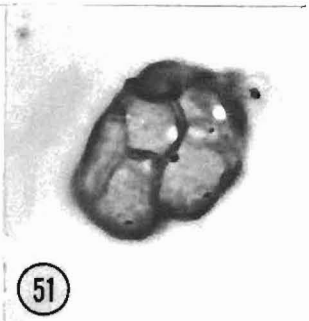

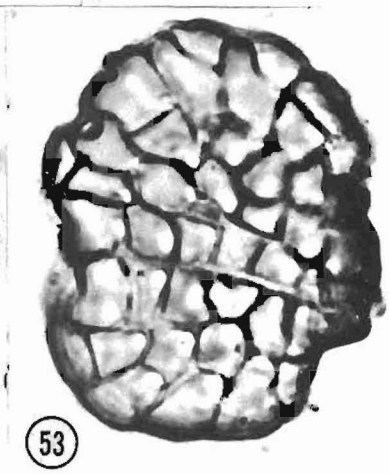

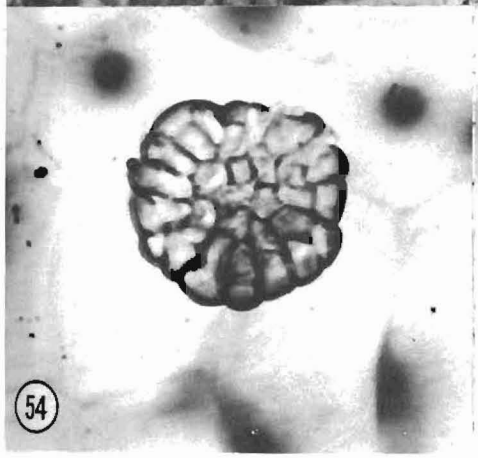

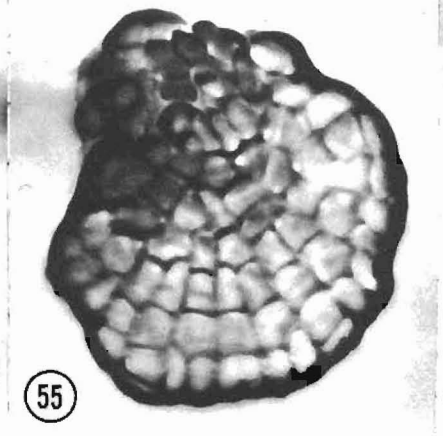

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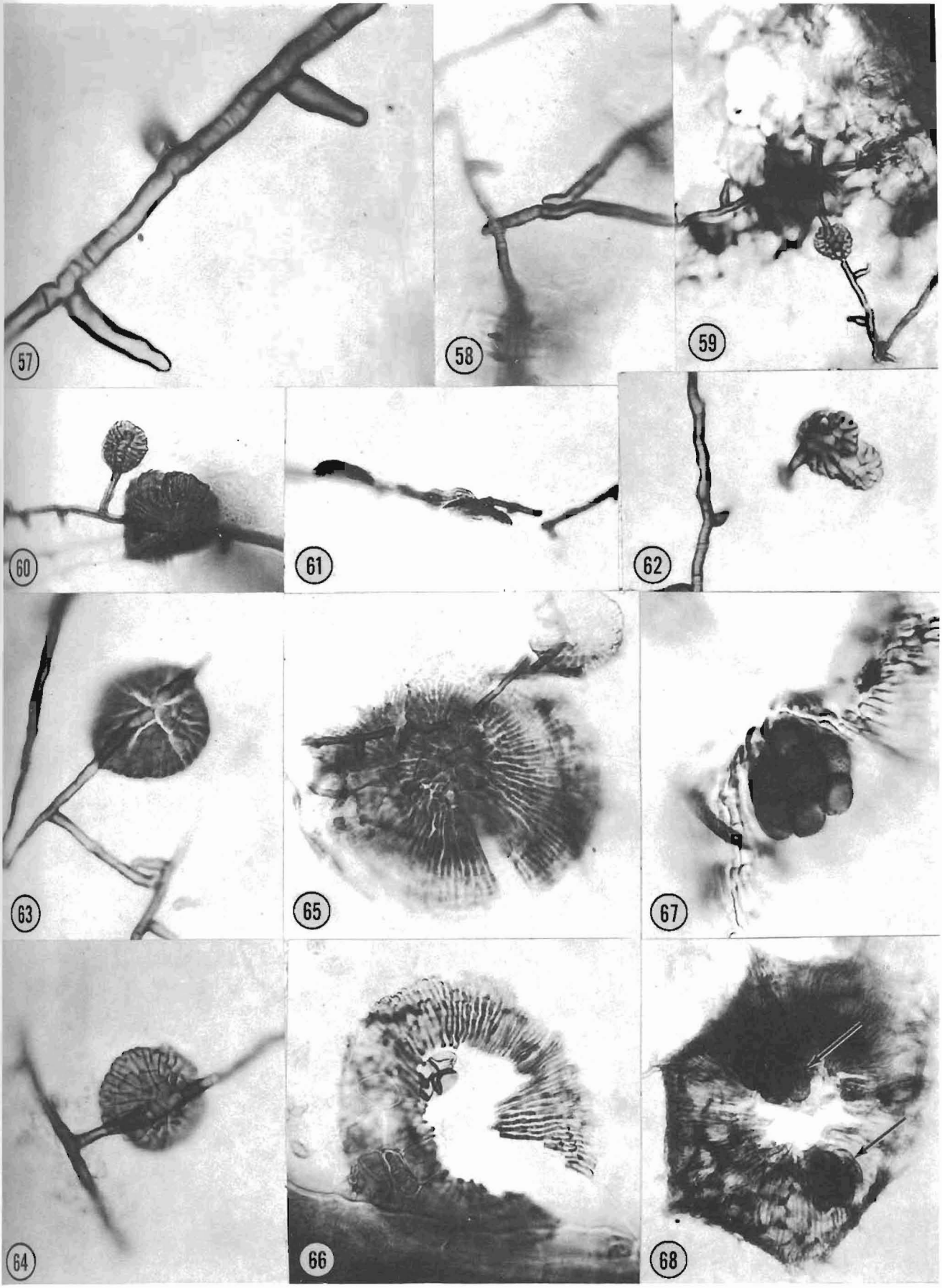

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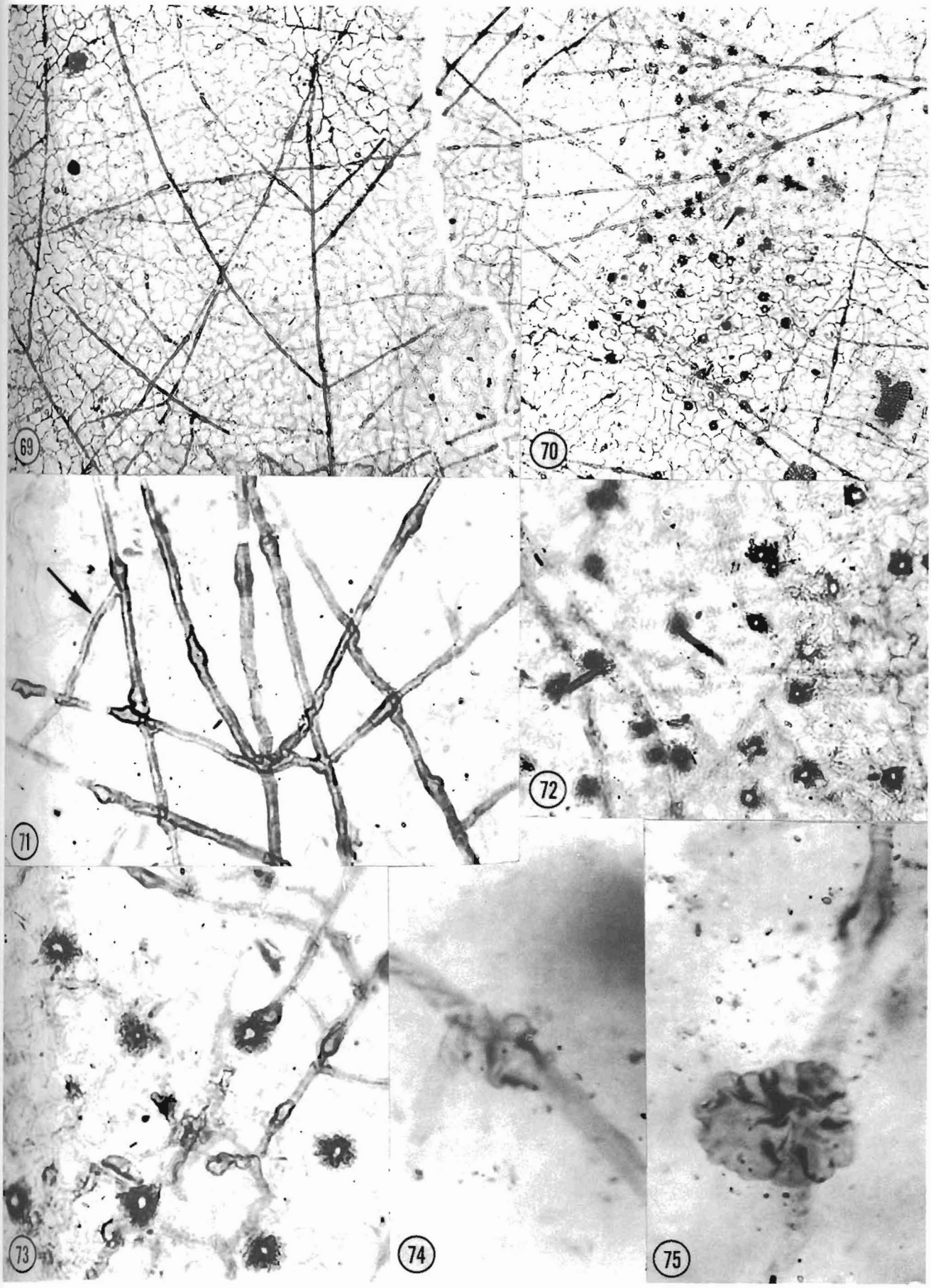

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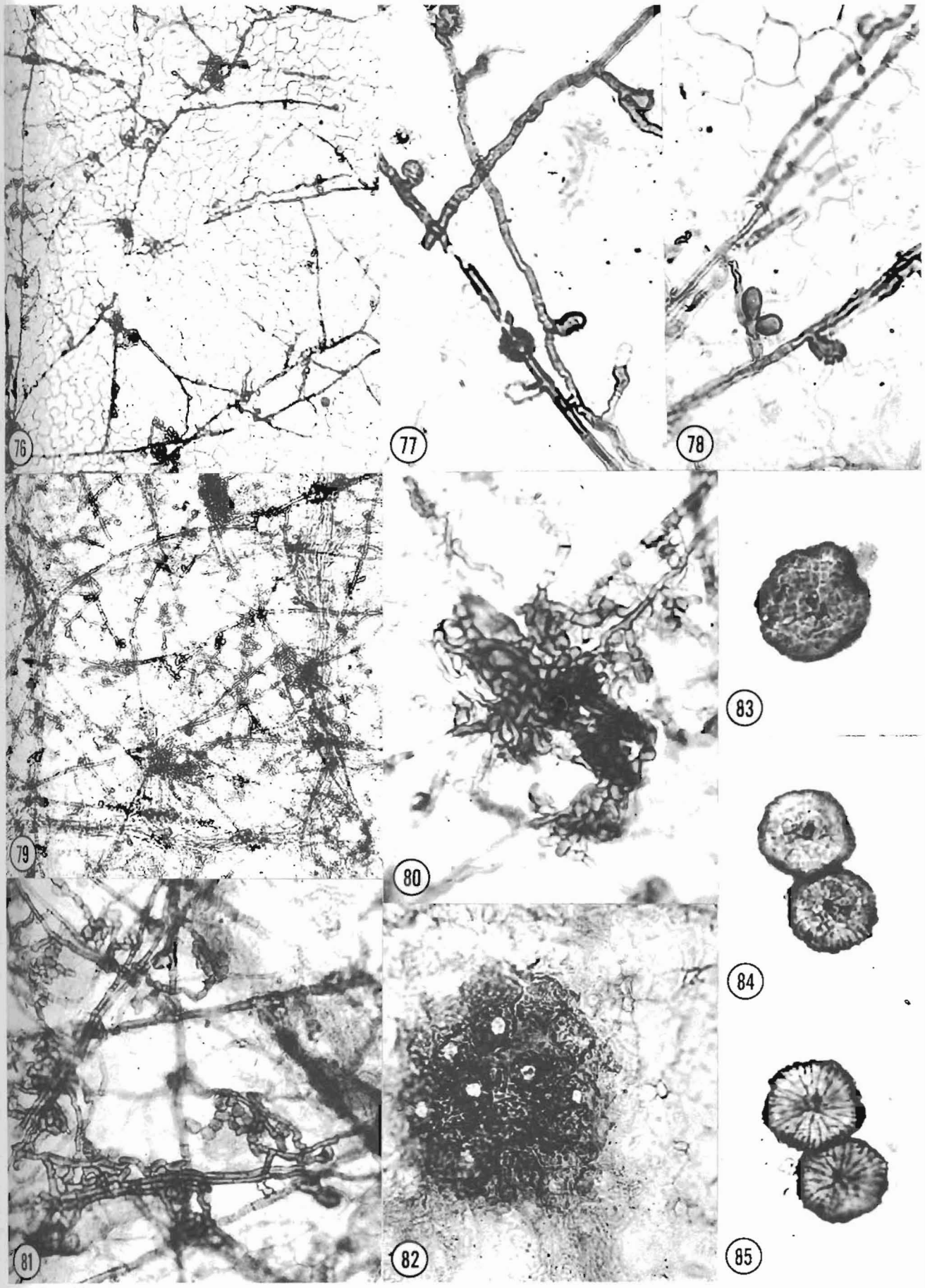

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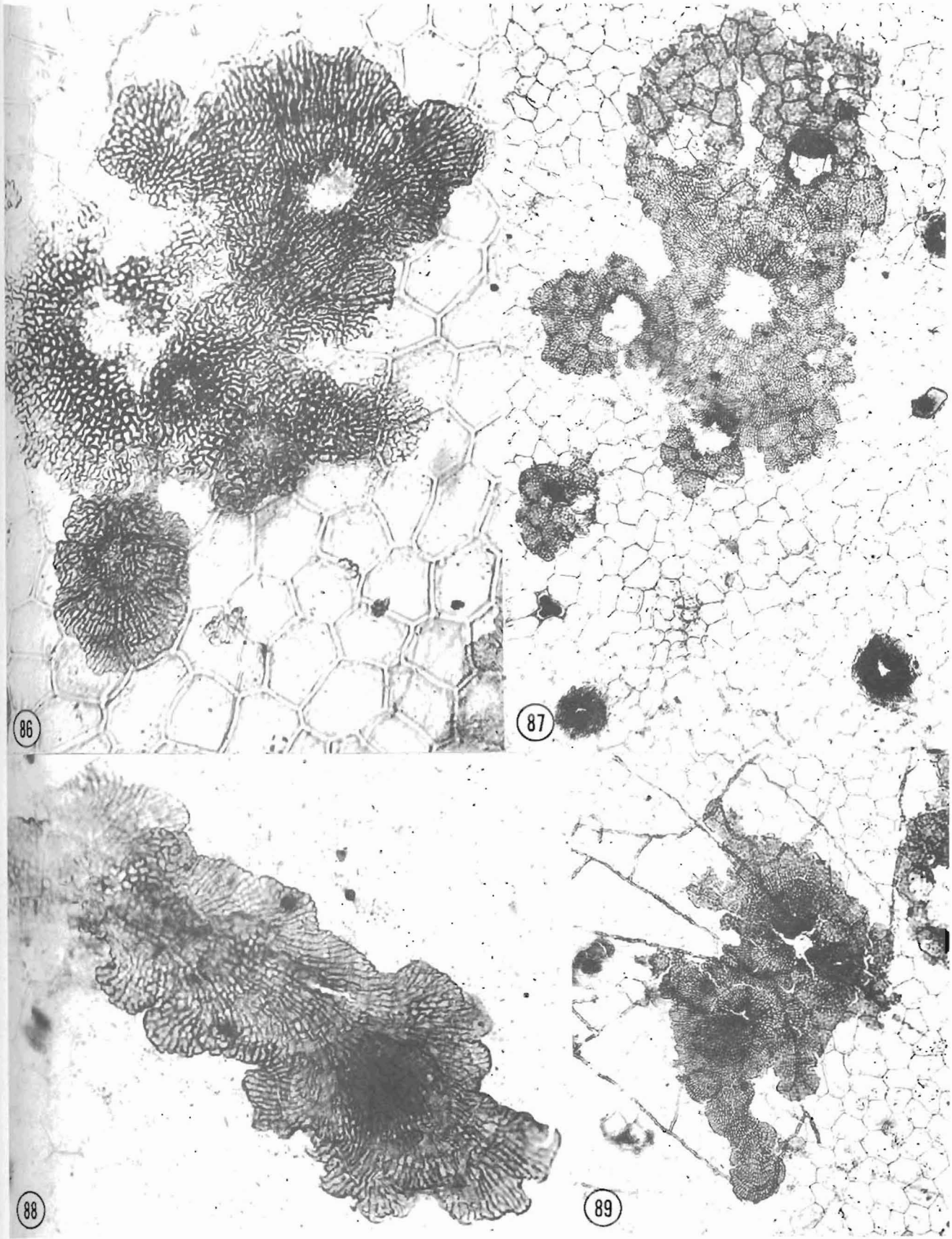

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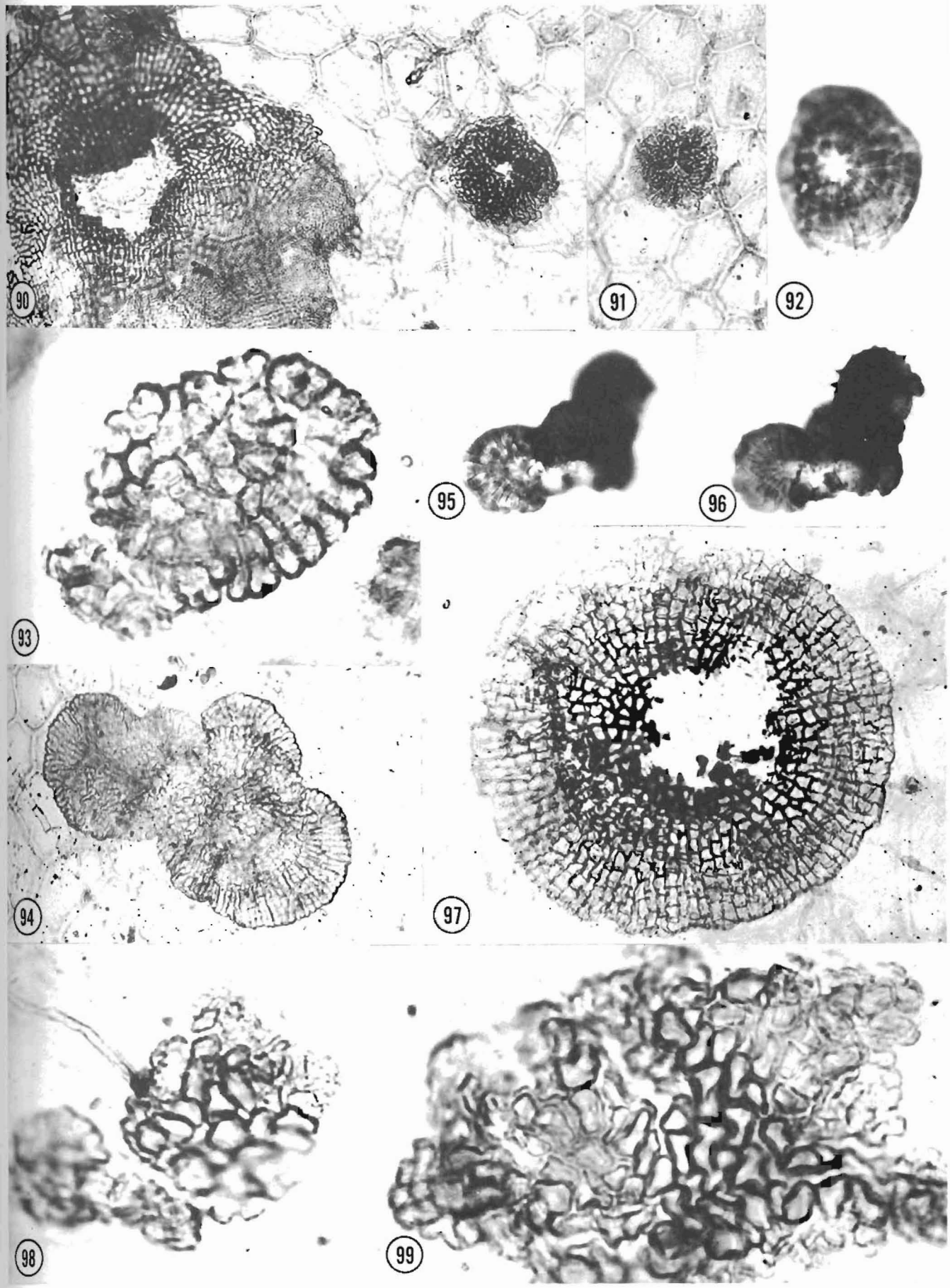

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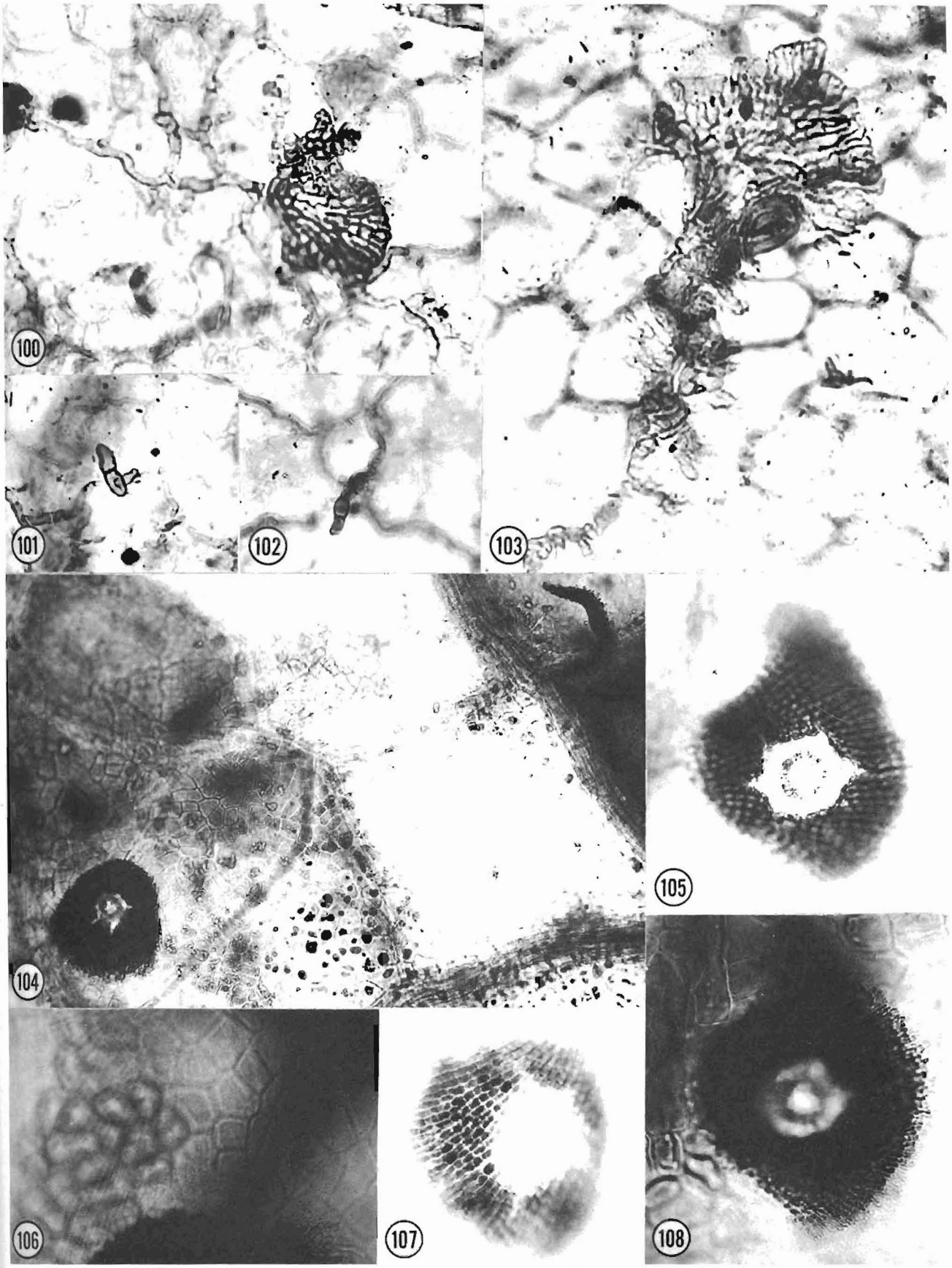

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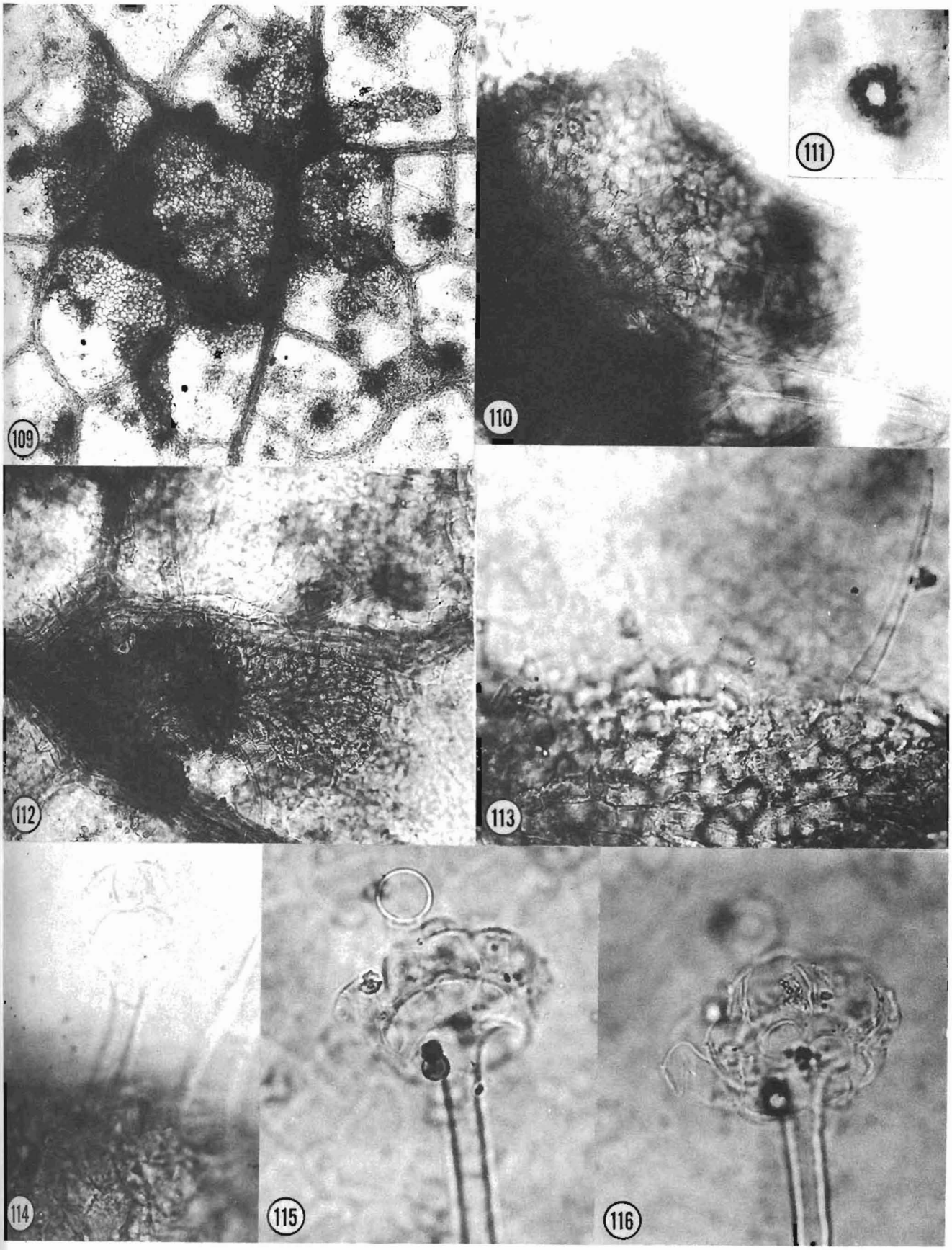

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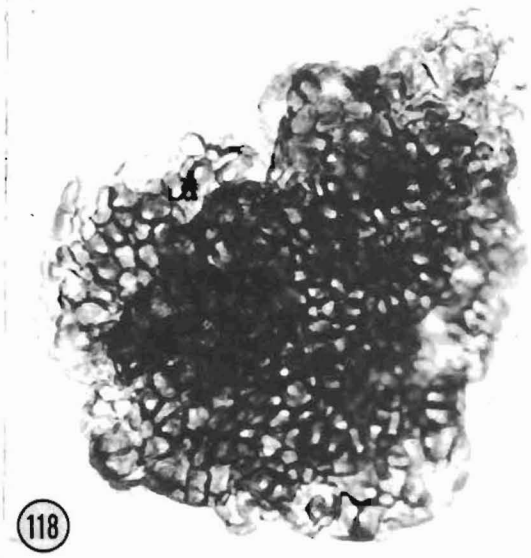

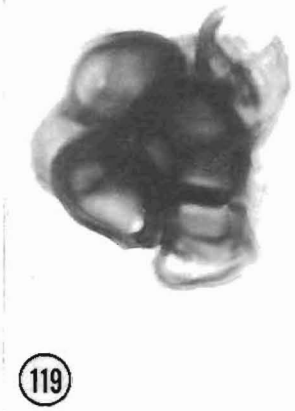

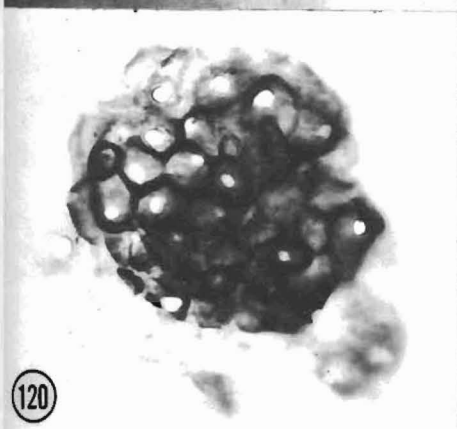

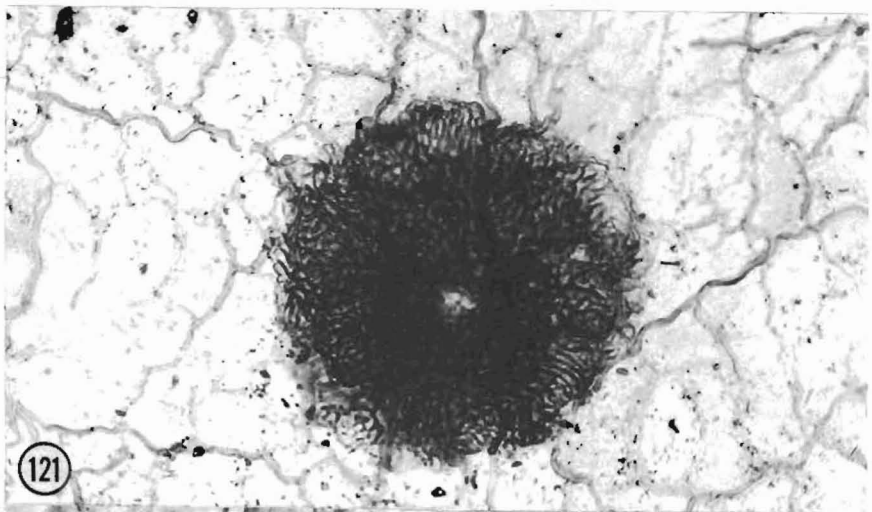

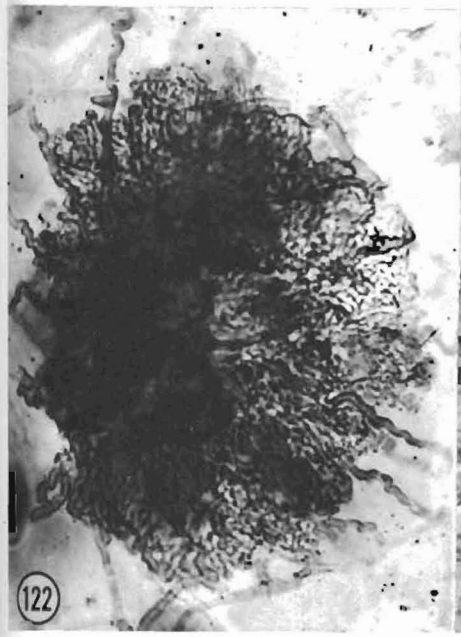

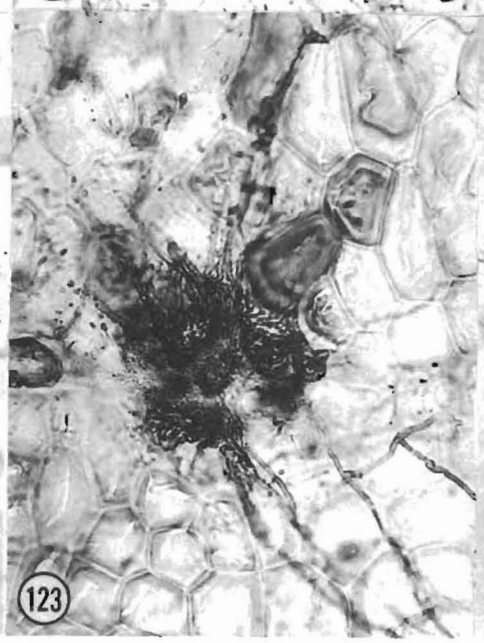

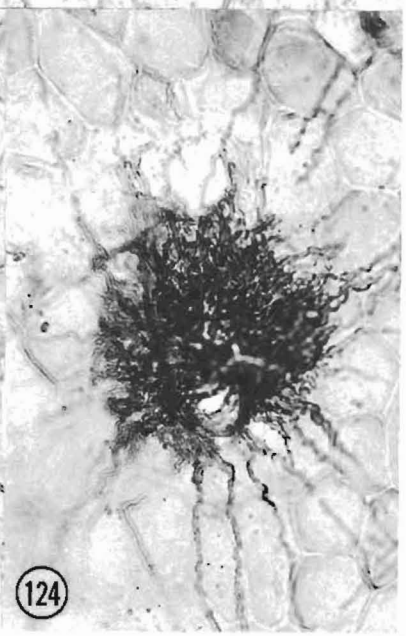

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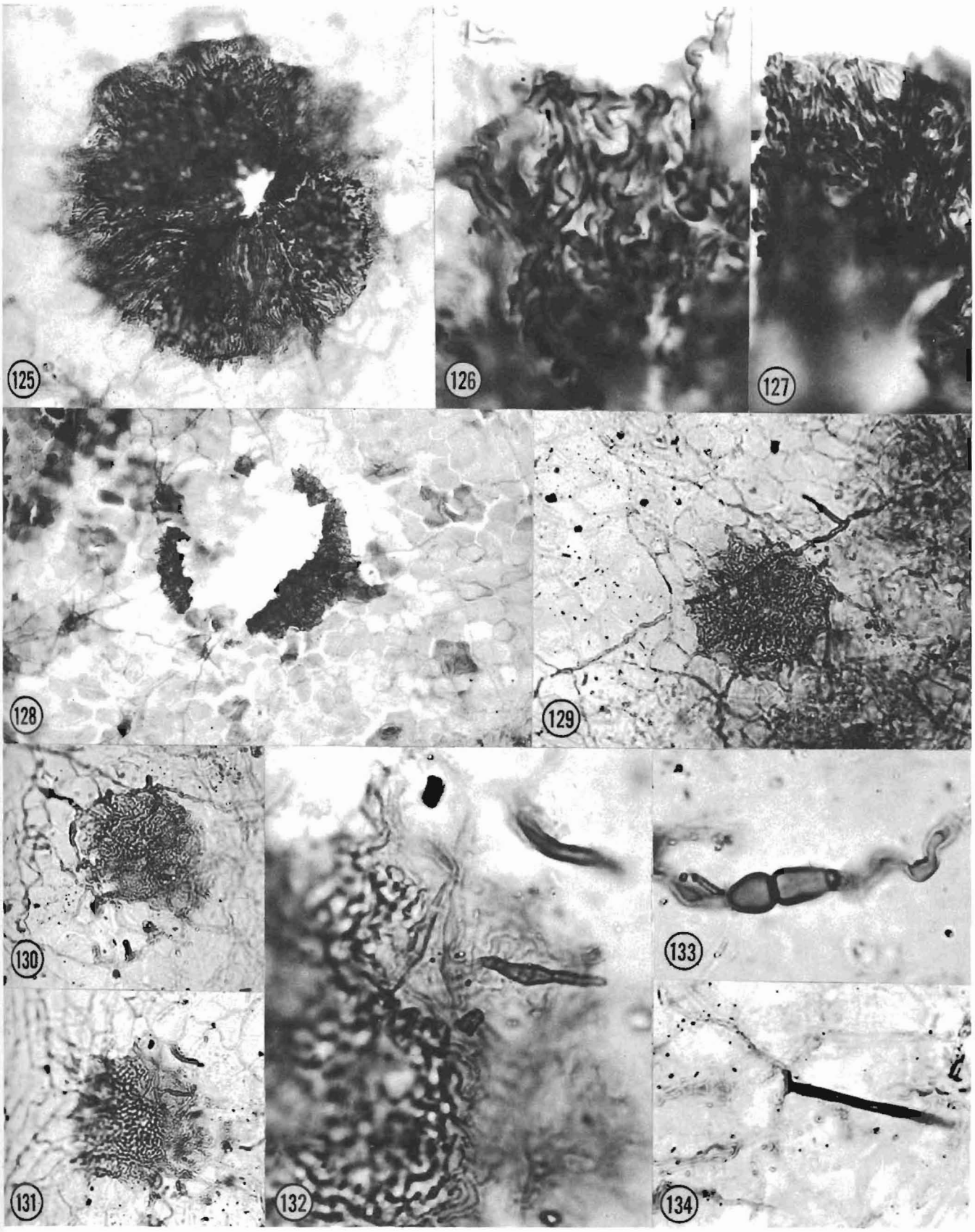

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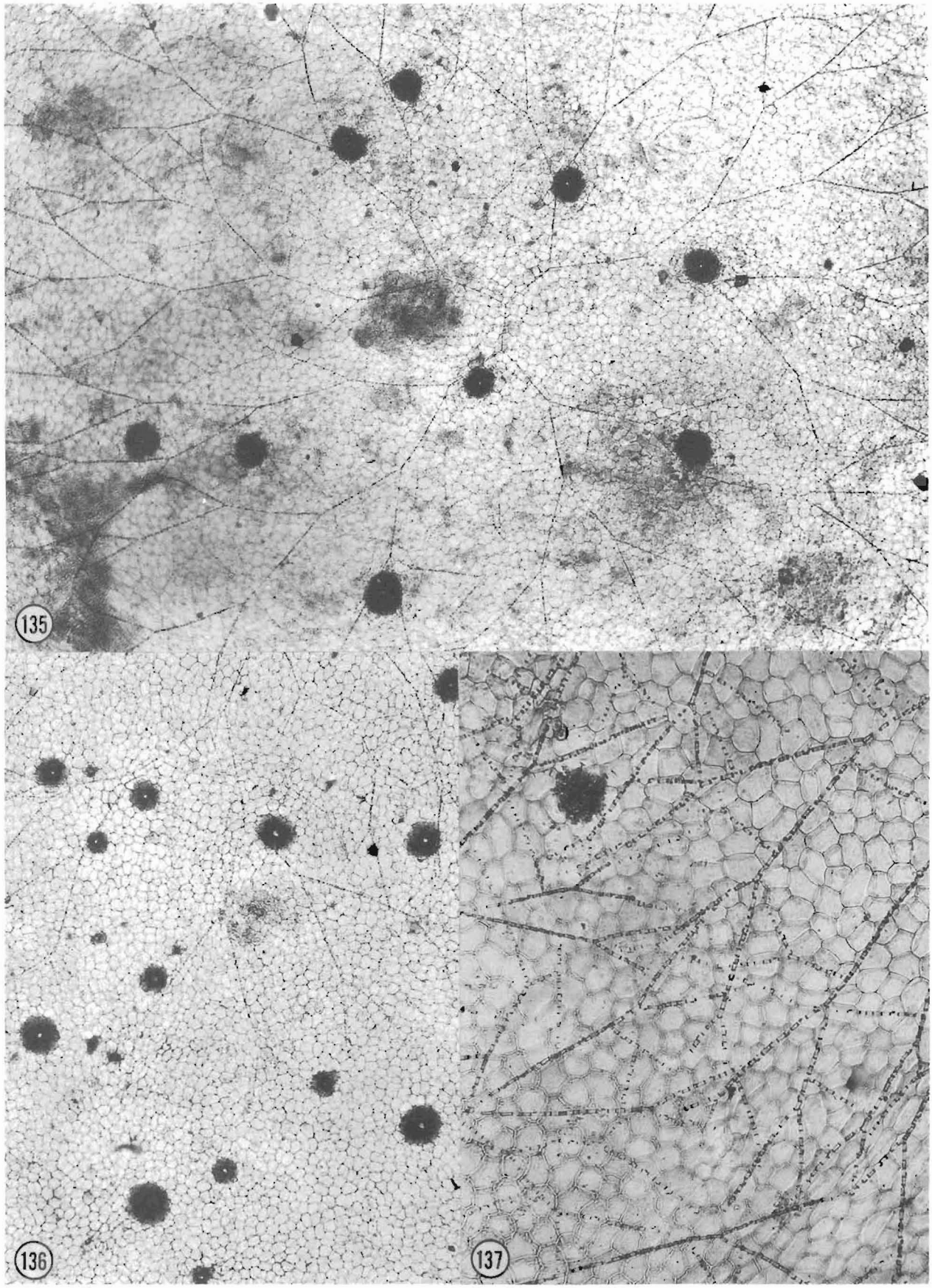

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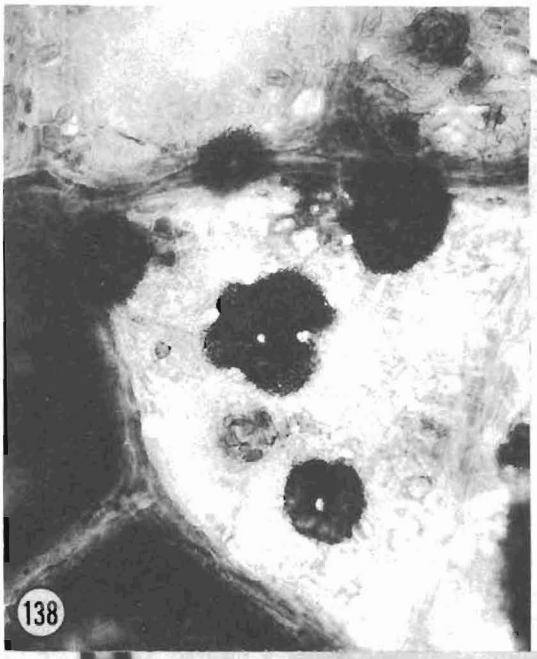
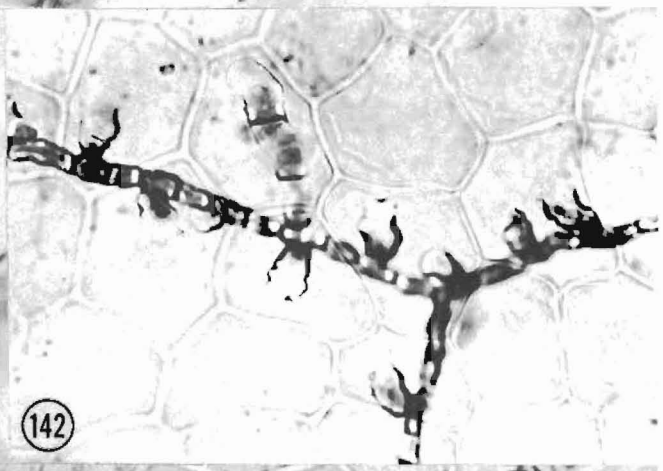
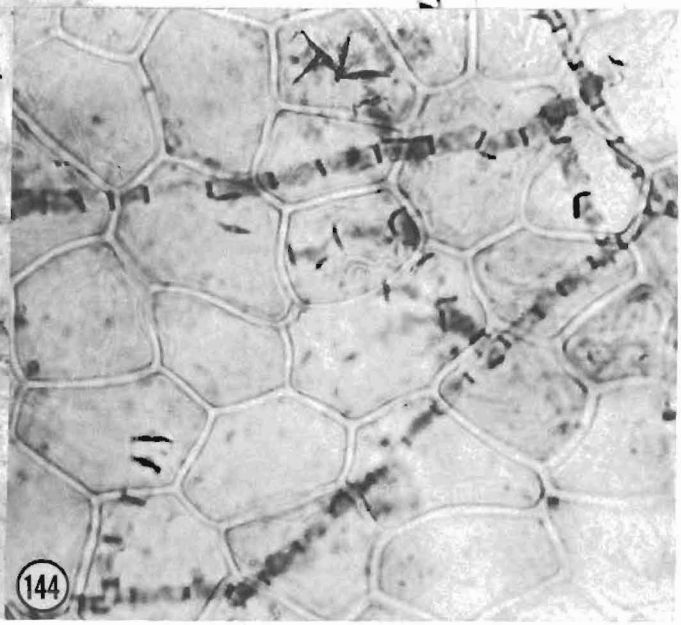
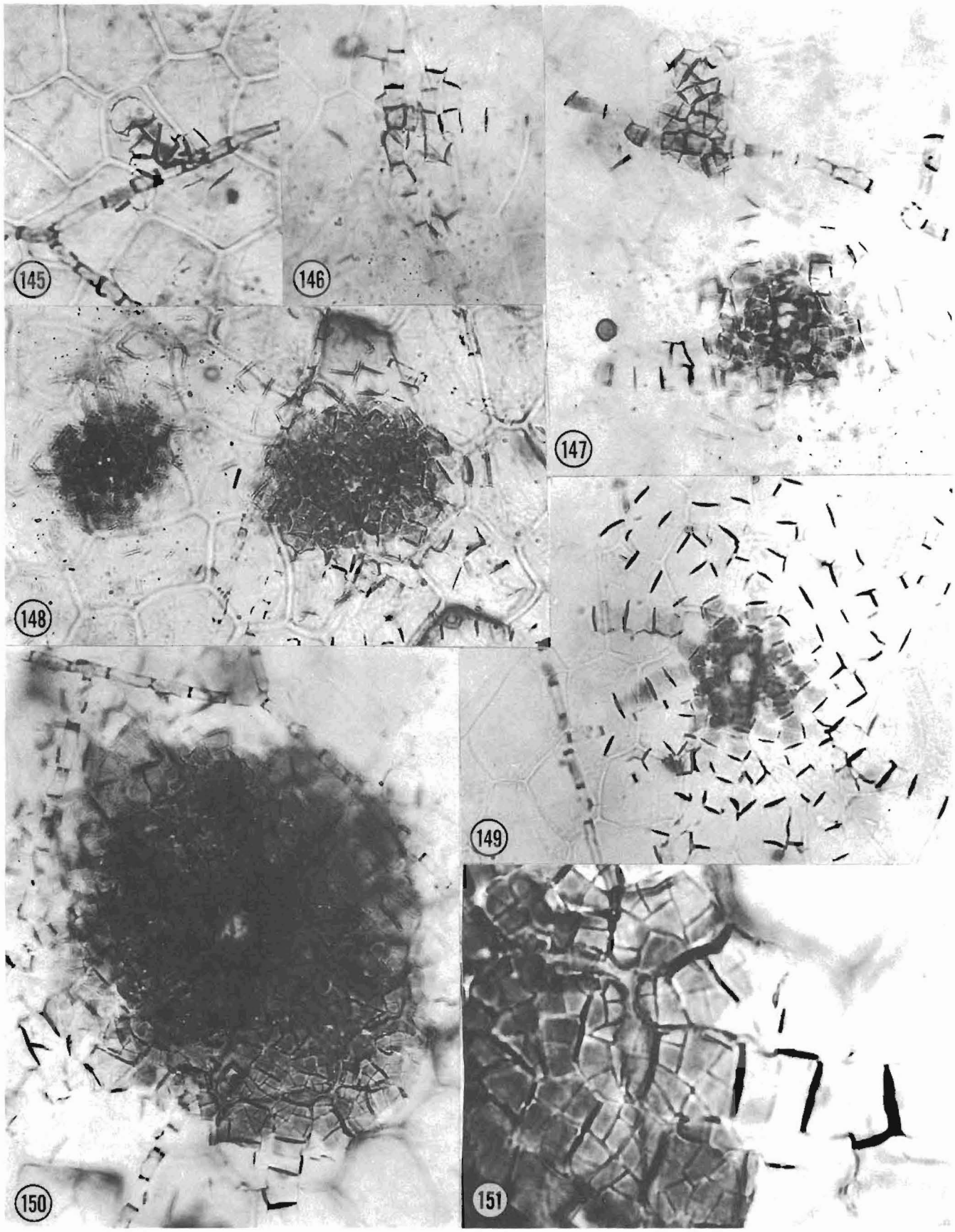






D. L. Dilcher: Epiphyllous fungi from Eocene deposits in Western Tennessee.



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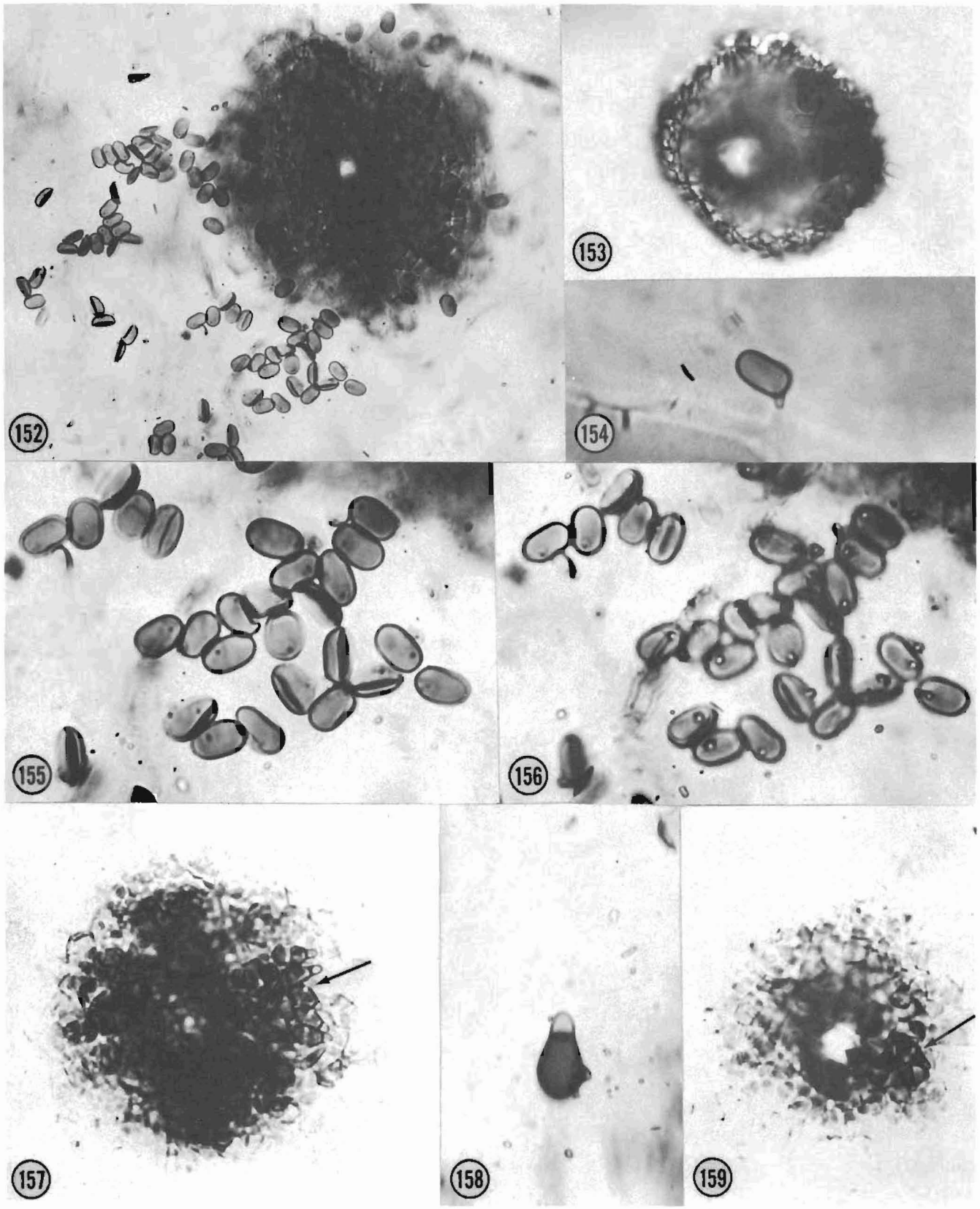
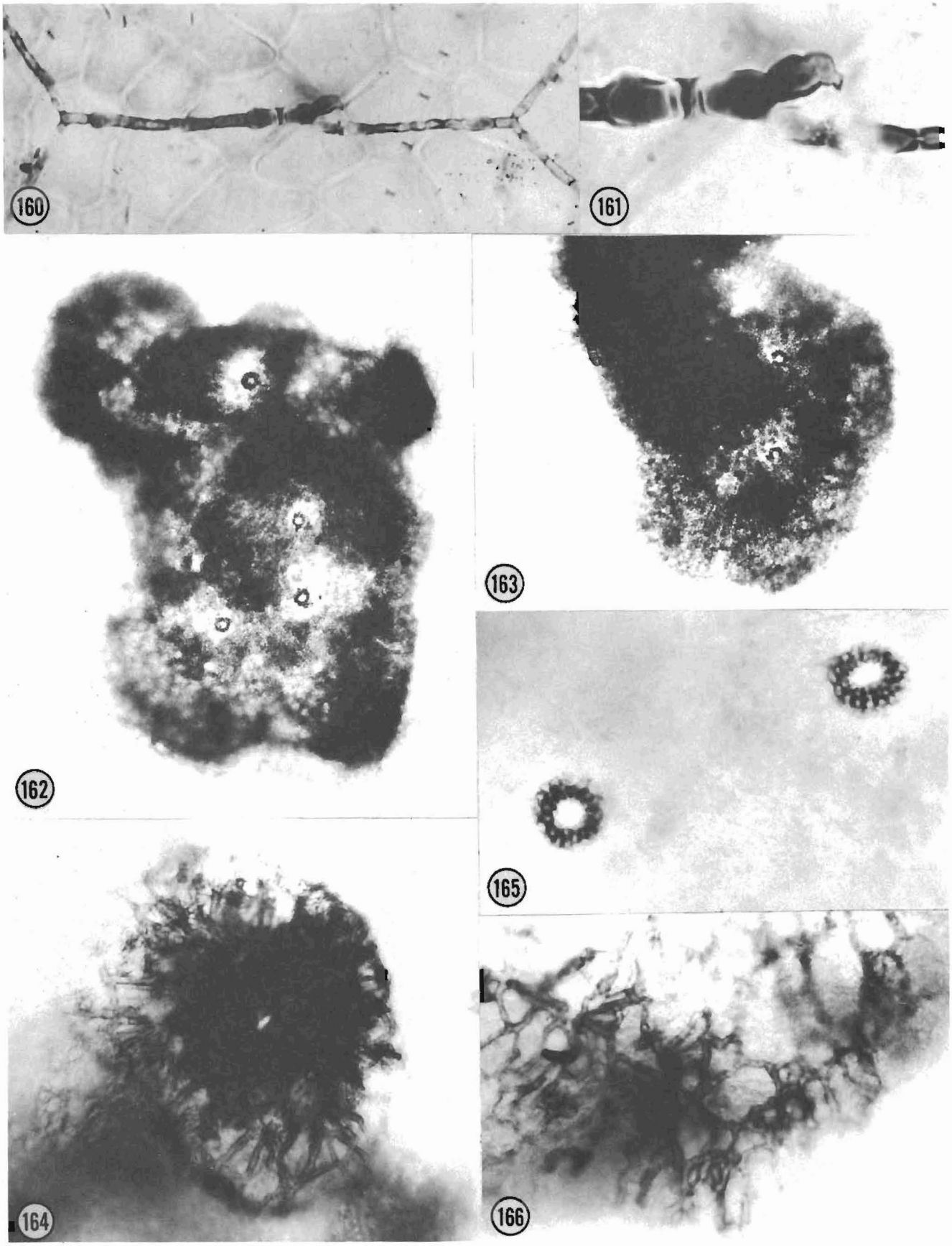
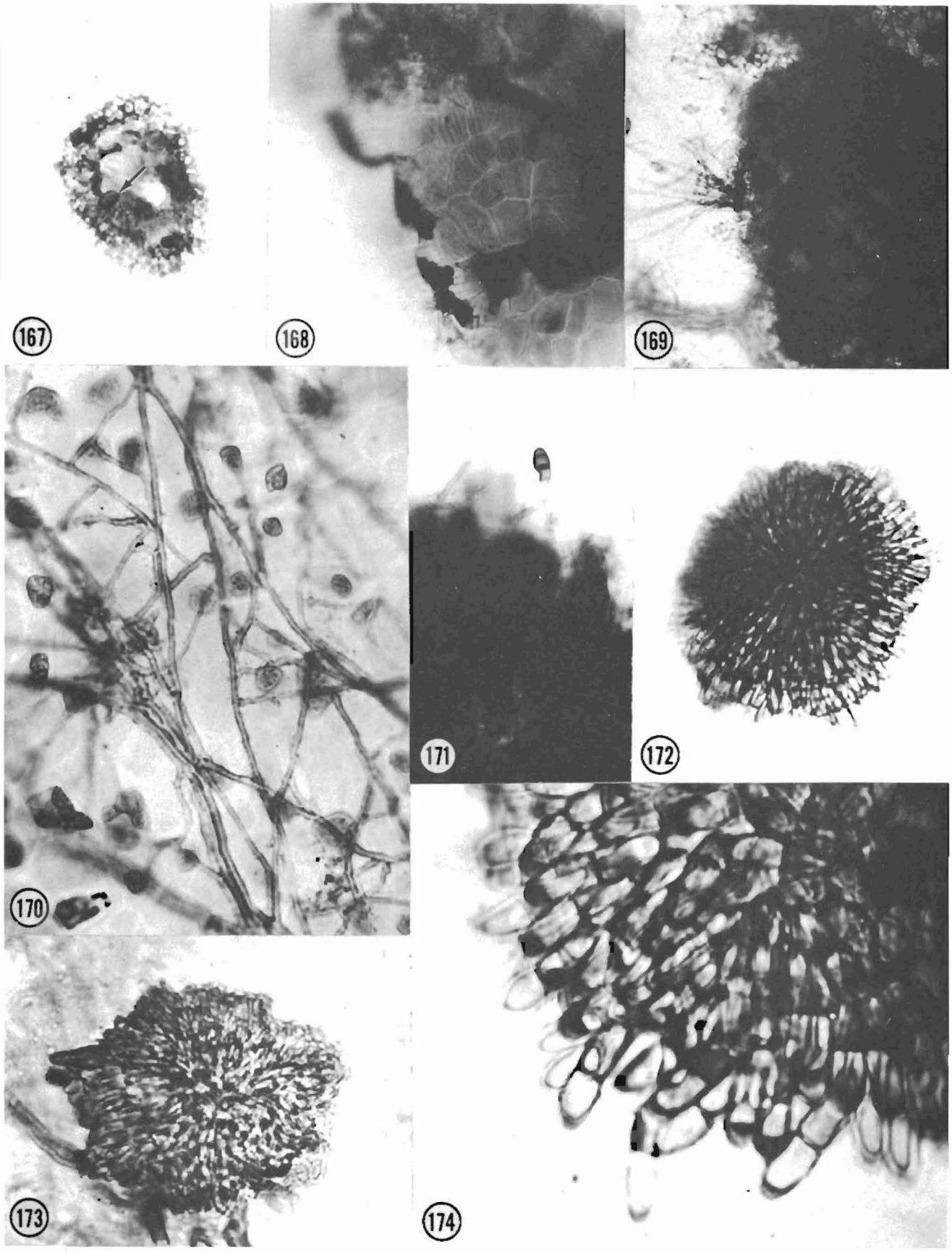


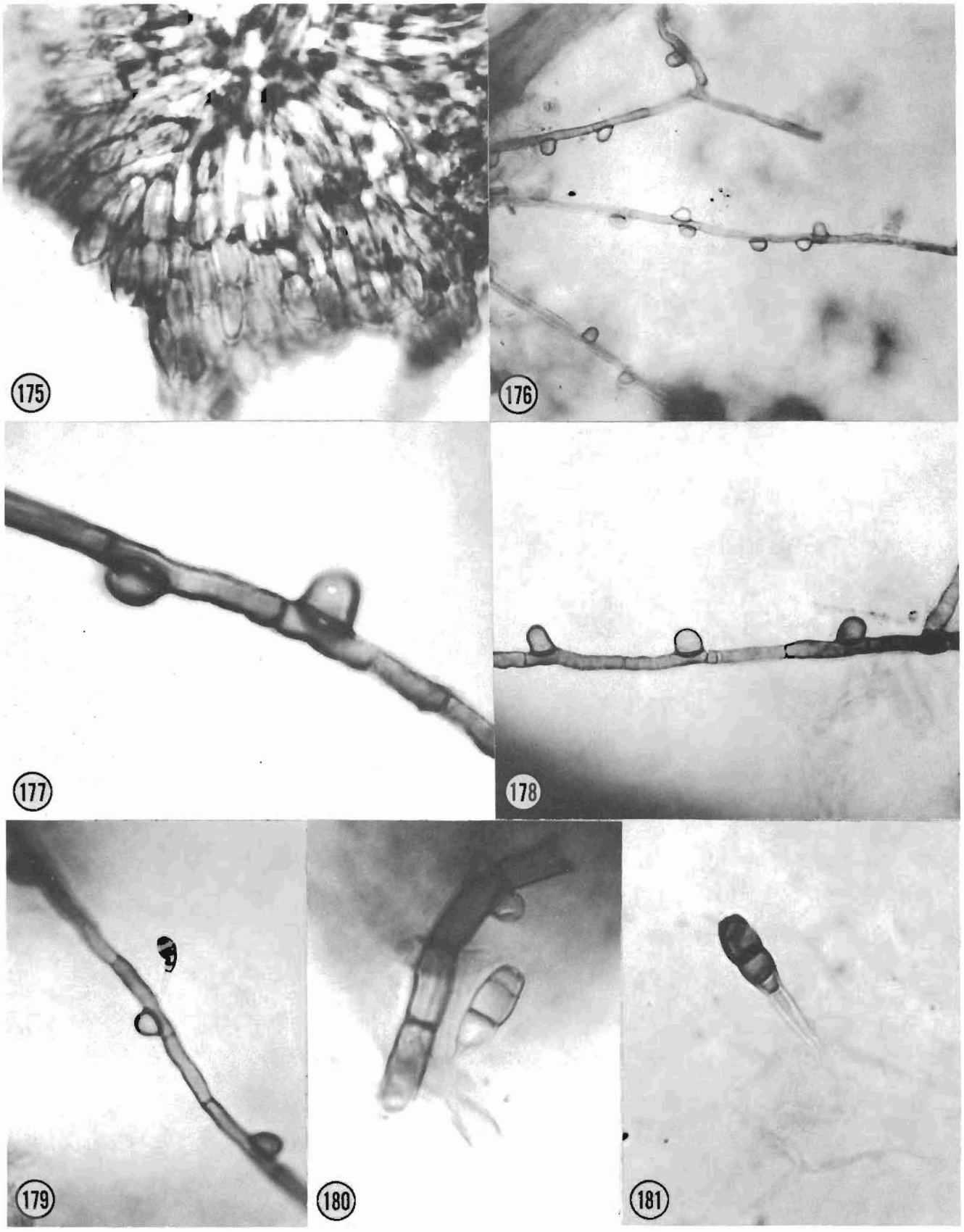
D. L. Dilcher: Epiphyllous fungi from Eocene deposits in Western Tennessee.



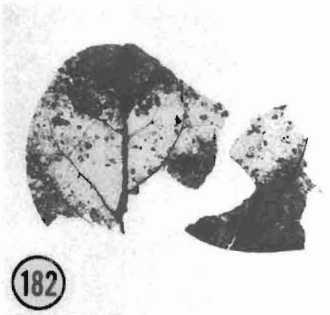
L. D Dilcher: Epiphyllous fungi from Eocene depositis in Western Tennessee.

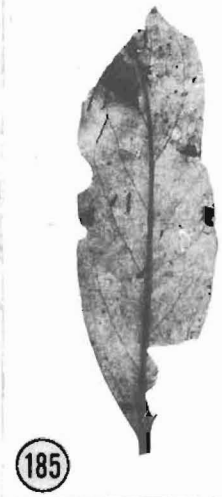


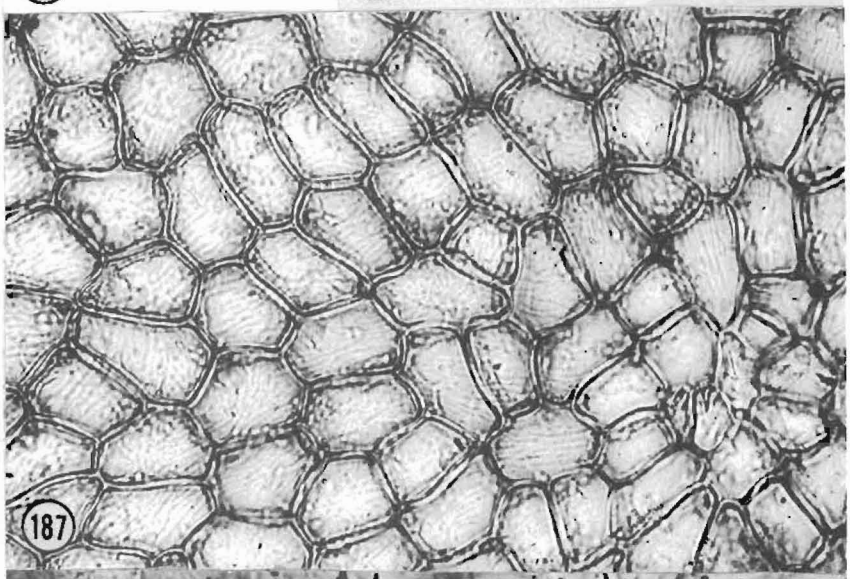
L. D. Dilcher · Epiphyllous fungi from Eocene depositis in Western Tennessee.

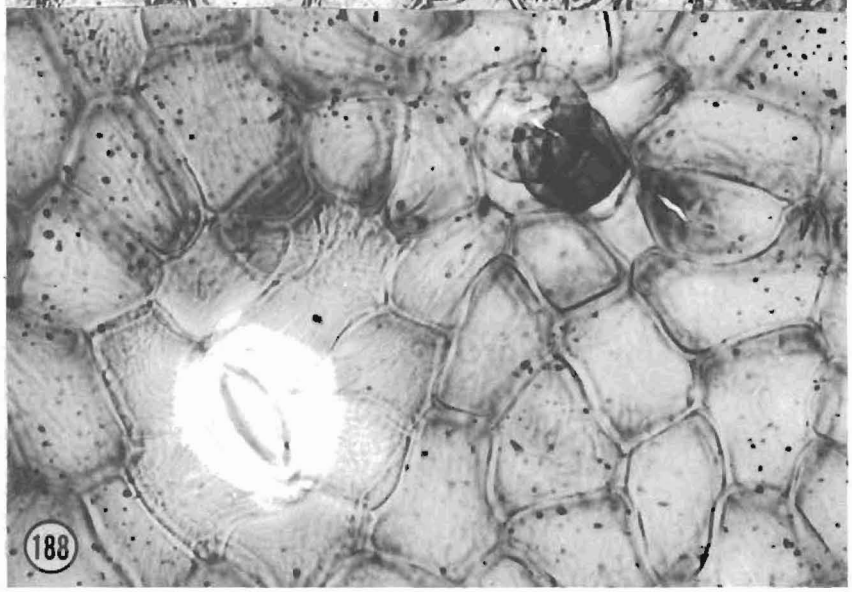


L. D. Dilcher. Epiphyllous fungi from Eocene depositis in Western Tennessee.

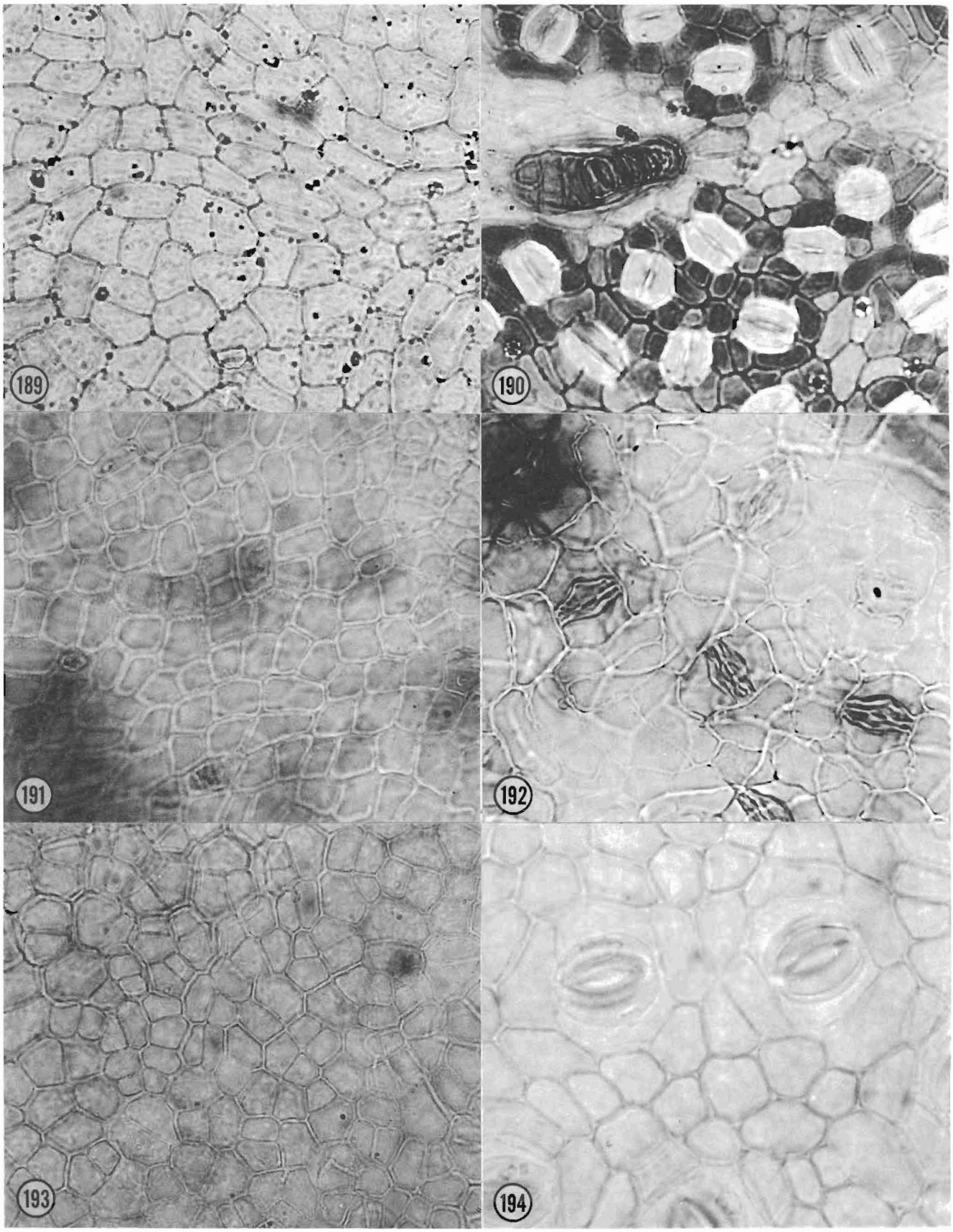








L. D. Dilcher: Epiphyllous fungi from Eocene depositis in Western Tennessee.



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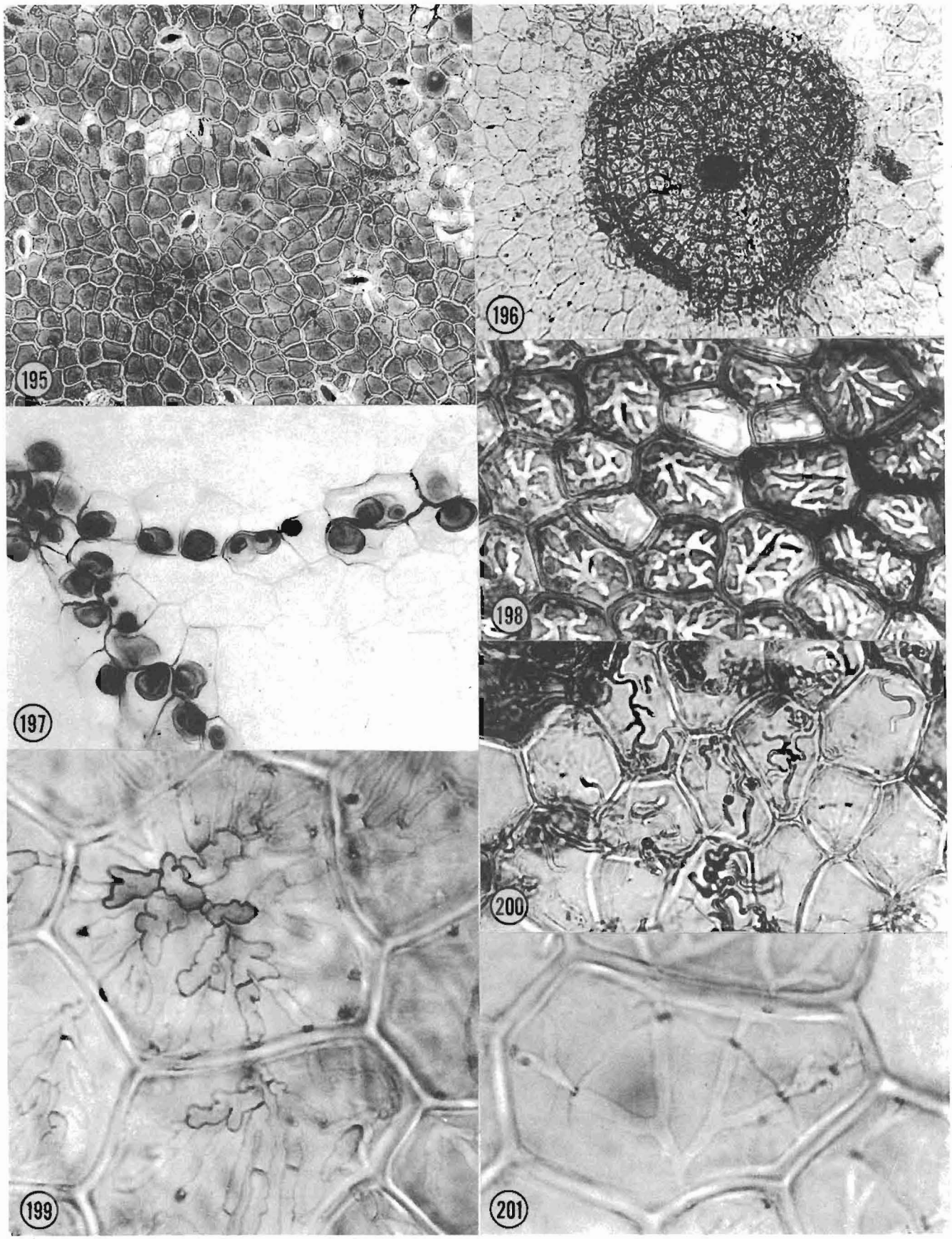

D. L. Dilcher: Epiphyllous fungi from Eocene deposits in Western Tennessee.