

A STUDY OF THE TROPICAL AMERICAN BLACK-MILDEWS^{1, 2}

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FOREWORD

The term "black-mildew" was proposed by Stevenson (1947),³ (although already used at his suggestion by Weiss (1940)), as a common name for those parasitic Ascomycetes with dark-colored, widely spreading, superficial mycelium in which small, globose ascocarps are seated. These fungi have formerly been classified with the Perisporiaceae and have been included under the general term of "sooty-molds". The epithet "sooty-mold" was found to be inappropriate, when applied to these fungi, because when handled they do not adhere to the hands and clothing as do the Capnodiaceae, for which family the name was originally coined. In the Capnodiaceae which grow on the secretions of scale insects, the black crusts are loose and easily detachable; but in the so-called Perisporiaceae they are closely appressed to the leaf surface and persistent. Because of the similarity in gross appearance of all superficial parasitic Ascomycetes with extensive dark-colored mycelium, investigators began to designate as "sooty-mold" any fungus with these characters. As a result of this practice the term has been used to include fungi of different morphologic and biologic relations.

The acceptance of the limitation of the term "sooty-mold", as proposed by Neger (1918), to the dark epiphytes on the secretion of insects, deprived the other black, superficial Ascomycetes of a common name. Arnaud (1918) tried to remedy this situation. He proposed the term "Astérinées" for the remaining superficial Ascomycetes parasitic on leaves. A perusal of his work revealed, that, aside from the dark color of the superficial mycelium, which is a characteristic of most Astérinées, the fungi assigned here vary considerably. The morphological external characters and the internal features of the ascogenous portion, divide this tribe into two structural groups.

The first group, for which we will retain Arnaud's Epithet, includes those fungi, like *Asterina* Lév., where the asci are produced in a stroma provided by a peculiar radial covering that breaks at maturity in a stellate fashion. The second structural group is represented by species in which the mycelium, like that of the first, produces crusts of radiating hyphae. In this group the ascocarp is peritheciump-like, small, globose, parenchymatous, and at maturity opens by a small lysigenous pore at the summit, or breaks out, but not in a stellate form. In the first group the ascomata are discoid and approach the Discomycetes; in the second, they are sphaeroid and resemble the fruit bodies of the Pyrenomycetes. Species formerly assigned to the

³ The year following author's name is the key to the citation in Literature Cited, p. 84.

Perisporiaceae are included in the latter. It is these that are here termed the "black-mildews".

The reasons for recognizing four different common names, representing four families of superficially occurring Ascomycetes on living leaves, will be evidenced from the discussion that follows. These four common names are "sooty-molds", "asterinaceans", "powdery mildews" and "black-mildews".

I, PROLEGOMENON

The past 50 years have witnessed a great number of changes in systematic mycology. Not only have there been established scores of new genera and families; but also, because of innumerable revisional works, the old limits of genera, families, and orders have been greatly modified. Consequently the keys in the standard works are of very limited value and in some groups an orientation is not now possible unless one is willing to undertake the *difficult and tedious search of the widely distributed literature*.

The vicissitudes suffered by the Perisporiales, a name coined by Lindau (1897) for an order of the Pyrenomycetes, have hardly been surpassed by any other group of fungi. The name was created to conform with the then current Rules of Nomenclature, thus replacing Perisporiae Fries (1823). The order has been subjected to a wide range of interpretation and, consequently, there has occurred a great deal of shifting, not only of the original genera, but of the families as well. These changes have resulted in the complete elimination of the order. However, by this action, the original genera and those later incorporated have been left, in many instances, unassigned to their respective places.

It is our belief that the time is ripe to correlate all of the available data, and at the same time, to attempt to clarify the situation in regard to the systematic position of the genera originally assigned to the family Perisporiaceae in Tropical America.

Apparently, the criterion that has guided modern authors in placing species of fungi under the Perisporiales is to be found in the introductory sentence of Theissen and Sydow's (1917) discussion of this order. They state that "Unter Perisporiales verstehen wir angiokarpe Askomyzeten mit mündungslosen kugeligen Gehäusen". The fact that they also mentioned the production of small fruiting bodies on a superficial mycelium has undoubtedly contributed to increase the diversity of opinions in regard to the limits of the group. This has led to the inclusion under it of forms of which their taxonomy has not been very clear because it has been based on weak and not well defined characters. This criterion has had the twofold effect of clumping together species which are distinct phylogenetically and excluding some others that are closely related.

In view of all the disagreement among works on the Perisporiales, following the publication of the monograph by Theissen and Sydow (l.c.), it occurred to us that we could make an adequate disposition of the genera only after a compilation of the literature, accompanied, when possible, by the study of critical material.

A. HISTORY

The first attempt to bring together these superficial forms was made by Winter (1887). He included under "Perisporiaceen" two subfamilies, Erysipheae and Perisporiae. Later Lindau (l.c.) revised Winter's concept and added the family Microthyriaceae, the members of which had been distributed by Winter under Perisporiae. After considerable study of these forms, Theissen (1913) excluded the Microthyriaceae from the Perisporiales and transferred them to his new order Hemisphaeriales. Saccardo (1913) divided the family Perisporiaceae into five tribes, none of which included the Microthyriaceae.

The modern concept of the group dates from Theissen and Sydow's (l.c.) revision of the order. In that publication four families are included: Erysiphaceae, Perisporiaceae, Englerulaceae, and Capnodiaceae. As there delimited, the order and many of the genera are not equivalent to those of the same names used by Lindau in Engler and Prantl's classification. It is clear that Lindau included in his order fungi of different characters merely because he regarded it as a temporary resting place for imperfectly known forms. The absence of a definite ostiolum was the sole basis for the inclusion of a superficial Pyrenomycete under the Perisporiales. It is curious to note, however, that this principal characteristic, the absence of an ostiolum had already been abandoned as a critical character by Fries (1823), the originator of the name "Perisporiae".

In recent years, much revisional work has followed the Theissen and Sydow contribution. Because the type-genus *Perisporium* Fr., does not correspond with the description, as Saccardo (1882) had discovered, Gwynne-Vaughan (1922) substituted the name of the order by Erysiphales based on the second oldest genus *Erysiphe*. In this, she has been followed by Bessey (1935), who, since *Perisporium* Fr. is untenable because the genus was typified by an imperfect fungus, accepted the change. He also substituted for the family name Perisporiaceae that of the best known genus *Meliola*, thus calling it the Meliolaceae. However Hansford (1946) recognized the Erysiphales in an entirely different and restricted sense, limiting the name as Arnaud did (1925) before him, to the "powdery-mildews". Martin (1941) raised the Meliolaceae to ordinal rank, as the Meliolales, and recognized two families: Meliolaceae and Englerulaceae. Arnaud (1918) considering

that all the superficial forms constitute a biological entity, proposed the name "Astérinéés" for the entire assemblage, including some of the Perisporiales. The name "Astérinéés" is rather confusing because of its similarity with that of the genus *Asterina* Lév. Among the Astérinéés Arnaud created the "Meliolinées" for the group with globose, superficial fruit bodies and mycelium with hyphopodia. This name is also used by Stevens (1927). Spegazzini (1918) distinguished between the biophilous and saprophilous species, reserving the older name Perisporiaea for the latter, and introducing Meliologiaea for the former. Gäumann and Dodge (1928) recognized the Perisporiales with three families: Erysiphaceae, Capnodiaceae, and Englerulaceae.

The latest treatments of the group are those of Hansford (l.c.) and Bessey (1950) in none of which appears the name Perisporiales. Hansford distributed the superficial forms among several orders, such as the Dothideales, Hypocreales, Sphaeriales and Erysiphales; while Bessey included six families under the Erysiphales: Erysiphaceae, Meliolaceae, Englerulaceae, Capnodiaceae, Trichothyriaceae and Atichiaceae. Miller (1949) excluded the Erysiphales from the Pyrenomycetes and placed them with the Plectomycetes.

In respect to the Capnodiaceae, Woronichin (1925) separated the family as a distinct order, Capnodiales; but Arnaud (1911) and also Fisher (1939) maintained that the members of this family belong to the Sphaeriales or the Dothideales. V. Hohnel (1917a) did not include the Capnodiaceae in his arrangement of the order Perisporiales; but Clements and Shear (1931), like Saccardo (1913), did so and in addition to the Capnodiaceae included six other families, one of which they called Perisporiaceae. Wolf and Wolf (1947) accepted the order name Erysiphales but recognized the Capnodiaceae as one of its families. Fisher (1933) used the name Capnodiaceae for a group of her "sooty-molds" and Perisporiaceae for another.

In the more recent treatments of the Ascomycetes, especially those of Miller (l.c.) and Namndfeldt (1932) the Perisporiales are entirely eliminated but no disposition of its components is made.

The above brief account of the many shiftings and concepts of the old order Perisporiales shows that there has been no accord among the several investigators as to its characterization and limits. Winter (l.c.) had already perceived the untenability of the order when he expressed the opinion that "die zum Teil sehr gut naturgemassen Anschluss bei Familien der Sphaeriacen finden können". Jaczewski (1894) found Winter's characterization deficient and after considering the order as purely artificial and heterogeneous, said that the species are united "pour caractère commun unique l'absence d'overture au sommet du perithèce".

Not only have there been shiftings due to diverse morphological interpretations of the order; but also, because its type-genus *Perisporium* Fr. was based on a saprophyte, the biological relations of its members have been altered. As originally conceived, the species comprising the group were saprophytic. According to Arnaud (1925) "elles . . . par conséquent, ne sont pas arrangés dans les fumaginées". Fumaginées is the French equivalent of "sooty-molds" and these have been defined by Neger (1918) and Fisher (1933) as pure epiphytes, thus complicating the interpretation of the order.

In an attempt to clarify this seemingly chaotic situation, we have examined as many available members of the group as possible. The criteria as to the limits and characters of the genera included herewith are those of their respective authors. The interpretation of the taxonomic position of the genera concerned, as will be evidenced from the discussion, is that of Miller (l.c.). We feel that he presents clear-cut characters to differentiate the various orders and a good working basis for ordinary determinations.

Since considerations of climate, geographical distribution, host relationships, and economic importance form a major part of the whole picture and contribute to a clearer understanding of the problem involved, these will also be considered here.

B. CLIMATE

To understand the climatic limitations of the old order name Perisporiales, as generally interpreted, one has to take cognizance of the habitat relations of its individual members. The ever-changing influences of the external environment are continually operating upon those species with external mycelium and fructifications. Species in which the mycelium is internal do not escape this influence either, since their fruiting bodies emerge to the surface of the hosts and, therefore, are exposed to the air.

Our observations in the Andes of Venezuela and Colombia and in the dry coastal plains of Cuba, Santo Domingo, and Puerto Rico, have convinced us that a constant humid atmosphere is an essential requirement for the abundant presence of these fungi; this of course, provided that the appropriate hosts are also present. As will be shown on page 36, these fungi, like the rusts, are restricted in their host relationships. Whether temperature plays any important role, cannot be implied from the data on hand. The fact that *Meliola nidulans* (Schw.) Cooke occurs as far north in the temperate zone as Switzerland, (Neger 1903) and as far south in the torrid zone as Colombia, (Toro 1930) is evidence that it is dependent upon the presence of the necessary host under the adequate environmental conditions. In epiphytotics of "powdery-mildews" in temperate climates it has been found

by Cherewick (1944) that temperature affects certain of these fungi indirectly, by increasing or decreasing the vigor of the host, rather than by acting upon the pathogen. In the Tropics the "black-mildews" are of importance, economically, because here humid conditions prevail during the growing season.

There is no doubt, that a definite correlation exists between rainfall and the number and extent of the colonies of these fungi. They are very susceptible to desiccation, although the thick-walled mycelium has the appearance of a xerophytic structure. Arnaud (1918) stated that the influence of a humid atmosphere is not only physiological but morphological as well. Fraser (1937) maintained that "notwithstanding the exposed nature of their habitat; the growth of "sooty-mold" fungi appears to be very sensitive to variations in the degree of atmospheric humidity". She (1933) observed that in New South Wales these fungi are abundant throughout the year but, more so, during the winter months (rainy season); while Arnaud (1910) claimed that in southern France, the dry summer conditions are not favorable for "fumaginée" development. Our own observations at Turrialba, Costa Rica, where the precipitation throughout the year is extremely high, reveal that humidity and not rainfall is the controlling factor in that environment.

Wind also exercises its influence by drying the surface of the leaves. Our findings on the Eastern Andes of Colombia testify to this. *Clethra brevifolia* Benth, is a small shrub that occurs on both sides of the Cordillera. The hot winds blowing from the plains favor precipitation on the windward side and insure the presence of a continuous sheath of damp air. The leeward side is drier. On the windward side there is not a single leaf of the shrub that is not infested with *Meliolina Chardoni* Toro; while not a trace of the fungus appears on the leeward side. On the other hand, at sea level in Puerto Rico and Santo Domingo there is an abundance of "black-mildews" and "sooty-molds". Here the temperature is high; nevertheless, fungi of this type are as prevalent as they are high up in the mountains where high humidity and low temperature prevail. In the case of the fungus on *Clethra* it may be interpreted as a response to the requirements of humidity and temperature in the altitudinal distribution of the fungus species. Diehl's (1937) definition of his so called "life-zones" are well illustrated by these conditions.

C. GEOGRAPHICAL DISTRIBUTION

When the tribe Perisporiae was first established by Fries (l.c.) only a few forms of general distribution were included and no speculations were made at the time in respect to their geographic distribution. However, when more genera and species were added and the geographical limits of many

forms became known, all workers began to recognize Fries' (1828) earlier observation when he assigned species to *Meliola*. "Genus in tropicis vulgatissimum ut Erysiphes in terris temperatis". The statement has been interpreted by all subsequent authors as meaning that the Erysiphaceae are temperate in distribution and the Perisporiaceae, tropical.

The discovery of many perisporiaceous forms in Temperate Zone climates and the recent reports of the ascigerous stages of *Erysiphe* in the Tropics (Seaver (1930), Abbott (1932)) demonstrated that Fries' original opinion is not entirely correct. It is true that the center of distribution of the Meliolaceae and other superficial Ascomycetes in tropical America is located between 20° N. latitude and 20° S. latitude; but it is also true that many erysiphaceous forms occur below the middle limit of the northern distribution and above this range, the two blend. It seems more proper to think, in harmony with the natural conditions, that the intensity of atmospheric humidity is the controlling factor in the geographic distribution of these fungi. They are more abundant near the tropical rain forests and also on the eastern portion of the Americas where a blanket of moist air is constantly covering the land. Neger (1903) observed that in cold climates *Meliola nidulans* (Schw.) Cke. developed only on the branches which are covered with moss. This observation strengthens the above statement because the moss maintained a constant humidity in the vicinity where the fungus grew.

The fact that with very few exceptions, conidial forms are absent in the Perisporiales is a point to consider in this connection. Another feature is the special adaptation of the ascus in some members of this group to absorb water during spore dehiscence. This may explain why the oidia of the Erysiphaceae often, in the absence of ascocarps, occur wherever the appropriate hosts grow; while many Perisporiaceous forms are absent from certain places.

The map in figure 1 shows that the geographical distribution of the "black mildews" follows a high incidence of humidity. We may conclude, therefore, that with certain broad limitations of temperature, they are abundant wherever there is an adequate supply of rainfall accompanied by high air humidity.

If we examine the records of *Meliola*, the genus most extensively studied in the group, we find that it follows the distribution of rainfall, and that temperature is of secondary importance. The species not only occur on the Equator, but in the mountains of France and Switzerland as well. However, the highest incidence of individuals and of species in the genus *Meliola* is from the Tropics; that of the Parodiopsidaceae is the highlands of inter-tropical regions; while the Pseudosphaeriaceae extend into extratropical climates.

D. HOST RELATIONS

As interpreted originally, the Perisporiales of Lindau (l.c.) included species growing upon a wide variety of substrata. The concept began to change



FIG. 1.—Map showing the geographical distribution of the black mildews and powdery-mildews: Meliolaceae ..□ ; Parodiopsidaceae ..○ ; Erysiphaceae ..● .

gradually until Spegazzini (1918) proposed the subdivision of the order into biophilous and saprophilous forms. The increment given to the foliicolous species by the different authors altered the interpretation of the order Perisporiales to such an extent that Theissen and Sydow (1917) do not

mention in their monograph a single saprophytic genus of the Perisporiaceae, except perhaps *Teratonema* Syd., which they report as occurring on bark. As only foliicolous or fungicolous species are today included in the group, a discussion of its biologic relations seems proper at this time.

1. Follicolous Species

The species occurring on the surface of leaves are all strict parasites as shown by the studies of Ward (1883), Maire (1908), Ryan (1926), and others. In this connection, the whole assemblage of external superficial forms comprises a closely related biologic group. They may differ in separation and color of the spores, type of fruiting body and position and color of the mycelium; but all agree in making contact with the living cells of the host through a more or less extended internal mycelium, and that this mycelium, when intercellular, sometimes produces haustoria. An exception is the Meliolaceae in which the haustoria arise from the external mycelium and are limited to the epidermal cells. Their origin is from underneath the capitate hyphopodia and the epidermis is not invaded except through the cuticle. Several cells may be penetrated in succession and then a necrotic spot of two or three epidermal dead cells may be observed under the high power of the microscope, or this necrosis may extend beyond the subiculum and then a spot becomes visible to the naked eye. Whether this killing of the cells is caused by a poisonous substance produced by the fungus or represents a defense mechanism of the host cannot be stated from the data available. However, in *Meliola chaetocloae* Stevens, where there appear as many necrotic spots as there are small colonies of the fungus, there seems to be a combination of both types of reactions. In *M. capsicola* Stev. there is a special discoloration of the cells surrounding the haustorium. *Toroa* Syd. is entirely cuticular and branches of the mycelium extend only intracuticularly, parallel with the superficial hyphae. In this respect this fungus is not parasitic, as no living cells of the host appear to be infested.

In species where there is invasion of the mesophyll, penetration may take place through the stomata. A feature that serves to differentiate the Paradiopsidaceae from the other Pseudosphaeriales is that the mycelium in the former do not penetrate beyond the palisade layer. However, in all cases, the mycelium is intercellular and infection is accomplished by haustoria.

There is no record of the time infection takes place or of the condition of the host necessary for infection. Our experience is that these fungi are not evident on young foliage but that only leaves that have already reached maturity are obviously infested. The cases of *Lasiostemma melioides* Th. and of *Meliola mangiferae* Earle exemplify this conclusion. In every instance observed there has been a complete coverage of the leaves of their

respective hosts, except the young ones. It appears in these particular cases that only mature leaves of susceptible hosts show signs of infection.

2. Fungicolous Species

The mycelium of the hyperparasite clings tightly to that of the host and envelopes its hyphae with a web of narrower threads. It has been observed that parasitized species tend to reduce the number of their fruiting bodies and even to become sterile. Close examination of such species has revealed that the hyperparasite usually fruits not on the mycelium of the host but upon the young ascocarps, where there is an increased amount of nutrients. This observation suggests biological control for those species that parasitize crop plants and which at the same time have hyperparasites.

E. ECONOMIC IMPORTANCE

The fact that these fungi develop on the surface of the leaves leads one to believe that they interfere with the photosynthetic process, thereby reducing the efficiency of these organs as a food-manufacturing mechanism. Since they also penetrate the host cells, either through haustoria or by direct ingress, they are likely to cause damage by depriving the parasitized cells of some of their nutrients. It was pointed out on page 33 that the Meliolaceae are exclusively epidermal in their association with the host and that in some cases there is evidence of necrotic damage, while in others, there is no apparent injury. The whole gamut of the host-fungus relations run from apparent symbionts to definite parasites with necroses. The Parodiopsidaceae are less extensive in their superficial habitat; but they penetrate deeper into the tissues of the host. The upper mesophyll is invaded and haustoria are sent into the cells. When a great many cells are invaded, there is a leaf-rolling, like that in *Parodiopsis Stevensii* Arn.; but unlike that in the Meliolaceae, there are no known necrotic lesions caused by members of this group. Their symptoms are thus hypoplasitic in nature.

All of the Capnodiaceae so far known are epiphytes upon scale insects or other fungi. The fungicolous Parodiopsidaceae develop only upon other fungi, usually on or near their fruiting bodies.

In all the "black-mildews" the interference with transpiration and photosynthesis is the result of the activities of the external mycelium. The damage to the host cells as degradation of nutrients, comes from the internal mycelium. Since both the external and the internal mycelium differ in place, time and structure, they are discussed in connection with the morphologic characters (page 36).

Few plants of economic importance are subject to serious attacks of these fungi. Sweetpotatoes, pepper, avocados, mangoes, coconuts, cocoa, coffee,

and citrus are among their economic hosts, but since the damage is slight, and furthermore, is restricted to leaves and does not occur to the fruits, the affected plants always produce a sound crop.

II, MORPHOLOGICAL FEATURES

As stated on page 29, the external environment exerts a great influence upon those fungi which live upon the surface of their hosts. The accompanying map of their distribution (fig. 1) also shows that they abound in regions of high humidity and bright sunlight. It is not impossible then, that under the influence of a constantly humid surrounding, forms with diverse origins might have suffered such evolutionary changes that, at present, they show convergence in a number of common morphological characters. An acceptance of such possibilities will only then justify the erection of the Astérinéés as a unified group, although, as Arnaud (1918) stated "qui ne constituent pas une entité systématique, mais bien une remarquable unité biologique et surtout climatologique". A classical example of this probable convergent evolution is found in the *Meliola*-*Actinodothis*-*Amazonia* complex. Here the character of mycelium, hyphopodia, asci, and spores are like those in the Meliolaceae, the stromatic covering forming the ascocarps are, on the other hand, dothideaceous, coccoideaceous, or microthyriaceous, respectively. V. Hohnel (1917) and Ryan (1926) studied the development of the fruit bodies in *Meliola* and the Microthyriaceae and found some fundamental differences in the two. Ryan (l.c.) stated that *Amazonia* develops like the Microthyriaceae. Our observations in *M. capsicola* show that this species possesses both microthyriaceous and meliolaceous types of development.

Numerous observations of these fungi tend to point toward the presence of identical characteristics not only in respect to the mycelium, but to host relationships as well. A possible explanation for the existing discrepancies may be found in the several interpretations given to the particular structures. The following discussion of their morphological features will perhaps help in elucidating this problem.

A. THE MYCELIUM

The foliicolous species comprising the superficial Ascomycetes form black crusts on the surfaces of their hosts, hence the term "sooty-molds" often erroneously applied here. The mycelium radiates from an epicentrum, clinging to the surface in a way that reminds one of the "runners" of certain flowering plants. This mycelium is distributed externally and internally; each type playing a different role. The internal functions in the absorption of nutrients; the external in growth and reproduction. Penetra-

tion of the external mycelium is either through the cuticle or the stomata, the former being more common.

1. Internal Mycelium

This portion of the vegetative structure of these fungi is limited to that which lies inside the host tissues. Contact with the living cell is invariably made by haustoria that penetrate it. In this respect the foliicolous superficial Ascomycetes are, like the rusts, strict parasites. Although Bornet (1851) was among the first to call attention to the fact that certain species of *Meliola* caused damage by discoloring the cells underneath, it was left to Maire (1908) to prove that these blemishes were produced by the action of a prolonged association of the haustoria with the living cells. Our observations demonstrate that this killing is restricted to host cells beneath the older portions of the mycelium and also that the hyphae immediately above, die simultaneously. We have seen numerous cases in which there has been a complete disappearance of the fungus tissue from the center of the dead spot, but that further on, upon living tissue, the mycelium continues growing. This is an analogous situation to that occurring in *Marchantia*, where the plant dies from behind, but these fungi die because they cannot derive nutrients from necrotic host cells. The Meliolaceae, as well as some other fungi with hyphopodia, lack internal mycelium. They make contact with the host only at the epidermis, by means of a haustorium that penetrates the cuticle. In all cases, however, the internal mycelium is thinner than the external and lacks its dark coloration. It is always intercellular and in some groups is restricted to the epidermis, in others it extends to the palisade; but it very seldom invades the spongy parenchyma, unless it has first penetrated through the lower surface of the leaf.

2. External Mycelium

In general, the external mycelium attains an unmistakable physiognomy, in spite of the presence of occasional structures in particular groups (hyphopodia, setae, nodules, etc.). Its characteristics are well determined and hereditarily fixed. It is brown, cylindrical, tough, and may or may not bear setae, hyphopodia, or nodules. In the Capnodiaceae the cross walls are near each other, giving the mycelium a moniloid appearance; in all other groups, the transverse septa are far apart. The hyphae are closely appressed to the surface of the host and no instance has been observed in which one branch of the mycelium crawls over the other. Whenever two hyphae come in contact, either at the tip or the sides, they anastomose.

In the Meliolaceae, which we have studied in detail, the capitate hyphopodia have the characters of appresoria. Each possesses a round central

body indicative of the penetration canal into the cuticle. Martin (1885) was the first to qualify the hyphopodia of *M. manca* E. & M. and to call them haustoria. However, Marie (1908) following Gaillard's (1891) implications insisted that "Les hyphopodies capitées ne sont autre chose que les premiers rudiments des périthèces". This conclusion is partly right. We believe that the function of hyphopodia in ascocarp formation is incidental. The abundance of nutrients near the source of absorption facilitates the development of the reproductive structures. The same relation exists in those species penetrating the stomata in that the ascocarps are produced from stomopodia at the place of entrance.

B. THE ASCOCARPS

Although in these superficial foliicolous Ascomycetes there is a close analogy in the character of the mycelium, this does not hold true for the fruiting bodies. Those of *Amazonia*, for example, are so distinct from those of *Meliola*, that the two genera have been placed in widely separated orders by different authors. This can be interpreted on the basis of the adaptability of the vegetative structures to a rapid hereditary adaptation to the conditions of a humid environment. Since the tissues external to and surrounding the centrum, are also vegetative in character, these have been influenced by the environment also. Hence, the ascocarps are generally round, small, uniloculate, and composed of only a few layers of cells. During the course of development of the ascocarp, the tissue is differentiated into an inner, hyaline, parenchymatous centrum in which the asci grow, and an outer, dark-colored several-layered rind. The fruiting bodies always appear seated upon the mycelium. From underneath these fruiting bodies there radiate a cushion of short mycelial branches which make up a subiculum.

III, SYSTEMATIC CONSIDERATIONS

To understand the corresponding position of the species that were assigned to the Perisporiales, one has to consider the interrelationships of the Myriangiales on the one hand and the Dothideales on the other, and their probable connection through the Pseudosphaeriales. According to von Höhnel (1918) the loculi in the Dothideales contain many asci while in the Myriangiales and the Pseudosphaeriales they always contain only one ascus. Theissen (1918) however, was of the opinion that this character is of secondary importance. Petrak (1923) followed a developmental series from the myriangian to the dothideal type and argued that in the myriangial form the "askogener Potenz" is distributed without apparent order in the stroma tissue; that in the dothideal type, certain parts of the stroma give rise to a bundle of numerous asci and that in the pseudosphaerial type the ability

to produce asci is confined to a limited basal portion. In this last type there is a wall-like periphery and a pore for dehiscence of the spores. The first series culminates in the Discomycetes, the last, in the Pyrenomycetes.

This Petrakian concept leaves unexplained the origin and course of the ascogons and of the paraphyses. Miller (1928) called attention to the untenability of the relationships of the Pseudosphaeriales and Dothideales to the Sphaeriales. According to him, the Myriangiales, Dothideales, and Pseudosphaeriales agreed in having the asci pushing their way through the stroma during their growth, while in the Sphaeriales the archicarp is adjacent in the stroma and, during development, the ascogon and the ascogenous hyphae are surrounded by a wall of loose fine hyphae originating from the basal cell of the ascogon. This wall encloses a "centrum" in which the ascogenous hyphae lie. The centrum enlarges and from its inner wall the paraphyses grow free from one another. By dissolution and absorption of the upper portion a narrow pore, the ostiolum, is formed and this is bound by periphyses. Accordingly, the Sphaeriaceae can be distinguished by a true perithecial wall, an ostiole lined with periphyses and free paraphyses between asci. The Perisporiaceae he considered, together with the Myriangiales, Pseudosphaeriales, and Dothideales, to be "distinguished by the absence of a true perithecial wall and the asci being borne in locules in the stroma". In a latter publication (1949) Miller excluded the Perisporiaceae entirely and considered the Myriangiales in the Plectomycetes.

Arnaud (1918), as a result of his studies on the biological group of superficial leaf inhabiting fungi, which he called "Astérinées", presented a classification of the Pyrenomycetes. He made no mention of the Perisporiales, but included some of the present forms with other families of the Pyrenomycetes. Some genera of the Capnodiaceae (1911) he had already included in other described genera of the Sphaeriales. Thus *Capnodium citri* became a *Pleosphaeria* and *Capnodium salicinum* a *Teichospora*.

Fraser (1935) in an account of several "sooty-molds" studied by her, found that in *Aithaloderma ferruginea*, the ascogenous fruits originate by the division of two or more adjoining cells of hyphae to form a thread of short wide cells. Further division gives rise to a flat disk, similar to the manner described by Arnaud (1910) for *Capnodium citri*. The young stroma increases in size by the growth of hyphae beneath this disk, and consists of a layer of dark-brown cells toward the outside and thin-walled interwoven hyphae, inside. The base of these inner hyphae are in contact with the leaf surface. From this the archicarp arises and grows at the expense of the core cells surrounding it. Both the archicarp and the stroma grow concurrently and digestion of the cells results in a globular fruit body. On the base of this fruit body there arises a system of ascogenous hyphae and the asci commence to be formed. As the ascospores mature, a pore develops.

Fraser (l.c.) studied three other species of Capnodiaceae and found that all agree in certain general characters with other species studied by different authors. They all have the same type of mycelium. The pycnidia are formed upwards, meristogenously, underneath a vegetative stroma. From the archicarp the developmental history is identical in all species in regard to the growth of the asci, the insertion of the ascogenous hyphae, and the continued formation of asci. They differ only on details of structure and extension of the stroma.

In the Capnodiaceae studied by v. Hohnel (1918), Arnaud (1912), Fisher (1933), Fraser (l.c.) and others, the fruit bodies resemble perithecia; but developmentally, they are stromata. To determine their systematic position in the light of these findings, one has to consider the differences between the Sphaeriales and the Dothideales.

In the Sphaeriales a perithecial wall is developed from the base of the ascogon. This wall is initiated as a result of the sexual process. In the Dothideales, there is no wall and the asci are produced in locules in the stroma. In the Capnodiaceae studied by Fraser (l.c.) there is no wall formed from the archicarp and so the ascocarp is a stroma. This is the character of the section "Chaetothyriae" Theiss, (Theissen & Sydow 1917) of the Capnodiaceae which in our opinion belongs to the Dothideales. On the other hand, the section "Eucapnodiae" Th. & Syd. (l.c.) agrees with the Amphisphaeriaceae and is certainly in the Pseudosphaeriales.

The Erysiphales (sensu stricto) is, according to our belief, a modified biological group from the Plectascales. Morphologically, the structure of the ascocarp is likewise characteristic of this order, consisting of an outer, brownish, parenchymatous, somewhat brittle envelope, and a hyaline, nurse tissue from which the asci develop. Unlike the fruit bodies of most of the members of this order, and the generalized condition in the Ascomycetes with ostiola or pores, those of the Erysiphales are differently adapted for the dissemination of the species. In some forms there is no disintegration of the peridial rind at the time of maturity of the spores; but the entire ascocarp acts as a disseminating organ. Neger (1902) discovered that he could divide the members of the order on the basis of their method of transport. In one, the appendages are interwoven with the mycelium so that the fruit bodies cling to the substrate and only later are they, in toto, washed away. In the second, the ascocarps break loose at their lower portion and they are carried away by external agents.

The white color of the external mycelium, the obligate parasitic habit and the unusual method of dehiscence, separate the Erysiphales from the pathogenic Plectascales; but the general structure of the ascocarps and the tendency for decline of sexuality are as in this last order.

The results of the investigations of v. Hohnel (1918), Theissen and Sydow

(1918), Petrak (1923), and many others have definitely established that a number of well-marked characters are continually associated with the Pseudosphaeriales. Among these may be mentioned the fact that the ascogons occur enclosed by a stromatic tissue and that during their growth this tissue is partially absorbed by the ascogenous hyphae and the developing asci. It can also be added that they are very thick-walled at the apex and this enables the asci to grow within the stromatic tissue. Other characters associated with the order are the occurrence of colored spores, which are usually multicellular to muriform, the parenchymatous tissue surrounding the individual asci, at least in the juvenile condition, and the nonreaction of the ascus to staining blue with iodine. Because these characters appear more or less also in the Myriangiales and others, Nannfeldt (l.c.) proposed for all such forms the name "Ascoloculares".

One picture characteristic of the Pseudosphaeriales is the copious production of imperfect forms of very different kinds, particularly of the hyphomycetous and sphaeropsidaceous types. Sometimes the correlation in resemblance of the spores of the imperfect and perfect forms is so close, that one can determine with a high degree of assurance the relation of one to the other, as for example, *Macrosporium* and *Pleospora*. In others, more than one spore type is associated with certain genera in a particular family, as demonstrated by Petrak (1924) for *Cucurbitaria* which has *Camarosporium*, *Diplodia* and *Haplosporella* as conidial stages or only one imperfect stage may occur as in the *Fusicladium-Venturia* association. In other instances, not only the spores of the two stages are similar; but the structural characters of the fructifications are indistinguishable externally, as in the *Hendersonia-Leptosphaeria* series observed by Dodge (1937).

If the anatomical characters of the fruit bodies could be correlated in all instances with definite perfect and imperfect spore types, then, the natural grouping of the Ascomycetes would be relatively easy. But when one thinks that Klebahn (1918) encountered sphaeriaceous, dothideaceous, and even myriangiaceous forms of *Mycosphaerella* whose imperfect stages could be assigned indistinctly to *Cercospora*, *Ramularia*, *Septoria*, etc., one realizes the impossibility of such arrangement.

Many of the superficial Pseudosphaeriales do not possess conidial forms; others are capable of developing upon the dead tissues of the host. On account of the uniformity of insertion of their fruit bodies, the only plausible separation at present seems to depend on the host-parasite relations and the structural features of the elements in the ascocarps. On this basis we are segregating from the old family Perisporiaceae those parasitic forms with abundant external mycelium and fruit bodies seated on the mycelium and calling them the Parodiopsidaceae. On page 64 we present our views of the characteristics required for the recognition of the family. In this connection,

the erection by Toro (1926) of the Pseudoperisporiales on the false observation of the existence of an ostiolum has no ground of justification and is here discarded.

In sexual reproduction, the Pseudosphaeriales run the whole gamut of variation. Spermogonia produced spermatia which effect fertilization through a trichogyne, as in *Mycosphaerella tulipifera* (Schw.) Higgins (1936), or fertilization takes place by nuclei produced in antheridia and entering through a pore at the tip of a trichogyne fused with nuclei in the ascogone, as in *Venturia* (Frey 1924) and so forth, until we find complete suppression of sex organs, as in *Pleospora herbarum* (Pers. ex Fr.) Rab. (Cavara and Mollica, 1907).

In recent years, two attempts have been made to separate certain forms from the Pseudosphaeriales. Falck (1947) created a new class of fungi which was called "Haerangiomyces". They based this class on the deliquescence of the asci and the peculiar arrangement of the spores in certain species of *Ceratostomella* and *Melanospora*. The spores are said to be arranged like the segments in an orange and the ascus is here termed an "octophore". Dehiscence of spores takes place by a mass of mucus which pushes them into a funnel-like structure, the "haerangium", made up of threads from the inside of the fruiting body. The untenability of this arrangement is clear. Deliquescent asci with mucus formation for spore dehiscence is found in the Chaetomiaceae, Meliolaceae, Aspergillaceae, Elaphomycetaceae, and others. The morphological characters of the ascocarps of these forms agree with either the Plectascales, Pseudosphaeriales, or Sphaeriales.

Kirschstein (1939) established a new family, Niessliaceae, for those formerly recognized sphaeriaceous forms, like *Coleroa*, *Antennularia* etc., with minute fruit bodies. Petrak (1940) showed that all the forms included by Kirschstein in his new family were good members of the Pseudosphaeriaceae.

The occurrence of dark-colored superficial mycelium, the production of small, globose ascocarps upon this mycelium and the strict parasitism of its members, are characters of sufficient importance to recognize as a separate family a group displaying these characters. Because of their peculiar biologic behavior and color, fungi as depicted above can properly be called "black-mildews". Like the mildews, they are parasitic on leaves and their reproductive structures, as well as their external vegetative phase, are entirely superficial.

IV, TAXONOMY

The tropical American species that have been previously assigned to the Perisporiales Lindau (l.c.) fall, in greater part, within the Pseudosphaeriales as this order has been interpreted by Miller (1949). Winter (l.c.) and

also Jaczewiski (l.c.) related the order Perisporiales to the Sphaeriales. Arnaud (1918) considered the Perisporiales as a "groupe sans valeur aucune"; while Nannfeldt (l.c.), in a deprecating manner, said of it that "felht jedlich Existenzberechtigung".

It was pointed out on page 27 that the concept of the Perisporiales, as newly defined by Theissen and Sydow (1917), lacks concatenation with the expressed concept of its author Lindau (l.c.). Petrak and Sydow (1923) considered the type-species of *Perisporium* Fr., type-genus of the family Perisporiaceae, to be a juvenile stage of a Discomycete. However, v. Hohnel (1919), following Corda's (1838) definition of the genus *Perisporium* redescribed it on the light of this new concept and selected as type *P. vulgare* Corda. That *Perisporium* Corda (nec Fries) could not be used again as a genus name is clearly seen from a study of that portion of the "International Rules of Botanical Nomenclature" related to homonyms. Neither can an order name be used with an entirely different meaning, even when attributing the name to the original author. While the Perisporiales, in the sense of Lindau, was composed of saprophytic and parasitic forms, the same order, in the sense of Theissen and Sydow, was made up of foliicolous species and hyperparasites on other fungi.

Spegazzini (l.c.) was the first definitely to call attention to the variety of meanings in the order and to divide the family Perisporiaceae into two tribes: Perisporiae for saprophytic and Meliolae for parasitic, species. The multiplicity of interpretations, naturally, resulted in a great deal of confusion with regard to the systematic position of the species therein included. In this connection, Petrak (1924) pointed out that "weil man heute noch gar nicht weiss, was eine Perisporiazee ist und wie ein Pilz beschaffen sein muss, um als Perisporiazee gelten zu können". Toro (1929) also claimed that "en tales circunstancias se impone una revisión completa del grupo y el establecimiento de un concepto definitivo". These two remarks summarized clearly the existing situation.

As a result of his studies of the Astérinéés, Arnaud (1918) showed that *Meliola* Fr. and its related genera were not at all to be allied with the other components of the Perisporiales. He created for them a new tribe: "Meliolinéés". In this conception of the group he was followed by Stevens (1927) and by Hansford (l.c.) Arnaud's idea of the tribe differed from that of Spegazzini's, whom Bessey (1935) and Martin followed by recognizing the tribe Meliioleae as a family, Meliolaceae. However, Hansford used the family name Meliolaceae also but followed Arnaud in its interpretation. It is in the latter sense that we recognize the family in this paper.

The 19 genera included by Theissen and Sydow (1917) in their monographic treatment of the Perisporiaceae have been shifted around according to the subjective interpretation of the individual investigator. Clements

and Shear (l.c.), who followed the classification of Saccardo raised the number of recognized genera to 43; Stevens (1913), who followed Lindau in Engler and Prantl's (1897) work had only 24. Bessey (1950) limited this number to 11, while Martin (l.c.) mentioned only the representative genus. Spegazzini (l.c.) recognized 22 genera.

It is our purpose here to follow the final disposition of the tropical American genera, hitherto considered as Perisporiaceae, which were included by Theissen and Sydow (1917) in the "Synoptische Tafeln".

A. DISPOSITION OF THE GENERA

1. Theissen and Sydow's Perisporiaceae

a). *Alina* Rac. Bull. Acad. Int. Sci. Sracovia 1909: 374.

This genus is mentioned here because *Jaffuela* Speg. (Bol. Acad. Ci. Córdoba 25: 41. 1921) has been considered a synonym of it. *Alina* Rac. was first removed from the Perisporiaceae by Arnaud (1918) and placed in the tribe Balladynées, near *Balladyna* Rac. Theissen and Sydow (l.c.) included *Balladyna* in the Capnodiaceae and Hansford (l.c.) assigned it to the Parodiellinaceae with the remark that "the black colour of this fungus renders it doubtful whether it is a true member of the Parodiopsidae". Since Gäumann and Dodge (l.c.) agreed with Arnaud in that the genus is closely related to *Balladyna*, it is clear that *Alina* and with it its synonym *Jaffuela* are to be placed in the Capnodiaceae and therefore excluded from the "black-mildews".

b). *Lasiobotrys* Kunze, Myk. Hefte 2: 88. 1823.

Lasiobotrys affinis Hark. is the only species of this Temperate Zone genus that had been reported within the geographic range of this work. The genus was studied by v. Hohnel (1919b), Arnaud (1918) and Petrak (1927); and all agreed in that the genus belongs in the Dothideaceae.

c). *Stomatogene* Theiss., Ann. Myc. 14: 404. 1916.

The presence of hyphopodia in the mycelium suggests affinities either with the Meliolaceae or the Englerulaceae. It will be shown later in this paper (page 49) that the former family name is restricted to *Meliola* and its allied genera. Since the latter family, as demonstrated by Petrak (1928), is composed of a heterogenous group of unrelated forms, and Hansford (l.c.) had placed this genus between *Balladynastrum* Hans. and *Parenglerula* v. Hohnel, it is assumed that the latter author considered it a member of the Englerulaceae and, therefore, excluded from the Perisporiaceae.

d). *Piline* Theiss., Ann. Myc. 14: 409. 1916.

The type-species was *Asterina splendens* Pat. Theissen (l.c. ut supra) in establishing the genus mentioned the spores as two-celled. In this respect it is identical with *Parodiopsis* Maub. However, Arnaud (1918) studied and figured the type-species and some of the spores appeared three-celled

and brown; but Theissen and Sydow (l.c. fig. 25b) showed them biseptate with the cross wall on the upper third of the spore. If Arnaud's observation is correct, and if the species is phragmosporous, then *Piline* is, as he stated, identical with *Perisporiopsis* P. Henn. If, on the other hand, as Arnaud (1921) later showed, the species is didymosporous, then the genus is a synonym of *Parodiopsis* Maub. In either case it is to be excluded because it is a synonym.

e). *Irene* Th. & Syd., Ann. Myc. **15**: 194. 1917.

This is a *Meliola* devoid of setae and is considered here under the Meliolaceae.

f). *Cleistosphaeria* Syd. Ann. Myc. **14**: 74. 1916.

Both v. Hohnel (1918d) and Arnaud (1923) studied this genus. According to the former it is a Capnodiaceae with a pseudosphaerial nucleus; according to the latter it is a true member of the Parodiellinaceae. The illustration by Theissen and Sydow (1917 fig. 25a) does not reveal the typical capnodiaceous mycelium. Clements & Shear (l.c.) spell the genus *Clistosphaeria*. Gonzalez-Fragoso and Ciferri (1925) described a *Cleistosphaeria Bromeliae* sp. nov. (Ciferri No. 136, Haina, Sto. Domingo) which we have examined and found to be identical with *Toroa dimerosporioides* (Speg.) Syd. We are considering the genus here in the sense of Arnaud under the Parodiopsidaceae.

g). *Meliola* Fr. Syst. Orb. Veg. **1**: 111. 1825.

Discussed in this paper in connection with the Meliolaceae.

h). *Dimeriella* Speg. Rev. Mus. La Plata **15**: 12. 1908.

This genus was critically studied by us (1939) and rejected because the original species placed under it were found to belong to other existing genera. However, one of the earliest species described for this genus had already been assigned to a new genus name, *Lasiostemma* Th. & Syd.; its characters correspond with those described by Theissen and Sydow (1917) for *Dimeriella*. *Lasiostemma* Th. & Syd. was selected by the writer to replace *Dimeriella* (auct.) nec Speg. From studies of the type specimen (Curtis Herb. No. 1355) and other material from South America and the West Indies (fig. 6, A) it is clear that the fungus belongs to the Pseudosphaeriales.

i). *Phaeodimeriella* Speg. Rev. Mus. La Plata **15**: 13. 1908.

This is one of the few genera in the original group of Theissen and Sydow (l.c.) that has suffered no shifting, although Clements and Shear (l.c.) changed the spelling to *Phaeodimeris*. It is treated by Hansford (l.c.) in the superficial Sphaeriaceae; but since together with *Dimerina* and *Phaeostigme* it forms a biologic entity, called by Theissen (1912) the *Dimerinae*, with pseudosphaericeous characters, it is herewith assigned to that group.

j). *Meliolina* Syd. Ann. Myc. **12**: 553. 1914.

Two tropical American genera have been considered as synonyms of this

oriental form. They are *Hyalomeliolina* Stev. and *Stevensula* Speg. According to the description, *Meliolina* is a *Meliola* without hyphopodia. *Hyalomeliolina* Stev. is not related to *Meliola* and according to its diagnosis is identical with *Nematostoma* Syd. The species of *Meliolina* Syd. reported by Stevens (1927) from the West Indies are parasitic upon the mycelium of *Meliola* and therefore do not belong here. They are reported by Hansford (l.c.) under his genus *Phaeophragmeriella* Hans. *Stevensula* Speg. is also parasitic on *Meliola* and according to the description is identical with *Phaeophragmeriella* Hans. Since Spegazzini's name has precedence over Hansford's we are considering the latter as a synonym. *Meliolina* Syd., because of the absence of hyphopodia, has to be excluded from the Melioliaceae and included with *Nematostoma* Syd. and *Stevensula* Speg. in the Pseudosphaeriales.

k). *Dimerina* Th. Beih. Bot. Cent. 29²: 46. 1912.

TABLE 1.—Distribution of Tropical American parasitic species of *Perisporium*

Old name	Host	Transfer to	Family
Bromeliae	Bromelia	Toroa	Paradiopsidaceae
Irenicolum	Meliola	Stevensula	do.
Meliolae	do.	do.	do.
Paullinae	do.	do.	do.
Lantanae	Lantana	Nematostoma	do.
Portoricense	Calophyllum	Perisporina	Parodiellinaceae
Wrightii	Opuntia	Myriangium	Myriangiaceae

Discussed in this paper in connection with *Dimerium* Sacc. & Syd. with which it is related.

l). *Parodiopsis* Maub. Bull. Soc. Myc. France 31: 3. 1915.

Placed in the family Parodiellinaceae, among the Hypocreales, by Arnaud (1918) but considered in this paper as the type of the family representing the newer concept of the Perisporiaceae (auct.) nec Fr.

m). *Dimerium* Sacc. & Syd. Syll. Fung. 17: 537. 1905.

Excluded here because it is a "genus confusum" (See page 46).

n). *Perisporina* P. Henn. Hedwigia 43: 357. 1904.

According to Arnaud (1923) the genus belongs to the Parodiellinaceae. It replaces in part the old name *Perisporium* (auct.) nec Fr. when applied to forms parasitic on leaves. The genus *Perisporium* Fr. is a phragmosporous saprophyte. Because of this, species belonging to different fungus groups have hitherto been described under *Perisporium*. Table 1 shows the present tentative distribution of some of the tropical American *Perisporium* species.

As is evidenced in table 1, *Perisporium*, in the sense of the authors, has

been segregated into a number of different genera, the parasitic members of which are differentiated as follows:

Ascocarps superficial in an external mycelium, spores several celled, brown

Ascocarps setose

Mycelial setae absent

Parasitic on leaves.....*Nematostoma*

Parasitic on fungi.....*Stevensula*

Mycelial setae present

Soluble dye evident.....*Nematostigma*

Soluble dye absent.....*Meliolina*

Ascocarps glabrous

Parasitic on leaves

Spores appendaged.....*Ceratosperma*

Spores unappendaged

Asci early evanescent.....*Toroa*

Asci persistent.....*Perisporina*

Ascomata in stroma, asci scattered, spores muriform.....*Myriangiium*

Of the 19 genera discussed by Theissen and Sydow (l.c.), 14 have representatives in tropical America and these have been treated above. The remaining 5 genera *Pampolysporium* Magn., *Teratonema* Syd., *Rizalia* Syd., *Haraea* Sacc. & Syd. and *Chrysomyces* Th. & Syd. have a geographic range beyond the treatment of this paper and have not been considered.

2. DIMERIUM Sacc. & Syd., A Nomen Confusum

The name *Dimerium* was originally proposed by Saccardo and Sydow (1904) as a subgenus for the brown-spored species of *Dimerosporium* Fuckel. Later under the authority of Saccardo and Sydow (1905) the name was raised to generic rank. V. Hohnel (1910) showed that *Dimerosporium* Fckl. was a microthyriaceous fungus whose type species possessed brown spores and that it was identical with *Asterina Veronicae* (Lib.) Cooke. This discovery invalidated the name *Dimerium*. Arnud (1918) proved that *Dimerosporium* Fckl. was a distinct genus from *Asterina* Lév., although it possessed the same type of spores and the same kind of microthyriaceous characters. In this sense, also, *Dimerium* Sacc. & Sydow is a synonym of *Dimerosporium* Fckl. Theissen (1912) after studying abundant material agreed with v. Hohnel's findings and decided that the hyaline spores forms of *Dimerosporium* (auct.) nec Fuckel with globose ascocarps constituted a distinct genus. He called it *Dimerina* and under this name it has been accepted as good by recent students of the group.

When the subgenus *Dimerium* was created, the first species under it was *D. pangerangense* P. Henn. & Nym. Whether this or any of the other mentioned species was to be considered as the type was not specified; how-

ever, *D. pangerangense* is a synonym of *Lembosia crustacea* (Cke.) Th. Most of the species of *Dimerium* recorded in the two above-cited volumes of the Sylloge belong to other recognized genera and nowhere in that work can there be found any indication as to what the type of *Dimerium* really is.

In the same year, the Sydows (1904) used the name *Dimerium* Sacc. & Syd. for their species *D. olivaceum*, a species which the young Sydow himself, as co-author (1917b) later made the type of the new genus *Hypophlegma*. In view of this fact and because no type species had been designated Theissen and Sydow (1917) selected one of the already described species and reinstated the name in the light of a newer concept. This designation of the type species not only changed the concept of *Dimerium* Sacc. & Sydow, but its morphological characterization as well. In other words, *Dimerium* Sacc. & Syd. was not equivalent to *Dimerium* Th. & Syd. In the minds of these last authors the fungus is perisporiaceous; ("Wie Dimerina, Sporen braun"); for the originators of the name it was microthyriaceous ("A Dimerosporio differt sporidiis coloratis nec hyalinis"). For subsequent authors, however, the concept was variable. It is in the sense of Theissen and Sydow that the genus is at present recognized with *D. pulveraceum* (Speg.) Th. as the type species.

When we consider that nearly all the original species of *Dimerium* belonged to different genera and that the newer concept of the genus does not correspond with its first interpretation, it is proper, for the sake of expediency in the application of the Rules of Nomenclature, to discard *Dimerium* Sacc. & Syd. (a synonym) and to select a new name for its homonym *Dimerium* Th. & Syd. There are a number of generic names which agree with the latter. Among these, the oldest and best known is *Phaeostigme* Syd., which, according to the characterization by its author, differs from *Dimerium* in the presence of paraphyses. It has been shown (Miller 1949) that the term paraphyses, when used in this group of fungi refers to the loose pseudoparenchymatous hyphae of the interascicular tissue (fig. 17) and therefore, are not of taxonomic significance in this instance.

Phaeostigme Sydow, Ann. Myc. **15**: 199. 1917.

Dimerium Th. & Syd. Ann. Myc. **15**: 464. 1917 (nec. Sacc. & Syd., Syll. Fung. **17**: 537. 1905).

Bolosphaera Syd. Ann. Myc. **15**: 201. 1917.

Phaeocapnidula Speg., Bol. Acad. Nac. Ci. Cordoba **26**: 369. 1923.

Pseudodimerium Pet., Ann. Myc. **22**: 21. 1924.

Hyperparasite on Ascomycetes; mycelium superficial, light-brown, without setae or hyphopodia; ascocarps sessile, globose, glabrous, light brown to blue black, astomous or with a pore with age; asci cylindrical clavate, thickened at the apex, 8-spored, early separated by thin strands

of pseudoparenchymatous tissue, this tissue disintegrating with age; spores two-celled, brown. Conidia in pycnidia, brown.

HOLO-type: *P. PICEA* (B. & C.) Syd. (*Dimerium piceum* (B. & C.) Th.) The species occurs throughout the geographical range of the hosts which are either *Meliola* or *Asterina*. It is the commonest of the hyperparasites of these fungi. A complete synonym is given by Hansford (l.c.) and an illustration by Toro (1930).

The fundamental differences between *Phaeostigme* Syd., *Bolosphaera* Syd., and *Pseudodimerium* Pet. lie in the characters of the wall surrounding the unilocular stroma that makes up the ascocarp. In *Phaeostigme* the wall is membranaceous, usually one-layered and olivaceous; in *Bolosphaera* it is reddish to blue and somewhat fleshy while in *Pseudodimerium* the wall is olivaceous to dark brown and several-layered. *Phaeocapnidula* Speg. is intermediate between the last two. However, the four genera intergrade. In his discussion of the Pseudosphaerial-question Miller (1928) stated that "such characters as the thickness or thinness of the stromatic wall or of the number of locules in the stroma apparently have no value".

3. *TONDUZIA* Stevens, A Nomen Excludendum

The name *Tonduzia* has been proposed as a generic name by three different authors. Two of the names belong in the Angiosperms and the other in the Ascomycetes. When first used it was to describe a species in the Cyperaceae (*Tonduzia* Boeck. Bull. Herb. Boiss. **3**: 464. 1895). Several years later it was used again to describe another species in the Apocynaceae (*Tonduzia* Pittier Cont. U. S. Nat. Herb. **12**: 103. 1908). The last time it was for a fungus (*Tonduzia* Stevens, Ill. Biol. Monog. **11**: 168. 1927). It is clear that Steven's name is a homonym by reason of being antedated.

Four genera of scolecosporous fungi have been reported among the Perisporiaceae. Of these, two are doubtfully of this family. The other two, according to their descriptions, seem to be synonymous. However, Petrak (1934) and Petrak and Sydow (1935) considered them as separate and distinct and we are doing likewise on their authority. The biological relations are the basis of their separation. *Tonduzia* Stev., in addition to the superficial mycelium also possesses an internal one while *Trichospermella* Speg. is entirely restricted to the trichomes and does not make contact with the leaf surface. Though representing a good genus, the name *Tonduzia* Stev. has to be replaced because it is a homonym. We propose the following name:

Ticomycetes nom. nov. (from Tico, a corruption of Costarican).

Tonduzia Stev. Illinois Biol. Monog. **11**: 168. 1927 (nec Pittier, nec Boeck.)

Fungi in follis parasitici; mycelio intramatricialis parco ex hyphis hyalinis composito; mycelio superficialis brunneo, hyphopodiis et setis ca-

rentes; ascomatis superficialis, glabris, poro pertusis donatis; asci cylindracei, octospori; sporiis filiformis, hyalinis.

Fungi parasitic on leaves; superficial mycelium brown, hyphopodia and setae absent; internal mycelium hyaline, scant; ascocarps globose, parenchymatous, with a pore, dark brown; asci cylindric, 8-spored; spores filiform, hyaline.

Holo-type: TONDUZIA PSYCHOTRIAE Stevens

Ticomycetes psychotriae (Stev.) comb. nov.

Tonduzia psychotriae Stevens, l.c.

This fungus was critically studied by Petrak (1934) and the description amended by him. The colonies are small, scattered, and brown; the external mycelium thin, septate, and without setae or hyphopodia; the internal mycelium hyaline and intercellular; the ascocarps sessile, small, globose, at maturity, with a pore for dehiscence of spores, wall dark, membranous, the asci cylindric, separated by ribbon-like hyphae with thin walls, 8-spored; the spores hyaline, filiform (ex. desc. Petrak).

On *Psychotria brachiata* Sw. La Colombiana, Costa Rican Fungi, F. L. Stevens No. 570 July, 19, 1923. (sp. non visa).

B. MELIOLA AND RELATED GENERA

1. MELIOLACEAE (Bessey 1935) emend. Hansf. 1936

Parasitic on leaves; mycelium superficial, colored, hyphopodiate; haustoria in epidermis, penetrating through cuticle; stroma perithecium-like, parenchymatous, superficial; asci evanescent; spores 3-4 septate, colored. Conidial stage absent (see fig. 2).

Neo-type:—MELIOLA Fr. emend. Bornet.

The Meliolaceae as herewith considered is restricted to Arnaud's concept of the Meliolinées (1918). It excludes the Englerulaceae which, according to Petrak (1928) is a heterogenous assemblage of diverse forms. The mycelium of the Englerulaceae possesses hyphopodia; but the asci are persistent and the ascocarps are made up of one layer of parenchymatous cells, which at maturity becomes slimy (fig. 3, A). Hyphopodia are also present in the Microthyriaceae, but here the mycelium is thinner, the ascocarps are applanate and at maturity break open in a stellate fashion. Imperfect forms are usually present in both these families.

In the Meliolaceae, especially at the time of maturity of the ascocarps (fig. 4, A and B, and fig. 5, E) there are multicellular threads which are connected above and below, separating the individual asci. This makes the structure appear as if each ascus occurs in a separate niche which is not in agreement with the statement of Theissen and Sydow, (1917) that they always form a "grundständigen Doldenstrauß". Sometimes, they are found

at different heights (fig. 5, A), thus indicating a relationship with the Myriangiales. On the other hand, the deliquescent asci excludes the family from the latter order.

In his characterization of the Pyrenomycetes, Arnaud (1925) emphasized that "le tissu interne qui entoure les asques n'est jamais filamenteux-cot-

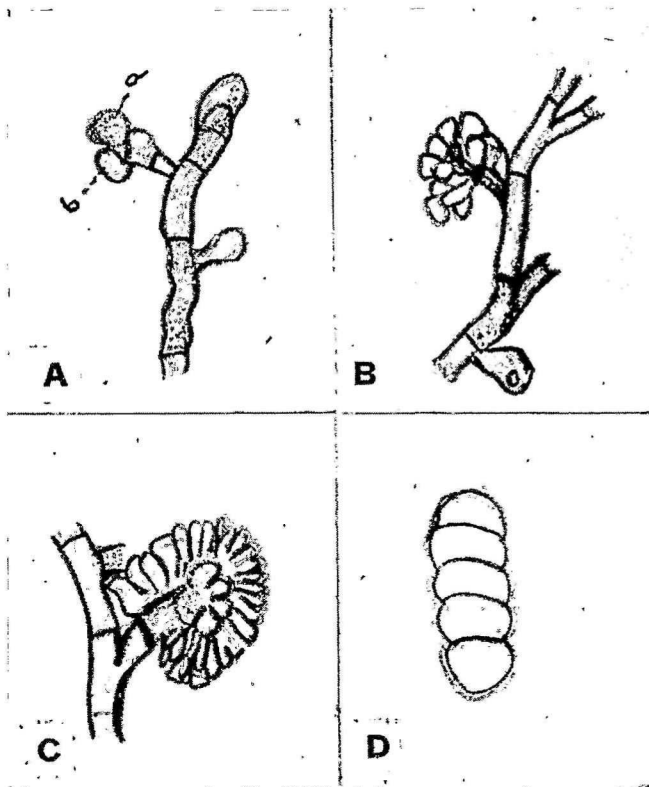


FIG 2.—Meliolaceæ; initiation of ascocarp in *Amazonia Psychotriæ* (P. Henn.) Th.: A, -a) Swollen tip from upper cell of hyphopodium; b) Lateral projection which by further growth encloses the swollen tip. B, Indentations develop after the projection cell has divided several times. The new cells elongate to form radial hyphae. C, By further growth of the radial cells the dimidiate character of the ascocarp begins to take shape. D, Matured spore.

toneux, comme chez les Plectascinées". Thus for him, a cottony-filamentous envelope is the distinguishing character of the Plectascales. In the Meliolaceæ, there is a distinct parenchymatous corè of several layers of cells, and, therefore, the fungus is Pyrenomycetous in the sense of Arnaud. The

centrum is formed by the dissolution of a few internal cells while the remaining cells become, by elongation, either the asci or the interthecial threads.

The Plectomycetes of Gwynne-Vaughan (1922) included all those forms which neither possess the cup-shaped apothecium of the Discomycetes, nor the flask-shaped perithecium opening by a pore, of the Pyrenomycetes. In this group she included the Perisporiaceae. It has already been shown (page 27) that Gwynne-Vaughan's concept of the Erysiphales is the same as that of the rejected Perisporiales and therefore, forms with little or no relationships inter se are included by her. Simplicity of construction is the only character common to the whole group.

Although some of the characters mentioned for the Pseudosphaeriales on page 40, are present in the Meliolaceae, others are highly modified. Among these modifications are the absence of a typical wall in the ascus and, consequently, the method of spore-ejection is distinctive. This difference in the morphological and physiological features of the ascus and in the biological significance of such characters, may be interpreted as a response of adaptation to the influences of a humid environment of the species concerned.

The results of the investigations of recent workers in the higher Ascomycetes have shown that in all the families of the class there is either an ascolocular or an ascohymenial type of development. The former is the more prevalent and the morphological structure by which it is represented does not correspond to the concept of a perithecium as interpreted by Miller (1928). This fact led v. Hohnel (1918b) to term this peritheciumlike fruit body a "pseudothecium". However, there has been a semantic tendency to call each type of divergence from the typical perithecium or apothecium by a different name (cleistothecium, thyriothecium, etc.), thus expanding the existing terminology. We will refrain from using such names and follow Miller's (1949) terminology: the fruit-body which has been so far considered as a "perithecium", will be called an "ascocarp"; what has been previously included within the "perithecial wall" will now be named the "centrum"; the "ostiolum" will become the "pore" and the "paraphyses" of authors, which are not the true paraphyses, will be regarded as "paraphysoids", when the interthecial hyphae have been dismembered or, simply "interthecial hyphae", when entire.

Inasmuch as the basic classes of Ascomycetes have been distinguished, regardless of their origin, according to the form and function of their spore-producing and spore-dispersing organs, it seems proper that the nomenclatural categories of division into lower groups be based on homologous structures. Since morphological characterization of the spore-bearing structure

has been indisputably used to distinguish the different groups of Ascomycetes, their functional characteristics may be utilized with the same justification.

The ascus is defined by Gäumann and Dodge (1928) as "a gonotocont in which the spores are formed endogenously through free cell formation". However, all workers in the Ascomycetes have conceived of this structure as made up of three essential morphological parts: The wall, the epiplasm, and the spores, each of which plays a separate role in the life history of the species.

The wall of the ascus consists of elastic membranes, those at maturity are strongly distended by osmotic pressure. These membranes either rupture at the apex in a definite fashion (operculate or inoperculate) or the external wall may break and the internal one increases to many times its original size. The increase in size represents a molecular transformation of the epiplasm at the onset of maturity. There are two agencies involved in ascus dehiscence: The elastic membrane and the osmotically potent epiplasm.

That the ascus has to be considered both with respect to its morphological structure and its physiological role there seems to be no doubt. In structure it is a sac for the endogenous formation of a number of spores following the course of a definite caryological development. In function, it is charged with the role of ejecting the mature spores in a definite direction. An analysis of the Meliolaceae in the light of these features will perhaps aid in elucidating the systematic position of the family.

In the ascus of the Meliolaceae a definite elastic inner wall is absent and the spores, very early, lie free in the ascocarp. Nor is there evidence of the presence of a separate thin wall, as this structure is interpreted in mycological literature. The spores during their development are surrounded by a

FIG. 3.—A, Meliolaceae: Surface view of mycelium, hyphopodia and ascostroma of *Irenina obtusa* Toro on *Tontanea canescens* (Willd.) Stand. (Fungi of Colombia, C. Garcés No. 408. Las Palmas, Antioquia, March 31, 1942). B, Englerulaceae: Surface view of *Paranglerula bulbifera* sp. nov. on *Eupatorium* sp. showing bulbiltes, anhistous ascocarps, mycelium and hyphopodia. (Fungi of Colombia, C. Garcés No. 1669. Las Palmas, Antioquia. Oct. 16, 1949). C, Parodiopsidaceae: Mycelium, hyphopodia and ascocarps of *Paradiopsis bicoronata* Garcés. On *Inga* sp. (Fungi of Colombia, C. Garcés No. 560. Envidado. Oct. 10, 1942). D, Meliolaceae: Undetermined. Mycelium, hyphopodia and ascocarps differ from No. 3 above. On *Paullinia* sp. (Fungi of Colombia. Dugan O. J. García No. 1187. Fundación, Magdalena. Jan 18, 1940). E, Trichothyriaceae: Conidia and conidiophores of *Trichothyrium* sp. on *Meliola trichostroma* (Kze) Toro. On *Psidium Guajavn* L. (Fungi of Puerto Rico. C. E. Chardón No. 1536. Mayaguez. Nov. 5, 1947). This and No. 8 below are not members of the "black-mildews" but of the "sooty-molds". They are shown here to contrast their external appearances. F, Capnodiaceae: Pycnidia of a Capnodiaceous fungus on citrus. Notice the characteristic dematioid mycelium (Fungi of Costa Rica. R. A. Toro No. 97, Turrialba, Aug. 15, 1949).

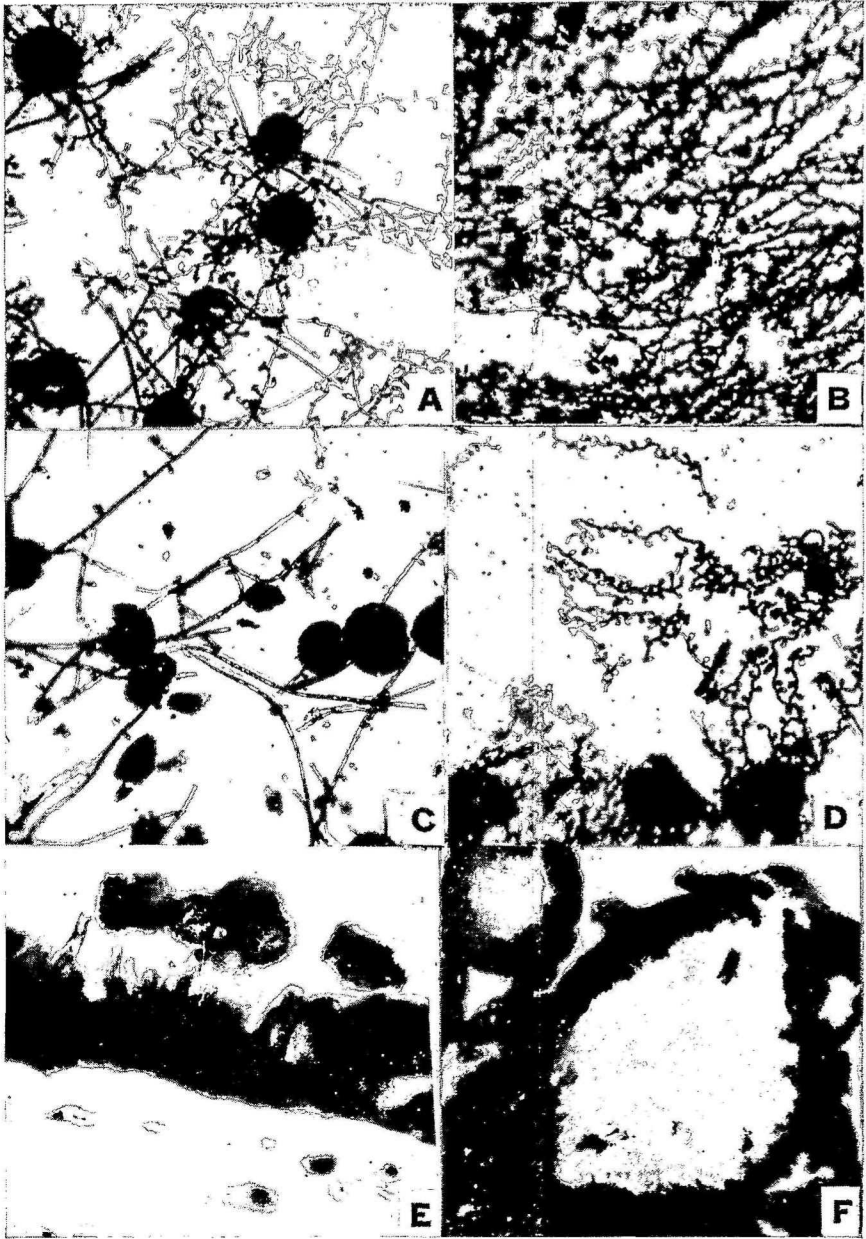


FIG. 3



FIG. 4.—A, Median cross-section of sterile ascocarp of *Meliola trichostroma*. All of the interthecial threads have the appearance of emaciated interascicular stroma and protrude thru the lysigenously formed pore. This condition appears on heavily parasitized specimens. B, Same but fertile. Notice that the interthecial threads are plump and may develop into asci or pseudostroma.

very dense epiplasm whose peripheral portion is a denser refractile zone not comparable to the definite wall of most of the higher Ascomycetes. In this



FIG. 5.—A, Median cross section of ascocarp of *Meliola trichostroma*. The pointed ends of the matured spores is characteristic of the species. The upper portion was broken during the course of sectioning but the centrum is intact. B, Young stage in the development of *Meliola capsicola*. Notice the centrum formed by homogenous, hyaline, parenchymatous tissue with no evidence of sex organs. C, An advanced stage of No. 12. The center cells have segregated into elongate ascus-like tissue and the cavity begins to be differentiated. D, Median section of mature ascocarp of *Meliola capsicola*. The lower portion shows two spores held in contact thru their elongate plane and appeared as if flattened on the sides. E, Ascocarp of *Phaeostigma picea* showing the general organization of the centrum.

respect the family differs from the members of the Pseudosphaeriales and corresponds to some of the Plectascales.

The structural features characterizing spore formation in the Meliolaceae are the entire absence of the typical ascus wall, the early dissolution of the epiplasm surrounding the young spores and irregular distribution of the mature spores inside the ascocarps. (See Graff's (1932) fig. 12-13-14).

If Nannfeldt's (l.c.) disposition of the Ophiostomataceae in the Plectascales is accepted, there is no doubt that the Meliolaceae, with equal right can be placed here. In both, the ascocarp is perithecium like and there is a clearly differentiated opening for the dehiscence of the spores. Moreover among the Plectascales, *Microascus* Zukal and *Acaulium* Olsen possess these characters in common with *Ophiostoma* H. & P. Sydow; while they also can be connected through *Thielavia* Zopf. with the Aspergillaceae. (See Emmons 1930).

KEY TO THE GENERA OF MELIOLACEAE

Stromata globose, of several layers

Mycelial setae present..... *Meliola*

Mycelial setae absent

Stromata with veriform appendages..... *Irene*

Stromata with setae..... *Irenopsis*

Stromata without setae or appendages..... *Irenina*

Stromata applanate, of few layers..... *Amazonia*

2. The Genus MELIOLA

MELIOLA (Fr.) Bornet, Ann. Sci. Nat. 3 16: 267. 1851.

Meliola Fr. Syst. Orb. Veg. 1825: 111.

Amphitrichum Nees ex. Spreng. Pl. Crypt. Trop. 1820: 46 p.p.-

Sphaeria Fr. Syst. Myc. 2: 513. 1823 p.p.

Myxothecium Kze. ex. Fr. Syst. Myk. 3: 232. 1829.

Couturea Cast in Fries ex Summa Veg. Scand. 1846: 407.

Asteridium Sacc. Syll. Fung. 1: 49. 1882.

Mycelium superficial, brown, radiating, hyphopodiate; mucronate hyphopodia bottle shaped, one celled; capitate hyphopodia two celled, upper celled usually round or angular with a refractile pore from which the haustoria arise; haustoria elongate, epidermal, arising from beneath the pore; mycelial setae present; ascocarps superficial, globose, black, without setae or appendages, of two or three layers of parenchymatous cells, astomous or with age, with a pore at the summit from the disintegration of the apical cells; asci evanescent, two-four spored; spores usually free; at different heights, in groups of two or four, separated by pseudostroma of hyaline thin walled threads; spores 3-4 septate, brown, sometimes muriform. Conidial phase unknown.

Lectotype: MELIOLA PSIDII Fr.

The genus comprises several hundreds of described species. It is of frequent occurrence in the Tropics, especially in angiospermous hosts. The discovery of its strict parasitism have convinced recent investigators that, like the rusts, the Meliolas cannot be differentiated on the basis of morphological characters. Existing species on widely separated host families can be split up into a number of distinct species on the basis of host specialization.

We have studied three species of this genus: *M. psidii* Fr., *M. capsicola* Stev., and *M. bicornis* Wint. We have followed the development of the fruit body and the formation of the asci in *M. capsicola* Stev. Our observations do not harmonize with the findings of Graff (1932) for *M. circinans* Earle, and for that reason we deem it important to record them here. That the group cannot be arranged on the basis of sexuality is revealed by Graff's inability to discover nuclear fusion in his species, in spite of his claim of the presence of the gametangia. That there is, on the other hand, a marked reduction in sex organs is shown by our findings in *M. capsicola*.

The ascocarps are formed in two different ways. In one, there is division along different planes in a two-celled, short, lateral branch until a globose structure, several layers of cells thick is formed. The fact that this lateral branch is short and two-celled, with the upper cell round (fig. 2) has probably been the cause of its confusion with the capitate hyphopodium, and, perhaps is responsible for the repeated erroneous statements that the fruiting bodies arise from the latter. Gaillard (1892) was the first to express this dubious conception of the capitate hyphopodia although he was careful to qualify his statement with the remark that "le nombre de celles qui atteignent ce developement est bien minime". In the capitate hyphopodium there is always a light-colored, refractile, round structure from which the haustoria grow from underneath. (fig. 2). In the short lateral branch this refractile body is absent and, therefore, the surface appears uniform. A median section of the fruiting body at the stage mentioned above, shows a layer of thick dark cells on the outside surrounding several layers of thin walled hyaline cells in the centrum. All fruiting bodies developing in this manner appear seated upon a subiculum of superficial mycelium (fig. 5, A).

We failed to observe any sex organs. When the hyaline centrum has attained three or four parenchymatous cells in thickness, it is uniform throughout. As more cells are produced, in a centripetal fashion, the central cells, which are the oldest, become detached and a cavity begins to form. (fig. 5, B). Further growth results in the increasing of the cavity. Some of the cells that have remained attached elongate along the vertical plane as the ascocarp grows. (fig. 5, C). These will form the interascicular pseudostroma. Those cells that have detached and become free, round up and then elongate,

becoming the initials of the asci. No nuclear fusion has been observed. The young asci are uninucleate, probably diploid, because of the larger size of the nucleus. When the spores mature each cell has one small nucleus, except the central one which is binucleate. Our observations on *Meliola capsicola* Stev. do not agree with the accounts of Graff (l.c.) for *Meliola circinans* Earle. According to that author there is an oogone and an antheridium formed from nearby hyphae, of the same nature as those described by Harper (1895), (1905) for *Sphaerotheca*, *Erysiphe* and *Phyllactinia*, the only difference being one of orientation. The sex organs of *Meliola* were reported to grow parallel, instead of perpendicular, to the host surface. Not only are the sex organs said to be of the Erysiphaceous type but the whole story of the development of *Meliola*, as described by Graff, follows Harper's account.

In *M. capsicola* the fruiting bodies arise from short side branches, resembling hyphopodia, which Arnaud (1918) termed stigmopodia or by the arching over of two cells which fuse at their tips. No fusion of the nuclei in these end branches was observed. The nearby hyphae give rise to the stroma or in the case of development from the stigmopodia, an appanate structure is formed which very soon rounds up (fig. 2) and the tissue therein is differentiated into an outer dark stromatic zone and an inner, hyaline, thin-walled portion of nurse cells. These cells later make up the asci and the interthecial stroma.

The asci are formed consecutively as small protuberances of the nurse cells adjacent to the wall surrounding the centrum. These elongate and the spores are differentiated in the manner explained by Graff for *M. circinans*. The two maturing spores lie in close connection along one phase of the long axis (fig. 5, E). At maturity the surface of contact of the spores appears flat because of proximity to the adjacent walls during growth. It is in the course of development of the spores, from the inception of the small protuberance with a plasmatic membrane to its growth and differentiation of the spores that any similarity to an ascus can be recognized in *M. capsicola*. The mature spores lie loose, irregularly distributed, and filling the cavity of the ascocarp (fig. 5, E). However, sometimes in specimens from dry places, as represented by *M. nigra* Stev. (Steven's P.R. fungi No. 363 on *Laguncularia racemosa* (L.) Gaertn.), the asci do not deliquesce too early and then it is possible to observe that the wall is made up of two membranes, the inner one closely surrounding the ascospores, the outer one thicker in the upper part and terminating in a short pedicel in the lower.

3. The Story of MELIOLA

The story of the genus *Meliola* Fr., like that of many old genera, is full of incongruities. As far as can be judged from our findings, the genus is one of those that could be classed under "genera confusa" and discarded.

However, *Meliola* is so well known and the number of species described under it so great, that it is proposed that the name be maintained in the list of "genera conservanda", if not on the basis of priority, at least for the sake of usage.

The first specimens which later became *Meliola* were described by Sprengel (1820) under the name *Amphitrichum* Nees. Fries (1823) placed the three specimens described by Sprengel under the provisional name *Sphaeria? amphitricha* (Spreng) Fr. and each of the species was made a variety thus, *S.? amphitricha* var. *Hibisci*, *S.? amphitricha* var. *Araliae* and *S.? amphitricha* var. *Sacchari*. Later (1825) Fries created the genus name *Meliola* and gave a description of it; but did not assign any species. From his own words 3 years later (1828), it is evident that he intended to include as species of *Meliola* each one of the three varieties of Sprengel. His statement "*Sphaeria? amphitricha* S. M. 2 p 513—Genus *Meliolae* constituent" clearly shows that such was his purpose. Therefore, at the time of the publication of the "Systema Mycologicum" (1821–1832), starting point for the Ascomycetes, there were recognized three species of *Meliola*:—*M. Hibisci* (Spreng.) Fr., *M. Araliae* (Spreng.) Fr. and *M. Sacchari* (Spreng.) Fr.; but no *M. amphitricha* Fr., since this binomial had been eliminated by the statement in the "Ellenches Fungorum" quoted above.

Kunze (1827) established the genus *Myxothecium*, whose type species, *M. Musae* Kze. was shown by Montagne (1838) to belong to *Meliola*. Although Kunze's name was accepted by Fries (1829), its recorded identity with *Meliola* makes it a synonym.

In 1846 Fries included the genus *Couturea* Cast. In a note to this genus he called attention to its identity with *Meliola* but lacking asci. The fact that in *Meliola* the asci are early deliquescent may account for the absence of asci in the genus *Couturea* Cast.

Our present concept of the genus dates from Bornet's (1851) careful studies of the morphology and biology of the species existing at that time and his redescription of the generic characters. However, Gaillard's monograph (1892) has contributed more than any other work to establish definitely what is a *Meliola*.

4. MELIOLA Fr. (1825), A Synonym

Should it be possible to prove that an authentic species of *Meliola* was represented in any one of the three original specimens of Sprengel, there would be no problem in connection with the validity of the name. The numerous inquiries made have brought out that the results obtained by all students of the genus can be summarized in the following conclusions:

1. There is no known species of *Meliola* on *Hibiscus* and therefore, *M. Hibisci* (Spreng.) Fr. must be something else.
2. There is no species of *Meliola* on *Saccharum* in Surinam, the locality

of Sprengel's specimens; although some other "sooty-molds" have been reported on this host from there.

3. Of the three original specimens reported by Sprengel, the only one studied by recent authors turned out to be an *Irene* and not a *Meliola* (vide *Irene Araliae* (Stevens 1927).

Therefore, *Meliola* Fr. (1825) could be an *Irene* Th. & Syd., a "sooty-mold" or something else.

5. Proposal

Consideration of the above statements should warrant discarding the genus name *Meliola* by invoking from the International Rules of Botanical Nomenclature the pertinent article dealing with the rejection of names proved to be synonyms. Nevertheless, by appealing to the principle of usage and basing our contention on the following introduction to the type-question, the proposal to conserve the genus name can be expedited by applying either one or both of these two criteria:

1. That, although *Meliola* Fr. (1825) is not identical with *Meliola* Fr. (1830), as exemplified by the description of *M. psidii* Fr. (1830), the latter, nevertheless, falls within the generally accepted dates for the *Systema Mycologicum* (1821-1832); moreover, the same person is the author in the three instances.

2. That the number of known species of *Meliola* is so great, and the characters of the genus have been so well established since Gaillard's monograph (1892), that nomenclatural chaos, rather than cosmos, would be the result of the adoption of a new name.

6. The Question of the Type-species

In 1830, Fries described the species which, because of a typographical error, was spelled *Melida psidii*. This is undoubtedly a misprint for *Meliola*, since the description as well as the specimen upon which this was based correspond with the present concept of this genus. Moreover, all subsequent students of the genus have recognized *Meliola psidii* Fr. as the accepted binomial for that species. Because the question of the type-species has not hitherto been definitely established, we are inclined to recognize *M. psidii* Fr. as the lecto-type.

Several type-species of *Meliola* have previously been selected at different times by as many authors, but none of these fits the nomenclatural concept of the type. Arnaud (1918) was the first to call attention to the fact that there has never been designated a type for this genus. He therefore chose the first species included under that name, *Meliola Hibisci* (Spreng.) Fr., and made it a "pseudo type". This he defined as the first species in a list accompanying a new genus. That this selection is erroneous and contrary to the accepted "Rules" is evident from a consideration of the circumstances.

which should lead to the establishment of the species. In the first place, Fries (1823) raised *Sphaeria? amphitricha* var. *Hibisci* to specific rank under the condition "si genere distingueretur"; but, as shown above, there is no species of *Meliola* on *Hibiscus*. The species existed in print only. In the second place, the name *Meliola*, as first used, represented a collective species whose entities are no longer included in the genus.

The same objections can be raised to the designation by Theissen & Sydow (1917) of two types for *Meliola*: *M. Araliae* (Spreng.) Mont. or *M. amphitricha* Fr. Montagne (1838-1842) studied a specimen collected by Bertero in Puerto Rico and described it as *Meliola Araliae* Mont. This is not *M. Araliae* (Spreng.) Fr. The former, according to the description, is a very good species of the genus; the latter, according to Stevens (1927) is an *Irene*. Since the binomial *Meliola Araliae* was preoccupied, Montagne's name became a later homonym, and is thus invalid. Judging from the description, this homonym can most likely be referred to *M. didimopanicis* P. Henn.

In his monograph of the genus *Meliola*, Stevens (1927) did not designate a type species. He stated that *M. amphitricha* Fr. and *M. hibisci* (Spreng.) Fr. have been mentioned as types. However, since *M. amphitricha* Fr. never existed because the combination name was eliminated when *Sphaeria? amphitricha* became *Meliola* (see above) and, since there has never been a specimen of *M. hibisci*, Stevens' designations are of no significance. (Art. 39 bis, 7th Int. Bot. Cong. 1950).

M. nidulans (Schw.) Cke. is another species that has been designated as the type (Clements and Shear 1931). This, although a good species of *Meliola*, should not typify the genus for several reasons: first, *Meliola* is considered a genus of tropical fungi and *nidulans* is one of its few species in temperate climates; second, this fungus occurs in an aberrant way, usually on the stems, protected by mosses. *Meliola* is generally conceived as a leaf parasite. Third, there is an older, typical species, *M. psidii* Fr., widely distributed wherever the host grows and well represented in all collections of tropical fungi. And last, it is more advisable and more in harmony with the established International Rules of Nomenclature to select as the lectotype a species represented by a specimen of the original material upon which the author of the genus and species described it. *M. psidii* Fr. fulfills these requirements.

7. The Identity of *M. psidii* Fr.

The description of *M. psidii* Fr. (1830) was based on a specimen distributed by Weigelt (leg. exsicc. Weigelt 1827 det Kunze) from Surinam on leaves of *Psidium pomiferum* and to which Kunze (in herb.) gave the name *Sphaeria? trichostroma*. We examined a specimen (Plant Industry Station Collections, Beltsville, Md.) of this original gathering and it represented

what is now known as *M. psidii* Fr. The specimen is accompanied by a diagnosis of the species. According to the suggestions guiding the application of the 1950 Rules in the selection of the nomenclatural types, specimens should be given preference over descriptions. (Article 16, Appendix 4c). Since in addition to the specimen, there is also a published name with a description, *S.?* *trichostroma* Kunze, should have preference over *M. psidii* Fr. (Appendix 4d). Even at the time, Fries suspected the identity of his species with that of Kunze when he stated under *S?* *trichostroma* "A quo genere Melidae vis nisi peculiari vegetatione recedunt". Furthermore, Sydow (1926) called attention to the identity of *M. psidii* and *S. trichostroma* and that perhaps Kunze's name had priority; but he let the names stand as if they represented two different genera.

In view of the identity of the two mentioned species we propose the adoption of the older name for *M. psidii* and offer the following combination and synonymy.

Meliola trichostroma (Kze.) comb. nov.

Sphaeria? *trichostroma* Kze. in Weigt. Exsicc. 1827.

Meliola Psidii Fr. Linn. 5: 549. 1830.

Meliola amphitricha Mont. (nec Fr.) Pl. Cell. 1838. p. 326.

Meliola moerenhoutiana Mont. p.p. ibid.

Meliola horrida Ell. & Ev. in Bull. Univ. Iowa 2: 396. 1893.

C. PSEUDOSPHAERIALES

The family Pseudosphaeriaceae was erected by v. Hohnel (1907) for genera, like *Wettsteinina* v. Hohn. and *Pseudosphaeria* v. Hohn., which possess stromata that are peritheciump-like having a single cavity with monoascular loculi in which each ascus is separated by a pseudostroma. Later Theissen and Sydow (1918) raised the family to ordinal rank and divided the order into seven families: Epipoloaceae, Parodiellaceae, Pleosporaceae, Cucurbitariaceae, Botryosphaeriaceae, Sphaerellaceae, and Pseudosphaeriaceae. As a tribe of the last family they included Dothioreae, a group which formerly belonged to the Myriangiales. Gäumann and Dodge (l.c.) considered the Pseudosphaeriaceae within the Myriangiales and derived this family from *Bagnisiella* and *Dothiora* thru degeneration of the stroma.

The three orders Myriangiales, Dothideales, and Pseudosphaeriales contain interascicular tissue and, therefore, there is no clear-cut morphological character of the centrum by which to differentiate them. For convenient classification, if the stroma is extensive and contains many cavities in a row (or even if reduced to one cavity), without definite walls, we call the fungus dothideaceous; if the stroma is peritheciump-like, with pseudoparaphyses forming a wall or between the asci, then we say it is pseudosphaeriaceous. In both kinds the asci are numerous, at the same level and the

threads between them, at maturity, may break up to give the appearance of paraphyses. In the Myriangiales there is only one ascus in each cavity; the few to many asci in the stroma occur scattered, at different levels and each is separated by well-defined parenchymatous tissue.

If we limit the Pseudosphaeriales to those forms with regularly arranged, more or less parallel asci, each ascus separated, at least when young, by an interascicular layer of septate threads, then, we will be confronted with an order containing the largest and most important groups of the Ascomycetes. These were formerly included under the Pyrenomycetes; but Miller (1928) has limited the concept of this class to forms possessing a perithecium. Later (1949), however, he expanded this concept further to include all Ascomycetes in which the ascocarps open by a pore. He distinguished the Pseudosphaeriales from the Dothideales by the absence of a definite wall and interthecial threads in the latter. To obtain a clear picture of the Pseudosphaeriales one has first to determine which family represents the center of development. From this one can deviate toward the extremes. It is these extreme forms, which naturally are transitory, that are difficult to classify in a particular system because their placement depends upon the subjective interpretation of the individual investigator. They may either be considered as belonging to the family from which they root or, with equal right, to the family to which they lead.

Our interpretation of the order will make the Pleosporaceae the center of the Pseudosphaeriales not only because the earliest recognized Pseudosphaeriaceae, *Pseudosphaeria* and *Wettsteinina* belong here; but also because *Leptosphaeria* and *Pleospora* have been the subjects of intensive studies as to the limits and significance of the group. As Petrak (1923) has discovered, the organization of the centrum of the fructification extends in two directions from the typical pseudosphaeriaceous: One toward the dothideal; the other to the sphaerial. This same observation made previously on *Leptosphaeria* Ces. & Not. by v. Hohnel (1918) led that author to adopt two series of developments: one dothideal-*Leptosphaeria* sensu stricto, based on the type of the genus; the other—sphaerial, which he identified with *Nodulosphaeria* Rabh. A short time later, the same author (1918b) differentiated a third type which he called pseudosphaerial; *Scleroplella* v. Hohn. The views of v. Hohnel and of Theissen and Sydow were criticized by Petrak (1923) because he felt these authors did not grasp the true meaning of the group. However, that author also failed to qualify his conception of the morphology and homology of the perithecium, the ostiolum and the paraphyses. Miller (l.c.) tried to remedy this situation by distinguishing between the remnants of partially dissolved stromatic pseudoparenchyma and paraphyses, and between perithecial wall and stroma. Later (l.c.) he clarified his interpretation of the former structures and stated that the threads grow downward from the archicarp before the asci are formed.

A condition similar to that of *Leptosphaeria* arises in connection with many genera (*Pyrenophora*, *Pleospora*, *Mycosphaerella*, *Meliola* etc.) occurring on hosts belonging to all classes of plants. In these genera, not only are there transitions in the organization of the centrum, (probably because of the influence of the particular host on the fungus species) but of the stroma and spores as well. Although the parasitic species of these genera are limited in host range, the spectra of their hosts, per se, are collective as this term is defined by Gäumann (56) and therefore, the fungus may be subject to a wide variety of cross fertilization. Species of this nature are apparently in a continuous flux of evolution and they can be interpreted only on the basis of their characteristics at the time of examination.

In view of the above considerations we are recognizing as Pseudosphaeriales those Ascomycetes with perithecioid ascocarps in which a single cavity with numerous asci without true paraphyses, occur. Miller's (1949) characterization of the order fulfills this requirement.

The seven families included in the order by Theissen and Sydow (1918) were separated on the basis of their insertion and also the extent of the stroma. The superficial elements of this order, in which mycelium was present or absent, were included in the tentative family Epipoloaceae. Some of the genera in this family belong to the "black-mildews". Arnaud (1918) established the family Parodiellinaceae and placed it under the Hypocreales because of a colored soluble substance produced by the mycelium. Later (1920) he divided this family into two tribes: one without external mycelium, Parodiellineae; the other with superficial mycelium, Parodiopsidae. In a later publication (1921) he added the Erysipheae, thus reducing the family Erysiphaceae to a tribe. We feel that there was no justification for depriving such a well-known family as the latter of its rank, especially since presence or absence of mycelium and its color have for long been used as good characters to differentiate among higher taxa.

There are good bases for recognizing three families, one for each of the three tribes under Arnaud's Parodiellinaceae. The first family, Parodiellinaceae, is based on the absence of a superficial mycelium and includes his tribe Parodiellineae, plus some of the Epipoloaceae of Theissen and Sydow. The second family, which we propose to call Parodiopsidae (fig. 6, C) is characterized by the presence of abundant, dark-colored mycelium upon which the ascocarps are seated. It includes the Epipoloaceae p.p. and the tribe Parodiopsidae of Arnaud. Here will be included the majority of the Perisporiaceae of Theissen and Sydow (1917). The third is the Erysiphaceae, with hyaline mycelium. These three families constitute a closely related morphological and biological group with connections thru certain general and specific characters. Among these characters may be mentioned:

- (1) That all the members of these families are strict parasites either

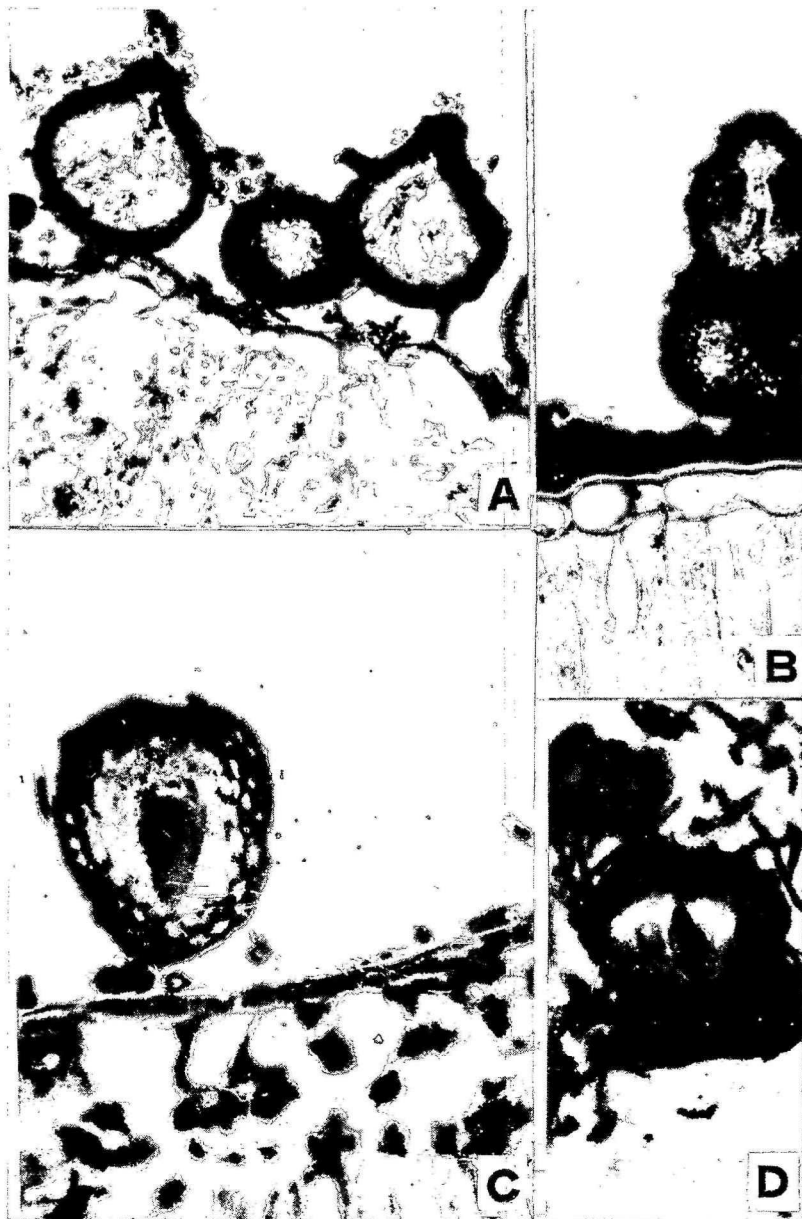


FIG. 6.—A, Parasitized sterile ascocarps of *Lasiostemma melioloides*. B, *Phaeostigma piceae* developing upon another hyperparasite of *Meliola*. C, Ascocarp of *Perisporina* showing a single big uninucleate ascus. D, Cross section of ascocarp of *Toroa dimero-sporioides* showing the deliquescent ascus, with 4 spores and numerous setae around it.

upon the leaves of flowering plants or upon the mycelium of similar fungi.

- (2) That they all contain a yellowish soluble substance which sometimes stains the host.
- (3) That the ascocarps are small, globose, and never carbonaceous and brittle.
- (4) That conidial fructifications are common.

The following key shows the position of our new family among those to which it is related:

External mycelium absent; conidia and ascocarps formed on cushions produced by the errumpent internal mycelium at the stomata.....	Parodiellinaceae
External mycelium present; ascocarps formed entirely superficial and scattered upon the mycelium.	
Hyphae colored; conidia not Oidiumlike	Parodiopsisaceae
Hyphae hyaline; conidia Oidiumlike.....	Erysiphaceae

1. PARODIOPSISACEAE Fam. Nov.

Fungi in foliis parasitici; mycelium omnino superficiale, ex hyphis brunneis, septatis compositum; haustoria intramatricialis connexis efformata; ascomata superficialis, brunnea vel atra, nucleo saepe paranchymatice, uniloculata, sessilia; asci pauci vel numerosi, 8-sporei.

Holo-Typus—PARODIOPSIS Maubl.

Fungus parasitic on leaves; external mycelium consisting of wide, brown, septate hyphae which penetrate the host by way of the stomata or the cuticle and giving rise to internal mycelium and haustoria; ascomata peritheceum like, superficial on the external mycelium, brown to brownish black; locules at the onset filled with delicate hyaline parenchyma in which the few to many 8-spored asci develop.

Holo-type: PARODIOPSIS Maubl.

The family name proposed here will include those Pseudosphaeriaceous fungi with small, globose, dark-colored fruit bodies seated on a superficial mycelium. (fig. 6, C). This corresponds with the concept of the Perisporiaceae as defined by Theissen and Sydow (1917) and which, for reasons already discussed, is untenable. It also corresponds in part, with the Epipoloaceae, Th. & Syd., which is not valid because the name was proposed "ad interim" to include the superficially seated Pseudosphaeriales. The difference between the above two families, as recognized by their authors, lie in the emphasis given to the structures. The Perisporiaceae were recognized on the basis of the dehiscence of the ascocarps; the Epipoloaceae, on the organization of the centrum. That this is so, can be inferred from the fact that Clements and Shear (1931) include *Ophiomeliola* Starb. and *Lasiosstemma* Th. & Syd., two of the Epipoloaceae in the Perisporiaceae, while the remaining genera are treated as superficial Sphaeriaceae. Arnaud's

(1920) characterization of the Parodiopsidae is based on the orientation of the internal mycelium from stomopodia at the stomata. When the three points of view were harmonized and the genera included were analyzed, it was found that their authors refer to the same group of organisms.

2. Key to the Genera of the Parodiopsidaceae

- Mycelium parasitic on leaves..... Parodiopsidae Arn.
 Spores hyaline
 Ascocarps setose
 Spores two-celled
 Mycelium dematioid..... 1. *Eumela*
 Mycelium filamentous..... 2. *Lasiostemma*
 Spores three-septate..... 3. *Aphanostigma*
 Spores filiform..... 4. *Ophiomeliola*
 Ascocarps glabrous
 Spores one-celled..... 5. *Cleistosphaeria*
 Spores two-celled..... 6. *Eudimeriolum*
 Spores three-septate..... 7. *Gomezina*
 Spores filiform
 Mycelium scanty, on trichomes..... 8. *Trichospermella*
 Mycelium abundant, on epidermis..... 9. *Ticomycetes*
 Spores brown
 Ascocarps setose
 Spores two-celled..... 10. *Mirandia*
 Spores x-celled
 Mycelium glabrous..... 11. *Nematostoma*
 Mycelium setose..... 12. *Meliolina*
 Ascocarps glabrous
 Spores two-celled..... 13. *Parodiopsis*
 Spores x-celled
 Mycelial setae present
 Hyphae penetrating through stomata..... 14. *Meliolinella*
 Hyphae entirely superficial, in cuticle..... 15. *Toroa*
 Mycelial setae absent..... 16. *Perisporina*
 Spores filiform..... 17. *Ophioparodia*
 Mycelium parasitic on fungi..... Dimerinae Th.
 Spores hyaline
 Ascocarps setose
 Spores filiform..... 18. *Leptascospora*
 Ascocarps glabrous
 Spores two-celled
 Parasitic on Ascomycetes..... 19. *Dimerina*
 Parasitic on rusts..... 20. *Eudarlucia*
 Spores x-celled..... 21. *Mycophaga*
 Spores brown
 Ascocarps setose
 Spores two-celled..... 22. *Phaeodimeriella*
 Spores x-celled..... 23. *Stevensula*
 Ascocarps glabrous
 Spores two-celled..... 24. *Phaeostigma*

3. Discussion of the Genera

a) *Parodiopsidae*(1) *EUMELA* Syd. Ann. Myc. **23**: 335. 1925.

This is a monotypic genus from Costa Rica. It is close to *Lasiostemma* Th. & Syd. from which it differs in the character of the mycelium, the insertion of the ascocarps and the presence of a conidial stage. It forms extensive black crusts which are entirely superficial and as in *Meliola*, the haustoria are epidermal.

The type-species is *Eumela Chiococcae* Sydow.

MATERIAL EXAMINED: On *Chiococca racemosa* L. Petrak's Mycotheca Germanica. No. 17. (Iso-type) Leg. H. Sydow, San Pedro de San Ramon, Costa Rica, Jan. 1925. (In Mycol. Coll. Pland Ind. Sta. Beltsville, Md.)

(2) *LASIOSTEMMA* Th. & Syd. Ann. Myc. **15**: 218. 1917. emend. Petrak in Sydowia **4**: 379. 1950.

Dimeriella Auct., nec. Spegazzini, p.p.

Chaetostigme Syd. Ann. Myc. **15**: 199. 1917.

Capnodinula Speg. Physis **4**: 288. 1918.

Pseudoperisporium Toro, Sci. Surv. Puerto Rico **8**²: 42. 1926.

Acarothalium Syd. Ann. Myc. **35**: 266. 1937.

The reasons for using this genus name in preference to *Dimeriella* are given on page 44 of this work. This genus differs markedly from *Eumela* in having an extensive internal mycelium. In a previous paper, the author (1934) had given his views of the nomenclatural status of this genus and that of those considered here as synonyms. The original description of the genus *Lasiostemma* is misleading because the author stated that "Sonst wie Parodiella", a fact which if true, would make the two genera related.

Type-species: *Lasiostemma melioides* (B. & C.) Th. & Syd.

1. *LASIOSTEMMA MELIOLOIDES* (B. & C.) Th. & Syd. Ann. Myc. **15**: 218. 1917.

Asterina melioides B. & C., Grevillea **4**: 10. 1875.

Meliola baccharidis B. & Rav., Grevillea **4**: 158. 1876.

Dimerosporium melioides (B. & C.) Martin, Journ. Myc. **1**: 146. 1885.

Dimerosporium baccharidis (B. & Rav.) Sacc., Syll. Fung. **1**: 53. 1882.

Dimerosporium melioides (B. & C.) Ell. & Ev., N. Am. Pyr. **1892**: 32.

Dimerosporium vestitum Earle, Bull. N. Y. Bot. Gard. **2**: 338. 1902.

Dimeriella melioides (B. & C.) Th., Ann. Myc. **10**: 1. 1912.

Chaetostigme melioides (B. & C.) Syd., Ann. Myc. **22**: 295. 1924.

This is the type species of the genus and the fungus is the common species on *Carduaceae* in continental United States. The upper portion of the asco-

carp is adorned by very long stranded radiating hyphae, a feature peculiar to this species.

MATERIAL EXAMINED: On *Baccharis halimifolia* L. Curtis Herbarium No. 1355. Daytona Beach, Florida. (In Herb. New York Bot. Garden).

2. LASIOSTEMMA CORONATA (Speg.) Toro, Journ. Univ. Puerto Rico **23**: 82. 1939.

Asteridium coronatum Speg. Anal. Soc. Ci. Argentina **26**: 18. 1888.

Dimerosporium Puiggarii Speg., Bol. Acad. Nac. Ci. Cordoba **11**: 485. 1889.

Dimerosporium annulatum Rehm, Hedwigia **35**: 53. 1896.

Asterella longiseta Starb., Bih. K. Svensk. Vet. Akad. Handl. **253**: 25. 1899.

Dimeriella longiseta (Starb.) Th., Broteria **9**: 12. 1910.

Dimeriella erigeronicola Stev., Trans. Ill. Acad. Sci. **10**: 166. 1917.

Pseudoperisporium erigeronicolum (Stev.) Toro, Sci. Surv. Puerto Rico & Virg. Is. **8**: 41. 1926.

Chaetostigme erigeronicola (Stev.) Stev., Illinois Bio. Monog. **11**²: 169. 1927.

In a previous paper (Toro 1939) we included under this species all previously described forms the ascocarps of which were arranged in concentric rings. However, since there are variations in spore characters and measurements in specimens on different hosts, we are at present limiting this species to the genus *Leptilon* and excluding from it those occurring on other hosts.

MATERIAL EXAMINED: On *Leptilon pusillum* (Nutt.) Britton. Puiggari No. 2586. Apiaphy São Paulo, Brazil, April 1888. (In Farlow Herbarium, Harvard Univ.); Cornell Univ. Exp. of Puerto Rico, Whetzel, Kern & Toro No. 2637, Ciales, July 20, 1924.; Fungi of Venezuela Kern & Toro No. 1709, Ocumare, March 1932.

On *Leptilon bonariensis* (L.) Small. Fungi Venezuelani, H. Sydow No. 249, Pto. La Cruz, Jan. 16, 1928. Fungi of British Guiana, F. L. Stevens No. 204, Fumatumari, July 11, 1922.

On *Leptilon chinense* (Jacq) Britton. Fungi of Costa Rica, R. A. Toro No. 234, Turrialba, July 10, 1949.; F. L. Stevens, Puerto Rico Fungi No. 2048, Quebradillas. (Plate 4 Fig. 16).

3. LASIOSTEMMA CORDICOLA (P. Henn.) Toro, Journ. Univ. Puerto Rico **23**: 83. 1939.

Dimerosporium cordicolum P. Henn., Hedwigia **43**: 455. 1904.

Dimerosporium cordiae P. Henn., Hedwigia **48**: 4. 1908.

Dimeriella cordiae (P. Henn.) Th., Beih. Bot. Cent. **26**: 67. 1912.

Dimerium Stevensii Garman, Mycologia **7**: 337. 1915.

Chaetostigme cordiac (P. Henn.) Stev. Illinois Biol. Monog. **11**: 169. 1927.

This is the species selected by Theissen and Sydow (1917) as the type of *Dimeriella* Speg. Studies of abundant material from different localities revealed that at maturity the spores are brown. In this case then *Dimeriella* Th. & Syd. nec. Speg. is a brown-spored form. *Mirandia* Toro then would become a synonym because it postdates this. But since the Theissen and Sydow's name is pre-occupied by Spegazzini's, still *Mirandia* would be the adequate name. *Lasiostemmella* Petrak (Sydowia 4: 376. 1950) then will become a synonym of *Mirandia* Toro, and the species herein discussed should be transferred to *Mirandia cordiicola* (P. Henn.) comb. nov.

MATERIAL EXAMINED: On *Cordia* sp. Ule's Herb. Brasilensis, No. 2950, Est. Amazonas Sept. 1901 (In Herb. Harvard University).

On *Cordia corymbosa* (L.) G. Don. Puerto Rico Fungi, F. L. Steven No. 934, College grounds, Mayaguez; Fungi Venezuelani, H. Sydow No. 41, Catia, Dec. 16, 1927. (In Herb. C. E. Chardón).

3. **APHANOSTIGME** Syd. Ann. Myc. 24: 368. 1926.

Dimeriollopsis Stevens, Illinois Biol. Monog. 11: 170. 1927.

The genus was described from Costa Rica and placed in the Dothideaceae. It is an epiparasite of the leaf hairs and there is no penetration either through the cuticle or the stomata. It is closely related to *Acanthostigma* De Not. from which it differs in being epiphyllous rather than saprophyllous in woody substrata. The two species of *Dimeriollopsis* Stev. that have been described from tropical America are herewith transferred to this older genus name.

Type species *Aphanostigme solani* Syd.

1. **Aphanostigme costarricensis** (Stev.) comb. nov.

Dimeriollopsis costarricensis Stev. l.c.

The spores in this species were unequally two-septate, the central cell being larger, as if a septum were missing. The mycelium occurs on the leaf trichomes, a character typical of the genus. The fungus was reported as occurring on *Cannavalia* sp.; but the specimens examined show the host to be *Phaseolus* sp.

MATERIAL EXAMINED: On *Phaseolus* sp. F. L. Steven's Fungi of Costa Rica No. 783 and 785. Swamp mouth. Aug. 8, 1923. (In Myc. Coll. Plant Ind. Sta. Beltsville, Md.).

2. **Aphanostigme heterotrichi** (Toro) comb. nov.

Dimeriollopsis heterotrichi Toro Mon. Univ. Puerto Rico 2: 110. 1934.

The mycelial hyphae are of a yellowish color, giving the host an appearance as of being stained. The spores are fusoid with the upper portion obtuse and the lower pointed. A re-examination revealed that the fungus occurs on the grayish hairs of the host.

MATERIAL EXAMINED: On *Heterotrichum macrodon* Planch. Fungi of Venezuela, Chardon and Stelling No. 810. Carabobo, Aug. 6, 1932. (In Herbarium Cornell University).

4. OPHIOMELIOLA Starb. in Bih. Sven. Handl. **25**: 22. 1899.

The only material assigned to this genus which we have had the opportunity to examine is that of *O. Mangiferae* Chaves Batista on *Mangifera indica* L. This material agrees with the section Chaetothyriae of the Capnodiaceae. We have not studied authentic material. However, since the description of the genus, as well as the name, suggest affinity here, we are tentatively retaining it on the authority of Clements and Shear (1931) and of Hansford (1946).

The type is *O. Lindmani* Starb.

5. CLEISTOSPHAERIA Syd. Ann. Mycol. **14**: 74. 1916.

The type is *C. macrostegia* on *Piptadenia* sp. The species was re-examined by Arnaud (1923) who found it to agree with his family Parodiellinaceae. The presence of external mycelium makes it a member of our new family.

6. EUDIMERIOLUM Spig. Anal. Mus. Nac. Buenos Aires **23**: 36. 1912.

Dimeriopsis Stev. Trans. Illinois Acad. Sci. **10**: 17. 1917.

The biologic relations differentiate this genus from *Dimerina* Th. The former is parasitic on leaves and stems, the latter, on fungi. Spegazzini's name antedates that of Stevens and therefore, should be recognized, for reason of priority. The type is *Eudimeriolum elegans* Spig. We have examined the following specimens which agree with the description of the genus.

1. EUDIMERIOLUM JACQUINEAE (B. & H.) Hansf. Myc. Paper **15**: 49. 1946.

Lizonia jacquiniae B. & H. Rev. Myc. **1891**: 16.

Dimerina jacquiniae Garman, Mycologia **7**: 337. 1915.

Dimerina monensis Stevens, Bot. Gaz. **69**: 254. 1920.

The specimen collected by Stevens (On *Jacquinia Barbasco* (Loef.) Mez., Mona Island, No. 6087) was described as two different species, probably by mistake. We are recognizing the synonymy on the authority of Hansford (1946), since we have not examined specimens of the *Lizonia*; but from the description it seems to be correct.

2. Eudimeriolum arthrotylidicolum (Stev.) comb. nov.

Dimeriopsis arthrotylidicola Stevens, Trans. Illinois Acad. Sc. **10**: 171. 1917.

The occurrence of the ascocarps underneath the mycelium, the large size of the spores and the adherence of the structures of the centrum make this species unique.

MATERIAL EXAMINED: On *Arthrotylidium sarmentosum* Pilg., F. L. Ste-

vens, Puerto Rico Fungi No. 4722. Utuado. Dec. 1915. (In Herbarium Insular Experiment Station, Rio Piedras, P.R.).

3. *Eudimeriolum dominicanum* (Toro) comb. nov.

Dimerina dominicana Toro Mycol. 19: 72. 1927.

A re-examination of the type specimen showed that the fungus is parasitic on leaves and therefore is not a *Dimeria*.

MATERIAL EXAMINED: On *Wallenia laurifolia* Sw., San Cristobal, R. D., Kern & Toro No. 178; March 13, 1926. (In Herbarium Cornell University).

7. GOMEZINA Chardon and Toro, Monog. Univ. Puerto Rico 2: 111. 1934.

The genus differs from *Aphanostigme* Syd. in possessing glabrous ascocarps. It is based on *Gomezina araguata* C. & T., the mycelium of which, not abundant and of a yellowish-brown color, imparts a similar coloration to the epidermal hairs of the host. In this respect the genus shows affinity with the Parodiopsidaceae.

MATERIAL EXAMINED: On *Croton niveus* Jacq. Road to Parapara, Aragua. Mycol. Exp. of Venezuela, Chardon and Toro No. 714. July 27, 1932. (In Herbarium Cornell University).

8. TRICHOSPERMELLA Speg., Anal. Mus. Nac. Buenos Aires 23: 38. 1912.

This genus, like *Gomezina* and *Aphanostigme*, is restricted to the leaf tomentum. The fruit bodies are astomous and the mycelium upon which they are seated is grey-brown. No material has been examined of its only species *T. pulchella* Speg. on *Cestrum* sp.

9. *Ticomycetes* nom. nov. *Tonduzia* Stev. Illinois Biol. Mon. 11: 168. 1927. (nec *Tonduzia* Boeck, nec *Tonduzia* Pit.)

Si genere hoc validum habendum est, nomen novum *Ticomycetes* proponendum, quia jam extant genere *Tonduzia* Boeck 1905.

On page 48 we explained why *Tonduzia* Stev. cannot be recognized. We have not been able to study the type-species, but Petrak (1934) had recognized it as a good genus and amended its description. The type is from Costa Rica on *Psychotria brachiata* Sw.

10. MIRANDIA Toro, Mon. Univ. Puerto Rico 2: 106. 1934.

The original description placed this genus near *Piline* Th., from which it differed in the presence of paraphyses. However, Arnaud (1918) showed that in *Piline splendens* (Pat.) Th. the spores are usually three-celled and therefore it is identical with *Perisporiopsis* P. Henn. Moreover, should the spores be two-celled, then *Piline* is identical with *Parodiopsis*. *Mirandia* differs from the latter in that the ascocarps are setose.

The type species is *Mirandia Fourcroyae* Toro.

MATERIAL EXAMINED: On *Fourcroya Humboldtiana* Trel. Explorations of

Venezuela, Chardon and Toro No. 550. Ocumare-Los Teques Road. July 9, 1932. (In Herbarium Cornell University).

11. NEMATOSTOMA Syd. Ann. Myc. **12**: 16. 1914.

Hyalomeliola Stev. Illinois Biol. Mon. **8**: 193. 1923.

The synonymy and inclusion of the genus here is based on Hansford's studies of the type species. He included the following two species which we have not seen: *N. guianense* on *Licania* from British Guiana and *N. costaricensis* on *Tetracera volubilis* from Costa Rica. One other species from Puerto Rico, which undoubtedly belongs here is *Perisporium Lantanae* Stev., but since there are two other related species on the same host, all of which may be synonyms, we omit conclusions until we are able to study the material.

12. MELIOLINA Syd. Ann. Myc. **12**: 553. 1914.

This is one of the several phragmosporous genera that have been identified with *Perisporium* auct. Its occurrence as a parasite on living leaves makes it unlike the latter; the absence of hyphopodia with epidermal haustoria excludes it from the Meliolaceae, while the formation of ascocarps upon an external mycelium incorporates it with the Parodiopsidaceae. Stevens (1918) described several species of *Perisporium*, parasitic upon the mycelium of *Meliola*, which he later (1927) transferred to *Meliolina*. However, we are using this genus name in a restricted sense. The type-species *M. cladotricha* (Lev.) Syd. is a leaf parasite; fungous parasites are therefore excluded. On page 45 is given a key to differentiate genera previously considered identical with *Perisporium* auct.

1. MELIOLINA CHARDONII Toro Ann. Myc. **32**: 113. 1934.

The species is characterized by the abundance and length of the ascocarpic setae, the large size of the spores and the acute character of their end cells.

MATERIAL EXAMINED: On *Clethra brevifolia* Benth. Explorations of Colombia, Chardon No. 779. Pamplona, Sept. 1932. (In Herbarium Cornell University).

13. PARODIOPSIS Maub. Bull. Soc. Myc. France **31**: 22. 1915.

Piline Th. Ann. Myc. **14**: 409. 1916.

Hypoplegma Th. & Syd. Ann. Myc. **15**: 135. 1917.

Chrysomyces Th. & Syd. Ibid. 139. 1917.

Schistodes Th. & Syd. Ibid. 465. 1917.

Meliolidium Speg. Bol. Acad. Nac. Ci. Cordoba **26**: 336. 1923.

Episphaerella Pet. Ann. Myc. **22**: 126. 1924.

This is the best known genus of the family and it has been extensively studied by Arnaud (1921). The following is a translation from his description.

Mycelium brown, reticulate, with setae and stomopodia from which

the internal mycelium with haustoria arise; ascocarps superficial on the external mycelium, globose, astomous, glabrous; wall of several layers; asci separated by interthecial threads, 8-spored, ellipsoid; spores ellipsoid, 2-celled, hyaline at first, becoming brown with age. Conidial stage present.

The type-species is *Parodiopsis melioloides* (B. & C.) Maub.

With the exception of the last two genera mentioned in the synonymy above all the others are given by Arnaud. *Meliolidium* Speg. is based on *M. portoricense* and is described as having one-celled, hyaline spores. However, the author remarked that perhaps there are four two-celled spores which separate early into unicellular fragments. Since Stevens and Higley (1917) found the same situation of fragmentation of the spores in the species they described as *Perisporium portoricense* but they were sometimes colored, we are for the present including Spegazzini's genus under *Parodiopsis*, with the conviction that further studies of the type material and of the method of distribution of the internal mycelium will reveal the true identity.

Episphaerella Pet. has as the type *Parodiopsis manihotis* (P. Henn.) Arn. This is one of the species which Arnaud (1921) studied and figured, but since the spores appeared juvenile and hyaline at the time, he placed it under the genus with a question mark. Should the spores prove to be hyaline at maturity, then *Episphaerella* Pet. becomes a synonym of *Eudimerium* Speg., an older name.

1. PARODIOPSIS BICORONATA Garces Mycologia 36: 433. 1944.

The character, both microscopic and macroscopic agreed closely with those described for the species, except that the hyphopodia are widely separate (called stomopodia by the author), and the mycelium is setulose (fig. 3, C).

MATERIAL EXAMINED: On *Inga* sp. C. Garcés No. 560 Envidado Sept. 1942. (In Myc. Coll. Pl. Ind. Sta. Beltsville.)

2. PARODIOPSIS STEVENSII Arnaud, Ann. Epiph. 9: 22. 1923.

The species occurs on the same material with *Perisporium truncatum* Stev. The presence of the conidial stage and the large size of the asci and spores is very characteristic.

MATERIAL EXAMINED: On *Inga Inga* (L) Britton. Puerto Rico Fungi, F. L. Stevens No. 7049, Mayaguez, July 1913. (In Herb. Insular Experiment Station).

3. PARODIOPSIS MELIOLOIDES (B. & C.) Maubl. Bull. Soc. Myc. France 31: 22. 1915.

Sphaeria melioloides B & C., Journ. Linn. Soc. 10: 387. 1868.

Parodiella melioloides Wint., Hedwigia 24: 257. 1885.

Dimerosporium Urbanianum P. Henn. Hedwigia **33**: 231. 1894.

Dimerium melioloides Garman, Mycol. **7**: 336. 1915.

As in the case of *Meliola*, there probably exists a great deal of specificity in this genus and the numerous reports of the species on different hosts may turn out to be separate species.

MATERIAL EXAMINED: On *Clusia rosea* Jacq. F. L. Stevens Puerto Rico Fungi No. 816. Maricao, July 1914. (In Herb. Insular Experiment Station, Rio Piedras).

14. MELIOLINELLA Hansf. Kew Myc. Paper **15**: 69. 1946.

Meliolinopsis Stev., Illinois Biol. Mon. **8**: 193. 1923. (nec Beeli, 1920).

Because Stevens' name was preoccupied by that of Beeli, and because the former was found to be a good genus, Hansford proposed the substitution above and transferred its only species, *M. palmicola* to the new combination *Meliolinella palmicola* (Stev.) Hansf. The species occurs on *Bactris* sp. in British Guiana.

15. TOROA Syd. Journ. Dept. Agric. Puerto Rico **10**: 19. 1926.

Perisporium auct. p. p.

The type-species of the genus, *Toroa dimerosporioides*, possess the yellowish-brown soluble dye characteristic of Arnaud's Parodiellinaceae. Because it has an external mycelium it falls in his Tribe Parodiopsidae. The mostly three septate spores are brown and constricted at the septa, and the end cells are short, obtuse, and lighter in color. The asci, mostly four-spored are, like those of the Meliolaceae, early evanescent. The mycelium is reticulate and provided with long, stiff setae. Stomopodia are produced at the stomata but the internal mycelium is mostly subcuticular.

1. TOROA DIMEROSPORIOIDES (Speg.) Syd. Journ. Dept. Agric. Puerto Rico **10**: 21. 1926.

Asteridium dimerosporioides Speg. Fungi Guar. **2**: 17. 1888.

Zukalia dimerosporioides (Speg.) Sacc. Syll. Fung. **9**: 434. 1891.

Gibberella dimerosporioides (Speg.) v. Hohnel, Frag. Myk. **359**: 9. 1909.

Perisporium bromeliae Stev. Trans. Illinois Acad. Sci. **10**: 168. 1917.

Chaetosphaeria bromeliae Frag. & Cif. Bol. R. Soc. Española Hist. Nat. **25**: 449. 1925.

As evidenced from the above synonymy, the species has been assigned to a variety of genera in different families, from the Capnodiaceae to the Nectriaceae. However, the presence of abundant reticulate, superficial, hyphopodiate mycelium, arising from stomopodia, following the deep vein indentations of the leaves, with superficial ascocarps on the mycelium,

makes this fungus a member of this family, for which there is no other available genus.

MATERIAL EXAMINED: On *Bromelia Pinguin* L. F. L. Stevens No. 7034. Mayaguez, Dec. 25, 1913. (In Herb. Insular Experiment Station, Rio Piedras). R. A. Toro No. 580, Juan Diaz, July 10, 1949. (In Herb. Inst. Nac. Agric. Turrialba, Costa Rica). This is the first report of the species from Costa Rica. (fig. 6, D).

16. PERISPORINA P. Henn. Hedwigia **43**: 357. 1904.

Perisporium Auct. pp.

Like *Toroa*, *Perisporina* possesses a superficial mycelium and the glabrous ascocarps are seated upon this mycelium. However, the internal mycelium of *Perisporina* is extensive and produce haustoria in the mesophyll. Like *Parodiopsis*, it is a leaf parasite and differs from it in being phaeophragmoporous.

The type-species is *P. manoensis* P. Henn.

1. PERISPORINA PORTORICENSIS (Stev. & Higley) Toro. Sci. Surv. Puerto Rico **8**: 38. 1926.

Perisporium portoricensis Stev. & Higley Trans. Ill. Acad. Sci. **10**: 169. 1917.

This species is very characteristic. The mature spores separate at the septa, leaving a great number of unicellular segments. The same situation happens in the case of *Meliolidium portoricense* Speg., on the same host, the same locality, only that the spores in the latter are described as two-celled, four in number and hyaline. Whether we are dealing with the same species at different stages of maturity cannot be stated at present. We defer this question until we have the opportunity to collect and study abundant material.

MATERIAL EXAMINED: On *Callophyllum antillanum* Britton. F. L. Steven's Puerto Rico Fungi No. 7489. Mayaguez, July 1913. (In Herb. Insular Experiment Station, Rio Piedras).

2. PERISPORINA TRUNCATA (Stev.) Arnaud Ann. Epiph. **9**: 33. 1923.

Perisporium truncatum Stev. Trans. Illinois Acad. Sci. **10**: 167. 1917.

This species is peculiar in that the asci are few in number and very large. It also produces conidia abundantly.

MATERIAL EXAMINED: On *Inga* sp. Herb. Inst. Nac. Agric. Turrialba, Costa Rica. R. A. Toro No. 473. Grecia, Aug. 5, 1949.

In his treatment of the genus *Stevensula*, Spegazzini transferred two other species of *Perisporium*, parasitic upon the mycelium of *Meliola*, to *Perisporina*. As we are considering the genus in a strict sense, for parasitic species with extensive endogenous mycelium with haustoria in the mesophyll,

Spegazzini's latter combinations will be dealt with in connection with *Stevensula*.

17. OPHIOPARODIA Pet. & Cif. Ann. Myc. **30**: 223. 1932.

This genus with *Ophiomeliola*, *Ticomycetes* and *Trichospermella* form a closely related group of scolecosporous forms. They can be differentiated as follows:

Ascocarp setose.....	<i>Ophiomeliola</i>
Ascocarp smooth	
Internal mycelium absent.....	<i>Trichospermella</i>
Internal mycelium present	
Endogenous hyphae superficial.....	<i>Ticomycetes</i>
Endogenous hyphae in the mesophyll.....	<i>Ophioparodia</i>

The type species is *O. pulchra* from Santo Domingo. The fact that it contains a conidial stage of the *Septoidium* type (Arnaud 1923) is indication of its affinity with the Parodiopsidaceae.

b) *Dimerinae*

18. LEPTASCOSPORA Speg. Physis **4**: 284. 1918.

Like *Darluca* Speg., this genus occurs on the uredinia of rusts. There is only one species known, *L. uredinis* (Rac.) Speg. Another doubtful species which agrees in spore and ascocarp characters, but differs in host relationships, is *L. Asterinae* Toro in herb. on *Asterina* sp. on *Hymenea* (West Indian Cryptogams. Collected by R. Thaxter, Port Spain, Trinidad, No. 7642.) (In Farlow Herb. Howard University).

19. DIMERINA Th. Beih. Bot. Cent. **29**²: 46. 1912.

Stigme Syd. Ann. Myc. **15**: 199. 1917.

Dimerinopsis Syd. ibid: 202. 1917.

Species of this genus are parasitic on the mycelium of *Meliola* or *Asterina*. Species parasitic on leaves and with the same characters have been placed under *Eudimeriolium* Speg.

Type of the genus is *Dimerina andirae* (P. Henn.) Hansf.

The following species is the most common of the genus in Tropical America.

DIMERINA MINDANAENSE (P. Henn.) Hansf. Imp. Inst. Myc. Paper **15**: 56. 1946.

Dimerosporium mindanaense P. Henn. Hedwigia **47**: 263. 1908.

Dimerina eutricha (Sacc. & Berl.) The. Beih. Bot. Cent. **29**²: 65. 1912.

Dimerosporium eutrichum Sacc. & Berl. Rev. Myc. **7**: 156. 1885.

Stigme costarricana Syd. Ann. Myc. **24**: 330. 1926.

This is prevalent on the mycelium of *Meliola*. It occurs throughout the range of the host species.

MATERIAL EXAMINED: On *Irenina hyptidicola* Stev. on *Hyptis capitata* Jacq. Stevens' Fungi of Puerto Rico No., 8526 Utuado July 16, 1915, Sydow Fungi Exotici Exsicatti No. 630, Grecia, Costa Rica, Jan 13, 1925; On *Hyptis mutabilis* (Poit) Eip., Fungi of Venezuela, R. A. Toro No. 73, El Valle, Dec. 15, 1930.

On *Meliola Psychotriæ* Earle on *Borreria laevis* (Lam.) Griseb. Puerto Rico Fungi, Herb. C. E. Chardon, Stevens' No. 8090, Utuado, July 8, 1915.

On *Irenina vilis* (Syd.) Stev. on *Valerianodes* sp. Fungi of Colombia, R. A. Toro No. 367, Salgar, Antioquia, April 15, 1927.

On *Irenina triloba* (Wint.) Stev. on *Pilea* sp. Fungi of Venezuela, Chardon, & Toro No. 255. La Cumbre, June 17, 1932.

20. EUDARLUCA Speg. Rev. Mus. La Plata 15: 22. 1908.

The type-species, *E. australis* Speg., differs from the species of *Dimerina* in being parasitic on the sori of rusts and in having its conidial stage in the genus *Darluka* Cast. It is exceedingly common in tropical America and has been reported from Santo Domingo, Puerto Rico, Venezuela, Colombia, Costa Rica, etc. on all plant rusts; but especially on the uredinial stage of *Puccinia*.

21. MYCOPHAGA Stev. Illinois Biol. Monog. 8: 197. 1923.

This monotypic genus has been reported from British Guiana on the mycelium of an unknown fungus occurring on *Anacardium* sp. We have not seen material, but the description of its type species, *M. guianensis* Stev. indicates that it belongs here.

22. PHAeODIMERIELLA Speg. Rev. Mus. La Plata. 15: 13. 1908.

Phaeodimeriella Th. Beih. Bot. Cent. 29²: 46. 1912.

Chaetostigmella Syd. Ann. Myc. 15: 199. 1917.

Phaeodimeris C. & S. Genera of Fungi p. 54. 1931.

As pointed out by Clements and Shear, both Spegazzini and Theissen used the same genus name and based it on the same type species: *Dimerosporium occultum* Rac. Authors have been attributing the genus name to Theissen; but as we pointed out (1934) Spegazzini's name has priority. The following species have been examined by us.

1). PHAeODIMERIELLA GUARAPIENSIS (Speg.) Speg. Rev. Museo La Plata 15: 15. 1908.

Dimerosporium guarapiensis Speg. Anal. Soc. Ci. Argentina 17: 130. 1884.

Dimerosporium appendiculatum Earle Bull. New York Bot. Garden 3: 303. 1905.

Phaeodimeriella guarapiensis (Speg.) Theis. Beih. Bot. Cent. 29²: 68. 1912.

Phaeodimeris guarapiensis (Speg.) Toro Sci. Surv. Puerto Rico
8²: 216. 1932.

This fungus occurs on the mycelium of both *Meliola* and *Asterina*. The setae are located on the upper portion of the ascocarp, they are few to many in number and without cross walls. The spores are brown, small, unequally septate.

MATERIAL EXAMINED: On *Asterina diplocarpa* Cooke on *Sida carpinifolia* L. Herb. C. E. Chardon, Heller No. 6333, Puerto Rico, Dec. 1902.

On *Meliola cyperi* Pat. on *Cyperus* sp. Herb. C. E. Chardon, Puerto Rico Fungi, No. 390, Ponce. June 20, 1923.

2). PHAEODIMERIELLA CAYAPONIAE (Garman) Seaver & Toro, Sci. Surv. Puerto Rico 8: 38. 1926.

Dimerium cayaponiae Garman Mycol. 7: 335. 1915.

Phaeodimeris cayaponiae (Garman) Toro Sci. Surv. Puerto Rico
8²: 216. 1932.

Although the description stated that the species have glabrous ascocarps, an examination of the type material revealed that it had three to four, short, cylindrical, hooklike setae. Also the fungus is parasitic on the mycelium of another fungus and not on the leaves as described.

MATERIAL EXAMINED: On unknown mycelium on *Cayaponia americana* (Lam.) Cogn. Puerto Rico Fungi, F. L. Stevens No. 408.

3). *Phaeodimeriella meliolinae* (Toro) comb. nov.

Chaetostigmella meliolinae Toro Ann. Myc. 32: 112. 1934.

The numerous, obtuse setae and the ellipsoid spores are the distinguishing characters of this species.

MATERIAL EXAMINED: On *Meliolina chardonii* Toro on *Clethra brevifolia* Benth. Fungi of Colombia. C. E. Chardon No. 779. Pamplona, Sept. 1932.

4). *Phaeodimeriella parasitica* (Toro) comb. nov.

Chaetostigmella parasitica Toro Monog. Univ. Puerto Rico 2:
108. 1934.

The setae on this species are septate, obtuse, and somewhat uncinata. The spores are triseriate in the ascus and equally septate.

MATERIAL EXAMINED: On *Xenostomella meridensis* Toro on *Miconia chaetodon* Naud. Fungi of Venezuela, Chardon No. 1102. Mérida, Sept. 3, 1932.

23. STEVENSULA Speg. Bol. Acad. Nac. Ci. Cordoba 26: 339. 1923.

Phaeophragmeriella Hansf., Proc. Linn. Soc 156: 107. 1944.

Perisporium auct. p.p.

In his discussion of the genus, Spegazzini clearly stated that the species is a parasite upon the mycelium of *Meliola*. Hansford's (1946) suggestion that this fungus represented a dark-colored setose *Perisporina* is baseless since he had included the latter in the Parodiellinaceae, all members of

which are strict leaf parasites. The view of Spegazzini (1923) that Stevens' (1917) species of *Perisporium* parasitic on *Meliola* should be referred to *Perisporina* is also incorrect. Already it has been shown that the old genus name *Perisporium* had a variety of meanings. In respect to *Phaeophragmeriella*, its characterization does not make it different, neither on morphological features nor biologic relations, from *Stevensula*. Perhaps the only apparent difference lies in the character of the setae which are described as short and uncinata for *Stevensula* and mycelial for *Phaeophragmeriella*.

The type-species is *Stevensula monensis* Speg.

1). *STEVENSULA MONENSIS* Speg. l.c.

The spores are three-septate, brown, slightly constricted at the septa, and with the end cells acute. The mycelium and ascocarps are setulose.

MATERIAL EXAMINED: On *Meliola monensis* Stev. on *Amyris elemifera* L. Puerto Rico Fungi. F. L. Stevens No. 6146. Mona Island, Dec. 20, 1923.

2). *Stevensula meliolicola* (Syd.) comb. nov.

Chaetosphaeria meliolicola Syd. Ann. Myc. **12**: 555. 1914.

Perisporium Paullinae Stev., Bot. Gaz. **65**: 228. 1918.

Perisporina Paullinae (Stev.) Speg. Bol. Acad. Ci. Cordoba **26**: 340. 1923.

Meliolina Paullinae (Stev.) Stev. Ann. Myc. **16**: 416. 1928.

Phaeophragmeriella meliolicola (Syd.) Hans. Proc. Linn. Soc. **156**: 107. 1944.

In our discussion of the genus *Meliolina* (page 44) we have already expressed our views with respect to the preferential use of *Stevensula* instead of *Phaeophragmeriella*. We have also shown that *Perisporium* is a composite genus name and that *Perisporina* is a leaf parasite, like *Meliolina*. The other genus name in the synonymy above, *Chaetosphaeria* Tul. has a lignicolous species as type, and therefore, is saprophytic.

An examination of Stevens' material showed that the fungus grows upon the remains of a *Meliola* and consequently is not parasitic on the leaf. The mycelium lacks abundant setae but the ascocarps have their outer wall in the lower portion prolonged into short, setaelike hyphae.

MATERIAL EXAMINED: On *Meliola Hessii* Stev. on *Paullinia pinnata* L. Herb. Ins. Experiment Station, F. L. Stevens Puerto Rico Fungi No. 1207, Mayaguez, May 4, 1913.

3). *Stevensula meliolae* (Stev.) comb. nov.

Perisporium meliolae Stev. Bot. Gaz. **65**: 228. 1918.

Perisporina meliolae (Stev.) Speg., Bol. Acad. Ci. Cordoba, **26**: 339. 1923.

Meliolina meliolae (Stev.) Stev. Ann. Myc. **26**: 416. 1928.

Phaeophragmeriella meliolae Hansf. Kew Myc. Paper **15**: 96. 1946.

The species differs from the other two above in the constant character

of the spores. They are always three-septate, as in the type-species, but smaller.

MATERIAL EXAMINED: On *Irene sororcula* (Speg.) Stev. on *Critonia portoricensis* (Urb.) Britton. Herb. Insular Experiment Station, Stevens Puerto Rico Fungi No. 7320. June 20, 1913.

24. PHAEOSTIGME Syd. Ann. Myc. **15**: 199. 1917.

Dimerium auct. nec Sacc. & Syd. Syll. Fung. **17**: 537. 1905.

Bolosphaeria Syd. Ann. Myc. **15**: 201. 1917.

Phaeocapnodinula Speg. Bol. Acad. Ci. Cordoba **26**: 369. 1923.

Pseudodimerium Pet. Ann. Myc. **22**: 21. 1924.

As has been shown on page 46 the genus name *Dimerium* is not valid and must be rejected. We have proposed the oldest and best known synonym as a substitute for it. The mycelium in this genus is parasitic on other fungi, without hyphopodia or setae. The ascocarps are small, globose, glabrous, and dark-colored. The spores are two-celled, brown, eight in each persistent, ellipsoid, ascus. The conidial stage is either *Ectosticta* or *Cicinnobella*.

Type-species is the following:

1. PHAEOSTIGME PICEA (B. & C.) Syd. l.c.

Asterina picea B. & C. Journ. Linn. Soc. **10**: 374. 1868.

Dimerium piceum (B. & C.) Theiss. Ann. Myc. **10**: 3. 1912.

Dimerosporium piceum (B. & C.) Sacc. & Th. Ann. Myc. **10**: 3. 1912.

About 10 other species of *Dimerium* are regarded as synonyms of this, but since we have not examined them, we do not include them here as such. The species is widely distributed and prevalent on the mycelium of *Meliola* and *Asterina*. It forms tightly enclosed mats of olivaceous hyphae upon which are seated globose, superficial, glabrous, dark-olivaceous ascocarps with indistinct pores at maturity. The asci, separated by interthecial threads, are cylindric, obtuse, thickened at the apex and eight-spored. The spores are usually biseriate, ellipsoid, one-septate, constricted, brown, one-cell slightly shorter than the other, and broader. (fig. 5,D, fig. 6,B).

MATERIAL EXAMINED: On *Meliola capsicola* Stev. on *Capsicum annum* L. Fungi of Costa Rica, R. A. Toro No. 43. Turrialba, June 10, 1949.

On different species of *Meliola* and *Asterina* on a variety of hosts. Herb. Insular Experiment Station. Puerto Rico. Also reported from Continental Tropical America and the West Indies.

2. PHAEOSTIGME ISAZANUM Toro Journ. Dept. Agric. Puerto Rico **14**: 234. 1930.

The small size of spores and ascocarps tends to identify this species with *Dimerium minutum* (Pat.) Sacc, which also occurs on *Asterina* on Melastomaceae. However, we shall regard our species as different until material of its supposed predecessor is obtained.

MATERIAL EXAMINED: On *Asterinella antioquiensis* Toro on *Miconia ciliata* (L. C. Rich.) DC Mycological Explorations of Colombia, R. A. Toro No. 246. Angelopolis, July 27, 1927: (In Herb. Cornell University).

Conclusion

The results obtained from the studies herewith presented have convinced us that, in determining relationships among the fungi, their mode of existence is important, as well as their morphological characteristics. There appear to exist three biological groups of superficial fungi each including forms which can be arranged on the basis of their morphological features. These three groups are as follows:

(1) *Species directly parasitic on leaves*: To this group are assigned the Erysiphaceae with hyaline mycelium and Oidiumlike conidia; the Parodiellinaceae, with no external mycelium and superficial ascocarps arising from stomopodia; the Meliolaceae, with extensive colored mycelium, epidermal haustoria arising from underneath the hyphopodia and without a conidial stage; the tribe Parodiopsidae of the Parodiopsidaceae, with abundant color, external mycelium, conidial stage not Oidium like. Here also can be included the Microthyriales with inverse-radiate ascocarps and some of the Englerulaceae, with anhistous fruiting bodies at maturity. (fig. 3, A-D)

(2) *Species that are purely superficial and therefore saprophytic*. To this group are assigned the Capnodiaceae with dematioid mycelium forming a black layer which is easily separable and fruit bodies never of straight-walled cells; the Trichothyriaceae, with mycelium like above but not dematioid and fruit bodies formed directly from the mycelial pellicle. (fig. 3, E, F).

(3) *Species parasitic on other leaf parasites and hence epiphytic*. To this group are assigned the Dimerinae tribe of the Parodiopsidaceae, some Trichothyriaceae, Englerulaceae, Hypocreaceae and Hemisphaeriaceae. (figs. 5, D and 6, B).

With the exception of the Capnodiaceae, no member of any other of the above-mentioned groups has ever been cultivated on artificial culture media. Therefore, all conform with the concept of parasites as generally interpreted.

The results of intensive taxonomic studies during the past 50 years have made possible the separation of the old order Perisporiales into a number of different orders and families. This separation has been made not only on the basis of their morphology, but on their biology as well. This dual agreement has the advantage of permitting the recognition of nomenclatural entities in the old order Perisporiales through the application of "nomen communis" to the taxa. Table 2 shows this relation.

The two families concerning us in this study are the Meliolaceae and the Parodiopsidaceae, the present successors of the Perisporiaceae.

The Meliolaceae are strict leaf parasites, with abundant external mycelium and no conidial stage. Contact with the living cells is made through haustoria which arise from the capitate hyphopodia and enter the host by way of the cuticle. The haustoria are confined to the epidermal cells. No internal mycelium is present. The ascocarps are peritheciiumlike; the asci are early-evanescent and the spores appear distributed at different heights in the centrum. If we judge the family by these characteristics we may conclude that it represents the culmination of ectoparasitism in the Plectascales.

TABLE 2.—Common and scientific names of the morphologic and biologic groups of the old perisporiales.

Common name	Scientific name	Biologic relation	Morphologic characters
Powdery mildews	Erysiphales	Parasitic	Hyaline mycelium conidia, Oidiumlike, ascocarps colored, astomous
Asterineans	{ Microthyriales Hemisphaeriales	{ Parasitic Epiphytic	Colored mycelium, usually with hyphopodia, fruit bodies inverse-radiate
Sooty-molds	Capnodiales	{ Saprophytic Epiphytic	Colored mycelium dematioid or straight, fruit bodies of meridian hyphae; whole easily detachable as a superficial black pellicle
Black-mildews	{ Pseudosphaeriales Meliolaceae	{ Parasitic	Mycelium of straight walls, colored, ascocarps parenchymatous, pellicle persistent

The type-genus of the family Meliolaceae is *Meliola*. In spite of the hundreds of species that have been described under it, a type-species has never been designated. Our studies of the early-described species and of the specimens representing them brought forth that *M. trichostroma* has to be regarded as its lecto-type.

The Parodiopsidaceae possess the centrum organization typical of the Pseudosphaeriales. Its type genus is *Parodiopsis*. From this genus two biologic groups can be differentiated, one in which all the members are leaf parasites with abundant superficial mycelium. The host cells are penetrated through the stomata and here the mycelium forms stomopodia from which

the abundant internal mycelium arise. This group comprises the tribe Parodiopsidae. The other biologic entity is composed of fungous parasites. The mycelium is abundant, but there is no penetration of the leaf tissues. This group is termed the Dimerinae. In both the mycelium is brown, the ascocarps are seated upon it, and the asci are separated by interthecial threads which at maturity resemble paraphyses.

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