Wehmer in one of his keys based upon single characters has brought together some short-stalked species of Aspergillus\(^1\) without indicating that the number of correlated characters found might justify more than an arbitrary grouping. He calls this section "Schwachwuchsige" or weak growers in spite of the fact that its best-known members, *A. fumigatus* and *A. nidulans*, are cosmopolitan and aggressive forms. If we substitute for this designation the designation short-stalked Aspergilli with calyptriform heads, we will bring together two green series typified by *A. fumigatus* and *A. nidulans*, and an ill-defined group of species whose colors are given as avellaneus, fawn, cinnamon, or reddish brown but not green. In long-continued culture of certain of the green and yellow-green forms within this group, the color changes in the conidial masses have been followed. Greens, blue greens, and yellow greens may run into each other; any of them may develop dark shades in age which mask the original color, but they do not transform into avellaneus or related colors. Similarly the rosy or cinnamon series do not show any trace of green.

Many cultures of members of this general group have been brought together. Some of these forms are readily aligned with species described in the literature. Others diverge more or less widely. Some of these are either entirely undescribed or so inadequately described as to make identification hopeless. All of these forms have stalks short, rarely exceeding 500 μ in length, and heads usually small in diameter with conidial masses in columns (calyptriform), not as separate chains or masses of chains radiating from the vesicle (radiate).

* Published by permission of the Secretary of Agriculture.

The conidia found are mostly globose and range in diameter from 2.5 to 4.5 μ.

A species in the avellaneus series which has been intensively studied will be discussed first. The name *Aspergillus terreus* is proposed for this species, which has been under observation for about five years. It was first studied from soil cultures made by Prof. W. M. Esten in Connecticut. It was afterward found in soil cultures by Mr. F. M. Scales in Virginia and California, by Mr. S. A. Waksman in New Jersey, and by Mr. F. C. Werkentin in Texas. It has been isolated from feces by Mr. G. W. Turesson at Seattle, Washington, from decaying avocado in Florida by Prof. H. S. Fawcett, and by the writers from decaying forage in Kansas, from cornmeal ground in Indiana, from musty tobacco, from waters bottled on the American mainland and in Porto Rico, as well as from numerous chance inoculations. It is readily recognized and not uncommon in routine cultures from decaying and soil-contaminated substances.

Some of the cultures obtained reproduce the morphology and reactions of the strain first studied within the degrees of variation found in successive transfers of the same pure culture. With the accumulation of material, however, we find ourselves with a series of related strains rather than a single organism. These vary in colony characters and in details of reaction but present close resemblances in essential characters which render separate descriptions for most of them impossible, as in the case of the forms of *A. niger*. It is entirely possible that investigation, strain by strain, might show equally conspicuous differences in their activities as among the black forms. A technical description has, therefore, been drawn in broad enough terms to include the more closely related of these forms. Whether some of them may ultimately be separated as varieties, upon physiological grounds, is not determined.

*A. terreus* Thom²

Colonies upon Czapek's solution agar from tints of pinkish cinnamon through cinnamon (at times near avellaneus of Saccardo's


³ Published without description marked Thom MS, by Göte Turesson in Svensk Botanisk Tidskrift 16: 5 et seq. 1916, in his discussion of "The presence and significance of moulds in the alimentary canal of man and higher animals."
Chromotaxia) to deeper brown shades in age (see Ridgway, Pl. XXIX, 15). Klincksieck and Valette, Nos. 103D, 112, 113, 108; spreading, velvety or in some strains developing definite floccosity or anastomosing ropes of aerial hyphae; reverse and agar from pale or bright yellow to fairly deep browns. Odor, none in some strains, at least transiently present in others, or developing with the addition of high percentages of cane sugar. Conidiophores 5–8 μ in diameter, 50–150 μ or even 250 μ in length, more or less flexuous, with walls smooth, up to 1 μ thick, septate or unseptate, with apex enlarged to form a vesicle commonly 12–18 μ, occasionally up to 25 μ in diameter, bearing sterigmata usually in two series upon its dome-like upper surface; primary sterigmata 2–2.5 μ by 7–9 μ, secondary 2–2.5 μ by 5–7 μ closely packed; heads becoming solid columnar masses up to 500 μ long by 50 μ in diameter; conidia slightly elliptical to globose, 2.2–2.5 μ or even to 3 μ in diameter, smooth, in long, parallel, adherent chains. Perithecia not found. Grows at 37° C. liquefies gelatin.

Habitat.—Common in soil and in decaying vegetable matter, throughout the United States.

Turesson reports the spores of this species as viable after passing

4 Saccardo, P. A. Chromotaxia seu Nomenclator Colorum, Patavii. 1891.
through the human digestive tract. This led him to feed cultures of this species to a rabbit, which afterwards died. *A. terreus* was recovered in culture from numerous portions of the intestine (Turessson, loc. cit., p. 20). Further studies upon the possible relation of this form to toxin production are necessary.

Some experiments were made to find whether this form is an active inhabitant of the soil or merely present in spore form. Two forms of soil, a light sandy loam from Texas and a clay type from Indiana, were obtained from the soil fertility laboratory; a third sample was obtained from the greenhouses of the Arlington Farm. Finely divided soil to a depth of about 5 cm. was tamped into test tubes and sterilized. Part of the series was given fractional sterilization in steam, the remainder 30 minutes in the autoclave at 15 pounds pressure. Three cc. of water were added to the light soil and 2.7 cc. to the heavy soil. The water was added before heating, in the case of the fractional sterilization, but after heating, in the case of autoclaving the tubes. These differences of manipulation seemed to have no effect upon the growth of the organisms tried.

The test tubes of soil were inoculated by sprinkling spores on the surface of the soil in the test tubes. For comparison of growth, three strains of *A. terreus*, one of *A. nidulans*, six of *A. flavus*, one of *A. clavatus*, one of *A. oryzae*, three of the Citromyces section of Penicillium, *P. pinophilum* and *P. luteum*, were used. Each is representative of a group of related forms repeatedly found in soil. After a period of approximately two months, the typical conidial masses of *A. terreus* could be seen not only upon the surface but in the open spaces in the sandy soil to a depth of 3 cm. The organism was recovered in pure culture from the deepest areas, where growth was not visible, by breaking the tips of the test tubes and transferring some particles of soil to culture media. Although cultures showed the mold to be present, traces of mycelium were often very difficult to find by microscopic examination. Mycelia under such conditions are much less evident. Short zigzag hyphae are found in intimate contact with soil particles rather than richly branching mycelia ramifying through wide areas. Spores are produced from short stubby branches extending into small open spaces. Hyphae and heads under these conditions are not recognizable by data based upon pure culture in artificial media. Nevertheless, it is clear from the table that *A. terreus* and many others of these species planted upon its surface are
capable of growing into soil to considerable depths and even capable of producing spores under conditions in which many fungi fail to fruit at all.

The tabulated data (Table 1) from these comparative cultures show that these organisms, which were selected because they are constantly obtained in studies from the soil, are capable of actively growing within the soil.

**Table 1**

<table>
<thead>
<tr>
<th>Name</th>
<th>Race</th>
<th>Clay Soil, Depth in Cm.</th>
<th>Sandy Soil, Depth in Cm.</th>
<th>Greenhouse Loam, Depth in Cm.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Spores Visible</td>
<td>Recovered, in Culture</td>
<td>Spores Visible</td>
</tr>
<tr>
<td>A. castaneus</td>
<td>3565</td>
<td>*</td>
<td>*</td>
<td>Surface</td>
</tr>
<tr>
<td>A. clavatus</td>
<td>4083</td>
<td>*</td>
<td>*</td>
<td>2 cm.</td>
</tr>
<tr>
<td>A. flavus</td>
<td>128</td>
<td>*</td>
<td>*</td>
<td>5 cm.</td>
</tr>
<tr>
<td>A. rehmi</td>
<td>1763</td>
<td>*</td>
<td>*</td>
<td>1.5 cm.</td>
</tr>
<tr>
<td>A. fumigatus</td>
<td>2750</td>
<td>*</td>
<td>*</td>
<td>1.5 cm.</td>
</tr>
<tr>
<td>A. nidulans</td>
<td>3557.6</td>
<td>*</td>
<td>*</td>
<td>5 cm.</td>
</tr>
<tr>
<td>A. terreus</td>
<td>3557.9</td>
<td>*</td>
<td>*</td>
<td>5 cm.</td>
</tr>
<tr>
<td>A. oryzae</td>
<td>4006.2</td>
<td>*</td>
<td>*</td>
<td>5 cm.</td>
</tr>
<tr>
<td>A. terreus</td>
<td>4010.4</td>
<td>*</td>
<td>*</td>
<td>5 cm.</td>
</tr>
<tr>
<td>Penicillium (Citromycetes)</td>
<td>444</td>
<td>*</td>
<td>*</td>
<td>5 cm.</td>
</tr>
<tr>
<td>Penicillium (Citromycetes)</td>
<td>442</td>
<td>*</td>
<td>*</td>
<td>5 cm.</td>
</tr>
<tr>
<td>Penicillium (Citromycetes)</td>
<td>333</td>
<td>*</td>
<td>*</td>
<td>5 cm.</td>
</tr>
<tr>
<td>P. luteum</td>
<td>2467</td>
<td>*</td>
<td>*</td>
<td>Interstices</td>
</tr>
<tr>
<td>P. pinophilum</td>
<td>4019.2</td>
<td>*</td>
<td>*</td>
<td>Interstices</td>
</tr>
<tr>
<td>P. luteum</td>
<td>4083</td>
<td>Bottom of tube</td>
<td>5 cm.</td>
<td>*</td>
</tr>
<tr>
<td>P. luteum</td>
<td>11</td>
<td>Bottom of tube</td>
<td>5 cm.</td>
<td>*</td>
</tr>
<tr>
<td>* No information.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The literature was searched to find a name and description applicable. In form and habit of colony *A. terreus* resembles *A. fumigatus*. 

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* Ridgway, loc. cit.
Fres. and *A. nidulans* Eid., both of which are abundant in soil cultures in America. Both of these species are green; *A. terreus* is never green. All three forms have small spores (2.5 μ to 4 μ), short stalks and dense columnar or calyptriform masses of conidia. They thus have the form given for *A. calyptratus* by Oudemans.7 *A. fumigatus* has one set of sterigmata in all heads. *A. terreus* shows one set of sterigmata occasionally in young heads but two sets in well-developed heads. *A. rehmii* has double sterigmata but is described as yellow. In *A. calyptratus* the conidial column although described as black is so colored in Oudemans's figures as to suggest *A. terreus*. More recently Werkenthin8 identified one strain of *A. terreus* as obtained from soil in Texas with *Sterigmatocystis veneta* of Massalongo.9 This form is described as having "fasciculate fertile hyphae" and to be in color pale or dirty yellowish ("pallide vel sordide luteolis"). The Texas strain has superficial, interlacing, trailing ropes of hyphae from which short conidiophores arise. The same condition is produced in our original strain of *A. terreus* when grown upon peptone-beef-juice agar with cane sugar. The description of Massalongo does not appear to justify this identification.

A considerable number of species have been described in color as avellaneous, cervinus, cinnamomeus, roseus, or by technical names falling within this related series of colors. These color-terms have been used so vaguely as frequently to mean only that the color so designated comes into the group, not that it has a definite tint or shade. Cultural study, moreover, shows that the same strain when grown under a series of differing cultural conditions may be successively described by a whole series of these names. These variations have been studied in detail for certain series of forms with reference to the Code de Couleurs by Klincksieck and Valette10 and the recent work of Ridgway.11 While exact duplication of culture-color in the charts is rare, the variations within closely related series tend to fall in the columns of Ridgway's plates; that is, in tints and shades of

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11 Ridgway, loc. cit.
single mixtures of primary colors. The young culture may first show
color as one of the paler tints of a series, then become successively
deeper, and not infrequently in age change to some one of the darker
shades of the same series. A change in the primary mixture fre-
quently develops in the same colony with age. Such changes with
rare exceptions bring combinations closely related to the original,
such as are found in adjacent columns or upon the same page in
Ridgway.

An organism showing one of these colors must, therefore, be
critically compared in all its characters with those described as show-
ing any of the related colors. In making this comparison these
descriptions have been brought together and considered. Before de-
scribing A. terreus as new the original descriptions of this series were
examined in every case and frequently all references in the literature
were followed. The original citations have been included in the
synopsis of the group presented and where possible an opinion is given
upon the proper placing of the form.

In habit and colony appearance A. terreus, A. fumigatus and A.
nidulans resemble each other more closely than they resemble such
forms as A. niger, A. ochraceus or A. flavus. They may, therefore,
be taken as typical forms in three related series. A brief review
of the history of the two series of forms typified by A. fumigatus of
Fresenius

and A. nidulans of Eidam

will be followed by a synoptical
presentation of the whole group as far as the material could be inter-
preted.

Aspergillus fumigatus Series

A. fumigatus was described by Fresenius in 1850. References to
molds in the human ear go some years farther back, but no previous
author gives an adequate description of the form. The figures of
Fresenius fix a type of conidiophore and fruiting head which is readily
found by examination of cultures today. However, since organisms
with this morphology are found everywhere and upon a wide variety
of substrata, the student of comparative cultures soon finds strains
with this conidial morphology but cultural characters diverging fairly
widely and apparently fairly stable. It is not surprising to find

Fresenius, J. B. G. W. Beiträge zur Mykologie. P. 81, pl. 10, figs. 1–11.
Frankfurt. 1850.

Eidam, E. Zur Kenntniss der Entwicklung der Ascomyceten. Cohn’s
some of them described as separate species. This type of organism is reported from the tongue, the ear, the cornea of the eye, and the human lung. As a cause of aspergillosis in birds, it is found in the lungs of various species. Cultures have been extensively tested and found pathogenic in varying degrees to fowls, rabbits, guinea pigs, and dogs. We have received it from soil bacteriologists working in widely separate regions, and recovered it many times from forage and musty or moldy grains. This type of mold has proved to be a regular inhabitant of soil at least in America, hence may be expected in cultures from any substance contaminated with dirt. All of these strains grow at the temperature of warm-blooded animals, this being a prerequisite to pathogenesis. The pathological literature with reference to Aspergillus is extensive. The literature of the group was critically examined in 1905 by Costantin and Lucet\(^1\) who recognized the close relationship of the whole series of forms. They retained as species Aspergillus Lindt, A. bronchialis Blumentritt, A. lignieresii Cost. & Lucet, A. fumigatus Fres., A. virido-griseus Cost. & Lucet, and A. penicilloides Speg.

They regarded the other forms already described as synonyms or unrecognizable. Comparison of long series of cultures from different sources confirms belief in the ability of races or strains to maintain specific cultural characters in Aspergillus as has been already described for A. niger (Thom and Currie, loc. cit.). Some of these forms can probably be described in morphological and physiological terms which will identify them. It is probable, however, that the number of races showing at least slight differences is very much greater than these investigators believed and that by sufficient search connecting forms would be found which would make up a fairly complete series. The determinations of pathogenicity already reported (Costantin and Lucet, loc. cit.) show that the strains so far studied vary markedly in this respect. Physiological differences of marked degree are not necessarily correlated with morphological characters. This has been demonstrated for A. niger by Thom and Currie, and is clearly shown in the studies of relative pathogenicity of Aspergillus as reported by Costantin and Lucet.

Perithecia have been reported for Aspergillus by Behrens\(^2\) and


\(^2\) Behrens, J. Centralbl. Bakt. 11: 335. 1892.
The validity of both of these determinations is disputed by Vuillemin who probably correctly regards the perithecia found by Behrens as belonging to the *A. glaucus* series and makes those described by Grijns the basis of *A. pseudo-nidulans* Vuillemin. On the other hand, the descriptions of perithecia for *A. fumigatoides* by Bainier and Sartory and for *A. fischeri* by Wehmer are scarcely questionable. Both of these forms reproduce the conidial form of *A. fumigatus* within the limits of variation reported for this form

![Diagram](image-url)

**Fig. 3.** *A. nidulans* (American soil strain no. 131). *a*, diagrammatic section of vesicle with two sterigmata; *b*, *c*, primary and secondary sterigmata, × 1,500; *d*, a group of conidia, × 1,500; *e*, *f*, *g*, *h*, *j*, diagrams of stalks and heads; *k*, peritheciun surrounded by sterile hyphae and Hülle-cells (*L*); *l*, Hülle-cell enlarged showing the thick walls and the granular cell contents; *m*, a group of ascospores.

as it is causing aspergillosis of birds. We have recently studied a form obtained from two separate sources in which the conidial areas were much reduced when cultivated at 20°-25° C. but developed characteristic areas of the *A. fumigatus* type at 37° C. Perithecia in both strains begin to appear abundantly within the first few days on Czapek's solution agar but not at all in plain agar (beef-extract-
peptone agar of the bacteriologists). They originate in coiled hyphae similar to the process described for *A. fumigatoides* or by DeBary\textsuperscript{20} for *A. repens*. The measurements and markings are a composite of those of *A. fischeri*, *A. fumigatoides*, and *A. malignus* Lindt. Clearly these forms are closely related and just as certainly may be regarded as members of the *A. fumigatus* group. How many of the entire series will stand critical examination is still in doubt. With this group as in previous papers (Thom, Thom and Currie),\textsuperscript{21} it seems best to retain in the literature of the series the specific names found applied to such well-described forms as may represent in typical manner particular lines of variation. In general, however, it must be recognized that all the forms thus far reported grow at 37° C. or higher, that all of them as far as tests have been reported in the literature have proved pathogenic to some of the usual experimental animals, that the conidial apparatus in all of them corresponds closely to the description by Fresenius. Even in ascospore production the common characters found overshadow the differences which are limited to contrasts in size and in details of spore markings. (See synopsis of the group, p. 97.)

**Characterization from Cultures** *(see also Table 2).*—Colonies on Czapek’s solution agar in some strains strictly velvety, in others with varying amounts of tufted aerial mycelium up to felted floccose forms, green to dark green, becoming almost black in age, spreading. Reverse and substratum, in some strains uncolored, in others showing varying amounts of yellow, this occasionally becoming reddish in age. Conidiophores short, usually densely crowded, up to 300 μ (occasional strains to 500 μ) long by 2–8 μ in diameter, frequently more or less green colored, especially in the upper part, arising directly from submerged hyphae or as branches from aerial hyphae, septate or unseptate, gradually enlarged upward, with apical flask-shaped vesicles up to 20–30 μ in diameter, fertile only on the upper half, bearing sterigmata in one series, usually about 6–8 μ (varying from 5–10 μ) by 2–3 μ, crowded, closely packed with axis parallel to axis of the stalk; chains of conidia form solid columns up to 400 μ by 50 μ, but usually much shorter; conidia dark green in mass, globose, 2–3.5 μ


mostly 2.5–3 μ in diameter. Perithecia not found in most of the strains investigated, abundantly produced in certain strains [data from No. 4188.21] up to 300 μ in diameter, not colored, or very pale salmon, with walls scarcely colored, consisting of a single layer of cells, crushing easily, covered by a loose network of uncolored sterile hyphae; asci abundant, filling the perithecium within a few days, from 8 μ by 10 μ to 10 μ by 12 μ, subglobose, breaking down quickly to leave the perithecium full of ripe ascospores; ascospores bi-convex, 7 μ by 4 μ, consisting of a central body 5 μ by 4 μ, with two frilled equatorial bands about 1 μ in width and 3 to 4 similar but narrower and Anastomosing bands on each convex surface, separating into 2 valves in germination.

All strains grew over a wide range of temperature, better at 37° C. or higher than at lower temperatures. A few strains produce green conidial areas only at high temperature.

Habit.—Variable and widely distributed in soil and soil-contaminated substances, on forage, and on grain, as a cause of aspergillosis in birds.

**Table 2**

Comparative Measurements of *Aspergillus fumigatus* and Allies

<table>
<thead>
<tr>
<th>Name</th>
<th>Habit</th>
<th>Stalk</th>
<th>Vesicle</th>
<th>Sterigmata</th>
<th>Conidia</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. avianus</em></td>
<td>*</td>
<td>7.5†</td>
<td>20–30</td>
<td>*</td>
<td>2–2.5</td>
</tr>
<tr>
<td><em>A. bronchialis</em></td>
<td>*</td>
<td>280–300 x 9</td>
<td>12–19</td>
<td>*</td>
<td>3–4.2</td>
</tr>
<tr>
<td><em>A. fischeri</em></td>
<td>*</td>
<td>300 x 6–7</td>
<td>20</td>
<td>5.7 x 2.5</td>
<td>2.4–3.5</td>
</tr>
<tr>
<td><em>A. flavo-viridescens</em></td>
<td>*</td>
<td>150–310 x 52</td>
<td>30–35</td>
<td>8–14 long</td>
<td>2–3 x 2</td>
</tr>
<tr>
<td><em>A. fumigatoideus</em></td>
<td>*</td>
<td>150–340</td>
<td>16–30</td>
<td>*</td>
<td>2.5</td>
</tr>
<tr>
<td><em>A. fumigatus</em></td>
<td></td>
<td>Flocose</td>
<td>250 x 2.8</td>
<td>5–6 long</td>
<td>3 ave.</td>
</tr>
<tr>
<td><em>A. granulosis var. exigua</em></td>
<td>*</td>
<td>–3 diam.</td>
<td>20–35</td>
<td>3–6 long</td>
<td>*</td>
</tr>
<tr>
<td><em>A. keratitidis</em></td>
<td></td>
<td>Flocose</td>
<td>180–230 x 6.8</td>
<td>–24</td>
<td>–6 long</td>
</tr>
<tr>
<td><em>A. lignieri</em></td>
<td></td>
<td>Flocose</td>
<td>*</td>
<td>1000 x 3</td>
<td>22–24</td>
</tr>
<tr>
<td><em>A. malagutus</em></td>
<td></td>
<td>Data entirely lacking.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. olivaceus</em></td>
<td></td>
<td>Flocose</td>
<td>–100 x 4.5</td>
<td>10–12</td>
<td>3–4 x 2.5</td>
</tr>
<tr>
<td><em>A. penicilloides</em></td>
<td>*</td>
<td>–200 x 3–7</td>
<td>10–12</td>
<td>–8.5 x 2.5</td>
<td>–3</td>
</tr>
<tr>
<td><em>A. pusillus</em></td>
<td></td>
<td>Flocose</td>
<td>50–74 x 3–4</td>
<td>10–12</td>
<td>3 x 1.5</td>
</tr>
<tr>
<td><em>A. quininae</em></td>
<td></td>
<td>6–7 diam.</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td><em>A. ramus</em></td>
<td></td>
<td>Hallier’s figures are the only clue to identity.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. viridogriseus</em></td>
<td></td>
<td>Flocose</td>
<td>400–600 x 6–15</td>
<td>25–36</td>
<td>–5 long</td>
</tr>
</tbody>
</table>

* No information.
† All measurements given are in micromillimeters.
ASPERGILLUS FUMIGATUS, A. NIDULANS, A. TERREUS N. SP.

ASPERGILLUS NIDULANS SERIES

Eidam (loc. cit.) in 1880 described *A. nidulans* as obtained from the nest of some type of wasp or bee in the botanical garden at Breslau. Conidial forms corresponding to Eidam's figures and description have been found in many situations since that time. Members of this series have been shown to be pathogenic, by animal inoculation. As far as tested, they all grow at 37° C. or higher. Saito\(^{22}\) has reported them from the air in Japan. *A. nidulans* var. *nicolletii* has been described as a cause of disease in man. Forms with this morphology have been repeatedly isolated from soil in various parts of America and by us from soil-polluted substances. This conidial type appears to be cosmopolitan and in America, at least, a characteristic inhabitant of the soil in which experiments show its ability to multiply (see table).

The ascospore of *A. nidulans* repeats the general structure originally described by DeBary\(^{23}\) for *A. repens*. It is more or less lens-shaped. When such an ascospore germinates the purple cell wall separates into two valves like those of a shellfish. These sometimes remain in contact at one edge but commonly remain attached to opposite sides of the germinating cell as figured by Eidam. Eidam reported no markings upon these ascospores. Grijns found a single equatorial band where the two valves meet. Vuillemin reports this band as double. One of our cultures shows a slight equatorial furrow with traces of a ridge in each side—approximately the form of the ascospore in *A. repens*. In all other cultures observed, there are two definite bands of varying width between which is the line at which the valves separate. These bands and the surface markings on the valves when present have the appearance presented by the wrinkled, folded, or at times closely fitting primary wall of the conidium as described for Penicillium by Thom\(^{24}\) and for *A. niger* by Thom and Currie.\(^{25}\)

*Aspergillus fumigatus* has strictly a single series of sterigmata or conidia-bearing cells upon the vesicle. *A. nidulans*, on the contrary, has both primary and secondary sterigmata in every head, hence has

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\(^{23}\) Loc. cit.
been called a Sterigmatocystis. That usage is disregarded in this paper. Comparative study of these two groups of races, *A. fumigatus* and *A. nidulans*, brings cumulative evidence of close relationship. *Aspergillus rehmii* Zukal and *Sterigmatocystis sydowi* Bainier and Sartory have both been cited as *A. nidulans* but this does not seem to be justified by examination of all the data given. *Aspergillus flavo-viridescens* Hanzawa appears to be more closely related to *A. versicolor* than to *A. nidulans*. *S. glauca, S. minor*, and *S. prasina* of Bainier and *S. olivacea* Van Tieghem might have been varieties of *A. nidulans*. The descriptions are inadequate for identification.

**Group Characterization of *A. nidulans* from Cultures**—Colonies on Czapek's solution agar, white to yellowish green, finally fairly deep green, velvety to more or less floccose in purely conidial areas, definitely floccose when perithecia are forming, reverse and agar usually more or less reddish to dark red or reddish brown, conidiophore more or less flexuous with the walls colored in shades of cinnamon brown, septate or unseptate, usually 50–100 μ but up to 200 μ long by about 3–5 μ in diameter, increasing gradually to a dome-like vesicle 7–15 μ in diameter, bearing sterigmata in two series, parallel with axis of the stalk; primary sterigmata varying, 5 by 3 μ to 7–8 μ by 2–3 μ; secondary sterigmata 7–10 μ by 2–2.5 μ; conidia globose up to 3 μ or 3.5 μ, occasionally to 4 μ in diameter, smooth or rough, greenish, in parallel chains adherent into a solid column 30–50 μ in diameter and up to 100–200 μ in length.

Perithecia becoming globose, up to 200–300 μ in diameter surrounded by floccose white to gray mycelium, the branches producing, either terminally or in a terminal series, yellowish to cinnamon globose cells up to 25 μ in diameter with walls 4–5 μ in thickness (the Hülle); perithecial walls thin, brittle, consisting of one or two layers of polygonal cells from pink to deep red, almost black, turning blue with the addition of alkali and red again with acid. Asci pink to purple, numerous, filling the perithecia, 8-spored; ascii and ascospores varying in size with the race or species. The following variations may be described:

1. *A. nidulans* Eidam. Asci 10.5–11 μ, ripening slowly over a period of many weeks; ascospores slightly oval, about 5 by 4 μ, smooth with deep purple walls, separating into two valves in germination. A culture with this type of ascospores has recently been found by us among the soil forms isolated by Waksman in New Jersey.
2. *A. pseudo-nidulans* Vuillemin.—Asci 9 by 14 μ; ascospores 4 by 4.5 μ, lenticular, with double equatorial bands, these being extensions near the edges of the valves of the ascospore. Vuillemin regards this as the form which Grijns reports as an ascosporic *A. fumigatus*. The double character of the equatorial band is so distinct that it is difficult to believe that Grijns failed to see it if present. The possibility of finding Grijns’s organism with a single equatorial band therefore remains open.

We have three variations of this ascosporic series distinguished as follows:

3. No. 110, received from Dr. Westerdijk at Amsterdam. Asci ripening slowly a few at a time over a period of several weeks, 10–13 μ in diameter; ascospores lens-shaped, about 4–5 μ in diameter and 3–3.5 μ in thickness with a plaited, folded, or wrinkled equatorial band as a free extension of the margin of each valve to a width of 1.5–1.8 μ (the double equatorial band of authors).

4. No. 4110, from flax straw and the same, No. 131, from soil, shows perithecia full of ripe ascospores within a few days; the asci mostly break down quickly, leaving the perithegium full of free ascospores; ascospores measuring as in No. 110, except that the equatorial bands are 1 μ or less in width.

5. No. 4138T11 differs from No. 4110 in the appearance of ridges and folds on the valves of the ascospore. It was obtained by Waksman from New Jersey soil.

**Synopsis of Whole Group**

* A. Green series.
  B. Sterigmata simple. *A. fumigatus* series.  
  Characterization page 90.
  C. Relationship to *A. fumigatus* distinct.
  D. Ascospores known.
  E. Ascospores with double band.
    1. Asci 14–18 μ; ascospores 6–8 μ in longest diameter...*A. malignus* Lindt.
    2. Asci 10–12 μ; ascospores 7 μ in longest diameter.
    B. C. No. 4188.21.
    3. Asci 20–26 μ x 12–18 μ; ascospores 3–3.5 μ...*A. fumigatoidees* B. & S.
  EE. Ascospores with single band.

F. Asci and ascospores colorless.
4. Asci 10–12 μ; ascospores 5.6 μ x 4.2 μ...A. fischeri Wehmer

FF. Asci and ascospores red.
5. Asci 9 x 14 μ; ascospores 4 μ x 4.5 μ.
Grijns' strain. (See
A. pseudo-nidulans.)

DD. Ascospores not found.

G. A. fumigatus Fres. (See type description.)
6. Probable synonyms. A. qui-
ninae Heim, A. keratitis
Ball, A. bronchalis Blum.,
A. ovarious Peck, A. ramo-
sus Hallier, A. nigrescens
Robin, A. microsporus
Böke, A. olivaceus Preuss,
A. glaucoides Spring.

GG. Strains separated from A. fumi-
gatus by cultural details. A.
lignieresii Cost. & Lucet, A.
virido-griseus Cost. & Lucet,
A. fumigatus var. tumescens
Blum.

CC. Relationship indistinct or doubtful.

H. Diminutive forms. (a and b
probably not related.)
b. Conidia 1 μ. .......... A. pusillus Massee

III. Vigorous active green colonies...A. gracilis Bainier,
A. gracilis var. exigus B. & S.

HHII. Descriptions inadequate. A.
Nöting Hallier, A. Hageni
Hallier, A. heterocephalus
Spring, A. ageni.

BB. Sterigmata in 2 series.
I. Perithecium known. (A. nidulans series.)
K. Asci developed slowly (several
weeks).
1. Asci 10.5–11 μ diam. Ascospores without band or frill; A. nidulans Eidam
1a. Soil culture 4163c28-produced Eidam's de-
scription.
1b. Var. pathogenic to man; A. nidulans var.
Nicollei Pinoy
2. Asci 10–13 μ diam. Ascospores with 2 bands 1.5–1.8 μ in width. (Culture.) Amsterdam strain.

**KK.** Asci developed quickly (a few days).

3. Ascospores with a single band. *A. fumigatus (?)* Grijns
5. Ascospores with 2 bands 1 μ or less in width. (Culture.) American soil strain. Probably the same as no. 4.

6. Ascospores with 2 bands, also ridges and folds on valves. (Culture.) New Jersey strain.


**AA.** Colonies never green—some mixture of yellow-orange and neutral gray, avellaneous, clay, cinnamon, etc.

**M.** Forms with 1 series of sterigmata.
- Heads (cervinus) fawn color (culture). *A. cervinus* Massee
- Heads rosy. *A. roseus* Link
- Heads in a dark brown to black column (culture by Oudemans). *A. calyptratus* Oud.

**MM.** Forms with 2 series of sterigmata.
- Flesh-color. *S. carnea* van Tiegh.
- Cinnamon to avellaneous (culture). *A. terreus* n. sp.
- Coremiform, tufted. *S. veneta* Massalongo

**List of Published Species**

The citations of the original descriptions of the species mentioned in this paper are given in alphabetical order by species names. The initial A. or S. indicates that the describer regarded the species as *Aspergillus* or *Sterigmatocystis* respectively. Except where indicated the original description has been examined. This list includes some forms not closely related to the species considered in the paper but which have been referred to by authors as belonging with these forms.

*A. africanus* Durieu & Montagne, Fl. Alg. p. 342. 1849. Reference is made to this description because the form is described as reddish brown; the spores were described, however, as 20 μ in diameter.
A. ageni. This name is cited by Lindt, Arch. Exp. Path. Pharm. 25: 265. 1889, as taken from Saccardo's Syllgoxe. Search for this reference leads to the conclusion that in this citation A. Hageni was made to read A. ageni.

A. aviarius Peck, N. Y. State Museum Rept. 44: 25. pl. 4. figs. 9–12. 1891. The description of this form leads to the belief that the organism was some strain of A. fumigatus.

A. bronchialis Blumentritt, Ber. Deutsch. Bot. Ges. 19: 442–446. pl. 22. figs. 1–6. 1901; also ibid. 23: 419–427. pl. 19. figs. 1–3. 6–7. 8–19–23. 1905. This colony is described as floccose in contrast to the commoner forms of A. fumigatus which are velvety or produce very little aerial mycelium. Close relationship to A. fumigatus is evident.

A. calyptratus Oudemans, Arch. Neerl. II. 7: 283. pl. 13. 1902. Conidial chains forming a black column are reported by Oudemans but the mass is figured as brown, thus possibly A. terreus, or a species of Haplographium.


A. cervinus Massée, Kew Bull. Misc. Inf. 4: 158. 1914. A fawn-colored species from African soil with morphology close to A. fumigatus. A culture with closely similar characters was contributed by Dr. J. R. Johnston from Porto Rico soil (3522,36).

A. fischeri Wehmer, Centralbl. Bakt. II. 18: 390–2. fig. 5. 1907. The conidial morphology reported is not different from A. fumigatus. Perithecia are described, see p. 93.

A. flavescens Wreden, Compt. Rend. Acad. Sci. Paris 65: 368–371. 1867. Also, St. Petersb. Med. Zeitschr. 13: 133–184. 1867. This species has been regarded as related to A. flavus but the conidia described are 2–3 μ in diameter and the upper parts of the stalks are described as yellowed. This establishes a strong probability that it was some strain of A. nidulans.


A. fumigatoides Bainier & Sartory, Bull. Soc. Myc. France 25: 112. pl. 5. 1909. The conidial apparatus described is hardly distinguish-
able from *A. fumigatus*. Perithecia were found with ascospores differing in detail from *A. fischeri, A. malignus* and the form we have described.


*A. fumigatus* var. *tumescens* Blumentritt, Ber. Deutsch. Bot. Ges. 23: 419–427. pl. 19. figs. 5, 6, 18, 19, 20, 21. 1905. The culture described produced a dense, buckled, pseudo-parenchyma-like felt of mycelium with fruiting bodies not differing to any significant degree in measurements from *A. fumigatus*. Secondary heads from the outgrowth of sterigmata, branching stalks and septate stalks are figured. It is probably correctly characterized by the author a “culture cripple,” since the differences are such as occur very commonly as a result of some unfavorable condition.

*S. glauca* Bainier, Bull. Soc. Bot. France 27: 29. 1880. The description of this Sterigmatocystis is not complete enough to indicate its relationships.

*A. glaucoides* Spring, Bull. Acad. Sci. Belg. 19: 560–572. 1852. The name without description was given to a colony which grew in an egg under experiment. The same form was afterward found in another egg. It is recorded as closely related to, if not identical with, the mold found in air sacs of birds, hence probably *A. fumigatus*.


*A. gracilis* var. *exiguus* Bainier & Sartory, Bull. Soc. Myc. France 28: 47. pl. 2. 1912. According to the description this variety differs in physiological characters slightly from *A. gracilis* Bainier.

*A. griseus* Link, Sp. Pl. 6: 69. 1824; Bonorden, Handb. Allg. Myk. p. 112. fig. 188. 1851. This was referred to by Wehmer (Monogr. p. 90) as probably *A. fumigatus*. Neither the description of Link nor the description and figure of Bonorden can be identified with certainty.

Florentin. 1892; syn. Otomyces Hageni Hallier, Zeitschr. Parasit. 1: 195. 1869; and 2: 22, 233, and 259. pl. 5. 1870. In the latter article the descriptions are inadequate while the figures given include under Otomyces hageni fruiting hyphae which evidently represent Mucors, Penicillia, and probably at least 2 species of Aspergillus. This citation is included because most of the pathogenic Aspergilli seem to belong to the A. fumigatus or the A. nidulans series.

A. heterocephalus Spring, Bull. Acad. Sci. Belg. 19: 568. 1852. This name was given to colonies in a hen’s egg which showed small heads globose and large heads columnar. Since no adequate figure or description was offered it may be discarded as a nomen nudum.

A. keratitis Ball, Amer. Med. 2: 31. 1901. This organism was found in an ulcer in the human cornea. No adequate description was given.

A. lignieresi Cost. & Lucet, Ann. Sci. Nat. IX. Bot. 2: 137. pl. 5. figs. 19–23. 1905. This culture from the lung of a penguin differs in cultural details from typical A. fumigatus, especially by the presence of swollen groups of cells in the mycelium.

A. malignus Lindt, Arch. Exp. Path. Pharm. 25: 256–271. figs. 1–11. 1889. While the description of this form is more or less incomplete and does not mention calyptriform heads, ascospore formation closely similar to that described by Lindt has been found by us in cultures with conidial fruits duplicating typical A. fumigatus.

A. microsporus Böke. The description and figures given by Cattaneo and Oliva in Arch. Lab. Bot. Critt. Garovaglio 5: 123. pl. 6. fig. 9. 1888, have been seen. No earlier or more complete description has been found. The organism was obtained from the human ear and has been listed as A. fumigatus but Wehmer (Monogr. p. 88) notes that the heads are figured as radiate, not calyptrate. The identity of Böke’s form must remain doubtful.

S. minor Bainier, Bull. Soc. Bot. France 27: 30. 1880. The description as given is not sufficient to separate this from A. nidulans.


A. nidulans var. Nicollei Pinoy, Compt. Rend. Acad. Sci. Paris 144: 396. 1907. This variety was found fruiting within human tissue in a subject affected with “Madura-foot.”

A. nigrescens Robin, Histoire Naturelle des Végétaux Parasites. p. 518. atlas. pl. 5. fig. 2. Paris. 1853. The organism of Robin has been called A. niger by Wilhelm (Beiträge zur Kenntnis der
culture was found upon quinine solution but the description given will not separate it from A. fumigatus.

A. ramosus Hallier, Zeitschr. Parasit. 2: 266-269. pi. 6. figs. 1-6. 1870. The figures and descriptions evidently represent a strain of A. fumigatus.

A. rehmii Zukal, Oesterr. Bot. Zeitschr. 43: 160. pi. 11, 12. figs. i-10. 1893. This species has been regarded as close to A. nidulans by some but Zukal's figures do not support that placing. The description given by Saito (Centralbl. Bakt. II. 17: 158) clearly places his organism in the A. flavus group.

A. roseus Batsch, Elench. Fung. 58; Fries, Syst. Myc. 3: 386. 1829. The only information given is "sporidiis roseis" with citations from Batsch, Sowerby, Persoon, Link, and Albertini and Schweinitz. The reference to this form is included because the colony color as in A. terreus approaches shades often designated as rosy.

A. roseus Link; Berkeley in J. E. Smith, Engl. Fl. 5: 340. 1836, cites A. roseus and attributes it to Link. Examination of Link, Sp. PI. 6: 68. 1824, correctly carries the name back to Batsch (see preceding citation).


S. veneta Massalongo, Boll. Soc. Bot. Ital. 1900. p. 259. This form is described as forming yellowish hemispherical colonies upon rotten twigs; the fertile hyphae are fasciculate (form coremia?). Werkenthin (Fungous flora of Texas soils, Phytopathology 6: 247-249. 1916) identified certain cultures from Texas soil as A. venetus on account of fasciculate aerial hyphae. Cultures of these forms received from Werkenthin show that he had the form here described as A. terreus. We cannot agree with the identification of this form with A. venetus Massalongo.


A. virido-griseus Cost. & Lucet, Ann. Sci. Nat. Bot. IX. 2: 140. 1905. The describers find this form to be pathogenic to rabbits not to fowls, and to be floccose whereas A. fumigatus is pathogenic also to fowls and is not floccose.

S. olivacea van Tieghem, Bull. Soc. Bot. France 24: 103. 1877. The data given are "common," "heads olive-green" and "on cochineal"; it must be dropped for lack of information.

A. olivaceus Preuss, Linnaea 25: 77. 1852. Schroeter (Cohn, Krypt. Schles. 3°: 216. 1893) notes that this description does not separate Preuss's material from A. fumigatus Fresenius.

A. penicilloides Spegazzini, Rev. Agrar. Veter. La Plata. p. 245. 1896. The description of this species might place it near to A. fumigatus. The organism was obtained from sugar-cane in Argentina. We have recently received a culture from Owen, in Louisiana, which probably represents the form described by Spegazzini but is not closely related to A. fumigatus.

S. prasina Bainier, Bull. Soc. Bot. France 27: 31. 1880. This form is not recognizable from Bainier's description. It might have been a strain of A. nidulans.

S. pseudo-nidulans Vuillemin, Arch. Parasitologie 8: 540-542. 1904. Vuillemin transfers the ascospore form described by Grijns as A. fumigatus in Centralbl. Bakt. II. 11: 330. 1903, to this specific name, amending Grijns's description by indicating the double nature of the band by which he separates his form A. nidulans as described by Eidam. The discussion by Vuillemin tallies with the commonest of our American soil forms of this group.

A. pusillus Massee, Kew Bull. Misc. Inf. 4: 158. 1914. From the description this is a very small gray colony from soil in Africa, which would be readily distinguished from other members of the group. A relationship to the A. fumigatus series is possible.

culture was found upon quinine solution but the description given will not separate it from *A. fumigatus*.

*A. ramosus* Hallier, Zeitschr. Parasit. 2: 266–269. pl. 6. figs. 1–6. 1870. The figures and descriptions evidently represent a strain of *A. fumigatus*.

*A. rehmii* Zukal, Oesterr. Bot. Zeitschr. 43: 160. pl. 11, 12. figs. 1–10. 1893. This species has been regarded as close to *A. nidulans* by some but Zukal’s figures do not support that placing. The description given by Saito (Centralsbl. Bakt. II. 17: 158) clearly places his organism in the *A. flavus* group.

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