PERSOONIA
Published by the Rijksherbarium, Leiden
Volume 3, Part 1, pp. 9-16 (1964)

PHOMA HERBARUM WESTEND., THE TYPE-SPECIES OF THE FORM-GENUS PHOMA SACC.

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(With two Plates)

The type of *Phoma herbarum* is selected and the characteristics of the species are redescribed from recently isolated material. Synonyms of this ubiquitous saprophytic fungus are *inter alia: Phoma urticae* S. Schulz. & Sacc., *Phoma oleracea* Sacc., *Phoma violacea* (Bertel) Eveleigh (described from paint), *Phoma hibernica* Grimes & al. (described from butter), and *Phoma lignicola* Rennerfelt (described from wood).

In the course of diagnostic mycological work with diseased or dead plant material we quite often isolated a typical *Phoma*. This fungus was characterized by its ability to develop a great number of thin-walled pycnidia on different kinds of substrata and by the production of only a small amount of aerial mycelium. Another peculiarity was that it maintained for a long time its ability to sporulate when cultivated *in vitro*. Only hyaline one-celled pycnidiospores were produced and no chlamydospores. The fungus appeared to belong to Group X of *Phoma* strains described by Dennis (1946) to which *Phoma urticae* S. Schulz & Sacc., *P. oleracea* Sacc., and *P. hibernica* Grimes & al. were assigned.

We informed Dr. R. W. G. Dennis that the fungus occurred on all kinds of plant material, whereafter he commented that it might be *Phoma herbarum* Westendorp (1852), a very common fungus on vegetable debris according to older literature. Dr. J. A. von Arx, Baarn, on examining the fungus on the seedcoat of *Brassica* spp. came to the same supposition. The suggestion made by these two mycologists was confirmed after consultation of the type material of *P. herbarum*, preserved in the Herbarium at Brussels.

Though in the course of time many mycologists determined fungi as *P. herbarum* (Saccardo, 1884; Allescher, 1901; Grove, 1935) the identity of this fungus remained doubtful. This is attributable to the fact that the identity of any species of *Phoma* is fully established only if the characters and variability of the fungus growing on an artificial substrate are known.

At the 8th International Botanical Congress at Paris (Lanjouw, 1956) it was laid down that *Phoma herbarum* Westend. be regarded as type-species of the form-genus *Phoma* Sacc. (nomen genericum conservandum). So a study of the characteristics of *P. herbarum* may lead to a better understanding and interpretation of the genus *Phoma*.

PHOMA HERBARUM Westend.

Phoma herbarum Westend. *in* Bull. Acad. Belg. **19** (3): 118.1852. — Lectotype: Herb. Crypt. belge, Fasc. 20 (1854) no. 965 on *Onobrychis viciifolia* Scop. ("Sainfoin") (BR). — Syntype: Herb. Crypt. belge, Fasc. 20 (1854) no. 965 on *Urtica dioica* L. ("Ortie") (BR).

Phoma urticae S. Schulz. & Sacc. *in* S. Schulz., Schwämme Pilze Ung. Slav. 700. 1869. — *Leptophoma urticae* (S. Schulz. & Sacc.) Höhn. *in* Hedwigia **59**: 262.1917 (misapplied).

Phoma oleracea Sacc. *in* Michelia **2**: 91–92. 1882.

Phoma oleracea var. *helianthi-tuberosi* Sacc., Syll. Fung. **3**: 135. 1884.

Phoma oleracea var. *scrophulariae* Sacc., Syll. Fung. **3**: 135. 1884.

Phoma oleracea var. *urticae* Sacc., Syll. Fung. **3**: 135. 1884.

Aposphaeria violacea Bertel *in* Öst. bot. Z. **54**: 205, 283, 288. 1904. — *Phoma violacea* (Bertel) Eveleigh *in* Trans. Brit. mycol. Soc. **44**: 577. 1961.

Phoma pigmentivora Massee *in* Kew Bull. **1911**: 325.

Phoma hibernica Grimes, O'Connor & Cummins *in* Trans. Brit. mycol. Soc. **17**: 99–101. 1932.

Phoma lignicola Rennerfelt *in* Svenska SkogsvFören. Tidskr. **35**: 60. 1937.

DESCRIPTIONS.—Dennis *in* Trans. Brit. mycol. Soc. **29**: 33–35. 1946 (*P. hibernica*, *P. oleracea*, *P. urticae*); Eveleigh *in* Trans. Brit. mycol. Soc. **44**: 578–582. 1961 (*P. violacea*); Grimes, O'Connor & Cummins *in* Trans. Brit. mycol. Soc. **17**: 100–101, 105–110. 1932 (*P. hibernica*).

DIAGNOSTIC CHARACTERS IN VIVO. — Pycnidia mostly superficially formed, simple or compound; wall of pseudoparenchymatic texture; simple pycnidia mostly globular, sometimes lenticular or flask-shaped, 80–260 μ diameter; compound pycnidia generally much larger. Ostioles somewhat protruding, oozing pinkish or yellow-white spore masses. Pycnidiospores 4.5–9.5 × 1.7–3.0 μ, commonly 5.0–5.5 × 2.0–2.5 μ.

DIAGNOSTIC CHARACTERS IN VITRO. — Aerial mycelium usually sparse. Pycnidia abundant, simple or compound; wall of pseudoparenchymatic texture; simple pycnidia mostly globular, sometimes lenticular or flask-shaped, 50–500 μ diameter; compound pycnidia sometimes even larger. Ostioles distinct, 1 in simple pycnidia, 2–3 or more in compound pycnidia. Spore mass abundant, completely covering the pycnidia at maturity, usually salmon pink, but sometimes yellow or white. Pycnidiospores 3.3–10.0 × 1.5–5.0 μ, commonly 4.5–5.0 × 2.0–2.5 μ (Pl. 2, fig. 6).

VARIABILITY IN VITRO. — The fungus grows well on various artificial media (compare Pl. 1, figs. 5, 6), but the rate of growth is influenced by the composition and acidity of the nutrient substrate (Eveleigh, 1961 A; as *P. violacea*). Optimal temperature 20–25° C. Growth both in darkness and daylight (Eveleigh, 1961 A; as *P. violacea*). Some strains of the fungus mainly develop small pycnidia and other strains mainly large ones. However, it often happens that sectors with small pycnidia occur alongside sectors with large pycnidia in the same culture. The quantity of aerial mycelium depends on the strains and the media. Often the fungus in culture shows sectors with a dense mycelial growth with only occasional pycnidia alternating with sectors with less copious aerial mycelium and abundant pycnidia ('dual phenomenon'—Hansen, 1938).

A characteristic of *Phoma herbarum* in culture is the typical pigment formation which also varies with the strains and the media. On cornmeal agar, oatmeal agar and potato-glucose agar the pigmentation is often well developed. The colour of the

pigment is mostly pink, sometimes orange-red or red-violet. The pH influences the pigmentation, in an acid medium the colour darkens as the pH is raised. Some strains produce little pigment. In culture some sectors may also show striking differences in pigmentation. Strong pigmentation is often associated with abundant aerial mycelium Light is also known to stimulate the formation of pigment (Eveleigh, 1961 A, 1961 B; as *P. violacea*).

DEVELOPMENTAL CHARACTERISTICS OF THE PYCNIDIA. — The pycnidial primordium may develop by repeated divisions out of the pycnidiospores: conidiogenous origin. This may be observed by inoculating an agar plate with pycnidiospores suspended in sterile tap water. The spores inflate, bud out, and divide crosswise and diagonally until a rounded or irregular mass of cells is formed. Hyphal threads mostly branch from the mass. In a growing colony such a pycnidial primordium usually arises by the simple meristogenous method (Kempton, 1919). This is well seen by staining an agar culture with Cotton blue and examining it microscopically after washing and mounting. A few adjacent cells in a single hypha inflate, divide both crosswise and diagonally, inflate, and divide again. This rounded or elongated mass continues to enlarge, just as in the case of conidiogenous origin, also with hyphal branches budding from it (Pl. 2, figs. 1–3). In a few cases closely adjacent hyphae may take part in the formation, which then becomes compound meristogenous, but the typical method of development is the simple meristogenous one from a few cells of a single hypha. Occasionally, due to later anastomosis, the development of the primordium seems to be symphogenous (pseudosymphogenous).

The cavity containing the spores apparently comes into being by a combined process of lysis (breaking up, disorganization) and celldivision (compare Dodge, 1923; lysigenetic origin). At first the central pseudoparenchymatic cells are gradually substituted by a meristematic tissue consisting of ellipsoid and ovoid small-celled elements. Thereafter this meristematic tissue is gradually reduced to a thin layer at the periphery of the cavity. In the meantime spore-formation takes place. The origin of the first spores is not clear. Possibly they are of endogenous origin (Pl. 2, fig. 4; compare Klebahn, 1933). Soon after the cavity is formed an ostiole is produced which is marked by dark hyphal cells. Structural provisions for the production of the ostiole are apparently already present in the primordium and hence the ostiole of the pycnidium of *Phoma herbarum* is a predetermined opening. The young pycnidial knot, which now has already all the essential characters of a pycnidium, becomes larger and larger until it attains the (variable) diameter of a mature pycnidium.

The peridium of such a mature pycnidium merely consists of a few cell-layers. The outer cells are relatively large and have a dark colour. The inner cells are mostly radially arranged and resemble a meristematic tissue. They are hyaline but their contents become strikingly stained in Cotton blue. The spores filling the whole cavity of the mature pycnidium project in rows from the hyaline cells lining the cavity. These cells are mostly somewhat cuspidate. The spores apparently originate by extrusion of parts of the plasm via a small pore in the point of those cells (Pl. 2, fig. 5), a process which Luttrell (1963) termed porogenous. It actually differs little from an endogenous spore-forming process, as was clearly explained by Goidanich & Ruggieri (1947). Since the spore-producing cells do not constitute a true hymenium, but are actually slightly differentiated pseudoparenchymatic peridial cells, the fructification of *Phoma herbarum* may be characterized as a histopycnidium (see Goidanich & Ruggieri, 1947).

HABITAT. — The fungus occurs on very diverse substrata, such as dead and dying herbaceous and woody plants, soil, water, milk, butter, paints, etc.

DISTRIBUTION. — World-wide.

SPECIMENS EXAMINED. —

Exsiccata: Lectotype on *Onobrychis viciifolia* Scop. and syntypes, Herb. crypt. belge, Fasc. 20 (1854) no. 965 (BR, PAD); *Phoma hibernica*, dried culture (1944) of type-isolate made by Prof. Grimes (K); *Phoma urticae*, Saccardo, Mycoth. ital. 1267 (PAD) and dried culture (1944) of isolate made by Dr. Dennis (K).

Cultures: *Phoma hibernica*, isolate from butter (1937), Vet. Landb. Maelkeri Lab. København (CBS); *Phoma lignicola*, culture of type (CBS); *Phoma pigmentivora* (*Aposphaeria violacea*), isolate used in U.S.A. for fungus resisting testing of white lead paint (1956) (ATCC–12569), isolate made by Cartwright (CBS), isolate from white lead paint, England (1952) (CMI–49.948), and isolate from bathroom paintwork, H. M. S. Vanguard (1950) (CMI–90.179).

The type exsiccatum of *Phoma herbarum* Westend. (Herb. crypt. belge, Fasc. 20 (1854) no. 965; BR) (syntype, sensu Troupin, 1949) contains fungal fructifications on a stem of nettle, *Urtica dioica* L. ("Ortie") and stem-pieces of sainfoin, *Onobrychis viciifolia* Scop. (Pl. 1, figs. 1,2). The descriptions follow.

The stem-pieces of sainfoin are closely covered with brownish black pycnidia. The latter are spherical, 70–170 μ diameter, or oval, 80–260 × 70–135 μ, with parenchymatic texture. Ostioles mostly 1, occasionally 2 or 3. Pycnidiospores more or less cylindrical, 4.5–9.5 × 1.7–3 μ, mean 5.5 × 2.2 μ. Microtome sections show these spores to develop from certain hyaline peridial cells which are mostly somewhat cuspidate.

The stem-piece of the nettle is for the greater part irregularly covered with pycnidia. These are subepidermal, erumpent, spherical or ellipsoid, 90–250 × 90–140 μ, with one distinct ostiole. A dark brown mycelium gives rise to macroscopically visible brown discolouration around the pycnidia. Pycnidiospores variable as to shape and size, generally cylindrical, 5–13.6 × 2–3.5 μ, mean 6.9 × 2.5 μ. Some pycnidia containing 2-celled spores 9.5–13.5 × 2.5–4 μ.

Occasional pycnidia on the nettle stem appear more superficially formed, agreeing wholly with those on sainfoin. These pycnidia lack the brown mycelium, while their pycnidiospores agree well with those of the fungus on sainfoin as to shape and size.

With regard to the nettle material, therefore, two clearly different fungi may be distinguished, the fungus commonly occurring on the sainfoin as well as in places on the nettle stem being considered to represent *Phoma herbarum* Westend. (lectotype: on sainfoin).

The pycnidial fungus isolated by us from various kinds of dead or dying plant material and other substrata, has the same characteristics as this type of *P. herbarum*. This was also verified by 'inoculation' of different strains of the isolated fungus on various dead sterilized herbaceous stems. This agreement, coupled with Westendorp's statement (1852) that *P. herbarum* occurs on dead stems of various herbaceous plants, leads to the conclusion that the *Phoma* described above is identical with *P. herbarum*.

The fact that the syntype material of *Phoma herbarum* contains two pycnidial fungi, explains why various taxonomic handbooks (e.g. Allescher, 1901; Grove, 1935) give the spore dimensions too large. In the original description of *P. herbarum*, Westendorp (1852) omitted spore dimensions. The first description to mention them was by Saccardo (Syll. Fung. **3**: 133. 1884 [1]). Apparently these spore dimensions were determined from a syntype of *P. herbarum* in the herbarium of Saccardo (Gola, 1930). This syntype, like the one at Brussels, contains, apart from *P. herbarum*, the second pycnidial fungus (on nettle, see above) with larger spores. Consequently, identifications based on Saccardo's spore measurements often refer to other fungi. Probably this holds especially for various alleged formae of *P. herbarum* which need further investigation.

The common *P. herbarum* has often been described under other names, as is evident from the synonyms listed. These are discussed below.

Saccordo already supposed (1884) that *Phoma urticae*, described from stems of *Urtica dioica* L., was a form of *P. herbarum*. The only exsiccatum of *P. urticae* in Saccardo's herbarium (see Gola, 1930) represents a *Phoma* which morphologically agrees completely with *P. herbarum*. As *P. herbarum* occurs widely on nettle stems (the syntype of *P. herbarum* is also on nettle stem, see above) *P. urticae* undoubtedly is a synonym of *P. herbarum*. It may be pointed out that Dennis (1946) gave the current name *P. urticae* to his strain 25 which turned out to be *P. herbarum*.

There are several indications which suggest that *Phoma oleracea*, described from stems of *Brassica oleracea* L., is a synonym of *P. herbarum*. Saccardo himself already stated that *P. oleracea*, of which type material is not known to be in existence, closely resembles *P. herbarum*. Slight differences in spore size were recorded but spore dimensions in *P. herbarum* are now known to vary a great deal.

The relation between *P. oleracea* and *P. lingam* (Tode ex Fr.) Desm. (basionym: *Sphaeria lingam* Tode), the well-known cause of dry rot and canker (black leg) of turnip and swede, has been much discussed (Henderson, 1918; Cunningham, 1927; Grove, 1935). It was generally believed that *P. oleracea* was probably identical with *P. lingam*. However, it was not realized that species of *Brassica* often harbour saprophytic *P. herbarum* in addition to pathogenic *P. lingam* (Pl. 1, figs. 3, 4), and that the first mentioned agrees well with Saccardo's description of *P. oleracea*. Saccardo was well acquainted with *P. lingam*, of which various exsiccata in his herbarium, some collected in Italy, bear witness (see Gola, 1930). Besides, he reported *P. lingam* from Italy (Saccardo, 1884). It must therefore be assumed that Saccardo considered *P. oleracea* different from *P. lingam*.

Both the "Centraalbureau voor Schimmelcultures" (CBS) and the "Phytopathologisch Laboratorium" (WCS) at Baarn used to record *P. lingam* and *P. oleracea* separately. The latter name was always applied to a fungus which has now proved

[1] In his description of *P. herbarum* Saccardo referred to his previous publication (*in* Michelia **2**: 92. 1880), but this contained only the description of f. *humuli* and some other forms, not of *P. herbarum* proper. The same applies to an earlier publication (*in* Michelia **1**: 523. 1879), where f. *galiorum* was described (compare Saccardo, Syll. Fung. **3**: 133. 1884).

to be identical with *P. herbarum*. This explains further why Cunningham (1927), who studied the cultures of *P. lingam* and *P. oleracea* from the CBS, found that the latter was not parasitic to *Brassica* spp. Both his description and the photograph of his culture of *P. oleracea* are characteristic of *P. herbarum*. Cunningham concluded nevertheless that this *P. oleracea* was an aberrant strain of *P. lingam*, assuming it had lost its pathogenicity and acquired the capacity to produce many fruit-bodies, which does not seem probable.

Also, in a recent report of the WCS (Baarn) in which the influence of seed infection by *P. lingam* on the attack of *Brassica* spp. was discussed, Kok (1962) mentioned non-pathogenic *P. oleracea* separately from parasitic *P. lingam*. Subsequent examination proved the former species to be the fungus now known as *P. herbarum* (compare Pl. 1, fig. 3).

From all these facts it was concluded that what had been understood by *P. oleracea* was identical with *P. herbarum* and that this species was different from *P. lingam*.[2]

Several varieties of *P. oleracea* (Saccardo, 1884) said to differ from the typical variety only by their occurrence on other host plants must also be regarded as synonyms of *P. herbarum*. This applies in any case to *P. oleracea* var. *helianthi-tuberosi*, *P. oleracea* var. *scrophulariae* and *P. oleracea* var. *urticae*. Further investigation is required in order to assess the other varieties described with deviating spore dimensions (Saccardo, 1884) and the formae mentioned in Rabenhorst, Kryptogamenflora (Allescher, 1901).

Phoma violacea, also known as *Aposphaeria violacea* or *Phoma pigmentivora*, and known to be the cause of a disfiguration of painted surfaces, also proved identical with *P. herbarum*. This conclusion was based on the study of cultures of this fungus received from the ATCC at Washington, the CMI at Kew, and the CBS at Baarn, as well as on isolations from paint made by the author. Disfiguration of white lead paint and coloured oilpaints has often been found in this country. The red discolouration and the formation of pycnidia in concentric rings are a very striking feature.

Application of Eveleigh's laboratory tests (Eveleigh, 1961 A) revealed that strains of *P. herbarum* from plants cause symptoms on paint like those of the original paint strains. This is in accordance with Eveleigh's conclusion (Eveleigh, 1961 B) that *P. violacea* must be a saprophytic organism, occurring among other substrata on dead wood (see below: *P. lignicola*). Eveleigh's study of the characters of *P. violacea* (Eveleigh, 1961 C) viz. variability of growth *in vitro*, formation of sectors, presence of one or more nuclei, and the formation of pigment, can now be considered to hold also for *P. herbarum*. The observations concerning *P. herbarum* strains from herbaceous material wholly agree with Eveleigh's data on *P. violacea* from paint (Eveleigh, 1961 C).

Phoma hibernica, described from butter, is also a synonym of *P. herbarum*. Dennis

[2] *P. lingam* is not a typical *Phoma*. We follow von Höhnel (1911) in placing the species in *Plenodomus* Preuss; its correct name is *Plenodomus lingam* (Tode ex Fr.) Höhn.

(1946) did not find significant differences between the original culture of *P. hibernica* and his *Phoma* strains 25 and 26, which can now be identified as *P. herbarum*. He only found that the mean spore dimensions of *P. hibernica* were somewhat larger and that this fungus showed some deviations on malt agar. These differences, however, are within the range of variation observed by the author to occur in several strains of *P. herbarum*. It also appeared that a dried culture of *P. hibernica* on malt agar obtained from the Herbarium at Kew was not different from certain Dutch strains of *P. herbarum* isolated from plants. It was finally ascertained that various Dutch strains of *P. herbarum* from plants grew well on butter. These cultures were not different from cultures on butter of a fungus determined by the CBS as *P. hibernica* apart from the fact that the latter did not sporulate. This culture, however, had been isolated from butter in Denmark as long ago as 1937 and its age may explain its sterility.

It seems therefore justified to conclude that *P. hibernica* is identical with *P. herbarum*. This fits the observations of Bisby, Timonin and James (1933) who isolated *P. hibernica* three or four times from soil at Manitoba, Canada. As *P. herbarum* occurs on all kinds of plant material it is of course widespread in soil. In this connection it is also worth mentioning that Borut & Johnson (1962) cultured *P. hibernica* many times from estuarine sediments in coastal North Carolina, U.S.A., while Bisby (1935) isolated *P. hibernica* from the air near the coast of Ireland.

The type culture of *Phoma lignicola* present at the CBS appeared not different from strains of *P. herbarum* producing a red-violet pigment. Rennerfelt isolated *P. lignicola* from woodpulp and described it as a new species, stating that comparison with the species mentioned by Grove (1935) and Allescher (1901) was not possible, as these were all connected with certain host plants. Although, indeed, *P. herbarum* is predominantly found on herbaceous plants, it is also frequently isolated from woody plants and wood.

There is no doubt that in the course of time further species will be reduced to the synonymy of *Phoma herbarum*.

The forementioned data should make it possible for mycologists to recognize in future whether isolated *Phoma*-like fungi are identical with the ubiquitous *Phoma herbarum*. The great variability shown by this fungus, however, will often make it desirable to compare cultures. For this purpose the "Plantenziektenkundige Dienst" at Wageningen preserves a great number of cultures of *P. herbarum*, both dried and living, which are sent on request.

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EXPLANATION OF PLATES 1, 2

PLATE 1

Figs. 1–3, 5, 6. *Phoma herbarum* Westend. — 1. Type material at Brussels, showing stems of nettle and sainfoin. — 2. Detail of stem of sainfoin covered with pycnidia (lectotype). — 3. Seed of *Brassica* sp. showing protruding pycnidia. — 5. Two strains on malt agar producing different sectors. — 6. Two strains on Ashby's medium.

Fig. 4. *Plenodomus lingam* (Tode ex Fr.) Höhn. — Seed of *Brassica* with protruding pycnidia.

PLATE 2

Figs. 1–6. *Phoma herbarum* Westend. — 1–3. Three stages of pycnidial primordium; simple meristogenous origin (free hand drawings). — 4. The first spores in the central cavity seem to be of endogenous origin. — 5. Porogenous spore production in mature pycnidium. — 6. Pycnidiospores showing their variability (camera lucida drawings).

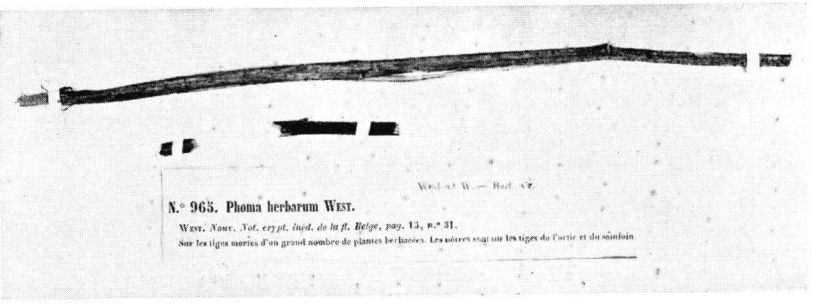

Fig. 1

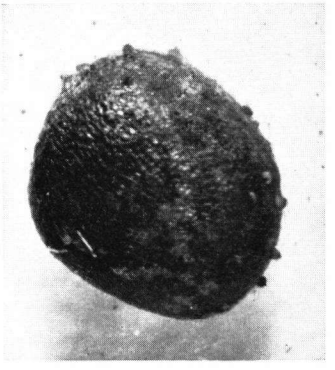

Fig. 3

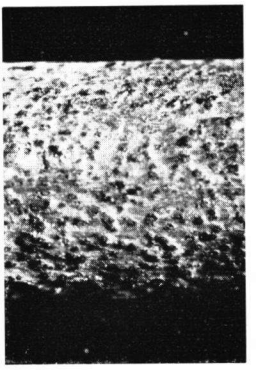

Fig. 2

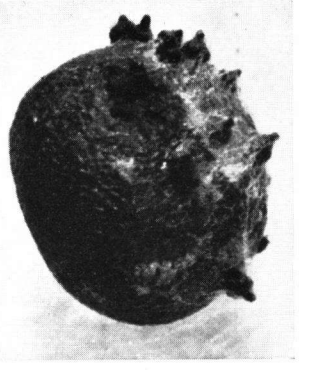

Fig. 4

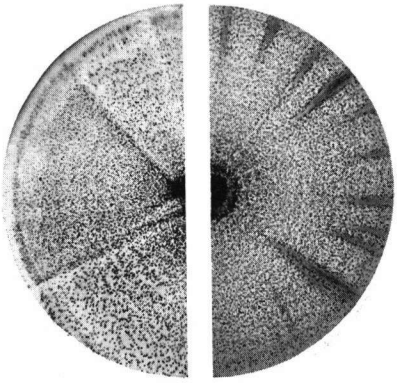

Fig. 5

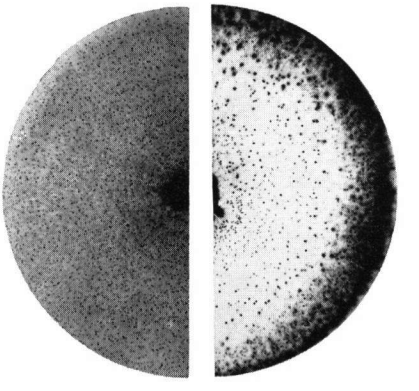

Fig. 6

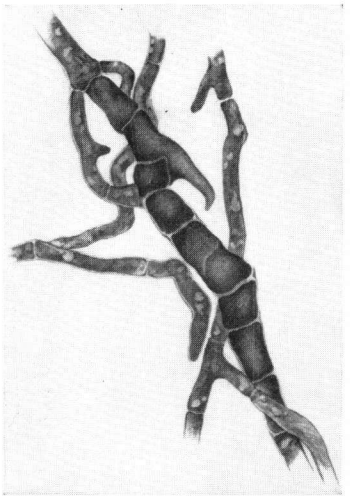

Fig. 1

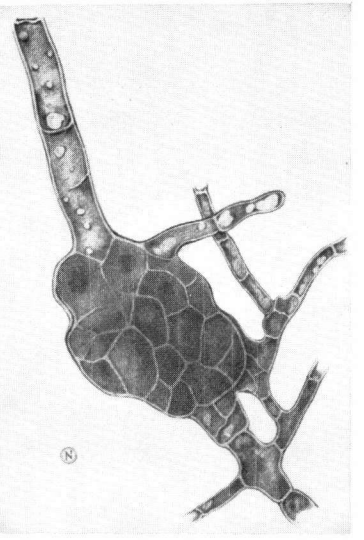

Fig. 2

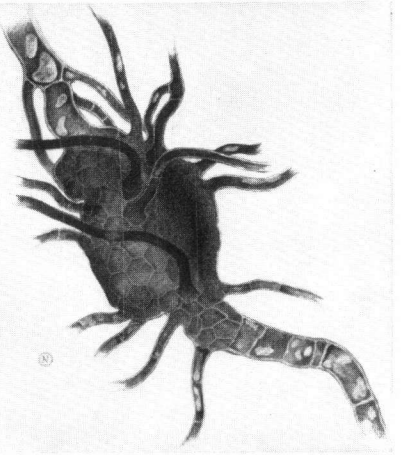

Fig. 3

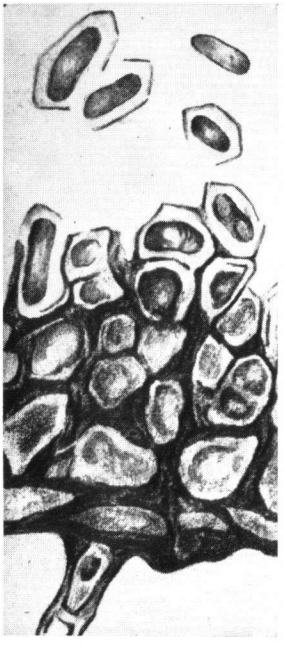

Fig. 4

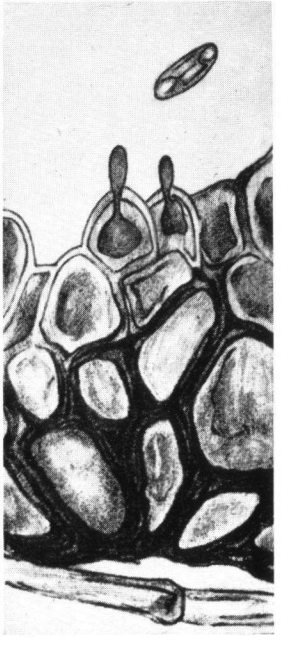

Fig. 5

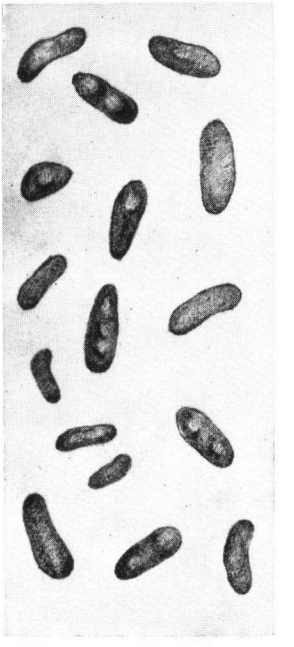

Fig. 6