INTERIM REPORT ON TAXONOMY OF GRAMINICOLOUS DOWNY MILDEWS ATTACKING MAIZE

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The year 1976 is the centennial of graminicolous downy mildews (DM). *Protomyces graminicola* Sacc. [*Sclerospora graminicola* (Sacc. & Schroet.)] was described in 1876 on *Setaria verticillata* (L.) Beauv. from Italy. It was not reported on maize *(Zea mays* L.*)* until 1909; in the interval, two other DMs were recorded on maize: *Sclerospora maydis* (Racib.) Butl. from Java in 1897 (as *Peronospora maydis* Racib.) and *Sclerophthora macrospora* (Sacc.) Thirum. *et al.* (as *Sclerospora macrospora*) from Italy in 1902.

Since the last summary concerning the taxonomy of the graminicolous DMs on maize (12), several significant taxonomic developments have occurred. In articles published by Payak *et al.* (6) and Shaw (11) (both of which appeared in the DM issue of Indian Phytopathology), the former authors stated "Sclerophthora: sporangiophores determinate...." (p. 184), while the latter author stated "Sporangiophores indeterminate.. *Sclerophthora*". Payak (personal communication) informed me that the basis for their statement was the cited abstract published by Thirumalachar (14).

Thirumalachar and Shaw were two of the three authors originally describing the genus *Sclerophthora* (15). Reference to that publication clarifies the apparent discrepancy. Apical growth of the sporangiophore is determinate and is terminated by a single large sporangium. However, subsequent additional sporangia are produced in basipetalous succession; the result is a cluster of 3-5 sporangia. Thus, development of the terminal sporangium does not end sporangiophore development. Consequently, the present writer considered overall development of the sporangiophore and its sporangia indeterminate in the sense of both Snell and Dick (13:p. 180) who include the phrase "without definite margin or edge", and Ainsworth (1:p.290) who includes "edge not well defined". These phrases more appropriately apply to margins of leafspots as indicated by Ainsworth. I now recognize the confusion resulting from application of the term indeterminate to the sporangiophore of *Sclerophthora* and support its description as determinate.

The basic and significant point is that the sequence of sporangial development is entirely different in *Sclerophthora* and *Phytophthora*. In *Phytophthora*, sporangiophores develop indeterminately in the sense that this term is usually applied to sporangiophores and conidiophores. Furthermore, sequential sporangial formation and elongation of the sporangiophore is acropetalous, not basipetalous as in *Sclerophthora*.

These differences in sporangiophoric development, combined with the typically obligate parasitism of all species of *Sclerophthora* and the difference in oogenesis between species of *Sclerophthora* and *Phytophthora* not only justify the continued recognition of two distinct genera, but also the placement of *Sclerophthora* in the Peronosporaceae, not the Pythiaceae (16)

Herbarium material of *Sclerophthora* and *Sclerospora* spp., whether of species producing sporangia or conidia, consistently contains a paucity of good asexual material. Even when present, the asexual stage is usually collapsed and badly distorted even if examined after being mounted in 3% KOH and warmed. A very few specimens in various herbaria, however, contain

excellently preserved asexual material. This state in *Sclerospora* and *Sclerophthora* is produced between midnight and dawn and is ephemeral under natural conditions. However, if collected between 4:00 and 8:00 AM, and promptly pressed, good herbarium specimens of the asexual stage can be obtained. Most of Weston's original collections of species known to produce the asexual stage, now in the Farlow Herbarium at Harvard University, contain excellent asexual material. Weston's publications (e.g., 18) on Philippine *Sclerospora* emphasize the noctural production of the conidia and conidiophores. He made certain that material he preserved was collected while still turgid and he pressed and dried it quickly.

The manuscript in which the genus *Peronosclerospora* (11, 12) will formally be published and the species of *Sclerospora* producing conidia and conidiophores transferred to it is in final preparation. No one has raised any objection either in print or in personal communication to this proposal; indeed, many colleagues have indicated their conviction for the necessity of this genus.

A question has arisen as to whether germination of the sporangia of *Sclerospora graminicola* and species of *Sclerophthora* ever occurs by germ tube. Direct germination occurs in *Phytophthora infestans* (Mont.) DeBary, and has been shown to be temperature related [optimum zoospore formation at 12°C and germ tube production at 25°C (2)]. Except in *Bremia* spp. (5), I consider most reports of germ tube germination in sporangial producing species of the Peronosporaceae doubtful. Pupipat (9) has provided illustrations clearly demonstrating what is usually the basis of reports of germ tube germination by such species. Photomicrograph No. I-11 of *Sclerophthora rayssiae* Kenneth *et al.* var. *zeae* Payak and Renfro shows zoospores escaping from the sporangium; note that two are laggards. No. I-9 clearly shows a zoosporangium in which one zoospore has encysted, and the cyst has subsequently germinated; its germ tube took the path of least resistance and grew out through the pore left by detachment of the apical operculum on the sporangium. Note that the pore is obviously larger than the diameter of the germ tube. Another shows three empty sporangia; the apical pores mark the location of opercula prior to zoospore discharge. No. I-12 is more difficult to interpret, but apparently three zoospores encysted within the sporangium, and one has produced a germ tube which again has egressed through the apical pore. Reports of direct germ tube germination are suspect in most sporangial Peronosporaceae for the reason that the germ tube is consistently described or illustrated as emerging apically, not indiscriminately at any point on the circumference of the conidium as in conidial *Sclerospora philippinensis* (17).

Until recently, I considered the nine species of *Sclerospora* and *Sclerophthora* reported on maize fairly well defined. At the same time, the species of Peronosporaceae occurring on Gramineae obviously have demonstrated great physiologic (= pathologic) plasticity in their adaptiveness to new hosts. All species occurring on maize have moved to that host from other hosts (12); there were no *Sclerospora* species reported on maize in North America prior to 1961 (4). But how are we to interpret the information presented by our colleague (8) concerning DM on maize in Thailand? One might hypothesize that additional species not yet recognized occur on native graminicolous hosts in Thailand, and are just now adapting to maize for the first time. But when, as a result of inoculations with single conidia of *Sclerospora sorghi* Weston and Uppal, conidia and conidiophores typical of *S. sacchari* Miyake and *S. philippinensis* Weston, as well as of *S. sorghi*, are obtained, one must admit the possibility of considerable morphologic plasticity in some *Sclerospora* species as well. All are multiple infections occurring; i.e., in addition to the artificially induced infections, are natural infections also occurring followed by anastomoses of hyphae within the host and the establishment of new heterokaryons and perhaps even the occurrence of parasexuality? These possibilities must be considered and careful experiments conducted to exclude multiple infections before we modify our current widely accepted concepts of species within the graminicolous DMs. Just

because such phenomena have not been recorded in the past is no reason why we should not now encounter and recognize them as more and different sources of germplasm of maize and sorghum are grown in increasing numbers of locations in Thailand and elsewhere in the world.

Workers in India (10) now refer to the "maize race" and the "sorghum race" of *Sclerospora sorghi*. The maize race occurs in Rajasthan, produces abundant conidia on maize, but oospores have not been yet found on this host. This race also readily infects *Heteropogon contortus* Beauv., which is considered a collateral host (3). It does not infect sorghum. Dr. Dange has provided a microscopic display of oospores from *H. contortus*. These oospores are different from those produced by *S. sorghi* on either sorghum or maize. Oospores from *H. contortus* are distinctly tuberculate and, while the tubercules are in contact with the oogonial wall, the oogonial wall and the exosporium certainly are not completely fused, as is so often and incorrectly stated to be a universal character of the genus *Sclerospora*. In contrast to the tuberculate markings of oospores produced on *H. contortus*, those produced by *S. sorghi* on maize and sorghum in the Mysore area and elsewhere in the world are typically irregularly polygonally-angled, with the oogonial wall in contact with and apparently fused to the oospore wall over most of their respective surfaces. Oospores produced on both *H. contortus* and *Sorghum* spp. are deep golden brown; those found in *Zea mays* are much lighter in color.

Distinct differences in oospore wall markings and relative thickness of the exosporium, mesosporium and endosporium are significant characters in the taxonomy of the Peronosporaceae. Wall color is less reliable; it is apparently dependent on the host species and even host variety involved, the stage of host development, and natural pigmentation of the host. Oospores of *S. sorghi* are produced less frequently and abundantly on maize than on sorghum. When found, they are usually produced in young plants under cool conditions, not in mature, senescent plants.

Thus, we are faced with the question whether the "maize race" in India is a distinct species which has moved from a native grass to maize. Further study could fully justify such disposition. A similar problem continues to exist in regard to *Sclerophthora macrospora*, which has now been reported on more than 140 different hosts (7; K. M. Safeeulla, personal communication). Critical examination of oospores from a number of these hosts reveals extreme morphologic variability (plasticity) -- probably too much to justify referral of material collected on all these hosts to a single species.

At this stage, however, the formal description of new species for either the "maize race" of *S. sorghi* or for segregates from the *Sclerophthora macrospora* complex is premature.

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