Notes on the Change of the Causal Species of Cucurbit Powdery Mildew in the U.S.

James D. McCreight

U.S. Department of Agriculture, Agricultural Research Service, 1636 E. Alisal St., Salinas, California 93905 U.S.A.

Beginning with the first report of powdery mildew (PM) on melon in Imperial Valley in 1925 (Jagger, 1926) through 1967, the causal organism of powdery mildew on melon and other cucurbit species in the U.S. generally regarded as Erisvphe was cichoracearum (Ec). Walker (1952)identified both Ec and Sphaerotheca humuli var. fuliginea, which is synonymous with Sphaerotheca fuliginea (Sf) (Braun, 1995), as causal organisms of PM, but stated that Ec "is the prevalent pathogen in the United States and apparently the most common generally." Moreover, the cleistothecial stage of Ec had been observed on cucumber in the U.S. (Randall and Menzies, 1956). In 1968, while Sf was named as the cause of PM without mention of Ec in a semi-popular article on control of PM on cucumber and squash (Paulus et al., 1968), two reports on genetic resistance to PM referred only to Ec (Harwood and Markarian, 1968a; Harwood and Markarian, 1968b). Two subsequent peer-reviewed reports on chemical control of PM on cucurbits referred only to Sf as the causal organism of PM (Paulus et al., 1972; Paulus et al., 1969). Two abstracts from U.S. researchers referred to Sf as the causal organism on cucumber, melon and Cucurbita spp. without specifying criteria for the identification of the pathogen (Sowell and Clark, 1971; Sowell and Corley, 1969). Shanmugasundaram et al. (1971) recognized both species as causal agents of PM in the introduction of their report of a genetic resistance to PM in cucumber, but they did not clearly state the criteria used to identify Sf as the pathogen in their research. In a review on breeding cucurbits for disease resistance, Sitterly (1973) referred only to Ec as the cause of PM. In the first comprehensive review of the described

genes of cucurbits, Robinson et al. (1976) referred only to Sf as the causal organism of PM on cucumber, melon, watermelon and Cucurbita. In 1978, Thomas stated that Sf "...a production-limiting was factor throughout all cantaloup-growing areas of the United States." There was an abrupt change in the identity of the causal organism of PM on cucurbits, melons in particular, across the U.S. without any apparent scientific documentation. The change from Ec to Sf should not be confused with the nomenclatural changes for these two species (Jahn et al., 2002).

Pertinent literature on this problem first appeared Homma in 1937. (1937)distinguished the fibrosin bodies in Ec and Sf and their utility in distinguishing the two species. Hirata (1955) found differences in the germ tubes of Ec (single, inconspicuous appressoria) and Sf (some are forked) useful to distinguish the two species. Zaracovitis (1965)was also examining conidial characters for distinguishing powdery mildew fungi.

In 1961, G.W. Bohn and T.W. Whitaker reported a new host of cucurbit mildew, and after a concise review of the literature available to them concluded "The fungus reported here is considered to be a conidial clone of an unknown species of the Erysiphaceae since it has not been observed to produce perithecia." Moreover, they cited the conflicting host-range reports in the literature, the presence of two biological races in southern California (Jagger et al., 1938), strains with different temperature requirements (Yarwood et al., 1954), absence of heterothallism on cucurbits in the U.S., and wide host range as reasons for research to determine the "...true identity or identities..." of the causal organism(s) of PM of cucurbits (Bohn and Whitaker, 1961).

Ballantyne reviewed the PM situation in Australia including the observations of fibrosin bodies in all specimens from cucurbits in New South Wales, Queensland and western Australia. She cited the statement by Weiss (1960) of the lack of any report of Sf from the U.S., and the 1961 report by Bohn and Whitaker. She noted that the reported reactions of various melon cultigens to PM in the U.S. were similar to those observed in Australia, and concluded that "such close agreement would be of considerable significance in the field of plant breeding if Sf were the only cucurbit PM present in Australia and Ec the only such fungus in the U.S.A." (Ballantyne, 1963)

At about this same time, Sf was being recognized as the dominant species causing PM on cucurbits in The Netherlands (Boerema and Kesteren, 1964) and India (Jhooty, 1967).

Kable and Ballantyne first reported a positive identification of Sf in the U.S. on cucurbits in Ithaca, N.Y. based on the presence of fibrosin bodies (Kable and Ballantyne, 1963). Yarwood and Gardner (1964) stated that PM on cucurbits they examined "...usually contain fibrosine bodies and perithecia are not formed...," and they further stated that the host ranges of Ec and Sf overlap. Sowell, Corley and Clark identified Sf as the pathogen in screening tests of cucurbit germplasm for host plant resistance to PM in Georgia and Iowa (Clark, 1975; Sowell and Clark, 1971; Sowell and Corley, 1969), but did not clearly state their criteria for identifying the pathogen. These few reports appear insufficient for a complete change in the identity of the causal species of PM in the U.S., but Sitterly (1978) noted in his review that either Ec or Sf predominates, or is the only species present.

Correspondence between G.W. Bohn, formerly Research Geneticist and Plant Pathologist, USDA-ARS, La Jolla and Brawley, Calif., and two colleagues provides insight into the change reflected in the literature cited above. A letter from Barbara Ballantyne, which followed the report by her and Kable (Kable and Ballantyne, 1963), and dated 10 September 1963 continued a sequence of interchanges on breeding melons for resistance to powdery mildew, but with a new focus on the identity of the pathogen in the U.S.: "Do you know if the California mildew resembles Sphaerotheca fuliginea in the characteristics mentioned in this paper?" (Fig. 1). In a letter dated 25 October 1963, Bohn stated that "Conidia of our fungus mounted in aceto-carmine (after Homma) and in dilute iodine-potassium iodide appear to contain large fibrosin bodies." (Fig. 2). He then surmised that "Perhaps it is all Sphaerotheca fuliginea and Erisyphe cichoracearum does not occur on cucurbits." A letter to Ballantyne dated 8 November 1963 indicated that Bohn was going to examine PM conidia in KOH, and included two color photographic slides of PM conidia, one in iodine-potassium iodide, the other in aceto-carmine (Fig. 3). Dr. Ballantyne replied on 14 November 1963 and stated that the iodine-potassium iodide slide showed fibrosin bodies that resembled Sphaerotheca fuliginea in New South Wales, Australia (Fig. 4). Bohn in a letter dated 15 November 1963 stated that PM samples from South Carolina and Texas had fibrosin bodies (Fig. 5). A letter dated 6 December 1963 from Bohn stated "Powdery mildew conidia from cantaloupe in California, Texas, and South Carolina, and from the wild squash Cucurbita digitata in the southern California desert, all look like those of the N.S.W. fungus. All exhibit fibrosin bodies in 3% KOH and all have the same shape." (Fig. 6).

Correspondence between Bohn and D.M. McLean, formerly Research Plant Pathologist, USDA-ARS, Charleston, S.C., in 1969 shed additional light on the situation. McLean stated in a letter on 9 April 1969, "I am having difficulty finding Erisyphe cichoracearum and most collections about Charleston are Sphaerotheca fuliginea " (Fig. 7). On 14 April 1969 Bohn wrote, "I have examined specimens of cucurbit powdery mildew on muskmelons collected at several sites in California, Arizona, and Texas, and single sites in South Carolina and Michigan. Although I was unable to find the perfect stage, the conidia of all collections had inclusion bodies characteristic of Sphaerotheca fuliginea. In addition to that evidence, our breeding lines resistant to race 2 are resistant at nearly all sites tested in various parts of the world including those where Sphaerotheca fuliginea has been Therefore, our race 2 is described. Sphaerotheca fuliginea and that species is prevalent on muskmelons the one everywhere. Intended to publish a brief paper on it this year but I haven't written it yet. Would you like to join me in the effort?" (Fig. 8). In a final letter on 18 April 1969 McLean replied, "I have been waiting for someone to admit that part of the mildew problem in the U.S. was caused by Sphaerotheca fuliginea. Now I am satisfied that we are on the right track. I have examined specimens from Texas, California, and Beltsville and have tried paring different isolates hoping to get a perfect stage. I have failed to find Ervsiphe cichoracearum in any of these studies. I most certainly would like to join you in describing race 2 and will help where I can." (Fig. 9). In a 13 May 1970 request for a sample of Ec, McLean mentioned a request from an unnamed person at Cornell University for a sample of Ec (Fig. 10). McLean mentions difficulty in finding Ec. Bohn sent a sample of Ec found on sunflower to McLean on 26 October 1970 (Fig. 11).

Bohn was at that time largely occupied with research on resistance to the mosaic virus complex of the southwest desert U.S. and the proposed manuscript was never written.

He apparently had not been aware of the work by Homma (1937) on conidial characteristics of Ec and Sf as indicated by his handwritten note at the top margin of the 10 September 1963 letter from Ballantyne that he had requested a copy of that work from the National Agriculture Library (Fig. 1). He also was not aware of the differences in germ tubes between Ec and Sf described by Hirata (1965) as indicated by his request for an outline of the technique for germinating conidia in his letter of 6 December 1963 (Fig. 6). He was probably also unaware of the more contemporary report on using conidial characters to identify PM fungi (Zaracovitis, 1965)

The last publication authored by Bohn in which the causal organism of PM was attributed to Ec was in 1967 in a semipopular article on control of PM on melon (Paulus et al., 1967). When he determined experimentally to his satisfaction that Sf was the only species causing PM on cucurbits following the 1961 paper (Bohn and Whitaker, 1961), Bohn changed the U.S. literature beginning in 1968 (Paulus et al., 1968), but did not publish his experimental evidence. Positive identification of race 3 as Sf was based on presence of fibrosin bodies and forked germ tubes (Thomas, 1978). Thus, the change in identity of the predominant causal organism of PM in the U.S. followed a similar course of discovery and verification, but it was not so clearly documented as in Australia (Ballantyne, 1963), The Netherlands (Boerema and Kesteren, 1964), and India (Jhooty, 1967).

Erisyphe cichoracearum may still play an important role in causing PM on cucurbits in the U.S., but there has been little evidence in the past 40 years. Limited attempts in my laboratory to infect melon with Ec from lettuce (*Lactuca sativa*) in Salinas Valley, Calif. were negative (unpublished data). One North American isolate of Ec, UCSC1, recovered from *Arabidopsis thaliana*, was demonstrated to be pathogenic on melon, cucumber, watermelon, *Cucurbita pepo*, and *Cucurbita maxima* (Adam et al., 1999).

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ADDRESS ALL MAIL TO GPO BOX NO JOSYDNEX N.S.W., AUSTRALIA PMB No. 10 RYDALMERE. N.S.W. DEPARTMENT OF AGRICULTURE FARRER PLACE, SYDNEY IN REPLY PLEASE QUOTE:

10th September, 1963.

Dr. G. W. Bohn, U.S. Horticultural Field Station, P.O. Box 150, LA JOLLA. CALIFORNIA. U.S.A.

Dear Dr. Bohn,

Thank you for your letter of the 19th July. I was pleased to have your comments on the reaction in your area of some varieties and breeding lines developed in the eastern United States.

I would be happy to grow the breeding line 37128 and LJ430 here next season to determine their reaction to powdery mildew. It will be several months yet before any results would be available but I will let you know as soon as possible.

I am enclosing a reprint of/preliminary note on some observations on cucurbit powdery mildews. It is quoted in a note in the June issue of the Plant Disease Reporter which you have probably seen. I will be very interested to know of further observations on the identity of the cucurbit powdery mildew in the U.S.A. Do you know if the Californian mildew resembles Sphaerotheca fuliginea. in the characteristics mentioned in this paper?

The situation regarding PMR5 and PMR6 which we discussed in earlier correspondence has become more confused by later results. Last/season when PMR 6 was grown in one of the inland districts where a different race occurs it was free from powdery and exhibuted the necrotic spotting that had previously been observed on this variety.

I will be particularly interested to observe its reaction again next season.

I would be most grateful if you could arrange for my name to be placed on the mailing list of your Station for any publications dealing with cantaloupes or lettuce. With kindest regards,

Yours sincerely, Barbara Ballanty (Barbara Ballantyne)

Plant Porthol ogist

Fig. 1. Letter from B. Ballantyne to G.W. Bohn, 10 Sept. 1963.

BJB/rb

U. S. Horticultural Field Station P. O. Box 150 La Jolla, California 92038

October 25, 1963

Dr. Barbara Ballantyne PMB No. 10 RYDALMERE. N.S.W., Australia

Dear Dr. Ballantyne:

Many thanks for your good letter of September 10, 1963 and your very interesting note on the identity of cucurbit powdery mildews. Conidia of our fungus mounted in aceto-carmine (after Homma) and in dilute iodine-potassium iodide appear to contain numerous, large fibrosin bodies. I have not observed germinating spores, but thes and the resistance of American varieties in Australia both suggest that we have the same fungus. Perhaps it is all Sphaerotheca fuliginea and Erysiphe cichoracearum does not occur on cucurbits. The performances of 37128 and LJ430 should add some information on this matter, or you may want to test the 8 powdery mildew resistant lines mentioned in my 1961 paper on the nectarless gene and in a paper on resistance now in press.

Have I sent you any papers? I have placed your name on our mailing lists for melon and lettuce papers but I don't want to duplicate any that you have.

With best regards,

Sincerely yours,

G. W. Bohn Pathologist

GWB:ds

Fig. 2. Letter from G.W. Bohn to B. Ballantyne, 25 Oct. 1963.

U. S. Horticultural Field Station P. 0. Box 150 La Jolla, California 92038

November 8, 1963

AIR MAIL

Dr. Barbara Ballantyne Division of Science Services Department of Agriculture RIDALMERE. N.S.W. AUSTRALIA

Dear Dr. Ballantyne:

In response to your letter of October 30, 1963 and Aerogramme dated November 4, 1963: I am sending under separate cover 500 seeds each of powdery mildew resistant inbreds - P_2 - F_{10} , 36478 bulk selfs; $P_3 - F_{10}$, 36486 bulk selfs; $P_4 - F_{10}$, 36301 bulk selfs; $P_5 - F_{10}$, 37438 bulk selfs; $P_6 - F_{17}$, 36523 bulk selfs; $P_7 - F_{11}$, 36611 bulk selfs; and \pm 200 seeds of $P_8 - F_{13} + F_{14}$, 36424 and its bulk selfs; $P_{10} - F_{16}$, 36607 bulk selfs. P_1 and P_9 are omitted because they are the cultivars PMR 45 and PMR 6, respectively. Incidentally, 37128 is $P_3 - F_{10}$.

I will look up seeds of P.I, 179260 and 181910 when I visit our seed file in Imperial Valley next week.

Many thanks for the reprint of your paper, Observations on the cucurbit powdery mildew in the Ithaca district. I will compare conidia in KOH with your figure 1. You may be interested in the enclosed kodachrome of our cucurbit powdery mildew mounted in iodine-potassium iodide. and

I will review our reprint file and send any that are not on the list that you kindly furnished.

With kindest regards,

Sincerely yours

G. W. Bohn Plant Pathologist

ARS :CR :GWBOHN :ds 11/8/63

Fig. 3. Letter from G.W. Bohn to B. Ballantyne, 8 Nov. 1963.

NEW SOUTH WALES



ADDRESS ALL MAIL TO G.P.O. BOX No. 36, SYDNEY N.S.W., AUSTRALIA DIVISION OF SCIENCE SERVICES,

DEPARTMENT OF AGRICULTURE RYDALMERE. N.S.W. FARRER FLACE, SYDNEY

IN REPLY PLEASE QUOTE: B.B.662. BJB/MN. 14th November, 1963.

Dr. G.W. Bohn, Plant Pathologist, U.S. Horticulturalfield Station, P.O. Box 150, LA JOLLA, CALIFORNIA 92038, U.S.A.

Dear Dr. Bohn,

I was very pleased to receive the seed of the powdery mildew resistant inbreds - P2, P3, P4, P5, P6, P8 and P10. I was also interested to receive the kodachrome slides of your powdery mildew which you sent with your letter of 8th November. I will let you know of the results as soon as possible.

The iodine-potassium iodide mount shows the fibrosin bodies clearly and as far as I can tell your fungus certainly does resemble that present in New South Wales. When you compare conidia in KOH with the figure 1 of the Plant Disease Reporter note you may be interested to compare it also with the photo I am enclosing of the N.S.W. mildew in 3% KOH.

I have followed the method of Hirata in using onion epidermis strips for germinating powdery mildew conidia, and have found this quite satisfactory. If you are interested I could send the details to you.

Please accept my warmest thanks for your help.

With kindest regards.

Yours sincerely,

Barbara Ba BARBARA BALLANTYNE, Plant Pathologist.

Fig. 4. Letter from B. Ballantyne to G.W. Bohn, 14 Nov. 1963.

U. S. Horticultural Field Station P. O. Box 150 La Jolla, California 92038

November 15, 1963

AIR MAIL

Dr. Barbara Ballantyne Division of Science Services, Department of Agriculture Private Mail Bag No. 10 RYDAIMERE. N.S.W. AUSTRALIA.

Dear Dr. Ballantyne:

In response to your request of November 4, 1963: You will find, enclosed, seed samples of <u>Cucumis sativus</u>, Plant Introductions 179260 from Turkey and 181910 from Syria. Seed increase plots were grown at Ames, Iowa without controlled inoculations so the stocks probably contain some mixture.

A single selection of powdery mildew from South Carolina and another from Texas produced conidia with large fibrosin bodies. The South Carolina culture looked slightly different from the Texas and California cultures but the slight differences in plant structure could have resulted from environmental variation.

With best regards,

Sincerely yours,

G. W. Bohn Plant Pathologist

ARS:CR:GWBohn:ds 11-15-63

Enc.

Fig. 5. Letter from G.W. Bohn to B. Ballantyne, 15 Nov. 1963.

U. S. Horticultural Field Station P. O. Box 150 La Jolla, California 92038

December 6, 1963

AIR MAIL

Dr. Barbara Ballantyne Division of Science Services Department of Agriculture Private Mail Bag No. 10 RYDALMERE. N.S.W. AUSTRALIA

Dear Dr. Ballantyne:

Many thanks for your letter of November 14, 1963 and the very excellent photograph of conidia of the N.S.W. cantaloup powdery mildew fungus. Powdery mildew conidia from cantaloupes in California, Texas, and South Carolina, and from the wild squash Gucurbita digitata in the southern California desert, all look like those of the N.S.W. fungus. All exhibit fibrosin bodies in 3% KOH mounts and all have the same shape.

I would appreciate an outline of Hirata's technique for conidia germination.

 P_7 was omitted from your list of seeds received. A packet of P_7 (LJ 36611 bulk selfs) is herewith enclosed to complete the supply.

With kindest regards,

Sincerely yours,

G. W. Bohn Plant Pathologist

ARS: CR: GWBohn: ds 12-6-63

Enc.

Fig. 6. Letter from G.W. Bohn to B. Ballantyne, 6 Dec. 1963.

UNITED STATES DEPARTMENT OF AGRICULTURE AGRICULTURAL RESEARCH SERVICE CROPS RESEARCH DIVISION P. O. BOX 3348 CHARLESTON, SOUTH CAROLINA 29407

U. S. Vegetable Breeding Laboratory

April 9, 1969

Dr. G. W. Bohn Geneticist USDA, ARS, CR U. S. Horticultural Field Station P. O. Box 150 La Jolla, California 92037

Dear Dr. Bohn:

The powdery mildew on cantaloupe in the envelope arrived in the morning and the specimens of spuash (boxed) in the afternoon of the same day. Have you identified the species? I am having difficulty finding Erysiphe cichorocearum and most collections about Charleston are Sphaerotheca fuliginea.

Both of the above specimens arrived in good shape, I prefer the boxed because of the larger quantity of the specimen.

Will you kindly send me a copy of your article describing race II of the powdery mildew organism.

Sincerely yours,

19:m. Mc Lean

D. M. McLean Res. Plant Pathologist

Fig. 7. Letter from D.M. McLean to G.W. Bohn, 9 Apr. 1969.

CROPS RESEARCH DIVISION U. S. Horticultural Field Station P. O. Box 150 La Jolla, California 92037

April 14, 1969

Dr. D. M. McLean U. S. Vegetable Breeding Laboratory P. O. Box 3348 Charleston, South Carolina 29407

Dear Mac:

I have examined specimens of cucurbit powdery mildew on muskmelons collected at several sites in California, Arizona, and Texas, and single sites in South Carolina and Michigan. Although I was unable to find the perfect stage, the conidia of all collections had inclusion bodies characteristic of Sphaerotheca fuliginea.

In addition to that evidence, our breeding lines resistant to race 2 are resistant at nearly all sites tested in various parts of the world including those where <u>Sphaerotheca fuliginea</u> has been described. Therefore, our race 2 is <u>Sphaerotheca fuliginea</u> and that species is the one prevalant on muskmelons everywhere. Intended to publish a brief paper on it this year but I haven't written it yet. Would you like to join me in the effort?

With best regards,

Sincerely,

G. W. Bohn Research Geneticist

Fig. 8. Letter from G.W. Bohn to D.M. McLean, 14 Apr. 1969.

UNITED STATES DEPARTMENT OF AGRICULTURE AGRICULTURAL RESEARCH SERVICE CROPS RESEARCH DIVISION P. O. BOX 3348 CHARLESTON, SOUTH CAROLINA 29407

U. S. Vegetable Breeding Laboratory

April 18, 1969

Dr. G. W. Bohn Research Geneticist U. S. Horticultural Field Station P. O. Box 150 La Jolla, California 92037

Dear Wes:

I have been waiting for someone to admit that part of the mildew problem in the U. S. was caused by <u>Sphaerotheca fuliginia</u>. Now I am satisfied that we are on the right track. I have examined specimens from Texas, California, Beltsville and have tried paring different isolates hoping to get a perfect stage. I have failed to find <u>Erysiphe cichoracearum</u> in any of these studies.

Today I found a specimen affecting watermelon fruits in the greenhouse. I have observed infection on <u>Citrullus fistulosis</u> plants but never on the fruit.

I most certainly would like to join you in describing race 2 and and will help where I can.

Best regards.

Sincerely yours,

D. M. M. Lean

D. M. McLean Plant Pathologist

Fig. 9. Letter from D.M. McLean to G.W. Bohn, 18 Apr. 1969.

UNITED STATES DEPARTMENT OF AGRICULTURE AGRICULTURAL RESEARCH SERVICE CROPS RESEARCH DIVISION P. O. BOX 3348 CHARLESTON, SOUTH CAROLINA 29407

U. S. Vegetable Breeding Laboratory

May 13, 1970

Dr. G. W. Bohn U. S. Horticultural Field Station P. O. Box 150 La Jolla, California 92037

Dear Wes:

Can you send me a culture of <u>Erysiphe cichoracaerum</u>? I am having a little problem finding it among our cultures. Send it on any plant that you choose.

Cornell University asked us to let them know when I find \underline{E} . cichoracaerum. Apparently, they have difficulty locating it also.

Sincerely,

D. M. Mc Lean

D. M. McLean Plant Pathologist

Fig. 10. Letter from D.M. McLean to G.W. Bohn, 13 May 1970.

£ U, S, GOVERNMENT PRINTING OFFICE: 1961-615954 DATE AD-311 (7-61) U. S. DEPARTMENT OF AGRICULTURE 10/26/70 SPEED-MEMO SUBJECT то chen FROM MESSAGE Here is some sunflow Erysphe eichosacearum, homo e The. serithec lew mites ontain a ia men dle with case. indl ha regards SIGNATURE (DESTROY THIS PART 3 UPON RECEIPT OF REPLY)

Fig. 11. Memo from G.W. Bohn to D.M. McLean, 10 Oct. 1969.