On the Occurrence in Britain of the Ascigerous Stage of a 'Brown Rot' Fungus.

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With Plates VI and VII.

ALTHOUGH the Brown Rot diseases of fruit trees have been under review for over a hundred years, and have attracted the attention of numerous workers because of their economic importance, the systematic relationship of the fungi concerned is still a debatable subject. This is chiefly owing to the fact that the ascigerous forms are met with comparatively rarely, especially in Europe, with the result that observations and descriptions have been chiefly confined to the conidial (*Monilia*) forms. The variation in the morphological characters of these *Monilias* in response to changes in the environmental conditions has created apparent discrepancies in such descriptions and has led to some confusion. This variation is well shown by *Monilia cinerea*, Bon., the grey fungus commonly found on plums and cherries, particularly with respect to the size of its conidia; thus the average size of the conidia produced on mummied fruit and dead twigs in winter is about $11.5 \times 8 \mu$, while those conidia which develop on recently infected fruit in summer average about $17 \times 11 \mu$. That such variation is a specific character has been established experimentally (10) by cultivating pure line strains (each derived from a single conidium) and comparing their morphological characters when grown under varied conditions in the laboratory and on fruit trees in the open.

When Woronin (11), in 1888, published an account of the life-history of *Sclerotinia Vaccinii*, in which he showed that a *Monilia* found on the young shoots of the Cowberry, *Vaccinium Vitis-Idaea*, was the conidial form of a *Sclerotinia* which produced apothecia on the mummied fruit, it was surmised that the Brown Rot fungi *Monilia fructigena* and *M. cinerea* were also to be referred to that ascomycetous genus, and Schröter (8) in 1893 included them in his Kryptogamen-Flora as *Sclerotinia fructigena* and *S. cinerea*, although the corresponding ascigerous forms had not then been discovered. In 1902, however, Norton (5) found apothecia

developing from mummied peaches lying on the ground in a Maryland orchard and, assuming that they were the ascigerous fructifications of *Monilia fructigena*, Pers., named the fungus *Sclerotinia fructigena*. Since that date others have also found and commented on the *Sclerotinia* occurring in North America on peaches and plums; in the earlier records, e.g. those by Dandeno (3), Reade (7), and Pollock (6), Norton's naming was adopted, but the more recent papers by Matheny (4) and Bartram (2) lend support to the conclusion arrived at by Aderhold and Ruhland (1), who examined some of Norton's specimens, that the Brown Rot fungus commonly found on the stone fruit in America is not *Sclerotinia fructigena* but *S. cinerea*.

Aderhold and Ruhland (1) announced the discovery in Europe of apothecia on mummified apples and apricots, and in an interesting paper which appeared in 1905 gave descriptions of three apothecial forms under the names *Sclerotinia fructigena*, *S. laxa*, and *S. cinerea*. In 1912 Westerdijk (9) found a *Sclerotinia* on mummied cherries which did not quite conform to the description of any of the three species as defined by Aderhold and Ruhland; it was probably a Brown Rot *Sclerotinia*, but its genetic connexion with a *Monilia* stage was not traced. Until the present year these appear to be the only European records of *Sclerotinia* fructifications associated with conidial forms of the *Monilia fructigena* type, i.e. those in which the conidial fructifications consist of conidiophores (usually forming dense pulvinate tufts) bearing branched chains of ellipsoid or lemon-shaped conidia without disjunctors.

The descriptions given by Aderhold and Ruhland, and the conclusions they arrived at, have been generally accepted except by those who recognize but one species, viz. *Sclerotinia fructigena*, as responsible for the Brown Rot disease. Aderhold and Ruhland obtained cultures from the ascospores of the form which they found on apples, and conidial fructifications were produced conforming to descriptions of *Monilia fructigena*, Pers., thus justifying Schröter's adoption of the name *Sclerotinia fructigena* for this fungus.

Their conclusions with respect to *S. laxa* and *S. cinerea* are open to criticism however. In the first place, the specimens they named *Sclerotinia cinerea* were preserved material sent to them from America by Norton. Now it has been recently pointed out (10) that the Brown Rot fungus of America, although practically indistinguishable in its conidial stage from the grey *Monilia* occurring on plums and cherries in Europe, differs from the latter in certain cultural characters, and Aderhold and Ruhland's assumption that the American *Sclerotinia* is a stage in the life-history of the European *Monilia cinerea*, Bon., is untenable; moreover, a more recent examination of fresh material by several American mycologists, e.g. Pollock (6), Reade (7), Matheny (4), and Bartram (2), has shown that the dimensions of the asci and ascospores as determined by Aderhold

and Ruhland for *Sclerotinia cinerea* are too low for the American *Sclerotinia*. Again, Aderhold and Ruhland quote the size of the conidia as the chief distinguishing character of the *Monilia* forms of *S. laxa* and *S. cinerea*. They find the average size of the conidia of *S. laxa* to be $16.1 \times 10.8 \mu$ and that of *S. cinerea* $13.8 \times 9.95 \mu$; the former, however, is approximately the average size of the summer conidia of *Monilia cinerea*, Bon., the latter rather higher than that of the winter conidia of the same fungus.

In order to throw further light on the relationship of these forms, attempts have been made by the writer to induce the development of apothecia by exposing mummied fruit on the ground and in pots of soil in the open. These attempts at first met with no success, as the 'mummies' gradually decayed, leaving only the stones and cores. Early in the present year, however, apothecia were found on mummied plums; these were naturally infected fruit which had been collected during the winter of 1918-19, and in January, 1919, were placed in an ordinary flower-pot, which was then exposed on the ground in the open and left undisturbed for over a year. In the middle of March, 1920, the contents of the pot were examined, and it was found that, although the great majority of the plums had decayed, leaving only the bare stones, in the débris at the bottom of the pot a few black, wrinkled, skin-like bodies remained, one of which still enclosed a plum-stone, and growing out of them were apothecia in various stages of development. On one of the 'mummies' as many as twelve sporophores were counted.

DESCRIPTION OF THE *SCLEROTINIA* FOUND ON MUMMIED PLUMS.

The sporophores arose from a thin, wrinkled, sclerotium-like body (enclosing a plum-stone or taking the general shape of the stone which had fallen out), 0.3 to 0.5 mm. in thickness, and consisting of closely interwoven hyphae, together with disintegrated particles of the fruit; the outer and inner surfaces of the sclerotium were black, but the internal hyphae were hyaline.

Each apothecium was stipitate, the stipes measuring from 0.4 to 2.8 cm. and in some instances bearing rhizoids towards the base. The lower portion of the stipes was dark brown, almost black; the upper light brown, merging into the darker outer surface of the receptacle. The young sporophores were claviform, but the older ones had expanded at the apex and become at first crateriform, later plane (but usually with a depressed centre), and finally convex, and often split at the margin to form lobes. The apothecia examined were, when fully expanded, from 4 to 9 mm. in diameter; the hymenium was brown at first, but later became more or less pruinose, and at maturity grey or almost white. The asci were cylindrical, narrowed below, rounded above, and when treated with iodine each showed a bluish 'pore' at the apex; each ascus contained eight spores.

Microscopic examination of an apothecium which is liberating spores shows that when the ascospores are fully developed they are situated in the upper half of the ascus, at first in a single row (monostichous) and usually with their long axes oblique to the axis of the ascus, but shortly before they are expelled they become more or less distichous nearer the apex of the ascus, which meanwhile increases in size and becomes vacuolate, a single vacuole finally extending from the apex almost to the base. After discharging its spores the ascus contracts, and its wall shows minute striae; an ascus which measured $192 \times 12 \mu$ immediately before its spores were set free contracted to $162 \times 9 \mu$ after dehiscence (Fig. 5, *d* and *e*).

The ascospores are non-septate (a few spores with a single median septum were seen on one occasion), variable in size and shape, usually irregularly ovoid, some broadly ovoid, others elongate, sometimes flattened on one side; the ends are generally rounded, but often narrowed and almost pointed, occasionally one end mucronate (Fig. 7).

Paraphyses are present; they are approximately the same length as the asci before the latter elongate to discharge their spores, $2-2.5 \mu$ in diameter, and are either simple or bear from one to three branches; they are usually very slightly dilated towards the apex, but in some cases the tip was distinctly swollen (Fig. 6).

Since the dimensions of asci and ascospores are usually quoted as characters of primary importance in distinguishing the apothecial forms found on stone-fruit, careful measurements were made of asci and ascospores of three of the apothecia found on plums and the ascospores of a fourth. The first apothecium examined was probably not quite mature, for although the spores were fully formed in many of the asci and were readily set free on tearing out a portion of the hymenium in water, no asci with distichous spores (as seen later in older specimens) were observed; the second and third had asci with monostichous and others with distichous spores, as well as a number which had discharged their spores, while the fourth apothecium had become dry after reaching maturity, and when examined, after soaking in water, the asci were found to be disintegrated, though numerous spores were to be obtained.

The results obtained are given in the following table:

DIMENSIONS OF THE ASCI OF THE PLUM *SCLEROTINIA*.

Apothecium.	Asci with monostichous spores.			Asci with distichous spores.		
	Number of asci measured.	Range of variation.	Average size.	Number of asci measured.	Range of variation.	Average size.
No. 1	25	$124-163 \times 7.5-10.5$	143.6×8.8	None present	—	—
2	25	$128-170 \times 8.0-10.0$	151.0×8.9	10	$164-198 \times 11-13.5$	184.4×12.5
3	25	$150-188 \times 7.5-9.5$	168.0×8.4	30	$162-226 \times 10-12.5$	194.6×10.8
Result	75	$124-188 \times 7.5-10.5$	153.4×8.7	40	$162-226 \times 10-13.5$	192.0×11.2

DIMENSIONS OF THE ASCOSPORES.

<i>Apothecium.</i>	<i>Number of spores measured.</i>	<i>Range of variation.</i>	<i>Average size.</i>
No 1	100	11.0-18 × 5.0-7	13.6 × 6.1
2	100	8.5-17 × 4.5-8	12.2 × 6.0
3	100	9.5-19 × 4.5-8	12.3 × 6.3
4	100	7.0-19 × 4.5-8.5	11.9 × 6.3
Result	400	7.0-19 × 4.5-8.5	12.5 × 6.2

CULTURAL AND INOCULATION EXPERIMENTS.

The ascospores germinated readily in distilled water and on prune-agar, and germ-tubes up to 250 μ in length developed within twenty-four hours at room temperature (18°-20° C.) ; the germ-tubes produced in distilled water were about 3 μ in diameter, and few produced branches during the first twenty-four hours (Fig. 8), while on agar the germ-tubes were 6-7 μ in diameter, and many were branched (Fig. 9). At the end of forty-eight hours the germ-tubes had produced numerous branches, and those growing on the agar had, in some instances, grown to a length of 2 mm.

Cultures were obtained by isolating ascospores on prune-agar plates and transferring the uncontaminated sporelings to other plates when two days old ; in this way pure line strains were obtained, each derived from a single ascospore. These cultures on prune-agar plates showed the zoned and lobed growth (characteristic of strains of *Monilia cinerea*, Bon., obtained from plums, cherries, and peach twigs in this country) which distinguish it from the American *Sclerotinia*.

On transferring a little of the mycelium from the plate cultures to sterilized potato in test-tubes, white hyphae grew out at first, but within five days, at room temperature, grey tufts of conidiophores bearing chains of conidia of the *Monilia cinerea* type developed. 100 conidia from each of three such cultures on potato, eight days old, were measured, and the following measurements obtained :

(1) 9.0 × 6-24.0 × 15.5 μ	Average 16.4 × 11.9 μ
(2) 9.5 × 7-24.5 × 18.5 μ	„ 15.9 × 11.9 μ
(3) 9.0 × 8-23.5 × 17.5 μ	„ 15.2 × 11.5 μ

These results are similar to those given by strains derived from conidia taken from plums naturally infected with *Monilia cinerea* ; thus for seven such strains, when cultivated on steamed potato, and the average dimensions of 100 conidia produced on the medium determined for each, the averages varied from 15.5 × 11.5 μ to 16.0 × 12.5 μ and 17.0 × 12.0 μ .¹

In order to confirm the evidence supplied by the cultural studies that the *Sclerotinia* and the grey *Monilia* found on plums and cherries are forms

¹ See Annals of Appl. Biol., vol. iii, p. 179.

of the same fungus, inoculation experiments were carried out on trees in the open, using conidia obtained from cultures derived from an ascospore. Inoculations were made on plum flowers and fruit, cherries (fruit), and apple flowers.

(a) *Inoculation of Plum Flowers.*

The inoculations were made by placing conidia on the stigmas of fourteen flowers of Victoria plum trees in the College plantation; the early symptoms of Brown Rot infection, i.e. brown discoloration of the stigmas and styles, were evident within four days, control flowers showing no such discoloration at this stage; the ovary was killed in every case, and on the twelfth day after inoculation nine of the flowers had grey *Monilia* pustules on the styles, and in some cases pustules appeared on the pedicels and calyx. About this time a gale removed all the inoculated flowers, and the question as to whether the fungus can establish itself in the flowering spurs and twigs was not determined. The experiment shows, however, that the fungus is capable of killing plum flowers by infection through the stigmas.

Measurements were taken of 100 conidia taken from the pedicel of one of the infected flowers, and the dimensions found to be $10 \times 8.5 - 20 \times 14 \mu$, average $14.8 \times 10.8 \mu$. The dimensions of conidia taken from a naturally infected flower in another plantation were $9.5 \times 7.5 - 28 \times 18 \mu$, average $14.5 \times 10.6 \mu$.

(b) *Inoculation of Plums (fruit).*

Conidia were placed in punctures made with a sterilized needle; seven of the eight plums inoculated became infected, and within nine days bore many grey *Monilia* pustules, while in one instance infection had already extended to a plum in contact with one of those inoculated. Conidia taken from one of the plums had dimensions of $10 \times 8 - 22 \times 17 \mu$, average $17.5 \times 13.0 \mu$.

As a control experiment eight plums were similarly punctured but not inoculated; these did not become infected.

(c) *Inoculation of Cherries (fruit).*

Cherries similarly inoculated were also readily attacked; in one instance pustules appeared within four days, on the rest pustules were observed on the sixth day. As in the case of the plums, where a sound cherry was in contact with an inoculated one, it became infected at the point of contact. Conidia taken from one of the cherries had dimensions of $11.5 \times 9 - 22.5 \times 18 \mu$, average $17.6 \times 13.2 \mu$.

It has been shown (10) that the average size of the conidia of *Monilia cinerea* when growing on fruit in summer is about $17 \times 11 \mu$, and it will be seen that the above dimensions for the conidia of the ascosporic strain produced under similar conditions are of the same order.

(d) *Inoculation of Apple Flowers.*

Apple flowers (variety James Grieve) were inoculated on the stigmas with conidia of the plum *Sclerotinia*, and simultaneously on the same tree others were inoculated with a strain of *Monilia cinerea* isolated from a dead flowering spur of an apple tree. For each strain eight inflorescences were selected and two flowers were inoculated on each inflorescence; thus sixteen flowers were inoculated with the *Sclerotinia* strain and sixteen with the apple strain of *Monilia*.

Of the eight inflorescences inoculated with the apple *Monilia* seven were killed outright, with all their flowers and leaves, the wilting of the leaves (which indicates that the fungus has extended from the infected flowers into the axis of the inflorescence) being noticeable in from twelve to seventeen days after inoculation of the stigmas.

Of the eight inflorescences inoculated with the plum *Sclerotinia* strain the flowering axis was not invaded in any one instance, although the inoculated flowers themselves showed the early symptoms of infection by a browning of the stigmas and styles when no such discoloration was observable on control flowers; one of these inoculated flowers, however, developed into fruit, while the rest fell off.

The results obtained from the inoculation experiments offer no evidence that the mode of parasitism of the fungus is modified in any way by the interpolation of the ascigerous stage, and confirm the conclusions given in a previous paper (10) that *Monilia (Sclerotinia) cinerea* is represented in Britain by two 'biologic forms', one of which causes a 'Blossom Wilt and Canker Disease' of apple trees, whilst the other is unable to extend farther than the pedicel of the inoculated apple flower. From its mode of growth in cultures, its parasitic habit, and the morphology of its conidial stage when growing on plums and cherries, together with its inability to invade the flowering spurs of apple trees, the *Sclerotinia* found on plums is shown to be the ascigerous stage of *Monilia cinerea* forma *pruni* referred to in that paper.

A COMPARISON OF THE BROWN ROT SCLEROTINIAS.

The following table summarizes the results obtained with respect to dimensions of asci and ascospores of Brown Rot Sclerotinias as determined by various authors:

Author.	Fungus.	Asci.	Ascospores.
Norton	<i>S. fructigena</i>	45-60 × 3-4	6-7 × 3-3.5
Reade	<i>S. fructigena</i>	125-215 × 7-10	10-15 × 5-8
Pollock	<i>S. fructigena</i>	130-179 × 9.2-11.5	11.4-14.4 × 5-7
Matheny	<i>S. cinerea</i>	From apothecia on peaches 135-190 × 6.9-10.5 Mostly 163 × 8.9	10.5-14.5 × 5.2-7.5 Mostly 12.5 × 6
		From apothecia on plums 135-173 × 6.8-10.8 Mostly 151 × 9.4	9.3-14.2 × 5-7.4 Mostly 11.8 × 6.3
Bartram	<i>S. cinerea</i>	Average 150.4 × 8.8	Average 10.1 × 7.1
Aderhold and Ruhland	<i>S. fructigena</i>	120.0-180.0 × 9.0-12.0	11.0-12.5 × 5.6-6.8
	<i>S. laxa</i>	121.5-149.9 × 8.5-11.8	11.5-13.5 × 5.2-6.9
	<i>S. cinerea</i>	89.3-107.6 × 5.9-6.8	6.2-9.3 × 3.1-4.6
Westerdijk	<i>Sclerotinia</i> on cherries	158.4-171.6 × 7.9-8.5	13.2-16.8 × 4.3-5.2
The <i>Sclerotinia</i> found on plums at Wye		Asci with monostichous spores 124-188 × 7.5-10.5 Average 153.4 × 8.7 Asci with distichous spores 162-226 × 10-13.5 Average 192 × 11.25	7-19 × 4.5-8.5 Average 12.5 × 6.2

With regard to the foregoing nomenclature and dimensions the following points are to be observed. As already mentioned, Aderhold and Ruhland established the connexion between the apothecial form they named *Sclerotinia fructigena* and the conidial form *Monilia fructigena*, Pers.; the ascospores of this fungus are described and figured as having pointed ends ('sporideis . . . ovato-fusoideis, utrinque acutis'). For their description of *S. cinerea* they used preserved material sent by Norton, and found that the ascospores had rounded ends; Reade examined fresh apothecia also obtained from Norton. It seems certain, therefore, that the earlier records of the *Sclerotinia* in America were not of *S. fructigena*, (Pers.) Schröter, and the more recent records show that the American form is one of which the conidial fructifications are indistinguishable from those of *Monilia cinerea*, Bon. It is to be noted that Reade's figures are higher than those of either Norton or Aderhold and Ruhland, and are of the same order as those obtained by Pollock, Matheny, and Bartram. Of thirteen strains of *Monilia* obtained by the present writer from various sources in North America, each has proved to be a fungus with a *Monilia* stage very similar to the grey *Monilia* common in Britain, but differing from the latter in its mode of growth when growing on agar, and in its more copious development of conidia when cultivated on artificially prepared culture media, while strains of *Monilia* isolated from mummied plums obtained from France and Holland have proved to be culturally similar to the form occurring in Britain. The American *Sclerotinia* would appear therefore to be either a distinct species or at least a form culturally distinct from the European *Monilia cinerea*, Bon.

There remain for consideration Aderhold and Ruhland's *Sclerotinia laxa* and Westerdijk's *Sclerotinia* on cherries; the asci and spores of the latter are greater than those found on *S. laxa*, but it will be seen that both

sets of dimensions are practically included in those given by the asci with monostichous spores of the *Sclerotinia* found on plums. The spores of *S. laxa* are described as 'fere semper monostichis, raro subirregulariter dispositis, utrinque obtusissimis, saepe 2-3 guttulis'; this general description of the spores conforms to Westerdijk's description and figures of the asci and spores of the cherry *Sclerotinia*. In neither case are asci with distichous spores mentioned, but as this is a condition which obtains only when the apothecia are quite ripe and liberating (or just about to liberate) spores, it might not have come under observation where suitable material was very limited.¹

The sclerotia from which *Sclerotinia laxa* developed were thicker (1 mm.) than those of the plum *Sclerotinia* (0.3-0.5 mm.), but this variation is probably merely due to a difference in the texture or size of the fruits.

Aderhold and Ruhland obtained cultures from the ascospores of the apricot *Sclerotinia* and reproduced the conidial stage; this they describe as appearing, to the naked eye, similar to *Monilia cinerea*; they found, however, that the conidia of the former were larger than those of the latter. Thus the dimensions of the conidia of *M. laxa* are given as $12.4-23.8 \times 9.3-15.5 \mu$ with an average of $16.1 \times 10.8 \mu$, those of *M. cinerea* as $9.3-14.5 \times 6.2-12.4$, the average size being $13.8 \times 9.95 \mu$. It will be seen from the inoculation experiments described in this paper that the dimensions obtained for the conidia of the plum *Sclerotinia* when growing on plums and cherries were in fact rather higher than those quoted for *Monilia laxa*.

Having regard to these facts, it would appear, therefore, that the *Sclerotinias* recorded for Europe as occurring on apricots, cherries, and plums show no essential morphological differences. To determine whether they are to be distinguished culturally, or biologically, with respect to their host plants will require further study. Aderhold and Ruhland suggest that there is a feeble specialization of parasitism, and that *S. laxa* is more or less confined to the apricot. Thus they had observed on one occasion that apricots were found severely attacked by Brown Rot, while neighbouring peaches and cherries were free from the disease; again, from their inoculation experiments, although they were able, with *S. laxa*, to infect the flowers not only of apricots but also of cherries, plums, and apples, they found that 'gegenüber *Sclerotinia laxa* die Pflaumenblüten sich relativ resistent erwiesen'. Though this evidence is suggestive it is not conclusive, and positive proof can only be obtained by parallel series of inoculations with strains of *Sclerotinia* from the various hosts.

¹ Aderhold and Ruhland appear to have obtained but one fully developed apothecium on apricots; they write, 'Von den beiden am 1. Mai Fruchtkörper zeigenden Aprikosen-Mumien trug die eine ein wohlentwickeltes und ein kleineres Apothecium, die andern 3 unvollkommen ausgebildete Apothecien'.

SUMMARY.

1. A *Sclerotinia* found on mummified plums at Wye in March 1920 has been shown, by cultural experiments in the laboratory and inoculations on fruit trees in the open, to be the apothecial stage of the grey *Monilia* commonly found on plums and cherries in Britain.

2. The fungus, of which a description is given, is to be referred to *Sclerotinia cinerea*, (Bon.) Schröter.

3. The dimensions of its asci and ascospores are, however, greater than those of the fungus described under that name by Aderhold and Ruhland; on the other hand, its morphological characters are not inconsistent with those of *Sclerotinia laxa* as defined by them.

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EXPLANATION OF PLATES VI AND VII.

Illustrating Mr. H. Wormald's paper on the Occurrence in Britain of the Ascigenous Stage of a 'Brown Rot' Fungus.

PLATE VI.

Fig. 1. Two mummified plums bearing sporophores of *Sclerotinia cinerea*. Nat. size.

Fig. 2. Isolated sporophores.

Fig. 3. Four sporophores *in situ*. $\times 2\frac{1}{2}$. The uppermost one bears rhizoids at the base of the stipes.

Fig. 4. Culture, on prune-agar, grown at room temperature : the product of a single ascospore 22 days after isolating the spore (cf. Ann. of Bot., vol. xxxiv, No. 134, Plate IV, Fig. 5).

PLATE VII.

Fig. 5. Asci of *Sclerotinia cinerea*. $\times 500$. *a* and *b*. With monostichous spores. *c*. An ascus becoming vacuolate ; spores not strictly monostichous. *d*. An ascus with a single large vacuole and distichous spores ; condition a few seconds before the ascus dehisced. *e*. The same ascus shown at *d*, but after dehiscence. *f*. An ascus with three abnormally small spores.

Fig. 6. Types of paraphyses. $\times 500$.

Fig. 7. Ascospores, showing variation in shape and size. $\times 1,000$.

Fig. 8. Ascospores germinating in distilled water : at end of 20 hours at room temperature (18° - 20° C.). $\times 500$.

Fig. 9. Ascospores germinating on prune-agar : at end of 20 hours at room temperature. $\times 500$.

1.

2.

3.

4.

WORMALD-BROWN ROT.

Huth coll.

6.

9.

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