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Microcyclic conidiogenesis in powdery mildews and its association with intracellular parasitism by *Ampelomyces*

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Abstract Microcyclic conidiogenesis (MC), a process defined as the production of conidia on a spore without any, or only a minimal, involvement of hyphal growth, has recently been reported in a little known powdery mildew species, *Oidium longipes*. To investigate whether this was an isolated case or it is a more general phenomenon in powdery mildew fungi, germinating conidia of eight species of the *Erysiphales* were examined using light microscopy. The following species were included in this work: *Erysiphe necator* on grapevine, *Blumeria graminis* f. sp. *hordei* on barley, *Podosphaera xanthii* on cucumber, *Erysiphe* sp. on *Ligustrum vulgare*, *O. longipes* on *Petunia x grandiflora*, *O. neolycopersici* on tomato, *Golovinomyces cichoracearum* on *Rudbeckia laciniata* and *Sawadaea* sp. on *Acer negundo*. In all these species, up to 4% of the germinated conidia exhibited MC. Moreover, when colonies of *E. necator* and *O. neolycopersici*, on detached grapevine and tomato leaves, respectively, were treated with a conidial suspension of *Ampelomyces*, the intracellular pycnidia of these mycoparasites appeared in microcyclic conidiophores. This represents a yet undescribed method of accelerating asexual reproduction in this mycoparasite. In the life cycle of powdery mildews, the importance of MC is still not clear but it should be taken into consideration when conidial germination is studied on the host surface for purposes such as epidemiology or species identification.

Keywords Microcyclic conidiation · Conidial germination · *Erysiphales* · Mycoparasitism

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The life cycle of many powdery mildew species (*Erysiphales*), the well known obligate biotrophic pathogens of many crops and wild plant species, has been studied in detail (Braun 1987; Braun et al. 2002; Bolay 2005). Studies of asexual and sexual reproduction especially of powdery mildews of important crops have been intensely explored with a view to pin-pointing potential chemical, biological or agro-technical strategies that may stop, or reduce, their spread and/or infection. The part of the life cycle involving conidial germination and infection of the host has always received special attention, e.g. through light microscopy, scanning and transmission electron microscopy and other direct methods (for a review, see Green et al. 2002). Host resistance to

many species of powdery mildew has also been extensively studied (e.g., Xiao et al. 2003; Li et al. 2009; Nonomura et al. 2009a).

In addition, the germination patterns of powdery mildew conidia have been investigated for identification purposes. It has long been known that the site of emergence of the germ tubes on the conidium as well as germ tube length and the morphology of their tips, are diagnostic for distinct groups of powdery mildews (Zaracovitis 1965; Braun 1987; Braun et al. 2002; Bolay 2005). A recent study revealed new germination types in some species (Cook and Braun 2009). However, it should be noted that germination tests done for species identification purposes have often been set up on artificial surfaces. These included glass slides (Zaracovitis 1965; Fletcher et al. 1988), water agar (Vági et al. 2007), lid of a plastic Petri dish (Cook and Braun 2009) and non-host plant materials such as epidermis of onion scale (To-anun et al. 2005). In some cases, however, germinated conidia were collected directly from host plant surfaces and investigated to support the identification of the powdery mildews infecting the source plant species (e.g., Kiss et al. 2001; Liberato 2006) or for other purposes (Oichi et al. 2006; Nonomura et al. 2009b).

In the light of all these extensive studies on conidial germination in the *Erysiphales*, it was surprising to find an additional factor associated with germination in *Oidium longipes*, a little known, and only recently described, powdery mildew species infecting petunia, eggplant and some other solanaceous plants (Kiss et al. 2008). Approximately 2 to 5% of the already germinated conidia produced functional conidiophores directly on their surfaces, thus favouring earlier propagation of young colonies. Similar processes of conidiogenesis taking place directly on fungal spores have been described in a large number of fungal species in various conditions and these phenomena were called microcyclic (or microcycle) conidiation or microcyclic conidiogenesis (for a review, see Hanlin 1994). We prefer the last term which we here abbreviate to MC. This phenomenon, found on *O. longipes* conidia, was the first documented case of this process in the *Erysiphales*.

To investigate whether this was an isolated case or it is a more general phenomenon in powdery mildew fungi, germinating conidia of eight species of the *Erysiphales* were repeatedly collected from their host plants and examined using bright-field, dark-field, phase contrast and differential interference contrast (DIC) microscopy. The following powdery mildew and host plant species and cultivars were included in this work: *Erysiphe necator* ex grapevine (*Vitis vinifera* cv. Chardonnay), *Blumeria graminis* f. sp. *hordei* ex barley (*Hordeum vulgare* cv. GK Omega), *Podosphaera xanthii* (formerly known as *Sphaerotheca fuliginea* or *S. fusca*) ex cucumber (*Cucumis sativus* cv. Rajnai Fürtös), *Erysiphe* sp. ex privet (*Ligustrum vulgare*), *O. longipes* ex petunia (*Petunia x grandiflora*), *O. neolycopersici* ex tomato (*Solanum lycopersicum* cv. Kecskeméti Jubileum), *Golovinomyces cichoracearum* ex *Rudbeckia laciniata* and *Sawadaea* sp. ex ash maple (*Acer negundo*). Powdery mildew-infected grapevine, barley, cucumber, petunia and tomato leaves were collected from plants kept in pots in a greenhouse for maintenance of the respective species of the *Erysiphales*. Powdery mildew-infected privet, *R. laciniata* and ash maple leaves were collected from the field for this study. Powdery mildew mycelia, which usually contained germinating conidia, were collected at random from the host plant surfaces with transparent adhesive tape, as described by Cook et al. (1997), or after boiling a small piece of powdery mildew-infected leaf tissue in lactic acid as described by Shin and La (1993). For each of the seven powdery mildew species studied, a total of 150–500 germinating conidia were examined at different time intervals to find as many cases of MC as possible.

In all the eight powdery mildews studied, approximately 0.5 to 4% of the germinated conidia exhibited MC. This was detected in *E. necator* on grapevine leaves (Fig. 1a, b), *Sawadaea* sp. on ash maple (Fig. 1c), *Erysiphe* sp. on privet (Fig. 1d), *P. xanthii* on cucumber (Fig. 1e), *G. cichoracearum* on *R. laciniata* (Fig. 1f), *O. neolycopersici* on tomato (Fig. 1g), *O. longipes* on petunia (Fig. 1h), as described earlier by Kiss et al. (2008), and *B. graminis* on barley (Fig. 2). Sometimes even two microcyclic conidiophores arose from a single conidium (Fig. 1h). These eight powdery mildews belong to five different groups based on conidiophore and conidial morphology (Cook et al. 1997; Braun et al. 2002), germ tube types (Cook and Braun 2009) and molecular phylogenetic analyses (for a review, see Takamatsu 2004): *G. cichoracearum, O. longipes*, *P. xanthii*, *Sawadaea* sp. and *B. graminis* produce catenate conidia, and represent four distinct subgenera

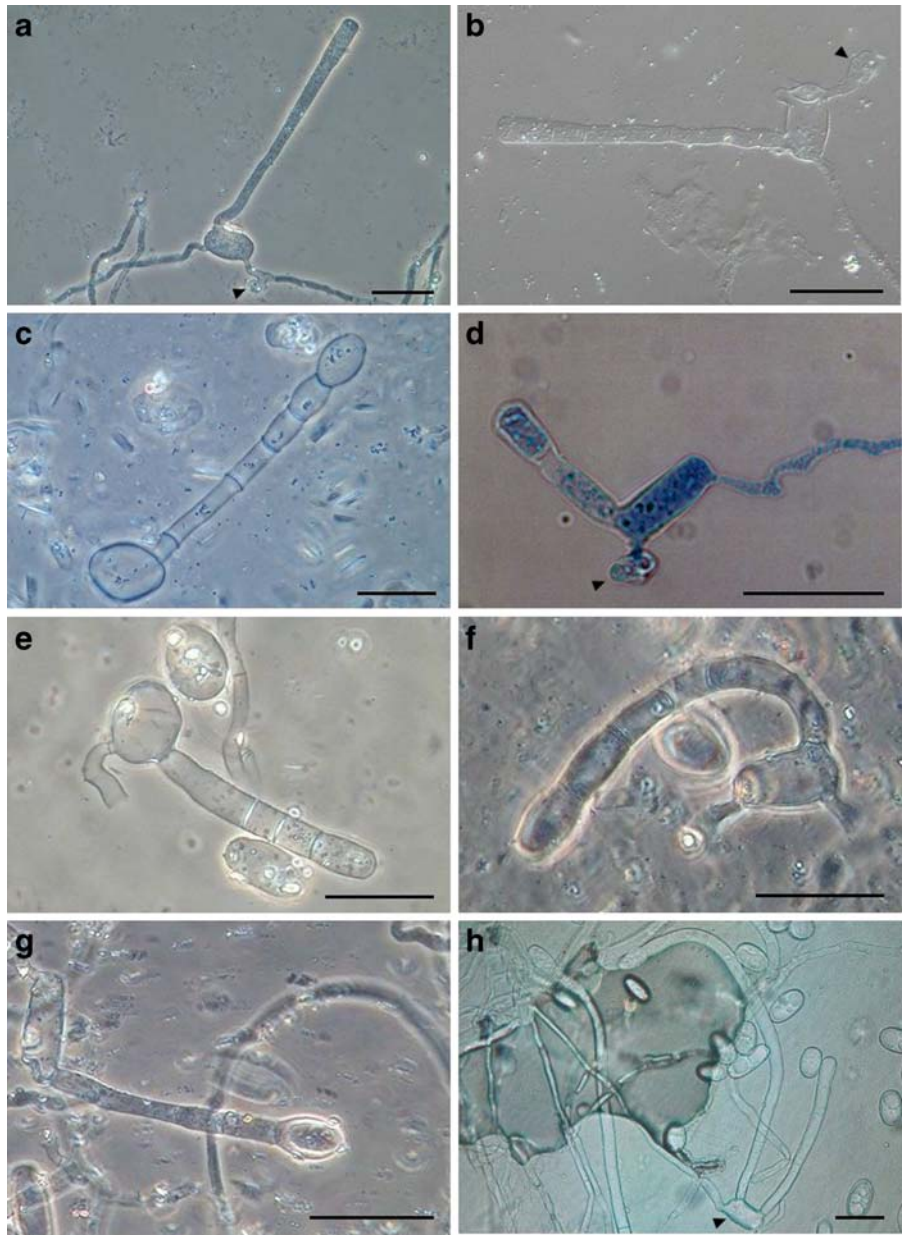

Fig. 1 Microcyclic conidiogenesis (MC) in germinated conidia of seven powdery mildew species. The production of germ tubes and hyphae by all the conidia with microcyclic conidiophores is visible in most cases. (**a**) and (**b**) Single conidia of *E. necator* with microcyclic conidiophores collected from grapevine leaves. **Arrows** point to primary germ tubes with lobed appressoria typical of the *Pseudoidium* type. (**c**) Conidium of *Sawadaea* sp. with a microcyclic conidiophore collected from an ash maple leaf. (**d**) Conidium of *Erysiphe* sp. from a privet leaf developing a pseudoidium-type microcyclic conidiophore. **Arrow** shows a short germ tube terminating in a lobed appressorium typical of the *Pseudoidium* type. (**e**) MC involving a conidium of *P. xanthii* collected from cucumber. (**f**) Conidium of *G. cichoracearum* with a microcyclic conidiophore collected from *R. laciniata* and showing a club-shaped germ tube typical of the *Reticuloidium* type. (**g**) Conidium of *O. neolycopersici* with a microcyclic conidiophore collected from tomato. (**h**) Conidium of *O. longipes* (**arrow**) collected with adhesive tape from petunia and producing two microcyclic conidiophores. Bars equal 30 μm

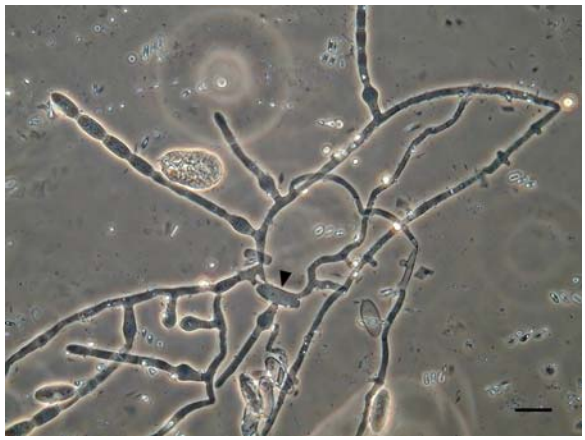

Fig. 2 Conidium of *Blumeria graminis* f. sp. *hordei* (**arrow**) from a barley leaf producing a still immature microcylic conidiophore from its side wall. The hyphae emerged from this conidium have already developed mature and immature conidiophores. Bar equals 30 μm

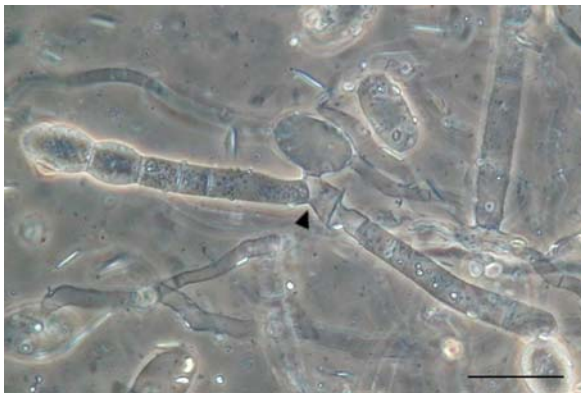

Fig. 3 Conidium of *P. xanthii* from a cucumber leaf showing a primary lateral forked germ tube (**arrow**) where the left hand arm has developed into a mature conidiophore and the right hand arm was developing a younger conidiophore. The basal part of the latter appears shrivelled on this figure. Lateral forked germ tubes (*brevitubus* subtype of *Fibroidium* germination type) are characteristic of *P. xanthii*. Bar equals 30 μm

of the genus *Oidium*, namely subgen. *Reticuloidium, Fibroidium, Octagoidium* and *Oidium*, respectively, while *E. necator*, *Erysiphe* sp. on privet and *O. neolycopersici* mature conidia singly, and all belong to the genus *Oidium* subgen. *Pseudoidium*. In addition, a recent paper showed a microphotograph of MC in a newly described anamorphic species, *O. aloysiae*, belonging to the subgen. *Striatoidium* (teleomorph *Neoerysiphe*) (Takamatsu et al. 2008, Fig. 6C). Thus MC has so far been detected in six major groups suggesting it is a widespread phenomenon in the *Erysiphales*. It is noteworthy that the microcyclic conidiophores always arose from a position on the conidium known to be a potential site for germ tube initiation as described by Cook and Braun (2009). It was from the shoulders (sub-terminal positions) as in the examples shown in Fig. 1 or, as in Figs. 2 and 3, from a side wall (lateral position often seen in *Blumeria* and typical of *P. xanthii*).

In addition to primary germ tubes, all the germinated conidia bearing microcyclic conidiophores had produced hyphae, sometimes termed 'secondary germ tubes' (Celio and Hausbeck 1998) that integrated the conidium with the superficial mycelium. The primary germ tubes were typical of the respective *Oidium* subgenera (equating to the holomorph genera) as described by Cook and Braun (2009) and are seen clearly in Figs. 1a, b, d (*Pseudoidium* germination type) and Fig. 1f (*Reticuloidium* germination type). In a germinating *P. xanthii* conidium, conidiophores arose directly from a forked primary germ tube (Fig. 3). Forked germ tubes are typical of this species (*brevitubus* subtype within *Fibroidium* germination type). This process is not considered as a MC but shows that mature conidiophores can rapidly develop after conidial germination, sometimes much faster than previously thought.

The hyphae, conidiophores, conidia and the young, immature sexual fruiting bodies of the *Erysiphales* are commonly parasitized worldwide by intracellular mycoparasites belonging to the genus *Ampelomyces* (for a review, see Kiss et al. 2004). Their hyphae are transported within parasitized, but usually living, airborne powdery mildew conidia and then continue their growth intracellularly if the living conidia land on a host plant surface, germinate and produce a new colony there. Thus a powdery mildew colony can be parasitized by *Ampelomyces* from its inception. This mycoparasite produces its asexual fruiting bodies (pycnidia) mostly in one or two cells of the conidiophores of powdery mildews. The pycnidia contain numerous unicellular and hyaline conidia. Thus, if a parasitized conidium underwent MC, the conidiophore so produced should contain intracellular pycnidia of *Ampelomyces*.

To determine whether *Ampelomyces* could form intracellular pycnidia in conidiophores arising from a parasitized conidium undergoing MC, detached

grapevine leaves infected with *E. necator* and detached tomato leaves infected with *O. neolycopersici* were sprayed with conidial suspensions of an *Ampelomyces* strain, designated DSM2222, as described in different mycoparasitic tests done by Szentiványi and Kiss (2003). The treated grapevine and tomato leaves were placed on filter papers soaked in water in large Petri dishes, 16 cm diameter, and kept in growth chambers at 20°C and 16 h daily illumination. Plates were opened every two days to water the filter papers and these movements were expected to contribute to the detachment of newly produced and parasitized conidia from their mother conidiophores. Control leaves were sprayed with water and kept as described for the treated leaves. Ten to 12 days after spraying, pieces 2–3 cm^2 were excised from both treated and control leaves, boiled in lactic acid as described in Shin and La (1993), and examined for the presence of germinated conidia of *E. necator* and *O. neolycopersici*. These tests were repeated several times until MC was found on both the *Ampelomyces*-treated and the control leaves.

MC was detected in both *E. necator* and *O. neolycopersici* sprayed with *Ampelomyces*: intracellular hyphae (Fig. 4a), as well as young pycnidia (Fig. 4b) and fully mature pycnidia (Figs. 4c, d) were found in the microcyclic conidiophores of both powdery mildew species. Curiously, the mature pycnidia shown in Figs. 4c, d were produced in conidiophores which arose laterally from the conidium. Lateral emergence of germ tubes is infrequent in *Oidium* subgen. *Pseudoidium* (Cook and Braun 2009) where the anamorph of *E. necator* belongs. It is possible that the presence of the mycoparasite had influenced the site of germination in these instances.

All the germinated conidia containing *Ampelomyces* hyphae had been previously penetrated by the mycoparasite, during their formation on parasitized powdery mildew colonies, before being detached from their mother conidiophores. In spite of the presence of *Ampelomyces* hyphae in these conidia, and *Ampelomyces* pycnidia in their microcyclic conidiophores, these cells were not killed by the mycoparasite and were able to produce new parasitised conidia that in turn might have given rise to new, and already parasitized powdery mildew colonies on grapevine and tomato leaves. Thus, mycoparasitised MC led to the rapid production of *Ampelomyces* conidia before

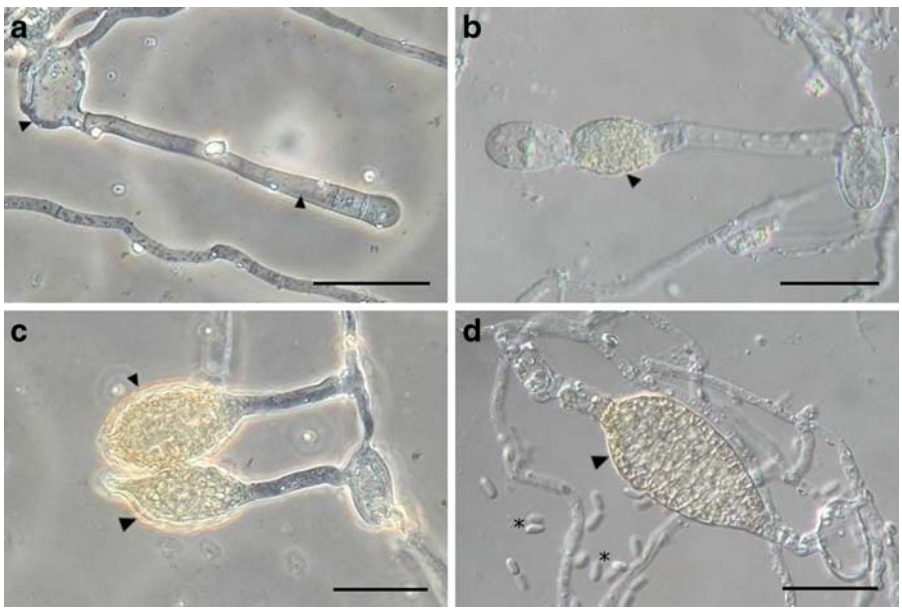

Fig. 4 Microcyclic conidiophores of *E. necator* conidia parasitized internally by *Ampelomyces* mycoparasites on grapevine leaves. (**a**) Intracellular hyphae of *Ampelomyces* (**arrows**) inside a conidium and a microcyclic conidiophore. (**b**) Young intracellular pycnidium of *Ampelomyces* (**arrow**) in a fully developed microcyclic conidiophore. (**c**) An intracellular pycnidium of *Ampelomyces* (**arrow**) in a microcyclic conidiophore and another one (**arrow**) in a conidiophore developed on the emerged hypha. (**d**) Fully mature intracellular pycnidium of *Ampelomyces* (**arrow**) produced in the second cell of a microcyclic conidiophore. Conidia of *Ampelomyces* released from the pycnidium are marked by an asterisk. Bars equal 30 μm

normal asexual reproduction could occur on an established colony. The presence of *Ampelomyces* pycnidia in microcyclic conidiophores is a new finding and represents a previously undescribed method of accelerating asexual reproduction in this mycoparasite. Observations by Hashioka and Nakai (1980) and Sundheim and Krekling (1982) had shown that the first interactions between *Ampelomyces* and the parasitized powdery mildew cells were apparently biotrophic (although the invaded cells were finally destroyed). Thus, parasitized powdery mildew colonies were able to continue their radial growth, albeit with decreased sporulation (Shishkoff and McGrath 2002). Therefore, *Ampelomyces* conidia released from pycnidia produced in microcyclic conidiophores could germinate on the host plant surface and promptly penetrate healthy powdery mildew colonies, thus contributing to a more rapid spread of *Ampelomyces* than previously thought possible. Therefore it is likely that this mechanism would allow *Ampelomyces* to spread more rapidly in the field.

MC has been described in a large number of fungal species (Anderson and Smith 1971; Bacon and Hinton 1991; Lapaire and Dunkle 2003; Ahearn et al. 2007) and it has also been studied from a practical point of view to ensure the synchronized production of large amounts of conidia of different strains in the shortest possible time for industrial or other mass production purposes (e.g., Cascino et al. 1990; Maheshwari 1999; Krasniewski et al. 2006). In all these cases, MC was defined as the production of conidia on a spore without any, or only a minimal, involvement of hyphal growth. However, in fact, considerable morpho-physiological differences could be found among the various processes described as MC. In all the powdery mildew species studied in this work, conidia exhibiting MC have also produced one or more primary germ tubes and also hyphae that may have already penetrated one or more host cells to ensure the biotrophic uptake of nutrients by the young, developing mycelium. However, in some cases the MC was clearly a very early process being completed before conidiogenesis started on the young hyphae (e.g., Figs. 1a, b). Thus, in these cases conidia originating from MC would have been among the first produced by the young colonies, thus ensuring their rapid propagation. In other cases, however, normal conidiogenesis had started on the emerged hyphae before MC occurred (e.g., Fig. 2). This showed that the germinated conidium, when it is part of the already formed young mycelium, can simply serve as a site for conidiogenesis similar to other cells of the hyphae. In some cases, e.g. as shown in Fig. 1h, or seen during other microscopic investigations, it was not possible to clearly distinguish the order of appearance of conidiophores found on hyphae and germinated conidia. Most probably, different types and sub-types of MC could be distinguished in the fungal world but these have not been categorised in the literature.

In some industrially or otherwise important fungi, the nutritional and/or environmental factors necessary for a synchronized MC in artificial conditions are well-known (e.g., Cascino et al. 1990; Krasniewski et al. 2006). In other fungi, where MC has been reported, but not studied in detail, almost nothing is elucidated in this respect (e.g., Lapaire and Dunkle 2003; Ahearn et al. 2007). The present study has shown that MC does occur in a number of phylogenetically different powdery mildew species but its occurrence is apparently rare; only one to four germinated conidia out of 100 exhibited MC in this work. Similar low values were reported for other fungi, such as *Aspergillus* spp. (Ahearn et al. 2007). Thus, the importance of this phenomenon in the life cycle of the *Erysiphales* is still not clear but it should be taken into consideration when conidial germination is studied on the host surface for purposes such as epidemiology or identification of species.

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