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RECOGNITION OF APHID PARASITOIDS BY HONEYDEW-COLLECTING ANTS: THE ROLE OF CUTICULAR LIPIDS IN A CHEMICAL MIMICRY SYSTEM

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Abstract—The aphidiid wasp *Lysiphlebus cardui* parasitizes in ant-attended *Aphis fabae cirsiiacanthoidis* colonies without causing aggressive behavior in the ant *Lasius niger*. By contrast, *Trioxys angelicae*, another aphidiid parasitoid of aphids, is rapidly recognized and vigorously attacked by the ants. *L. niger* workers also responded differently to dead individuals of *L. cardui* and *T. angelicae*. Dead *L. cardui* parasitoids were often ignored when encountered by *L. niger*, whereas dead *T. angelicae* individuals were immediately grasped by ants that discovered them. However, hexane-washed parasitoids caused a similar reaction pattern in the ants, in that both aphidiid species were tolerated in the aphid colony. Lure experiments demonstrated that chemical stimuli on the cuticle are major cues for the ants to distinguish between the parasitoids. The hexane extract of *L. cardui* transferred to washed individuals of *T. angelicae* resulted in ant responses characteristic towards *L. cardui*, and *L. niger* workers displayed the typical removal pattern they normally showed towards *T. angelicae* when *T. angelicae* extract was applied to *L. cardui* individuals. Both parasitoid species treated with the hexane extract of *A. fabae cirsiiacanthoidis* were similarily treated by the ants as were aphid control individuals. The suggestion that the aphidiid wasp *L. cardui* uses chemical mimicry is discussed.

Key Words—*Aphis fabae cirsiiacanthoidis*, Homoptera, Aphidae, ants, ant-parasitoid interactions, Hymenoptera, Formicidae, Aphidiidae, parasitoids, *Lysiphlebus cardui*, *Trioxys angelicae*, cuticular lipids, chemical mimicry.

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INTRODUCTION

Insects that are associated with ants in a symbiotic relationship often provide sugar-rich secretions to the ants. In return, ants can act as effective guards in warding off predators and parasites (Banks, 1962; El-Ziady, 1960; El-Ziady and Kennedy, 1956; Flanders, 1951; Way, 1963). However, this ant protection is not perfect. Many predators and parasitoids of the nutrition-providing insects manage to integrate in a mutualistic association to gain access to their prey or host organism (Eisner et al., 1978; Mason et al., 1991; Pontin, 1959). Some species of the family Aphidiidae successfully overcome the defense mechanism of honeydew-collecting ants. Takada and Hashimoto (1985) described species-specific interactions between the root aphid *Sappaphis piri* Matsumura, the ant species *Lasius niger* (L.) and *Pheidole fervida* F. Smith, and the aphid parasitoids *Aclitus sappaphis* Takada & Shiga and *Paralipsis eikoae* (Yasumatsu). *A. sappaphis* was tolerated by the ant *P. fervida*, but vigorously attacked by *L. niger*. By contrast, *P. eikoae* was tolerated by *L. niger* and attacked by *P. fervida*.

In the aphid–ant system *Aphis fabae cirsiiacanthoidis* Schrank and *Lasius niger* on creeping thistle, *Cirsium arvense* (L.) Scop., the aphidiid wasp *Lysiphlebus cardui* (Marshall) that displays a cryptic behavior when searching in aphid colonies is either disregarded or tapped with the antennae by honeydew-collecting ants (for quantitative data see Völkl, 1992; and Völkl and Mackauer, 1993). In contrast, the aphidiid wasp *Trioxys angelicae* (Haliday) showing a "nervous" searching behavior in aphid colonies is readily attacked by ants; in some encounters the wasp manages to escape by flying off the plant, in others the parasitoid is seized by worker ants and killed (Völkl, 1992; Völkl and Mackauer, 1993). Völkl and Mackauer (1993) could demonstrate by using lightly anesthetized living females of both parasitoid species that behavioral cues of the wasps were not primarily responsible for the difference in the response of the ants. Furthermore, ants of different and unrelated genera responded in a similar pattern towards the parasitoid species. These authors suggested that *L. cardui* mimics the cuticular lipid profile of the aphid host, *A. fabae cirsiiacanthoidis*, to avoid attack by the ants. Such a strategy of being chemically "invisible" is known from a number of inquilines of social insects (e.g., Howard et al., 1980, 1982, 1990a, b; Vander Meer and Wojcik, 1982; Vander Meer et al., 1989).

The aim of this study was to test the hypothesis of Völkl and Mackauer (1993) that chemical cues on the cuticular surface rather than behavioral or morphological features prevent *L. cardui* from being recognized and attacked by honeydew-collecting ants. Experiments with dead nontreated and hexane-treated individuals of *L. cardui*, *T. angelicae*, and *A. fabae cirsiiacanthoidis*, as well as lure experiments with these parasitoids and aphids, were carried out to demonstrate the major role of epicuticular lipids as recognition cues in this aphid–ant–parasitoid system.

METHODS AND MATERIALS

Source of Parasitoids and Aphids. L. cardui parasitoids were obtained by collecting *A. fabae cirsiiacanthoidis* mummies on *C. arvense* in the vicinity of Bayreuth, Germany, at the beginning of July 1991 by cutting off whole thistle plants. In the laboratory, the mummies were removed from the plants with forceps and placed in a gauze-covered cage (28 × 20 × 36 cm), where the parasitoid females could eclose. Thus, *L. cardui* individuals had no contact to either living aphid hosts or to the host plant of the aphids. The females were tested the day after eclosion.

From a laboratory culture of *T. angelicae* parasitizing *A. fabae cirsiiacanthoidis* on *C. arvense* in a climate chamber (20°C ± 1°C, 16:8 hr light–dark), aphid mummies were removed from the plants and kept in a gauze-covered glass vial (8 cm diam., 12 cm high) in the laboratory until adult eclosion. Similar to *L. cardui*, *T. angelicae* parasitoids did not experience either their host aphids or the aphid host plant. For the experiments, the females were tested the day after eclosion.

To gain unparasitized *A. fabae cirsiiacanthoidis* individuals, potted thistle plants infested with this aphid species were kept in a gauze-covered cage (100 × 50 × 110 cm) in the field to exclude aphid parasitoids. During the whole season, no mummy could be detected.

General Aspects of the Experiments. Field experiments were conducted in a roof garden between early July and the end of August 1991. Four potted *C. arvense* plants, each infested with a mixed-age colony of about 500 individuals of *A. fabae cirsiiacanthoidis*, were placed close to a naturally established colony of *L. niger*. Within a few days of exposure, each aphid colony was visited by honeydew-collecting workers of this ant species. The trials were carried out during periods when ant activity was at a maximum at temperatures ranging between 18°C and 28°C. Four experiments with *L. cardui*, *T. angelicae*, and *A. fabae cirsiiacanthoidis* were performed to test the hypothesis that cuticular lipids on the surface of the parasitoid species were the major recognition cues for the ants.

Experiment 1: Introduction of Dead Parasitoids and Aphids. Living females of both parasitoid species (*L. cardui*: $N = 31$; *T. angelicae*: $N = 35$) were transferred singly in small glass tubes (1 cm diam., 3 cm high) and killed by freezing at −50°C for 2 min. After freezing, the dead parasitoids were kept at room temperature at least for 1 min before testing began. For the bioassay, a dead parasitoid was carefully placed into a leaf axil of the plant that was frequently passed by *L. niger* workers, without disturbing the foraging behavior of the ants. The same procedure was conducted with dead aphids of different developmental stages ($N = 39$). When encountering the test individual, the ants either ignored it or removed it from the plant. The ant that finally removed the individual was recorded.

Experiment 2: Introduction of Dead Hexane-Washed Parasitoids and Aphids. To test the significance of chemical stimuli on the surface of the parasitoids for triggering removal behavior of the ants, an organic solvent was used to wash off the epicuticular lipids of the test individuals (Gilby, 1980; Jackson and Blomquist, 1976; Lockey, 1988). Dead females of both parasitoid species previously killed by freezing were twice immersed in 250 μl hexane for 1 min each. Subsequently, the insects were transferred on filter paper and kept in the laboratory for 24 hr for drying. The next day, the hexane-washed parasitoids (*L. cardui*: $N = 22$; *T. angelicae*: $N = 21$) were tested by carefully placing an individual into a leaf axil of the aphids' host plant. The same procedure was carried out with dead hexane-washed aphids of different developmental stages ($N = 20$). The recording of the ants' behavior was the same as in experiment 1.

Experiment 3: Introduction of Dead Parasitoids Treated with Hexane Soak of Other Parasitoid Species. Freeze-killed females of *T. angelicae* and *L. cardui* were twice soaked in 250 μl hexane for 1 min each. The extract portions of one species were combined and kept for the subsequent transfer procedure. The hexane-washed individuals were allowed to air dry for about 5 min. Subsequently, conspecific individuals were placed into a glass vial and covered with the hexane soak of the other parasitoid species; that is, *T. angelicae* parasitoids ($N = 23$) received the hexane extract of *L. cardui*, while the *T. angelicae* extract was deposited on *L. cardui* parasitoids ($N = 22$). The solvent was removed under nitrogen, and as a result, the lipids should coat the test individuals. After the treatment, the test individuals were allowed to air dry for 24 hr at room temperature. To check whether the technique of transferring epicuticular lipids was successful, control experiments were conducted to demonstrate that the specific reaction of *L. niger* ants towards the parasitoid species did not change. For this purpose, control individuals (*L. cardui*: $N = 24$; *T. angelicae*: $N = 23$) were prepared by treating the washed parasitoids with the hexane soak of conspecific females. Each parasitoid lure was covered with the equivalent of an extract of three parasitoids either from conspecific females or from alien females. Preliminary experiments with lower cuticular lipid concentrations showed that the recovery of the lipids was too low to result in a clear behavioral response of the ants. The introduction of the parasitoid individuals into an aphid colony and the recording of the behavioral response of the ants followed experiment 1. Each lure was used only once in an experiment.

Experiment 4: Introduction of Dead Parasitoids Treated with Hexane Soak *of* A. fabae cirsiiacanthoidis. Freeze-killed unparasitized *A. fabae cirsiiacanthoidis* of different developmental stages were solvent-washed as explained for the parasitoids in experiment 3. The hexane soak of the aphids was applied on both hexane-washed *L. cardui* ($N = 20$) and *T. angelicae* ($N = 20$) females. As control individuals, washed aphids ($N = 22$) received their own extract. Each lure and control individual was covered with the equivalent of the extract of four aphids. After the transfer procedure, the insects were allowed to air dry for 24 hr at room temperature. The next day, the parasitoid lures and the aphid control were tested in the same way as described in experiment 1. Each lure was only used once in an experiment.

Statistical Analysis. The performance of a three-way table analysis with the factors species, treatment, and ant behavior resulted in a significant three-factor interaction term. In this case, according to Sokal and Rohlf (1981) we analyzed the data by employing separate two-way table tests of independence (chi^2 test, two-tailed) with the Yates' correction for continuity for small sample sizes (Sokal and Rohlf, 1981). Moreover, due to the small sample sizes of the test series, we pooled the removal events of the second and subsequent ants for each species and compared them with the respective number of removals by the first ant coming across the test individual.

RESULTS

Introduction of Dead Parasitoids and Aphids (Experiment 1). L. niger workers responded significantly different towards dead individuals of both parasitoid species and aphids. Figure 1 shows the distribution of *L. niger* ants that removed the test individuals. About 40% of *L. cardui* and 80% of *T. angelicae*

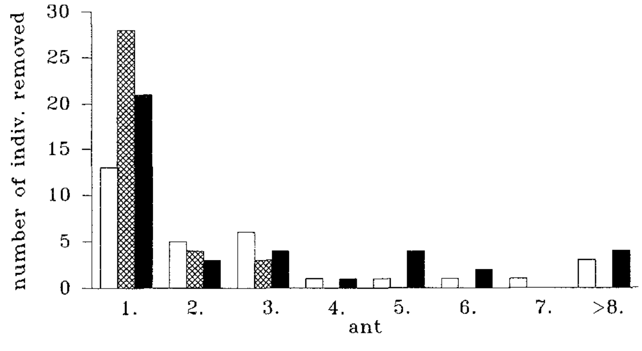

FIG. 1. Frequency distribution of the removal of dead nontreated test individuals by *Lasius niger* workers. Open bars: *Lysiphlebus cardui* ($N = 31$); cross-hatched bars: *Trioxys angelicae* ($N = 35$); shaded bars: *Aphis fabae cirsiiacanthoidis* ($N = 39$).

were seized by the first ant encountering the wasps (Figure 2); all *T. angelicae* individuals were finally removed by the third ant, in contrast to about 75% of *L. cardui* females. Half of the dead *A. fabae cirsiiacanthoidis* were immediately carried off by the ants after discovery. The response of *L. niger* workers towards dead individuals of both parasitoid species was significantly different when comparing the data of removal by the first ant to the pooled removal events of the subsequent ants ($\text{chi}^2 = 8.57$; $P = 0.003$; $N = 66$). In addition, ants showed also a significantly different response towards aphids and *T. angelicae* ($\text{chi}^2 = 4.53$; $P = 0.03$; $N = 74$). *L. cardui* females and aphids released a similar removal behavior in the ants ($\text{chi}^2 = 0.56$; $P = 0.45$; $N = 70$).

Introduction of Dead Hexane-Washed Parasitoids and Aphids (Experiment 2). Dead *L. cardui* and *T. angelicae* parasitoids immersed in hexane prior to the experiment induced similar removal reactions of *L. niger* workers (Figure 2, B: $\text{chi}^2 = 0.64$; $P = 0.425$; $N = 43$). Half of the *L. cardui* females and about one third of the *T. angelicae* females were taken by the first ant encountering the test individual. For *A. fabae cirsiiacanthoidis* only every fifth dead individual was removed by the first ant. The statistical analysis revealed no difference in ant behavior towards hexane-washed parasitoid species and aphids (*L. cardui–A. fabae cirsiiacanthoidis*: $\text{chi}^2 = 2.90$; $P = 0.09$; $N = 42$; *T. angelicae–A. fabae cirsiiacanthoidis*: $\text{chi}^2 = 0.37$; $P = 0.54$; $N = 41$).

A comparison of the results prior to solvent-washing and after the hexane treatment within a test group showed that *L. niger* workers displayed a similar

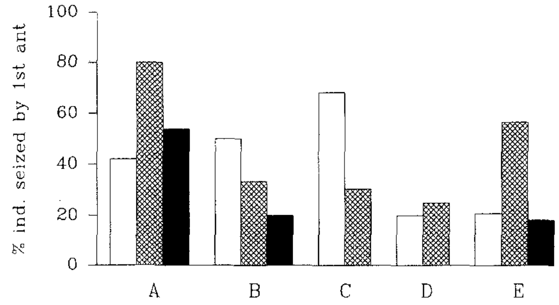

FIG. 2. Response of *Lasius niger* to nontreated and differently treated aphid parasitoids of *Lysiphlebus cardui* and *Trioxys angelicae*, and *Aphis fabae cirsiiacanthoidis*. The bars represent the proportions of test individuals that were removed by the first ant when encountering the individual in the aphid colony. (A) Nontreated; (B) hexane-washed; (C) treated with the hexane soak of the other parasitoid species; (D) treated with the hexane soak of *Aphis fabae cirsiiacanthoidis*; (E) control individuals (treated with the hexane soak of conspecifics). Open bars: *Lysiphlebus cardui*; cross-hatched bars: *Trioxys angelicae*; shaded bars: *Aphis fabae cirsiiacanthoidis*. Numbers of tested individuals were between 20 and 39 (for the exact numbers see Methods and Materials).

removal response when encountering dead *L. cardui* females in the aphid colony ($\mathrm{chi}^2 = 0.09$; $P = 0.76$; $N = 53$). By contrast, dead nontreated and solvent-washed *T. angelicae* individuals induced a significantly different reaction of the ants ($\mathrm{chi}^2 = 10.29$; $P = 0.0013$; $N = 56$). Similarily, the ants' response towards dead nontreated and hexane-washed individuals of *A. fabae cirsiiacanthoidis* differed significantly ($\mathrm{chi}^2 = 8.33$; $P = 0.004$; $N = 79$). This could probably be due to the release of alarm substances from the siphons when removing the live aphids with forceps from the colony before freezing. These signals could be still present on the siphons during the experiments, causing the first ant to remove the dead nontreated aphids immediately (Nault et al., 1976).

Introduction of Dead Parasitoids Treated with Hexane Soak of Other Parasitoid Species (Experiment 3). Control individuals of *L. cardui* (females treated with the hexane soak of conspecifics) were removed significantly less often by the first ant than control individuals of *T. angelicae* (Figure 2, E: $\mathrm{chi}^2 = 4.91$; $P = 0.03$; $N = 47$). Moreover, *L. niger* workers displayed a similar removal response towards nontreated and control individuals of both parasitoid species (Figure 2, A and E: *L. cardui*: $\mathrm{chi}^2 = 1.86$; $P = 0.17$; $N = 55$; *T. angelicae*: $\mathrm{chi}^2 = 2.65$; $P = 0.10$; $N = 58$). These results showed that the transfer of cuticular lipids was successful.

The behavior of *L. niger* workers differed significantly between *T. angelicae* and *L. cardui* females covered with the cuticular lipid extract of the other species ($\mathrm{chi}^2 = 4.99$; $P = 0.003$; $N = 45$). In almost 70% of the trials, *L. cardui* parasitoids treated with the hexane soak of *T. angelicae* induced an immediate removal by the first ant (Figure 2, C). This response did not significantly differ from the behavior the ants showed towards the *T. angelicae* control group ($\mathrm{chi}^2 = 0.25$; $P = 0.62$; $N = 45$). When encountering dead test individuals of *T. angelicae* with the solvent extract of *L. cardui* parasitoids, *L. niger* workers removed them with a similar probability as *L. cardui* control individuals (Figure 2, C: $\mathrm{chi}^2 = 0.18$; $P = 0.67$; $N = 47$).

Introduction of Dead Parasitoids Treated with Hexane Soak of A. fabae cirsiiacanthoidis *(Experiment 4).* When *A. fabae cirsiiacanthoidis* individuals treated with the solvent extract of conspecifics were offered in an aphid colony, foraging *L. niger* workers rarely responded immediately at discovery. Only a fifth of the tested individuals ($N = 22$) were removed by the first ant. However, a comparison of the ants' response to nontreated (experiment 1) and control individuals of *A. fabae cirsiiacanthoidis* revealed a significant difference (Figure 2, A and E: $\mathrm{chi}^2 = 6.00$; $P = 0.01$; $N = 61$). This result might be due to alarm substances present on the nontreated aphids (see explanation above). A possible contamination of test individuals with such alarm substances in the aphid hexane extract could be ruled out because these lures were dried for 24 hr, during which time these alarm substances should evaporate. *L. niger* responded to dead parasitoids of *L. cardui* ($N = 20$) and *T. angelicae* ($N = 20$)

treated with the hexane soak of *A. fabae cirsiiacanthoidis* (Figure 2, D) in a similar way. Eighty percent of the *L. cardui* lures and 75% of the *T. angelicae* lures were ignored by the discovering ant. The observations did not reveal any difference in the removal behavior of the ants towards the tested parasitoid individuals compared to the aphid control (*L. cardui–A. fabae cirsiiacanthoidis*: $\mathrm{chi}^2 = 0.0$; $P = 1.0$; $N = 42$; *T. angelicae–A. fabae cirsiiacanthoidis*: $\mathrm{chi}^2 = 0.03$; $P = 0.87$; $N = 42$).

DISCUSSION

To gain access to nests or to resources of social insects, predators and parasitoids may use several strategies. Morphological adaptations are used by myrmecophilous staphylinid beetles to integrate into ants' nests (Kistner, 1966, 1979). Behavioral mechanisms play a role in the beetle *Amphotis marginatus* Fabr. (Nitidulidae) begging for food from ants of the species *Lasius fuliginosus* (Latreille) (Hölldobler and Wilson, 1990). A similar behavior is also known from aphid parasitoids of the genus *Paralipsis* Förster (Aphidiidae) (Maneval, 1940; Takada and Hashimoto, 1985). In addition, chemical cues are involved in many inquilines of social insects either in using chemical secretions as appeasement and integrating substances (Hölldobler and Wilson, 1990) or in mimicking the specific cuticular lipid pattern of the host species (Howard et al., 1980, 1982, 1990a, b; Vander Meer and Wojcik, 1982; Vander Meer et al., 1989). Chemical mimicry was supposed to play a role in the relationship between the aphidiid wasp *L. cardui* and the ant *L. niger* in colonies of the aphid *A. fabae cirsiiacanthoidis* (Völkl and Mackauer, 1993). Völkl and Mackauer (1993) assumed that *L. cardui* mimics the cuticular lipid profile of its host aphid, thus being tolerated in the host colony by honeydew-collecting ants.

The present results demonstrate that recognition of *L. cardui* and *T. angelicae* parasitoids by ants is based on chemical cues located on the cuticular surface of the wasps. Dead nontreated *L. cardui* and *T. angelicae* offered in an aphid colony elicited a different removal response of the ants when being discovered (experiment 1). While *L. niger* workers rarely cared for dead *L. cardui* parasitoids in the aphid colony, dead *T. angelicae* individuals were readily removed by ants encountering them. This specific ants' reaction is comparable to that ants showed towards living parasitoids when searching in an aphid colony: *T. angelicae* females are immediately attacked by honeydew-collecting ants, while *L. cardui* wasps search unmolested for appropriate aphid hosts (Völkl and Mackauer, 1993). Moreover, the ants' removal response towards dead *L. cardui* resembled their response when encountering dead aphids in the colony. Consequently, ants were able to distinguish between dead individuals of the two parasitoid species, that is, the different searching behavior of the wasps is not the major cue for triggering aggressive reactions of *L. niger* ants.

The removal of the cuticular lipids from the surface of the parasitoids by immersion in an organic solvent (e.g., Gilby, 1980; Jackson and Blomquist, 1976; Lockey, 1988) resulted in an identical removal response of the ants when hexane-washed individuals of *L. cardui* and *T. angelicae* were offered (experiment 2). Consequently, *L. niger* ants could not discriminate between two aphidiid species when deprived of their species-specific lipid layer. Hexane-washed aphids also elicited a tolerant ant response. The significant difference in the behavior of the ants towards nontreated and hexane-washed *T. angelicae* suggests that these individuals lost their specific recognition cues after the solvent extraction, which obviously triggered the aggressive behavior of the ants. The hexane immersion of *L. cardui* individuals did not alter the response of *L. niger* compared to its reaction towards nontreated conspecific parasitoids. These findings also show that any possible morphological feature of the parasitoid species important for species recognition by the ants could be ruled out.

To confirm the presumption that chemical cues on the cuticular surface are responsible for the recognition of the parasitoids by *L. niger*, the lure experiments were conducted. The results showed that the cuticular lipids caused them to be ignored or removed by the ants. The transfer of *L. cardui* extract to individuals of *T. angelicae* had the effect that *L. niger* ants treated *T. angelicae* lures similar to *L. cardui* controls. The removal behavior of the ants towards *L. cardui* individuals covered with the hexane extract of *T. angelicae* also was in accordance with the results of the *T. angelicae* control. Similarily, the transfer of *A. fabae cirsiiacanthoidis* soak onto *L. cardui* and *T. angelicae* parasitoids caused the same response of *L. niger* as towards the aphid control.

The experiments confirm the hypothesis that the aphidiid wasp *L. cardui* uses chemical cues located on the cuticular surface to avoid attacks by aphid-guarding ants (Völkl and Mackauer, 1993). These recognition cues are hexane-soluble and can be artificially transferred to other nonconspecific parasitoids. Moreover, the almost identical removal behavior of *L. niger* workers towards dead aphids and *L. cardui* suggests that *L. cardui* mimics the cuticular lipid profile of its aphid host. The use of epicuticular lipids to escape attack is known from a number of inquilines of ants and termites (Howard et al., 1980, 1982, 1990a, b; Vander Meer and Wojcik, 1982; Vander Meer et al., 1989). Most of these intruders known by now mimic the cuticular hydrocarbon pattern of their host species. Another strategy to incorporate into a host's nest is by producing the typical fatty acid bouquet of the host. This could be demonstrated with the death's head hawkmoth, *Acherontia atropos* L. (Moritz et al., 1991). The detailed chemical background of the adaptation of *L. cardui* to avoid attacks from honeydew-collecting ants is still unknown. However, the cuticular lipids of the species involved in this aphid–ant–parasitoid system are already under chemical investigation to find out why *L. cardui* is chemically invisible to ants.

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