BIOLOGY AND DISTRIBUTION OF *AEDES ALBOPICTUS* AND *AEDES AEGYPTI* IN MADAGASCAR

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ABSTRACT. The biology and distribution of the 2 Malagasy *Stegomyia* species, *Aedes aegypti* and *Aedes albopictus*, is updated and reported. *Aedes aegypti* is present in the western and southern regions and *Ae. albopictus* in the east and on the high plateau. Some unusual locations are noted. The ranges of *Ae. albopictus* and *Ae. aegypti* on Madagascar overlap only slightly. *Aedes aegypti* is present in the west and in the south, while the *Ae. albopictus* distribution area is in the east and on the central high plateau. Climatic factors (number of dry months, annual rainfall and temperature), rather than competitive interactions, appear to be the major determinants of the distribution of these species. *Aedes aegypti* is just slightly anthropophilic, contrary to *Ae. albopictus*. Babanki virus and MMP 158 virus were isolated from *Ae. aegypti*; no virus has been isolated from *Ae. albopictus*.

INTRODUCTION

Madagascar, an island east of Africa, shows particularly diversified biotopes, ranging from humid tropical forest to subarid areas. Twenty-nine species of *Aedes* have been recorded, of which 13 are endemic. The subgenus *Stegomyia* is represented by *Ae. aegypti* (Linn.) and *Ae. albopictus* (Skuse). Although much data have been compiled about *Aedes aegypti* (Dégallier et al. 1988), and *Aedes albopictus* (Hawley 1988), these two species are still relatively unknown in Madagascar.

Within the framework of a survey on arbovirus diseases initiated by the Institute Pasteur in Madagascar, we visited numerous regions within various bioclimatic zones. During this survey, we studied the biology and distribution of these two major culicids. We show that they are generally allopatric and that their range expansions depend on bioclimatic factors.

Two different viruses were isolated from Malagasy *Ae. aegypti* and none from *Ae. albopictus*. It should be noted that yellow fever and dengue viruses have never been isolated in Madagascar. In contrast, dengue has been conspicuous in the neighboring islands and in East Africa for a decade. In the northwestern part of Madagascar, the detection of antibodies that inhibit hemagglutination in man appears to show that a serotype (probably dengue 1) may have circulated in this region in preceding years (Fontenille et al. 1988).

DISTRIBUTION

Figure 1 shows the distribution of *Aedes aegypti* and *Ae. albopictus* in Madagascar. "Unusual" localities are noted.

Figure 2 shows the different bioclimatic zones, with their main characteristics (Atlas de Madagascar 1969).

Table 1 shows the climatic parameters of the 2 "classical" areas of distribution for *Aedes aegypti* and *Ae. albopictus*.

There are 4 bioclimatic regions in Madagascar:

— On the east coast, the climate is subequatorial with rainfall exceeding 1,500 mm and sometimes 3,000 mm, with less than 2 ecologically dry months and high temperatures throughout the year. The vegetation is a mosaic of evergreen rainforest and secondary grass.

— On the plateau, the climate is tropical-humid. The rainfall still exceeds 1,500 mm with a dry season of 0 to 5 months and a mean temperature in the coldest month of between 10° and 15°C, except above 2,000 m where the mean temperature is near 5°C. Natural vegetation has nearly completely disappeared.

— On the western plain, the dry season lasts from 5 to 8 months. Rainfall is around 1,500 mm in the north, 500 to 1,500 mm in the south. Temperatures are high throughout the year. The vegetation is a mosaic of dry deciduous forests and grasslands.

— In the south, rainfall is sparse and highly irregular. The climate is semiarid. The natural vegetation is a dry thorn scrub.

BIOLOGY OF *AEDES ALBOPICTUS* IN MADAGASCAR

As noted by several authors, *Ae. albopictus* is abundant in all the localities within its distribution area. This species was found in Madagascar for the first time by Ventrillon in 1904.

Aedes albopictus is very anthropophilic and closely associated with man. In one area of Toamasina, in June 1983, the average biting rate of *Ae. albopictus* was 14 per man-hour between 1630 and 1830 hours. Ravaonjanahary (1978) recorded 100 bites per man per day during the

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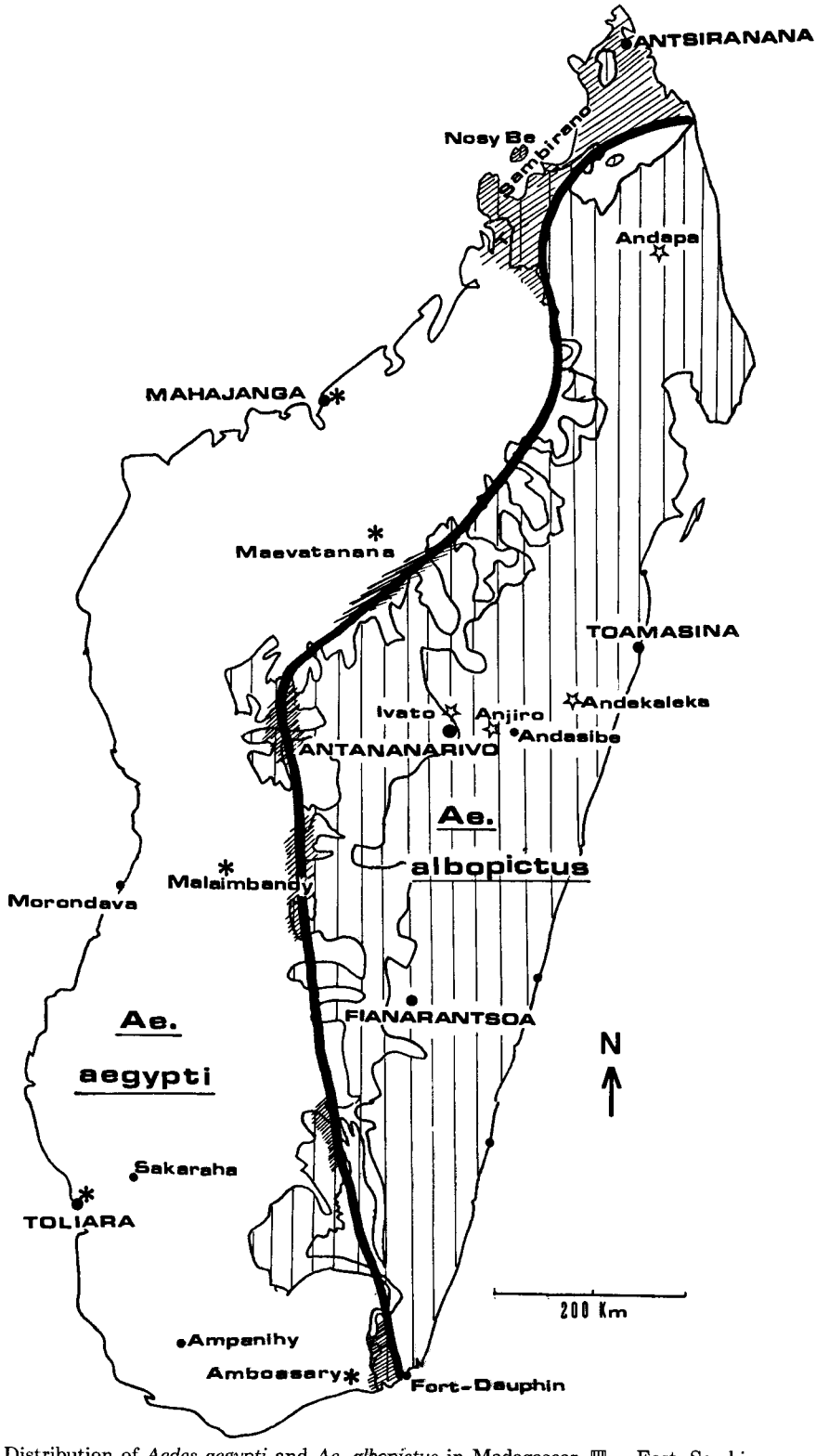

Fig. 1. Distribution of *Aedes aegypti* and *Ae. albopictus* in Madagascar. ▥ = East, Sambirano and Center regions; □ = West and South regions; Heavy black line = limit of the distribution between *Ae. aegypti* (West) and *Ae. albopictus* (East); ▨ = sympatric zones; ☆ = unusual locations of *Ae. aegypti*; * = unusual locations of *Ae. albopictus*.

wet season in Tsaramandroso (Mahajanga region). It is rare in natural forests. In the humid tropical forest near Andasibe, only 2 *Ae. albopictus* were captured on man out of 16,131 mosquitoes collected, of which 6,142 were *Aedes* species (surveys from 1982 to 1986). This species is mainly diurnal, usually biting in the late afternoon, but, in certain regions, it was captured while biting man during the night, e.g., in Nosy Be. In this region, it was possible to attract *Ae. albopictus* with *Lemur fulvus* as bait, but its attraction to lemurs seems to be low. A survey on artificial breeding places carried out in March 1984 in Tamatave revealed that the Breteau index for *Ae. albopictus* was 50, the "House" index was 45, and the "container" index was 22. On Nosy Be island in April 1986, the Breteau index was 47. These data show a high degree of urban colonization by this species. Shelters are primarily domestic and peridomestic (flower pots, tin cans, cans for water storage, used tires, cut bamboos, tree holes). This species is frequently found associated with *Culex quinquefasciatus* Say. Depending on the region, it was also found associated with *Culex carleti* Brunhes and Ravaonjanahary, *Cx. antennatus* (Becker), *Ae. aegypti, Uranotaenia* sp., *Cx.* (*Neoculex*) sp. and *Cx.* (*Culiciomyia*) sp. On the High Plateau we noticed that some habitats stay dry, with eggs remaining quiescent for more than 5 months. Eggs hatched at the first immersion.

Madagascar is the western range limit for this essentially Oriental species. It is likely that this species was introduced into Madagascar by man during immigration from Indonesia in the 12th or 13th century (Mattingly 1953).

Aedes albopictus was also found in the following five western and southern localities, away from its "classical" distribution zone (Fig. 1):

— It was found in Majunga, urban and surrounding areas as far as Tsaramandroso, 100 km southeast of Majunga. Larvae develop in tree holes, barrels, used tires and various containers (Rodhain et al. 1980);

— in Maevatanana, in February 1987, at 100 m altitude, (1,800 mm of annual rainfall with 5 to 6 dry months per year). The coldest month is July with an average temperature of 22°C. We caught this species on man;

— in Malaimbandy, in December 1986, at 150 m altitude. This area has 750 mm of rainfall annually, 7 dry months, average temperature of the coldest month is 22°C. Three adults of this species were caught among 113 mosquitoes;

— in Toliara, in 1978 and 1987, along the coast, (annual rain: 300 mm, 8 dry months, the average temperature of the coldest month is 20°C). This species has been found to colonize used tires;

— in Amboasary, in April 1984, two females among 3,110 mosquitoes, were captured on man in inhabited areas during the day. This region has a dry tropical climate (less than 600 mm of rain annually, 8 dry months).

In Madagascar, *Ae. albopictus* is not known to be a vector of any pathogenic agent. In 1976, Gubler and Rosen showed that among different strains of *Ae. albopictus* from 13 regions in the world, the Malagasy mosquito population from Antananarivo could be infected orally by four dengue serotypes. Tesh et al. (1976) also showed that this population was receptive to Chikungunya virus.

BIOLOGY OF *AEDES AEGYPTI* IN MADAGASCAR

Despite its major epidemiologic importance, there have been few attempts to study this mosquito in Madagascar[3,4]. *Aedes aegypti* exhibits substantially feral behavior. This species is represented everywhere by *Ae. aegypti formosus* (Walker) (dark, forest form). This mosquito seems to show few anthropophilic tendencies, except in southern regions where a more domestic behavior is observed. In the Ampijoroa native forest, over 15,163 mosquitoes were captured (from 1982 to 1987); among them 9,553 *Aedes* of which 304 were *Ae. aegypti* (3.2% of *Aedes*). *Aedes aegypti* was less frequently captured when attracted with *Lemur fulvus* as bait. In the surrounding villages, one *Ae. aegypti* per man-hour was the average capture during favorable hours at the end of the day. However, when bamboo ovitraps were installed in the forest, more than 50% of them were colonized by this species. Similar results were obtained from more than 15,497 mosquitoes in the Morondava region: only 295 *Ae. aegypti* were captured on man out of a total of 10,185 *Aedes*. These data reveal the low anthropophily of this species in western Madagascar. Capture of this mosquito was less frequent after sunset.

Surveys carried out in the south of Madagascar by us and other authors showed that this species is more domestic in the south than in the west or in the north. Its behavior is close to the African form which evolved to become do-

[3] Brunhes, J. and C. Ravaonjanahary. 1969. Enquête sur la répartition et la sensibilité aux insecticides d'*Anopheles funestus* et sur la répartition d'*Aedes aegypti*. Doc. ORSTOM Tananarive, 14 p. (unpublished report).

[4] Subra, R. and C. Ravaonjanahary. 1973. Répartition et fréquence d'*Aedes aegypti* Linné 1762 à Madagascar. Enquêtes de saison sèche dans le Moyen-Ouest, le Nord-Ouest et le Sud. Doc. Centre ORSTOM Tananarive, 25 p. (unpublished report).

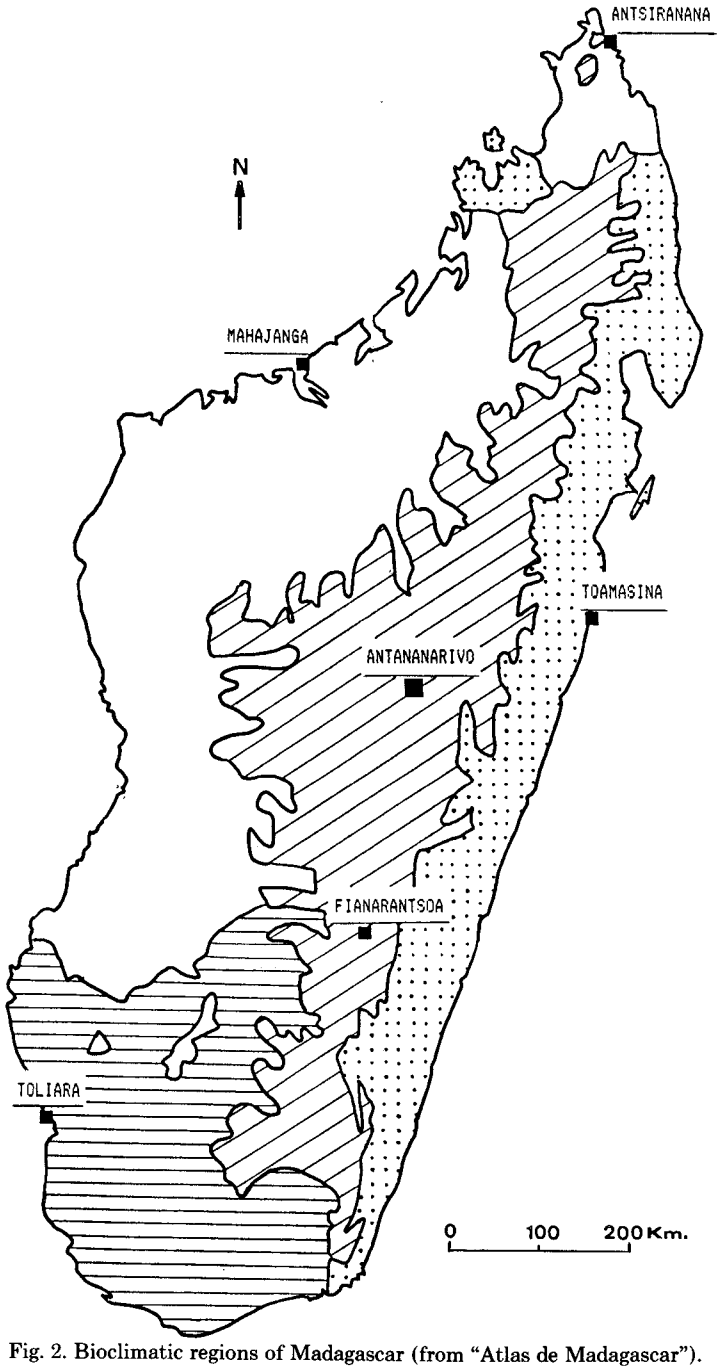

Fig. 2. Bioclimatic regions of Madagascar (from "Atlas de Madagascar").

	Climate type	Rainfall (mm)	Average temp. coldest month	No. of dry months
▩	Tropical-humid (altitude < 900 m)	R > 1,500	t > 15°C	0–2
▨	Tropical-altitude (altitude > 900 m)	R > 1,500	5° < t < 15°C	0–5
□	Tropical dry	2,000 > R > 500	t > 20°C	5–8
▤	Semiarid	800 > R > 400	t > 20°C	8–9

Table 1. Climatic parameters of *Aedes aegypti* and *Ae. albopictus* zones in Madagascar.

Parameter	Zones with *Ae. aegypti*	Zones with *Ae. albopictus*
Geographic regions	West and South Madagascar	Central High Plateau and Eastern region
Maximum altitude	900 m	1,500 m
No. of dry months	0–9	usually < to 6
Rainfall	<2,000 mm	usually > 1,000
Average temperature of the coldest month	>18°C	>12°C

mestic and more susceptible to yellow fever virus (Rodhain 1983, Powell 1985). In April 1987, we captured an average of 5.3 *Ae. aegypti* per man-hour at the end of the day in Sakaraha village. Bamboo ovitraps left for 15 days were all colonized. This was previously noted in similar research carried out in 1983 at Ampanihy. In April 1984, we captured 1,264 *Ae. aegypti* on man in the native Amboasary forest, of which 43 were captured at night. This species represented 40.7% of total captures.

Depending on the strain origin, colonization of this species varies in difficulty. Specimens from the forest settlement at Ampijoroa and Morondava were hard to establish as breeding groups. Fecundity is low and mortality is high. Moreover, they fed poorly on guinea pigs and even less on man. In contrast, the urban specimens from Sakaraha were easily colonized.

Aedes aegypti was found away from its classical distribution zone 4 times: on the High Plateau near Antananarivo, where a small colony appears to remain in Ivato; near Andapa, in Anjiro and in Andekaleka, near the east coast (Fig. 1). This phenomenon has been discussed elsewhere (Fontenille 1986).

In March 1985, we isolated MMP 158 virus from specimens captured in undisturbed forests near Morondava. This virus was isolated for the first time in Kenya in 1968 (East Africa Virus Research Institute) and was later found again in Sudan and Uganda. Its pathogenicity for man is not known.

A current survey carried out by the Institute Pasteur in Paris shows that the Morondava population of *Ae. aegypti* is susceptible to dengue 2 and dengue 4 viruses. No test has been carried out for yellow fever virus.

In March 1988, one strain of Babanki virus (Alphavirus) was isolated from 17 specimens caught on man, in Anjiro.

DISCUSSION

Aedes aegypti and *Ae. albopictus* live together elsewhere, and larval competition between the two species occurs, generally in favor of *Ae. aegypti* (Surtees 1966, Gilotra et al. 1967, Moore and Fisher 1969). Although this theory is not accepted by all (Chan et al. 1971), several authors noted that in sympatric zones, particularly in southeast Asia, fecundity of *Ae. aegypti* is higher, mortality is lower and development is more rapid. Some factors may be dependent on metabolites such as the Growth Retardant Factor (Moore and Whitacre 1972, Dye 1984). In contrast, *Ae. albopictus* appears to have replaced *Ae. aegypti* in Hawaii (World Health Organization 1986).

In Madagascar, the situation varies and competition seems less important. As shown above, the distribution of each species is closely related to rainfall and temperature. This is demonstrated by the occurrence of *Ae. albopictus* in the Sambirano enclave region (Nosy Be), which has a climate similar to that of the eastern region. In Madagascar, the preferred habitat of the two species differs. Some habitat characteristics are undoubtedly more important than others. Some factors that may limit the distribution of each species are:

Annual rainfall. High rainfall would not be expected to limit the distribution of species with aquatic larvae, unless larval habitats are flushed by hard rains. We have no evidence that such flushing occurs for either species. Therefore, the east, with rainfall all the year long, would be favorable for the two species. In contrast, the west with less than 1 m annual rainfall may be too dry for *Ae. albopictus*, which is only present in particular habitats such as tires or domestic containers.

Number of dry months. So far, *Ae. albopictus* occurs in regions with 0 to 6 dry months in a year, while *Ae. aegypti* can endure 9 dry months in the year, although this species does not develop in regions with less than 5 dry months (except in Sambirano enclave with only 3 dry months). The number of dry months corresponds the period in which natural larval habitats dry up. However, it is worth noting that during the rainy season, in the dry regions, the drying of larval habitats is very short. Nevertheless, we observe continuous breeding of *Ae. aegypti*. In our insectarium (26°C and 80% RH), only 4 to 8 days of drying, is enough for the hatching of the eggs of the Malagasy strains.

Temperature of the coldest month. The coldest months occur during the "dry season" (May–October), and the eggs are in dry places. Temperature dropping below 8°C may not affect the survival of these lasting eggs. In general, *Ae. aegypti* is not found in regions with a minimal monthly average temperature less than 18°C, and for *Ae. albopictus* less than 12°C. No *Ae. albopictus* adults were observed when the monthly average temperature was below 16°C.

Annual average temperature. Although the west is generally hotter than the east, *Ae. aegypti* also occurs in regions that are colder than areas in which *Ae. albopictus* occurs. Thus, average annual temperature does not appear to limit the distribution of either species.

Altitude. Aedes aegypti is not usually found above 900 m nor *Ae. albopictus* above 1,500 m.

Thus, in Madagascar, the major factors affecting the distribution of these species are:

For *Ae. aegypti*:
— Mean temperature of the coldest month must be at least 18°C.
— The dry season should last no longer than 3 months.
— Annual rainfall of no more than 1,400 mm [although in Cameroon, *Ae. aegypti* is present in areas with annual rainfall more than 1,500 mm (Rickenbach and Button 1977)].

For *Ae. albopictus*:
— Temperature of coldest months no less than 12°C.
— A dry season no longer than 6 months.
— At least one meter annual rainfall [but this species was found in an area of Pakistan with a mean annual rainfall of 460 mm (Qutubuddin 1960)].

It is noted that these species do occur sympatrically in parts of Madagascar. The two species may coexist and share habitats in forest areas and villages, particularly in tree holes (*Mangifera indica*). No field or laboratory survey has been carried out in order to determine whether one of the two species dominates the other in these regions.

Unusual presence of *Ae. aegypti* on the east coast results either from accidental introduction of noncolonizing individuals (e.g., adults carried in vehicles) or from new and very small populations, as in Ivato and Anjiro, where we found adults at an interval of several months.

In contrast, the presence of *Ae. albopictus* on the west coast and in the south, particularly in Toliara and Mahajanga, reveals that this species could find suitable conditions, although far from preferred habitats (Toliara: 8 dry months, 300 mm annual rainfall). This species develops in very particular breeding places (tires in Toliara and various peridomestic habitats in Mahajanga). As far as we know, this species has not been reported in these regions before 1978[5], (Ravaonjanahary 1978). Further surveys in the coming years should reveal whether this species is really expanding its range on Madagascar.

CONCLUSIONS

Although *Ae. albopictus* and *Ae. aegypti* seem to be little involved in arbovirus cycles, their presence could become a problem. Study of these species is of greater interest since *Ae. albopictus* is expanding its range throughout the world, particularly in the USA and Brazil, and more and more regions surrounding Madagascar suffer from dengue.

Several field surveys enabled us to clarify the distribution of the two species. *Aedes albopictus* is mostly localized in the eastern and central regions, *Ae. aegypti* in the west and in the south. Their areas of distribution perfectly coincide with large climatic domains; sympatry zones are localized at the limit of the domains. Thus, we believe that the observed allopatric distribution of the two species is dependent on restrictive abiotic factors and probably not on competition.

[5] Coulanges, P., et al. 1978. Rapport définitif sur une mission épidémiologique sur les arbovirus à Madagascar (Province de Tuléar, Mars-Avril 1978), Doc. Institut Pasteur de Paris (Ecologie virale) (unpublished report).

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