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Evidence for a differentiated chromosomal race north of classical south European refuge areas in the garden dormouse *Eliomys quercinus*

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Abstract The dormouse *Eliomys quercinus* is a forest rodent undergoing long periods of winter hibernation. The species presents a surprisingly large diversity of chromosomal races, which geographic distribution was shown recently to predate the Pleistocene glaciations. Previously reported data on the karyotypes of the garden dormouse in France come from the northeast of the country, where the 2N=50 race occurs. New data are presented from specimens trapped near the Atlantic coast (departments of Vendée and Charente-Maritime), in the Pyrenees, the Alps and in the Massif Central. The French Alpine chain, close to the Italian border, is inhabited by the 2N=54 race. A karyotype with 2N=48 chromosomes, of Iberian type, is found north of the Pyrenees, near the central Atlantic coast and also in the south of the Massif Central, whereas the 2N=50 race occurs in the north of the massif. A hybrid between these two races (2N=49) was found in Vendée. These facts reveal that neither the Pyrenees nor the Alps constitute a biogeographic barrier to the dormouse and strongly suggest that the present population of northern France derives from a postglacial recolonisation movement initiated in the southernmost regions of France or in the Rhône valley.

Keywords Garden dormouse · France · Distribution · Karyotypes · Hybridization

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Introduction

The postglacial recolonisation patterns of forest rodents have been extensively studied in recent years (Deffontaine et al. 2005; Michaux et al. 1998, 2004; Nieberding et al. 2005). These studies demonstrated that most rodents survived the cold periods of the Quaternary in temperate southern refuges including Spain, Italy and the Balkans. This pattern may not be applicable to species displaying winter hibernation, and increased tolerance to cold temperatures, for which more northerly refuge areas might be expected. The garden dormouse (*Eliomys quercinus*) is a useful model species to test this hypothesis, sharing an ecological niche with rodents for which data are available, but having extensive periods of winter hibernation. Moreover, it has been previously shown that this species exhibits allopatric differentiated karyotypic races (Cristaldi and Canipari 1976; Filippucci et al. 1988b; Zima et al. 1994). The differentiation of these karyotypic races predates the Quaternary period and likely took place about 4 million years ago (Perez et al. 2012). During the Pliocene period, a rather warm climate prevailed in Europe (Fauquette et al. 1998), and the *Eliomys* genus was well distributed in Spain, in southern France, in Greece (Kowalski 2001), in northern Italy (Verona: Sala 1996) and in Sardinia (Kotsakis 1986). Thus, the dormouse chromosomal races were confronted to the contrasted climatic conditions that started with the Quaternary period.

This dormouse is currently found in forests of pine, larch and oak and in mixed coniferous and deciduous woods, orchards, vineyards, parks and villages, from sea level to the upper tree limit (currently to 2,300 m in the Alps or the Pyrenees, but still higher in southern Spain or Morocco at 2,500 and 2,800 m, respectively). It also lives in Mediterranean scrub, if not too dense, and utilises stony or rocky environments, colonising old buildings, ruins, dry stone walls as well as mountain boulders, karstic habitats, old quarries or cliffs. Some populations live in forested sand dunes (Marismas del Guadalquivir; northern Belgium). Throughout its distribution, it is found in close proximity to humans, in farms, huts, storehouses or attics (after Ognev 1963; Storch 1978 and personal observation).

The systematics of the genus *Eliomys* is still a question of debate and long-standing conflicting opinions. No less than 28 names have been proposed since 1766 (Holden 1993), and Miller (1912) recognised five extant species in Europe alone, whereas Ellerman and Morrison-Scott (1951) reduce the number of species to two: *E. quercinus* from Europe and north Africa and *Eliomys melanurus* from "south-west Asia" (i.e. the near-east). More recently, various authors have considered that a single species, formed by three distinct lineages, or subspecies, is present in Europe: the "*quercinus*", "*lusitanicus*" and "*melanurus*" lineages (Corbet 1978; Kahmann and Thoms 1981; Niethammer 1959; Storch 1978). These lineages are distinguished on the basis of the coloration pattern of the tail. However, this viewpoint is not universally accepted (Nadachowski et al. 1978; Nader et al. 1982). From karyological analyses and electrophoretical comparisons, Filippucci et al. (1988a, c) concluded that two distinct species existed, i. e. *E. quercinus* in Europe, including the Mediterranean islands, and *E. melanurus* in northern Africa (N=46 chromosomes) and the near-east (N=48 chromosomes).

Krystufek and Kraft (1997) collected skull samples throughout the north African, near-eastern and west European parts of the distribution of the dormouse and concluded that animals from the near-east are distinct from all the other ones. The border between *quercinus*' and *melanurus*' distribution ranges lies somewhere in Libya, between Cyrenaica and Tripolitana. Therefore, the *Eliomys* genus contains two species, but the question of their African distribution is still under debate.

The existence of different morphotypes and cytotypes in the European garden dormouse has long been recognised. However, as cytological studies progressed, it became evident that these morphotypes did not fully correspond to the karyological characteristics (Cristaldi and Canipari 1976; Krystufek and Kraft 1997).

In Europe, four chromosomal races have been found. One, with 2N=48 is distributed in the Iberian peninsula, central and southern Italy, Croatia (Vujosevic et al. 1993), Romania (Murariu et al. 1985), Russia (Graphodatsky and Fokin 1993) and the western Mediterranean islands, except Sardinia. The animals with 50 chromosomes are distributed from north-eastern France to Germany, Austria and Czech Republic and are present in Sardinia (Cristaldi and Canipari 1976; Zima et al. 1994, 1997). A Swiss form with 2N=52 was first reported by Matthey and Renaud (1937) and its presence confirmed later by Renaud (1938). Unfortunately, the location of the capture site (s) of the specimens analysed was not given. However, it seems that Renaud trapped small rodents in the "district de Lausanne" (*op. cit*., p. 350). Later, this form has been found in the Alps, from the Valle d'Aosta to the eastern part of the chain (Cristaldi and Canipari 1976; Filippucci et al. 1988b; Ramalhinho and Libois 2005). Another form with 2N=54 ranges from Liguria, near the Mediterranean coast, to the Valle d'Aosta and the upper Rhône valley (Cristaldi and Canipari 1976; Filippucci et al. 1988b; Zima et al. 1994).

Until now, there have been no reports of contact or hybrid zones between these different races, with the exception of the region of the Gran Paradiso where Cristaldi and Canipari (1976) observed the sympatry of both Alpine forms (52 and 54 chromosomes).

Surprisingly, in France the few data published have all reported a diploid number of 2N=50 chromosomes, except in Corsica where it is 48 (Italian race; Table 1; Orsini 1987). However, all the animals studied were trapped in the central and north-eastern part of the country, where a diploid number of 50 would be expected given the distribution of this chromosomal race in neighbouring countries (Fig. 1). No analysis has been done on dormice living either on the northern slopes of the Pyrenees nor in the French part of the Alpine massif, i.e. in the vicinity of other chromosomal races.

Recently, the postglacial recolonisation of Western Europe has been studied in several species, showing the significance of the Alps and of the Pyrenees on their phylogeographical pattern (Hewitt 1999; Michaux et al. 1998; Taberlet et al. 1998). This paper presents new information on the French distribution of *Eliomys* chromosomal races and discusses the role of these mountain chains as biogeographical barriers.

Methods

Animals were live trapped in LFA Sherman traps (7.5×8.9×22.9 cm) baited with a sardine and flour mixture in southern France, from the Atlantic coast to the Alps, and cytologically analysed. Microscope slides for observation of the chromosomes in somatic metaphases were prepared by direct treatment of the bone marrow (Baker et al. 1982). The G banding was obtained using Seabright's technique (1971). The diploid number (2N) and the morphological chromosome characteristics were analysed using a Leica Q500 image analyser and Leica Chantal and Qwin software.

Table 1 Localities and geographical coordinates of the dormice in France and the neighbouring regions

Figure 1	Country	Department/province	Locality	Latitude	Longitude	2N =	Number of animals F (female); M (male)	References
	Literature							
A	France	Corsica	Not mentioned	?	?	48	1	Orsini 1987
B	Spain	Catalonia	Figueras	42.27	2.96	48	15	Filippucci and Kotsakis 1994
C	Spain	?	Pyrenees	?	?	48	8 F, 6 M	Arroyo-Nombela et al.1982
D	France	Rhône	Region of Lyon	45.77	4.83	50	2 F, 1 M	Arroyo-Nombela et al.1982
E	France	Loiret	Not mentioned	?	?	50	?	Dutrillaux et al. 1979
F	Belgium	?	Not mentioned	?	?	50	?	Léonard et al. 1970
G	Germany	Rheinland- Pfalz	Koblenz	50.35	7.55	50	4	Filippucci and Kotsakis 1994
H	Germany	Hesse	Frankfurt	50.09	8.6	50	1	Filippucci (in litt.)
I	Germany	Baden Wurttemberg	Hinterzarten	47.91	8.1	50	1	Filippucci et al. 1990
J	France	Doubs	Besançon	47.24	6.00	50	1 M, 1 F	Filippucci et al. 1990
K	Switzerland	Vaud	Bassin	46.47	6.23	50	1 F	Filippucci et al. 1990
L	Switzerland	Vaud	Arziers	46.46	6.03	50	1 M	Filippucci et al. 1990
M	Switzerland	Vaud	"Lausanne"	46.55	6.65	52	7 M	Renaud 1938
N	Italy	Valle d'Aosta	Grivola/Valnontey	45.6	7.3	52	1 F, 1 M	Cristaldi and Canipari 1976
O	Switzerland	Valais	Ayer	46.18	7.6	54	1 F	Filippucci et al. 1990
P	Switzerland	Valais	Sembrancher	46.08	7.15	54	2 F, 1 M	Filippucci et al. 1990
Q	Italy	Valle d'Aosta	Dolonne/Entrèves	45.8	6.96	54	1 F, 1 M	Filippucci et al. 1988b
R	Italy	Valle d'Aosta	Grivola/Valnontey	45.6	7.3	54	2 F	Cristaldi and Canipari 1976
S	Italy	Liguria	Trioria	43.99	7.77	54	8 F, 2 M	Filippucci et al. 1988b
	This study							Date of capture
1	France	Pyrénées-Orientales	Les Angles (Bouillouses)	42.559	2.016	48	8 F, 3 M	June 19, 2000
2	France	Lozère	Mas-Saint-Chély	44.309	3.396	48	1 M	September 10, 2000
3	France	Charente-Maritime	Saint-Dizan-du-Gua	45.417	−0.729	48	1 F	July 1, 1999
4	France	Charente-Maritime	Salles-sur-Mer	46.104	−1.052	48	1	December 15, 1998
5	France	Vendée	Le Poiré-sur-Velluire	46.412	−0.896	48	1 F	June 1, 1998
6	France	Vendée	Saint-Benoist-sur-Mer	46.424	−1.357	48	1 M	October 5, 2000
7	France	Vendée	Lairoux	46.45	−1.267	49	1 F	October 7, 2000
8	France	Puy de Dôme	Manson	45.744	3.013	50	1 F	July 1, 2000
9	France	Loiret	Chilleurs-Aux-Bois	48.071	2.133	50	1 F	2003
10	France	Calvados	Saint-Philbert des Champs	49.209	0.282	50	1 M	October 8, 2000
11	Belgium	Hainaut	Manage	50.498	4.237	50	1 M	March 22, 2003
12	France	Meurthe et Moselle	Neuves-Maisons	48.615	6.104	50	1 F	2002
13	Italy	Valle d'Aosta	Antey Saint André	45.834	7.600	54	1 M	September 28, 2010
14	France	Savoie		45.667	6.773	54	1 F, 1 M	August 5, 2000

Table 1 (continued)

Figure1	Country	Department/province	Locality	Latitude	Longitude	2N =	Number of animals F (female); M (male)	References
			Bourg Saint-Maurice (Bettex)					
15	France	Hautes-Alpes	Névache (Vallée étroite)	45.053	6.657	54	1 F	August 3, 2000
16	France	Hautes-Alpes	Névache	45.026	6.658	54	3 F	August 3, 2000
17	France	Hautes-Alpes	La Chapelle-en-Valgaudemar	44.838	6.286	54	1 M	August 13, 2002
18	France	Hautes-Alpes	Le Saix	44.466	5.835	54	2 F	August 14, 2002
19	France	Alpes-Hte-Provence	Sainte-Anne la Condamine	44.469	6.718	54	1 F	August 1, 2000
20	Italy	Cuneo	Pietraporzio	44.332	7.030	54	1 M	August 2, 2000

The karyotype is mentioned based on the literature (letters from A to S) and on the present study (digits from 1 to 20)

Results

The location of the capture sites, the number of animals and their diploid number are presented in Table 1 and mapped in Fig. 1. Four different chromosomal races were observed in the garden dormice trapped in France.

The 25 Pyrenean animals (Table 1), one from Lozère (Causse Méjean) and those living near the Atlantic coast in the departments of Charente-Maritime and Vendée, were all characterised by a 48-chromosome karyotype. This was composed of four pairs of large-sized subtelocentric, eight pairs of metacentric, ten pairs of submetacentric and one pair of acrocentric chromosomes, where the X chromosome is a large metacentric and Y is punctiform (Iberian race) (Arroyo-Nombela et al. 1982; Diaz de la Guardia and Ruiz-Girela 1979). In contrast, the "Italian" race, as found in Corsica, also has 2N=48, but is characterised by three pairs of acrocentric autosomes (Cristaldi and Canipari 1976; Filippucci et al. 1988b; Gornung et al. 2010; Vujosevic et al. 1993).

A diploid number of 50 is found in one animal from Normandy, in another from Lorraine (near Nancy), a third from near Orléans and in a fourth from the Massif Central, near Clermont-Ferrand. The karyotype is the same as above, but with two more pairs of acrocentric chromosomes in place of one pair of submetacentric (Arroyo-Nombela et al. 1982; Filippucci et al. 1990; Leonard et al. 1970).

All the animals trapped in the Alps, between the Mont Blanc massif and the Mediterranean coast, had a diploid number of 54 chromosomes (south Alpine race). Their karyotype is composed of four pairs of large subtelocentric, seven pairs of metacentric, eight pairs of submetacentric and seven pairs of acrocentric chromosomes. The same chromosomal pattern was observed by Cristaldi and Canipari (1976) and Filippucci et al. (1988b).

A female from Lairoux (Vendée) had a karyotype of 2N=49 chromosomes (Fig. 2). Its autosomes comprised four pairs of large subtelocentric, eight pairs of metacentric, nine pairs of submetacentric, one pair of acrocentric chromosomes and three unpaired chromosomes: one submetacentric (A in Fig. 2) and two acrocentric ones (B and C in Fig. 2). These latter had a banding pattern corresponding clearly to each of the arms of the unpaired submetacentric chromosome.

Discussion and conclusions

The occurrence of the south Alpine race (2N=54) on the Italian slopes of the western Alps has already been demonstrated by Cristaldi and Canipari (1976) and Filippucci et al. (1988b). The present data show that its French distribution corresponds to the Italian one, extending at least from the

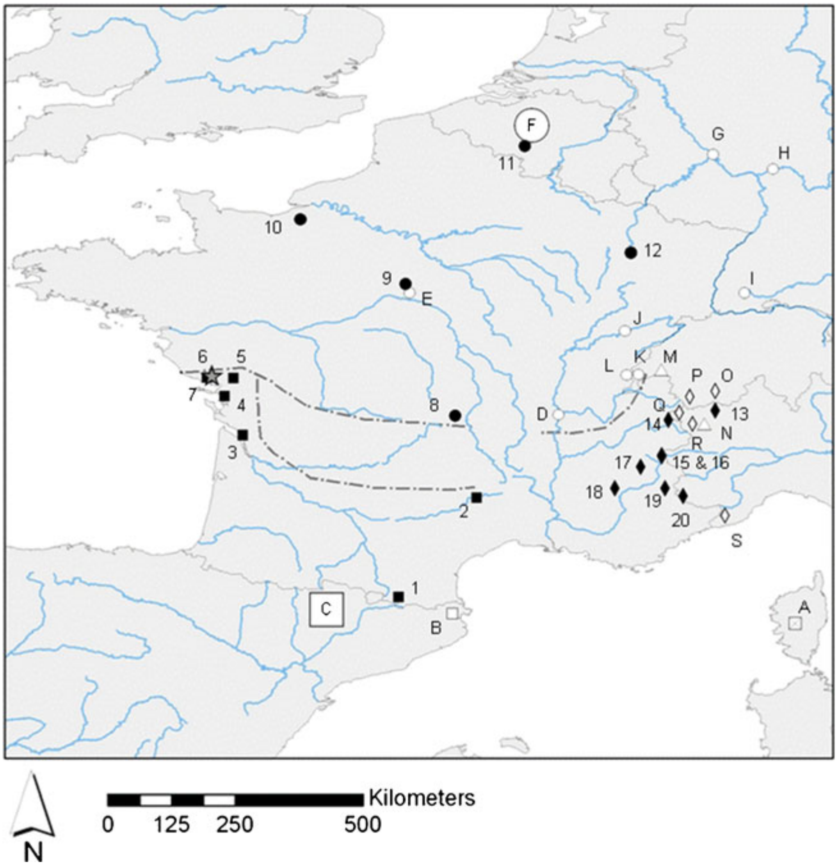

Fig. 1 Distribution of the chromosomic races of the garden dormouse, *E. quercinus*, in France and in neighbouring countries. Race with 48 chromosomes "Iberian" (*squares*), race with 48 chromosomes "Italian" (*cross inside a square*) (Corsica), race with 50 chromosomes (*circles*), race with 52 chromosomes (*triangles*) and race with 54 chromosomes (*diamonds*). The *grey star* indicates where the hybrid dormouse was trapped. *Symbols in grey*, data from the literature; in *plain*, data from this study. The *large symbols* refer to an imprecise sampling location (see Table 1). The *broken lines* tentatively delimit the hybrid zone (see main text). Please refer to Table 1 for digit vs letter numbers

Massif of Mont Blanc to Mercantour, along the Italian border and from the Italian border to the south-western part of the department of Hautes-Alpes. Our data from the French side of the Alps, reported here for the first time, suggest that the Alps do not act as a biogeographic barrier for the dormouse, although more data from the western extension of the south Alpine race are needed.

Similarly, the presence of animals with an "Iberian" karyotype seems well established, not only along the Atlantic coast up to La Rochelle but also in the southern part of the Massif Central. Therefore, it may be assumed that the present populations of south-western France might have survived in situ (Kowalski 2001). Alternatively, these populations may be derived from a postglacial recolonisation movement initiated either in the Iberian Peninsula or more probably from the Mediterranean coast or the Basque region in southern France, where some deciduous forests remained, even during the most severe frosts of the last glaciation

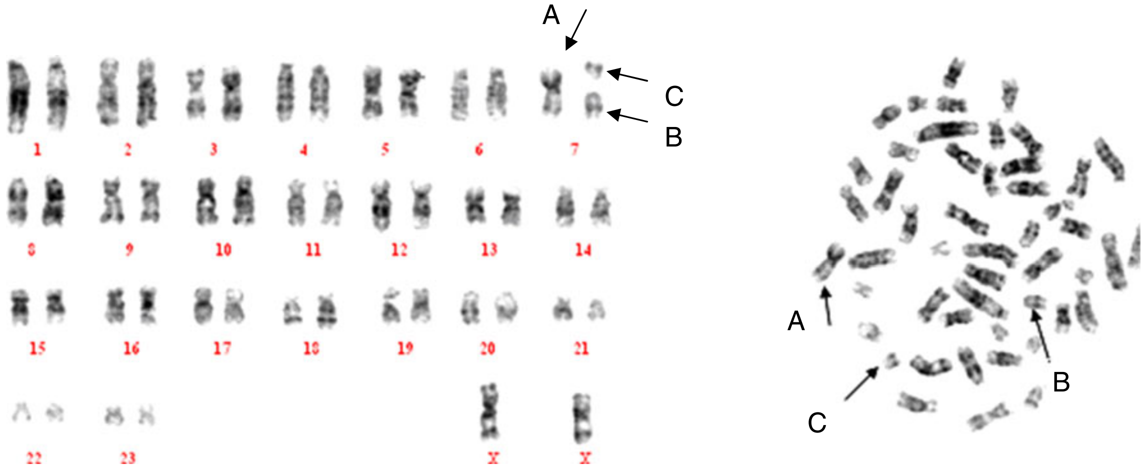

Fig. 2 Metaphase chromosomes and G-banded karyotype from a female 2N=49. Hybride from Lairoux (Vendée). The chromosomes are numbered according to the morphology of 2N=48 and 2N=50. One of the chromosomes (*7*) has fissioned originating from two acrocentrics

(Antoine et al. 1999; Blondel 1995). Indeed, fossil garden dormouse remains have been found throughout the Middle and Upper Pleistocene in Spain and in southern France (Chaline 1972; Kowalski 2001; Lopez-Garcia et al. 2007). In other forest rodents, the Pyrenees did not constitute a biogeographical barrier, either when they moved from the south to north (*Apodemus sylvaticus*: Michaux et al. 2003; *Myodes glareolus*: Deffontaine et al. 2005) or from north to south (*Apodemus flavicollis*: Michaux et al. 2004).

The female from Lairoux (2N=49) is a hybrid animal between the chromosomal races 2N=48 (Iberian) and 2N=50. This is the first time that a hybrid between two chromosomal races of the garden dormouse has been reported. The existence of fertile hybrids between chromosomal races was reported in several other species including the house mouse (*Mus domesticus*) in Madeira (Britton-Davidian et al. 2007), *Mus minutoides* in South Africa (Veyrunes et al. 2010) and the common shrew (*Sorex araneus*) in Siberia (Polyakov et al. 2011). The existence of a hybrid with 2N=49 shows that the two races 2N=50 and 2N=48 can interbreed. The race 2N=50 therefore probably results from a single Robertsonian rearrangement involving a submetacentric chromosome of a 2N=48 Iberian karyotype. The enzymatic data of Filippucci et al. (1988c) similarly suggest that the Iberian race 2N=48 is more closely related to the 2N=50 race than to the Italian race 2N=48. However, the western mtDNA (*cytb*) lineage (2N=50) is closer to the Alpine lineages than to the Iberian one (Perez et al. 2012).

The presence in Lairoux of an animal with 2N=49 chromosomes indicates that a hybrid zone exists in the south of the department of Vendée, i.e. that some populations of garden dormice with 2N=50 (northern race) must live in the vicinity. Extrapolating the geographical data so far obtained, it seems that the northern race reaches the south of Vendée and continues approximately from Niort to Limoges, Clermont-Ferrand and Lyon, as defined by the upper line in Fig. 1. On the other hand, the Iberian race extends at least to southern Vendée, and south of a line running roughly from Niort to Bergerac, Cahors, Rodez and Florac (as defined by the lower line in Fig. 1). There is thus support for the existence of a hybrid zone situated between these two lines.

The northern race of garden dormouse is currently located north of the 46th parallel where tundra, a hostile environment for the species, predominated during the last ice age (Blondel 1995). Similarly, the dormouse was probably absent from central Europe from Early Pleistocene to the Holocene and recolonised these regions recently during the sub-boreal time (4000–2800 BP) (Horacek 1986). Thus, the northern race of garden dormouse probably recolonised this region from central and northern France, during the Holocene. Although some chromosomal rearrangements may occur on a short time scale, as was shown in the mouse *M. domesticus* (Britton-Davidian et al. 2000), the dormouse chromosomal races match the mtDNA genetic lineages that differentiated long before the Quaternary glaciations, about 4.2±1 Myr ago (Perez et al. 2012). Therefore, *E. quercinus* does not show a pattern of postglacial recolonisation of northwestern Europe from the refuge populations in Iberia or Italy. During the last ice age, the northern race may have been repelled by the Iberian race during its expansion towards the north, or it may have found a suitable refuge in the lower part of the Rhone valley between Montpellier, Lyon and Cannes, for which no karyotypic information is yet available. This last scenario would suggest that the northern race may be better adapted to the cooler summers of the Atlantic climatic conditions than the Iberian race. Indeed, during the very last Weichselian period, garden dormouse fossil remains were found (Vaucluse, Older Dryas, Haute Loire and Gard: last Vistulian) in association with Artic lemmings (*Dicrostonyx torquatus*) (Crégut-Bonnoure and Paccard 1997; Kowalski 2001) and were found in the same locality for long periods of time during which the climate switched from cold (Saalian) to warmer (Eemian), and again colder episodes (Weichselian) (Soyons, Ardèche; Defleur and Desclaux 1997). Therefore, this race had to differentiate north of the classical refuges for temperate species.

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