Mitochondrial phylogeography and population history of pine martens *Martes martes* compared with polecats *Mustela putorius*

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Abstract

The flora and fauna of Europe are linked by a common biogeographic history, most recently the Pleistocene glaciations that restricted the range of most species to southern refugial populations. Changes in population size and migration, as well as selection, have all left a signature on the genetic differentiation. Thus, three paradigms of postglacial recolonization have been described, inferred from the patterns of DNA differentiation. Yet some species, especially wide-ranging carnivores, exhibit little population structuring between the proposed refugia, although relatively few have been studied due to the difficulty of obtaining samples. Therefore, we investigated mitochondrial variation in pine martens, *Martes martes*, in order to understand the extent to which they were affected by glacial cycles, and compared the results with an analysis of sequences from polecats, *Mustela putorius*. A general lack of ancient lineages, and a mismatch distribution that is consistent with an expanding population, is evidence that the present-day *M. martes* and *M. putorius* in central and northern Europe colonized from a single European refugium following a recent glaciation. There has also been interspecific mitochondrial introgression between *M. martes* and the sable *M. zibellina* in Fennoscandia.

Keywords: conservation genetics, control region, introgression, mitochondrial DNA, phylogeography, pine marten

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Introduction

The flora and fauna of Europe are linked by a common biogeographic history, most recently the Pleistocene glaciations that restricted the range of most species to southern refugial populations (Taberlet et al. 1998; Hewitt 1999). Changes in population size and migration, as well as selection, have all left a signature on the genetic differentiation that is present today. However, the exact nature of the differentiation depends upon the species and their dispersal abilities. Thus some species, in particular those of low mobility, split into separate races and even species, originating from the refugia in which they diverged. Wherever they meet and mate, the races now form hybrid zones with varying degrees of introgression. Many of these zones cluster in the Alps, central Europe, the north Balkans and the Pyrenees, because the postglacial expansion was limited by mountains to the north of the refugium (Taberlet et al. 1998; Hewitt 1999). Another major cluster of zones is in central Sweden, probably produced by the final melting of the Scandinavian ice cap, allowing colonists from the east and west to meet (Jaarola et al. 1999).

Thus, Iberia (Spain and Portugal), Italy, the Balkans and the Caucasus have been proposed as the main European refugia, and three paradigms of postglacial colonization have been described, inferred from the patterns of DNA differentiation (Hewitt 1999). Common to all three, the Balkans were apparently the source for most populations to the east, and many in the west. In the meadow grasshopper *Chorthippus parallelus* (paradigm no. 1), individuals have a similar genetic background across the whole of Europe,
including the Balkans, except in Turkey, Greece, Italy and Spain, which have a large proportion of unique haplotypes (Lunt et al. 1998). This implies that an expansion from the Balkans colonized most of Europe, and that the climatic conditions, or the barrier of the mountains, prevented populations in other refugia from migrating. Alternatively, sequences from the west European hedgehog Erinaceus europaeus (paradigm no. 2) imply colonization from three glacial refugia: a western/Spanish one, a central/Italian one and an eastern/Balkan one (Santucci et al. 1998). Finally, the brown bear Ursus arctos (paradigm no. 3) appears to have colonized most of Europe from two refugia, in Iberia and the Caucasus/Carpathians (Taberlet et al. 1994, 1995).

Yet some species, especially wide-ranging carnivores and birds, exhibit little population structuring across Europe, so that the same mitochondrial haplotype may sometimes be recovered between very distant sites (Vila et al. 1999). We have therefore undertaken a study on pine martens, Martes martes, using mitochondrial control region sequences, and the results are compared with a further analysis of sequences from polecats, Mustela putorius, as well as the European mink Mustela lutreola (Davison et al. 1999, 2000). The ultimate aim is to advise on units for the conservation of martens in Britain and Europe.

Martes martes are a circumboreal species, remaining widespread throughout most of western Europe, including Fennoscandia, but excluding parts of the Low Countries (Mitchell-Jones et al. 1999). They are present, though uncommon, in Northern Spain and along the border with Portugal. They are rare or absent in much of the rest of southern Europe, with many of the records old and impossible to verify, including Greece (absent), Slovenia (rare), Croatia (rare), Serbia (extremely rare), Bulgaria (extremely rare), and the Black Sea coast, in Anatolia. Finally, many of the island populations were introduced up to 1000 years ago, for their fur, including to the Balearics and possibly Corsica, Sardinia and Ireland (Yalden 1999). In northern and central Europe, Martes martes are broadly sympatric with beech martens, M. foina (Mitchell-Jones et al. 1999), though the latter are much more common in the south. M. martes and M. foina do not hybridize, as far as is known.

Further east, the data on species distributions are sketchy (Anderson 1970; Bakeyev & Sinitsyn 1994). The sable M. zibellina is distinguished from M. martes by pelt and skull characters (Anderson 1970), but is not present in western Europe (Mitchell-Jones et al. 1999). It replaces M. martes at some point east of the Ural mountains, and the two species may hybridize when they meet (Grakov 1994). M. zibellina is replaced by M. flavula (yellow-throated marten) in East Asia and M. melanopus in Japan (Japanese marten). In North America, two species are present, M. pennanti (fisher) and M. americana (American pine marten), although the latter may actually be two species that occasionally hybridize, coastal/western M. a. caurina and continental/eastern M. a. americana (Carr & Hicks 1997; Demboski et al. 1999).

The situation is similar with polecats, which also have a wide European distribution. Mu. putorius (European polecat) is replaced by the steppe polecat Mu. eversmanni in the east. The degree of sequence divergence between the two and North American Mu. nigripes (black-footed ferret) is slight (Davison et al. 1999). In contrast, European mink Mu. lutreola are limited to Russia, France and northern Spain, and Romania (Davison et al. 2000). Morphological and molecular analyses strongly suggest that Mu. lutreola hybridizes with Mu. putorius (Heptner et al. 1967; Davison et al. 2000).

Materials and methods

Sampling

Samples of 139 Martes martes were obtained from 14 European countries (Table 1; approximate location shown in Fig. 1). Since martens are hunted for their fur in some northern European countries, relatively large numbers could be collected. In southern European countries, such as Spain, martens are either protected or very rare, so occasional road traffic accident animals or museum specimens in alcohol were used. Fewer samples were available. We attempted to keep the distance between samples within a single population to a minimum, relative to the distance between populations. The shortest distance between population samples was approximately 300 km (Germany/the Netherlands).

In England and Wales, marten samples were very difficult to collect. Six animals were sampled during the 1990s from England (Jeffertes & Critchley 1994; Birks et al. 1997), and latterly one from Wales using a faecal sample (Davison et al. 2001). In addition, six samples were also taken from captive stock in two British wildlife parks. The study book suggests that these animals originated from the former Czechoslovakia. The DNA sequences from these latter animals were excluded from the population structure analysis.

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Molecular analyses

Genomic DNA was extracted from either liver, blood, or skin and hair specimens, alongside an extraction blank, using Qiagen Blood/Tissue purification kits. Nucleon phytopure™ kits were used to extract DNA from the faecal sample, described in detail in Davison et al. (2001).

Two separate mitochondrial DNA (mtDNA) fragments, control region and cytochrome b, were amplified, resulting in approximately 320 and 364 base pairs of sequence, respectively.
The methods, along with the cytochrome b primers, have been described previously in Davison et al. (1999). For the control region amplification, the primers L15774 and H16498 were used initially (Shields & Kocher 1991). However, this combination did not always yield a clean polymerase chain reaction (PCR) product, so a slightly smaller product was amplified using either LRCB1 (5'-TGGCTCTGTAAAACCAA- AAATGG-3') or LRCB3 (5'-AGACTCAAGGAAAGCA-AC-3') and H16498. Samples were screened for sequence variation in the control region using a combination of single-strand conformation polymorphism analysis (SSCP) on PCR amplified material (Sunnucks et al. 2000), and DNA sequencing. Where possible, at least three haplotypes were sequenced from each haplotype, and common haplotypes were sequenced more frequently. Nucleotide sequences were determined using either the dRhodamine or Big Dye ABI sequencing kit (Applied Biosystems), and aligned by eye. Arguably, there has been near complete mitochondrial introgression between Mustela putorius and Mustela lutreola (Davison et al. 2000). Therefore, Mu. putorius and Mu. lutreola haplotypes were analysed together, because they might represent a single evolutionary unit. Of course, this may not be justified, so variation in the Mu. putorius sequences was also analysed separately. There was insufficient sequence variation to do the same with Mu. lutreola. A similar problem was encountered with the marten sequences, with probable introgression between Martes zibellina and M. martes. Thus, the analyses were performed on all sequences together and also a selection of sequences (see Results for further justification).

Descriptive statistics
Nucleotide diversity, \( \pi \), was estimated using the program dnasp (Rozas & Rozas 1997). The D\(^p\) and P\(^d\) tests, first suggested by Fu & Li (1993) and also implemented in dnasp, were used to test the hypothesis that control region variation does not differ from neutral expectations. The tests compare the number of singleton mutations to the total number (D\(^p\)), and the average number of nucleotide differences between pairs of sequences (P\(^d\)), both under a neutral model. Statistical significance was determined by comparison of the measured value with the values of Fu & Li (1993).

The relationship between unique haplotypes was described using a minimum spanning network, with the sequences as nodes of a network instead of the terminal tips of a tree. Networks are useful when many of the sequences may be derived from the same ancestral genotype. The algorithm used was MINDSNET, a program within ARLEQUIN 2.0 (Schneider et al. 2000).

Phylogenetic analyses
Phylogenetic trees were constructed using the neighbour-joining method with PAUP* version 4 (Swofford 1998). Multiple hits were corrected using the general time-reversible (GTR) model. The rate matrix, base frequencies, proportion of invariant sites and shape parameter (\( \alpha \)) of the gamma distribution (based on 16 rate categories) were estimated using likelihood, by iteration from an initial neighbour-joining tree. Parameters estimated from the initial tree were used to make a new neighbour-joining tree. The parameters were then re-estimated, and the process was repeated until there was no further improvement in likelihood. Bootstrap values were then calculated using 1000 replicates. Maximum likelihood methods were also performed on the control region sequences, using DNAEL in PHYLIP (Felsenstein 1993). Tree searching for maximum parsimony used a heuristic procedure with tree–bisection–reconnection branch swapping.

Analyses based on coalescent theory
Population bottlenecks and expansions, selective sweeps on the mtDNA, and mutational rate heterogeneity may all result in a Poisson distribution of substitutional differences between pairs of haplotypes (Slatkin & Hudson 1991; Rogers & Harpending 1992). Therefore, the ‘mismatch distribution’ of differences was calculated in dnasp (Rozas & Rozas 1997), and compared with a fit to the Poisson model.

Analyses of population structure
Population genetic structure was analysed for samples with five or more individuals, with an analogue of \( F_{ST} \), \( \Theta_{ST} \), as implemented in an analysis of molecular variance (AMOVA in ARLEQUIN 2.0; Schneider et al. 2000). The method estimates the proportion of genetic variation at different hierarchical levels, using information from the geographical distribution of haplotypes and the pairwise distances between them. The covariance components of variation were calculated among populations and within populations. The significance of estimates was determined by a Markov chain analysis (Schneider et al. 2000). All multiple tests of significance were corrected by the ‘sequential Bonferroni’ method (Rice 1989).

Evidence for an association of geographical distance with genetic distance was tested by plotting a regression of \( \Theta_{ST} \) values against ln (geographical distance), with significance determined by a randomization (Mantel) test in the program RT (Mantel 1967; Manly 1997). The geographical distances were estimated using ‘Distance Finder’ (http://www.indo.com/distance).

Results
Phylogenetic analyses
Twenty-five control region sequences from 139 martens fell into three major clades (groups I, II and III) in a
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10% sequence divergence

Fig. 2 Neighbour-joining control region tree for martens (gamma shape parameter of a = 0.16, transition/transversion ratio = 72). Bootstrap support is shown for nodes found in greater than 50% of 1000 trees. The sequences have GenBank accession numbers AF336949–AF336973.

neighbour-joining tree, with limited bootstrapping support (Fig. 2; GenBank AF336949–73). The same clades were evident using maximum likelihood and maximum parsimony methods. Group I lineages, found throughout Europe (Fig. 1), may further subdivide into a paraphyletic group Ia and outgroup Ib, although again, this is not supported by bootstrapping (Fig. 2). Group II lineages were found in Finland and Sweden only (Fig. 1). Finally, two very divergent haplotypes, group III, were found in two martens from the north of England (Northumberland).

The relationship between different marten species has been investigated by various authors using partial cytochrome b sequences (Carr & Hicks 1997; Demboski et al. 1999; Kurose et al. 1999). Most recently, Hosoda et al. (1999, 2000) used the complete cytochrome b sequence to show that Martes martes and Martes zibellina are reciprocally monophyletic sister taxa, and this was supported by bootstrapping. We therefore sequenced a fragment of the cytochrome b gene from 19 martens as a comparison: seven from Britain (u, v, and five v haplotypes), three from Ireland (all p), four from Germany (l, d, b, and m), two from Sweden (r and q), and three from Finland (s and two v).

Five haplotypes were discovered. Over the cytochrome b region studied, the single group Ia sequence (d, b, l, a) was identical to northwestern Russian and German M. martes sequences (GenBank AB051237, AB051251–3), and the single group Ib sequence (m, p) differed by a single base (the new sequence has GenBank reference AF336975). Cytochrome b sequences from group II control region haplotypes were identical to previously reported M. zibellina sequences from Khabarovsk in the Russian Far East (Hosoda et al. 1999; s and q identical to AB029420; r and v identical to AB029421). The simplest explanation is that the group II lineages originated by introgression from M. zibellina. Finally, the two English martens from group III had an identical sequence to M. americana caurina from Southeast Alaska and the Queen Charlotte Islands, British Colombia (Demboski et al. 1999; GenBank AF13468–9). This is consistent with morphological data that suggest that the animals were descendents of American martens that have previously escaped from captivity (Colin Simms, personal communication).

Control region diversity

Within group I, 11 polymorphic sites were identified from 325 aligned sites (3.4%); seven sites (2.6%) were polymorphic within group II (Fig. 3). Within groups (I and II) 15 sites were polymorphic (4.6%), increasing further to 43 sites (13.2%) when group III sequences and the outgroup, M. foina, were included (Fig. 3). Two regions of insertions–deletions were difficult to align, and were thus excluded in all further analyses (around positions 116 and 126 in Fig. 3); total aligned sequence = 305 bases. Similar hypervariable regions were found previously in Mustela putorius and Mustela lutreola (Davison et al. 2000).

Differentiation between individual haplotypes within groups was low, with most separated by single base substitutions. The minimum spanning network that describes the relationships between the group I and II haplotypes is shown in Fig. 4. The maximum difference was between haplotypes r and l, r and g (both 16 sites), or r and t (17 sites). Group Ia and Ib differ by three base substitutions in the minimum spanning network (Fig. 4).

The nucleotide diversity (θ) of group I haplotypes in M. martes (0.013, SD = 0.001) was low, as was the same estimate in Mu. putorius (0.009, SD = 0.001). When group I and II haplotypes were considered together, the nucleotide diversity was higher, and the same as that found when using introgressed Mu. putorius and Mu. lutreola haplotypes (0.021, SD = 0.003; 0.021, SD = 0.002, respectively). Values for θ* and P* were 0.65 and 0.53, respectively, but –0.20 and –0.26 when group I haplotypes alone were considered. Similar values were obtained for the Mu. putorius
Fig. 3 Variable sites of the mitochondrial DNA control region in martens. Identity with the first sequence is denoted by a dot, and a gap in the alignment by ~.

Fig. 4 A minimum spanning network constructed using mitochondrial control region sequences, excluding insertion/deletions. All haplotypes differ by single steps except where shown. The divergent group, haplotypes s, q, r and v, were found in Fennoscandia and probably introgressed from Martes zibellina. Haplotypes e and k differ by an insertion/deletion only, so are shown together.

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and *Mu. lutreola* sequences. However, in all instances values did not deviate significantly from zero.

The distribution of the pairwise number of differences in the control region did not differ significantly from the null Poisson model in all comparisons (Fig. 5a–d), although the best fit was obtained using *M. martes* group I haplotypes, or *Mu. putorius* sequences alone (Fig. 5a,c). The mean number of differences was very similar in martens compared with *Mu. putorius*/*Mu. lutreola* (Fig. 5a, mean = 3.9 and Fig. 5c, mean = 3.2; Fig. 5b, mean = 6.4 and Fig. 5d, mean = 7.2).

**Population structure**

Within-population nucleotide diversity was highly variable, because some populations were monomorphic, others had both group I and II lineages and also, due to sampling bias (Table 1; Fig. 1). Consequently, the most diverse populations were those in Fennoscandia. There was some evidence for structuring between group Ia and Ib haplotypes, because the former were the predominant type in Sweden, Scotland, France, Germany, Latvia and the Netherlands (Fig. 1). However, small sample sizes mean that this result should be interpreted with caution.

The *AMOVA* on control region variation indicated significant differentiation between certain sites, mostly involving comparisons with Ireland, Finland, or Scotland. Among-population differentiation explained 64.8% of the covariance component; within-population differentiation explained 35.2% (*θ ST = 0.65, P = 0*, based on 4970 permutations). No evidence for an isolation-by-distance was found, following the regression of log (distance between populations) against *θ ST*.

**Discussion**

The phylogeography of *Martes martes* and *Mustela putorius* in Europe

The absence of ancient lineages in *Martes martes* and *Mustela putorius* (with the exception of the introgressed *Martes zibellina* haplotypes, see below), as well as a mismatch distribution that is consistent with an expanding population (Fig. 5), is evidence that the present-day *M. martes* and *Mu. putorius* in central and northern Europe colonized from a single European refugium following a recent glaciation. The refugium was not necessarily the
same for each species, nor does it rule out unsampled divergent lineages in southern Europe. These lineages may exist but they have probably not contributed to the present day diversity in the rest of Europe. Low levels of mitochondrial variability have been reported in other mustelids, such as wolverines (Walker et al. 2001) and otters (Cassens et al. 2000), suggesting that a similar process may be responsible. This could be because they are predominantly northern species. The south Mediterranean is near their range limits, except during glaciations, so the relics of the refugial populations have periodically become extinct. An alternative explanation is that they have a low effective population size, so diversity is rapidly lost. It suggests that there may be a spectrum of biogeographic patterns across Europe, instead of three paradigms (Hewitt 1999).

Nevertheless, there are two minor mitochondrial lineages in M. martes (Fig. 2), and Mu. putorius are similarly differentiated (Davison et al. 1999, 2000). These types may represent postglacial recolonization from different refugia, with subsequent intermixing, but it is impossible to confirm without further sampling. As mentioned, sampling of M. martes in southern Europe was especially difficult, so it is possible that some undiscovered lineages remain (Fig. 1).

In wolves (Canis lupus) statistical parsimony, AMOVA analysis and Mantel tests all showed a lack of genetic differentiation by distance, and it has been argued that this is due to the multiple expansions and contractions into refugia, combined with their extreme mobility, dispersal over 1000 km has been recorded, and they have crossed the Bering land bridge a number of times (Vila et al. 1999). For mustelids, it is possible that the distribution of alleles is patchy as a consequence of a leptokurtic dispersal following recolonization (Ibrahim et al. 1996), but other more ‘current’ explanations are possible, such as population fragmentation and isolation.

Mitochondrial introgression in mustelids

Mustelid species often hybridize when sympatric (Griffiths 2000). Hybridization has previously been detected by altered pelt and cranial features, between Mu. putorius and Mu. lutreola, and between M. martes and M. zibellina. It is now clear that the history of hybridization has had an impact upon the mitochondrial diversity as well. In Mu. putorius and Mu. lutreola at least one haplotype is shared between the species (Davison et al. 2000). The remainder of the haplotypes are so similar that the mitochondrial phylogeny does not resolve the species, although this could be because of the recent speciation of Mu. lutreola, rather than hybridization (Davison et al. 2000). Similarly, the most likely explanation for the divergent group II lineage in Fennoscandian M. martes is that it originated by introgression from M. zibellina, because the same type was found in M. zibellina from the Russian Far East, over 6000 km away. Presumably, M. zibellina further west also have this sequence but they have not been sampled. Alternative explanations, such as the diffusion of M. martes mitochondrial to the Far East or the retention of an ancestral polymorphism are less plausible.

In addition, introgression has been reported in other Fennoscandian taxa, such as field voles (Jaarola et al. 1999). This is because Fennoscandia was completely covered with ice at the height of the last glaciation, c. 18000 years BP (Jaarola et al. 1999). As the ice melted with the onset of the Holocene, immigrants arrived both via a southern land bridge and via a northward route suggested by the southern and northeastern colonizers was established around 9000 years BP, so there is now a cluster of hybrid zones in central Sweden (Jaarola et al. 1999). In the field vole, Microtus agrestis, the southern mitochondrial lineages probably derive from a Balkan refugium, whereas the northeast lineage arrived via Russia. Similar phylogeographic patterns have also been observed in bank voles Clethrionomys glareolus, the common shrew Sorex araneus and the brown bear Ursus arctos (Taberlet et al. 1995; Jaarola et al. 1999). Furthermore, bank voles in northern Sweden and Finland have mtDNA originating from a different species, the red-backed vole Clethrionomys rutilus.

At present, it is impossible to know exactly how the introgression occurred between martens in Fennoscandia, nor whether the original M. martes colonization was bi-directional. However, as M. zibellina is an eastern species that is better cold adapted than M. martes, it may have been the first to colonize the northeast of Fennoscandia. As the climate ameliorated, M. martes could have replaced M. zibellina, with mitochondrial introgression as the dwindling M. zibellina population mated with M. martes.

An alternative scenario is suggested by reports from hunters’ bags. M. zibellina is generally limited by the Ural mountains to the west, but occasionally penetrates deep into Europe. From the fifteenth to the seventeenth centuries, M. zibellina reached into northern Finland and Sweden at 50° N latitude (Heptner et al. 1967; Bakeyev & Sinitsyn 1994). They also moved southwest into Byelorussia, Lithuania and eastern Poland. This range extension coincided with a marked downturn in temperatures, between 1550 and 1850, which is known as the ‘Little Ice Age’. Similar cold effects were noted in the forests, as northern spruce extended its range up to 600 km southward. As the temperatures increased again, the range of M. zibellina was restricted once again to the Urals. During this period there will have been ample opportunities for contact between M. martes and M. zibellina, since records from the levying of taxes on pelts show that the species were sympatric for a number generations (Bakeyev & Sinitsyn 1994).

A significant problem with most of the studies that have reported bi-directional colonization in Fennoscandia is that nuclear markers have rarely been used. Results from
microsatellites or nuclear gene sequences do not always corroborate mitochondrial studies, though a distinction should be made between intra- and interspecific studies (Tegelström et al. 1988; Hare & Avise 1998; Avise 2000; Waits et al. 2000). In part, the explanation may be due to the smaller effective population size of mtDNA. However, a lack of correlation between mitochondrial sequences and microsatellites in a recent study on brown bears was explained by differences in the levels of male and female gene flow (Waits et al. 2000). Female bears are strongly philopatric. Between species, the patterns of introgression between two species will tend to be shaped by the type and extent of reproductive barriers.

Units for conservation in M. martes

In normal circumstances, group I and group II mitochondrial types might define an Evolutionary Significant Unit (ESU; Moritz 1994). However, defining ESUs based on a single molecular genetic marker is not ideal: combining ecological and genetic data (mitochondrial and nuclear; see Waits et al. 2000) is preferred (Crandall et al. 2000). The full description of ESUs in M. martes must await further samples from southern Europe and studies using nuclear markers.

In Scotland, the M. martes population continues to expand following their near extinction, whereas it has been extinct in England and Wales (Strachan et al. 1997). For five specimens in this study, the mtDNA type was the same as that for animals from Scotland, and different from captive bred animals. Further work using microsatellites could determine whether the English and Welsh M. martes are relicts from the original population, recent covert introductions from Scotland, or the result of introgression between the two. More worrying is the discovery of M. americana caurina mitochondrial haplotypes in northern England. Although M. martes and M. americana represent opposite ends of a Holarctic species group, it is likely that they may still hybridize given the opportunity. However, at present it is unknown whether there is an even extant population of M. americana in Northumberland, nor whether they were accidental escapes (perhaps from fur farms) or deliberate releases.

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References


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