Conservation Genetics and Phylogeography of the Threatened Corsican and Barbary Red Deer *(Cervus elaphus corsicanus* and *C. e. barbarus)*

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Abstract The two red deer subspecies *C. e. corsicanus* (Corsican red deer, endemic to the Tyrrhenian islands of Sardinia and Corsica) and *C. e. barbarus* (Barbary red deer, presently confined to a small area along the Tunisian-Algerian border) are classified by the IUCN as “Endangered” and “Lower risk (near threatened)”, respectively (until recently, the Barbary red deer’s status was “Vulnerable”). Both subspecies underwent severe bottlenecks in the twentieth century. We review our results on genetic variability and differentiation in these two subspecies at polymorphic microsatellite loci and sequences of the mitochondrial control region and discuss their bearing on conservation and phylogeography. Our analyses yielded very low genetic variability for *C. e. corsicanus*. The Barbary red deer also showed low variability values in a European comparison, but diversity was not as low as might have been feared in the light of the population’s history. Analyses of molecular variance, assignment tests and factorial correspondence analysis did not yield any signs of differentiation among the Tunisian subgroups studied, whereas there was clear evidence of a differentiation between the Sardinian and the Corsican red deer population. The phylogeographic analysis showed close relationships between *C. e. corsicanus* and autochthonous Italian deer at two unlinked sets of nuclear loci, suggesting as the most likely scenario an introduction of Italian mainland red deer to the Tyrrhenian islands, from where animals were probably translocated to North-Africa.

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1 Introduction

The red deer (*Cervus elaphus*) is not an endangered species as a whole. Two genetically and morphologically distinct Western-Palearctic populations, however, are listed by the World Conservation Union as "Endangered" (*C. e. corsicanus*, the Tyrrhenian or Corsican red deer) and "Lower Risk" (near threatened) (*C. e. barbarus*, the North-African Barbary red deer). In the present review, we shall give a summary on our work on these two subspecies with regard to (1) genetic variability and differentiation of subpopulations and (2) the phylogeographic origin of the Tyrrhenian red deer and its relationship to the Barbary red deer.

2 Conservation Genetics

2.1 Barbary Red Deer

Apart from recent introductions, the Barbary red deer (*C. e. barbarus* Bennett, 1833) is the only African deer taxon. The historical range of this deer covered large parts of Algeria, Tunisia and possibly Morocco, but at present the Barbary deer is restricted to a small area of cork oak and pine forest on the Tunisian-Algerian border (Fig. 1) – a concentration which makes it particularly susceptible to diseases and forest fires, which are not uncommon in the region (Kock and Schomber 1961; Cowan and Holloway 1973; Dolan 1988; Oumani 2006). The Barbary red deer is listed in Appendix III by CITES (a recent proposal to list it in Appendix I was rejected in June 2007), and its IUCN status has recently been changed from "Vulnerable" to "Lower Risk (near threatened)" (Wemmer 1998; IUCN Red List 2007). Barbary red deer are characterised by a simplified antler structure (frequent lack of the bez tine) and by white spots running in longitudinal lines (Dolan 1988; Geist 1998). They suffered a severe bottleneck with only seven specimens left in Tunisia in 1962, two of them in Ain Baccouch and five in Ain Seraouia (Van Dijk 1972), which, however, were augmented by animals from Algeria crossing the border (Dolan 1988; Wemmer 1998). Consequently, hunting was banned, and in 1966, a reserve of 417 hectares with 17 individuals was established at El Feidja, about 190 km Southwest of Tunis, from where the deer can emigrate freely (Direction Générale des Forêts – hereafter abbreviated as DGF – 1994). This reserve is located within the El Feidja National Park, which also includes an additional enclosure for the Barbary deer. Subsequently, an area of ca. 200 km along the Mediterranean in Northern Tunisia was colonised (Meyer 1972; Dolan 1988).

Apart from Algerian immigrants, the El Feidja population is the origin of all Barbary deer present in Tunisia. Between 1978 and 1996, several reintroductions of this species into different reserves, mainly Ain Baccouch (Tabarka) and Mhebès (Séjnane), were carried out (DGF 1994). Population size at El Feidja seems to have been about 100 individuals since 1972 (Van Dijk 1972; Dhouib 1998; Oumani 2006).

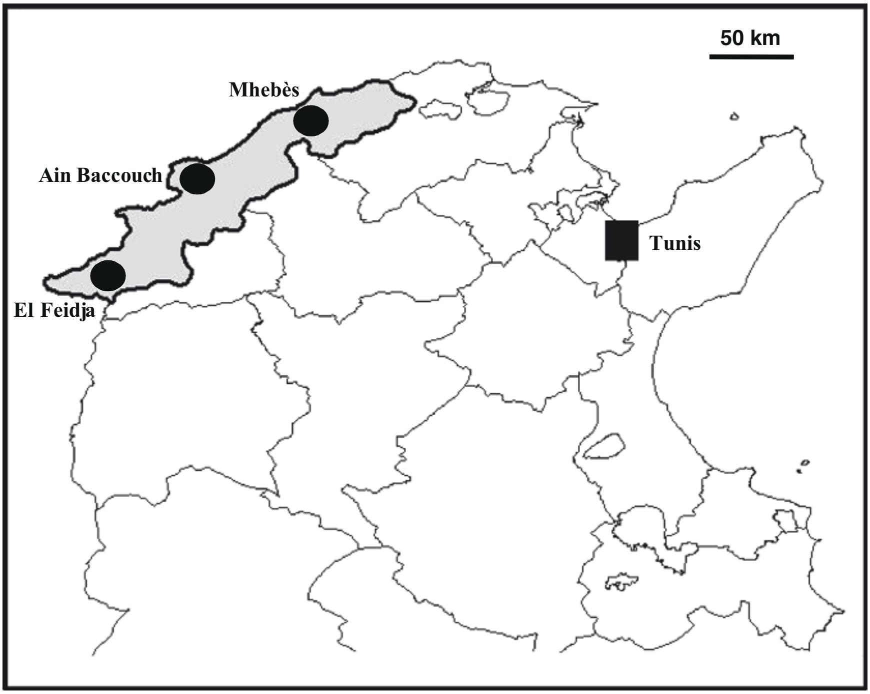

Fig. 1 Distribution of the Barbary red deer in Tunisia (*shaded area*) and location of sample sites. Figure taken from Hajji et al. (2007)

For Mhebès, Oumani recorded 80 individuals in 2002 and a similar number (70) in 2006 (Oumani 2006). The present number of deer at Mhebès is rather low compared with the number of founders (39 individuals) in 1979 (DGF 1994). The fact that neither of the two reserve populations (El Feidja and Mhebès) has increased is explained by Oumani (2006) with the dispersal of the deer from the reserve areas into adjacent habitats. Sadly, poaching is still also an important factor in limiting the population growth of the Barbary deer in Tunisia.

The total population size of *C. e. barbarus* in Tunisia was estimated by Oumani (pers. comm. 2006) to be about 800 individuals. This is in clear contrast to the census results obtained by the DGF according to which there are 2,000 deer in Tunisia (DGF 1994; see also Dolan 1988 who gives the same number). In addition to protection through government programmes, the WWF, in the context of the Regional Euro-Mediterranean Programme for the Environment (SMAP), is coordinating a project at El Feidja and Mhebès including studies on the population size and ecology of the deer in Northwestern Tunisia and the establishment of a deer enclosure at Mhebès. These conservation measures, however, are still sometimes thwarted by the government as was shown by the sale of 10 red deer from an enclosure in El Feidja in 2007 to a prince who wanted them for his private zoo in Morocco. In addition to these 10 animals, many more panicked during the capturing, jumped over the enclosure's fence and have not returned since.

Apart from the inclusion of some African samples in phylogenetic or phylogeographic studies (Polziehn and Strobeck 2002; Ludt et al. 2004; Hajji et al. 2008) there has only been one genetic study of Barbary red deer. Hajji et al. (2007) analysed 30 Tunisian Barbary red deer from El Feidja ($n=12$), Ain Baccouch ($n=8$) and Mhebès ($n=10$). Samples were collected in the field (faeces) or came from skin and hair of captured or accidentally killed or injured deer.

A stretch of 680 bp of the mitochondrial control region was successfully amplified and sequenced in 20 individuals. Amplification of 13 polymorphic microsatellites was successful in 19 red deer, a subset of 8 loci was amplified in all 30 individuals. Two distinct haplotypes were found differing by 16 transitions and being distributed evenly among the 20 specimens, occurring 11 and 9 times, respectively. This resulted in a low or intermediate haplotype diversity but in a rather high nucleotide diversity (Table 1), which is typical of populations having undergone a transient bottleneck where many haplotypes from the polymorphic original gene pool are lost through drift and those remaining are usually not closely related to one another (Nei et al. 1975).

The microsatellite loci analysed did not show any significant signs of linkage disequilibrium. Neither did tests for distortion of our results through stutter bands, large allele dropout or null alleles. Observed and expected heterozygosity values were 0.46 and 0.78, respectively, allelic diversity was 5.60 (Table 1).

A statistical test for a signature of the bottleneck in the microsatellite data (based on heterozygosity values relative to those expected under mutation-drift equilibrium and implemented in the Bottleneck software by Cornuet and Luikart 1996) was highly significant ($p=0.00018$).

We particularly tested our three sample sites El Feidja, Ain Baccouch and Mhebès for signs of (incipient) differentiation by calculating overall and pairwise F_{ST} and R_{ST} values (the latter being a microsatellite-specific analogue of F_{ST}) and by carrying out assignment tests in which individuals are assigned to the population of which their genotype is most typical. Additionally, a factorial correspondence analysis (FCA) was also conducted to see if this approach would yield any clusters of individuals related to their geographical origin. Positive signs of differentiation were not found in any of these calculations in that none of the F_{ST} or R_{ST} values were significantly different from zero; the assignment tests showed very high error rates (about 60%, which is not much lower than expected under random assignment to three populations); and there were no clusters of individuals in the FCA (not shown).

In Ain Baccouch, only one of the two haplotypes was found, but this is probably an artefact of the small sample size (control region amplification was successful in seven animals from Ain Baccouch) and may not be interpreted as evidence of differentiation. Consequently, the Tunisian red deer can still be considered a single, genetically homogeneous population.

The genetic data clearly reflect the population's bottleneck and show low genetic diversity for both mitochondrial control region sequences and nuclear microsatellite loci. However, compared to other populations known to be bottlenecked and/or inbred (e.g., Hasselbusch, Mesola or Corsica/Sardinia), variability values were not

Table 1 Genetic variability at microsatellite loci and the mitochondrial control region in the Tunisian and European red deer populations

Population	H_O	H_E	AD	HD	π [%]
Tunisia	0.46	0.78	5.6	0.529	1.266
Sardinia	0.48	0.66	–	0.872	0.473
Corsica	0.54	0.64	–	–	–
Mesola	0.51	0.62	–	0	0
Hasselbusch	0.58	0.66	4.9	0.493	0.337
Val di Susa	0.75	0.85	8.0	0.591	0.733
Tarvis	0.76	0.81	–	0.750	0.650
Southern Spain	0.65	0.80	–	0.652	1.318
Bulgaria	0.74	0.85	–	0.667	0.986
Romania	0.54	0.88	–	0.500	0.644
Spain	0.66	0.78	7.5	–	–
Scotland	0.44	0.81	–	0.478	0.536

H_O and H_E: observed and expected heterozygosity, AD allelic diversity (only given when sample size was comparable, i.e. between 16 and 22), HD haplotype diversity, π: nucleotide diversity. Mesola, Val di Susa and Tarvis are on the Italian mainland. The values for Corsica are from Hajji et al. 2008. Hasselbusch is a strongly inbred and isolated population in Northern Germany (see Zachos et al. 2007 for details). The data for Sardinia and Mesola are from Hmwe et al. (2006a), those for Val di Susa, Tarvis, Southern Spain and Bulgaria from Zachos et al. (2003), and the Spanish, Romanian and Scottish values are taken from Martinez et al. (2002), Feulner et al. (2004) and Hmwe et al. (2006b). For details of calculations see Hajji et al. (2007)

as low as might have been expected in the light of the population's demographic history (Table 1, Hmwe et al. 2006a). This may be due partly to immigration of Algerian animals. The Algerian population is estimated to have been about 300–400 head in the early 1950s before the Algerian war for independence and 400–600 in the mid-1970s (Salez 1959; Kock and Schomber 1961; Wemmer 1998; for an estimate on population density in Algeria cf. Burthey et al. 1992). The total Algerian population was estimated to be approximately 2,000 in the late 1980s (Dolan 1988) but since the official number for Tunisia is dubious, the same might also hold for Algeria.

Conservation measures should concentrate on the reduction of poaching, which still plays a major role in the mortality rates of Barbary red deer. At the moment, efforts are being made by the WWF to strengthen anti-poaching legislation. In addition, the distribution range of the Barbary red deer should be further extended to reduce its susceptibility to environmental stochasticity such as forest fires and diseases.

The analysis of Hajji et al. (2007) and ongoing field studies in Tunisia have yielded valuable data on *C. e. barbarus* but information about these deer outside Tunisia is much needed. There are still rumours of Barbary red deer having survived in Morocco. This sounds unlikely but should be investigated nonetheless. The most important future steps, however, must concentrate on Algeria. The population size in Algeria and the number of migrants between Algeria and Tunisia need to be known. An assessment of the genetic variability in Algerian red deer and whether they are differentiated from the Tunisian population or not are pre-requisites of an effective bilateral management which must be the ultimate goal in the conservation of these last African red deer. Fortunately, plans for such bilateral protection measures are under way at present.

2.2 *Tyrrhenian or Corsican Red Deer*

The Corsican red deer (*C. e. corsicanus* Erxleben, 1777) is the smallest of the existing red deer (Dolan 1988). It is confined to the Tyrrhenian islands Corsica and Sardinia and classified as "Endangered" by the IUCN (Wemmer 1998; IUCN Red List 2007). In the second half of the twentieth century, it underwent a severe bottleneck with only 100–200 animals remaining (Krumbiegel 1982; Dolan 1988; Kidjo et al. 2007 and references therein), but has recovered well since so that recently it has been suggested that the Tyrrhenian red deer be downgraded to "near threatened" in the IUCN Red List (Kidjo et al. 2007). Present numbers are given as at least 2,700 head by Lovari et al. (2007), but in line with Banwell (1998), who gives an estimate of only 1,500 specimens, another recent figure is "slightly >1,000" (Kidjo et al. 2007). After its extinction around 1970, the Corsican population was re-founded with altogether 14 Sardinian animals (of which one male died shortly after its introduction) between 1985 and 1994 (Dolan 1988; Gonzalez and Kidjo 2002; Kidjo et al. 2007). The introduced deer were at first kept in enclosures, but since 1998 there have been repeated releases into the wild so that in 2004, there were about 200 free-ranging animals on Corsica and another 50 in enclosures (see Kidjo et al. 2007 who give a detailed report on the extirpation and reintroduction history of the red deer on Corsica).

The first assessment of genetic variability based on five microsatellite loci and 332 bp of the mitochondrial control region yielded very low variability values for 17 Sardinian red deer in a European comparison (Zachos et al. 2003). A more recent study, based on a larger sample size of 29 Sardinian red deer and an extended panel of 12 microsatellite loci as well as a larger fraction of the mitochondrial control region (531 bp) confirmed these results (Hmwe et al. 2006a, see values in Table 1). Microsatellite variability was nearly as low as for Mesola, a relict population of truly autochthonous Italian mainland red deer which mark the lower end of genetic diversity in European-type red deer. The comparatively high number of eight haplotypes found (defined by seven polymorphic sites) may be a consequence of more than one colonisation of or introduction to the island. Only a few females would be enough to have caused this mitochondrial pattern without significantly increasing nuclear genetic variability. We have recently analysed a panel of eight further microsatellite loci, which show the same picture with respect to variability (Hajji et al. 2008), but also included 10 red deer from Corsica in our analysis. Genetic variability of the Corsican animals was still a little lower than that for Sardinia (observed and expected heterozygosity and allelic richness were 0.54, 0.64 and 3.50 for Corsica and 0.53, 0.71 and 4.40 for Sardinia), but the differences were

Fig. 2 Bayesian structure analysis of Corsican (1) and Sardinian (2) red deer with the STRUCTURE software (Pritchard et al. 2000). All Corsican animals were assigned to one cluster (*dark grey*) with high probabilities, whereas all but six Sardinian deer were assigned to a second cluster (*light grey*) with similarly high probabilities. When the data were tested for $K=3$ clusters (which yielded a higher overall probability but is not shown), only two of these six Sardinian specimens were grouped with the Corsican red deer, while the other 21 Sardinian red deer were assigned to two "non-Corsican" clusters

not significant. Interestingly, however, signs of considerable differentiation were found between the Corsican red deer and their population of origin on Sardinia. Pairwise F_{ST} for these two populations was about 15% and significantly different from zero, and the number of loci not in Hardy-Weinberg-Equilibrium due to an excess of homozygotes increased considerably (from two and zero in the single populations to five in the pooled data set), which is indicative of a Wahlund effect, i.e. a reduction in homozygosity relative to Hardy-Weinberg expectations due to substructuring of the total population. Further, assignment tests assigned more than 90% of the Corsican and Sardinian animals to their correct population of origin, and a Bayesian structure analysis without a priori assumptions of geographical origin also yielded distinct clusters roughly equivalent to the two islands (Fig. 2). Finally, a tree based on genetic distances among all individual red deer from Corsica and Sardinia also showed a non-random pattern in that one of the two main branches comprised exclusively Sardinian animals while the other comprised pre-dominantly Corsican deer (not shown).

3 Phylogeography of the Corsican Red Deer

The origin of the Corsican red deer has been a matter of considerable debate (reviewed in Vigne 1988 and Zachos and Hartl 2006). The two main questions are: (1) where did it come from and (2) how did it reach the Tyrrhenian islands – naturally during a glacial regression of the sea-level or through human introduction? The latter hypothesis was already put forward at the end of the nineteenth century (Lydekker 1898), and Groves (pers. comm. to Geist 1998) thought that the Tyrrhenian red deer were introduced from North-Africa by the Phoenicians. It has recently been shown that hares (*Lepus* sp.) were introduced to Sardinia from Africa (Scandura et al. 2007), so this might also hold for red deer. In line with this, Ludt et al. (2004) and Skog et al. (2009) found close relationships between Sardinian and Barbary red deer based on sequences of mitochondrial DNA (cytochrome b and control region; see also Sommer et al. 2008 for a review on red deer phylogeography). Flerov (1952) regarded the Corsican red deer to be closely related to the Barbary red deer and the Spanish subspecies *C. e. hispanicus*, and Zachos et al. (2003) and Hmwe et al. (2006a) found close similarities at the mitochondrial control region between Sardinian and Spanish red deer. This was, however, not corroborated in more comprehensive studies (Ludt et al. 2004; Skog et al. (2009). An early genetic hypothesis based on mitochondrial RFLP markers linked *C. e. corsicanus* with Bulgaria and the Near East (Hartl et al. 1995) but none of the subsequent analyses yielded further evidence in favour of this assumption.

The only other genetically substantiated hypothesis as to the origin of the Tyrrhenian red deer is based on nuclear microsatellite loci. Zachos et al. (2003) and Hmwe et al. (2006a) found close relationships between Sardinian and European mainland red deer, in particular those from the Mesola wood in the Po delta (the relationship of mitochondrial control region sequences derived from Sardinian and Mesola red deer was ambiguous). The Mesola population is important from a phylogeographic point of view as it is the only surviving, truly autochthonous red deer population in the Italian peninsula, thus very probably at least partially representing the original Italian gene pool (Mattioli 1990). This hypothesis matches with morphological analyses which showed close similarities between Holocene red deer from Southern Italy and samples from the extinct original Corsican red deer population (Vigne 1988). According to this hypothesis red deer either naturally colonised the Tyrrhenian islands from the Italian mainland during a glacial period in the Pleistocene when the sea-level was considerably lower (for details see Hmwe et al. 2006a) or were introduced to Sardinia and Corsica by man. Putative Pleistocene red deer fossils are known from Corsica (*C. e. rossii*, Pereira 2001), but the extant Tyrrhenian red deer can hardly be considered a descendant of these early deer because, in spite of a very well-analysed fossil record, no red deer were found between the early Holocene (ca. 11500 cal. BP) and the mid-Holocene (5000 cal. BP or later) (Vigne et al. 1997; Vigne 1999; Costa et al. 2003). Sites from the Late Neolithic (4500 cal. BP) in Sardinia and from Classical Antiquity in Corsica, however, have frequently yielded red deer bones (Fonzo 1987; Vigne 1988). This is clearly indicative of human introduction after the indigenous deer populations had become extinct (Vigne 1992, 1999; Schüle 1993; Masseti 1998, 2002a). The Corsican population, possibly much younger than the Sardinian one, could have been founded with introduced animals from Sardinia or directly from the Italian mainland. Such introduction events were not uncommon at the time, and deer are known to have been introduced to many islands as early as the eleventh millennium BP (Vigne 1993; Masseti 1996, 2002a,b).

To shed further light on this issue, red deer from Corsica and Sardinia together with a selective sample of numerous European-type red deer were analysed for the first time, among them both Mesola and North-Africa (Hajji et al. 2008; see Fig. 3).

The study, based on eight nuclear microsatellite loci, yielded close relationships of *C. e. corsicanus* to red deer from both Mesola and North-Africa, as reflected, for

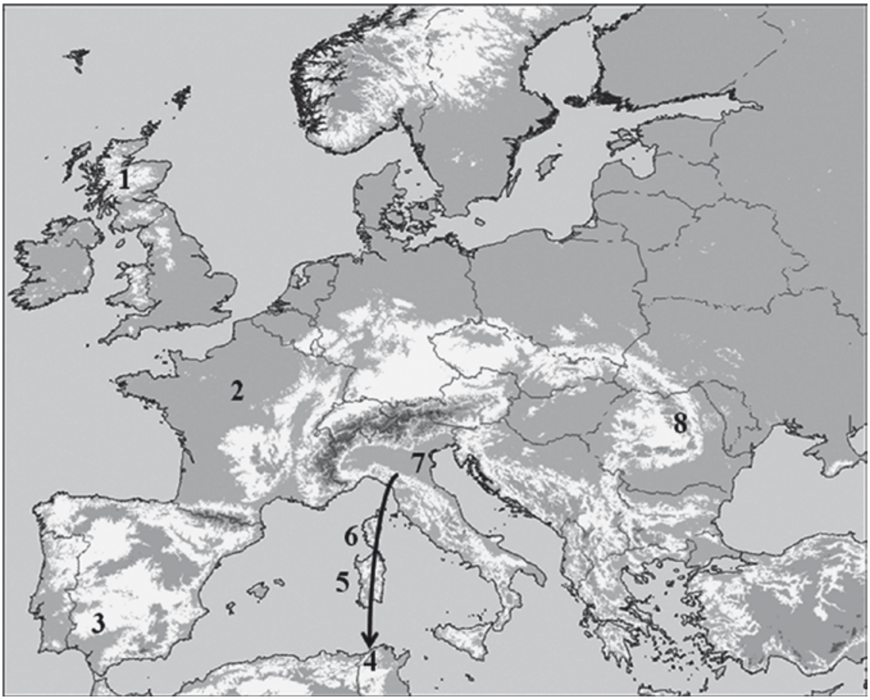

Fig. 3 Geographical location of sample sites studied in a phylogeographic analysis by Hajji et al. (2008). 1: Scotland (*C. e. scoticus*, *n* = 9), 2: France (*C. e. hippelaphus*, *n* = 14), 3: Southern Spain (*C. e. hispanicus*, *n* = 21), 4: Tunisia (*C. e. barbarus*, *n* = 30), 5: Sardinia (*C. e. corsicanus*, *n* = 23), 6: Corsica (*C. e. corsicanus*, *n* = 10), 7: Mesola (*C. e. hippelaphus*, *n* = 25), 8: Romanian Carpathians (*C. e. montanus*, *n* = 17). The arrow denotes the most probable direction of introductions

example, by the fact that more than 50% of all alleles found in Mesola and Tunisia, respectively, were alleles also recorded in the Tyrrhenian red deer. However, the analyses favoured Mesola as the closest relative of the Tyrrhenian red deer. This was evident from allele frequencies and distributions at single loci, from different parameters of genetic distance and from the resulting trees (see Fig. 4). Nei's standard distances (Nei 1972), chord distances (Cavalli-Sforza and Edwards 1967) and proportion-of-shared-alleles distances (Bowcock et al. 1994, calculated as 1-Dps) between *C. e. corsicanus* and Mesola were 0.745, 0.117 and 0.585, while the respective values between *C. e. corsicanus* and Tunisia were 1.015, 0.126 and 0.640. Assignment tests did not yield misassignments of *C. e. corsicanus* specimens except for the individuals incorrectly assigned between Sardinia and Corsica (see above).

Rather unexpectedly, the study also yielded a quite close genetic proximity between *C. e. corsicanus* and the French red deer population. This may be due to introductions from France to the Tyrrhenian islands (which cannot be totally ruled out, although there are no records confirming this) or, more probably, due to the limited number of loci (eight) used in the analyses and/or length homoplasy.

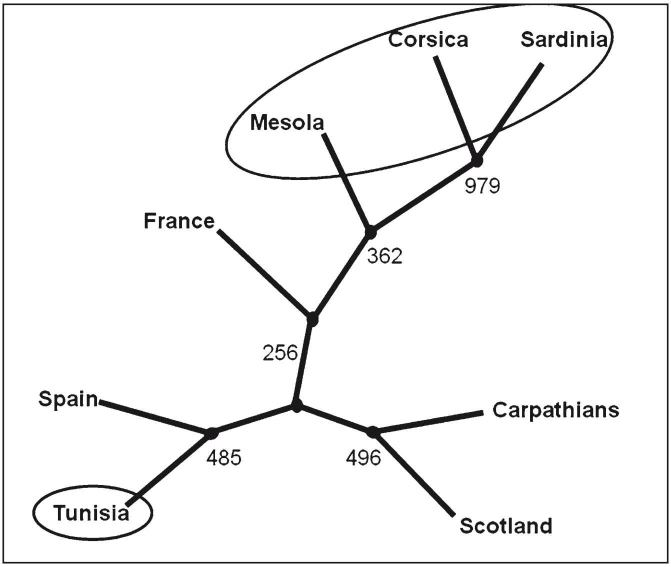

Fig. 4 Neighbour-joining tree based on pairwise chord distances derived from allele frequencies at eight nuclear microsatellite loci. Numbers at nodes refer to support from 1,000 bootstrap replicates. Figure modified from Hajji et al. (2008)

Perhaps the emerging picture would have been clearer had the animals been genotyped for more loci. This would also explain the rather low bootstrap support for nodes in our trees. Null alleles, stutter bands and allelic dropout, potential error sources known to be able to distort analyses based on microsatellites, were tested for with the MICRO-CHECKER software (van Oosterhout et al. 2004) and could be shown not to have influenced the data (see Hajji et al. 2008 for details).

In general, however, the results are in accordance with a priori expectations. They confirm those of Hmwe et al. (2006a) in that Mesola turned out to be the probably closest extant relative of the Tyrrhenian red deer. The recent study (Hajji et al. 2008) was based on eight completely different and unlinked nuclear loci, which further adds to the credibility of the main conclusion.

Nevertheless, although not as unequivocal as with mitochondrial sequence data, nuclear genetic analyses also confirmed a close relationship of Tyrrhenian and Barbary red deer. It is still unclear if there are true *Cervus* fossils in the Late Pleistocene of North-Africa (Cheylan 1991), and it is considered more probable that the modern Barbary red deer go back to introductions by humans in Holocene times (Kowalski and Rzebik-Kowalska 1991), although Hamilton (1978) thought that the Barbary red deer reached Africa via Sicily. Putting together both the palaeontological and the genetic results, it seems very likely that the Tyrrhenian red deer were introduced to Corsica and Sardinia from mainland Italy and that these deer were subsequently translocated to North-Africa (Fig. 3, see also Dobson 1998). This would neatly explain the seeming contradiction between nuclear and mitochondrial genetic data. The fact that the Mesola red deer do not show a mitochondrial haplotype unequivocally linked with those of the Tyrrhenian and the Barbary red deer is probably the result of drift in the small, long-time isolated and bottlenecked Mesola population. Effective population size is four times smaller for the mitochondrial than for the nuclear gene pool, which is why drift has a fourfold smaller effect on (nuclear) microsatellite allele frequencies than on control region sequences.

Apart from presenting a very probable solution to the debate about the origin of the Tyrrhenian red deer and its relative relationships with mainland Italian and African Barbary red deer, the study of Hajji et al. (2008) also highlights the need for taking into consideration all available sources – palaeontological, archaeozoological and genetic, and it is also a corroboration of previous studies, which warned against the exclusive use of mitochondrial DNA in phylogeographic analyses (e.g., Taberlet et al. 1998).

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