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Inheritance of the king coat colour pattern in cheetahs *Acinonyx jubatus*

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(With 1 plate and 1 figure in the text)

The paper describes the pedigree of nine King cheetahs born in captivity and provides evidence that the king coat colour pattern in *Acinonyx jubatus* appears to result from the action of a recessive allele at an autosomal locus.

Contents

Introduction

King cheetahs have been recorded sporadically over the past 50 years (Hills & Smithers, 1980) and, although once described as a leopard-cheetah hybrid (Cooper, 1926) and later recognized as a cheetah but described as a new species, *Acinonyx rex* (Pocock, 1927), it is today generally accepted to represent an abnormally marked variant of *A. jubatus*. Pocock (1939) acknowledged this and Robinson (1976) suggested that the change of the spotted pattern to blotches in these cheetahs is comparable to that of the so-called 'striped tabby' to the 'blotched tabby' in the Domestic cat *Felis catus*. This implies that the king coat colour pattern results from a mutation inherited as a single autosomal recessive allele. This paper describes the pedigree of the nine King cheetahs bred at the De Wildt Cheetah Research Centre (South Africa) between 1981 and 1984 and provides evidence that the expression of the aberrant coat colour results from the action of an autosomal recessive allele.

Materials and methods

The pattern of inheritance of the king coat colour pattern within the captive colony of cheetahs at the De Wildt Cheetah Research Centre was deduced from breeding records available for the 10-year period

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from 1975 to 1984. Husbandry and breeding of cheetahs at the Centre has been described elsewhere (Brand, 1980). The breeding system, where females were isolated from males except for mating purposes, provided the opportunity to select artificially breeding pairs. Suspected pregnant females were each housed separately in maternity enclosures after mating with a selected male. Males did not regain access to these females until the onset of the following mating season, thus ensuring the planned parentage of litters.

Shelters within each maternity enclosure were inspected daily for the presence of cubs or aborted foetuses, or any other signs of parturition, and the dates, sex composition and coat colours of all litters were recorded where possible. Cheetahs with a spotted coat colour pattern will, for the purpose of this discussion, be referred to as the 'wild type' and those with a blotched coat colour pattern, as 'kings'.

Results

The pedigree

The coat colour patterns of the nine King cheetahs are very different to those of the wild type (Plate I), but similar to those of the study skins of *A. rex*, as described and illustrated by Hills & Smithers (1980). These were all characterized by the partial replacement of the normal spots by broad bands forming whorls and spiral arrangements similar to those occurring in the blotched tabby Domestic cat.

The pedigrees of the nine King cheetahs produced are illustrated in Fig. 1. The three wild type mothers involved originated from two consecutive litters produced by a wild type male (Chris) and female (Lady) caught in SWA/Namibia and the northern Transvaal, South Africa, respectively. One of the three wild type males (Frik), which sired King cheetahs, was similarly captured as a free-ranging animal in the northern Transvaal. The other two males (Ben and M35) were born following matings between Frik and a wild type female (Gill), caught in the eastern Transvaal.

Matings between the wild type male Frik and two of the wild type daughters (Jean and Jumper) resulted in the birth of two King cheetahs. All the other King cheetahs were conceived by mating his male wild type progeny (Ben and M35) with the wild type females, Jean and F20 (Fig. 1).

A mating between Frik and Lady (wild type, wild caught mother of three siblings which in turn produced King cheetahs) did not produce a King. This suggests that Lady was not a carrier of the 'king' trait and indicates that her daughters inherited the character from the father, Chris. It should, however, be noted that these data do not preclude Lady from being a carrier.

Coat colour genetics

The hypothesis that the 'king' phenotype results from a single autosomal recessive mutation is supported by the fact that King cheetahs of both sexes were produced by wild type parents and offspring of these wild type parents. If the 'king' phenotype results from a mutation of a gene locus, homologous to the tabby locus in the Domestic cat, it is expected that the pattern of inheritance would be similar to that of the blotched tabby pattern and thus typical of a single autosomal recessive gene.

In designating the 'king' character as t^b and its dominant allele as $t+$, it follows that all King cheetahs must be of the genotype t^bt^b and wild types either $t+t^b$ or $t+t+$. King cheetahs will only be produced by $t+t^b$ or t^bt^b parents and wild type carriers by matings between $t+t+$ and $t+t^b$ or $t+t^b$ and $t+t^b$ or $t+t^b$ and t^bt^b parents.

PLATE I. The first King cheetah produced at the De Wildt Cheetah Research Centre.

The ratio of King cheetahs to wild type progeny resulting from matings between the different genotypes is in accordance ($\chi^2 = 0{\cdot}32$) with the hypothesis of a single autosomal gene, where the mutant allele 'king' is recessive to the wild type allele (Table I).

Since the grandparents of the King cheetahs failed to produce the king coat colour, we suggest that each of these original matings involved a $t+t+$ and $t+t^b$ individual. Early deaths precluded test-crossing to prove this, but at least one of these males (Frik), was, through his production of King cheetahs, positively identified as heterozygous for this character. At least two of the 12 progeny in three litters resulting from this male and the wild type female (Gill) were similarly proved to be heterozygous (Fig. 1). Furthermore, three (Jean, Jumper and F20) of the 18 wild type progeny of the wild type grandparents (Chris and Lady) have been provisionally identified as heterozygous carriers of the 'king' character.

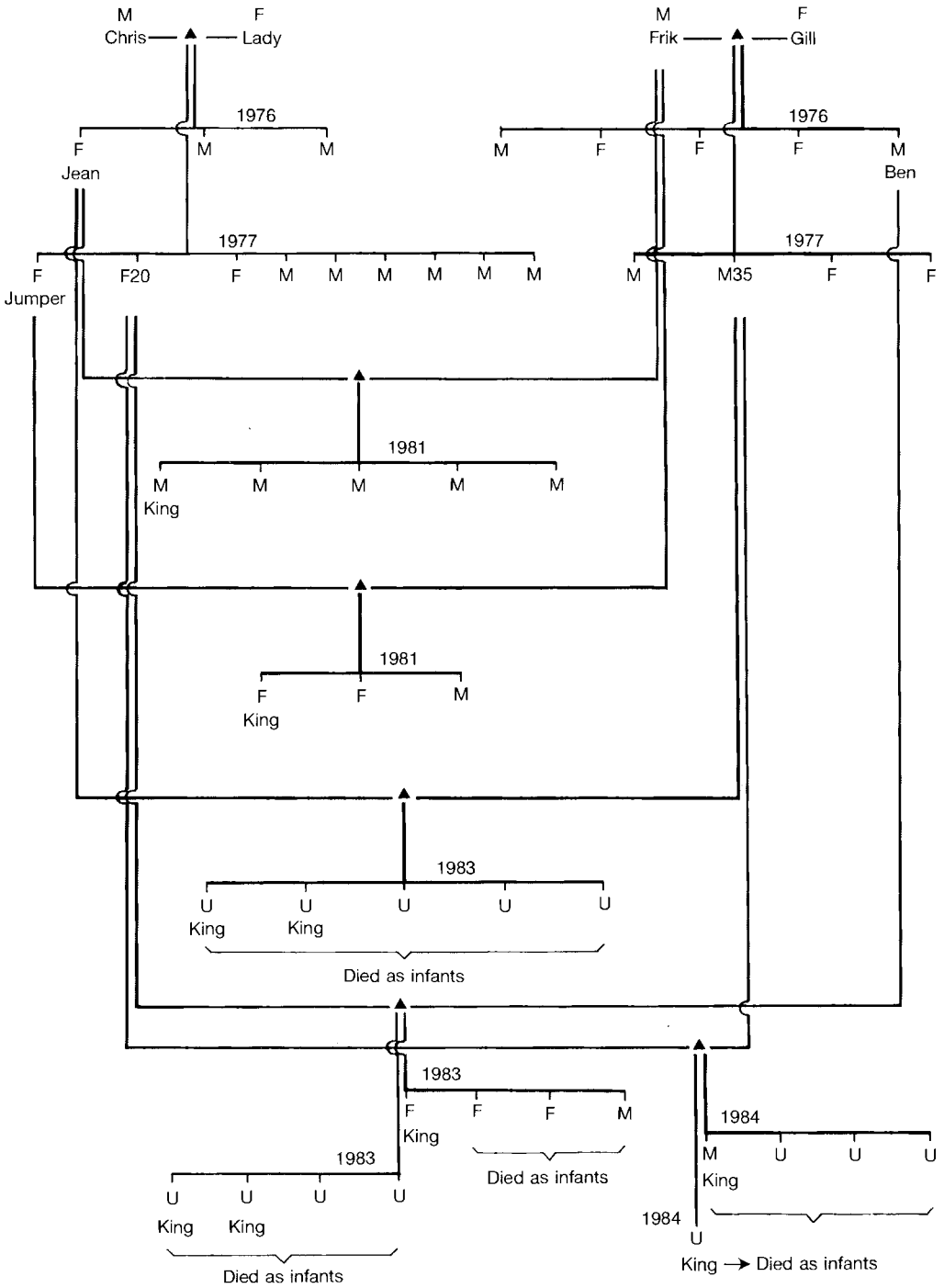

FIG. 1. Pedigree of the nine King cheetahs born at the De Wildt Cheetah Research Centre between 1981 and 1984 (M = males; F = females; U = sex unknown).

TABLE I

Observed and expected number of King and wild type progeny from matings between different presumed genotypes. The calculation of the expected numbers were based on the hypothesis that the King phenotype results from a single autosomal recessive mutant

Mating	Number of litters	Total progeny	Observed		Expected		χ^2 value
			King	Wild type	King	Wild type	
$t^+t^b \times t^+t^b$	8	26	9	17	6·5	19·5	0·32

TABLE II

The relationship between phenotype and survival of cubs produced during 1981, 1983 and 1984 at the De Wildt Cheetah Research Centre

Phenotypes	Number of cubs	
	surviving	dying
King	3	6
Wild type	23	49
Total	26	55

Mortality

The information in Fig. 1 indicates a high infant mortality amongst captive cheetahs, Kings also succumbing with only three surviving to adulthood. Two of them had to be hand-raised due to abandonment by the mother. However, the proportion of King cheetahs dying as infants did not differ significantly from the proportion of wild type individuals that died ($\chi^2 = 0{\cdot}01$; Table II).

Discussion

The breeding of King cheetahs from a captive group of wild type cheetahs removes all doubts regarding the specific status of *A. rex* and confirms earlier suggestions (Pocock, 1939; Robinson, 1976; Hills & Smithers, 1980) that the King cheetah merely represents a colour variant of *A. jubatus*. Furthermore, our information provides evidence that the king trait is inherited as an autosomal recessive allele, which probably arose from a mutation at the tabby locus. The concept of gene homology is generally accepted today (Robinson, 1970, 1976). Most felids have a characteristic and consistent striped, spotted or rosetted pattern of dark pigment overlaid on an agouti background (Robinson, 1976). Based on information available from Domestic cat breeding, this basic pattern appears to be controlled by a single locus, designated the tabby locus (Robinson, 1976).

The apparent similarities between the blotched tabby and king phenotypes and patterns of inheritance may be interpreted as suggesting homology and support the hypothesis that the King cheetah represents a colour variant resulting from a mutation at the tabby locus.

Death of one of the parents and all the grandparents of the King cheetahs, the present infertile status of the surviving male King cheetah, immaturity and a high rate of infant mortality, are still precluding a programme of test-crossing to prove fully that the king character is inherited as a recessive mutant. The future breeding programme will be adapted and orientated towards this end.

King cheetahs have been collected and observed in a restricted area in eastern and south-eastern Zimbabwe, the north-eastern Transvaal and eastern Botswana (Hill & Smithers, 1980). It is thus surprising that the grandfather (Chris) of the King cheetahs originated from SWA/Namibia. We, however, have no reason to think that the SWA/Namibia cheetah population is isolated from other populations, implying that the observed mutation is not restricted to a specific area.

Summary

The fortuitous breeding of King cheetahs at the De Wildt Cheetah Research Centre gives conclusive evidence that *Acinonyx rex* simply represents an unusual colour variant of *Acinonyx jubatus*. Consistency in the coat colour pattern of nine King cheetahs born at the Centre, and the pattern of inheritance thereof, suggests that it is controlled by a recessive allele at a single autosomal locus. The typical change of the spotted pattern to blotches is probably homologous to a mutation at the tabby locus of the Domestic cat.

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