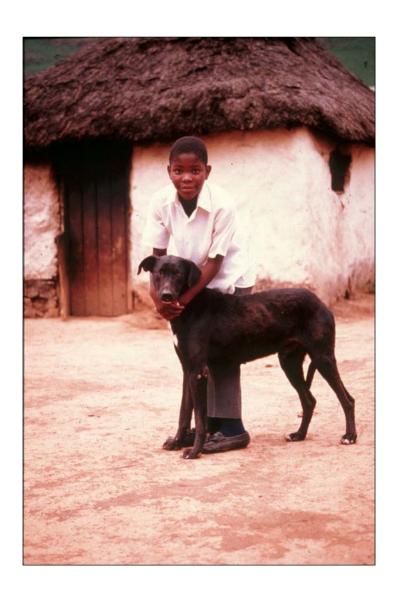
CHAPTER 1

INTRODUCTION



INTRODUCTION

1.1. TAXONOMY AND DISTRIBUTION OF CANIS FAMILIARIS

The Canidae is a morphologically diverse family of dog-like carnivores that includes 14 extant genera and 34 species (Stains, 1975). Morphological convergences is probably the main cause for conflicting classifications of this family (Huxley, 1880; Simpson, 1945; Langguth, 1969, 1975; Clutton-Brock et al., 1976; Van Gelder, 1978) In 1758 Linnaeus classified the domestic dog as Canis familiaris, a species designation, and also commented on the diversity within this species. Subspecies (or races) of dogs are referred to as breeds. Domestic dogs would almost certainly not be confined within a single Latin name by any mammalogist, were it not for humans viewing them as mere breeds (Jones, 1999). Honacki et al. (1982) suggested that the dog be reclassified as a subspecies of the wolf (Canis lupus) and be named Canis lupus familiaris. Although some scientists do refer to the domestic dog as C. l. familiaris (eg. Bårdgard and Brix, 1997a,b; Meek, 1999; Miller et al., 1999), it is still common practise to use the species designation, C. familiaris, by researchers from various fields of science, including physiology (Scantlebury et al., 2000), genetics (Thomas et al., 1999), veterinary research (Bingham et al., 1999), parasitology (Hoberg et al., 1999), zoology (Frid, 1999; Riede and Fitch, 1999), forensic sciences (Komar, 1999), comparative psychology (Fiset, 2000), population ecology and animal behaviour (Pal, 2001; Pal et al., 1998, 1999a, 1999b).

Dogs have the greatest world-wide distribution, amongst mammals, with the largest population in the genus *Canis*, and with the most distinctive physical and behavioural

variations. The only other mammal besides the dog with a similar, rare combination of genetic diversity and a widespread, well-mixed gene pool and distribution is man.

1.2. EVOLUTIONARY HISTORY OF THE DOMESTIC DOG

Canidae diverged from other carnivore families about 50 – 60 million years ago, if a constant rate of sequence evolution is assumed, which is near the time when canids first appeared in the fossil record (Flynn and Galiono, 1982; Wayne *et al.*, 1991b).

The results of allozyme and chromosome based analyses suggest that several phylogenetic divisions occur within the Canidae (Wayne, 1993):

- (1) the wolf-like canids, including domestic dogs, grey wolves, coyotes and jackals;
- (2) South American canids, including species of diverse morphology but common recent ancestry;
- (3) the red-fox-like canids of the Old and New World, including red foxes and kit foxes; and
- (4) monotypic genera (species such as the bat-eared fox and racoon dog) that have a long, separate evolutionary history.

These divisions began about 7 - 10 million years ago based on genetic distances and the fossil record (Wayne and O'Brien, 1987; Wayne *et al.* 1987a, b; Wayne, 1993).

There are reasonably clear mechanisms for the evolutionary divergence of dogs. All the species of the genus *Canis* are allelomorphic, which means that wolves, coyotes, jackals and dogs are karyotypically identical. They, therefore, share the same number

and shape of chromosomes, and the same mapping of genes on those chromosomes. There are only minor allelic differences in the base pairs of individual genes (Coppinger and Coppinger, 1998).

The most recent evidence obtained by sequencing mitochondrial DNA (mtDNA) of 67 dog breeds and wolves from 27 localities indicates that dogs may have diverged from wolves over 100 000 years ago (Vilà *et al.*, 1997). This was a very controversial topic in the scientific community, because some researchers believe that the molecular clock theory is not accurate. According to several scientists, the fossil records (e.g. Olson, 1985) do not support the theory of divergence 100 000 years ago. The debate is still ongoing between researchers and reports (Federoff *et al.*, 1997) are being published supporting both the opposing views.

The earliest remains of the domestic dog date back to 10 to 15 thousand years ago (Olson, 1985). Multiple domestication events are suggested at different times and in different places, due to the diversity of these remains (Wayne, 1993). Dogs may be derived from several different ancestral gray wolf populations and many dog breeds and wild wolf populations must be analysed in order to elucidate the genetic sources of the domestic dog gene pool, according to the latter author. In a comparison between seven dog breeds and 26 gray wolf populations from different locations around the world, using limited mtDNA restriction fragment analyses, it was shown that the mtDNA genotype of dogs and wolves are either identical or differ by the loss or gain of only one or two restriction sites (Wayne *et al.*, 1992). With a maximum difference of 0.296 of mtDNA sequence, the domestic dog is an extremely close relative of the gray wolf (Wayne and Jenks, 1991; Wayne *et al.*, 1992; Templeton,

1989). By comparison, the closest wild relative of the gray wolf, is the coyote, and they differ by about 4% mtDNA sequence (Lehman *et al.*, 1991). It can, therefore, be said that the molecular genetic evidence does not support theories that domestic dogs were derived from jackal ancestors (Lorentz, 1954).

Research based on canine ethology (Feddersen, 1978) clearly indicate that it were not individualistic jackals, but pack-living, social behaving wolves, which genetically transferred their behavioural patterns to the dog. Therefore, despite their diversity in size and proportion, dogs are 'domestic' gray wolves, and the wide variation in their adult morphology is most likely a result of simple changes in developmental rate and timing (Wayne, 1986). The wolf populations became smaller, due to a decrease in their habitat and, therefore, genotypes were fixed at random in the remaining populations, leaving a "fractured genetic landscape" (Wayne 1993). Furthermore, each population was preserved separately through captive breeding, which led to a continuation of artificial selection on a grand scale (Wayne, 1993).

It can therefore be safely said that dogs were domesticated from the wolf, as its sole ancestor. Different definitions can be used to define this concept and to explain this rather complex event. Domestication can be seen as active human intervention in natural selection, according to Hall (1987). Price (1984) explained domestication as follows: "...that process by which a population of animals becomes adapted to man and the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events recurring during each generation." In this sense, the process of domestication can then be seen as an evolutionary process, as well as a developmental phenomenon. The definition by

Price (1998), although simplified, "does not assume that genes and the environment operate as independent factors that additively combine to determine phenotypic outcome". It also means that the one process cannot be understood in isolation or separated from the other. Lickliter and Ness (1990) point out that the development of the domestic phenotype can only be understood as a complex interplay of organic, organismic and environmental factors during ontogeny. Because domestication implies change, it is expected that the phenotype of the wild animal and the domesticated version will differ.

1.3. MIGRATION OF THE DOG INTO AFRICA

The question now is, how the dog arrived on the Africa continent, as African wolves never existed? It is known that the domestic dog migrated with Mongoloid people to the Americas (Olson and Olson, 1977), arrived in Japan with early Jomo immigrants (Tanabe, 1991), later making its way with Eastern seafarers all along the archipelagos in the Pacific and finally reaching Australia where these dogs became the feral dingo (Corbett, 1995). The domestic dog arrived as an import into Africa in a similar manner, according to extensive research done by Gallant (1998/1999a,b,c; in prep.). At present, the earliest archaeological record on the African continent for *Canis familiaris* has been identified in the Nile estuary at Merimde-Benisalâme and Maadi (Boessneck, 1988). These fossils were dated to 4 500 BC. Archaeological findings indicate that, dating back to early Neolithic days, trade and cultural exchange existed between the people of the Nile valley and their contemporaries in the East (Hoffman, 1984) where, amongst other goods, dogs were used as trading products between nations and communities.

According to research and archaeological finds, the spreading of the dog throughout Africa happened in different directions and phases, which overlapped each other in time. These phases, as described by Gallant (1998/1999a,b,c; 1999; in prep.), are summarised as follows:

Phase 1: Pre-dynastic expansion along the Nile to Upper Egypt and Nubia

The dog, from its site of arrival in the Nile estuary, migrated throughout the Neolithic settlements along the lower Nile valley and further south into Nubia during the second part of the 5th millennium. This movement is not only substantiated by archaeological records and faunal finds, but also evident from art works and pottery in that era. The oldest known depiction of a dog in Africa is found on an Egyptian vase (dating back to 3 700 BC.) decorated with a hunting scene, in a cross-lined style typical for the first Naqada culture near Hierakonpolis (Hendirckx, 1992). This type of dog, which originated in the East, is called "Tesem" in Egypt and is related with the Schilluk and the present day Sloughi, Saluqi and other granioïds of the desert. A similar type of dog was described in a painting on a Naqada pot (Hiltzheimer, 1932). In both these cases, the dogs were all wearing collars.

A more sturdier, heavier-set type of dog (known as a 'molossian') was also represented in artworks from Hierakonpolis and on an ivory sceptre, and are typical for Sumarian statuettes from the same period (Quibell, 1900; Osborn and Osbornová, 1998). Sumerians were a non-semitic nation, which settled in Mesopotamia after coming from the Asian highlands and probably introduced the molossians (presumably descendants from the Chinese wolf). These dogs, together with the

granioïd Tesem, made their way to Egypt, but (unlike the Tesem) disappeared from the artistic scene and was only revived as from the XVIII dynasty, which could suggest an extinction of the early imported molossian stock (Osborn and Osbornová, 1998).

Remains of *Canis lupus familiaris* (these animals were not pure wolves anymore, but also not yet at the fully domesticated, dog classification stage) were found further south at Kadero, in Sudan, and was believed to be the furthest southward move of the dog at the time (Gautier, 1984a, b). Similar remains found in association with human skeletons at Kerma, Sudan, dated at 1 700 BC (Chaix, 1982, 1984).

Phase 2: Westward distribution with Saharan pastoral societies

Archaeological records show the domestic dog travelled westward, deep into the Sahara with the movement of the pastoral people (Smith, 1992; Roubet and Carter, 1984; Aumassip, 1984), partially overlapping in time with phase 1. This movement brought cultural unity between the Nile valley and the Saharan Neolithic people, as can be seen in their similar artistic expressions where the domestic dog is represented as from 3 700 BC (Camps, 1977; Brentjes, 1984).

Phase 3: Hesitant move of the Saharan frontier

The remains of two granioïd dogs were found in Niger, at the burial site of 'In Gall-Tegidda n Tesemt' and were dated at 1400 BC (Paris, 1984). Escavations in the Inland Niger Delta in Mali, yielded remains of domestic dogs that have been

identified as from *ca.* 250BC (Keech McIntosh, 1995), which suggested a very slow westward and south-westward radiation. More remains, dating back from approximately 400 – 1400 AD, were also found in a West African Iron Age site at Akumbu, in Mali (MacDonald, 1992). Researchers found a multitude of dispersed fragments of dogs that had apparently been eaten in a protohistoric site in Senegal (Van Neer and Bocoum, 1991). However, no entire skeletons were found.

Phase 4: The occupation of sub-Saharan Africa

Although no fossils of domestic dogs were identified, it can be assumed that the dog spread with the pastoral people from Sudan into Ethiopia and the tsetse free areas of the Central Rift of Uganda and Kenya as from the 4th millennium BC. People's dependence on domestic livestock such as sheep, goats and cattle between the 4th millennium BC and the 1st millennium AD in the Central Rift (Gifford-González and Kimengich, 1984) leads to the assumption that dogs were also part of the pastoral lifestyle. Similar to the movement in West Africa, the migration seemed to stop here for a period of time.

Evidence from comparative studies on ceramic styles and the relationship in language distribution has lead archaeologists to believe the spread of the Eastern Bantu speakers started from an area situated at the Cameroon-Nigerian border *ca.* 200 AD, which classifies it as Early Iron Age (200 – 1000 AD) (Huffman, 1997). It is important to note that a parallel migration of pastoralists were taking place much further south, which preceded the arrival of Early Iron Age people by a couple of centuries. The Stone Age Khoikhoi pastoralists travelled westwards through

Botswana, the south of Namibia and roughly followed the west coast to reach the present Cape of Good Hope just before Christianity reached these shores (Smith, 1992).

The routes of the Bantu expansion are not well known, but Gallant (1999) suggests that they became partially adapted to a well-settled pastoral life style, after contouring the equatorial forest, first in an eastward direction through the south of Sudan and then southwards through the Central Rift and interlacustrine region. They then acquired livestock and dogs and were possibly followed by more pariah dogs when they continued their migration through tsetse free corridors in Zambia, Zimbabwe and Botswana to reach South Africa.

Archaeozoologists have found the first bone fragments of dogs in South Africa dating back to about 570 AD at Diamant in the Northern Cape (Plug, 1996). By 650 AD the domestic dog reached the lower Thukela basin (Van Schalkwyk, 1994). It can thus be concluded that domestication of dogs did not occur in the Later Stone Age, and the first signs of domesticated dogs were found in the Iron Age settlements. Where these dogs came from and how they reached southern Africa is still speculative. Dogs presumably accompanied the Bantu-speaking people in their long migration southwards and were obtained by various means by hunter-gatherers who came in contact with new migrants (Voigt, 1983). It is also possible that the dogs were introduced to Bushman by Iron Age people; there is no record of any canid remains which definitely belong to *Canis familiaris* which pre-date the Iron Age. The only contender for this pre-Iron Age date, is a juvenile domestic dog that was found in a 'Strandloper' burial at Cape St. Francis (Chappel, 1968), which has been dated to

about 800 AD. There is sufficient scientific evidence to prove that, a thousand years before any possible serious Western influence in southern African canine development, the people in this part of the world were hunting with dogs that had become endemic to this area after migration from another part of Africa.

One of the most significant archaeological sites where fossils of domestic dogs were found is in Zimbabwe, at Mapungubwe. All these specimens found at Mapungubwe fit the description given by Von Petters (1934) of the basic South African native dog, which he describes as being a pariah type, with some greyhound features. The term "pariah dog" has been misunderstood and misinterpreted, Johan Gallant (representative of the Kennel Union of South Africa) has defined it as follows: "The primitive and original Early Neolithic pariah dog were offspring of protodogs, which had not been touched by domestication. Like their direct forebears they continued to roam as semi-wild scavengers in the vicinity of the ever-increasing human settlements. Their primitive state evolved over the years, but was also increasingly contaminated through occasional crossbreeding with domestic dogs or with domestic dogs that turned feral and joined their ranks" (Gallant, 1999). Therefore, when one considers the difference between feral and pariah dogs, the latter would be a dog that originates from primitive stock that had not been touched by domestication, and feral would strictly speaking refer to an animal of domestic stock that returned to a free roaming, scavenging state.

The fossils from Mapungubwe indicate two types or sizes: a slender, gracile form from South West Africa / Namibia and the Cape, and a more robust, stocky form from the old Transvaal and former Natal (KwaZulu-Natal) (Voigt, 1983). They were

generally medium-sized dogs with long muzzles and their coats differ in type and colour, with no standardised ear and tail carriage. These present-day dogs of the Bantu-speaking people have obviously been exposed to the influence of European breeds, especially the greyhound, but their basic form has a long and intricate history going back to the dogs of the Hottentots and larger dogs of the Transvaal Iron Age (Voigt, 1983).

The best example of these pariah type dogs (according to Gallant, pers. comm.) is those, which the Zulu people refer to as 'Isidqa' or 'Sica' (to name just one type). These dogs, registered as "Africanis", are the focus of this study and are found in most kraals and villages, north and south of the Tugela River, in KwaZulu-Natal.



Figure 1: An example of the Africanis breed found in southern Africa.

They are called different names by different tribes or communities, and also at different locations. Hall (1994a, b), a student at the University of Natal who previously studied anthropology at Rhodes University, described these variations in the endemic dogs as follows:

"The *I-Twina* is a gaze-hound hunting by sight and a sprinter, rather than a long-distance runner. It has the general conformation of a greyhound, and is identified by Zulu informants as having a wide chest and "large" stomach and a muzzle, which is shorter, and perhaps a little blunter.

The *I-Baku*, which means "big" or "floppy ears" in Xhosa, are still very popular, especially in Mpondoland, Transkei and southern Natal (KwaZulu-Natal). These dogs are also of the greyhound type, and true to their name, they have large, hanging ears, a coat that is usually long-haired, large, splayed paws characteristic of North African breeds suited to desert conditions and hind dew claws common to primitive dogs.

The *I-Nqeqe* among Xhosa-speakers or *I-Maku* among Zulu-speakers, seems to be the same dog, but again with local variations. It is shorter, more robust conformation, prick or semi-erect ears and curly tail, and its frequent ridge and plucky nature are almost identical to travellers portraits and descriptions of the Eastern Cape Khoi dog."

Dog breeding within the African community is mostly based on natural selection, rather than selective breeding by man. These dogs have their own inborn behavioural patterns, which include dominance between breeds and single partner preference displayed by dominant females. It is therefore possible that a kind of genetic unity is established and survives in these dogs.

1.4. PREVIOUS GENETICS STUDIES ON DOGS

No previous studies regarding the genetics of the endemic southern African dog breed have been done. Dogs, and especially their relationship with wolves and other canines, has however been the focus of several genetic studies by various scientists. Braend (1967), Steven and Townsley (1970) and Day *et. al.* (1971) were some of the first geneticists to report protein polymorphisms in canine serum. Similar studies in the late 1960's and early '70's provided proof of genetic polymorphisms of some enzymes in canine erythrocytes (e.g. Baur and Shorr, 1969; Braend and Austad, 1973; Meera Khan *et. al.*, 1973; Stevens and Townsley, 1970). Several polymorphisms in dogs (e.g. Fisher *et. al.*, 1976; Juneja *et. al.*, 1987; Lorenzini and Fico, 1995; Tanabe *et. al.*, 1991) have since then been identified and studied.

Although there seems to be a lack of genetic studies related to dogs in particular, the field of wolf genetics have been more widely explored and studied (e.g. Ferrel *et. al.*, 1980; Forbes and Boyd, 1996, 1997; Kennedy *et. al.*, 1991; Randi *et. al.*, 1993; Wayne *et. al.*, 1991a, 1992). The close relationship between dogs and wolves make these studies regarding wolf genetics therefore also valuable in the understanding and explanation of the genetics of dogs.

Several scientists were responsible for identifying and clarifying canine relationships and evolutionary histories, particularly with regards to the relationship between wolves and dogs, with the help of genetic techniques (e.g. Vilà *et. al.*, 1997; Wayne, 1986, 1993, 1996; Wayne and O'Brien, 1987; Wayne *et. al.*, 1987a, b).

All the above mentioned studies and investigations were done all using various different genetic techniques, ranging from allozyme electrophoresis (as in this present study) to DNA analysis. Analyses pertaining to the study of only the genetic core (DNA) of organisms have became more commonly accepted, with the advance of genetic technology in recent years (e.g. Forbes and Boyd, 1996, 1997; Wayne *et. al.*, 1991b, 1992). Protein electrophoresis has however remained a valuable and reliable technique for studying genetic issues and is still widely used (e.g. Ferrell *et. al.*, 1980; Kennedy *et. al.*, 1991; Lorenzini and Fico, 1995; Randi *et. al.*, 1993; Wayne and O'Brien, 1987; Wayne *et. al.*, 1991a).

1.5. AIMS FOR THIS STUDY

This is the first study to report on the genetic variation and differentiation between the southern African endemic breed and those of hybrids from less privileged communities in South Africa. Hybrid animals (i.e. mixed breeds) were selected due to relatively easy access to confiscated material from animal anti-cruelty societies, and to compare the expected high genetic variation values of these hybrids to that of the endemic breed. An indigenous, Middle Eastern dog population was also analysed to determine the genetic relationship between this type and the endemic population of southern Africa to indicate possible origin, migration and evolutionary patterns.

1. One of the primary aims of this study will be to determine if the genetic variation in the endemic Africanis breed is genetically distinct or differ markedly from levels present in other dog breeds.

- 2. Another main aim of this study is to determine the level of genetic diversity in Africanis dogs, in comparison with that of other domesticated dog breeds. This is important in order to ascertain if any significant genetic differences exist which would separate the Africaniss from common-known breeds.
- 3. The levels of genetic variation and differentiation in the endemic Africanis breed will help us to trace the origin and development of this endemic race, by comparing genetic characteristics of the Africanis with those of dogs from the Middle East, and thereby give insight into the evolution of these dogs. By studying the genetic similarity (or differences) between these breeds, a possible genetic relationship can be established.
- 4. The results of this study will be valuable in determining the conservation status of the endemic dogs, as well as providing a scientific basis for possible future breeding programs involving these animals.
- 5. This study will be able to shed some light on the usefulness of protein electrophoresis, concerning the controversy surrounding the various genetic techniques available for studying genetic related issues, and thereby support or disprove the value and viability of this method.