# Evolution of the brain of Plio/Pleistocene wolves

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Summary

The living subfamily Caninae can roughly be divided into three groups: the dogs, the foxes and the South American canids, which started to diverge somewhere in the Miocene. Here the evolution of the dogs is dealt with, starting with the genus *Eucyon*, which originated in North America during the Middle Miocene, and spread over the Old World. During the Pleistocene, the dogs were abundant in Eurasia, with as most well-known representative the Etruscan wolf, *Canis etruscus*, and later, during the Late Pleistocene the gray wolf, *Canis lupus*. The evolution of the dogs is followed on the basis of the evolution of their cerebrum. The specific patterns of grooves and folds on the cortex make an impression on the inner side of the neurocranium. By making a cast of this inner side, this pattern is revealed. The authors made such casts (endocasts) of all living dogs and red foxes, plus a number of fossil species and compared them mutually. It appears that foxes of the *Vulpes*-lineage have a short prorean gyrus, and a penthagon-like pattern of grooves on the sensory-motor region. Dogs (*Canis, Cuon, Lycaon*) have a long, broad and bilaterally compressed prorean gyrus, and an orthogonal pattern of the grooves on the sensory-motor region. *Eucyon* appears to be rather close to the *Vulpes*-pattern, whereas *Canis lepophagus* is very similar to living *Canis*. *Vulpes stenognathus* doesn't differ significantly from the living *Vulpes*.

Samenvatting

De huidige onderfamilie Caninae kan grofweg verdeeld worden in drie groepen: de honden, de vossen en de Zuid-Amerikaanse hondachtigen, die zich van elkaar scheiden ergens ver weg in het Mioceen. Hier wordt de evolutie van de honden besproken, die in het Midden Mioceen in Noord Amerika begon met het geslacht *Eucyon*, en zich daarna verspreidde over de oude wereld. In het Pleistoceen waren de hondachtigen talrijk in Eurazië, met als bekendste vertegenwoordiger de Etruskische wolf *Canis etruscus*, en in het Laat Pleistoceen de grijze wolf, *Canis lupus*. De evolutie van de honden wordt gevolgd aan de hand van de evolutie van hun grote hersenen. De specifieke patronen van groeven en windingen op de cortex geven een afdruk aan de binnenkant van de hersenschedel. Door een afgietsel van die hersenschedel te maken, wordt dat patroon zichtbaar. De auteurs hebben zulke afgietsels gemaakt van alle nu voorkomende wilde honden en vossen, plus van een aantal fossiele soorten en onderling vergeleken. De vossen van het geslacht *Vulpes* blijken een korte prorean winding te hebben, en een penthagon-vormig patroon van de groeven op de sensorische motorcortex. De honden (*Canis, Cuon, Lycaon*) daarentegen hebben een lange en samengeknepen prorean winding, en een orthogonaal patroon (als twee gebogen haakjes) op de sensorische motorcortex. *Eucyon* is nog dicht bij het *Vulpes*-patroon, maar de laat-pliocene *Canis lepophagus* is al echt *Canis*-achtig. De miocene *Vulpes stenognathus* wijkt niet significant af van de huidige soorten van het geslacht *Vulpes*.

## Introduction

Members of the canid subfamily Caninae are found all over the world, and radiated into many genera and species (fig. 1). Today, all living canids are classified in this subfamily. The other two subfamilies are the Hesperocyoninae and the Borophaginae (Tedford, 1978), both extinct. It is also this subfamily that entered the Old World, in contrast to the two others. They appeared quite successfull. One of our most common domestic animals, the dog, belongs to this group. And the two most common enemies of our other domestic animals (cattle and chickens), also belong to this same group: wolves and foxes.

It is therefore surprising that the evolution of features such as dentition and skull characters has been extensively studied for the Canininae, whereas the same cannot be said for the evolution of their brain cortex. Muscles leave scars on the bones, from which their shape and development can be inferred. The same is true for the brain, which leaves traces on the interior side of the neurocranium. This fact makes the study of the brain of fossil species possible, and thus the study of the evolution of this organ.

Radinsky (1973) reviewed the evolution of the canid brain as known sofar by that time, based on endocasts. Endocasts are casts, usually of latex or gypsum, made of the interior of whatever structure. They can be artificial, man made, or natural, caused by fossilization of infillings. The impressions of the inner surface of the structure are copied (in negative) on the endocast. In the case of the neurocranium, the endocasts reveal the

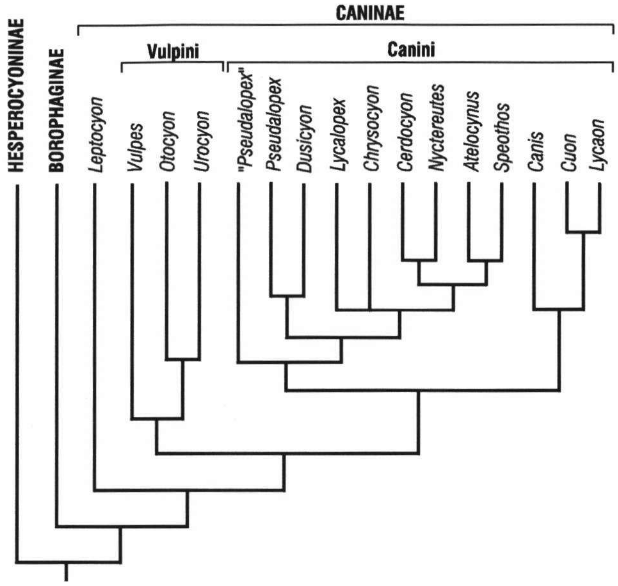

Fig 1 Cladogram of the family Canidae showing the phylogenetic relationships of the genera within the subfamily Caninae. Redrawn from Tedford, Taylor & Wang (1995)

Cladogram van de familie Canidae waaruit de verwantschap blijkt tussen de verschillende geslachten van de onderfamilie Caninae. De onderfamilies Hesperocyoninae en Borophaginae zijn uitgestorven, evenals het geslacht *Leptocyon*. Onder de vossen (Vulpini) vallen de rode vos, de grootoorvos en de grijze vos. De honden (Canini) vallen uiteen in twee hoofdgroepen. Aan de rechterkant: *Canis*, de dhole (Indische rode hond) en de hyenahond. Aan de linkerkant, van links naar rechts: de vijf Zuid Amerikaanse zorro's en manenwolf, de wasbeerhond, de kortoorvos en de boshond. Gebaseerd op Tedford, Taylor & Wang (1995).

impressions caused by the folds and grooves of the brain cortex during the animal's life. In this way, it is possible to study the cortical landscape of a specimen of which no brain is available. Especially for fossil specimens this is the only way to study the external morphology of the brain. The neurocranium is used as a mould to make a cast of the lost brain. In fact, the external morphology and the size of the brain are more acccurately seen on endocast than on fresh brains. This is because the brain changes its shape once it is freed from its hard bone shell (Edinger, 1948). Natural endocasts arise when the neurocranium is filled with hard matrix during fossilisation, after which the bone itself dissolves. A stone core remains, made of the sediment that used to fill the braincase. Natural endocasts are very rare.

Apart from Radinsky's work little has been published on brain morphology of fossil Caninae. Descriptions of endocasts of the cerebrum of fossil species are known only for the raccoon dog "*Nyctereutes sinensis*" (*Nyctereutes* sp. in Tedford & Qiu, 1991, and *N. procyonoides* in Soria & Aguirre, 1976) from the Pleistocene of Choukoutien (Pei, 1934), for a «*Canis*» sp. and *Nyctereutes* sp. from the Late Pliocene (Czyzewska, 1981), for a *Canis dirus* (Moodie, 1922), and of an arctic fox from the Late Pleistocene (Vanura, 1943).

From the scarce studies available, one thing immediately arises. There appears to be an amazing uniformity of the pattern of folds and the grooves separating them on the large brain all living Caninae. This uniformity can be extended into most of the extinct species, and is probably due to the fact that the adaptive radiation of the Caninae started in a not too remote past, somewhere during the Middle to Late Miocene. Small, crucial differences are, however, distinguishable, and on the basis of these differences, the evolution of the Canine brain can be followed along the phylogenetic path. We focus on the wolf lineage of North America, Eurasia and Africa, and omit the South American canids (several zorro's, maned wolf, bush dog). The South American canids started to radiate during the Late Pliocene with *Pseudalopex* and *Protocyon*, and are endemic to the subcontinent, and are not found elsewhere. Endemic species are known to radiate far beyond the extent seen on the mainland (De Vos & Van der Geer, in press), so South American canids quite probable do not follow the same evolutionary pattern as mainland relatives. For similar reasons we omit *Cynotherium sardous*, the pleistocene Sardinian dhole, which is endemic to Sardinia-Corsica.

## Materials and methods

The endocasts that are used in this study are made according to the technique described by Radinsky (1968). He developed a non-destructive technique of producing endocasts with the use of latex. A thin (1-2 mm) layer of latex is applied inside the braincase in successive layers. Since the latex is very elastic it can be pulled out through the foramen magnum, and once it is out of the braincase, it pops out in its original shape.

Endocasts were taken of all living Caninae species, except for the South American species, and from some fossil Caninae (for scientific names, see table 1). The endocasts of living species were mainly taken from the collections of the National Natural History Museum, Leiden, The Netherlands; the endocasts of fossil species were mainly taken from the collections of the American Museum of Natural History, New York. The endocasts used by Radinsky (1973) are stored in the Field Museum of Natural History, Chicago.

To describe the pattern of the grooves that separate the many well developed folds on the cerebral cortex, we use the (translated) names given for the folds and grooves of the domestic dog brain by Filimonov (1928, represented by Adrianov & Mering, 1959).

The endocasts are presented with the help of drawings to emphasize on characters that are typical for the species and in order to avoid individual variation. Special care has been taken on the preparation of the cerebrum, while all the other parts of the brain are draftly presented.

Key to Institutional Abbreviations:
AMNH American Museum of Natural History, New York
F:AM Frick Collection of the American Museum of Natural History, New York
NNML National Natural History Museum, Leiden, The Netherlands
GIN Geological Institute of Russian Academy of Sciences, Moscow
FMNH Field Museum of Natural History, Chicago

## History of Pliocene/Pleistocene canids

The first dog in Eurasia and Africa belongs to the genus *Eucyon* and occurs during the late Late Miocene (Late Turolian). Phylogenetically, it is linked to *Eucyon davisi* of the Late Miocene (Hemphillian) of North America (Rook *et al.*, 1991) and the Pliocene of China (Tedford & Qiu, 1996) and Greece (Koufos, 1997). *E. monticinensis* is the oldest Eurasian species (late Late Miocene; Italy and Spain), followed by *E. odessanus* (earlier "*Vulpes odessana*") of the Early Pliocene of the Ukraine (Tedford & Qui, 1996). Related forms *E. minor* and *zhoui*) are found in Pliocene deposits of China (Flynn *et al.*, 1991; Tedford *et al.*, 1991). Probably also "*Canis*" *kuruksaensis* from the Late Pliocene of Tadjikistan (Sotnikova, 1979) and the new genus? aff. *Canis brevirostris* from the Pliocene of Langebaanweg (Barry, 1987) are also related to the genus *Eucyon* (Sotnikova, in press; Rook, 1993).

A faunal turn-over, or faunal event in the sense of Repenning (1967) characterizes the boundary between the end of the middle Villafranchian (MN17; Senèze Faunal Unit, 1.8 Ma) and the beginning of the late Villafranchian (MN18; Olivola Faunal Unit, 1.7 Ma) in Europe, or the Plio-Pleistocene boundary, appointed to 1.77 Ma (Berggren *et al.*, 1995). The event is sometimes called the wolf-event (Azzaroli, 1983; Torre, 1992 *et al.*), and is marked by the disappearance of *Nyctereutes megamastoides, Gazella borbonica, Eucladoceros tegulensis, Pseudodama* cf. *lyra*, and the occurrence of *Pachycrocuta brevirostris, Panthera toscana, Eucladoceros dicranios, Pseudodama nestii* and the Etruscan wolf *Canis etruscus* after which the event was named (Azzaroli 1977, 1983; Masini *et al.* 1994). Before the Plio-Pleistocene boundary, finds of *Canis* are not only rare, but also phylogenetically speaking unsure. Examples are "*Canis*" *cipio* of the Late Miocene of Spain (Crusafont, 1950), "*Canis*" *michauxi* and "*Canis*" *adoxus* of the Early Pliocene of France (Martin, 1973; Tedford & Qiu, 1996; but *Vulpes adoxus* in Pons Moyá & Crusafont, 1976, and *Eucyon adoxus* in Rook, 1993), and possibly also "*Canis*" *senezensis* (Martin, 1973; however, the Senèze material is mixed (Azzaroli *et al.*, 1988), and this canid resembles *C. arnensis* of the Early Pleistocene, according to Rook & Torre, 1996). The first true *Canis* occurs in Italy during the Late Pliocene (Rook & Torre, 1996), but it is the Etruscan wolf that is well-represented in Early Pleistocene sites.

The dispersal of *Canis* in Eurasia started during the Late Pliocene (about 3 Ma), but originated in North America during the Late Miocene (about 5.5 Ma). There, a continuous fossil record is present from an archaic *Canis* through the coyote-sized *C. lepophagus* of the Late Pliocene to a variety of forms during the Pleistocene (*C. edwardii, C. cedazoensis, C. armbusteri, C. dirus*; Nowak, 1979), and finally to the gray wolf *C. lupus* (Rook, 1993).

The *Canis* dispersal to Eurasia is inferred from a *C. etruscus*-like form of about 3 Ma (Flynn *et al.*, 1991), and, slightly later, a *C. arnensis*-like form and a *C. falconeri*-like form (2.5 Ma) in deposits in China. The genus *Cuon* also appears during the Pliocene in China During the Pleistocene it dispersed both to North America and to Europe.

Thus, during the Early Pleistocene in Europe three dogs are recognized: a wolf-like *Canis*

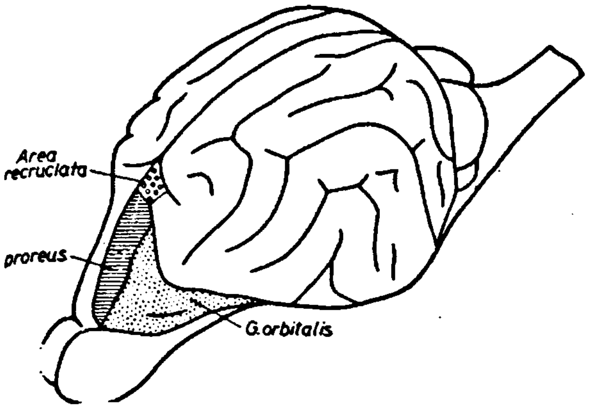

Fig 2 The frontal pole of the cerebral cortex of the dog with the prefrontal and sensory-motor regions. Redrawn after Kreiner (1964)

Het voorste deel van de cortex van de grote hersenen van de hond met de prefrontale regio (vertikale strepen) en de sensorische motorcortex (horizontale strepen). De sensorische motorcortex heeft op zijn beurt een belangrijke winding, de sigmoid winding, met de coronale, cruciate en de ansate groeven. De prefrontale regio is gekenmerkt door de orbitale en de prorean windingen. Gebaseerd op Kreiner (1964)

*etruscus*, a jackal-like *C. arnensis*, and the large *C. falconeri*. The terms wolf-like and jackal-like are mainly given on the basis of body size and possible ecological niche, and not on the basis of direct connection with the living forms. The systematic position of the hypercarnivorous *C. falconeri* (Europe: Early Pleistocene; China: Late Pliocene) is as yet unclear; and sometimes placed under a separate subgenus *Xenocyon* (Rook, 1993, 1994). *C. falconeri* was widely distributed.

Later, these three species were replaced by the species *C. mosbachensis* and *C. (Xenocyon) lycaonoides* during the Middle Pleistocene, and they on their turn by the modern gray wolf, *C. lupus*, during the Late Pleistocene.

In Africa the jackals prevail. The black-backed jackal occurred during the Early Pleistocene in Tanzania (Pohle, 1928) and South Africa (Ewer, 1955). Two large sized species, too, occur at that time: *C. africanus* and *C. atrox* (Ewer, 1995; Savage, 1978). The oldest record of the Cape hunting dog is from the Middle Pleistocene of South Africa (Hendey, 1974), but its origin is unknown. Rook (1993) relates it to the subgenus *Xenocyon*, in which he includes *C. falconeri*, *C. lycaonoides*, *C. africanus* and *C. atrox*, thus all larger sized Caninae with hypercarnivorous dentitions except for *Cuon*.

## Evolution of the brain

To follow the differences that evolved on the brain cortex during the phylogeny of the dogs, we studied especially the morphology of the frontal pole of the brain, which includes the so-called prefrontal cortex, and the sensory-motor region. The first region is represented on the endocasts by the orbital and prorean folds, the second region mainly by the sigmoid folds (fig. 2). It is known that the now living foxes of the *Vulpes*-lineage and raccoon dogs have a small prorean fold on the prefrontal cortex, whereas the wolves of today have a large and broad prorean fold, although they share a common ancestor. In addition, the first group have a significantly smaller brain. It would be interesting to know where exactly in the phylogeny of the canids these differences appeared, and also whether it can help us to solve taxonomical problems. It is known that the larger prorean fold appears after the branching off of the foxes and the raccoon dogs, somewhere in the Early Miocene, but before the appearance of the modern gray wolf. What happened between *Eucyon* and *Canis*, and do they differ from the younger *C. etruscus* and *C. arnensis*?

In order to follow the evolution of the brain it is useful to start with the known end products of this evolution: the living caninae. A second step is the analysis of their fossil ancestors, determined as such by numerous characters of dentition, skull, postcranials, mitochondrial and nuclear DNA, and allozymes. As a third step, with the help of the reconstructed evolution of the brain, it might be possible to interpolate taxonomically problematic taxa to their most likely sister taxa.

## Brain studies on the wild Caninae

The existing literature on the anatomy and other aspects of the nervous system of the domestic dog is enormous. In contrast, relatively few has been written on the brains of the wild dogs. Gervais (1870) was the first, followed by Krueg (1880), Mivart (1885), Klatt (1928), Atkins (1970), England (1973), Radinsky (1973), Atkins & Dillon (1971). Other studies are limited: Atkins (1978: red wolf, coyote) and Boulay & Verity (1973: gray wolf, coyote, raccoon dog).

From these studies and from personal observations it becomes clear that the external cerebrum anatomy of the modern dogs is amazingly uniform without important differences between the genera. All dog brains appear to have the same basic pattern of grooves and folds on the cortex. This gives you "the superficial impression that if you've seen one canid brain, you've seen 'em all" (quoted from Atkins, 1978). This basic pattern is not affected by brain size since it is the same form from the smaller species (raccoon dog: *Nyctereutes procyonoides*) to the largest species (gray wolf: *Canis lupus*). The only differences of allometric nature are that the grooves on the cerebral cortex of the larger brained dogs are more wavy and that there are more secondary grooves. These differences are due to the nature of the outer layer of the brain which is organized as a thin sheet with a limited thickness. It can therefore only increase by surface expansion, while the underlying white matter expands as a volume (see reviews by Sacher, 1970, Jerison, 1973).

However, there are two main distinctive features amongst the brains of the different dogs, both found in the frontal lobe. Firstly, the pattern of grooves of the sensory-motor region can roughly be divided into two types. Secondly, the shape and the relative size of the proreal fold differs considerably between fox-like canids and wolf-like canids.

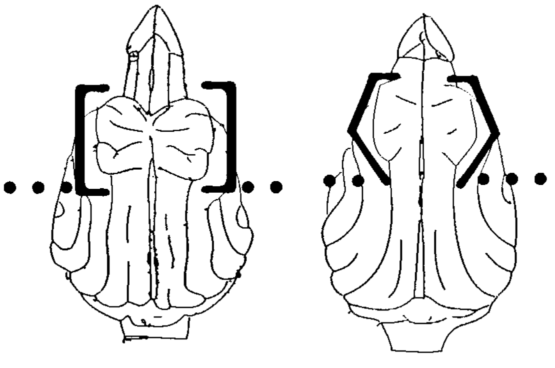

Fig 3 Different types of outlines of the coronal grooves on the dorsal surface of the cerebrum: the pentagon type (right), typical for *Vulpes*, and the orthogonal type (left), typical for *Canis*

De verschillende patronen op de bovenkant van de grote hersenen, gevormd door de coronale groeven op de sensorische motorcortex. De pentagon-vorm of vijfhoek (rechts) vinden we bij vossen van het geslacht *Vulpes* (rode vos); de orthogonale of rechthoekige vorm (links) vinden we bij hondachtigen van het geslacht *Canis* (wolf, coyote, jakhals) en nauwe verwanten (dhole of indische rode hond, hyenahond)

## Sensory-motor region

The sensory-motor region occupies the sigmoid fold, of which the outer lower borderline is formed by the coronal groove (Kreiner, 1964). Klant (1928) suggested that the sigmoid folds expand more abruptly in the dog group than in the foxes, but Radinsky (1973) noted that there is a considerable overlap in that feature, making this character unsuitable as distinguishing feature between the brains of the living Caninae genera. However, though indeed there is an overlap in the degree of expansion of these folds, the outline that is created by the coronal groove and the ansate groove on the dorsal surface of the large brain can roughly be distinguished into two types (fig. 3):

- ○ **the penthagon type: the coronal grooves diverge caudally more than rostrally, creating a «pentagon-like» outline. This type is typical for the genus *Vulpes*.**
- ○ **the orthogonal type: the sigmoid folds expand out more abruptly than in the previous groups. The ansate and the coronal grooves create an «orthogonal» outline like two brackets. This type is typical for the genus *Canis*.**

## The proreal fold

The differences in the shape and the relative size of the proreal fold were noted more than hundred years ago by Huxley (1880). He noted that this fold in some Caninae tends to be longer and narrower than in some others. This was one of the differences that were used by him to divide the Caninae into two groups, the *alopecoid* (fox-like) with a relatively small fold and the *thooid* (dog-like) with a relatively large fold, compared with the length of the large brain. The proreal fold tends to be longer and narrower in the larger species than in the smaller ones, but Radinsky (1973) concluded that this difference has nothing to do with size on itself. His major argument was that jackals like the black-backed jackal and the side-striped jackal have a longer and narrower proreal fold than foxes of comparable brain size like the gray fox and the common red fox.

## Endocasts of living wild dogs

In the group of wolf-like species are included animals of medium size (side-striped jackal, golden jackal, black-backed jackal) and of larger size (gray wolf, coyote, Simenian jackal, red wolf,

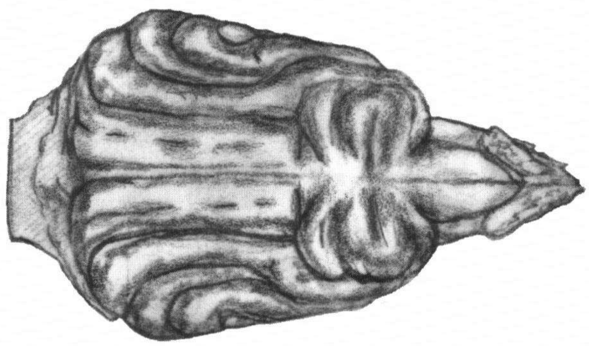

Fig 4 Endocast of the living coyote (*Canis latrans*)

Endocast van de coyote (*Canis latrans*) als voorbeeld van het typische *Canis*-patroon. De groeven op de sensorische motorcortex vormen een orthogonaal of rechthoekig patroon, en de prorean winding is lang en aan beide zijden vernauwd

dhole, Cape hunting dog). The gray wolf has the largest brain of all living wild Caninae.

The two halves of the large brain widen out quite abruptly immediately behind the presylvian groove. This is evident in all members of this group, but slightly less so in the dhole and the Cape hunting dog. The gray wolf has an angular profile. The gray wolf, the red wolf and the Simenian jackal have, relatively spoken, the narrowest prefrontal region. Although the gray and the red wolf have a similar long prefrontal region (England, 1973), this region is relatively thicker in the gray wolf than in the red wolf (Atkins, 1979). In general, in all members of the genus *Canis* the proreal pyrus is very long and bilaterally constricted, more than in any other member of the family Caninae. The proreal fold of the dhole and the Cape hunting dog is shorter but considerably thicker.

The orbital fold of the smaller species (golden jackal, side-striped jackal, black-backed jackal) has only one groove ( the proreal groove), which separates the orbital fold from the proreal fold. The coyote, dhole and Cape hunting dog have one more groove, the intraorbital groove which runs parallel to the lower section of the presylvian groove. The Simenian jackal and the gray wolf have three grooves in that region: the proreal groove, the intraorbital groove and another, unnamed groove that forms the dorsal boundary of the anterior portion of the orbital fold.

In all wild dogs the sigmoid folds expand very abruptly. This creates on the dorsal surface of the large brain an orthogonal outline of the ansate and the coronal grooves (fig. 4). The expansion of the sigmoid folds is smaller in the golden jackal and the side-striped jackal. This has probably to do with their smaller brain size, though the sigmoid folds of a only slightly larger jackal, the black-backed jackal, are expanded as in the other members of the *Canis* group (wolves, Simenian jackal, coyote).

In the coyote the coronal groove may continue onto the medial surface with the lesser cruciate groove, but this is not a constant feature.

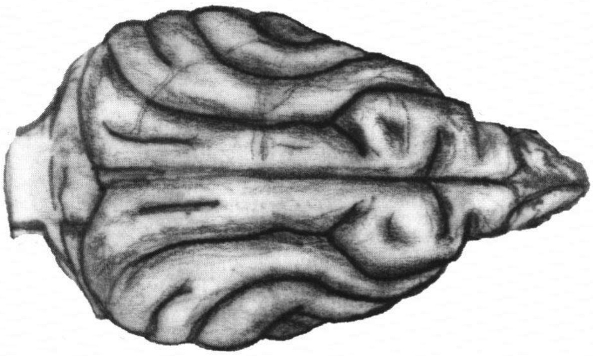

Fig 5 Endocast of the living red fox, *Vulpes vulpes*

Endocast van de rode vos (*Vulpes vulpes*) als voorbeeld van het typische *Vulpes*-patroon. De coronaal groeven op de sensorische motorcortex vormen een pentagon-vormig of vijfhoekig patroon, en de prorean winding is erg klein

The gray wolf, dhole and Cape hunting dog have a dimple in the middle of the coronal fold. The dhole and Cape hunting dog have a short groove that divides the anterior sigmoid fold into two parts.

## Endocasts of living red foxes

The foxes of the red fox lineage include animals of small or medium brain size. The desert fox, or fennec, has the smallest brain of all living Caninae. No important distinguishing features were found between the brains of the species of the genus *Vulpes* that were examined (common red fox, Bengal fox, cape fox, rueppellian fox, desert fox). In these species the proreal fold is very small and the coronal grooves form a pentagon- like outline (fig. 5). The large brain of the arctic fox differs slightly from the other *Vulpes* species. The frontal lobes are very high and the

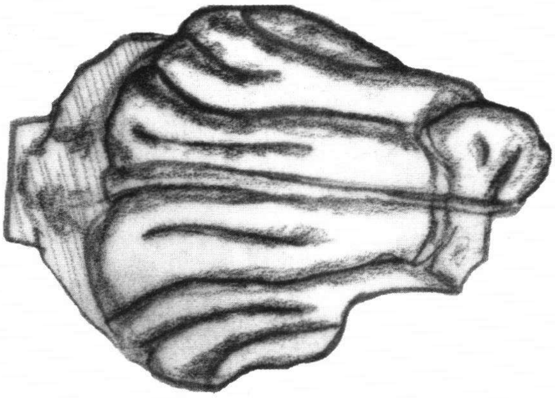

Fig 6 Endocast FMNH PM 58960 of *Vulpes stenognathus* from the Late Miocene of North America (F:AM 49284)

Endocast FMNH PM 58960 van *Vulpes stenognathus* uit het Laat Mioceen van Noord Amerika (F:AM 49284). De *bulbus olfactorius* ontbreekt aan beide zijden, evenals een deel van het voorste gedeelte van de grote hersenen. De sensorische motorcortex is beschadigd, maar toch lijken de groeven een pentagon-vormig of vijfhoekig patroon te vormen,

small brain is more overlapped. Furthermore, the proreal fold of the arctic fox is more developed than in any other fox. Also the ansate groove and the postcruciate groove are very well developed, and form a pattern of grooves on the sensory-motor region that is distinct from the other *Vulpes* species.

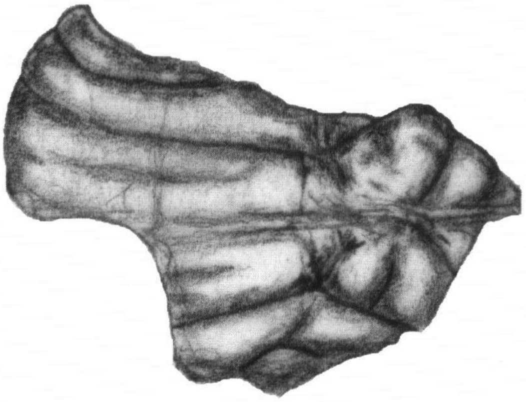

Fig 7 Endocast of *Eucyon davisi* from the Late Miocene of Arizona (F:AM 63005)

Endocast van *Eucyon davisi* uit het Laat Mioceen van Arizona (F:AM 63005). Hoewel dit exemplaar ernstig beschadigd is, is toch het grootste gedeelte van de sensorische motorcortex intact. De groeven vormen een pentagon-vormig of vijfhoekig patroon. Daarmee lijkt *Eucyon* meer op *Vulpes* dan op *Canis*

## Endocasts of fossil canids

### *Vulpes*

The first products of the Caninae principal radiation were *Vulpes* and *Eucyon* (Hunt, 1996). During the Late Miocene the first fox of the red fox lineage occurred in North America with the species *Vulpes stenognathus*. During the whole Late Miocene the species was very abundant, but it is seldom found in Pliocene localities. The red fox lineage dispersed to Asia during the Pliocene.

Specimen FMNH PM 58960 (described by Radinsky, 1973) is an endocast from skull F:AM 49284, coming from the Late Miocene of North America. It lacks the olfactory bulbs and part of its frontal region. Although the sensory-motor region is not well preserved, it can be observed that the cruciate groove is quite long and the sigmoid fold is well-developed. The expansion of the sigmoid folds is reflected in the bowing out of the coronal grooves. Also the postcruciate and ansate grooves are present (fig. 6). However, no distinguishing feature could be found between this endocast and that of comparable sized living *Vulpes* species.

### *Eucyon*

The genus *Eucyon* appears for the first time during the Middle Miocene in Orgeon and Nevada. Gradually it dispersed over the rest of North America, to Asia and to Europe (Middle Miocene - Early Pliocene). The last occurrence seems to be Late Pliocene (Yushe, China).

The fragmentary skull F:AM 63005 of *Eucyon davisi* originates from the Late Miocene of Arizona (described by Radinsky, 1973: 183, as a Pliocene coyote *Canis* cf. *C. latrans*). It preserves only the dorsal part of the large brain, the sensory-motor region and the region of the lateral grooves. Unfortunately the orbital and proreal folds are missing. The coronal and ansate grooves create a pentagon-like outline on the dorsal surface (fig. 7). The general groove pattern of the preserved region is similar to that of *Vulpes*, and not to *Canis*.

### *Canis*

At the end of the Miocene the first *Canis* species appears in North America, but not earlier than the Pleistocene members of the genus invaded Europe, Africa and South America. *Canis* is in general larger than *Eucyon*, and has a more advanced dentition. Gradually its size increases, and during the Late Pliocene it reaches the size of the living coyote. Sometimes the genus *Canis* is

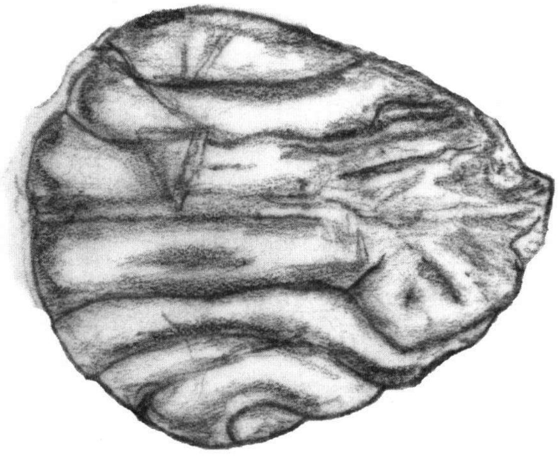

Fig 8 Endocast of *Canis lepophagus* from the Late Pliocene of Texas (AMNH 104782)

Endocast van *Canis lepophagus* uit het Laat Plioceen van Texas (AMNH 104782). Het voorste deel met de prorean en orbitale windingen ontbreekt, maar het lijkt erop dat de prorean winding net zo ontwikkeld is als bij de grijze wolf (*Canis lupus*). Het patroon van de windingen op de sensorische motorcortex is echter minder uitgesproken als bij de grijze wolf, en neigt naar een pentagon-vormig of vijfhoekig patroon als bij de rode vos

considered to include *Xenocyon* as a subgenus (for example, Rook, 1994). The oldest *Xenocyon* is *C. falconeri*, which occurred during the Pliocene and Early Pleistocene in Eurasia and Africa, and is replaced by *C. (Xenocyon) lycaonoides* during the Middle Pleistocene in Europe.

Specimen AMNH 104782 of *Canis lepophagus* is a cast of a nearly complete endocast from a Late Pliocene specimen of Texas (cast of WT 769), but lacks the rostral part of the proreal and orbital folds. The external brain anatomy is in essence the same as in living *Canis* species. Although the prorean fold is incomplete, it is not difficult to see that indeed it has a development similar to the modern wolf-like animals (fig. 8). However, the expansion of the sigmoid folds seems to be less than in the living *Canis*. This gives the impression that the groove pattern of the sensory-motor region had not yet attained its modern condition.

Specimen GIN 3722-144 is a complete endocast from an undescribed *Canis (Xenocyon) lycaonoides* from the Kolyma, Siberia, Middle Pleistocene (Sotnikova, pers. comm.). Its characters are typical for the now living wild dogs. The brain halves abruptly widen out immediately behind the presylvian groove. The frontal part is characteristically elongated and narrowed. The proreal fold is long and bilaterally constricted and there are two grooves on the orbital fold. The orthogonal type of groove pattern on the sensory-motor region is the typical configuration for the *Canis* group.

## Evolution of the Caninae cerebrum

Based on the endocasts of the living and fossil dogs that were described above, it is possible to reconstruct the evolution of the frontal part of their brain, from the Pliocene through the Pleistocene. Data on the phylogeny are mainly from Nowak (1979), Berta (1988), Tedford & Qui (1996), Rook (1992, 1993, 1994), Wang *et al.* (1999), Sotnikova (1989).

At the end of Middle Miocene the genus *Eucyon* made its appearance in North America (Tedford & Qiu, 1996). The groove pattern of the sensory-motor region is close to that of the foxes of the genus *Vulpes*, as the coronal groove and the ansate groove create on the dorsal surface a pentagon-like outline. The form of the prorean fold of *Eucyon* is at the moment unknown.

At the end of the Miocene the first *Canis* species appeared in North America. The external cerebrum anatomy of one of the earliest species, *C. lepophagus*, is similar to the living *Canis* species. The prefrontal region of *C. lepophagus* is very well developed like in living *Canis*, and the groove pattern on the sensory-motor cortex has the orthogonal-shape as in *Canis*. This latter feature is is a crucial difference with *Eucyon* and *Vulpes*, who have a pentagon-like shape. At this point of the evolution, the species of the wolf-lineage seems to have clearly departed from the red fox-lineage.
After *C. lepophagus* the Pleistocene dogs of Europe evolved, but the difference between *C. etruscus* and *C. (X) lycaonoides* on one side and the modern *Canis*, to which the gray wolf, the coyote and the jackals belong, on the other side, is only gradual. The dhole and the Cape hunting dog are *Canis*-like, but differ in the shape of the frontal pole, which is relatively thick and short compared to *Canis*. In addition, they have an extra median groove on the anterior sigmoid fold. The radiation of the wolf-lineage seems to have resulted in at least three Pleistocene products: the wolves, coyote, and jackals (*Canis, Xenocyon*), the dhole (*Cuon*), and the Cape hunting dog (*Lycaon*).

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