

External brain anatomy in relation to the phylogeny of Caninae (Carnivora: Canidae)

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Received July 2002; accepted for publication January 2003

Caninae is one of the most studied mammalian groups, nevertheless there are relatively few comparative studies on their neuroanatomy. This work contributes to a better knowledge of this subfamily, since it describes the external cerebrum anatomy of 29 out of the 35 living Caninae species, 11 of which are described for the first time. Information about their frontal region appears to be a welcome supplement to the study of the phylogeny. Two distinctive features are recognized, that can be traced back in the fossil record: the sulcal pattern medial to the coronal sulci, and the shape and relative size of the proreal gyrus. Four types are described for the first feature: (1) orthogonal: *Canis*, *Lycaon*, *Cuon*, *Atelocynus*, *Speothos*, (2) pentagonal: *Vulpes*, *Alopex*, *Otocyon*, †*Eucyon*, (3) parenthesis-like: †*Dusicyon*, *Pseudalopex*, *Chrysocyon*, (4) heart-shaped: *Urocyon*, *Cerdocyon*, *Pseudalopex culpaeus*, *Nyctereutes*. Three types are described for the second feature: (1) elongated and bilaterally compressed: *Canis*, *Cuon*, *Lycaon*, *Atelocynus*, *Speothos*, *Cerdocyon*, †*Dusicyon*, *Chrysocyon*, *Pseudalopex*, †*Nyctereutes sinensis*, †*N. tingi*, (2) small: *Vulpes*, *Otocyon*, *Urocyon*, *Alopex*, (3) wide and low: *Nyctereutes procyonoides*. On the basis of these features some phylogenetic interpretations are presented: the fossil Asian *Nyctereutes* is close to *Cerdocyon*, *Speothos* is close to *Atelocynus*, *Chrysocyon* is not related to *Canis*, *Urocyon* differs from *Vulpes* and *Pseudalopex culpaeus* differs from the rest of the *Pseudalopex* species. © 2003 The Linnean Society of London. *Zoological Journal of the Linnean Society*, 2003, 138, 505–522.

ADDITIONAL KEYWORDS: endocasts – Pleistocene – Pliocene – South American canids – taxonomy.

INTRODUCTION

The Caninae can be considered a successful group; members of this subfamily of Canidae are found all over the world. They are representatives of the vast canid radiation into many genera and species. All species of living canids are classified in this subfamily (Tedford, 1978). The relationships among the various genera within the Caninae are still a source of argument, in contrast to the concept of the subfamily itself, which has never been challenged (Rook & Azzaroli-Puccetti, 1997; Wayne *et al.*, 1997). The numerous systematic studies so far could not unequivocally solve the problem (e.g. Langguth, 1975; Clutton-Brock, Corbert & Hills, 1976; Van Gelder, 1978; Berta, 1987, 1988; Wayne & O'Brien, 1987; Wayne, Nash & O'Brien, 1987a,b; Wayne *et al.*, 1989, 1997; Tedford, Taylor & Wang, 1995).

In the present work a contribution to solving this problem is presented in the form of an analysis of the evolution of the external morphology of the anterior part of the cerebrum as it is reproduced on the endocranial casts (endocasts). In most mammals the endocasts reproduce almost every detail seen on the surface of the cerebrum, which makes it possible to study the external brain anatomy of species whose brains are not available. Contrary to the cerebrum, the cerebellum, as represented on endocasts, offers little information of phylogenetic value, and the ventral brainstem even less so (Atkins, 1978). They are therefore not described in this study. For information about the cerebellum of some wild canids, the reader is referred to Atkins (1970) for the maned wolf, the dingo and several foxes, and to Atkins & Dillon (1971) for the three jackals, the grey wolf and the red wolf, with some taxonomic and phylogenetic interpretations.

The existing literature on the anatomy of the nervous system of the domestic dog is extensive (Fox,

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1971; Beitz & Fletcher, 1993; and references quoted therein), in remarkable contrast to that of the wild members of the same subfamily. Early studies on the external brain anatomy of wild Caninae are known from Gervais (1870), Flower (1880), Huxley (1880), Krueg (1880), Mivart (1885) and Klatt (1928). More recent studies are those of England (1973) on the cerebrum of *C. latrans*, *C. lupus*, *Urocyon cinereoargenteus*, *V. vulpes* and the dingo, and of Atkins (1978) on *C. latrans* and *C. rufus*. Among the most elaborate works on the wild Caninae brain are those of Radinsky (1969, 1973a, 1978). He (Radinsky, 1973a) took several endocranial casts (endocasts) from all available living species and described and figured some foxes (*V. vulpes*, *V. zerda*, *Urocyon cinereoargenteus*, *Otocyon megalotis*), some dogs (*C. lupus*, *C. adustus*, *C. simensis*, *Lycaon pictus*), some South American canids (*Cerdocyon thous*, *Pseudalopex sechurae*, *Speothos venaticus*) and the raccoon dog (*Nyctereutes procyonoides*). In addition he gave brief comments on a few other members. Later, he figured *V. vulpes* again, and *C. mesomelas* (Radinsky, 1978). He also presented a series of endocasts from fossil Canidae (†*Leptocyon* spp., *Canis* cf. *C. latrans* (†*Eucyon davisii* in this study), *Vulpes* sp. (†*V. stenognathus* in this study), †*Nyctereutes megamastoides* (†*N. sinensis* in this study), most of them described for the first time (Radinsky, 1973a). He also made an attempt to reveal the evolution of their external brain morphology (Radinsky, 1969, 1973a), with functional and phylogenetic implications.

From these studies and from personal observations it becomes clear that the external morphology of the cerebrum of the modern Caninae is characterized by uniformity and the lack of important differences between the genera. All Caninae brains have the same basic sulcal pattern. As Atkins (1978) already noted, it creates the superficial impression that 'if you've seen one canid brain, you've seen 'em all'. This implies that macroscopic observations, without inquiring further into the anatomy of the cortex, may be sufficient to interpret cortical homologies. The problem of these homologies (see, amongst others, Haller Von Hallerstein, 1934; Kreiner, 1968; Campbell & Hodos, 1970) is less relevant in the case of Caninae, due to the amazing uniformity of the sulcal pattern of the cerebrum of all living, and most of the extinct Caninae.

However, from the present study it appears that there are two main distinctive features amongst the brains of modern Caninae: firstly, the sulcal pattern of the cortex medial to the coronal sulci and secondly, the shape and the relative size of the preoreal gyrus. On the basis of these two features some persistent problems of canid phylogeny are approached in this paper.

MATERIAL AND METHODS

Although Gervais (1870) was the first to use endocasts in a study of carnivore brain morphology, we follow Radinsky's (1968) method, described by Hildebrand (1968). The endocasts are produced according to a non-destructive technique using latex. With this method, successive thin (1–2 mm) layers of latex are applied on the interior surface of the braincase.

Each new layer is applied when the former has hardened. Since latex is very elastic it can be pulled out through the foramen magnum, and once it is out of the braincase, it resumes its original shape. All non-natural endocasts used in this study were made with this technique.

Endocasts were taken of 29 living Caninae species, mainly from the collections of the National Natural History Museum (Naturalis), Leiden, the Netherlands (Table 1), and also from some fossil Caninae, mainly from the collections of the American Museum of Natural History, New York (Table 2). These endocasts are compared with those made by Radinsky, now in the collection of the Field Museum of Natural History, Chicago.

The taxonomic arrangement in this work follows the classification by Wozencraft (1993). A more recent work was that of Tedford *et al.* (1995), which mainly agreed with Wozencraft's, with some exceptions. Tedford *et al.* (1995) considered *Alopex lagopus* as a species of *Vulpes*, they kept the genus *Lycalopex* (for *L. vetulus*), and they considered the South American zorros as paraphyletic (*Pseudalopex culpaeus*, '*P.*' *griseus*, '*P.*' *sechurae*, '*P.*' *gymnocercus*). Under the genus *Pseudalopex* only the culpeo fox is placed, whereas the three remaining species are without a proper generic name, and thus indicated by them with quotation marks. They lack a uniting synapomorphy, other than those uniting the South American clade as a whole. For alternative taxonomies see Thomas (1914), Kraglievich (1930), Cabrera (1931), Osgood (1934), Langguth (1969, 1970, 1975), Ewer (1973), Stains (1975), Clutton-Brock *et al.* (1976), Van Gelder (1978), Wozencraft (1989) and Zunino *et al.* (1995).

The nomenclature of the cortical convolutions follows Filimonov (1928; redrawn by Adrianov & Merling, 1959). Interpretations of homologies in sulcal pattern of extinct and living wild Caninae have been done on the basis of macroscopic morphological observations, with the use of sulcal maps from previous works on wild and fossil canid brains. Drawings of the endocast are presented instead of photographs in order to emphasize characters that are typical for the species and to avoid individual variation. Special attention has been taken on the preparation of the cerebrum, while other parts of

Table 1. List of specimens of living Caninae

Species	Number	Locality
<i>Alopex lagopus</i>	NNML cat. no. h.	–
<i>Alopex lagopus</i>	NNML cat. no. d.	–
<i>Atelocynus microtis</i>	AMNH(M) 76579	Peru
<i>Canis adustus</i>	NNML cat. no. h.	–
<i>Canis aureus</i>	NNML cat. ost. b.	–
<i>Canis aureus</i>	NMNH-Z 11597/378/3	Azerbaijan
<i>Canis latrans</i>	NNML cat. no. c.	USA
<i>Canis lupus</i>	NNML cat. no. l.	Austria
<i>Canis mesomelas</i>	NNML reg. no. 25891	SW Africa
<i>Canis mesomelas</i>	NNML cat. no. l.	SW Africa
<i>Canis rufus</i>	AMNH 112	USA
<i>Canis simensis</i>	NNML cat. no. b.	Ethiopia
<i>Cerdocyon thous</i>	NNML cat. no. b.	S. America
<i>Cerdocyon thous</i>	AMNH(M) 14853	Colombia
<i>Chrysocyon brachyurus</i>	NNML cat. no. a.	Brazil
<i>Cuon alpinus</i>	NNML reg. no. 1546	–
<i>Dusicyon australis</i>	NNML reg. no. 19111	Falkland Islands, S. America
<i>Dusicyon australis</i>	NNML reg. no. 19112	S. America
<i>Lycaon pictus</i>	NNML cat. no. c.	SW Africa
<i>Nyctereutes procyonoides</i>	NNML cat. no. d.	Japan
<i>Nyctereutes procyonoides</i>	NNML cat. no. h.	Japan
<i>Nyctereutes procyonoides</i>	NMHN-P 6433	Ukraine
<i>Nyctereutes procyonoides</i>	NMHN-P 6434	Ukraine
<i>Otocyon megalotis</i>	NNML cat no a.	S. Africa
<i>Pseudalopex culpaeus</i>	NNML reg. no. 620	Ecuador
<i>Pseudalopex culpaeus</i>	AMNH(M) 67088	Equator
<i>Pseudalopex griseus</i>	AMNH(M) 41509	Argentina
<i>Pseudalopex griseus</i>	NNML cat. no. a.	Chile
<i>Pseudalopex gymnocercus</i>	AMNH(M) 205782	Uruguay
<i>Pseudalopex sechurae</i>	NNML reg. no. 2381	Peru
<i>Pseudalopex vetulus</i>	NNML cat. ost. a	S. America
<i>Pseudalopex vetulus</i>	AMNH(M) 13398	Brazil
<i>Speothos venaticus</i>	NNML reg. no. 3224	Brazil
<i>Urocyon cinereoargenteus</i>	AMNH(M) 68527	Guatemala
<i>Urocyon cinereoargenteus</i>	NNML reg. no. 626	the Netherlands (zoo specimen)
<i>Vulpes bengalensis</i>	NNML cat. no. c.	Nepal
<i>Vulpes bengalensis</i>	NNML cat. no. b.	Nepal
<i>Vulpes chama</i>	NNML reg. no. 25900	SW Africa
<i>Vulpes corsac</i>	NMNH-Z 11616/527/4	Ukraine
<i>Vulpes corsac</i>	NMNH-Z 11614/383/2	Turkmenistan
<i>Vulpes rueppelli</i>	NNML cat. no. b.	Egypt
<i>Vulpes vulpes</i>	NNML cat. no. b.	Syria
<i>Vulpes vulpes</i>	NNML reg. no. 932	–
<i>Vulpes vulpes</i>	NMNH-P 6419	Ukraine
<i>Vulpes zerda</i>	NNML cat. no. c.	Egypt

the brain, such as the cerebellum and the brain stem, are not presented in detail. From the literature and our own observations, it appears that their macroscopic structure does not contribute much to the taxonomy, and therefore phylogeny, of the subfamily.

Institutional abbreviations

AMNH American Museum of Natural History, New York, USA; AMNH(M) American Museum of Natural History, Department of Mammalogy; F:AM Frick Collection, American Museum of Natural History; FMNH Field Museum of Natural History, Chicago, USA; GIN

Table 2. List of specimens of fossil Caninae

Species	Number	Epoch (Age)	Locality
<i>Canis lepophagus</i>	AMNH 104782 (Cast of WT 760)	Late Pliocene (Late Blancan)	N. Cita Canyon, Texas, USA
<i>Canis (Xenocyon) lycaonoides</i>	GIN 3722-144	Middle Pleistocene	Kolyma, North Siberia, Russia
<i>Eucyon davisi</i>	F:AM 63005	Late Miocene (Late Hemphillian)	Bird Bone Quarry, Arizona, USA
<i>Leptocyon</i> sp.	F:AM 49433	Late Miocene (Clarendonian)	Hollow Horn Bear Quarry, S. Dakota, USA
<i>Nyctereutes sinensis</i>	F:AM 96750	Late Pliocene	Hsia Chwang, Shansi, China
<i>Nyctereutes sinensis</i>	F:AM 96792	Late Pliocene	Hsia Chwang, Shansi, China
<i>Nyctereutes sinensis</i>	F:AM 22336 (Natural endocast)	Late Pliocene	Niu Wako, Shansi, China
<i>Nyctereutes tingi</i>	F:AM 96757	Early Pliocene	Nan Chuang Kou, Shansi, China
<i>Vulpes stenognathus</i>	FMNH PM 58960 (Endocast from F:AM 49284)	Late Miocene (Late Hemphillian)	Spring Valley, Lincoln Country, S. Nevada, USA

Geological Institute of the Russian Academy of Sciences, Moscow, Russia; NNHM National Natural History Museum, Kiev, Ukraine; NNML Nationaal Natuurhistorisch Museum (Naturalis), Leiden, the Netherlands.

THE CANINAE CEREBRUM

GENERAL FEATURES

In general, the basic sulcal pattern of the cerebrum of members of the subfamily Caninae does not appear to be affected by brain size, since it is the same from the smallest (*Vulpes zerda*) to the largest (*Canis lupus*) species (Radinsky, 1973a). The only differences of an allometric nature are that the sulci of the cerebral cortex of the larger brained Caninae tend to be more wavy, and that there are more secondary sulci in the larger brains. These differences are due to the nature of the neocortex, which is organized as a thin sheet that can only increase by areal expansion, while the underlying subcortical matter expands as a volume (see reviews by Sacher, 1970; Jerison, 1973). As in living mammals, the brain's information-processing capacity is closely related to the surface area of the cortex (Jerison, 1991), it is obvious that the more wavy the sulcal pattern is and the more secondary sulci there are, the higher this capacity is. Though this is generally true, such an analysis is beyond the scope of the present study. Besides, the present study focuses on a relatively uniform group as regards external brain anatomy (Atkins, 1978; see above), so that such differences in capacity are not likely to be of great taxonomic value.

In spite of the uniformity, two clearly discriminative features are recognized in the brains of modern Can-

inae, on the basis of which some groups can be distinguished. These features consist of the sulcal pattern of the cortex between the coronal sulci, and the shape and relative size of the prereal gyrus of the frontal pole. Differences in these features can be traced back in the ancestral canids as far as the Miocene.

CORTEX MEDIAL TO THE CORONAL SULCI

This region corresponds mainly to the sigmoid gyri, of which the outer borderline is constituted by the coronal sulci. Other sulci of this region are the cruciate, praecruciate, posteruciate and ansate (Fig. 1). In the domestic dog this region consists the major part of the sensory-motor cortex (Kreiner, 1964). Klatt (1928) suggested that the sigmoid gyri expand out more abruptly in the dog group than in the foxes. Radinsky (1973a) on the other hand considered this character unsuitable to distinguish between the brains of the living Caninae genera, due to the observed amount of overlap. However, although there is indeed an overlap in the expansion of the sigmoid gyri, we were able to roughly classify the outline that was created by the coronal and ansate sulci on the dorsal surface of the cerebrum into four groups (Fig. 2):

- the pentagonal outline: the coronal sulci diverge caudally more than rostrally, giving the impression of a five-angled figure.
- the parenthesis-like outline: the coronal sulci bow out laterally, giving the impression of an oval figure.
- the heart-shaped outline: the coronal sulci bow out laterally but diverge rostrally more than in the parenthesis-like outline.
- the orthogonal outline: the sigmoid gyri expand out more abruptly than in the previous groups, so that the

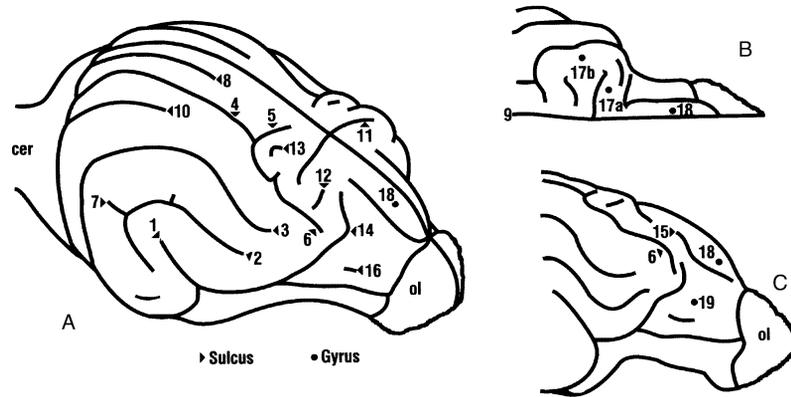


Figure 1. Sulci and gyri of the domestic dog cerebrum. (A) Anterodorsolateral view. (B) Dorsal view of the frontal pole of the right hemisphere. (C) Lateral view of the frontal pole of the left hemisphere. (1) Sylvian sulcus (*sulcus Sylvii*, *sulcus pseudosylvius*); (2) ectosylvian sulcus (*sulcus ectosylvius*); (3) suprasylvian sulcus (*sulcus suprasylvius*); (4) lateral sulcus (*sulcus lateralis*); (5) ansate sulcus (*sulcus ansatus*); (6) coronal sulcus (*sulcus coronalis*); (7) radial process (*processus acuminis*); (8) endolateral sulcus (*sulcus endolateralis*); (9) longitudinal fissure (*fissura longitudinalis cerebri*); (10) ectolateral sulcus (*sulcus ectolateralis*); (11) cruciate sulcus (*sulcus cruciatus*); (12) praecruciate sulcus (*sulcus praecruciatu*); (13) posterucuate sulcus (*sulcus posteruciatu*); (14) presylvian sulcus (*sulcus praesylvius*); (15) proreal sulcus (*sulcus proreus*); (16) intraorbital (*sulcus interprorealis*, *sulcus intraorbitalis*); (17) sigmoid gyrus: (a) anterior part (*pars anterior gyri sigmoidei*); (b) posterior part (*pars posterior gyri sigmoidei*); (18) proreal gyrus (*gyrus proreus*); (19) orbital gyrus (*gyrus orbitalis*); cer: cerebellum; ol: olfactory bulb.

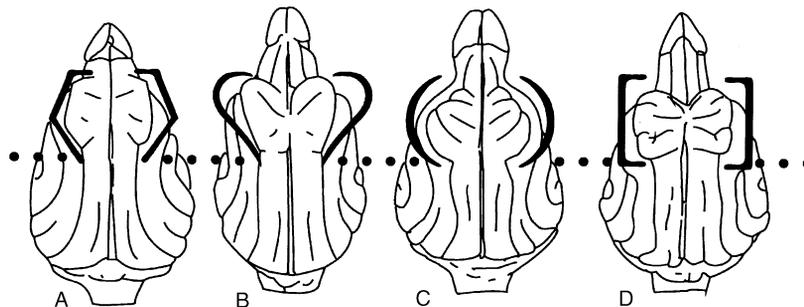


Figure 2. Different types of outlines that are created by the coronal and ansate sulci on the dorsal surface of the cerebrum: (A) pentagonal; (B) heart-shaped; (C) parenthesis-like; (D) orthogonal.

ansate and coronal sulci form a bracketed pattern, giving the impression of an oblong or square figure.

THE PROREAL GYRUS

The second discriminative feature which distinguishes between Caninae members is also found in the frontal pole. It appears that the shape and relative size of the proreal gyrus is not constant, as was already observed by Huxley (1880). He defined an alopecoid group characterized by a relatively small proreal gyrus and a thooid group characterized by a relatively large proreal gyrus.

Radinsky (1973a) paid much attention to this feature and also divided the Caninae into two groups, the

fox-like, corresponding to Huxley's alopecoid, and the dog-like, corresponding to Huxley's thooid, with the exception of *Nyctereutes*, which he placed in the fox-like canids. Although in general the proreal gyrus tends to be longer and narrower in the larger species than in the smaller, he considered this difference not to be allometric. His major argument was that jackals like *C. mesomelas* and *C. adustus* have longer and narrower proreal gyrus than foxes of comparable brain size like *Urocyon cinereoargenteus* and *V. vulpes*.

THE FOSSIL EVIDENCE

Caninae made their first appearance in North America during the Orellan (Early Oligocene) with the

genus †*Leptocyon* (Wang & Tedford, 1994), which remained the only representative until the Clarendonian (Middle Miocene). †*Leptocyon* is considered the stem taxon for the Caninae (Tedford *et al.*, 1995), from which a rapid radiation (cladogenesis) took place during the Pliocene and Pleistocene, resulting in their modern array (Wang, Tedford & Taylor, 1999).

The main evolutionary trends of the Caninae brain were illustrated by Radinsky (1973a) with a series of endocasts of †*Leptocyon-Vulpes*-†*Eucyon*. The most evident trend is the expansion and increased folding of the neocortex. In particular, the expansion of the frontal pole was expressed by the development of the sigmoid gyri and of the proreal gyrus.

The Clarendonian (early Late Miocene) †*Leptocyon* sp. (F:AM 49433) shows a sulcal pattern similar to that of modern Caninae. The sylvian sulcus is present, and concentrically wrapped around it the ectosylvian, suprasylvian and ectolateral sulci are arranged as a series of vertical arches; the lateral and entolateral sulci are horizontal grooves on the dorsal part of the cerebral cortex. The major difference between this †*Leptocyon* specimen and all later Caninae is found on the region medial to the coronal sulci, which is very narrow. This is particularly evidenced by the coronal sulcus (the outer lower borderline of the sigmoid gyrus), which does not bow out laterally and is almost on the same line with the lateral sulcus (Fig. 3).

In the later Caninae, the evolution of the brain took place mainly on the sigmoid, proreal and orbital gyri. All other structures of the brain seem to have already been established in the genus †*Leptocyon*.

Two early representatives of the Caninae radiation are the genera *Vulpes* and †*Eucyon* (Hunt, 1996; Tedford, Wang & Taylor, 2001). The Late Miocene †*Vulpes stenognathus* (F:AM 49284) and †*Eucyon davisi* (F:AM

63005) have a more developed region medial to the coronal sulci than †*Leptocyon*: the cruciate sulci are longer, the sigmoid gyri are more expanded and the postcruciate and ansate sulci are present, although the expansion of the sigmoid gyri is still relatively small. The sulcal pattern of the cortex between the coronal sulci in both genera appears to be similar.

In the later Caninae, the frontal region is very well developed. The Late Pliocene †*Canis lepophagus* (AMNH 104782) has considerably more expanded sigmoid gyri. Although the proreal gyrus is not completely preserved, it is not difficult to see that it has a development similar to living dog-like animals. This is particularly evident in the cerebral hemispheres, which widen out abruptly immediately behind the presylvian sulci, creating an angular profile at this region (Fig. 3).

The cortex rostral to the presylvian sulcus is also well developed in the brains of the Pliocene *Nyctereutes*. In the four available endocasts, †*N. tingi* (F:AM 96757) and †*N. sinensis* (F:AM 96750, F:AM 96792, F:AM 22336), the proreal gyrus is long and bilaterally constricted and the orbital gyrus is well developed. The other parts of the cerebrum are like those of the living *Nyctereutes* (*N. procyonoides*), although the fossil forms appear to be slightly more advanced as they have an ansate sulcus and more wavy cerebral gyri (see below for the description of the living form). The outline of the sulcal pattern of †*N. tingi* is not very clear, due to damage by cracking. The coronal sulci bows out laterally, but it is not possible to say whether it follows the heart-shaped pattern or the parenthesis pattern. The sulcal pattern in †*N. sinensis* (F:AM 96750, F:AM 96792) is much better preserved, and is clearly heart-shaped, though not as clear as in *N. procyonoides*. Specimen F:AM 22336 (*N. megamastoides*

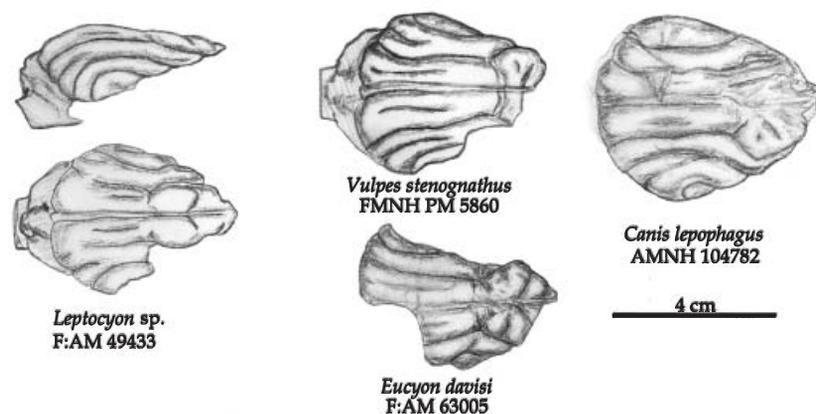


Figure 3. Endocasts from Neogene Caninae: †*Leptocyon* sp., F:AM 49433, lateral view (left side, reversed) and dorsal view; †*Vulpes stenognathus* FMNH PM 58960 (endocast from F:AM 49284), dorsal view; †*Eucyon davisi*, F:AM 63005, dorsal view; †*Canis lepophagus*, AMNH 104782 (cast of WT 760), dorsal view.

in Radinsky, 1973a) was compressed and damaged, becoming asymmetrical. The resulting pattern is therefore less clear than in the other specimens (Fig. 4).

The brain of the Middle Pleistocene †*Canis* (*Xenocyon*) *lycaonoides* (GIN 3722–144; Fig. 4) has the same morphology as the living wolf-like species (Fig. 5).

In the *Vulpes*-lineage, on the contrary, it appears that the external morphology of the brain was already more or less fixed in the Hemphillian (Late Miocene), as the brain of †*V. stenognathus* (FNMH PM 58960, endocast from F:AM 49284, Late Hemphillian) does not seem to differ essentially from that of the living *Vulpes* species, as was already noted by Radinsky (1973a). The frontal pole of F:AM 49284 is badly damaged, and only part of the sigmoid gyri can be judged. In any case, the coronal sulci bows out in such a way that they seem to form a pentagonal outline, which corresponds with the pattern seen in the living forms (see below).

From the morphology of the external brain of the available fossil Caninae, it appears that during the

Caninae radiation the evolution of the cerebrum took place mainly on the region medial to coronal sulci in the form of different sulcal patterns and in the region rostral to presylvial sulcus in the shape and relative size of the preoreal gyrus. During the adaptive radiation, several sulcal patterns and types of preoreal gyri evolved.

THE CEREBRUM OF THE LIVING CANINAE

Endocasts of all known Caninae species that are living today are described below, except for the foxes *Urocyon littoralis*, *Vulpes cana*, *V. ferrilata*, *V. macrotis*, *V. pallida* and *V. velox* as they were not available to us. As stated in the introduction above, there is no conclusive agreement on the generic rank of some species, thus here we followed the generally used taxonomy of Wozencraft (1993). In addition, for reasons of convenience in presentation, we classified the canids into three hypothetical groups: the dog-like species, the fox-like species and the raccoon dog. This does not necessarily mean that these groups are nat-

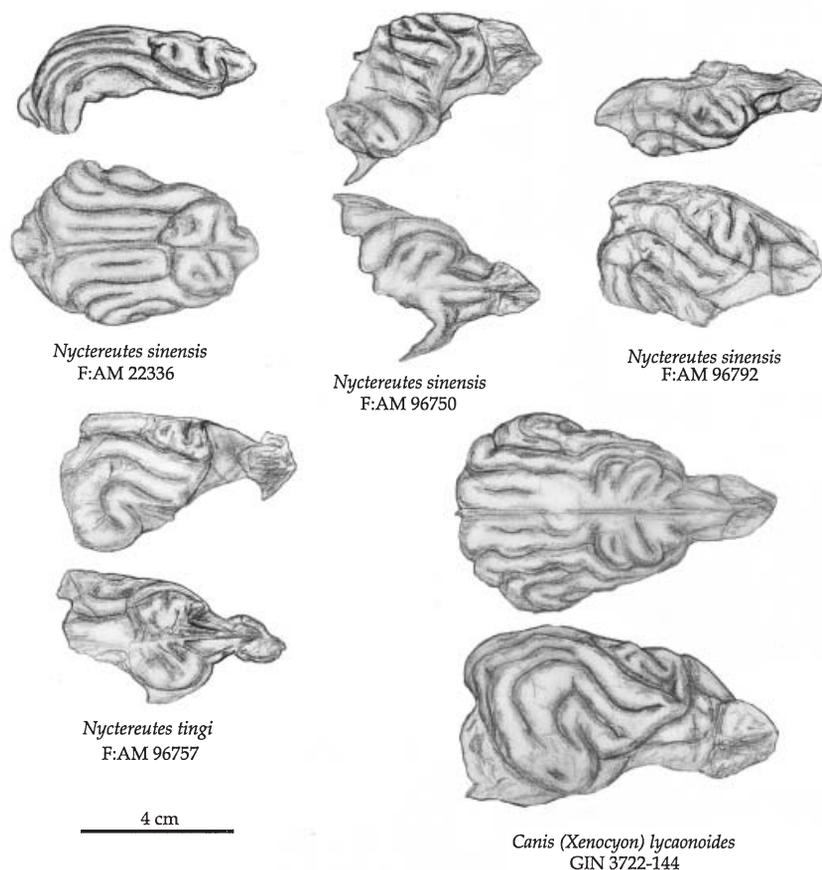


Figure 4. Endocasts from Pliocene *Nyctereutes* and Pleistocene †*Canis* (*Xenocyon*) *lycaonoides*, lateral and dorsal views. Lateral views of †*N. tingi* F:AM 96757, †*N. sinensis* F:AM 22336 and †*N. sinensis* F:AM 96750 reversed from the left side.

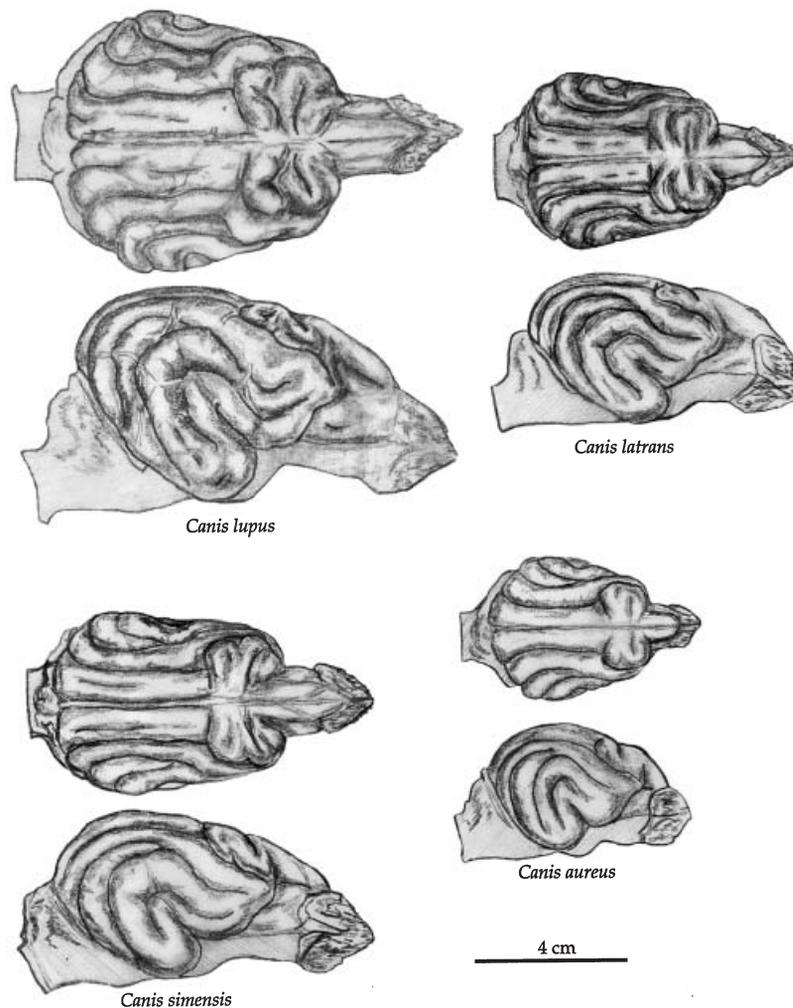


Figure 5. Endocasts from living *Canis* spp., dorsal and lateral views.

ural, in other words, that they have any phylogenetic value.

The phylogenetic position of the Asian raccoon dog (*Nyctereutes procyonoides*) is still unclear, and two recent papers presented significant conflicts. Tedford *et al.* (1995) placed *Nyctereutes* in the same group with the South American canids on the ground of osteological and dental similarities shared with *Cerdocyon thous*. This may imply a palaeo-biogeographical enigma, however, since *Cerdocyon* has also been reported from the Late Miocene–Early Pliocene of Central America (Torres & Ferrusquia, 1981) and North America (R.H. Tedford, pers. comm., 2002). In Wayne *et al.*'s (1997) combined analysis of mitochondrial DNA with Tedford *et al.*'s data, the Asian raccoon dog is neither related to the South American canids nor to any other living species. It is therefore unclear

whether we should include the raccoon dog in the dog-like or in the fox-like species.

DOG-LIKE SPECIES

In this group are included the jackals (*C. adustus*, *C. aureus*, *C. mesomelas*), the wolves (*C. lupus*, *C. rufus*, *C. simensis*), the coyote (*C. latrans*), the dhole (*Cuon alpinus*), the cape-hunting dog (*Lycaon pictus*), and the canids that are endemic to South America. Recognized South American species are the zorros (*Pseudalopex griseus*, *P. gymnocercus*, *P. sechurae*, *P. culpaeus*), the bush dog (*Speothos venaticus*), the hoary fox (*Pseudalopex vetulus*), the small-eared dog (*Atelocynus microtis*), the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Cerdocyon thous*), and the recently extinct Falkland Island wolf (*Dusicyon australis*).

In all dog-like species, the cerebral hemispheres widen out abruptly immediately behind the presylvian sulci. This is particularly evident in the genus *Canis*, with *C. lupus* having the most angular profile. *C. lupus*, *C. rufus* and *C. simensis* have relatively the narrowest proreal gyrus (Fig. 5). England (1973) also noted this elongation in *C. rufus* and *C. lupus*, but Atkins (1978) thought that the relative thickening of this region in *C. lupus* is greater than in *C. rufus*. In general, in all members of the genus *Canis* the proreal gyrus is very long and bilaterally constricted, more than in any other member of the family Caninae. The proreal gyrus of *Cuon*, *Lycaon*, *Atelocynus* and *Speothos* is shorter and considerably thicker

(Figs 6, 7). The proreal gyrus in the other South American species is also relatively large, although smaller than in the genus *Canis*. In all South American species, the proreal gyrus is bilaterally constricted (Fig. 8).

The orbital gyri of *C. aureus*, *C. adustus*, *C. mesomelas*, *Chrysocyon*, *Cerdocyon* and *Pseudalopex* have only one sulcus (the proreal sulcus) which separates the proreal and orbital gyri. *C. latrans*, *Cuon alpinus* and *Lycaon pictus* have one more sulcus, the intraorbital sulcus, which extends parallel to the lower section of the presylvian sulcus. *C. simensis*, *C. lupus*, *C. rufus*, and the two examined specimens of †*Dusicyon australis* have three sulci in that region: the proreal

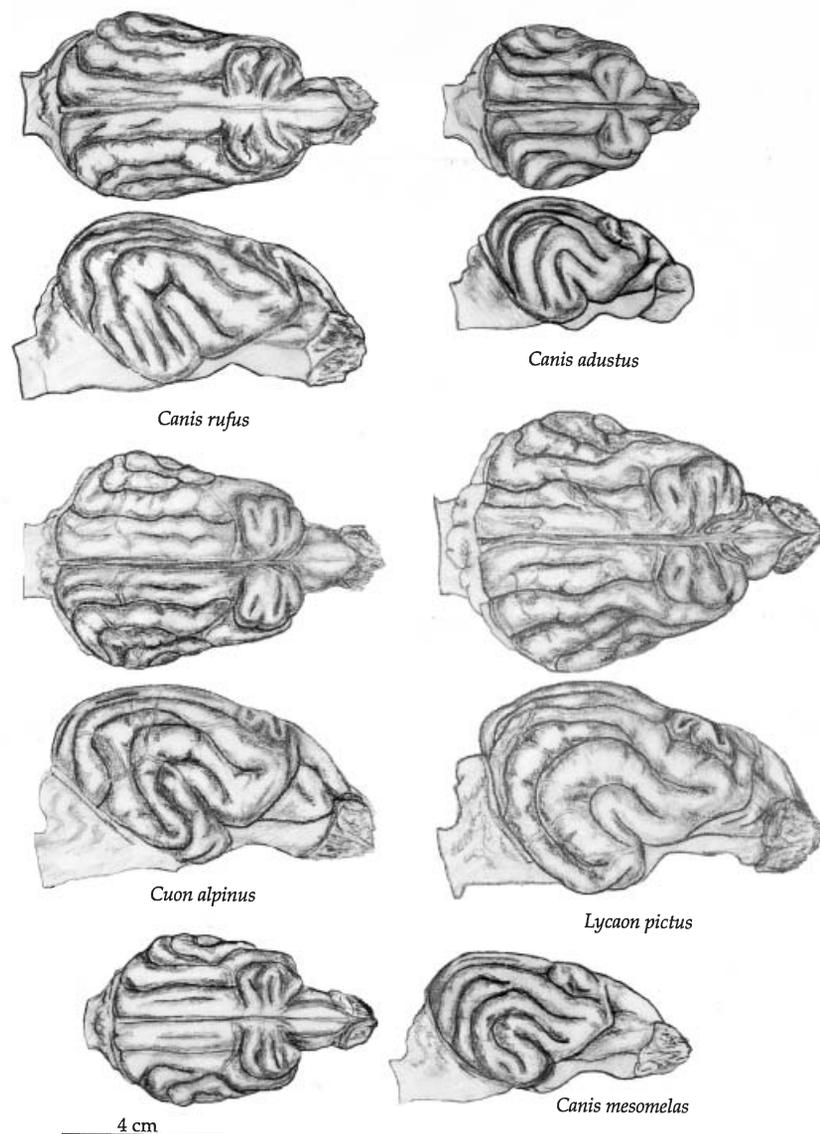


Figure 6. Endocasts from living *Canis* spp., *Lycaon pictus* and *Cuon alpinus*, dorsal and lateral views.

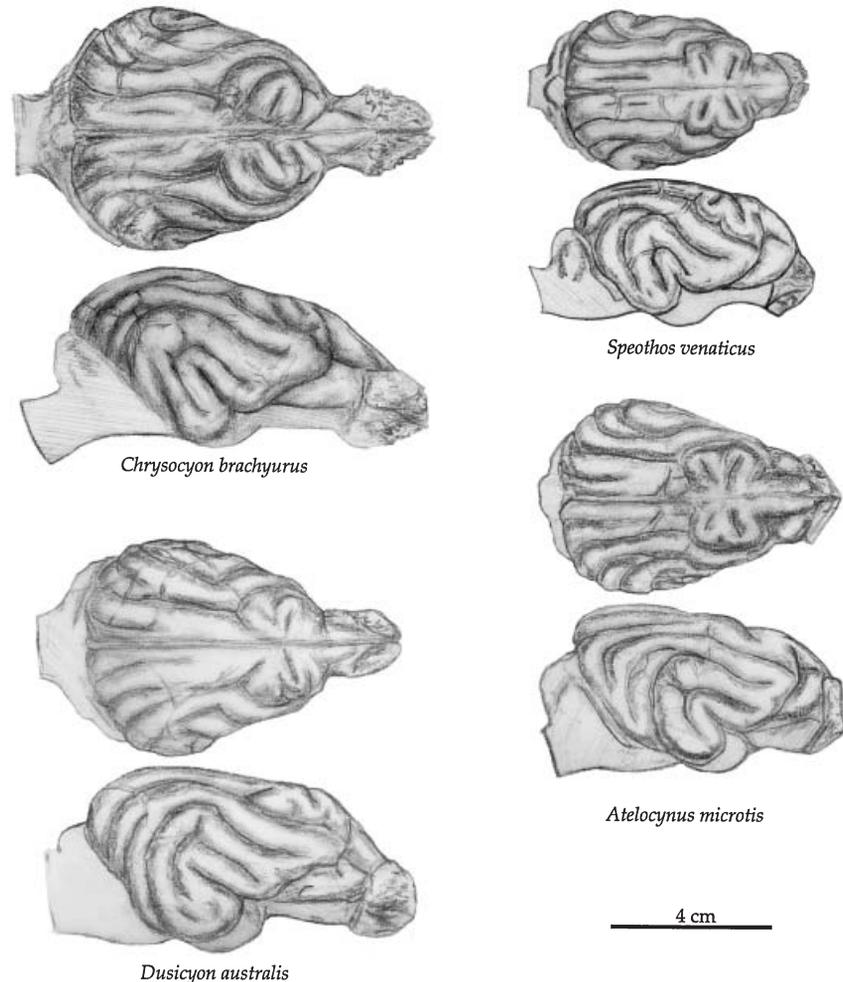


Figure 7. Endocasts from *Chrysocyon*, *Speothos*, *Atelocynus* and the recently extinct †*Dusicyon australis*, dorsal and lateral views.

sulcus, the intraorbital sulcus and a third sulcus, which is not found in the domestic dog, forming the dorsal boundary of the anterior portion of the orbital gyrus.

In the genera *Canis*, *Cuon*, *Lycaon*, *Atelocynus* and *Speothos*, the sigmoid gyri expand very abruptly. This creates on the dorsal surface of the cerebrum an orthogonal or oblong outline of the ansate and coronal sulci (Figs 5–7). The expansion of the sigmoid gyri is less in *C. aureus* and *C. adustus* than in the others. In *C. latrans* the coronal sulcus may continue onto the medial surface with the lesser cruciate sulcus, but this is not a constant feature (Atkins, 1978).

C. lupus, *Cuon alpinus* and *Lycaon pictus* have a dimple in the middle of the coronal gyrus. *Cuon alpinus* and *Lycaon pictus* have a short sulcus that divides the anterior sigmoid gyrus in two parts (Radinsky, 1973a).

In †*Dusicyon australis*, *Pseudalopex vetulus*, *P. sechurae*, *P. griseus* and *Chrysocyon brachyurus*, a parenthesis-like or oval outline is found, in which the coronal sulci bow out laterally on the dorsal surface of the cerebrum (Figs 7, 8). In the latter species, the posterior part of the sigmoid gyrus is more developed than in the other four. In *Cerdocyon thous* and *Pseudalopex culpaeus*, the coronal sulci diverge rostrally, creating a heart-shaped outline.

Thus, three patterns are observed in the dog-like species:

- 1 orthogonal outline: *Canis*, *Cuon*, *Lycaon*, *Atelocynus* and *Speothos*,
- 2 parenthesis-like or oval outline: †*Dusicyon australis*, *Pseudalopex sechurae*, *P. gymnocercus*, *P. griseus*, *P. vetulus* and *Chrysocyon*,
- 3 heart-shaped outline: *Cerdocyon* and *Pseudalopex culpaeus*.

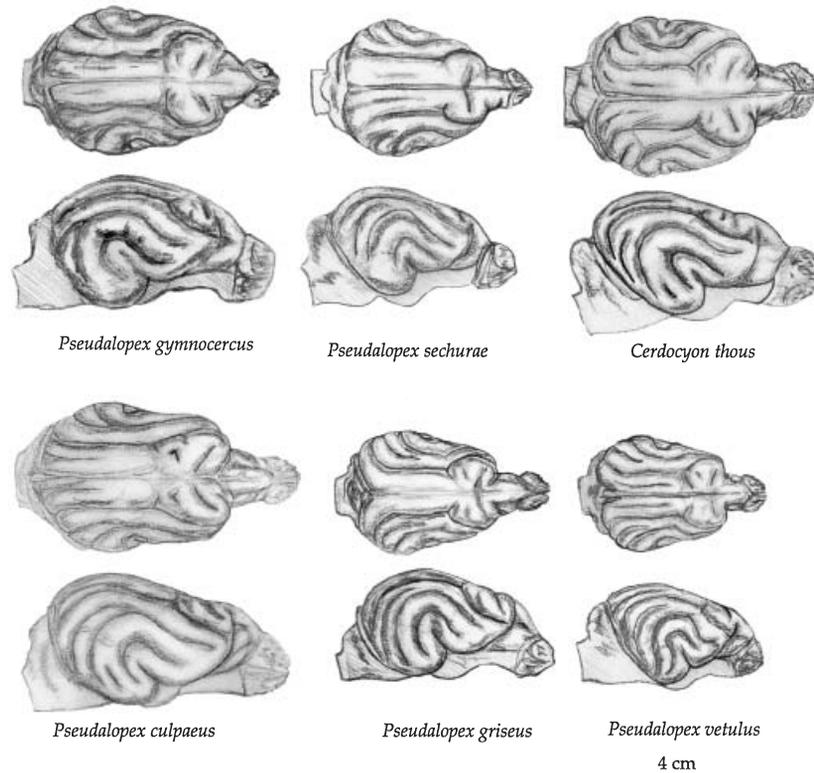


Figure 8. Endocasts from *Pseudalopex* spp. and *Cerdocyon thous*, dorsal and lateral views.

FOX-LIKE SPECIES

This group includes the *Vulpes* species (*V. vulpes*, *V. bengalensis*, *V. chama*, *V. rueppelli* and *V. zerda*), the arctic fox (*Alopex lagopus*), the bat-eared fox (*Otocyon megalotis*), and the grey fox (*Urocyon cinereoargenteus*).

No distinguishing features were found between the brains of the *Vulpes* species checked. In these species the prereal gyrus is very small and the coronal sulci create a pentagonal outline on the dorsal cerebral cortex (Fig. 9).

The cerebrum of *Alopex lagopus* has many features which distinguish it from that of the *Vulpes* species. The frontal lobes in *Alopex* are very high and the cerebellum is more overlapped. The proreal gyrus of *Alopex* is more developed than in any other fox. In addition, the ansate and postcruciate sulci are very well developed, creating a sulcal pattern at the region medial to the coronal sulci which is very distinct from the *Vulpes* species, although it approaches a pentagonal outline (Fig. 9).

The coronal sulci of *Urocyon cinereoargenteus* bow out laterally, thus creating a heart-shaped outline. There are two sulci on the orbital gyrus. The pro-

real gyrus is very small and similar to that seen in *Vulpes*.

Otocyon has the least overlapped cerebellum of all foxes. The frontal lobes are low and wide. The length of the cruciate sulcus is variable. The length and bilateral constriction of the proreal gyrus in *Otocyon* are also variable, and it is thought that they are affected by the size of the brain (Radinsky, 1973a).

RACCOON DOG

In *Nyctereutes*, there is only a slight angular depression in the lateral profile at the level of the presylvian sulcus. The region rostral to the presylvian sulcus gives the impression that it is not well developed. The relative length of the proreal gyrus approaches that of the dog-like species (Radinsky, 1973a); however, it is broad and low, and with hardly any bilateral constriction, which makes it comparable to that of *Alopex lagopus*. The coronal sulci create a heart-shaped outline on the dorsal aspect of the cerebrum (Fig. 10). The ansate sulcus is never present, while in the small foxes (some *Vulpes* spp. and *Urocyon*) it may be present or may not.

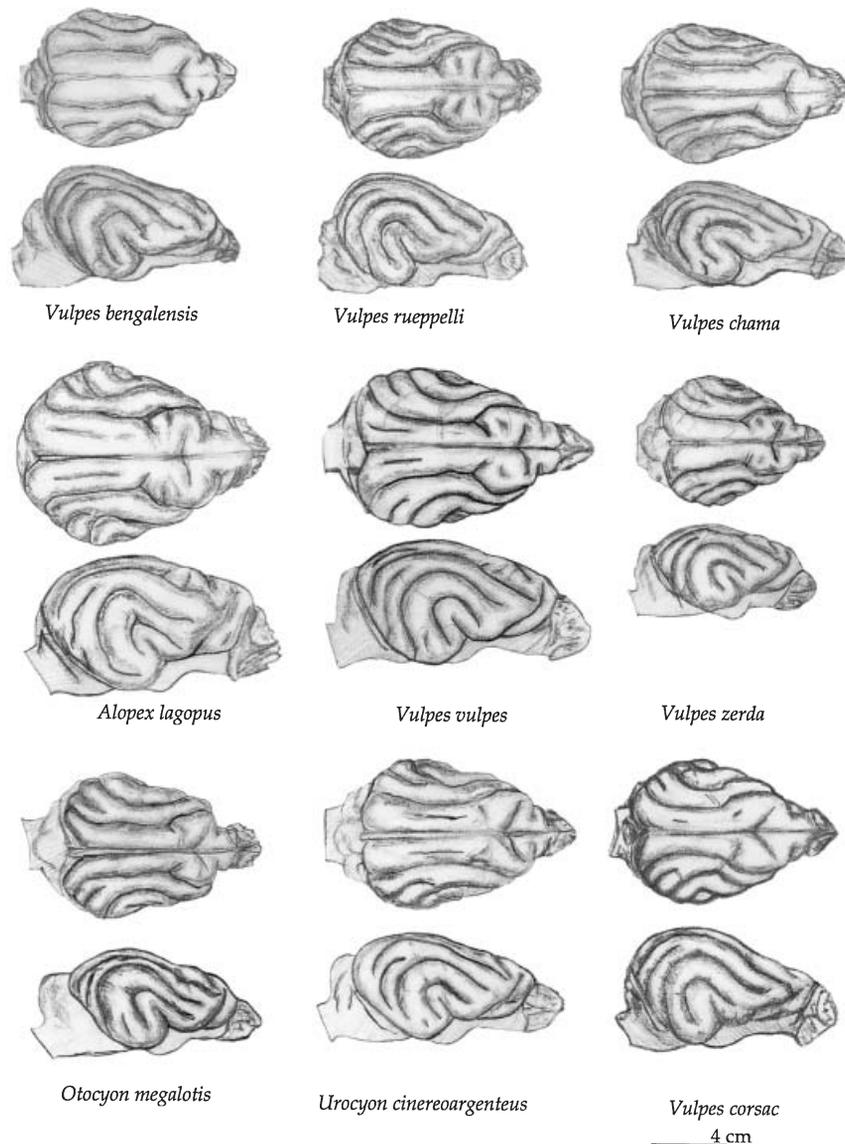


Figure 9. Endocasts from living *Vulpes* spp., *Otocyon megalotis*, *Alopex lagopus* and *Urocyon cinereoargenteus*, dorsal and lateral views.

PHYLOGENETIC IMPLICATIONS

Neurocranium endocasts reveal the external morphology of the brain. Therefore, they can be very useful for taxonomic purposes, in addition to the classical features of the skeleton and dentition, and modern biochemical analyses. In fact, the brain cortex is the only complicated soft tissue that can be reconstructed from skeletal impressions, as it can be relatively easily cast from empty skulls. In addition, natural endocasts of fossil species are also known, which can be compared to the endocasts of living species.

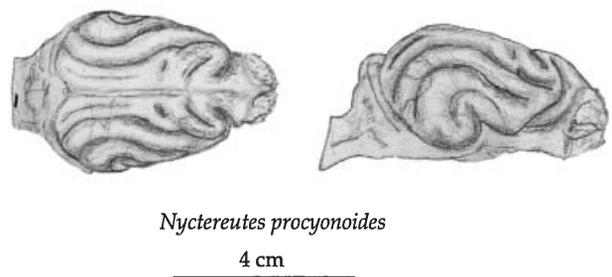


Figure 10. Endocast from *Nyctereutes procyonoides*, dorsal and lateral view.

The use of only living species to solve a phylogenetic problem has its limitations, due to the danger of so-called *Scalae Naturae* (pseudoevolutionary sequences) in which a living species is regarded as representative of the ancestral stage of another living species. In such a way, misleading phylogenetic schemes can be constructed, such as England's (1973) for carnivores. The reason for this is the possibility that the evolution of the mammalian cerebral cortex is affected by parallelisms (Edinger, 1962; Radinsky, 1971). To minimize parallelism in sulcal patterns, endocasts of fossil species are crucial.

The external macromorphology of the cerebrum has already been used in the past to clarify phylogenetic relationships in both living and extinct mammals, such as primates (Connolly, 1950), antilopes (Oboussier, 1972), mustelids (Radinsky, 1973b; Willemsen, 1980), viverrids (Radinsky, 1975), and marsupials (wynyardiids: Haight & Murray, 1981).

The same also has been done for the Caninae (Huxley, 1880; England, 1973; Radinsky, 1973a). Huxley (1880) divided the Caninae into two groups: the alopecoid and the thooid, using dental and cranial characters, but also the shape of the proreal gyrus. Based on the same characters, Radinsky (1973a) also divided the subfamily into two groups, the fox-like and the dog-like, respectively, and suggested that *Nyctereutes procyonoides* be classified under the fox-like Caninae. He also pointed out that there are no neuroanatomical data that support the classification of the desert fox (*Vulpes zerda*) into a separate genus *Fennecus* (see classifications of Ewer, 1973; Stains, 1975). In recent works on living Caninae most authors recognize these two species (Asian raccoon dog and desert fox), but disagree as to their exact phylogenetic and taxonomic position (see discussion below).

For our phylogenetic interpretations the sigmoid and proreal gyri are of particular importance (Fig. 11). This is because the rest of the brain structures seems to have been stable since the Middle Miocene (see above), before the beginning of the principal Caninae radiation. During this adaptive radiation all cortical structures of the brain remained basically the same, except for the latter two gyri.

Our approach was based on living canid species, with the addition of the actual fossil record. In this way, the phylogeny of the living canid species, based upon dental, skeletal, genetic, soft tissue and other biological features, included their ancestral taxa, which are known only by dental, skeletal and now also endocranial features.

NYCTEREUTES

The phylogenetic position of the *Nyctereutes* is not clear. Huxley (1880), using cranial and dental charac-

ters, considered it 'essentially a low Thooid of the South-American type', although it is an Old World canid. A century later, in their phenetic study, Clutton-Brock *et al.* (1976) placed *Nyctereutes* either together with *Pseudalopex sechurae* and *P. vetulus* (using teeth and cranial characters only) or alternatively in a clade on its own, not related to any other canid (using all the characters of their analysis). Later, again based on osteological and dental morphology, it was placed as a sister taxon of *Cerdocyon thous* (Berta, 1988; Tedford *et al.*, 1995). On the other hand it was also placed as a sister taxon to *Vulpes* (Wayne *et al.*, 1987a; Wayne *et al.*, 1987b), based on karyology using G-banded chromosomes. A biochemical analysis of allozymes yielded nothing more than a position somewhere at the stem of the Caninae multichotomy (Wayne & O'Brien, 1987). Finally, in Wayne *et al.*'s (1997) combined analysis of mitochondrial DNA and morphological data, the raccoon dog is not closely related to any other living species. Thus, *Nyctereutes* may be close to *Pseudalopex*, to *Vulpes*, to *Cerdocyon* or to none of the living canids.

The fossil Asian *Nyctereutes*, represented by the primitive †*N. tingi* and the derived †*N. sinensis*, are considered sister taxa, and appear suddenly somewhere in the Early Pliocene (Tedford & Qiu, 1991). †*N. tingi* became extinct in the Late Pliocene; †*N. sinensis* disappeared in the Middle Pleistocene, either through extinction, or through evolution into *Nyctereutes* sp. (Tedford & Qiu, 1991). This latter species was described by Pei (1934), but is also considered synonymous with *N. procyonoides* (Soria & Aguirre, 1976). The European forms, represented by the primitive †*N. donnezani* and the derived †*N. megamastoides*, became extinct before the beginning of the Pleistocene, without known descendants (Martin, 1971).

The brains of the fossil Asian *Nyctereutes* (†*N. tingi*, †*N. sinensis*) appear to be more advanced than that of the living species (*N. procyonoides*, Fig. 10), as the fossil species have cerebral gyri that are more wavy, and a more distinct ansate sulcus (Radinsky, 1973a). In addition, the proreal gyrus is long and narrow and the orbital gyrus wide in the fossils, compared to the living species (Figs 4, 10). A simple explanation might be that the brains of the fossil species were larger than the living raccoon dog: in our endocasts by about 25%. The degree of the complexity of the gyri is a common difference between brains of different size. Moreover, the absence of the ansate sulcus in the living raccoon dog could be due to their smaller brain. However, the differences in the proreal gyrus are significant, and it is easy to distinguish *Nyctereutes procyonoides* (Fig. 10) from *N. sinensis* (Fig. 8).

The fossil *Nyctereutes* is, in external brain morphology, not close to the living species. It appears to be sim-

ilar only to *Cerdocyon thous*. They not only have the same heart-shaped sulcal pattern, but they also have an ansate sulcus. A more important similarity is found in the preoreal gyrus, which has the same development and shape in †*N. tingi* and †*N. sinensis* as in *Cerdocyon thous*. If, however, we take the living raccoon dog into account, it appears that although the sulcal pattern is also heart-shaped, the postcruciate region in *N. procyonoides* is more elongated, and it misses the ansate sulcus. The most striking difference is found in the degree of development of the preoreal gyrus, which is long and bilaterally constricted in *Cerdocyon*, but not so in *N. procyonoides*. In fact, the endocasts of the fossil *Nyctereutes* have more similarities with *Cerdocyon* than with the living *Nyctereutes*. This implies that Berta's (1988) and Tedford *et al.*'s (1995) hypotheses might be confirmed as far as the fossil species are concerned (Fig. 12).

PSEUDALOPEX

There has been a general disagreement on the classification of the South American Caninae species *Dusicyon australis* (Falkland Island wolf), *Pseudalopex vetulus* (hoary fox) and the zorros *Pseudalopex culpaeus* (culpeo fox), *P. griseus* (Argentine grey fox), *P. gymnocercus* (pampas fox) and *P. sechurae* (sechuran fox). Earlier works (Thomas, 1914; Kraglievich, 1930; Cabrera, 1931; Osgood, 1934) each presented a different taxonomy of these species.

Langguth (1969, 1970) placed the hoary fox in the genus *Lycalopex* and the other species into the genus *Dusicyon*, giving them only subgeneric recognition. Later (1975) he moved these latter species to the genus *Canis*, as according to him they did not differ enough to grant a full generic rank. Clutton-Brock *et al.* (1976) noted that there were close similarities between the six species, and accordingly grouped them into the genus *Dusicyon*. Berta (1987, 1988), however, suggested that †*Dusicyon australis* should be separated from the others, and placed under the generic name *Pseudalopex* the species *Pseudalopex culpaeus*, *P. griseus*, *P. sechurae* and *P. gymnocercus*. She also moved the genus *Lycalopex* into *Pseudalopex*; this was, however, a taxonomic mistake as the generic name *Lycalopex* has priority above *Pseudalopex* (Zunino *et al.*, 1995). Tedford *et al.* (1995) kept the genus *Lycalopex* (for *L. vetulus*) and considered the *Pseudalopex* group (*sensu* Berta, 1988) as paraphyletic. Within the genus *Pseudalopex* they placed only the culpeo fox (*P. culpaeus*), while the three remaining species were indicated by quotation marks: '*Pseudalopex*' *gymnocercus*, '*P.*' *sechurae* and '*P.*' *griseus*. Wayne & O'Brien (1987), based upon allozymes, placed *P. vetulus* with *Cerdocyon*; later, Wayne

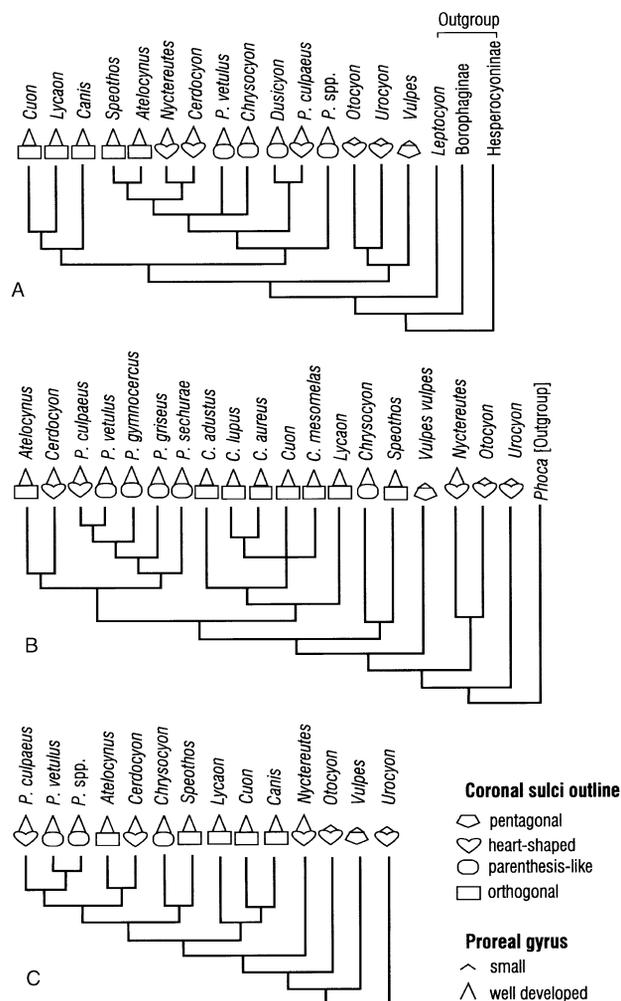


Figure 11. Probable phylogenetic relationships within the living Caninae and occurrence of different types of sulcal pattern. (A) Tedford *et al.*'s (1995) morphological cladogram; (B) Cladogram based on Wayne *et al.*'s (1997) molecular parsimony cladogram; C: Tedford's and Wayne's combined cladogram by Wayne *et al.* (1997). *P. spp.* indicates the species *Pseudalopex griseus*, *P. gymnocercus* and *P. sechurae*.

et al.'s (1997) analysis resulted in a dichotomy with *P. culpaeus* and *P. vetulus* on one side and *P. sechurae* on the other.

The brain morphology of the above mentioned South American species (including †*Dusicyon australis*) indicates that they are not directly related to the genus *Canis*. The patterns of the external cerebrum anatomy of *culpaeus*, *griseus*, *sechurae*, *gymnocercus* and *vetulus* are very similar (Fig. 8). Only *P. culpaeus* deviates, whose coronal sulci forms a heart-shaped outline on the dorsal cortex, whereas in *P. vetulus*, *P. griseus*, *P. gymnocercus*, *P. sechurae*,

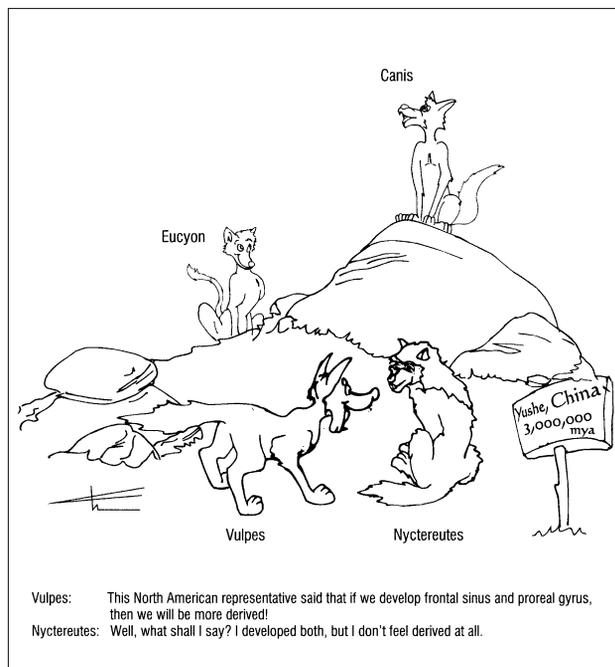


Figure 12. The living raccoon dog (*Nyctereutes procyonoides*) is considerably smaller than the fossil †*Nyctereutes sinensis*, which is considered its ancestor (see discussion in the text). As presented in this study, the fossil *Nyctereutes* species have a larger proreal gyrus than the living species. A similar development is seen in the frontal sinus, which is also larger in the fossil species than in the living form (Tedford *et al.*, 1995). These two points are the subject of the cartoon: in China 3 million years ago, a *Vulpes* (which lacks a frontal sinus and has a proreal gyrus very small) is very enthusiastic with the new ideas of a *Canis* (in which both features are very well developed), however, the *Nyctereutes* does not seem to be interested at all.

they form a parenthesis-like or oval outline (Fig. 8). This is the only difference seen in the anterior part of the brain that might support a separate generic status of *P. culpaeus*. There are no features of the brain morphology that distinguish *P. vetulus* from the others, so a separate generic status of the former cannot be defended from the point of view of anterior brain morphology.

CHRYSOCYON

Berta (1988) placed the maned wolf in a sister taxon of *Canis*. Others related it to *Canis*, *Cerdocyon* and *Speothos* on the basis of chromosomes (Wayne *et al.*, 1987a,b), to *Cerdocyon* and *P. vetulus* based on allozymes (Wayne & O'Brien, 1987), to South American Caninae based on morphology (Tedford *et al.*, 1995), or, based on a combined analysis of morphological data

and mitochondrial DNA, to *Speothos* alone (Wayne *et al.*, 1997).

Features of the external brain anatomy of *Chrysocyon* separated this genus from *Canis*, and support its classification within the South American Caninae. Its sulcal pattern, especially at the cortex medial to the coronal sulci, differs completely from that found in the *Canis* species. In the latter genus it is always orthogonal or oblong (Fig. 5), whereas in *Chrysocyon* it is more oval, parenthesis-like, and with a very well-developed posterior part of the sigmoid gyrus (Fig. 7). The parenthesis-like sulcal pattern is also found in *Pseudalopex*, †*Dusicyon* and *Cerdocyon* (Fig. 8), but these last three genera all lack the typical expansion of the posterior part of the sigmoid gyrus. The remaining South American canids, *Atelocynus* and *Speothos*, have an orthogonal sulcal pattern (Fig. 7) which is more or less similar to *Canis*. *Chrysocyon* should be placed with *Pseudalopex*, †*Dusicyon* and *Cerdocyon*, but we are not able to say where exactly.

SPEOTHOS

Speothos venaticus is grouped as a sister taxon to *Atelocynus* (Berta, 1988; Tedford *et al.*, 1995), to *Cerdocyon* and *Atelocynus* (Langguth, 1969, 1970) or to *Chrysocyon* (Wayne *et al.*, 1997).

The frontal pole in *Speothos* and *Atelocynus* is massive, which is not seen in the other dog-like species (Fig. 7). The proreal gyrus is broad in both, and the coronal sulci create an orthogonal outline, which is similar to *Canis*. These features clearly distinguish them from all other South American canids, and supports Berta's (1988) and Tedford *et al.*'s (1995) hypothesis.

UROCYON

Osgood (1934) considered that *Urocyon* has an affinity with the South American canids. Later, Clutton-Brock *et al.* (1976) suggested that *Urocyon* should be included in the genus *Vulpes*. Later works (Wayne *et al.*, 1987a,b; Berta, 1988; Tedford *et al.*, 1995) presented *Urocyon* as a separate genus, related to *Vulpes*. In Wayne & O'Brien's (1987) biochemical analysis of allozymes, *Urocyon* has a position somewhere at the stem of the Caninae multichotomy.

The region rostral to the presylvian sulcus of *Urocyon* is much smaller than in the dog-like species and in *Nyctereutes* (living and fossil), and is comparable to that of *Vulpes*. This seems to indicate a relationship with *Vulpes*. However, the sigmoid gyri form on the dorsal surface of the cerebrum has a heart-shaped outline, which separates *Urocyon* from all *Vulpes* spp. and *Alopex lagopus*, which have a pentagonal outline (Fig. 9), and relates it with *Otocyon*, *Nyc-*

tereutes and the South American canids *Pseudalopex culpaeus* and *Cerdocyon thous*. Based on these data it is not easy to ascertain the phylogenetic position of *Urocyon*, apart from its being not a member of the *Vulpes*-like species.

CONCLUSION

The external brain anatomy of the living Caninae is extremely uniform, except for two distinctive features which can be traced back as far as the Middle Miocene. The first feature consists of the pattern formed by the coronal and ansate sulci bordering the sigmoid gyri. Four patterns are distinguished (Fig. 2): an orthogonal or oblong outline, found in *Canis* spp., *Lycaon pictus*, *Cuon alpinus*, *Atelocynus microtis*, *Speothos venaticus*, †*Canis* (*Xenocyon*) *lycaonoides* (Middle Pleistocene), an oval or parenthesis-like outline, found in †*Dusicyon australis* (Holocene), *Pseudalopex vetulus*, *P. griseus*, *P. gymnocercus*, *P. sechurae*, *Chrysocyon brachyurus*, a pentagonal outline, found in *Vulpes* spp., *Alopex lagopus*, *Otocyon megalotis*, †*Eucyon davisi* (Late Miocene); and a heart-shaped outline, found in *Cerdocyon thous*, *Pseudalopex culpaeus*, *Urocyon cinereoagenteus*, *Nyctereutes procyonoides* and †*Nyctereutes sinensis* (Late Pliocene). The second feature consists of the shape and relative size of the proreal gyrus. A wide, broad proreal gyrus is found in *Nyctereutes procyonoides*; an elongated, bilaterally compressed gyrus is found in living *Canis* spp., †*Canis lepophagus* (Late Pliocene), †*Canis* (*Xenocyon*) *lycaonoides* (Middle Pleistocene), *Cuon alpinus*, *Lycaon pictus*, *Atelocynus microtis*, *Speothos venaticus*, *Cerdocyon thous*, †*Nyctereutes sinensis* (Late Pliocene) and †*Nyctereutes tingi* (Early Pliocene); a short and small gyrus is found in *Vulpes* spp., *Otocyon megalotis*, *Urocyon cinereoagenteus*, *Alopex lagopus*. In addition, there are some smaller differences, such as the presence of only one orbital sulcus (*C. aureus*, *C. adustus*, *C. mesomelas*, *Chrysocyon*, *Cerdocyon* and *Pseudalopex*), the presence of an additional intraorbital sulcus (*C. latrans*, *Cuon*, *Lycaon* and *Urocyon*), or of even a third groove (*C. simensis*, *C. lupus*, *C. rufus* and †*Dusicyon australis*).

These differences shed new light on some old phylogenetic problems. Based on the differences observed in endocranial casts of almost all living Caninae species and a number of fossil species, we are able to conclude that the fossil *Nyctereutes* is very close to *Cerdocyon* (in contrast to the living *Nyctereutes*), that *Pseudalopex culpaeus* might be separated from *vetulus*, *griseus*, *gymnocercus* and *sechurae*, that *Chrysocyon* is not directly related to *Canis*, but to *Pseudalopex*-†*Dusicyon*-*Cerdocyon*, that *Speothos* is not closely related to the other South American canids, with the exception of *Atelocynus*,

and that *Urocyon* should not be included in the *Vulpes*.

ACKNOWLEDGEMENTS

We are most grateful to Richard Tedford (AMNH) for sharing his extensive knowledge on canid evolution and for his permission to prepare endocasts from fossil canids in his charge. We wish to thank Marina Sotnikova (GIN) for the fruitful discussions we had with her, and for allowing us to make an endocast from a *Xenocyon* specimen. We also thank Dmitry Ivanoff (NNHM) and John De Vos, Chris Smeenk, Duncan Reeder and Reinier Van Zelst (NNML) who enabled us to study the skulls of living Caninae and gave permission to make endocasts. We thank Paul Sondaar (Zoologisch Museum, Amsterdam), Michael Dermitzakis and Constantine Doukas (University of Athens) for their support, and Harry Jerison (University of California) for the discussions we had with him. The contribution of George Papadopoulos (Aristotelian University of Thessaloniki) was very important, in helping us to interpret cortical sulcal maps. Finally we thank Lawrence Heaney, Bruce Patterson, Bill Stanley and Lorie Barber (FMNH) for access to the Leonard Radinsky collection, and Hans Brinkerink (Vista Natura, Baarn) and Jean Kelly (AMNH) for guidance in casting techniques. The visit to the AMNH was made possible thanks to the financial support by the 'Collection Study Grant' of that museum. The Archimedes Foundation (the Netherlands) covered part of the travel expenses.

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