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

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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, Nycytereutes. Three types are described for the second feature: (1) elongated and bilaterally compressed: Canis, Cuon, Lycaon, Atelocynus, Speothos, Cerdocyon, †Dusicyon, Chrysocyon, Pseudalopex, †Nycytereutes sinensis, †N. tingi, (2) small: Vulpes, Otocyon, Urocyon, Alopex, (3) wide and low: Nycytereutes procyonoides. On the basis of these features some phylogenetic interpretations are presented: the fossil Asian Nycytereutes 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.


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 & Azzaroni-Puccetti, 1997; Wayne et al., 1997). The numerous systematic studies so far could not unequivocally solve the problem (e.g. Langguth, 1975; Clutton-Brock, Corbet & 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,
venaticus (Lycaon pictus) paper. On the basis of these two features some persistent the shape and the relative size of the proreal gyrus. The brains of modern Caninae: firstly, the sulcal pattern of the cerebrum of all living, and most of the recent studies are those of England (1973) on the cerebrum of C. latrans, C. lupus, Urocyon cinereargenteus, 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. zarda, Urocyon cinereargenteus, 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 davisi 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, 1978), 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 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...
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

The Canine 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 Caninae, 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 proreal 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, postcruciate 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

### Table 2. List of specimens of fossil Caninae

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

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**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 (Xeno-
cyon) 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 proreal gyrus. During the adaptive radiation, several sulcal patterns and types of proreal gyri evolved.

**THE CEREBRUM OF THE LIVING CANINAЕ**

Endocasts of all known Caninae species that are living today are described below, except for the foxes Urocyon littoralis, Vulpes cana, V. ferrilata, V. macros-
tis, 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-

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**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.
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*, *Atelocyynus* 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.

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. griseus*, *Chrysocyon brachyurus*,
3. heart-shaped outline: *Cerdocyon* and *Pseudalopex culpaeus*.

Figure 7. Endocasts from *Chrysocyon, Speothos, Atelocynus* and the recently extinct †*Dusicyon australis*, 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 proreal 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 proreal 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 8. Endocasts from Pseudalopex spp. and CERDOCYON THOUS, 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 9. Endocasts from living Vulpes spp., Otocyon megalotis, Alopex lagopus and Urocyon cinereoargenteus, dorsal and lateral views.

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 pseudoevolutionary sequences (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), antelopes (Oboussier, 1972), mustelids (Radinsky, 1973b; Willemensen, 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 alope-coid 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-

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 proreal 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 proreal 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, since there was no proper generic name: ‘Pseudalopex’ gymnocercus, ‘P’ sechurae and ‘P’ griseus. Wayne & O’Brien (1987), based upon allozymes, placed P. vetulus with Cerdocyon; later, Wayne 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,
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 the former 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 Caninea 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-

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**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.
**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. 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. securae, 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 cinereoargenteus, 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 cinereoargenteus, 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 securae, 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.

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