The evolution of the brain in Canidae (Mammalia: Carnivora)

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Canid brain evolution followed three independent, yet convergent paths. Each of the three canid subfamilies (Hesperocyoninae, Borophaginae and Caninae) started with a simple brain, which gradually became more complicated as the cerebral cortex became larger and more fissured, the cerebellar hemispheres became larger and the vermis more twisted. The extent to which these evolutionary changes took place differs between the three canid subfamilies. Caninae, the living group, has the most advanced external brain anatomy. This is related to the general tendency of the carnivore brain to become more convoluted through geological time. A parallel development of similar sulcal patterns took place in independent lineages within the Canidae. As a result, some sulci appeared independently several times during canid evolution. The cruciate sulcus appeared four times; the Sylvian, endolateral, ectolateral and ectosylvian sulci appeared three times. The skulls of species with short rostra have a more posteriorly placed posterior border of the palate than those of their close relatives with long rostra. This arrangement affects the position of the cribriform plate (posterior to which the olfactory bulbs are housed), which is also moved backwards and, as a result, the frontal lobes appear more massive. Some canid lineages evolved large size and certain craniodental characters (e.g., deep jaws and large canines), which allowed them to prey on large-bodied animals. In these cases a stasis is noted in brain evolution. This phenomenon might be related to energetic constraints.

Contents

Introduction

Palaeoneurology is the study of the nervous system of fossil animals. Palaeoneurology is as old as palaeontology itself: Cuvier (1804) realised that casts of the brain cavity of fossil vertebrates could be informative concerning the external anatomy of the brain (Edinger, 1962). To prove this, he peeled away the dorsal surface of the neurocranium of a fossil mammal to reveal a natural stone cast of the brain, created by the

sedimentary rock that had filled the neurocranium after the animal's death.

Subsequently, the brain has received considerable attention from vertebrate palae-ontologists (for a review of the literature, see Edinger, 1977), but it was Edinger who reformed the scope of palaeoneurology from the mere description of incidental find-ings of fossil brains into the study of the evolutionary history of the brain, thus found-ing modern palaeoneurology (Buchholtz & Seyfarth, 1999). Edinger understood that by applying methods of comparative neuro-anatomy to endocranial casts of animal groups, whose evolutionary history is well established through independent phylogenetic and stratigraphic work, one could reveal the actual evolutionary transformations of brain.

Palaeoneurological data are the only direct evidence available about the brains of the past. Using only living species to reveal the evolutionary history of the brain has its limitations, due to the danger of so-called *Scalae Naturae* (pseudo-evolutionary sequenc-es) in which a living species is regarded as representative of the ancestral stage of an-other species. In such a way, misleading phylogenetic schemes can be constructed, such as for carnivores (England, 1973; see Preuss, 2000, for a further discussion of this prob-lem). To avoid the effects of parallelisms, the contribution of the fossil record is crucial (Radinsky, 1971; Lyras & Van der Geer, 2003). While comparative neurology tries to un-ravel evolution by comparing the brains of living animals only, palaeoneurology does so by observations on fossil brains. As Edinger (1962) noted, "paleoneurology intro-duced to comparative neurology a fourth dimension: time."

This palaeoneurological approach is an important contribution to comparative neu-ro-anatomy, because it helps us to resolve several misconceptions concerning brain evo-lution (Edinger, 1962; Dermitzakis, 2002). These misconceptions result from the way in which the problem of brain evolution was originally approached. In early theories, which were based mainly on the study of living species and a few fossil specimens, it was argued that brains evolve in a linear manner from fish to man (for a critique, see Hodos & Campbell, 1969), and that brain size is correlated with intelligence and, there-fore, with species success (for a critique, see Radinsky, 1982). These theories influenced, and in many cases still influence, neuro-anatomical studies (Striedter, 1998). Addition-ally, despite the great diversity of living animals, neuro-anatomy is founded on studies of very few model organisms, mainly rats, cats, pigeons and macaque monkeys, an ap-proach that further restricts our view of brain evolution (Preuss, 2000).

The present study is a contribution to the study of the evolution of the brain of the Canidae. This family includes wolves, jackals, foxes and many other less familiar spe-cies. In total there are 35 living species of wild canids (Wozencraft, 2005), that exhibit a wide range of morphological and ecological diversity, from the insectivorous *Otocyon megalotis* to the almost exclusively meat-eating *Lycaon pictus*. Fossil canids are even more spectacular. They belong to the oldest carnivore group still extant today and their past morphological diversity was even greater than currently, as they were not only filling ecological niches that today are occupied by canids, but also those occupied by hyenas, raccoons (Wang *et al.*, 2004) and, to a certain extent, cats (Van Valkenburgh, 1991).

Materials and methods

Endocranial casts — Soft tissues usually do not fossilize, yet there is good fossil evi-dence about brain morphology. This is because the brain is protected within the neuro-

cranium, a hard bony structure that is often fossilized, and which receives much attention during palaeontological excavations and subsequent conservation. Particularly in the case of placental mammals, the brain almost entirely fills the neurocranium, so that casts of the brain cavity (endocranial casts or endocasts) reveal most of the features of external brain anatomy. The only exceptions are the large-brained mammals such as dolphins and great apes, in which only the general shape of the brain is preserved. In all the other mammals, the reproduction of the morphology of the external cerebral morphology is so perfect, that it is better to study endocranial casts than the actual brains, which have the tendency to deform once they are out of the skull (Edinger, 1948). Cerebellar morphology is usually blurred, and only the outlines of the vermis and main lobes are visible.

In the present study, two types of endocranial casts are used. The first type is artificial latex casts that are made after removing the sediment from the brain cavity and by using the neurocranium as a mould to prepare the cast (for descriptions of this technique, see Radinsky, 1968; Hildebrand, 1968; Murrill & Wallace, 1971). The second type is natural stone casts of fossilized sediment that fill the neurocranium. These casts were further prepared either by removing part of the bone of the neurocranium (usually one half of the dorsal surface) or were created naturally by erosion.

Most of the endocranial casts used in this study were prepared by Radinsky and are now in the collection of FMNH (for institutional abbreviations, see below). Additional casts were prepared from AMNH, AMPG, GIN, NNHM, NNM, PIN, SASN specimens and are now in the collections of NNM or in the institution of their origin (see Appendices 1 and 2 for a list of endocasts).

Computed Tomography (CT scan) — A very rare canid skull (*Eucyon davisi*; F:AM 97057) was analyzed by high resolution computed tomography (CT) at the University of Texas X-ray CT facility. The original CT images (500 slices) were recorded in the coronal plane. They were further processed by the same laboratory in order to segment the endocast from the neurocranium and to construct an endocranial representation.

Two additional *Nyctereutes* specimens (*N. tingi*; AUT-MEL-1 and *N. megamastoides*; AUT-DFN-20) were scanned with a medical tomoscan at the Second Radiological Clinic of the University of Athens. The CT images (40 slices for each neurocranium) were acquired with a General Electric Hispeed scan and were further processed at AMPG.

Quantitative analysis of endocranial casts — Most quantitative studies deal with relative brain size or encephalization index. As this subject has been covered in previous works (e.g., Jerison 1973; Finarelli & Flynn, 2007; Finarelli, 2008), it has been left out of the present study. Instead, the quantitative analysis herein is based on the relative length of the superficially exposed gyri and sulci. Their length is correlated with the gyrification index (the ratio between the entire and the outer cortical surface) and, therefore, the evolutionary history of cortical folding can be investigated with these simple length measurements (Zilles *et al*., 1989).

The length of the gyri was measured directly from the endocasts with the use of a curvimeter (map-reading wheel). For the specimens that were CT-scanned, a stereological method was applied, in which the total length of the superficially exposed gyri (L) was calculated as the product of the total number of convexities (P) and the average

thickness of the slices (h): L=P*h. For details on both methods, see Elias & Schwartz (1971).

When a natural endocast or plaster copy of a latex endocast was available, its volume was determined from its water displacement. When a plaster copy of the endocast was not available, the volume was measured with mustard seed poured directly from the original skull. In cases in which parts of one hemisphere or the olfactory bulbs were missing, the missing parts were restored before measuring the volume based on the preserved parts of the same endocast or on endocasts of other individuals of the same species. These cases are indicated with an asterisk in Appendix 3.

The volume of the endocasts that were investigated with computed tomography was calculated as the product of the average thickness of the slices (h) and the sum of the surface area (Sn) of each section: $V=h*Sum(S1+S2+…..Sn)$. The Gyral Length Index (GLI) of an endocast is the ratio between the total length of the superficially exposed gyri (GL) and the cubic root of the endocast volume (V): $GLI=GL/(V^3)$.

Craniodental adaptations and dietary specialization — Most carnivores prey on other vertebrates. During the killing and eating of the prey, the heavy loads applied on the predator's skull can cause dental loss or damage (Biknevicius & Van Valkenburgh, 1996). In order to avoid this, predatory mammals have developed specific craniodental adaptations and killing techniques. These adaptations (such as short and broad maxilla, thick mandible and strong incisors) are particularly evident in highly carnivorous mammals, which include a very large percentage of meat in their diet and often prey on animals larger than themselves. Since specialization towards a highly carnivorous diet is associated morphologically with certain changes in the skull, mandible and dentition, we can rely on measurements of these changes in order to investigate the dietary specialization.

The estimation of certain cranial, mandibular and dental proportions was based on ratios that were developed by Van Valkenburgh & Koepfli (1993) in a study of predatory adaptations of the living Canidae. The values for living Canidae were taken from Van Valkenburgh & Koepfli (1993) and for most Borophaginae from Van Valkenburgh *et al*. (2003). For the rest of the Borophaginae, Hesperocyoninae and some other carnivore groups, the ratios were calculated from linear measurements (Fig. 1; Table 1) that were taken from AMNH specimens according to the method of Van Valkenburgh & Koepfli (1993). For a list of specimens, see Appendix 4. The ratios were analysed using principal component analysis in JMP (SAS).

Phylogenetic, taxonomic and stratigraphic framework — Phylogenetic and stratigraphic data are crucial for the outcome of this project. In order to formulate a complete picture of canid brain evolution, it is necessary to place the descriptions of the endocasts within a phylogenetic and chronologic framework.

Phylogenetic relationships follow Wang (1994) on Hesperocyoninae, Wang *et al*. (1999) on Borophaginae, Tedford *et al*. (1995) for the living Caninae, Wang *et al*. (2004, 2008) for the fossil North American Caninae and Berta (1987, 1988) for the fossil South American Caninae. Additional data were taken from the works of Nowak (1979), Tedford & Qiu (1991, 1996), Rook (1992, 1993, 1994), Sotnikova (2001, 2006), Lyras *et al*. (2006) and Wang *et al*. (2008). The stratigraphic framework (Fig. 2) follows the geo-

$$RBL = \frac{a}{f} \qquad RLGA = \frac{\sqrt{(e \cdot d) + (b \cdot c)}}{a} \qquad IxP4 = \frac{\sqrt[4]{\dfrac{\pi \cdot l \cdot g^3}{64}}}{k}$$

$$C1 = \frac{\sqrt{n \cdot m}}{r} \qquad I3 = \frac{\sqrt{p \cdot o}}{r} \qquad C1C1 = \frac{q}{r}$$
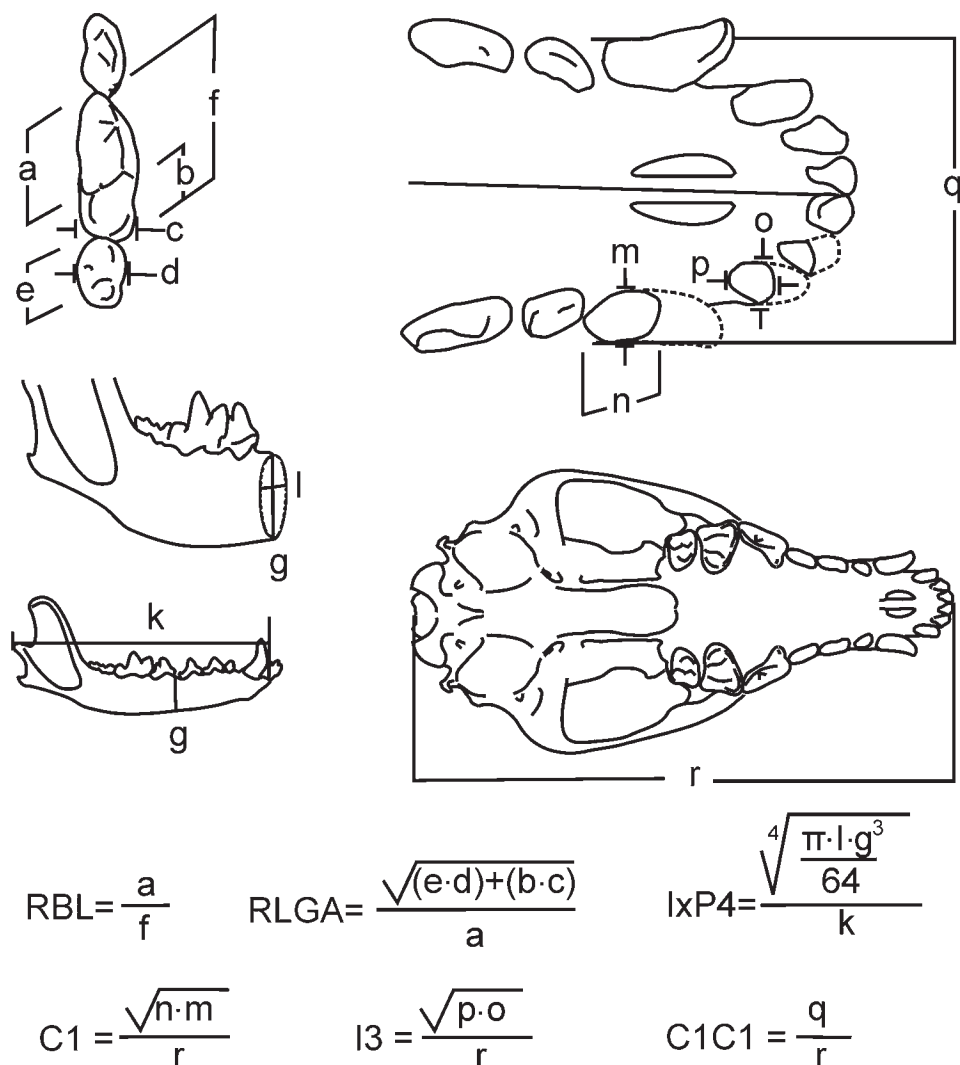
Fig. 1. Views (top) of the mandible and skull of a canid illustrating the measurements used in some of the Van Valkenburcgh & Koepfli's (1993) ratios (bottom) that were applied to quantify ecologic specialization. Key: RBL= relative blade length of the lower first molar (m1); RGLA= relative lower molar grinding area; IxP4= relative resistance of dentary to bending in the parasagittal plane (jaw rigity); C1= relative size of the upper canine (C); I3 = relative size of the upper third incisor (I3); C1C1 = relative rostral breadth. (a) Maximum length of the m1 trigonid. (b) Maximum length of m1 talonid. (c) Maximum breadth of m1 talonid (d): maximum breadth of the lower second molar (m2). (e) Maximum length of m2. (f) Anteroposteral length of the m1. (g) Maximum dentary height at the p3-p4 interdental gap. (k) The distance between the posterior margin of the mandibular condyle and the anterior margin of the lower canine. (l) Maximum dentary width at the interdental gap between the lower third and fourth molars (p3-p4). (m) Maximum breadth of C. (n) Maximum length of C. (o) Maximum breadth of I3. (p) Maximum length of I3. (q) Mediolateral breadth between lateral margins of the upper canines. (r) Skull (condylobasal) length.

Table 1. Variables (ratios) used in the analysis and their definitions (according to Van Valkenburgh *et al.,* 2003).

RBL	Relative blade length of the lower first molar (carnassial) measured as the ratio of trigonid length to total anteroposterior length of the m1.
RLGA	Relative lower molar grinding area measured as the square root of the summed areas of the m1 talonid and m2 divided by the length of the ml trigonid. Tooth area was estimated as the product of the maximal breadth and maximum length of the talonid and m2, respectively.
RUGA	Relative upper molar grinding area measured as the square root of the summed areas of the M1 and M2 divided by the maximum anteroposterior length of the P4 (carnassial). Tooth area was estimated as the product of maximum breadth and maximum length of the M1 and M2, respectively.
M1BS	Size of the cutting blade (trigonid) of the m1 relative to dentary length, estimated by dividing the maximum anteroposierior length of the trigonid by dentary length. Dentary length was measured as the distance between the posterior margin of the mandibular condyle and the anterior margin of the canine tooth.
M2S	Relative size of the m2 estimated by the square root of m2 area divided by dentary length. Tooth area was measured as in RLGA and dentary length as in M1BS.
IxP4	Relative resistance of the dentary to bending in the parasagittal plane as estimated by the second moment of area of the dentary relative to dentary length at the interdental gap between the third and fourth premolars. The second moment of area was calculated using the formula $Ix=(\pi*Dx*Dy^3)/64$ where Dx is maximum dentary width and Dy is maximum dentary height at the p3-p4 interdental gap. Ix relative to dentary length was then estimated as the fourth root of Ix divided by dentary length. Dentary length was measured as in M1BS.
IxM2	Relative resistance of the dentary to bending in the parasagittal plane as estimated by the second moment of area of the dentary relative to dentary length at the interdental gap between the ml and m2. Estimated as in IxP4 except that maximum breadth and height were taken at the ml-m2 interdental gap.
I2	Relative size of the upper second incisor estimated by the square root of the basal area of I2 divided by skull (condylobasal) length. I2 area was calculated as the product of maximum anteroposterior length and mediolateral breadth measured at the alveolar margin.
I3	Relative size of the upper third incisor estimated by the square root of the basal area of I3 divided by skull (condylobasal) length. I3 area was calculated as the product of maximum anteroposterior length and mediolateral breadth measured at the alveolar margin.
C1	Relative size of the upper canine estimated by the square root of the basal area of C1 divided by skull (condylobasal) length. C1 area was calculated as the product of maximum anteroposterior length and mediolateral breadth measured at the alveolar margin.
C1C1	Relative rostral breadth measured as the maximum mediolateral breadth between lateral margins of the upper canines, divided by skull (condylobasal) length.
UM2/1	Square root of M2 area divided by the square root of MI area. Areas estimated as in RUGA.
DIA	Relative spacing of the upper premolars estimated by the ratio of the sum of the anteroposterior lengths of Cl, P2-4 divided by the distance between the posterior margin of P4 and the anterior margin of C1.

Fig. 2. Simplified marine-continental chronologic correlation of the Cenozoic terrestrial faunas used in ▶ the text (see materials and methods for further information).

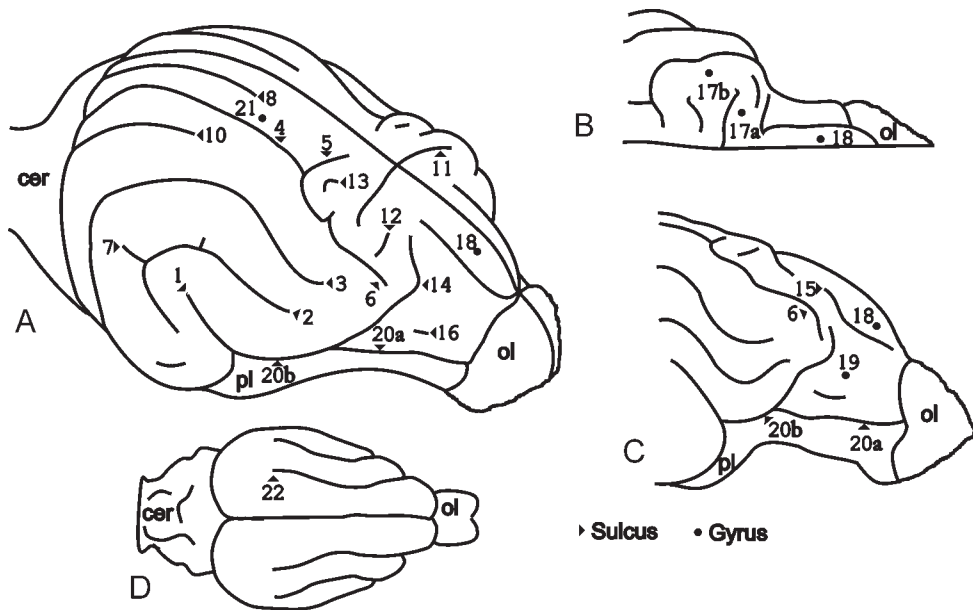| Epochs		Stage Age	European Mamm. Chrons.	Land Mammal Ages			
				North America	Europe	China	South America
Pleistocene	0.78			Irvingtonian	Biharian	Nihewanian	Lujanian 0.01
1 Early 1.80			MNQ19 MNQ18				Ensenadan
2 Late		Gelasian	MN17	Blancan	Villafranchian	Yushean	
3 Middle		Piacenzian	MN16				
Pliocene 4 Early 5 5.33		Zanclean	MN 15 MN14	4.7	Ruscinian		
	Late	Messinian 7.24	MN13 MN 12	Hemphillian	Turolian		
		Tortonian 11.60	MN 11 MN 10	9.0 Clarendonian 11.5			
10	Middle	Serravallian	MN 9 MN 8 MN 7 MN6	Barstovian			
Miocene 15		Langhian 15.97	MN 5	15.9			
	Early	Burdigalian 20,5	MN 4b MN 4a MN 3b MN 3a	Hemigfordian 19			
20		Aquitanian	MN 2b MN 2a MN 1	Arikareean			
23.03							
Oligocene	Late	Chattian	MP 30 MP 29 MP 28 MP 27 MP 26 MP24-25				
	Early	Rupelian	MP 23 MP 22 MP 21	30 Whitneyan Orellan			
Eocene	Late	Priabonian	MP 20 MP 19 MP 18 MP 17	Chadronian			

Fig. 3. Sulci and gyri of the brain of a domestic dog (A-C) and the Oligocene *Leptocyon gregorii* (D). (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. (D) Dorsal view. The drawings of A, B and C are addapted from Lyras & Van der Geer (2003).
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 acominis); 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 praecruciatus); 13. postcruciate sulcus (sulcus postcruciatus); 14. presylvian sulcus (sulcus praesylvius); 15. proreal sulcus (sulcus proreus); 16. intraorbital sulcus (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); 20. rhinal sulcus (sulcus rhinalis), a. anterior part (pars anterior sulcus rhinalis), b. posterior part (pars posterior sulcus rhinalis); 21. lateral gyrus (gyrus lateralis); 22. coronolateral sulcus (the coronal and lateral sulci together); cer. cerebellum; ol. olfactory bulb.

chronological time scale of Gradstein *et al*. (2004), and the definitions of the land mammal ages in Tedford *et al*. (1987, 1996) for North America, Flynn & Swisher (1995) for South America, Steininger *et al*. (1996) for Europe and Flynn *et al*. (1995) for China.

Anatomical nomenclature and homologies — The anatomical nomenclature of the skull and soft tissues (including the brain) follows that of Evans & Christensen (1993). The interpretation of homologous gyri and sulci on the cerebral cortex of extinct and living carnivores is done on the basis of macroscopic morphological observations, with the use of sulcal and gyral maps from previous works on this subject. The problem of ho-

mologies has been stressed in the past by several authors (including Haller Von Hallerstein, 1934; Kreiner, 1968; Campbell & Hodos, 1970; Uylings & Van Eden, 1990) and several criteria have been suggested. However, as in fossils, the actual brain is not available and only the macroscopic morphology can be used in this study. In evolutionary lineages for which a good representation of fossil endocasts is available, it is possible to track the evolutionary changes and identify the gyri of fossil specimens, simply by noting the sequence of gyral appearance.

The anatomical nomenclature of the cortical convolutions of canids follows Filimonov (1928; redrawn by Adrianov & Mering, 1959). The nomenclature of groups that have no living representatives and in which the sulcal pattern differs substantially from that of the living forms (e.g., Creodonta, Miacidae and Nimravidae) follows the nomenclature and identifying criteria summarized by Welker (1990).

Institutional abbreviations

AMNH	American Museum of Natural History, New York, U.S.A.
AMNH(M)	Department of Mammalogy, American Museum of Natural History, U.S.A.
AMPG	Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Athens, Greece.
AUT	Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki, Thessaloniki, Greece.
BMN	Natural History Museum, Basel, Switzerland.
CSCLA	California State College, Los Angeles, California, U.S.A.
F:AM	Frick Collection, American Museum of Natural History, U.S.A.
FMNH	Field Museum of Natural History, Chicago, U.S.A.
GIN	Geological Institute, Russian Academy of Sciences, Moscow, Russia.
IQW	Forschungsstation für Quartärpaläontologie, Weimar, Germany.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
NNHM	National Natural History Museum, National Academy of Sciences of Ukraine, Kiev, Ukraine.
NNM	Nationaal Natuurhistorisch Museum (Naturalis), Leiden, the Netherlands.
NNM RGM	Rijksmuseum van Geologie en Mineralogie (formerly, now Nationaal Natuurhistorisch Museum, the Netherlands).
NNM RMNH	Rijksmuseum van Natuurlijke Historie (formerly, now Nationaal Natuurhistorisch Museum, the Netherlands).
SASN	Soprintendenza Archeologica Sassari e Nuoro, Sardinia, Italy.
TMM	Texas Memorial Museum, University of Texas, Austin, U.S.A.
UNSM	University of Nebraska State Museum, Lincoln, U.S.A.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
YPM	Yale Peabody Museum of Natural History, Yale University, New Haven, U.S.A.

<center>**History of research**</center>

Extant canids —Although there is an extensive literature on the anatomy of the nervous system of the domestic dog (Fox, 1971; Beitz & Fletcher, 1993; and references cited therein), there are few publications on the brain anatomy of the wild canids. Early studies on the external brain anatomy of wild canids were published by Gervais (1870), Mivart (1885) and Klatt (1928). More recent studies are those of England (1973) on the cerebrum of *Canis latrans*, *C. lupus*, *Urocyon cinereoargenterus*, *Vulpes vulpes* and the dingo, and Atkins (1978) on *Canis latrans* and *C. rufus*. A more extensive study was that of Radinsky (1973), who described and figured twelve species of wild canids (*Vulpes vulpes*, *V. zerda*, *Urocyon cinereoargenterus*, *Otocyon megalotis*, *C. lupus*, *C. adustus*, *C. simensis*, *Lycaon pictus*, *Cerdocyon thous*, *Lycalopex sechurae*, *Speothos venaticus* and *Nyctereutes procyonoides*) and gave brief comments on a few other members. Radinsky (1978a) figured *Vulpes vulpes* and *Canis mesomelas*. Lyras & Van der Geer (2003) described and figured the external anatomy of the cerebrum of 29 living wild canids (*Canis lupus, C. adustus, C. aureus, C. mesomelas, C. sinensis, Lycaon pictus, Cuon alpinus, Atelocynus microtis, Speothos venaticus, Lycalopex culpaeus, L. griseus, L. sechurae, L. gymnocercys, L. vetulus, Dusicyon australis, Cerdocyon thous, Nyctereutes procyonoides, Urocyon cinereoargenterus, Otocyon megalotis, Vulpes lagopus, V. vulpes, V. zerda, V. bengalensis, V. corsac, V. rueppelli* and *V. chama*) and demonstrated the usefulness external brain anatomy for phylogenetic interpretations (Fig. 4).

Fossil canids — The earliest description of a fossil canid brain (Scott, 1895) was based on a natural endocast of *Cynodesmus.* Subsequently, brains of fossil canids have been described by several authors. Of particular interest are Moodie (1922), who described and figured an artificial endocast of *Canis dirus;* Pei (1934), who figured a natural endocast of *Nyctereutes* sp.; Tilney (1931) and Scott & Jepsen (1936), who gave a detailed description of a natural endocast of *Hesperocyon gregarius;* Jakway & Clement (1967), who figured and described a natural endocast of *Paratomarctus* (*Tomarctus* in their work); and Czyżewska (1981), who described two natural endocasts (*Nyctereutes* and *"Canis"*) from Poland.

The above mentioned papers were focused on the description of individual specimens and did not attempt to investigate the evolutionary history of the brain in the entire family. This was first done by Radinsky (1969), who gave an outline of canid brain evolution with the description of endocasts of four genera (*Hesperocyon, Mesocyon, Paratomarctus* and *Canis*). Subsequently, Radinsky (1973) described endocranial casts from 18 fossil canid genera (13 for the first time) and figured endocasts from several living species (see above). With the use of this endocranial material and with

Fig. 4. (A) Different types of outlines that are created by the coronal and ansate sulci on the dorsal surface of the cerebrum (from Lyras & Van der Geer, 2003). (B) Probable phylogenetic relationships within the living Caninae and occurrence of different types of sulcal pattern (from Lyras & Van der Geer, 2003).
Outline patterns: a, pentagonal; b, heart-shaped; c, parenthesis-like; d, orthogonal.
Caninae phylogenetic relationships: 1, Tedford *et al.* (1995) morphological cladogram; 2, Cladogram based on Wayne *et al.* (1997) molecular parsimony cladogram; 3, Tedford's and Wayne's combined cladogram by Wayne *et al.* (1997).
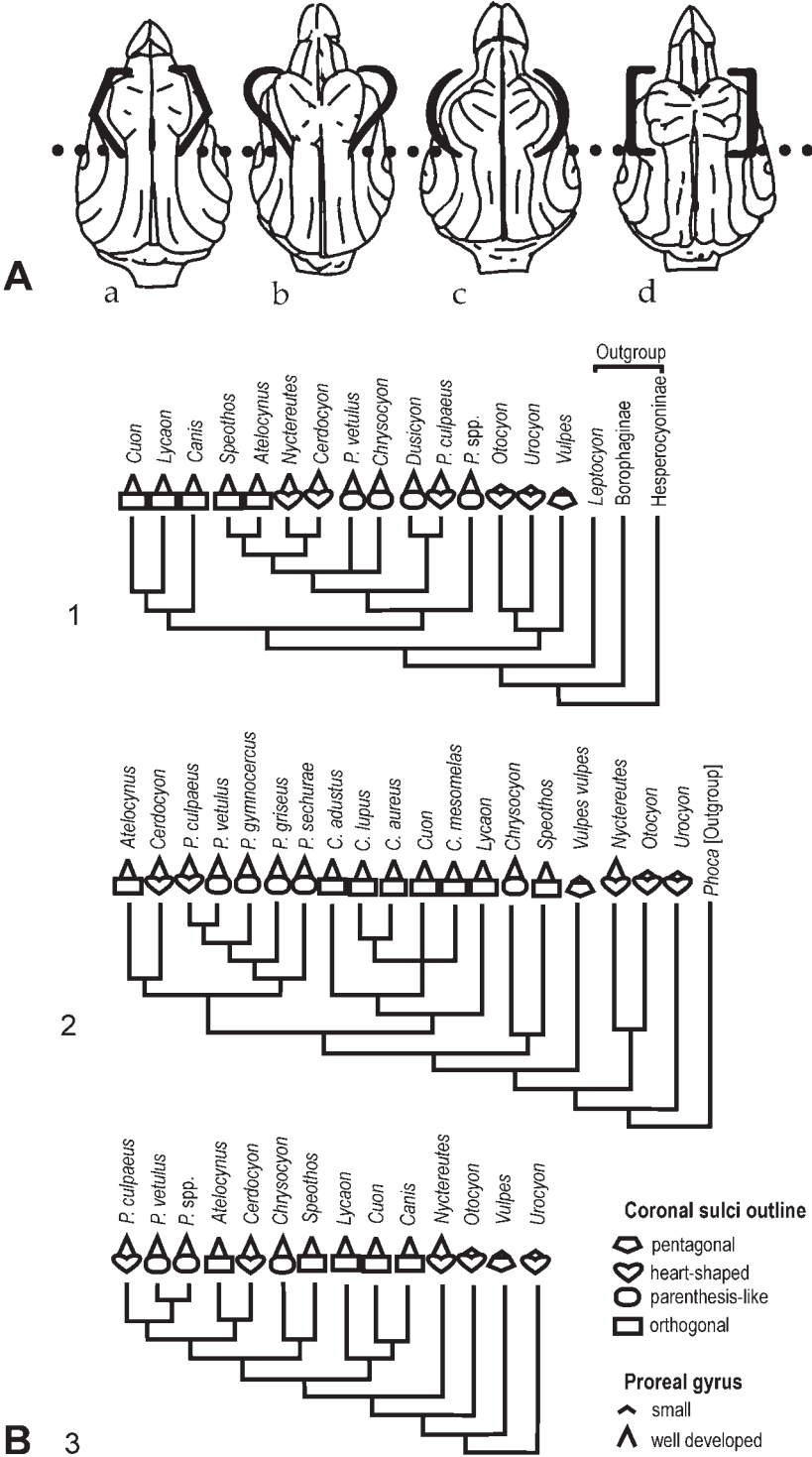
Table 2. List of fossil canid endocasts that were figured by Radinsky (1973).

Assignment in Radinsky (1973)	Specimen number	Present assignment
"unnamed new genus"	F:AM 67098	Osbornodon fricki
Enhydrocyon stenocephalus	USNM 7745	Enhydrocyon stenocephalus
Mesocyon sp.	AMNH 6946	Mesocyon sp.
Hesperocyon gregarius	YPM10068 & AMNH 69476	Hesperocyon gregarius
Leptocyon sp.	F:AM 49063	Leptocyon gregorii
Leptocyon sp.	F:AM 49433	Leptocyon sp.
Vulpes sp.	F:AM 49284	Vulpes stenognathus
Nyctereutes megamastoides	F:AM 22336	Nyctereutes sinensis
Canis cf. C. latrans	F:AM 63005	Eucyon davisi
Nothocyon sp.	F:AM 49031	Archaeocyon leptodus
Phlaocyon marslandensis	UNSM 26153	Phlaocyon marslandensis
Cynodesmus petersoni	F:AM 61300	Desmocyon matthewi
"Phlaocyon-like species "	F:AM 61009	Paracynarctus sinclairi
Aelurodon platyrhinus	F:AM 61746	Aelurodon ferox
Tomarctus cf. T. euthos	F:AM 61074	Paratomactus euthos
"unnamed new genus close to Osteoborus"	F:AM 61328	Carpocyon webbi
"unnamed new species of Aelurodon"	F:AM 61476	Epicyon haydeni
Osteoborus dudleyi	MCZ 3688	Borophagus dudleyi

SOUTH AMERICAN CANIDS AND NYCTEREUTES

WOLVES   FOXES

RECENT   PLIO-PLEISTOCENE   MIOCENE   PLIO-PLEISTOCENE   RECENT

1. Leptocyon sp. F:AM 49433
2. Eucyon davisi F:AM 63005
3. Canis lepophagus AMNH 104782
4. Canis lupus NNML cat.no.l.
5. Nyctereutes sinensis F:AM 96750
6. Chrysocyon brachyurus NNML cat.no.a.
7. Cerdocyon thous NNML cat.no.b.
8. Nyctereutes procyonoides NNML cat. no. d.
9. Pseudalopex culpaeus AMNH 27904
10. Urocyon cinereoargenteus AMNH(M) 68527.
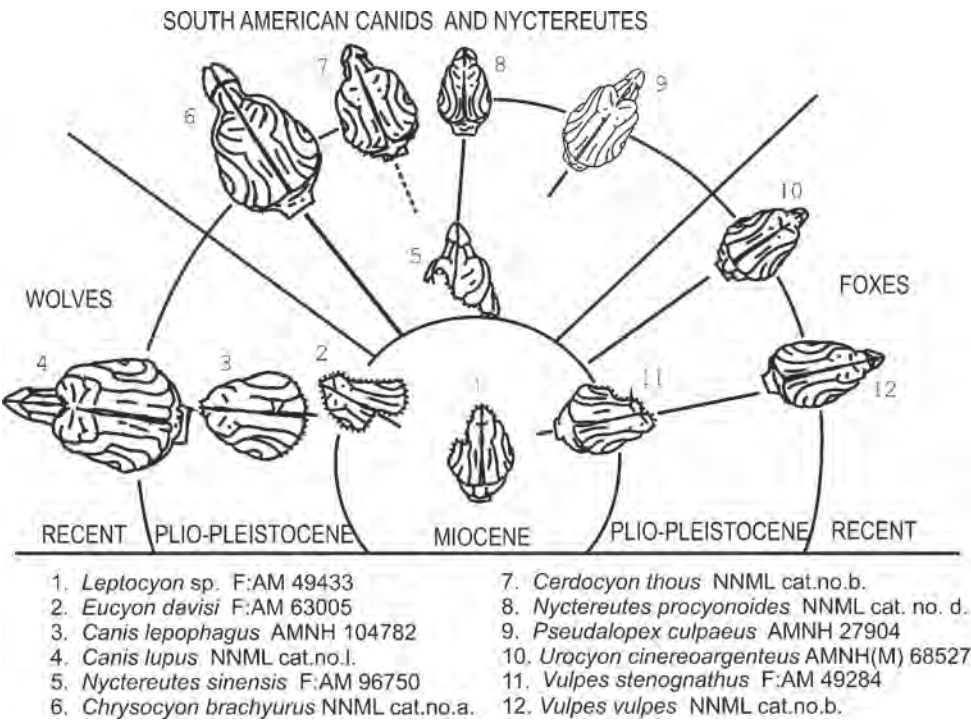11. Vulpes stenognathus F:AM 49284
12. Vulpes vulpes NNML cat.no.b.

Fig. 5. *Nyctereutes* as part of the evolutionary radiation of the Caninae brain (from Dermitzakis *et al.*, 2004).

phylogenetic data from an unpublished study by Tedford & Taylor, Radinsky presented the most rigorous work on canid brain evolution up to that time (Table 2).

Some of the most important conclusions of Radinsky's work include the brain of the first Canidae had fewer sulci than the brains of living species and even sulci that are almost ubiquitous in modern carnivores were absent in the early forms. During evolution, lobule VII of the cerebellar vermis became enlarged and twisted, the neocortex expanded and gradually more cortical folds appeared (by 25 Ma the ectosylvian, ectolateral and presylvian sulci appeared, and at about 12 Ma the sylvian sulcus). Expansion of the cortex in the early stages of canid evolution took place at the posterior and temporal lobe, and in later stages (particularly after the Late Miocene) at the anterior lobe. The most important difference among brains of the living canids is the relative size and shape of the proreal gyrus (long and bilaterally constricted in dogs, short and broad in foxes).

More recently, Lyras (2001) and Lyras et al. (2001) investigated some aspects of the evolutionary radiation of the Caninae brain that took place in the Mio-Pliocene. They noted the different sulcal patterns in Vulpini (foxes) and Canini (dogs), and that these appeared during the course of the evolutionary radiation. Lyras & Van der Geer (2003) presented more endocasts of fossil and living Caninae (see above) that gave additional evidence for the evolutionary radiation of their sulcal pattern. Finally, Dermitzakis et al. (2004) presented a paper on the evolutionary history of the brain of *Nyctereutes* (Fig. 5).

Outline of canid evolution — Simpson (1945, p. 222), in his classification of mammals, noted that "fossil canids are very abundant, and this richness is very embarrassing since it suffices to complicate rather than to elucidate..." This might have been true for his time, but during the last fifteen years a series of palaeontological and neontological studies (Berta, 1988; Rook, 1992, 1993, 1994; Wang, 1994; Tedford et al., 1995; Wang et al., 1999; Ivanoff, 2000, 2001; Sotnikova, 2001; Martìnez-Navarro & Rook, 2003), and molecular and karyological studies (Wayne et al., 1987a, b, 1997), as well as ecomorphology and functional morphology (Munthe, 1989; Van Valkenburgh, 1985, 1989, 1991; Van Valkenburgh & Koepfli, 1993; Van Valkenburgh et al., 2003; Andersson, 2003, 2005), have shed new light on canid evolution. The family is now one of the best known carnivore groups.

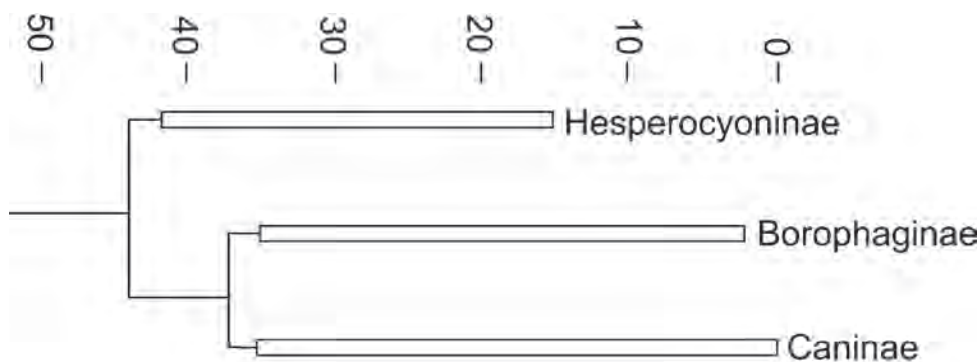
Fig. 6. Phyletic relationship of the major divisions of Canidae and their temporal ranges (redrawn from Wang et al., 1999).

Canid evolution is mainly a North American story. Most of their evolutionary history took place in North America, as canids were restricted to that continent from the Late Eocene until the Late Miocene. Contrary to the early studies (Matthew, 1930; Simpson, 1945; MacDonald, 1963), that agreed on a bipartite division of the family, recent works follow the suggestion of Tedford (1978), according to whom canids are divided into three subfamilies (Fig. 6): the Hesperocyoninae, which radiated mainly during the Oligocene; the Borophaginae, which radiated during the Oligocene and Miocene; and the Caninae, which radiated during the Plio-Pleistocene. Although their evolutionary radiations were sequential, their start was more or less contemporaneus: Late Eocene for the Hesperocyoninae, Oligocene for the Caninae and Borophaginae (Wang, 1994; Wang et al., 1999).

The first canids were small, fox-sized carnivores belonging to the genera *Prohesperocyon* (a transitional form between Miacidae and Canidae; Wang, 1994) and *Hesperocyon* (the first true canid and ancestor of all later forms). *Hesperocyon* appeared during the Duchesnean (Late Eocene) (Bryant, 1992), but it became abundant somewhat later, during the Chadronian (latest Eocene). The Oligocene was a critical period for the Canidae, since at that time many new forms appeared and canids reached their maximum species richness. This is because they entered several empty niches that originated from a faunal reorganization (Woodburne & Swisher, 1995) and environmental changes due to a long episode of Antarctic glaciation (Tedford et al., 1996).

The first subfamily to radiate was that of the Hesperocyoninae (Fig. 7). With the exception of one genus (*Osbornodon*), all Hesperocyoninae were small in size and had a clear tendency towards hypercarnivorous dental adaptations (such as reduced last molars and a trenchant talonid of the m1). These characters led Van Valkenburgh (1991) to suggest that many Hesperocyoninae were filling cat-like niches, which were empty at the beginning of the Miocene in North America. Wang (1994) recognised four main evolutionary lineages: *Paraenhydrocyon*, *Mesocyon - Enhydrocyon*, *Osbornodon* and *Ectopocynus*. Hesperocyoninae became extinct in the Middle Miocene.

The first Borophaginae were, like the Hesperocyoninae, small in size. Their dental adaptations tended towards hypocarnivory (an omnivorous diet with dental adaptations opposite to those of hypercarnivory, with an increased grinding area of the molars and reduced cutting section of P4/m1). Later Borophaginae included a wide spectrum of adaptations, and occupied several ecological niches that are today filled by raccoons, canids and hyenas. Wang et al. (1999) published a phylogenetic analysis of the subfamily in which four major clades were recognized (Fig. 7). Some of these lineages showed a clear tendency towards hypercarnivory. There were also species with dental adaptations comparable to those of the living hyenas (hence their common name "hyena-dogs"). Borophaginae became extinct during the Pliocene.

The earliest member of the Caninae is the genus *Leptocyon*. This genus was adapted to mesocarnivory (moderate carnivorous adaptations intermediate between hypo- and hyper-carnivory). The genus is not only the first, but also the only representative of the family for most of its history, ranging from Early Oligocene until Late Miocene. The radiation of Caninae started when several ecological niches became available again, due to the extinction of all small Borophaginae (Wang et al., 2004). During the early stages of this radiation all major clades of living Canidae appeared (Tedford et al., 2001).
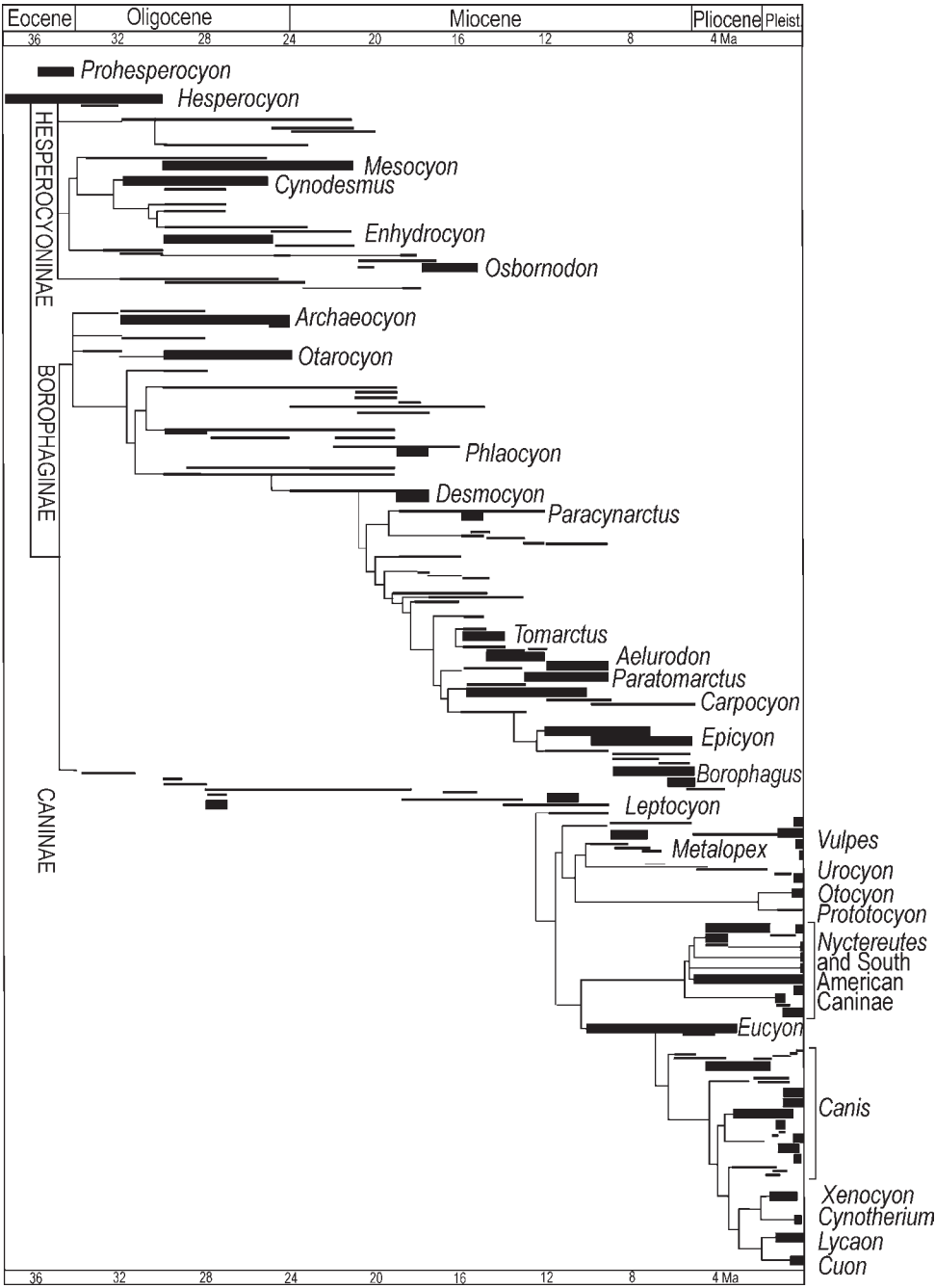
Fig. 7. Phylogenetic relationships of canid taxa. Temporal ranges are indicated by individual bars. The thick bars indicate species from which endocasts were available. These are discussed further in this study. Phylogenetic relationships and temporal ranges taken from Berta (1988), Wang (1994) and Wang *et al.* (1999, 2004, 2008).

At the end of the Miocene Caninae migrated into the Old World (Fig. 8). Their appearance in Eurasia is associated with the extinction of the small canid-like hyenas at the Miocene-Pliocene boundary (Werdelin & Turner, 1996). During the Plio-Pleistocene, several Caninae species appeared in the Old World, either as immigrants from North America or as new species. Some of those new canids returned to North America (Fig. 8). The migration of Caninae into South America began in the Pliocene after the establishment of the Panama Isthmus (Berta, 1988). Apart from the immigrants from the north, South America turned out to be an important place for diversification and many new endemic species, adapted to local conditions, evolved there (Hunt, 1996).

The first canids and
the Hesperocyoninae

The first canids, *Prohesperocyon* and *Hesperocyon,* appeared in North America in the Late Eocene. During the Oligocene, *Hesperocyon* gave rise to several canid clades, some of which were grouped by Wang (1994) within the subfamily Hesperocyoninae. This subfamily reached its maximum diversity during the Late Oligocene and went extinct in the Middle Miocene.

Late Miocene - Early Pliocene

Early Pliocene - Pleistocene

Late Eocene: *Prohesperocyon*

Phylogenetic position — *Prohesperocyon* is a transitional form between the Miacidae and Canidae (Wang, 1994). The dentition of *Prohesperocyon wilsoni*, the only known species in the genus, shows similarities to *Miacis* and *Procynodictis*. However, the anatomical features of its basicranium (fully ossified bulla, medially expanded petrosal and extrabullar position of the internal carotid artery) indicate that it is a canid (Wang & Tedford, 1994).

Material — *Prohesperocyon wilsoni* AMNH 127172 (plaster cast of TMM 40504-126) - Chadronian (Late Eocene) from the Airstrip Local Fauna, southern Sierra Vieja area, Presidio County, Texas, U.S.A.; skull with partially exposed natural endocast (Fig. 9).

Description — Natural erosion of the neurocranial wall of the only known skull of

◀ Fig. 8. Caninae dispersal through time (the dispersal routes are plotted on the present-day geography).
(1) Evolution of Caninae in North America: An evolutionary radiation at the end of the Miocene (Claren-donian and Hemphillian) resulted in the appearance of early members of all the major Caninae clades: *Vulpes*, *Urocyon* (Wang *et al.*, 2004), *Eucyon/Canis* (Tedford & Qiu, 1996), *Cerdocyon* (Torres & Ferrusquia-Villafranca, 1981; McKenna & Bell, 1997) and *Chrysocyon* (McKenna & Bell, 1997).
(2) Dispersal and evolution of Caninae in Eurasia: In the latest Late Miocene- Early Pliocene, Caninae underwent an extensive radiation in Eurasia, resulting in the appearance of new species of *Eucyon* (Rook, 1992; Tedford & Qiu, 1996) and *Vulpes* (Qiu & Tedford, 1990), the appearance of *Nyctereutes* (Tedford & Qiu, 1991) and some new, still undescribed genera (Tedford & Qiu, 1996; Ivanoff, pers. comm. 2003; Sot-nikova, 2006). The figure suggests that Caninae entered first the Far East (2a) and then Europe (2b). However, the fossil evidence suggests the opposite, as the first European fossils (later Late Miocene: Tourolian: MN12) are older than the Chinese ones (Early Pliocene). If the East-West-East immigration actually did take place, Caninae must have followed a route without leaving (or not yet found) fossil evidence (De Bonis *et al.*, 2007, suggested an African route), came to Europe and then moved to Asia (Zhang, pers. comm. 2004).
(3) At the Late Miocene Caninae entered Africa. They were represented by *Vulpes* (De Bonis *et al.*, 2007) and *Eucyon* (Morales *et al.*, 2005). The genus *Canis* is definitely present in Afrika at 3.5 Ma (Werdelin & Lewis, 2000) and probably at Laetoli slightly earlier (Weredlin & Dehghani, in press). *Nyctereutes*-like were present in Afrika in the Pliocene (Barry, 1987; Wedelin & Lewis, 2005).
(4) During the Late Pliocene-Pleistocene, North America continued to be a centre of canid evolution, with the appearance of several new *Canis* species (Wang *et al.*, 2004).
(5) Caninae entered South America after the establishment of the Panama Isthmus (around 3 Ma): The oldest canid record in South America is from the Late Pliocene (Berman, 1994). During the Early Pleis-tocene (Ensenadan), canid diversity increased with species of *Lycalopex*, *Chrysocyon, Theriodictis, Protocyon* and *Canis* (Berta 1988; Berman 1994; Prevosti *et al.,* 2005). At the end of the Pleistocene, all large canids, with the exception of *Chrysocyon*, became extinct in South America (Berta, 1987).
(6) Evolution of Caninae in Eurasia: During the Late Pliocene *Nyctereutes* was distributed throughout Eurasia. The genus became extinct in Europe before the beginning of the Pleistocene, while in Asia it survived to the present (Soria & Aguirre 1976; Tedford & Qiu, 1991). During the Plio-Pleistocene, new *Canis*-like species appeared in Eurasia. These belong to the genera *Canis, Cuon* and *Xenocyon* (Flynn *et al.*, 1991; Rook, 1993; Sotnikova, 2001). *Canis* appeared in Asia during the Pliocene (6a). The earliest record of *Canis* in Europe (6b) is from latest Pliocene (Rook & Tore, 1996), but it became abundant only after the Plio-Pleistocene boundary. Some *Canis*-like lineages (*Canis, Cuon* and *Xenocyon*) became a specialization towards hypercarnivory. *Lycaon* seems to be related to one of these lineages (Rook, 1994; Martínez-Na-varro & Rook, 2003). During the Pleistocene, several Eurasian Caninae (*Vulpes, Canis, Cuon* and *Xenocyon*) entered North America (Rook, 1993; Wang *et al.* 2004).
(7) Evolution of Caninae in Africa: During the Late Pliocene, *Nyctereutes* was present in Africa (Geraads, 1997). During the Pleistocene the jackals and *Lycaon* appeared (Werdelin & Lewis, 2005).

this species has exposed the dorsolateral part of its endocast. Although the exposure is not complete, it is sufficient to give a good picture of the brain of *Prohesperocyon*.

The cerebral hemispheres are pear-shaped, posteriorly broad, anteriorly tapering and decreasing in vertical as much as in transverse diameter. The temporal and, particu-larly, the frontal lobes are clearly smaller than those of any living canid. There are only two neocortical sulci: the coronolateral, which runs almost parallel to the longitutional fissure; and the suprasylvian, which forms a wide vertical arch on the lateral side of the brain. The overlap of the cerebellum by the cerebrum is small, leaving almost the entire vermis exposed. In dorsal view, the fissura prima lie half way between the rostral and occipital lobes of the vermis. Although the erosion of the endocast has removed much of the detail of the cerebellar hemispheres, it is clear that they are relatively narrow, as they do not extend further than the lateral margins of the foramen magnum.
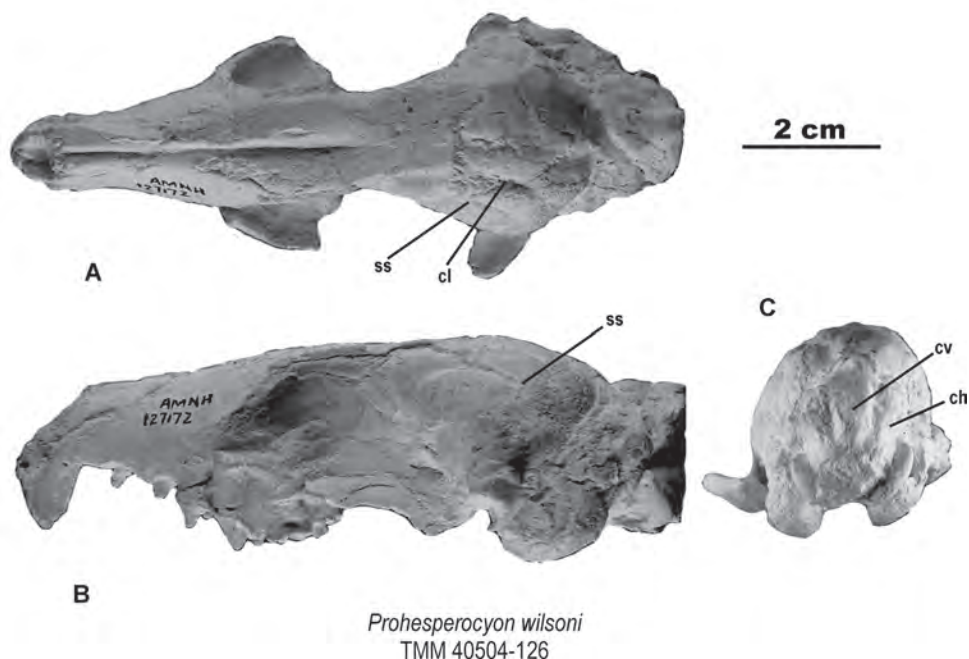
Fig. 9. *Prohesperocyon wilsoni* AMNH 127172 (plaster cast of TMM 40504-126). (A) Dorsal, (B) left lateral and (C) posterior views. cl: coronolateral sulcus, ss: suprasylvian sulcus, cv: cerebellar vermis, ch: cerebellar hemishere.

Late Eocene - Early Oligocene*: Hesperocyon*

Phylogenetic position — *Hesperocyon* gave rise to several lineages within the initial radiation of the Canidae (Wang, 1994; Munthe, 1998). Its earliest certain appearance is the Chadronian (Late Eocene), though there is dental evidence that extends its range into the Duchesnean (Bryant, 1992). These were small animals, with an elongated body, long tail and subdigitigrade forefeet with probably retractile claws (Wang, 1993). *Hesperocyon* is the most common fossil carnivore in the badlands of the northern Great Plains (reviewed by Wang, 1994) and several natural endocasts of this genus are preserved.

Material — *Hesperocyon gregarius* F:AM 50277 - Chadronian to Orellan (Late Eocene-Early Oligocene), upper end of Shack Draw, Wyoming, U.S.A. A nearly complete skull with a dorsally and laterally exposed natural endocast. The dorsal part of the cerebellum is hidden under the parietal bone and part of the cerebrum is covered by the field label. The olfactory bulbs are not exposed (Fig. 10 C, D).

Hesperocyon gregarius F:AM 76518 - Orellan (Early Oligocene), Herb Geike Ranch, Sioux County, Nebraska, U.S.A. Skull and mandible with partially exposed natural endocranial cast of the cerebrum and cerebellum. The rostral part of the cerebrum and the olfactory bulbs are hidden within the skull. The endocast is slightly distorted by lateral compression (Fig. 10A, B).

Hesperocyon gregarius F:AM 76520 - Orellan (Early Oligocene), Herb Geike Ranch, Sioux County, Nebraska, U.S.A. Partial skull with exposed cerebrum and part of the cerebellum. A fragment of the parietal bone intervenes between the cerebrum and right
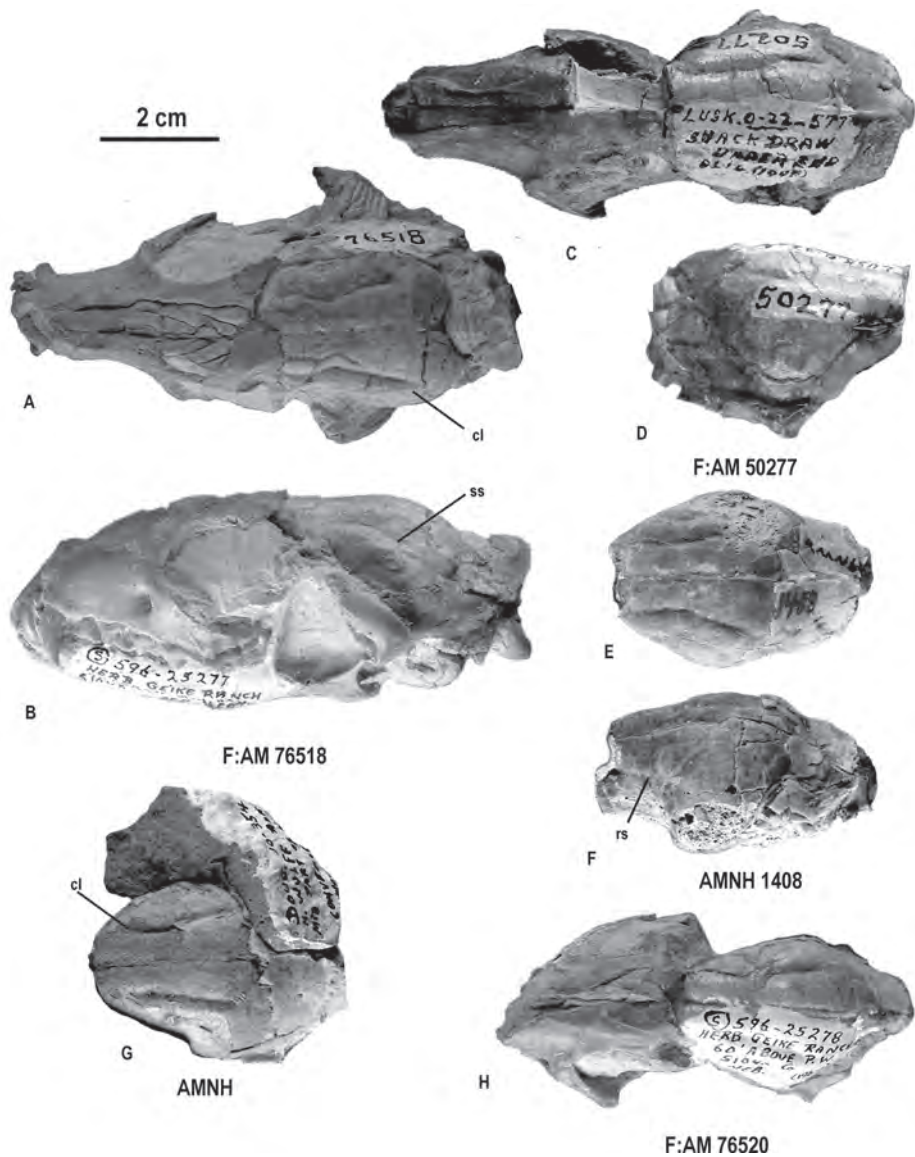
Fig. 10. Natural endocranial casts from Eocene and Oligocene *Hesperocyon*. *Hesperocyon gregarius* F:AM 76518, (A) dorsal and (B) left lateral views. *H. gregarius* F:AM 50277, (C) dorsal and (D) right lateral views; *H. gregarius* AMNH 1408, (E) dorsal and (F) left lateral views; *Hesperocyon* sp. AMNH-uncataloged (field number: Doug. 10-354), (G) dorsal view; *H. gregarius* F:AM 76520, (H) dorsal view. cl: coronolateral sulcus, ss: suprasylvian sulcus, rs: rhinal sulcus.

cerebellar surface. The left cerebellar hemisphere is covered by the field note (Fig. 10H).

    Hesperocyon gregarius AMNH 1408 - Early Oligocene, Oreodon Beds of Big Badlands, South Dakota, U.S.A. Natural endocast with partial skull, left ramus, left tarsus and metatarsus. The endocast is nearly complete with only the olfactory bulbs being

Fig. 11. Natural endocranial casts from Oligocene *Hesperocyon*. *Hesperocyon gregarius* AMNH 85888, (A) dorsal view; *Hesperocyon* sp. AMNH 129176, (B) dorsal view; *Hesperocyon* sp. AMNH 39476 (C) dorsal, (D) right lateral and (E) ventral views; *H. gregarius* F:AM 76166, (F) dorsal and (G) lateral views; *Hesperocyon* sp. AMNH 9766, (H) anterior, (I) posterior, (J) dorsal, (K) left lateral and (L) ventral views. cl: coronolateral sulcus, ss: suprasylvian sulcus, ol: olfactory bulb.

hidden within the cast of the nasal cavities. Its ventral surface is poorly preserved (Fig. 10E, F).

Hesperocyon sp. AMNH - uncatalogued (field number: Doug. 10-354) - Orellan (Early Oligocene), middle part of nodule zone, Wolff Ranch, southeast of Douglas area, Converse County, Wyoming, U.S.A. Natural endocast party covered by matrix. The olfactory bulbs and the occipital part of the cerebellum are missing (Fig. 10G).

Hesperocyon gregarius AMNH 85888 - Orellan-Whitneyan (Early Oligocene), "Middle" Brule Formation, Robert's Draw, Nebraska, U.S.A. Partial skull and natural endocast of the anterior cerebrum (Fig. 11A).

Hesperocyon gregarius F:AM 76166 - Orellan (Early Oligocene), upper part of nodular layer, Reno Ranch, Converse County, Wyoming, U.S.A. Endocranial cast of the cerebrum and part of the cerebellum of a nearly complete skull with mandible. The right cerebellar hemisphere is covered by the field label (Fig. 11F, G).

Hesperocyon gregarius YPM 10067 - Early Oligocene, South Dakota, U.S.A. Natural endocast that was described and figured by Scott & Jepsen (1936) under the name *Pseudocynodictis* (Radinsky, 1969, 1973; Edinger, 1977).

Hesperocyon sp. AMNH 129176 - Orellan (Early Oligocene), west of Ant Hill Locality, Brule Formation, Wyoming, U.S.A. A nearly complete natural endocast. The olfactory bulbs are missing and parts of the cerebellum are covered by bone (Fig. 11B).

Hesperocyon sp. AMNH 9766 - Early Oligocene, Oreodon Beds, Indian Creek, Big Badlands, South Dakota, U.S.A. An excellently preserved natural endocast (Fig. 11H-L). The specimen was figured and described in detail by Tilney (1931) under the name *Cynodictis* (Radinsky, 1969, 1973; Edinger, 1977).

Hesperocyon sp. AMNH 39476 - Early Oligocene, south of Scenic, South Dakota, U.S.A. Natural endocast from which only the rostral part of the olfactory bulbs is missing (Fig. 11C, D, E). Radinsky (1973) used it, together with YPM-10067 and YPM-PU 12732, for a composite drawing and description of the *Hesperocyon* brain.

Description and comparisons — The brain of *Hesperocyon* is slightly more globular than that of *Prohesperocyon*, but is otherwise similar in proportions and important features. The rhinal sulcus is relatively high, at about 25 % of the brain's total height. The olfactory bulbs are large and not covered by the cerebral hemispheres. The frontal lobe is short and narrow. There are only two cortical sulci, the coronolateral and the suprasylvian. In some specimens the coronolateral sulcus approaches to the dorsal midline at the level of frontoparietal suture and then bows out slightly. The extent of this is variable and is at a maximum in F:AM 76518 (Fig. 11A) in which the coronolateral sulcus forms a clear bend at the level of the frontopariental suture that distinguishes the rostral (the coronal) from the occipital (the lateral) part.

The more globular shape of the *Hesprerocyon* brain might be a result of differences in the general cranial proportions of the two genera. *Prohesperocyon* has a more elongated skull than *Hesperocyon* and differences in skull proportions are known to affect the general shape of the brain (Weidenreich, 1941; Seiferle, 1966; Radinsky, 1973).

Tilney (1931), Scott & Jepsen (1936) and Radinsky (1969, 1971, 1973, 1978a) gave detailed descriptions of the *Hesperocyon* brain based on some of the specimens mentioned above. The descriptions of Tilney (1931) and Scott & Jepsen (1936) are quite accurate, although as they were trying to locate the sulci of living carnivores in *Hesperocyon*, they incorrectly interpreted a small depression at the temporal lobe as the sylvian

sulcus (see below). In addition, Scott & Jepsen (1936) suggested that the endocasts do not reproduce all sulci present on the living brains, because the cruciate sulcus, which is present in all living carnivore families, is absent in *Hesperocyon.* Their problem was rather obvious; since all living carnivore families share the same sulci and the fossil canids do not have them, these sulci must have appeared either by parallel evolution or the fossils are misleading. Scott & Jepsen (1936) chose the second option, but Radinsky (1971) showed that most of the homologous sulci of the carnivores are actually the result of parallel evolution. According to Radinsky (1971), sulci with a universal distribution among living carnivores, like the cruciate sulcus, are absent from their early representatives and appeared independently at least five times. In addition, he indicated that

Fig. 12. Endocranial casts from *Mesocyon*. *Mesocyon* sp. AMNH 6946, (A) dorsal, (B) right lateral, (C) left lateral and (D) ventral views; *Mesocyon coryphaeus* AMNH 6920, (E) dorsal, (F) lateral and (G) ventral views. cl: coronolateral sulcus, ss: suprasylvian sulcus, es: ectosylvian sulcus, el: ectolateral sulcus, rs: rhinal sulcus. cl: coronolateral sulcus, ss: suprasylvian sulcus, es: ectosylvian sulcus, rs, rhinal sulcus, ol: olfactory bulb.

the reproduction of the external brain anatomy of *Hesperocyon* by the endocasts is as accurate as in the similar-sized exant canids (Radinsky, 1973).

Oligocene - Early Miocene: *Mesocyon, Cynodesmus, Enhydrocyon*

Phylogenetic position — This is the most diverse lineage of hesperocyonines, beginning with *Mesocyon,* and leading to *Enhydrocyon* through the transitional forms *Cynodesmus*, *Sunkahetanka* and *Philotrox*. The lineage is characterized by an increased trend towards hypercarnivory. Endocranial material is known from three genera: *Mesocyon*, *Cynodesmus* and *Enhydrocyon***.**

Fig. 13. Endocranial casts from *Cynodesmus* and *Enhydrocyon*. *Cynodesmus thooides* YPM-PU 10412, (A) dorsal, (B) left lateral and (C) right lateral views; *Cynodesmus thooides* F:AM 63373 (D) dorsal and (E) lateral views. *Enhydrocyon stenocephalus* FMNH PM 59036 (plaster cast of USNM 7745), (F) dorsal view.

Material — *Mesocyon coryphaeus* AMNH 6920 - Oligocene of Camp Creek, John Day Basin, Oregon, U.S.A. Partial skull and a plaster copy of its nearly complete endocranial cast; the skull roof is restored and, therefore, the original endocast is presently unavailable. The olfactory bulbs and part of the cerebrum are hidden within the cast of the nasal cavities (Fig. 12E-G). The specimen was used by Radinsky (1973), together with AMNH 6946 and F:AM 63373 (a *Cynodesmus*, see below) for a composite description of the *Mesocyon* brain.

Mesocyon sp. AMNH 6946 - Early Arikareean (Late Oligocene), Turtle Cove of John Day Formation, Oregon (no locality data), U.S.A. A complete and excellently preserved natural endocast (Fig. 12A-D). It was figured by Edinger (1956) under the name *Daphoenus,* and described and figured by Radinsky (1969, 1973, 1978a).

Cynodesmus thooides YPM-PU 10412 - Early Arikareean (Late Oligocene) of Smith River and Spring Creek, Meagher County, Montana, U.S.A. Partial skull and mandible. The roof and lateral walls of the neurocranium are eroded, exposing a natural endocast in which the dorsal and left lateral side are excellently preserved (Fig. 13A-C). The specimen was described by Scott (1895).

Cynodesmus thooides F:AM 63373 - Whitneyan to Early Arikareean (Late Oligocene) of Wounded Knee area, Brule Formation, Washabaugh County, South Dakota, U.S.A. Partly exposed natural endocast. The ventral and posterior part of the endocast is covered by bone. The anterior part of the cerebrum and the olfactory bulbs are missing (Fig. 13D, E).

Enhydrocyon stenocephalus FMNH PM 59036 (plaster cast of USNM 7745) - Early Arikareean (Late Oligocene), Turtle Cove Member of John Day Formation, Grant County, Oregon, U.S.A. Partial skull with a nearly complete natural endocast (Fig. 13F). The specimen was figured and described by Radinsky (1973, fig. 3).

Description and comparisons — Scott (1895) described the brain of *Cynodesmus* YPM-PU 10412, and Radinsky (1973) gave more extensive composite descriptions of *Mesocyon* and *Cynodesmus* brains based on YPM-PU 10412, AMNH 6946, F:AM 63373 and F:AM 61300. However, after the extensive work on canid phylogeny of recent years, many specimens have been taxonomically re-assigned. As a consequence, F:AM 63373 is no longer considered *Mesocyon,* but *Cynodesmus* (according to Wang, 1994). On the other hand, F:AM 61300 is not *Cynodesmus,* and certainly not "*Cynodesmus petersoni,*" which is a *nomen nudum* (Wang, 1994), but the borophagine *Desmocyon matthewi* (Wang *et al.,* 1999). As a result, it has become evident that several anatomical features were attributed by Radinsky (1973, p. 174) either to the wrong taxon or were characterised as "differences [of] evolutionary significance or [reflecting] individual variation." Therefore, in order to avoid confusion, the brains of *Mesocyon* and *Cynodesmus* are redescribed herein.

The brain of *Mesocyon* is almost twice as large as that of *Hesperocyon*. The general appearance of the brains of the two genera is similar. The frontal and temporal lobes are small, the rhinal sulcus of *Mesocyon* is somewhat lower than that of *Hesperocyon*, the overlap of the cerebellum is small and the posterior cerebellar vermis is straight. An advance in *Mesocyon* over *Hesperocyon* is the appearance of two more sulci; in addition to the coronolateral and suprasylvian sulci, there are also an ectolateral and an ectosylvian sulci. The ectolateral sulcus is short, but well defined. The ectosylvian sulcus is well defined on one side, and shallower and broken in two parts on the other (Fig. 12),

a condition that is seen in both specimens. In AMNH 6946, the coronolateral sulci diverge posterolaterally significantly more than in AMNH 6920.

Cynodesmus thooides has a brain that is of similar size and external anatomy to that of *Mesocyon*. The cerebral cortex of *Cynodesmus* seems somewhat less expanded than in *Mesocyon*. It has two main sulci, the coronolateral and suprasylvian, but lacks the ectolateral sulcus, while the ectosylvian sulcus is represented by a series of variable depressions (Fig. 13). An advance over *Mesocyon* is the presence of a small presylvian sulcus.

The brain of *Enhydrocyon stenocephalus* is characterised by high and wide frontal lobes, resulting in a rectangular outline in dorsal view in contrast to the more tapering brains of all the other canids of the Late Eocene-Early Miocene. Its brain has been described by Radinsky (1973, p. 176), who noted about its sulcal ... pattern that there is "a well defined ectolateral sulcus and an incomplete ectosylvian sulcus the left suprasylvian sulcus is broken with the two pieces slightly overlapped. A short presylvian sulcus delimits a narrow orbital gyrus." Further, the rhinal sulcus is as high as in *Mesocyon* and the overlap of the cerebellum, which has a straight cerebellar vermis, is small.

An interesting point in the evolutionary history of these three canids is their tendency towards hypercarnivory. *Enhydrocyon* is not only bigger than *Cynodesmus* and *Mesocyon*, but also has stronger and broader zygomatic arches, shorter and broader
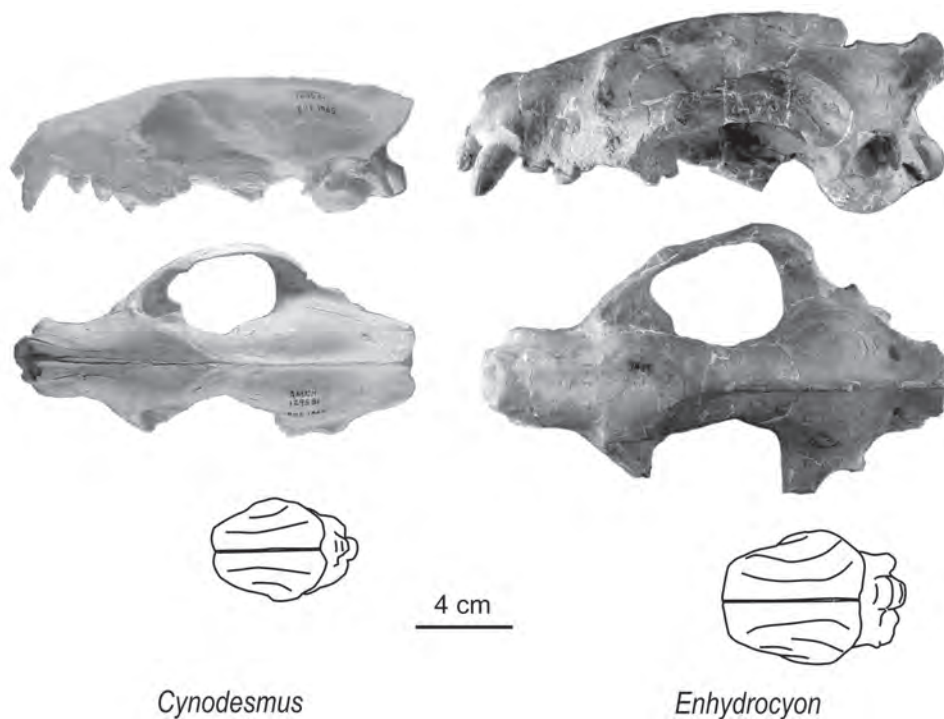

Fig. 14. Dorsal and lateral views of skulls and dorsal views of endocranial casts of *Cynodesmus* (left) and *Enhydrocyon* (right). The skull are *Cynodesmus thooides* AMNH 129531 (plaster cast of Black Hills Institute 1965) and *Enhydrocyon stenocephalus* F:AM 6901. Endocast drawings are based on YPM-PU 10412 (for *Cynodesmus*) and USNM 7745 (for *Enhydrocyon*).

maxillae, a thick mandible and rather modified teeth. Conversely, the changes in the brain are minimal (Fig. 14). The only important change is that of its general shape, which is anterodorsally more compressed in *Enhydrocyon.* However, this is mainly a side effect of cranial evolution. As the snout became shorter, the palatine bone and the ethmoid plate were pushed backwards, and, therefore, the frontal lobes of the brain became anteroposteriorly compressed. In other respects - sulcal pattern, overlap of the cerebellum, position of the rhinal sulcus and torsion of the cerebellar vermis - the brain of *Enhydrocyon* is comparable to those of *Cynodesmus* and *Mesocyon*.

Early Miocene: *Osbornodon*

Phylogenetic position — This genus, in contrast to the other hesperocyonines, is characterized by mesocarnivorous dental characters. It also has some other craniodental features that resemble those of Caninae. However, Wang (1994) considered *Osbornodon* as a member of the Hesperocyoninae based on the morphology of the m1 talonid. The stratigraphic range of *Osbornodon* is from the Orellan (Early Oligocene) to the Early Barstovian (Middle Miocene). From the seven described species of *Osbornodon* (see Wang, 2003), only one endocast is known, belonging to *Osbornodon fricki.*

Material — *Osbornodon fricki* - F:AM 67098 - Late Hemingfordian (Early Miocene) of Sioux County, Nebraska, U.S.A. A complete skull from which a latex endocast (FMNH PM 58964) has been prepared (Fig. 15). The endocast was figured and described by Radinsky (1973, fig. 4) as "unnamed new genus."

Description and comparisons — The brain of *Osbornodon fricki* is twice the size of that of *Mesocyon* and six times the size of that of *Hesperocyon*. Its overall morphology has neither the rectangular outline of *Enhydrocyon* nor the tapering brains of the other Eocene-Oligocene hesperocyonines. Its frontal lobes are more developed that those of
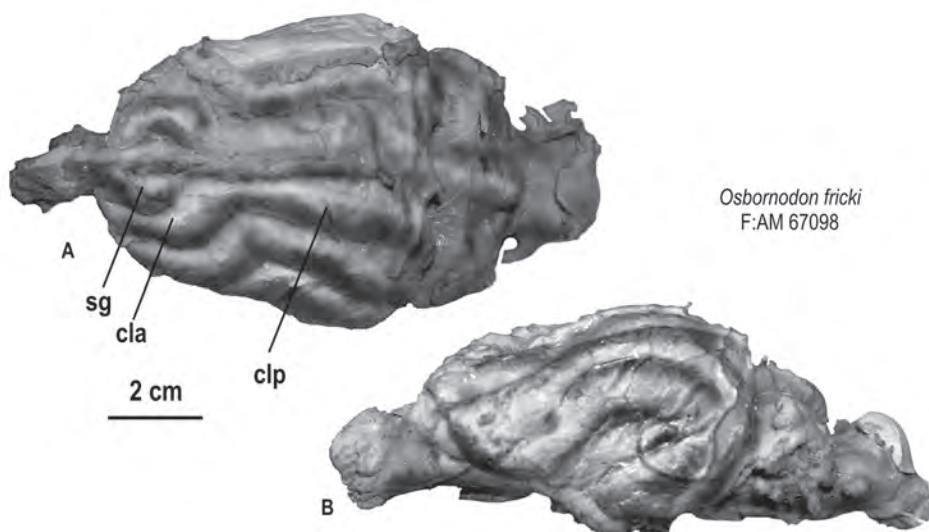

Fig. 15. Endocranial cast from *Osbornodon fricki* F:AM 67098. (A) Dorsal and (B) left lateral views. cla: anterior part of coronolateral gyrus; clp: posterior part of coronolateral gyrus; sg: sigmoid gyrus.

Hesperocyon and *Mesocyon*, the overlap of the cerebellum is larger, the olfactory bulbs are rostrally expanded and the cerebellar vermis is slightly twisted. The most important features of the *O. fricki* cerebral cortex were described by Radinsky (1973), who noted, in addition to the sulci seen on *Cynodesmus*, a large orbital gyrus, a small sylvian sulcus, a complete ectosylvian sulcus and large cruciate depression. This depression is at the centre of the anterior part of the two coronolateral sulci, which come closer to the dorsal midline at the level of the frontoparietal suture and then bow out laterally. This was considered by Radinsky (1973, p. 178) as "the first appearance of a distinct sigmoid gyrus." This tendency also can be seen in *Mesocyon* and *Cynodesmus*, and even in a couple of *Hesperocyon* specimens. However, it is in *Osbornodon fricki* that it becomes evident.

Summary and conclusions concerning the Hesperocyoninae brain

Remarks — *Prohesperocyon*, which is the transitional form between the Miacidae and the Canidae, has a brain with pear-shaped cerebral hemispheres and undeveloped temporal and frontal lobes. Its cortex has only two neocortical sulci (the coronolateral and suprasylvian). The cerebellum is widely exposed and has a straight cerebellar vermis and small cerebellar hemispheres. Of similar morphology is the brain of the first hesperocyonine, *Hesperocyon*. The major difference between the brains of the two genera is that the brain of *Hesperocyon* is more globular, something that is related to differences in cranial proportions.

The brains of the derived Oligocene hesperocyonines, *Mesocyon, Cynodesmus* and *Enhydrocyon,* have a more expanded cerebral cortex. The brain of *Mesocyon* is slightly more advanced than that of *Cynodesmus*. In *Mesocyon* there is an ectolateral and an ectosylvian sulcus, while in *Cynodesmus* there is no ectolateral sulcus and only a series of variable depressions in the place of the ectosylvian sulcus. However, *Cynodesmus* does have a presylvian sulcus. The brain of *Enhydrocyon* has four neocortical sulci (coronolateral, suprasylvian, ectosylvian and presylvian). The most important difference between *Enhydrocyon* and its ancestor (*Cynodesmus*) is that its brain has very high frontal lobes, a feature that is related to its cranial morphology (short rostrum).

The cerebral cortex of the Early Miocene hesperocyonine, *Osbornodon fricki,* is far more advanced than that of its Oligocene relatives. In addition to the sulci seen in *Cynodesmus*, it has a large orbital gyrus, a small sylvian sulcus, a complete ectosylvian sulcus and a large cruciate depression. The rostral parts of the coronolateral sulci bow out laterally, indicating a separation between the coronal and lateral parts, and the first appearance of the sigmoid gyri. Although such a cortical pattern appears for the first time in *Osbornodon fricki*, early signs of such an arrangement can be seen also in *Mesocyon* and *Cynodesmus*, and even in a couple of *Hesperocyon* specimens.

The Borophaginae

This group of canids is often called hyena-dogs, because some of them show a convergent evolution towards hyenas. During their evolutionary history, borophagines acquired a wide range of morphologies and filled several ecological niches (Wang *et al*., 1999).

Oligocene: *Archaeocyon, Otarocyon, Rhizocyon*

Phylogenetic position — During the Oligocene many new canid species appeared. Most of them had numerous derived characters, and were classified by Tedford (1978) and Wang (1994) within the subfamily Hesperocyoninae. Other canids, however, do not present any clear distinguishing characters and placing them in any of the three canid subfamilies is problematic. Although there is a lack of cladistic resolution, Wang *et al.* (1999) considered them as early members of the Borophaginae (*Archaeocyon, Otarocyon, Oxetocyon* and *Rhizocyon*). The same authors also suggested an alternative scenario, in which these taxa may be independent clades of an evolutionary radiation. Four endo-

Fig. 16. Endocranial casts of Oligocene Borophaginae. *Archaeocyon leptodus* F:AM 49033, (A) dorsal, (B) right lateral and (C) detail of the posterodorsolateral views. *Archaeocyon leptodus* F:AM 49031 (D) dorsal and (E) posterior views. *Otarocyon cooki* F:AM 49043, (F) dorsal, (G) lateral and (H) ventral view; *Rhizocyon oregonensis* AMNH 6879, (I) dorsal and (J) lateral views.

casts of these canids, belonging to three genera, were studied, namely *Archaeocyon*, *Otarocyon* and *Rhizocyon*.

Material — *Archaeocyon leptodus* F:AM 49031 - Medial Arikareean (Late Oligocene) of Muddy Creek, Niobrana and Platte Counties, Wyoming, U.S.A. Incomplete skull from which the left part of the roof and sidewall of the neurocranium have been removed in order to expose a natural endocast (Fig. 16A-C). The specimen has been figured and briefly described by Radinsky (1973, fig. 3) under the name *Nothocyon*.

Archaeocyon leptodus F:AM 49033 - Same locality and stratigraphic position as the previous specimen. Partial skull with a dorsally exposed natural endocast (Fig. 16D, E).

Otarocyon cooki F:AM 49043 - Early Arikareean (Late Oligocene) of Little Muddy Creek, Niobrana County, Wyoming, U.S.A. Left ramus and posterior part of skull from which a latex endocast (FMNH PM 58987) has been prepared (Fig. 19F-K). The endocast was briefly described by Radinsky (1973) under the name *Nothocyon*.

Rhizocyon oregonensis AMNH 6879 - Early Arikareean (Late Oligocene) of John Day Basin, Oregon, U.S.A. Skull and left ramus. Parts of the dorsal and lateral walls of the neurocranium are missing exposing a partial natural endocast (Fig. 16L, M).

Description and comparisons — Some aspects of the brains of *Archaeocyon* and *Otarocyon* were discussed by Radinsky (1973), who used two of the above listed specimens (F:AM 49031 and F:AM 49043) for the description of *Nothocyon*. Today, this genus is considered to be an arctoid (Wang & Tedford, 1992), and the two specimens are attributed to *Otarocyon* (F:AM 49043) and *Archaeocyon* (F:AM 49031). Radinsky (1973, p. 174) described F:AM 49043 as being "similar to *Hesperocyon*, except for showing a short presylvian sulcus on one side" and F:AM 49031 as "10 % longer, [having] a slightly more posteriorly extended coronolateral sulcus and a short but distinct ectolateral sulcus."

Actually, the two endocasts are quite different from each other, which is explained by the fact that they belong to different genera. The brain of *Otarocyon* is about the same size as that of *Hesperocyon*. Its general shape is dorsoventrally more compressed, due to the proportions of its skull, which is short-snouted, and its neurocranium is laterally expanded. The most characteristic feature of *Otarocyon* brain is the small expansion of its neocortex; the rhinal sulcus is very high, almost a third of the total height of the brain, and the coronolateral and suprasylvian sulci are short, even shorter than those of *Hesperocyon*. As Radinsky (1973) noted, an advance over *Hesperocyon* is the presence of a short presylvian sulcus. In total, *Otarocyon* is the canid with the least derived brain in terms of external brain anatomy. The simplicity of its brain comes ito sharp contrast with its rather derived cranial anatomy (Fig. 17). The skull of *Otarocyon* has many derived characters and is similar morphologically to the living fennec fox of Africa and Arabia (*Vulpes zerda*) (Wang et al., 1999). Its brain, on the other hand, is much simpler.

In contrast to *Otarocyon*, the brain of *Archaeocyon* has more similarities with that of *Hesperocyon*. As Radinsky (1973) noted, its only differences are its size (the brain of *Archaeocyon* is a bit larger), the more caudally extended coronolateral sulcus and the presence of a short ectolateral sulcus (Fig. 16).

The brain of *Rhizocyon* is known only from a partly exposed specimen (Fig. 16K, L). From what is exposed, its brain has the general morphology similar to that of *Archaeocyon*, although there is no trace of an ectolateral sulcus and the coronolateral sulcus does not extend quite as far caudally.
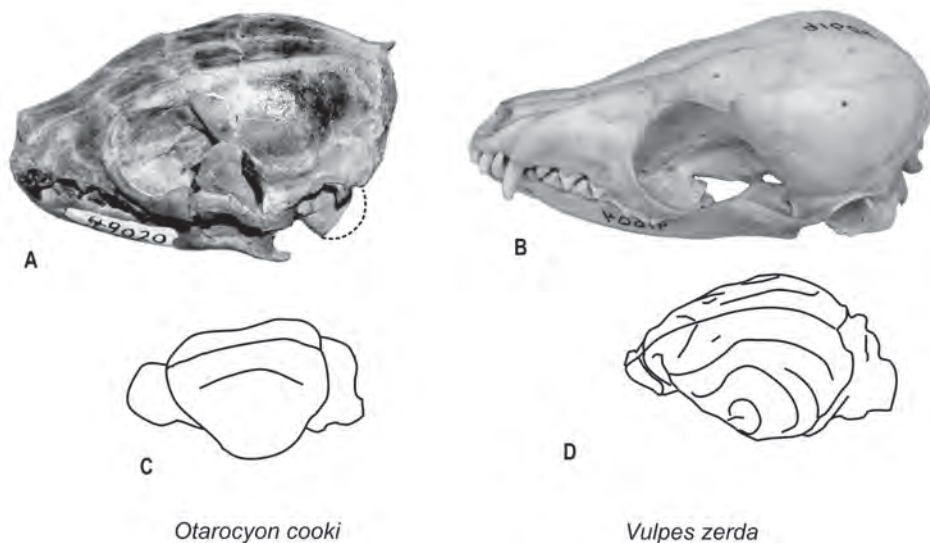
Fig. 17. Dorsolateral views of skulls and endocranial casts from *Otarocyon cooki* and *Vulpes zerda*. (A) *Otarocyon cooki* F:AM 49020; (B) *V. zerda* FMNH 91604 (reversed from the right); (C) *O. cooki* F:AM 49043 (endocranial cast FMNH PM 58987); (D) *V. zerda* NNM RMNH cat ost c.

Oligocene - Early Miocene: *Phlaocyon*

Phylogenetic position — *Phlaocyon* is one of two genera of the tribe Phlaocyonini. Members of this group converge on procyonids dentally (Munthe, 1998) and therefore it is believed that they occupied raccoon-like ecological niches (Wang *et al.*, 2004).

Material — *Phlaocyon marslandensis* UNSM 26153 - Early Hemingfordian (Early Miocene) of Runningwater Formation, Box Butte County, Nebraska, U.S.A. Partial skull from which a latex endocast (FMNH PM 58977) has been prepared (Fig. 18A). The cerebellum and the occipital part of the right cerebral hemisphere are missing. The specimen was figured and described by Radinsky (1973, fig. 4).

Description and comparisons — The brain of *Phlaocyon* has three main sulci, the coronolateral, ectolateral and ectosylvian. The rostral part of the coronolateral sulcus bows out lightly laterally and, in this way, the coronolateral gyrus becomes broader. In the medial part of this widening there is a depression in contact with the dorsal midline, which according to Radinsky (1973, p. 176) represents an incipient cruciate sulcus. According to the same author this sulcus appears to be "the extension onto the dorsal cerebral surface of a continuation of the splenial sulcus [...] rather than the beginning of a new sulcus." He also noted that the rostral end of the coronolateral sulcus is forked; a feature unique among canids.

Early Miocene: *Desmocyon*

Phylogenetic position — *Desmocyon* is a transitional form. It gave rise to all the later borophagines (Wang *et al.*, 1999).

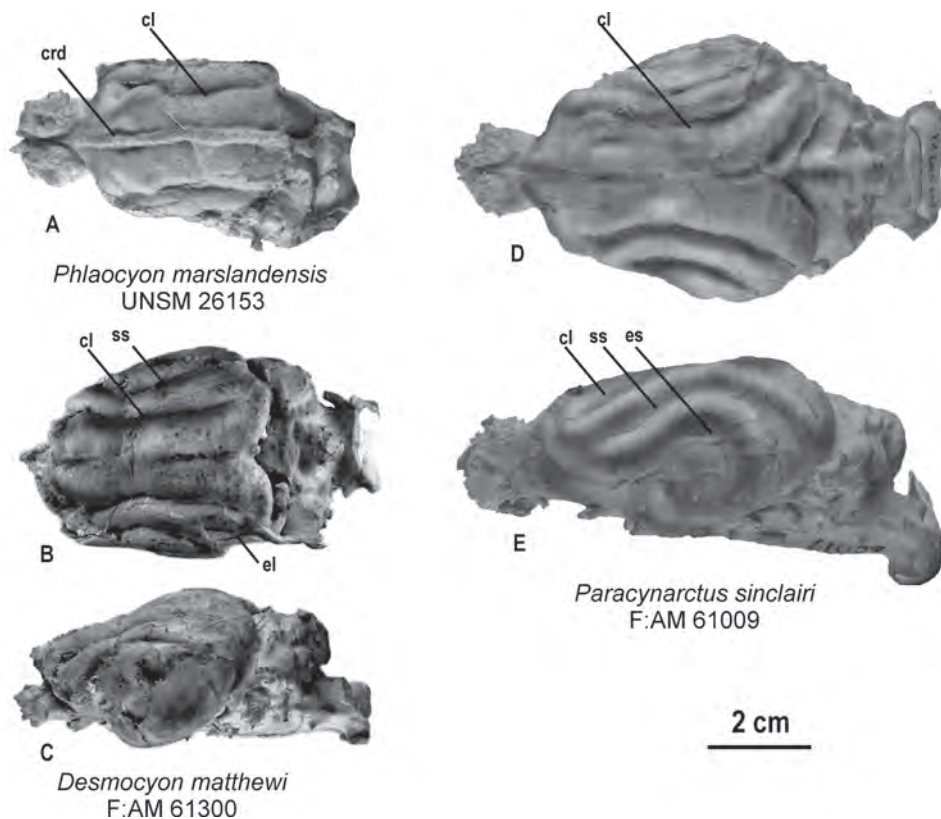*Material* — *Desmocyon matthewi* F:AM 61300 - Early Hemingfordian (Early Miocene)

Fig. 18. Endocranial casts from *Phlaocyon*, *Desmocyon* and *Paracynarctus*. *Phlaocyon marslandensis* UNSM 26153 (endocranial cast FMNH PM 58977), (A) dorsal view; *Desmocyon matthewi* F:AM 61300 (endocranial cast FMNH PM 58983), (B) dorsal and (C) lateral views; *Paracynarctus sinclairi* F:AM 61009 (endocranial cast FMNH PM 58973), (D) dorsal and (E) lateral views. crd: cortical depresion at the position of cruciate sulcus; cl: coronolateral sulcus; ss: suplasylvian sulcus; es: ectosylvian sulcus; el: ectolateral sulcus.

of Runningwater Formation, Dawes County, Nebraska, U.S.A. Partial skull from which a latex endocast (FMNH PM 58983) has been prepared (Fig. 18B, C). The endocast is almost complete, lacking only the orbital gyri and a part of the left hemisphere. It was used by Radinsky (1973), together with a *Cynodesmus* endocast, for a composite description of the brain of *Cynodesmus*.

Description and comparisons — The rhinal sulcus is lower than in *Phlaocyon*, and there is an angle between its occipital and rostral parts. The cerebrum has three sulci, the coronolateral, suprasylvian and ectolateral. The coronolateral sulcus forms a clear bend at the level of frontoparietal suture and bows out anteriorly, forming a wider coronolateral gyrus. The suprasylvian sulcus extends further posteroventrally than in the earlier borophagines. The ectolateral sulcus is small, but well defined, and the suprasylvian sulcus form a wide vertical arch on the lateral side of the cortex. The cerebellum is widely exposed. The cerebellar hemispheres are well developed, with the paramedian and ansiform lobules twisted as in living canids. The cerebellar vermis is straight.

An interesting detail in the brain of *Desmocyon* is that there is no indication of a cruciate sulcus. The coronolateral sulcus is broader in the rostral part, just as in *Phlaocyon*, but *Desmocyon* lacks a depression on the cortex in contact with the dorsal midline of the brain (see Fig. 18A, B). Since later borophagines have a cruciate sulcus (see descriptions below) and since they all evolved from *Desmocyon* (see phylogenetic analyses by Wang *et al.*, 1999), that sulcus must have appeared independently twice within the borophagines.

Miocene: *Paracynarctus*

Phylogenetic position — During the Miocene, borophagines reached their maximum diversity. Wang *et al.* (1999) recognized several clades, including the Cynarctina, which includes *Cynarctus* and *Paracynarctus*. Its members were adapted to hypocarnivory.

Material — *Paracynarctus sinclairi* F:AM 61009 - Early Barstovian (Middle Miocene) of the Olcott Formation, Sioux County, Nebraska, U.S.A. Complete skull from which a latex endocast (FMNH PM 58973) has been prepared (Fig. 18D, E). The specimen was figured and described by Radinsky (1973, fig. 4) as an unnamed new genus of a *Phlaocyon*-like canid.

Description and comparisons — The brain of *Paracynarctus sinclairi* is about 20 % larger than that of *Desmocyon*. Radinsky (1973) noted that it has four sulci, the coronolateral, ectolateral, suprasylvian and ectosylvian; that there is no indication of a cruciate sulcus, that there is a well developed orbital gyrus; and that the cerebral vermis is slightly twisted. He also suggested that a sylvian sulcus might be present.

The outline of the brain of *Paracynarctus* is more comparable to that of *Desmocyon* than to *Phlaocyon*. This is to be expected, as phylogenetically *Paracynarctus* is more distantly related to *Phlaocyon*, something that also explains the absence of a cruciate depression in *Paracynarctus*, although it is present in the stratigraphically earlier *Phlaocyon*.

Miocene: *Tomarctus, Microtomarctus, Aelurodon*

Phylogenetic position — *Tomarctus* and *Aelurodon* form a Borophaginae clade that originated in the Barstovian with *Tomarctus hippophagus* and ended in the Clarendonian with *Aelurodon taxoides* (Wang *et al.*, 1999). The lineage is characterized by increased hypercarnivory, a tendency that is particularly evident in *A. ferox* and *A. taxoides* (Baskin, 1980). *Microtomarctus* is phylogenetically related to *Tomarctus* (Wang *et al.,* 1999). Seven endocasts from this group are used.

Material — *Tomarctus hippophagus* F:AM 61179A - Early Barstovian (Middle Miocene) of the Olcott Formation, Sioux County, Nebraska, U.S.A. Part of a skull from which a latex endocast (NNM RGM 195225) has been prepared. The complete left hemisphere, the cerebellum and part of the right hemisphere are preserved (Fig. 19A, B).

Tomarctus hippophagus F:AM 61179B - Posterior part of skull from the same locality and stratigraphic position as the previous specimen. A latex endocast (FMNH PM 58959) has been prepared (Fig. 19C-E). The endocast preserves the part that is caudal to the frontoparietal suture.

Tomarctus brevirostris F:AM 61179C - Posterior part of a skull from the same locality and stratigraphic position as the previous specimens. A latex endocast (FMNH PM 58957) has been prepared (Fig. 19F, G), which, as in the previous specimen, preserves only the part of the brain that is caudal to the frontoparietal suture.

Microtomarctus confertus F:AM 27534 - Early Barstovian (Middle Miocene), ''First Division,'' Barstow Formation, San Bernardino County, California, U.S.A. Partial skull from which an artificial endocast (FMNH PM 58967) was made (Fig. 20D). The endocast preserves only a small part of the left hemisphere.

Aelurodon ferox F:AM 61746 - Late Barstovian (Middle Miocene), Devil's Gulch Member, Valentine Formation, Brown, Cherry, and Keyapaha Counties, Nebraska, U.S.A. Skull with left ramus and partial skeleton. From the skull, an almost complete

Fig. 19. Endocranial casts from *Tomarctus*. *Tomarctus hippophagus* F:AM 61179A (endocranial cast NNM RGM 195225), (A) dorsal and (B) lateral views. *T. hippophagus* F:AM 61179B (endocranial cast FMNH PM 58959), (C) dorsal, (D) posterior and (E) left lateral views; *T. brevirostis* F:AM 61179C (endocranial cast FMNH PM 58957), (F) dorsal and (G) left lateral views. pl: pyriform lobe; ra: anterior part of the rhinal sulcus; el: ectolateral sulcus; rp: posterior part of the rhinal sulcus.
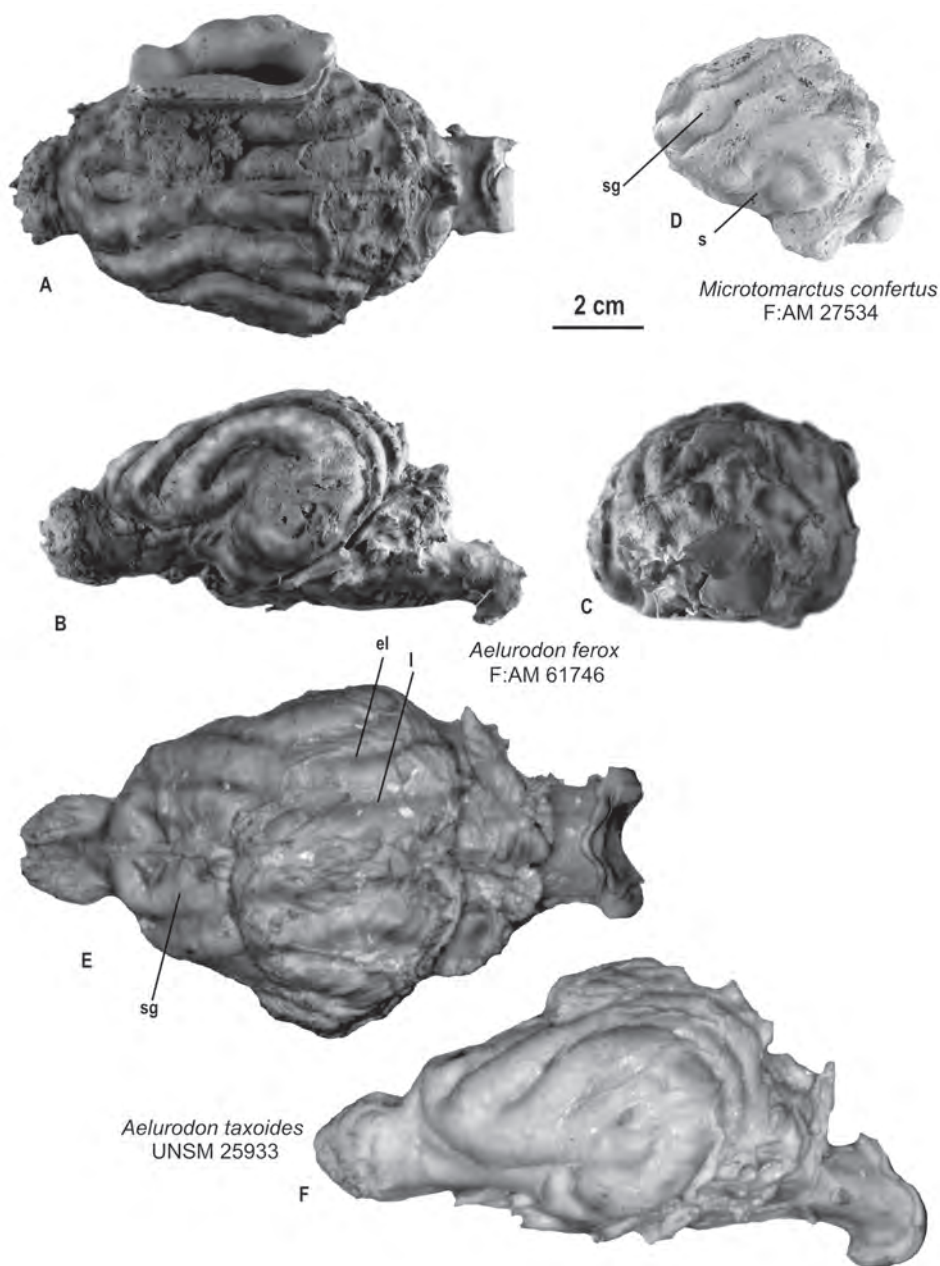
Fig. 20. Endocranial casts of *Aelurodon* and *Microtomarctus*. *Aelurodon ferox* F:AM 61746 (endocranial cast FMNH PM 58965), (A) dorsal, (B) lateral and (C) posterior views; *Microtomarctus confertus* F:AM 27534 (endocranial cast FMNH PM 58967), (D) lateral view; *A. taxoides* UNSM 25933 (endocranial cast FMNH PM 58969), (E) dorsal and (F) lateral views. sg: sigmoid gyrus; s: Sylvian sulcus; el: ectolateral sulcus; l: lateral sulcus
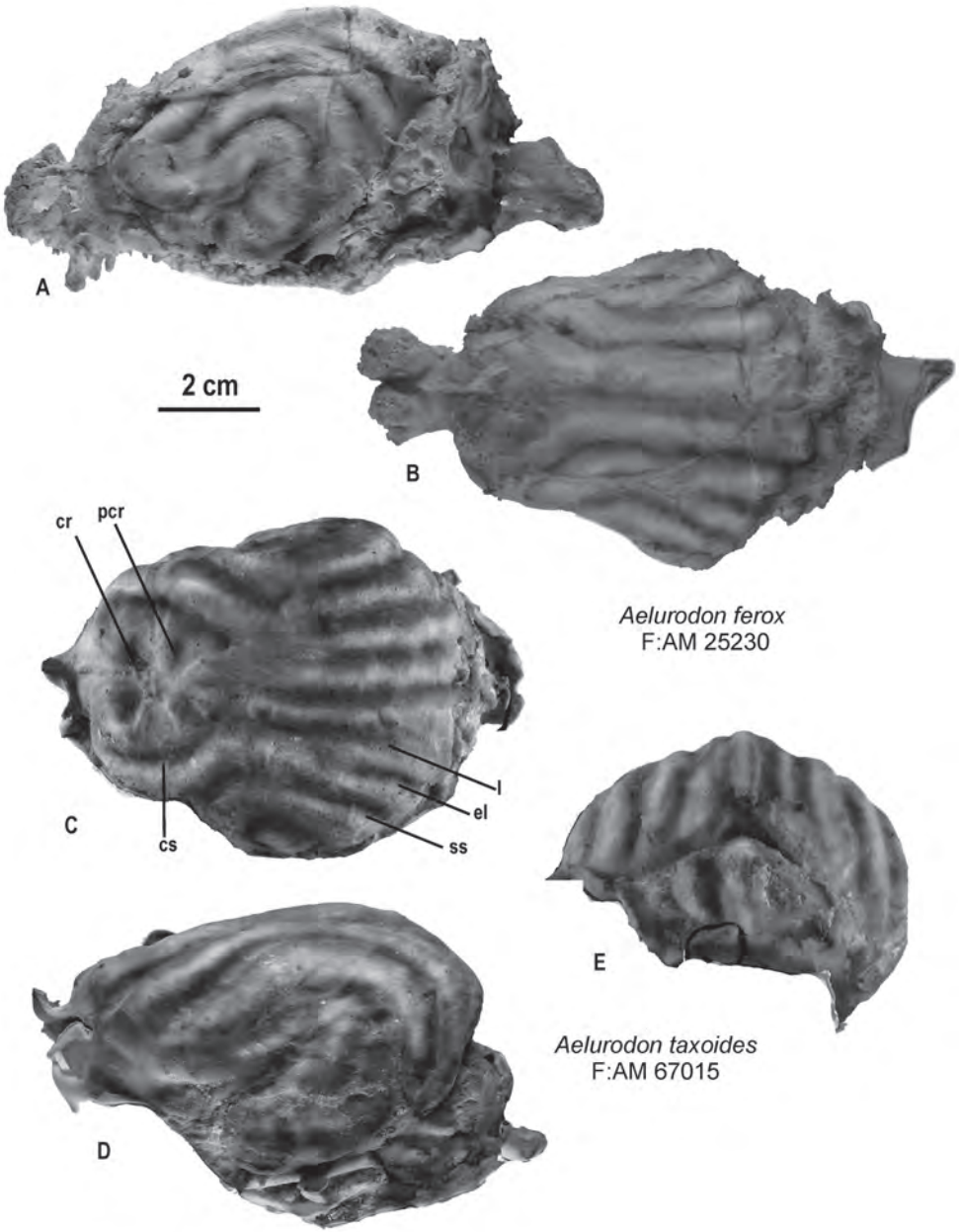
Fig. 21. Endocranial casts of *Aelurodon*. *Aelurodon ferox* F:AM 25230 (endocranial cast FMNH PM 58951), (A) left lateral and (B) dorsal views; *A. taxoides* F:AM 67015 (endocranial cast FMNH PM 58971), (C) dorsal, (D) lateral and (E) posterior views. cr: cruciate sulcus; pcr: postcruciate sulcus; cs: coronal sulcus; ss: suprasylvian sulcus; el: ectolateral sulcus; l: lateral sulcus.

endocast (FMNH PM 58965) was prepared (Fig. 20A-C). The specimen is excellently preserved, being incomplete only in the right hemisphere where a hole was opened in the neurocranial wall during the preparation of the endocast. The endocast was figured and described by Radinsky (1973, fig. 5) together with F:AM 25230 as *Aelurodon platyrhinus*, a synonym of *A. ferox*.

Aelurodon ferox F:AM 25230 - Skull with mandible from the same location and stratigraphic position as the previous specimen. A complete endocast (FMNH PM 58951) was prepared (Fig. 21A, B), which was used by Radinsky (1973) for a composite description of the brain of synonymous *Aelurodon platyrhinus.*

Aelurodon taxoides UNSM 25933 - Clarendonian (Middle Miocene), lower part of the Ash Hollow Formation, Banner County, Nebraska, U.S.A. Complete skull from which a latex endocast (FMNH PM 58969) has been prepared. The endocast is complete, although the reproduction of part of its dorsal surface is not good (Fig 20E, F).

Aelurodon taxoides F:AM 67015 - Clarendonian (Middle Miocene), Ash Hollow Formation, Sheridan, Brown, Cherry and Hitchcock Counties, Nebraska, U.S.A. Partial skull, from which a latex endocast (FMNH PM 58971) has been made (Fig. 21C-E). The endocast preserves most of the cerebellum, the right hemisphere and part of the left hemisphere. The olfactory bulbs and the brainstem are missing. It was mentioned by Radinsky (1973) as "unidentified species of *Aelurodon.*"

Description and comparisons — Before the publication of the phylogenetic analysis of Borophaginae by Wang *et al.* (1999), *Tomarctus* was one of the most confusing canid taxa and several species of that genus were erected. Previous palaeoneurological studies were based on the assumption that these species (later assigned to *Tomarctus*, *Microtomarctus* or *Paratomarctus*) all belonged to *Tomarctus.* Therefore, in order to clear out this confusion, the brains of these genera are described again (*Tomarctus* in this section and *Paratomarctus* below).

The brain of *Tomarctus* is about the same size as that of *Paracynarctus*. The cerebellar vermis is straight. The posterior part of the rhinal sulcus forms a sharp angle with its rostral part and, in this way, the posterior part of the pyriform lobe is more covered by the neocortex. The lateral sulcus steadily diverges caudally. The coronal sulci swell out only slightly, just a bit laterally to the lateral sulcus. The caudal part of the coronal sulcus is situated more laterally than the rostral part. In the centre of the cortex area between the coronal sulci there is a depression, which seems to represent an incipient cruciate sulcus. There is a short Sylvian sulcus. There are no ansate and endolateral sulci.

The available material from *Microtomarctus* is rather limited (Fig. 20D). The coronal sulci bow out laterally and, just as in *Tomarctus*, the caudal part of the coronal sulcus is more laterally expanded than the anterior. There is a very short cruciate and a Sylvian sulcus.

The brain of *Aelurodon* is about 30 % longer than that of *Tomarctus*. The posterior cerebellar vermis is straight or slightly twisted. The lateral sulcus extends straight back rather than diverging caudally (Radinsky, 1973) as in *Tomarctus.* The Sylvian sulcus is better developed.

In an early form of *Aelurodon*, *A. ferox*, there is no clearly formed cruciate sulcus and, just like in *Tomarctus,* there are no endolateral and ansate sulci. In a later species, *A. taxoides*, the sigmoid gyri are more expanded and there are clearly formed cruciate and postcruciate sulci (compare Figs. 20 with 21).

Miocene-Pliocene: Paratomarctus, Carpocyon, Epicyon, Borophagus

Phylogenetic position — The last Borophaginae group appeared at the Middle Miocene. It originated with *Paratomarctus*, which at the end of Miocene gave rise to *Carpocyon* and to *Epicyon-Borophagus*. The species of *Carpocyon* were jackal-sized canids with meso-hypocarnivorous dentitions (Wang *et al.,* 1999). The species of *Epicyon* and *Borophagus* were large (*E. haydeni* is the largest canid ever lived) and had craniodental adaptations that parallel those of the Old World hyenids (Werdelin, 1989; Baskin, 1998; Van Valkenburgh *et al.,* 2003). In the Pliocene, *Borophagus* was the only surviving member of the subfamily.

Fig. 22. Endocranial casts from *Paratomarctus*. *Paratomarctus temerarius* F:AM 61070 (endocranial cast FMNH PM 58958), (A) dorsal, (B) left lateral, (C) right lateral and (D) anterior views; *Paratomarctus* sp. CSCLA 207, (E) dorsal, (F) lateral and (G) ventral views. cr: cruciate sulcus; pcr: postcruciate sulcus; s: Sylvian sulcus; sg: sigmoid gyrus; pl: pyriform lobe; ra: anterior part of the rhinal sulcus; rp: posterior part of the rhinal sulcus.

Material — *Paratomarctus temerarius* F:AM 61070 - Late Barstovian (Middle Miocene) from Mouth of Snake River, Crookston Bridge Member, Valentine Formation, Cherry and Brown Counties, Nebraska, U.S.A. Skull with partial ramus from which a latex endocast (FMNH PM 58958) has been prepared (Fig. 22A-D). The specimen was described and figured by Radinsky (1969) as *Tomarctus* and later (Radinsky, 1973, 1978a) as *Tomarctus* cf. *T. euthos.* The specimen number was misprinted in Radinsky's papers as F:AM 61074.

Paratomarctus sp. CSCLA 207 - Late Barstovian (Middle Miocene) from San Bernardino County, California, U.S.A. Isolated natural endocast. The specimen is almost
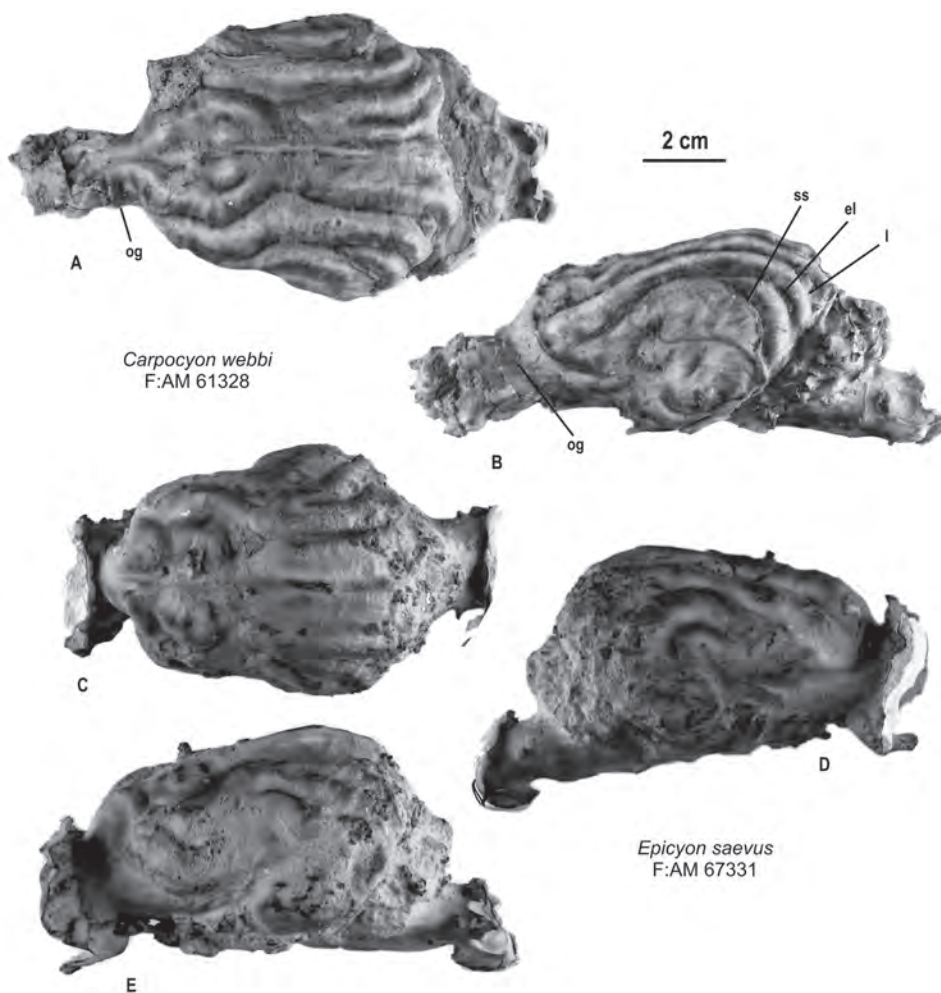

Fig. 23. Endocranial casts of *Carpocyon* and *Epicyon*. *Carpocyon webbi* F:AM 61328 (endocranial cast FMNH PM 58964), (A) dorsal and (B) lateral views; *E. saevus* F:AM 67331 (endocranial cast FMNH PM 58970), (C) dorsal, (D) right lateral and (E) left lateral views. og: orbital gyrus; ss: suprasylvian sulcus; el: ectolateral sulcus; l: lateral sulcus.

complete, lacking only the olfactory bulbs (Fig. 22E-G). It was figured and described by Jakway & Clement (1967) as *Tomarctus* sp. CSCLA 207 is a natural endocast without cranial material; the attribution to *Paratomarctus* is based on the similarity of the external brain anatomy between F:AM 61070 and CSCLA 207 (see description below and Fig. 22).

Carpocyon webbi F:AM 61328 - Late Late Barstovian (Middle Miocene) from Midway Quarry, Burge Member, Valentine Formation, Cherry County, Nebraska, U.S.A. Skull
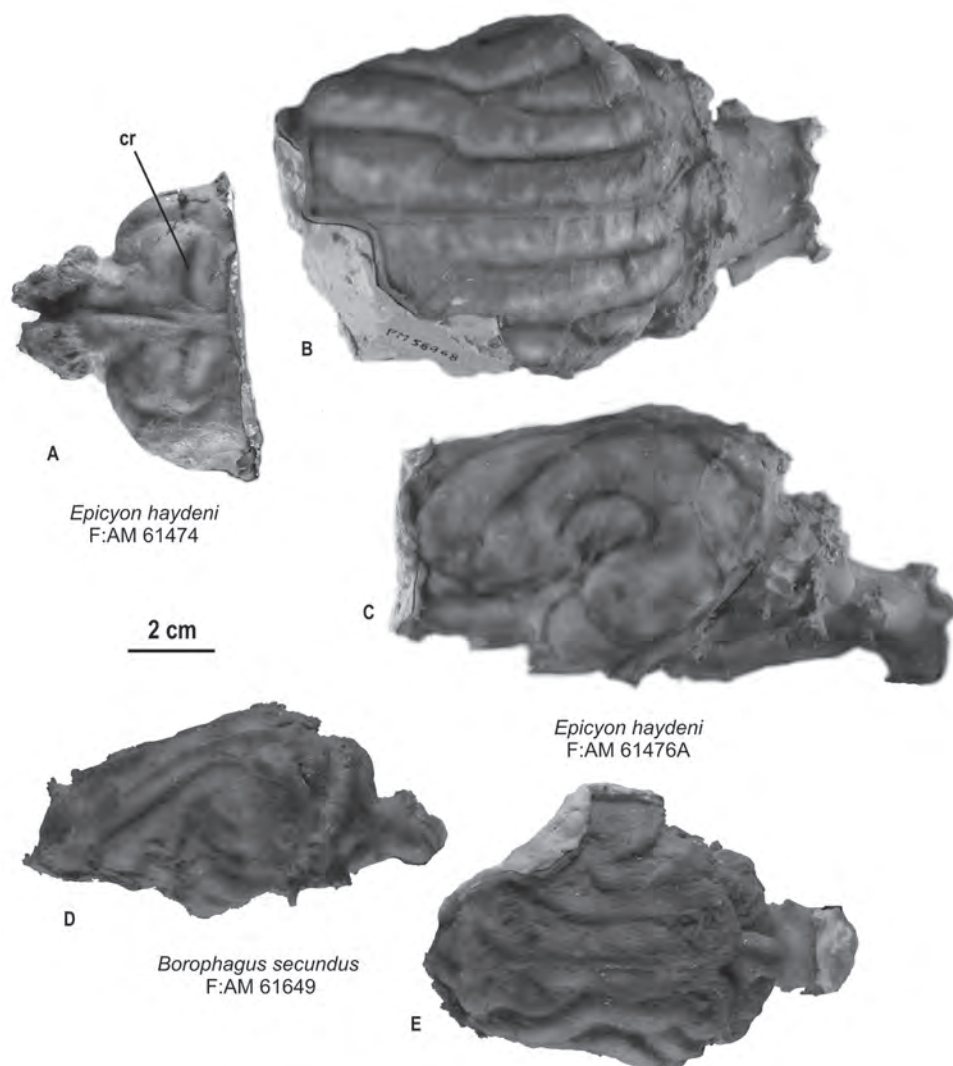

Fig. 24. Endocranial of from *Epicyon* and *Borophagus*. *Epicyon haydeni* F:AM 61474 (endocranial cast FMNH PM 58976), (A) dorsal view; *E. haydeni* F:AM 61476A (endocranial cast FMNH PM 58968), (B) dorsal and (C) lateral views; *B. secundus* F:AM 61649 (endocranial cast FMNH PM 58954), (D) lateral and (E) dorsal views. cr: cruciate sulcus.

from which a latex endocast (FMNH PM 58964) has been prepared (Fig. 23A, B). The endocast is complete, and was figured and described by Radinsky (1973, fig. 5) as "unnamed new genus close to *Osteoborus*."

Epicyon saevus F:AM 67331 - Late Clarendonian (Middle Miocene) from the Ash Hollow Formation, Brown and Cherry Counties, Mensinger Quarry, Nebraska, U.S.A. Partial skull with I1-P1 alveoli and P2-M2 from which a latex endocast (FMNH PM 58970) was made. The endocast is almost complete, lacking only the rostral part of the olfactory bulbs (Fig. 23C-E). It was mentioned by Radinsky (1973) as *Aelurodon* cf. *salvus*.

Epicyon haydeni F:AM 61476A - Early Hemphillian (Late Miocene) from Jack Swayze Quarry, Ogallala Group, Clark County, Kansas, U.S.A. Posterior part of a skull from which a latex endocast (FMNH PM 58968) has been prepared. The specimen lacks the anterior part of the brain (olfactory bulbs, orbital and anterior sigmoid gyri) and part of the left temporal lobe (Fig. 24B, C). It was used by Radinsky (1973), together with F:AM 61474, for a composite description of the *Epicyon* brain (under the name "unnamed new species of *Aelurodon*").

Epicyon haydeni F:AM 61474 – Early Hemphillian (Late Miocene) from F. Sebastian Place, Ogallala Group, Decatur County, Kansas, U.S.A. Anterior half of skull from which a latex endocast (FMNH PM 58976) has been prepared. The specimen preserves only the olfactory bulbs, and the orbital and sigmoid gyri (Fig. 24A). Radinsky (1973) used it, together with F:AM 61476A, for a composite description of the *Epicyon* brain (see previous specimen).

Borophagus secundus F:AM 61649 - Late Hemphillian (Late Miocene) from Edson Quarry, Ogallala Group, Marshall Ranch, Sherman County, Kansas, U.S.A. Part of a skull from which a latex endocast (FMNH PM 58954) has been prepared. The specimen is incomplete as the olfactory bulbs and a small part of the brain stem are missing. It was mentioned by Radinsky (1973) under the name *Osteoborus cyonoides* (synonym of *Borophagus secundus*).

Borophagus dudleyi MCZ 3688 - Late Late Hemphillian (Late Miocene) from the phosphate pits near Mulberry, Bone Valley Formation, Polk County, Florida, U.S.A. Complete skull from which a latex endocast (FMNH PM 58963) has been prepared (Fig. 25). The endocast is of excellent preservation. It was figured and described by Radinsky (1973, fig. 5).

Description and comparisons — The brain of *Paratomarctus* is quite similar in size and general morphology to that of *Tomarctus* (see description above). There are, however, some distinguishing features: the sigmoid gyri bow out more; there are clearly formed cruciate and post-cruciate sulci; there is an endolateral sulcus; and the posterior part of the pyriform lobe is exposed. Additionally, the brain of *Paratomarctus* has posterior sigmoid gyri that bow out more laterally than the anterior sigmmoid gyri, there is no ansate sulcus and there is a complete ectosylvian sulcus.

The brain of *Paratomarcus* is far more derived than that of *Tomarctus* and, despite its smaller size, is comparable to that of *Aelurodon taxoides*. *Carpocyon webbi* has a brain that is twice the size of that of *Paratomarctus*. The most characteristic features are the long orbital gyrus and that the olfactory bulbs are more pedunculate (rostrally extended) (Fig. 23A). The morphology of the lateral gyrus is similar to that of *Paratomarctus*. There are endolateral and postcruciate sulci. The cruciate sulcus is in the form of a depression. The posterior cerebellar vermis is slightly more twisted than that of *Paratomarctus*.

The brain of *Epicyon saevus* is in many ways similar to that of *Aelurodon ferox*. It is of about the same size and shares some features of the cortical pattern; the species was considered by Radinsky (1973) as *Aelurodon*. Just like *Aelurodon*, and unlike *Paratomarctus* and *Carpocyon*, it has no endolateral sulcus and the lateral sulcus extends straight back. However, *E. saevus* has many features that distinguish it from *Aelurodon:* the cerebellum is more overlapped; the vermis is slightly more twisted; the pyriform lobe is less exposed; the sigmoid gyri are more expanded; and there are clearly formed cruciate and postcruciate sulci. In addition, the Sylvian sulcus is more pronounced.

Epicyon haydeni has a much larger brain than all previous mentioned canids as is to be expected of the largest canid that ever lived. Its brain is similar to that of *E. saevus*. The cruciate sulcus is longer (Fig. 24A) and the frontal lobes are more massive.

The brain anatomy of *Borophagus* is known in two species. The coronal sulci bow out more in *B. secundus* than in the older borophagines. The cortex between the coronal sulci is even more expanded in the later species, *B. dudleyi*. Further, that species has a longer Sylvian sulcus and the most massive frontal lobes of any Borophaginae (Fig. 25).
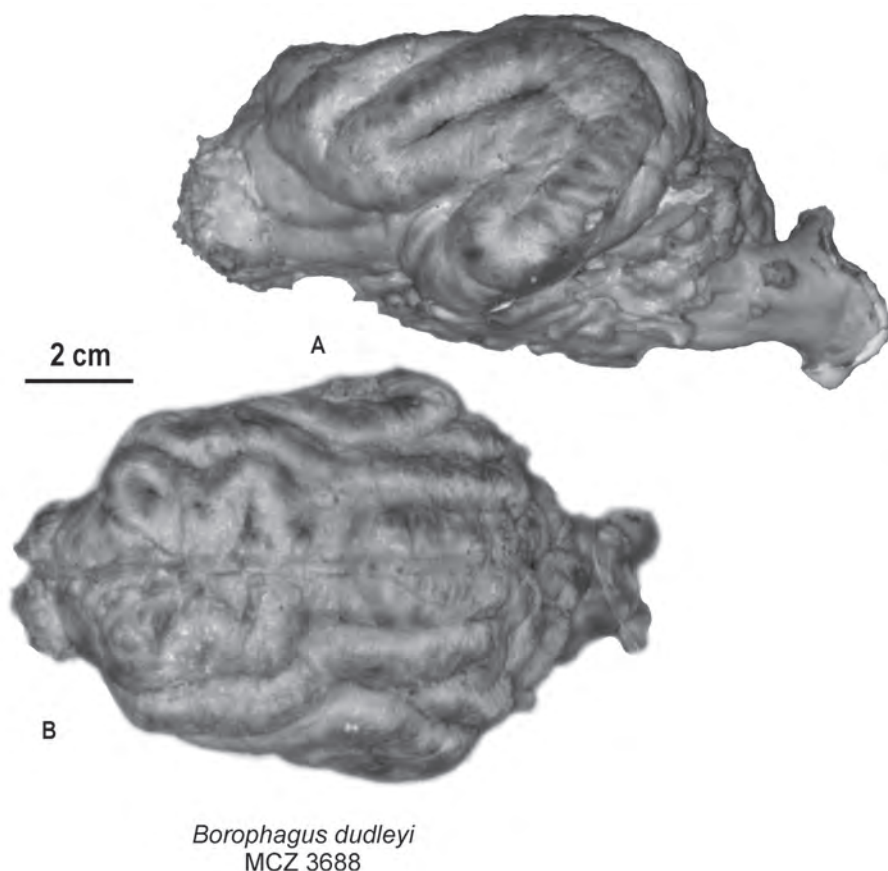

Fig. 25. Endocranial cast of *Borophagus dudleyi* MCZ 3688 (endocranial cast FMNH PM 58963), (A) lateral and (B) dorsal view.

Summary and conclusions concerning the Borophaginae brain

Remarks — The first borophagines (*Archaeocyon, Rhizocyon, Otarocyon)* have brains similar in size, lobation and fissuration to that of *Hesperocyon*. The differences between them and *Hesperocyon* are small: *Archaeocyon* has a more posteriorly extended corono-lateral sulcus and has a short ectolateral sulcus. On the other hand, *Rhizocyon* has no ectolateral sulcus and the coronolateral sulcus is shorter. *Otarocyon* has a neocortex with a very small expansion (the rhinal sulcus is very high, and the coronolateral and supra-sylvian sulci are very short), yet it has a short presylvian sulcus, which is not present in the other forms.

The differences between *Hesperocyon* and *Archaeocyon* indicate that some small changes took place in the brain from one genus to the other. The presence of a presyl-vian sulcus in *Otarocyon* suggests that, at least concerning brain evolution, this genus followed a different path from the other early borophagines.

Further advances can be seen in *Phlaocyon* and *Desmocyon*. The brain of *Phlaocyon* has three main sulci (the coronolateral, ectolateral and ectosylvian). Additionally, there is a widening of the rostral part of the coronolateral gyrus and, in the middle of this area, an incipital cruciate sulcus. The rostral end of the coronolateral sulcus is forked, a feature that is unique among canids. This feature and the presence of an incipient cruci-ate sulcus distinguish *Phlaocyon* from the rest of the canids. The presence of a cruciate sulcus is not, of course, a unique feature. However, in this particular case, it is unrelated to the cruciate sulcus of the other borophagines. This can be inferred from an examina-tion of the external brain anatomy of *Desmocyon* (the genus from which all later borophagines evolved); it has a brain with similar fissuration (three main sulci) and gyrification (a wider anterior part of the coronolateral gyrus) as *Phlaocyon*, yet its gen-eral shape is very different and it has no indication of a cruciate sulcus. Since later borophagines have a cruciate sulcus, this structure must have appeared independently twice within the subfamily.

Paracynarctus is a later borophagine. The outline of its brain is comparable to that of *Desmocyon*. Its cortex has four sulci (the coronolateral, ectolateral, suprasylvian and ectosylvian), perhaps a very small Sylvian sulcus and a well developed orbital gyrus. The posterior cerebellar vermis is slightly twisted.

The evolutionary history of the Middle and Late Miocene borophagines followed two major paths, the *Tomarctus-Aelurodon* and *Paratomarctus-Borophagus* clades. Both clades show a tendency to increase brain (and body) size, expansion of the occipital and temporal lobes, and expansion of the cortex medial to the coronal sulci. The expansion of the cortex of the occipital lobe is expressed in the larger overlap of the cerebellum and the expansion of the temporal lobe by the elongation of the Sylvian sulcus. The cortex medial to the coronal sulci expanded by bowing out of the coronal sulci, and by developing the cruciate and postcruciate sulci.

The cortical expansion was not the same in both groups. The *Paratomarctus-Boropha-gus* group began at a more advanced stage of gyral complexity and carried its develop-ment much further than did the *Tomarctus-Aelurodon* group. In both groups the poste-rior cerebellar vermis remained straight or (in some later forms) was only slightly twisted.

The coronal sulci of *Tomartus* bow out only slightly and there is an incident cruciate sulcus in the form of a depression. A similar condition is seen in *Aelurodon ferox*, but in

a later species, *A. taxoides*, the sigmoid gyri are more expanded, and there are clearly formed cruciate and postcruciate sulci.

In *Paratomarcus* the sigmoid gyri bow out more, and there are clearly formed cruciate and postcruciate sulci. The sigmoid gyri are further expanded in *Epicyon saevus,* and the cruciate and postcruciate sulci are clearly formed. An even longer cruciate sulcus can be seen in a later species of *Epicyon* (*E. haydeni*) and in *Borophagus*.

The development of the sigmoid gyri took place independently in *Paracynarctus*, *Paratomarctus* and *Tomarctus*. In general, this area expanded independently several times in carnivore evolution. There are also some morphological differences between the sulcal patterns of these genera that support the hypothesis of parallel evolution. It is, however, somewhat implausible to suggest that out of the three available specimens, all three are cases of parallel evolution. A more reasonable explanation is that the development of the sigmoid gyri started with *Desmocyon matthewi* and then an evolutionary radiation in the brain took place. Such a case of radiation in the sulcal pattern around the sigmoid gyri took place during the major evolutionary radiation of the Caninae at the latest Miocene and earliest Pliocene (Lyras & Van der Geer, 2003). It is possible that the same evolutionary process took place in the Middle Miocene during the evolution of the Borophaginae. However, the analysis of Caninae was based on many more specimens, while in this case, due to the limited material, this idea should only be considered a working hypothesis.

An interesting detail is the form of lateral gyrus in the early and later forms of the two clades. The lateral sulcus diverges caudally in *Tomarctus* and *Paratomarctus*, while in *Aelurodon*, *Epicyon* and *Borophagus* it extends straight back. In addition, there is an endolateral sulcus in *Paratomarctus*, but not in *Epicyon* and *Borophagus*. Finally, *Carpocyon webbi* has a long orbital gyrus and the olfactory bulbs are more pedunculate (rostrally extended), yet in contrast *Epicyon haydeni* and *Borophagus dudleyi* have more compressed and massive frontal lobes than their close relatives.

Otarocyon has a rather simple brain, which, although comparable to that of contemporareous canids, contrasts with its rather derived ear anatomy and general cranial morphology (which can be compared with that of the living *Vulpes zerda*).

The Caninae

Remarks — The Caninae first appeared in the Early Oligocene. Their major radiation occurred much later, during the latest Miocene - Early Pliocene, and is probably still ongoing (Laidlaw *et al.*, 2007). For the description of the evolution of the Caninae brain, not only endocasts from fossils will be used, but also from extant taxa.

Oligocene - Miocene: *Leptocyon*

Phylogenetic position — *Leptocyon* is the earliest representative of the Caninae (Tedford, 1978). During the course of its evolution the mesocarnivorous *Leptocyon* remained small and inconspicuous (Wang *et al.*, 2004).

Material — *Leptocyon gregorii* F:AM 49063 - Late Arikareean (Early Miocene) of Keeline, Niobrana County, Wyoming, U.S.A. A nearly complete skull from which a latex endocast (FMNH PM 58961) has been prepared (Fig. 26A). The specimen was figured and described by Radinsky (1973, fig. 6) as *Leptocyon* sp.
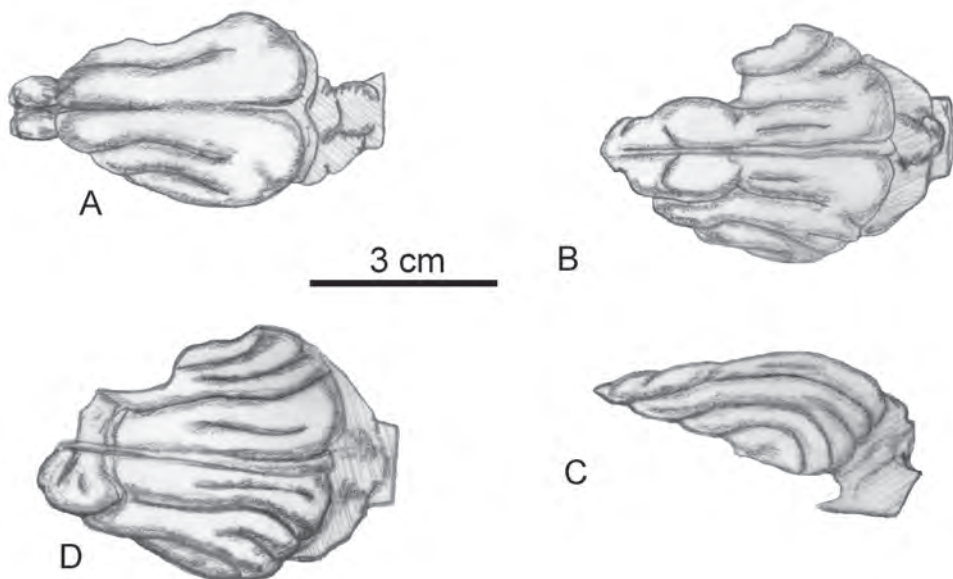
Fig. 26. Endocranial casts from *Leptocyon* and *Vulpes*. (A) Dorsal view of *Leptocyon gregorii* F:AM 49063 (endocranial cast FMNH PM 58961); (B) dorsal and (C) lateral views of *Leptocyon* sp. F:AM 49433 (endocranial cast NNM RGM 195222); (D) dorsal view of *Vulpes stenognathus* F:AM 49284 (from Lyras, 2001).

Leptocyon sp. F:AM 49433 - Clarendonian (Late Miocene) of Hollow Horn Bear Quarry, South Dakota, U.S.A. An isolated brain case from which a latex endocast has been prepared (NNM RGM 195222 and FMNH PM 58959). The endocast is incomplete and lacks the olfactory bulbs, orbital gyrus and part of the left hemisphere (Fig. 26B, C). The specimen was figured and described by Radinsky (1973), Lyras (2001) and Lyras & Van der Geer (2003).

Description and comparisons — The earliest available *Leptocyon* endocast (Fig. 26) is from the Early Miocene, which is much later than the appearance of *Leptocyon* itself. Its morphology is comparable to that of the early members of the other two subfamilies (such as *Hesperocyon* and *Archaeocyon*). According to Radinsky (1973), who described the specimen, there is no ectolateral sulcus (except for a dimple), the coronolateral sulcus does not extend very far caudally and there is a small presylvian sulcus. Another interesting feature of the *Leprocyon gregorii* brain is the shape of the coronolateral sulcus; its rostral and occipital parts are separated by a slight approach of the sulcus to the cerebrum midline at the level of the frontoparietal suture.

The brain of the Clarendonian *Leptocyon* has a more overlapped cerebellum and more twisted cerebellar vermis than any canid described above. Its sulcal pattern is similar to that of modern Caninae: the Sylvian sulcus is present and concentrically wrapped around with the ectosylvian; suprasylvian and ectolateral sulci are arranged as a series of vertical arches; and the lateral and endolateral sulci on the dorsal part of the cerebral cortex. The region medial to the coronal sulci is narrow. This is particularly evident in the shape of the coronal sulcus, which is the outer lower border of the

sigmoid gyrus. This sulcus does not bow out laterally and is almost in line with the lateral sulcus.

Miocene - Holocene: *Vulpes, Urocyon* and *Otocyon*

Phylogenetic position — The first foxes appeared in North America in the latest Miocene. They were primitive species of *Vulpes*, *Urocyon* and another, still unde-scribed, genus (Tedford, pers. comm. 2005). The evolutionary history of *Urocyon* is restricted to the New World, where it continues to the present. *Vulpes* migrated to the Old World and, during the Pliocene, became widespread in Eurasia (Qiu & Tedford, 1990). Today, *Vulpes* is a rather complex genus with several species that together oc-cupy a wide geographic range. During the Pliocene, *Otocyon* (or a closely related form) appeared in Africa (Werdelin, pers comm., 2008). *Otocyon* is also known from the Pleistocene of Africa (Werdelin & Lewis, 2005) and still occurs there (*O. megalotis,* the bat-eared fox).

Material — *Vulpes stenognathus* F:AM 49284 - Late Hemphillian (Late Miocene) of Spring Valley, Lincoln County, South Nevada, U.S.A. The specimen was figured and described by Radinsky (1973), Lyras (2001), Lyras *et al.* (2001) and Lyras & Van der Geer (2003).

Living species of the genera *Vulpes, Urocyon* and *Otocyon*: *Vulpes vulpes* (NNM RMNH cat. no. a, NNM RMNH cat. no. b. NNM RMNH reg. no. 932, NNMH-Z 6419, FMNH 67413, AMNH(M) 21847), *Vulpes bengalensis* (NNM RMNH cat. no. b. and NNM RMNH cat. no. c), *Vulpes rueppelli* (NNM RMNH cat. no. b), *Vulpes corsac* (NNHM-Z 11616/527/4, NNHM-Z 11614/383/2), *Vulpes chama* (NNM RMNH reg. no. 25900), *Vulpes zerda* (NNM RMNH cat. no. c, FMNH 90369, FMNH 91748, FMNH 91743), *Vulpes lago-pus* (NNM RMNH cat. no. d, NNM RMNH cat. no. h, FMNH 74070, FMNH 74068, FMNH 9871), *Urocyon cinereoargenteus* (NNM RMNH reg. no. 626, AMNH(M) 68527) and *Otocyon megalotis* (NNM RMNH cat. no. a, FMNH 38419, AMNH(M) 169093, AMNH(M) 169099). All are complete or nearly complete endocasts, taken from skulls of Recent foxes (see Appendix 2).

Description and comparisons — The brains of foxes are more advanced than any of the canid brains described so far. Their cerebrum has all the main sulci and gyri found on any living canid, as is evident from their earliest known representative, *Vulpes stenog-nathus* (F:AM 49284). The brain of this species has, in addition to sulci seen in *Leptocyon*, ansate and postcruciate sulci, a more expanded sigmoid gyrus and a longer cruciate sulcus. The overlap of the cerebellum is larger (but slightly smaller than in most mod-ern foxes) and the external anatomy of the cerebellum is the same as that of the living species of *Vulpes*. The proreal gyrus is not preserved in F:AM 49284, but it is likely that its development was limited, since in all living *Vulpes* species this gyrus is very small.

There are some small differences in the size and general shape of the brains of the living *Vulpes* species checked, yet no reliable distinguishing feature can be noted, as these differences are related mainly to cranial proportions. Somewhat different from the other foxes is the arctic fox, *V. lagopus,* the frontal lobes of which are very high and the cerebellum more overlapped. The proreal gyrus of *V. lagopus* is more developed than in any other fox (Lyras & Van der Geer, 2003). Further, the ansate and postcruciate sulci are very well developed, creating a sulcal pattern at the region medial to the coro-nal sulci that is very distinct from the rest *Vulpes* species, although it also approaches a pentagonal outline (Fig. 27).
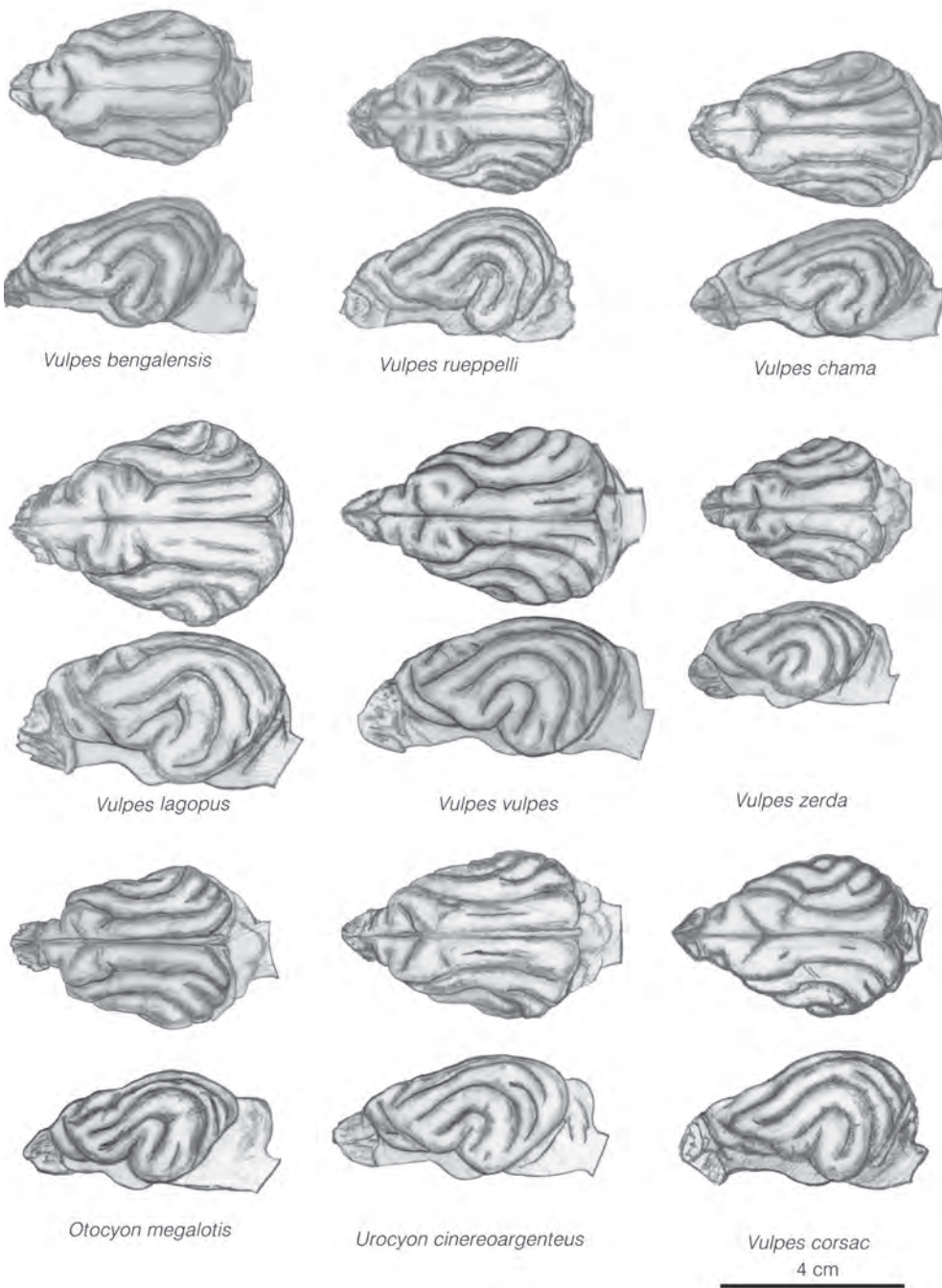
Fig. 27. Endocranial casts from living foxes (from Lyras & Van der Geer, 2003).

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 the one seen in *Vulpes*.

Otocyon has the least overlapped cerebellum of all foxes. The frontal lobes are low and wide, and the length of the cruciate sulcus is variable. According to Radinsky (1973), 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.

Miocene - Pliocene: *Eucyon*

Phylogenetic position — *Eucyon* is a transitional form between the Vulpini and the Canini (the *Canis*-like and South American canids). Its exact phylogenetic position is still a matter of discussion. Tedford & Qiu (1996), who first recognised the genus, considered it as the sister group to the South American canids and the *Canis*-like species. Wang *et al*. (2004, fig. 2.1) placed *Eucyon* closer to the South American canids. More recently, Wang *et al*. (2008) placed *Eucyon* closer the *Canis*-like species.

In North America, *Eucyon* is represented by *E. davisi* (late Middle Miocene - Late Miocene, also Early Pliocene of Eurasia). At the end of the Miocene, *Eucyon* migrated to Eurasia, where it underwent a radiation that gave rise to several new forms. Formerly, finds of these canids were considered to belong to either *Canis, Vulpes* or *Nyctereutes* (for example, Teilhard de Chardin & Piveteau, 1930; Odintzov, 1967; Martin, 1973). In recent years, researchers have recognized that these fossils belong to either *Eucyon* (*E. davisi, E. monticinensis, E. minor, E. zhoui*) or new, *Eucyon*-like, genera (*Nurocyon chonokhariensis, "Canis" adoxus, "Vulpes" odessana*) (Rook, 1992, 1993; Tedford & Qiu, 1996; Koufos, 1997; Wang *et al*., 2004; Sotnikova, 2006; Spassov & Rook, 2006). Some of these canids have several derived characters, and represent either transitional forms between *Eucyon* and true *Canis* or examples of convergent evolution towards *Canis* or *Nyctereutes* (Sotnikova, 2006).

Material — *Eucyon davisi* F:AM 63005 - Late Hemphillian (Late Miocene) of Bird Bone Quarry, Arizona, U.S.A. Maxilla and dorsal part of skull from which a partial latex endocast (NNM RGM 195215) has been made. The endocast preserves only the dorsal part of the cerebrum (Fig. 28). It was figured by Radinsky (1973, fig. 6) under the name *Canis* cf. *C. latran*s, and described and figured by Lyras (2001), Lyras *et al*. (2001) and Lyras & Van der Geer (2003).

Eucyon davisi F:AM 97057 - Early Pliocene of Hsia Kou, Shansi, China. Complete skull from which a digital endocast (Fig. 29) was created at the University of Texas.

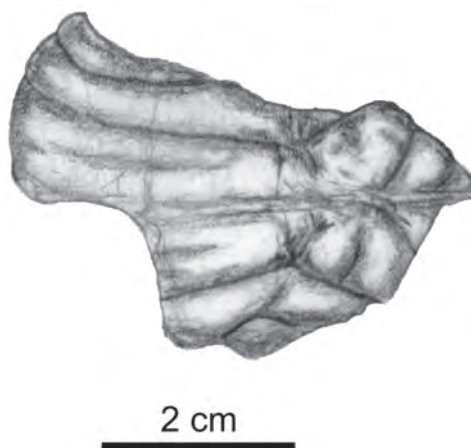*Description and comparisons* — The brain of *Eucyon davisi* is very similar in

Fig. 28. Dorsal view of endocranial cast of *Eucyon davisi* F:AM 63005 (endocranial cast NNM RGM 195215) (from Lyras & Van der Geer, 2003).

size, proportions and general arrangement of the sulcal pattern to that of small jackals such as *Canis adustus*. However, there are some very important differences in the sulcal pattern which distinguish the brain of *Eucyon* from that of *Canis*. The proreal gyrus is bilaterally constricted in *Eucyon*, but it is shorter than that of similar-sized living *Canis*. The expansion of the sigmoid gyri of *Eucyon* is comparable to that of *Vulpes*. The cruciate and postcruciate sulci are better formed and there is a short ansate sulcus. The pyriform lobe is more exposed than in jackals and the ectolateral sulcus is not connected to the suprasylvian sulcus. In F:AM 63005 there is no clear endolateral sulcus, while in F:AM 97057, which is slightly younger, there is a very shallow endolateral sulcus. Over-
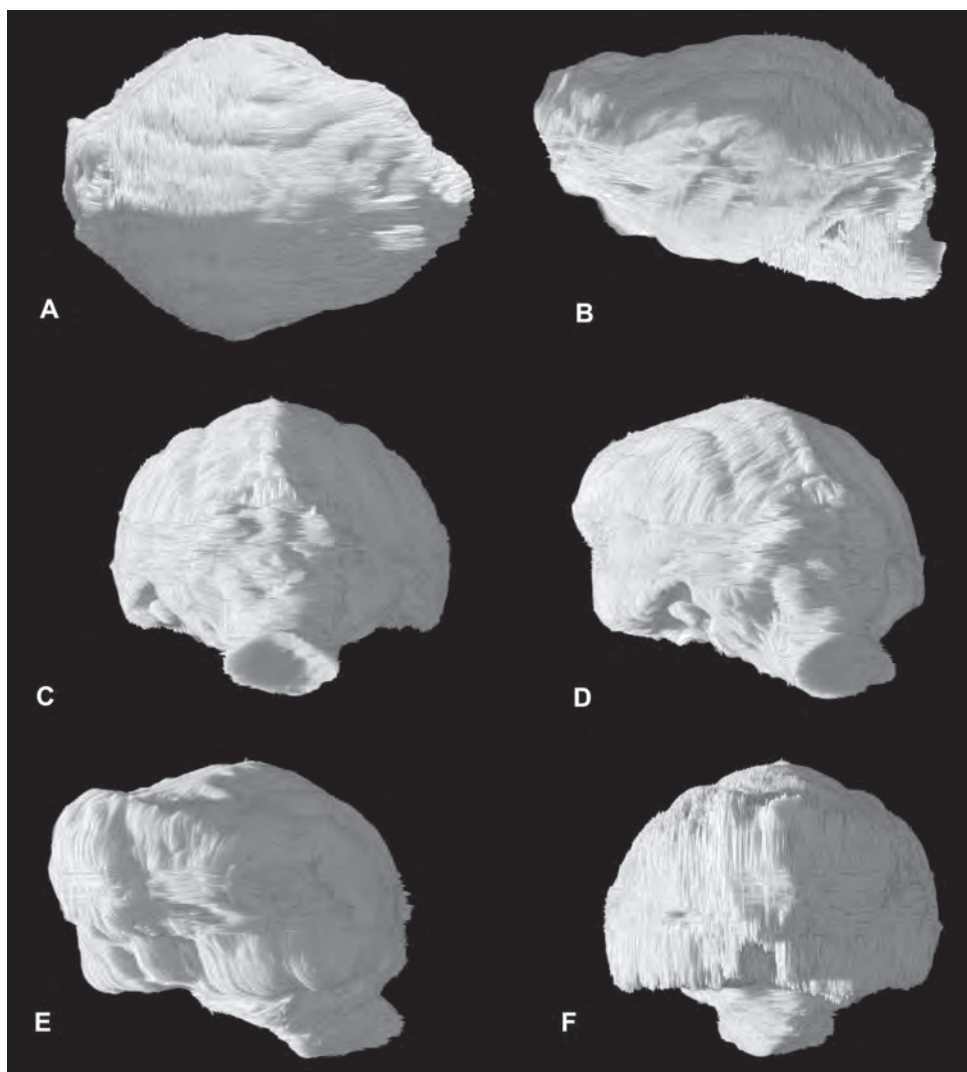

Fig. 29. Digital representation of endocranial cast of *Eucyon davisi* F:AM 97057. (A) Dorsal, (B) lateral, (C) posterior, (D) posterolateral, (E) anterolateral and (F) anterior views.

all, the brain of *Eucyon davisi* is more primitive than that of *Canis* and in many aspects comparable to that of *Vulpes*.

Miocene - Holocene: *Cerdocyon* and *Nyctereutes*

Phylogenetic position — Molecular studies find no direct relationship between the living representatives of *Nyctereutes* and *Cerdocyon* (Wayne *et al.*, 1997; Lindblad-Toh *et al.*, 2005). Morphological (Tedford *et al.*, 1995), palaeontological (Berta, 1988) and palaeoneurological evidence (Lyras & van der Geer, 2003; Dermitzakis *et al.*, 2004), on the other hand, support a very close relationship between them.

Based on the fossil record, their evolutionary history started in North America with the appearance of *Cerdocyon* at the end of the Miocene (McKenna & Bell, 1997). Soon after its appearance it dispersed to the Old World, where it rapidly evolved into *Nyctereutes*. During the Early Pliocene, there were two species of *Nyctereutes* in Asia, *N. tingi* and *N. sinensis.* The first, *N. tingi*, might be a transitional form between *Cerdocyon* and the more derived *Nyctereutes sinensis.* In Europe, *Nyctereutes* is represented by *N. tingi* and *N. donnezani.* During the Late Pliocene there were two species of *Nyctereutes* in Eurasia, *N. sinensis* in Asia and *N. megamastoides* in Europe. However, the distinction between the European and Asian forms is often based on geographic criteria, and it is possible that *N. sinensis - N. megamastoides* and *N. tingi - N. donnezani* are variations of the same species (Tedford & Qiu, 1991).

In Europe, *Nyctereures* became extinct before the beginning of the Pleistocene (Martin, 1971), while in Asia it has persisted to the present day with the living species *N. procyonoides*. During the 20th Century, individuals were introduced for their fur into western Russia, and subsequently the genus has again spread through most of Eastern and Central Europe.

Unlike *Nyctereutes*, *Cerdocyon* has an exclusively New World history. During the Late Miocene-Early Pliocene, *Cerdocyon* was present in Central America (Torres & Ferrusquia-Villafranca, 1981). After the establishment of the Panama Isthmus about 3 million years ago, it dispersed to South America (Berta, 1988), where it continues to live today with the species *Cerdocyon thous*.

Material — *Nyctereutes tingi* AUT MEL-1- Early Pliocene of Megalo Emvolon, Macedonia, Greece. Complete skull from which CT scan images were acquired (Fig. 30).

Nyctereutes tingi F:AM 96757 - Early Pliocene of Nan Chuang Kou, Shansi, China. Partial skull from which a latex endocast (NNM RGM 195216) has been prepared. The endocast preserves the sigmoid gyri, the orbital and proreal gyri, and the anterior part of the right temporal lobe (Fig. 31A-C). It was figured and described by Lyras (2001), Lyras & Van der Geer (2003) and Dermitzakis *et al*. (2004).

Nyctereutes sinensis F:AM 96750 - Late Pliocene of Hsia Chwang, Shansi, China. Partial skull from which a latex endocast (NNM RGM 195223) has been prepared. The endocast preserves the left sigmoid, the orbital and proreal gyrus, and the anterior part of the left temporal lobe (Fig. 31D, E). It was figured and described by Lyras (2001), Lyras & Van der Geer (2003) and Dermitzakis *et al*. (2004).

Nyctereutes sinensis F:AM 96792 - Late Pliocene of Hsia Chwang, Shansi, China. Partial skull from which a latex endocast (NNM RGM 195218) was prepared. The endocast, which is laterally compressed, preserves the anterior and part of the left temporal lobe
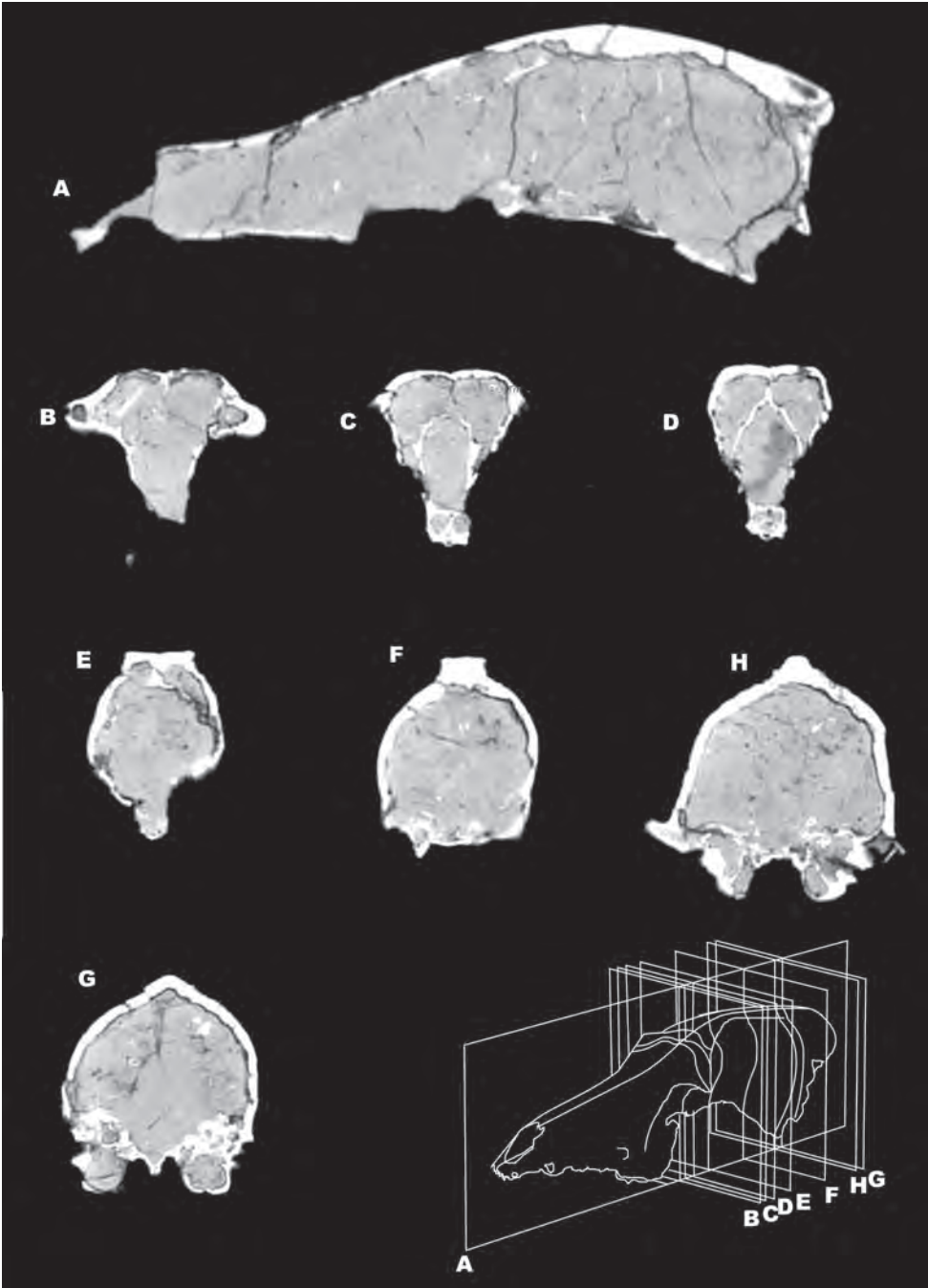
Fig. 30. CT slices from *Nyctereutes tingi* AUT-MEL-1. The position and orientation of the slices is indicated in the drawing at the right corner.
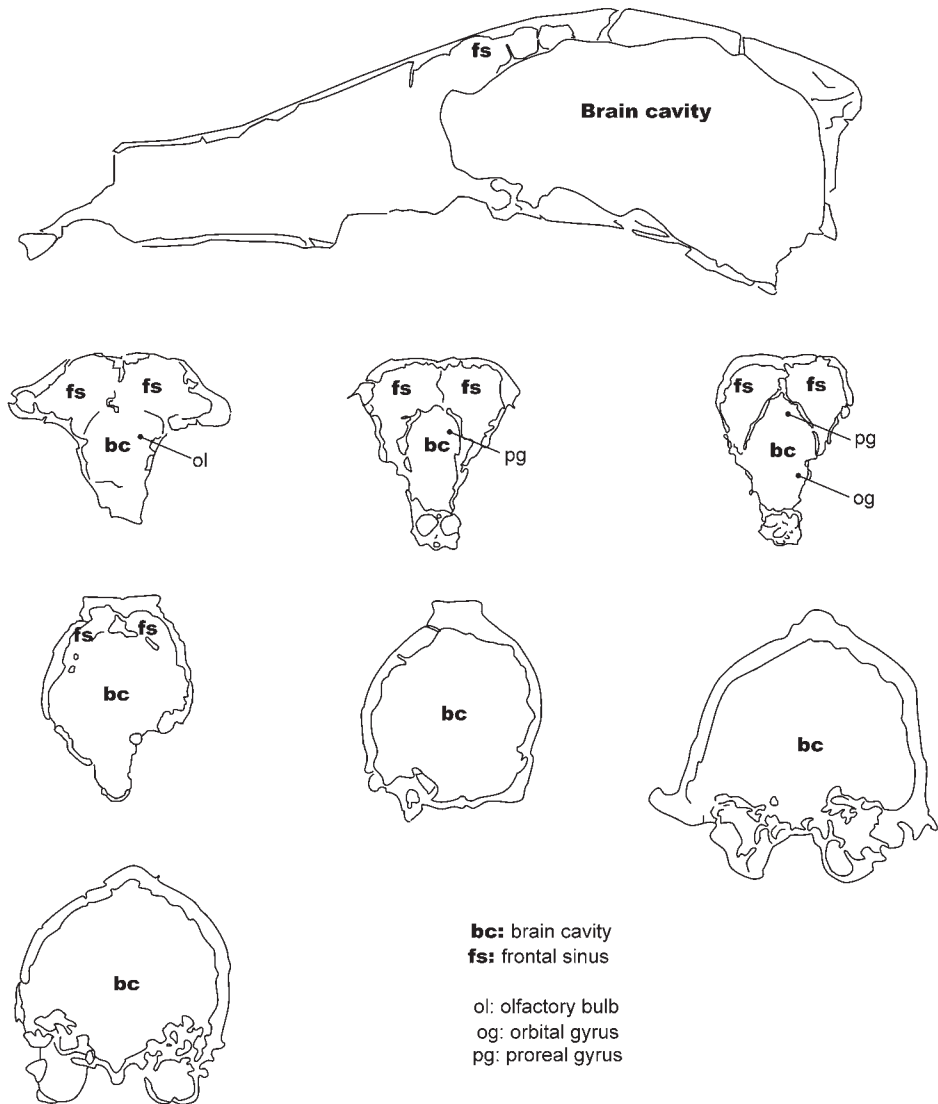
Fig. 30. Continued.

(Fig 31F, G). It has been figured and described by Lyras (2001), Lyras & Van der Geer (2003) and Dermitzakis *et al*. (2004).

Nyctereutes sinensis F:AM 22336 - Late Pliocene of Niu Wako, Shansi, China. Complete skull from which a partial natural endocast (NNM RGM 195219; Fig. 32A, B) has been prepared by removing part of the neurocranial roof. The endocast, which is dorsolaterally compressed, was figured and described by Radinsky (1973, as *N. megamastoides*), Lyras (2001), Lyras & Van der Geer (2003) and Dermitzakis *et al*. (2004).

Nyctereutes megamastoides GIN uncatalogued - Late Pliocene of Beregovaya, Russia; Nearly complete skull from which a latex endocast (NNM RGM 195220) has been prepared (Fig. 32D). From the endocast only a part of the brainstem is missing.

bc: brain cavity
fs: frontal sinus

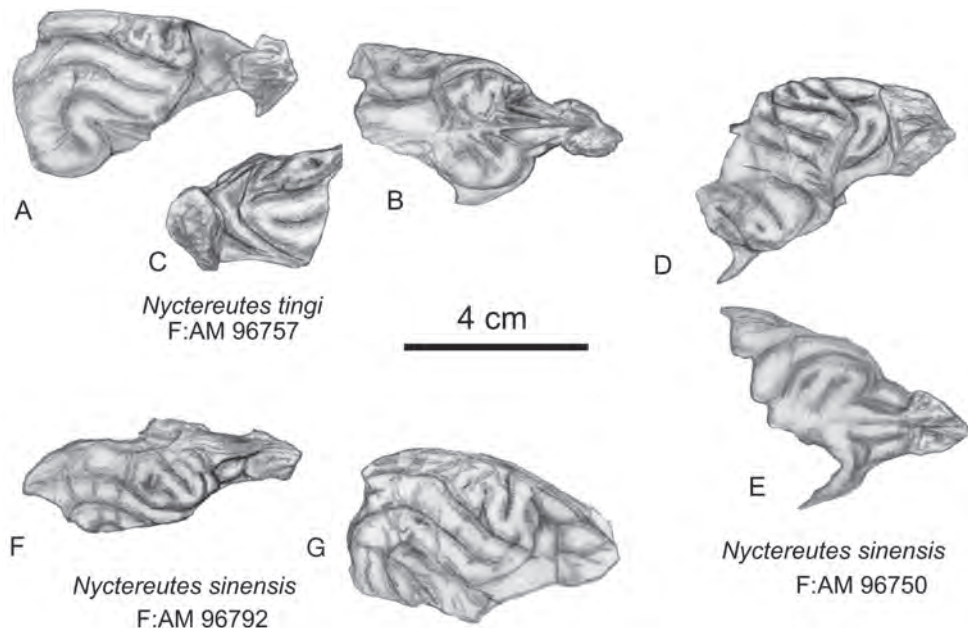ol: olfactory bulb
og: orbital gyrus
pg: proreal gyrus

Fig. 31. Endocranial casts from Pliocene *Nyctereutes*. (A) Right lateral, (B) dorsal and (C) left lateral views of *Nyctereutes tingi* F:AM 96757 (endocranial cast NNM RGM 195216); (D) lateral (mirrored from the left) and (E) dorsal views of *Nyctereutes sinensis* F:AM 96750 (endocranial cast NNM RGM 195223); (F) dorsal and (G) left lateral views of *Nyctereutes sinensis* F:AM 96792 (endocranial cast NNM RGM 195218). From Lyras & Van der Geer (2003) (exept C).

Nyctereutes megamastoides AMPG(V)-Σ 384 - Late Pliocene of Sesclo, Thessaly, Greece. Part of skull from which a latex endocast has been prepared (endocranial cast NNM RGM 195221). The endocast preserves the entire brain exept of its brainstem (Fig. 32C).

Nyctereutes megamastoides AUT-DFN 17 - Late Pliocene of Dafnero, Macedonia, Greece. Complete skull from which CT scan images were acquired (Fig. 33).

Endocasts from skulls of living crab-eating foxes and raccoon dogs: *Cerdocyon thous* (NNM RMNH cat. ost. no. b., AMNH (M) 14853, FMNH 20205, FMNH 20436 and FMNH 68889), *Nyctereutes procyonoides* (NNM RMNH cat. ost. no. a., NNM RMNH cat. ost. no. d., NNM RMNH cat. ost. no. h., NNHM-P 6433, NNHM-P 6434 and FMNH 36002).

Description and comparisons — The cerebral hemispheres of *Cerdocyon thous* widen out abruptly immediately behind the presylvian sulcus, thereby creating an angular profile in dorsal view (Fig. 34). The proreal gyrus is long and bilaterally constricted, and the coronal sulci create a heart-shaped outline on the dorsal aspect of the cerebrum.

In the living raccoon dog, *Nyctereutes procyonoides*, there is only a slight incurvation in the lateral profile at the level of the presylvian sulcus. The region rostral to the presylvian sulcus gives the impression of not being well developed. The relative length of the proreal gyrus approaches that of most Canini (Radinsky, 1973). However, it is broad and low, and with hardly any bilateral constriction, which makes it comparable to that of *Vulpes lagopus*. The coronal sulci create a heart-shaped outline on the dorsal aspect of
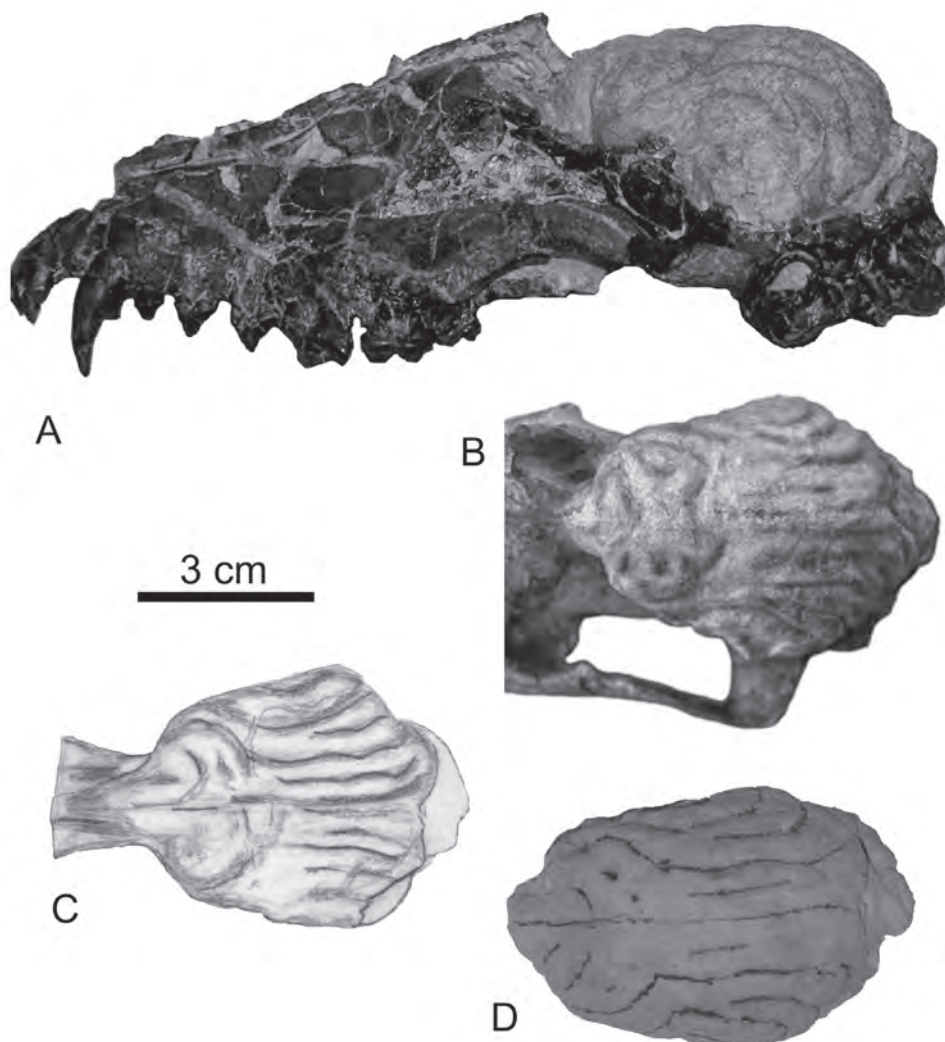
Fig. 32. Endocranial casts from Pliocene *Nyctereutes*. (A) Lateral and (B) dorsal views of *Nyctereutes sinensis* F:AM 22336 (endocranial cast NNM RGM 195219); (C) dorsal view of *Nyctereutes megamastoides* AMNH (Y)-Σ 384 (endocranial cast NNM RGM 195221); (D) dorsal view of *Nyctereutes megamastoides* GIN (endocranial cast NNM RGM 195220).

the cerebrum (Fig. 34). The ansate sulcus is never present, while in the small foxes (some *Vulpes* spp. and *Urocyon*) it may or may not be present.

In fossil *Nyctereutes*, most parts of the cerebrum are like those of the living species, *N. procyonoides*, though the fossil forms differ from the living in that they have an ansate sulcus and more wavy cerebral gyri (Radinsky, 1973). This difference might be simply the result of allometry, as the degree of complexity of the gyri is a common difference between brains of different size. The outline of the sulcal pattern of *N. tingi* is not very

clear, due to damage in the form of cracks on F:AM 96757 and the low resolution of the CT-scan of AUT-MEL-1. On the other hand, the sulcal pattern in *N. megamastoides* (AMPG(V)-Σ 384) and *N. sinensis* (F:AM 96750, F:AM 96792) is much better preserved, and is clearly heart-shaped. The specimen F:AM 22336 was compressed and damaged, and thus became asymmetrical. The resulting pattern is therefore less clear than in the other specimens.
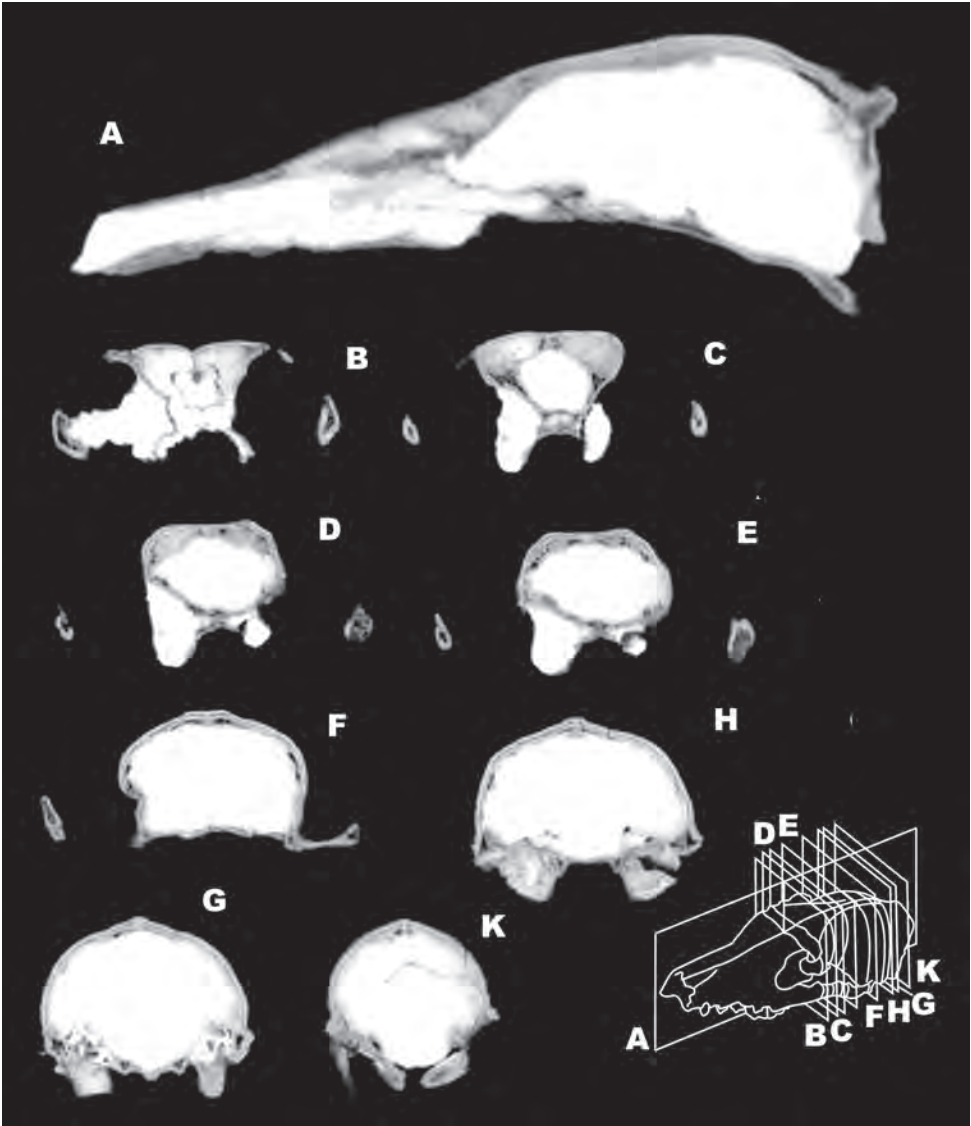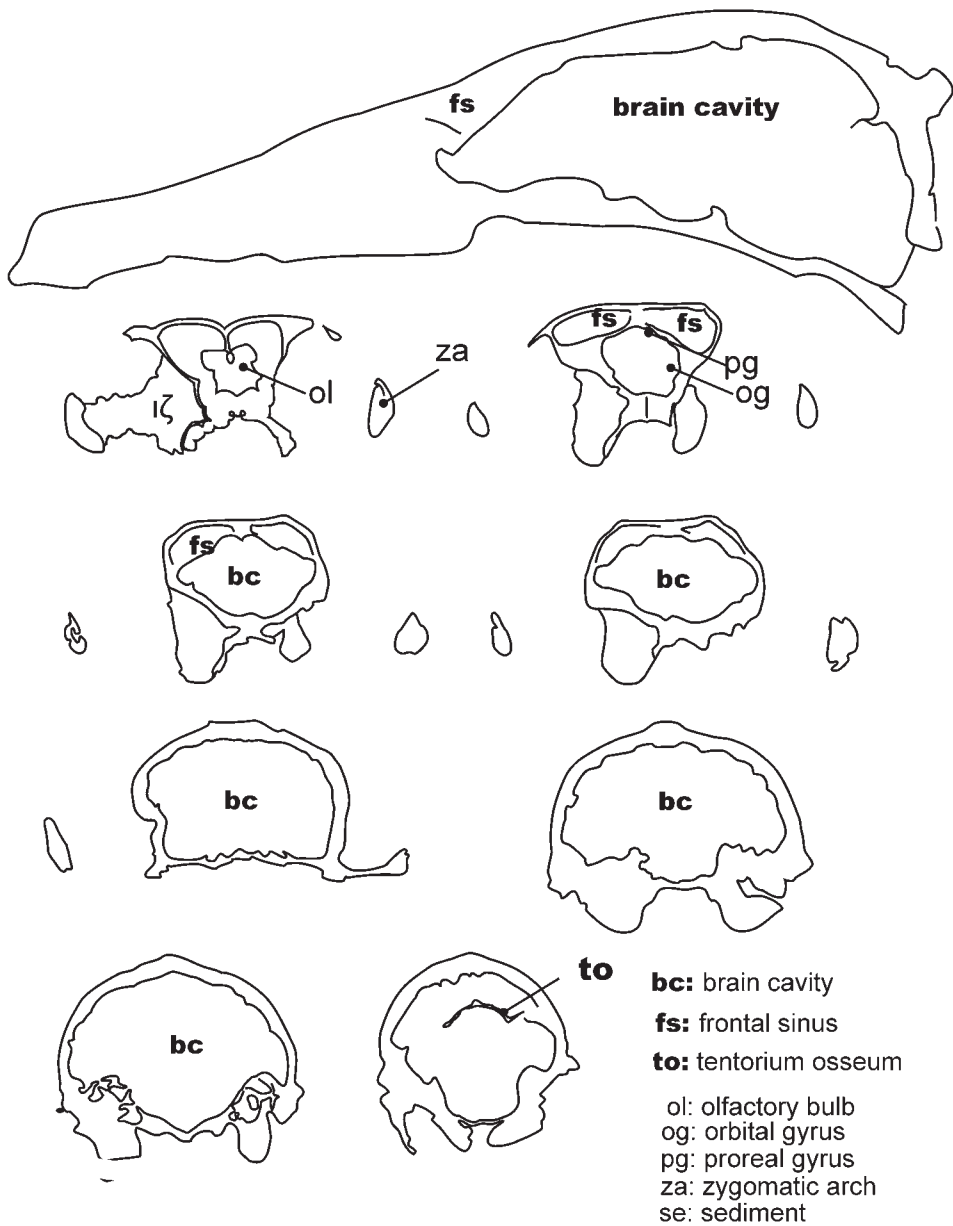

Fig. 33. CT slices of *Nyctereutes megamastoides* AUT-DFN-17. The position and orientation of the slices are indicated in the drawing at the right corner.

Fig. 33. Continue.

The most important difference between living and fossil *Nyctereutes* has to do with the development of the cortex rostral to the presylvian sulcus (Lyras & Van der Geer, 2003). In *N. tingi* (F:AM 96757), *N. sinensis* (F:AM 96750, F:AM 96792, F:AM 22336) and *N. megamastoides* (GIN-uncatalogued), the proreal gyrus is long and bilaterally constricted, and the orbital gyrus is well developed. An exception is the *N. megamastoides* specimen from Sesclo (AMPG(V)-Σ 384), in which the proreal gyrus is slightly shorter and broader.

bc: brain cavity
fs: frontal sinus
to: tentorium osseum

ol: olfactory bulb
og: orbital gyrus
pg: proreal gyrus
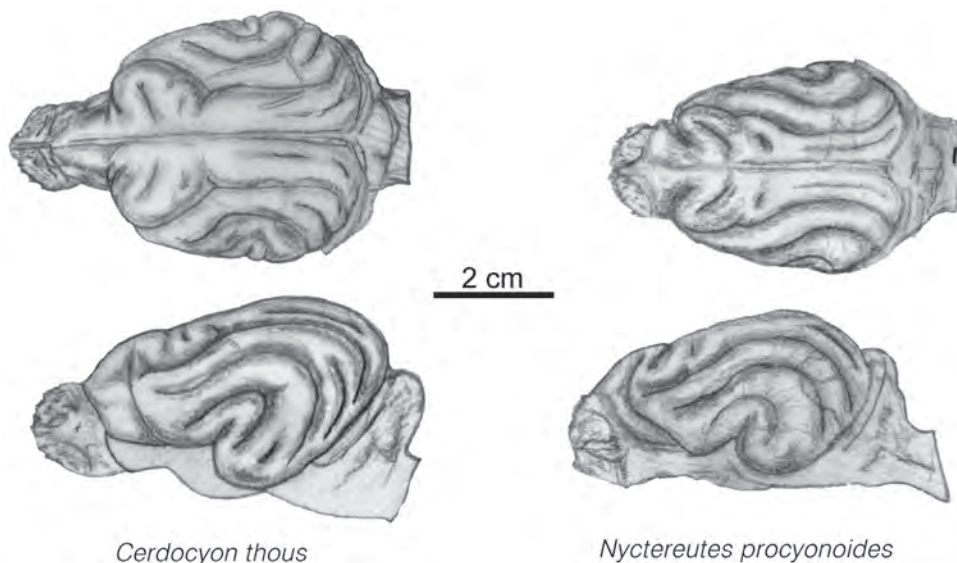za: zygomatic arch
se: sediment

Fig. 34. Endocranial casts from living *Cerdocyon* and *Nyctereutes* (from Lyras & Van der Geer, 2003).

A key point towards a better understanding of the differences in the shape of the proreal gyrus between living and Pliocene *Nyctereutes* (with the exception of that from Sesclo) is the differences in their cranial anatomy. The Sesclo material differs from the rest of the Pliocene specimens, not only in the brain, but also in a number of craniodental characters, two of which are the relatively short and broad rostrum, and that the caudal border of the palatine lies at the end of the tooth row (Athanasiou, 1998). These differences are even more obvious when the living raccoon dog is taken into considera-

tion; it has a shorter rostrum and the caudal palatine border is situated even further back than in Pliocene *Nyctereutes* (Fig. 35). These cranial differences seem to have an effect on the morphology of the proreal gyrus. All canids that have relatively short faces such as *Lycaon*, *Enhydrocyon*, *Borophagus* and *Speothos*), also have relatively high and massive frontal lobes (Radinsky, 1973) and a caudal palatine border that extends caudal to the tooth row (Fig. 36). The same seems to be the case in many domestic dog breeds that have short faces (Seiferle, 1966).

Thus, the broader proreal gyrus of the fossil *Nyctereutes* from Sesclo and, particularly, of living *Nyctereutes procyonoides* can be due to the same morpho-
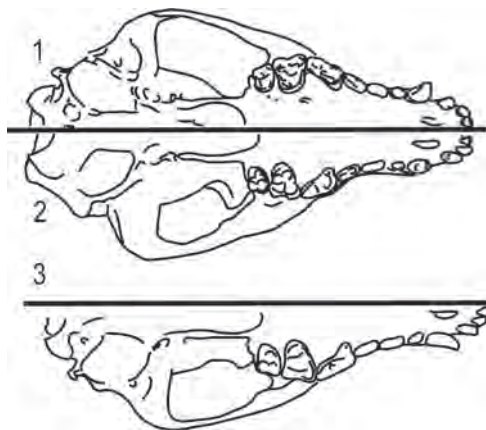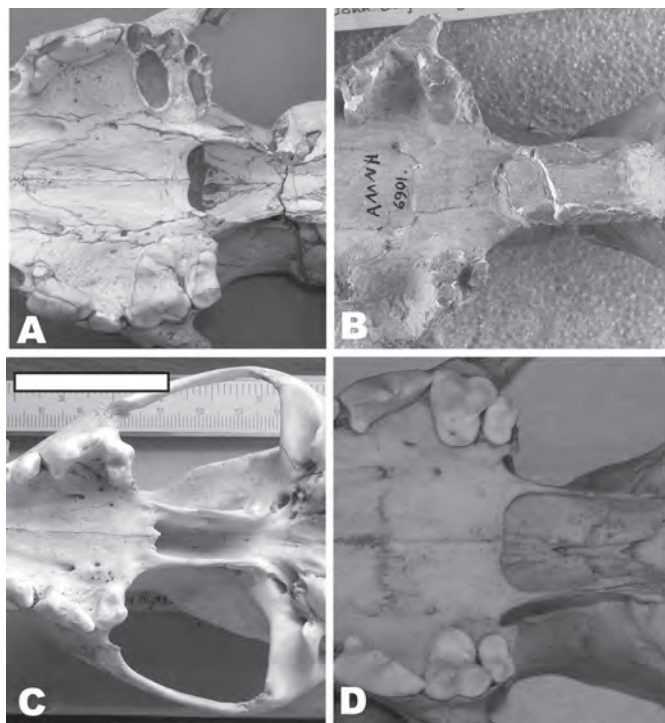

Fig. 35. Ventral view of skulls of (1) *Nyctereutes procyonoides*, (2) *Nyctereutes sinensis* and (3) *Cerdocyon thous*. All skulls are depicted to the same condylobasal length.

Fig. 36. Detail of the ventral view of four Canidae skulls. (A) *Canis variabilis* (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing); (B) *Enhydrocyon stenocephalus* AMNH 6901; (C) *Speothos venaticus* AMNH (M) 76806; (D) *Lycaon pictus* AMNH(M) 81853. The length of the white bar is 3 cm.

genetic factors that affect the shortening of the facial region. From observations on living and fossil canids, it appears that the caudal palatine border always lies below the cribriform plate that houses the olfactory bulbs of the brain. As the caudal palatine border moves backwards, the cribriform plate does the same, resulting in the anterior lobe of the brain becoming anterodorsally compressed. Since there is no direct functional relationship between the olfactory bulbs and the nasal pharynx, it is possible that this anatomical relationship is the result of ontogenetic restrictions. Evans & Christensen (1993) indicated that the basicranium follows a different ontogenetic pattern than the rest of the skull; therefore, it is possible that changes in that part of the brain are more constrained.

Miocene - Holocene: *Chrysocyon, Lycalopex, Dusicyon, Atelocynus* and *Speothos*

Phylogenetic position — During the Pleistocene, several new canid species appeared in or migrated to South America, where they underwent radiation that gave rise to the divergent group of South American canids. Their exact phylogenetic history and even taxonomy is still a matter of discussion (see, for example, Lyras & van der Geer, 2003; Zrzavý & Řičánková, 2004; Wang *et al.*, 2004). The evolutionary history of the canids mentioned in this section can be summarized as follows.

Chrysocyon appeared in North America at the end of the Miocene (Berta, 1987; McKenna & Bell, 1997). The extant species, *Chrysocyon brachyurus*, is known from the Lujanian (Middle and Late Pleistocene) - Holocene of Bolivia and Brazil (Berta, 1988).

A more diverse group of South American canids includes the genera *Lycalopex* and

Dusicyon. According to Berta (1988), the "ancestral" stock that gave rise to them is an early member of the genus *Lycalopex*. This genus appeared in the Late Pliocene ("*Dusi-cyon*" *cultridens*; see Berman, 1994) and today is represented by six species (*Lycalopex culpaeus, L. fulvipes, L. griseus, L. gymnocercus, L. sechurae* and *L. vetulus*). *Lycalopex* is phylogenetically close to *Dusicyon*. This genus is known from two species, one as a fossil from mainland South America (Burmeister, 1866) and the other as the wolf of the Falkland Islands. This wolf, which is not phylogenetically related to the members of the genus *Canis*, was endemic to the Falklands, were it became extinct in 1876 (Nowak & Paradiso, 1983).

Atelocynus and *Speothos* are two rather peculiar canids of similar appearance (Sheldon, 1992). Phylogenetically, they are probably related to *Cerdocyon* and *Nyctereutes* (Berta, 1987, 1988; Tedford *et al.*, 1995); see, however, Wayne & O'Brien (1987) and Wayne *et al.* (1997) for alternative assessments.

Material — *Lycalopex culpaeus* AMNH 27904 - Middle Pleistocene of Ecuador. Skull with mandible. Part of the left wall of the neurocranium is missing. From the specimen a latex endocast has been prepared (NNM RGM 195227). It preserves the cerebellum and the greater part of the right cerebral hemisphere, with only the anterior lobe missing (Fig. 37).

Dusicyon australis NNM RMNH reg. no. 19111 and NNM RMNH reg. no. 19112: Endocasts from the recently extinct Falkland Islands wolf (Fig. 38).

Living species of the genera *Chrysocyon, Atelocynus, Speothos* and *Lycalopex* (Figs. 38, 39): *Chrysocyon brachyurus* (NNM RMNH cat. no. a., AMNH(M) 133940, USNM 361013), *Atelocynus microtis* (AMNH(M) 76579, FMNH 98081, FMNH 146277), *Speothos venaticus* (NNM RMNH reg. no. 3224), *Lycalopex culpaeus* (NNM RMNH reg. no. 620, AMNH(M) 205782), *Lycalopex sechurae* (NNM RMNH reg. no. 2381) and *Lycalopex vetulus* (NNM RMNH cat. ost. no. a., AMNH(M) 68527). Endocasts were taken from skulls of these Recent South American canids.

Description and comparisons — Features of this group, including the general shape of the brain, are morphologically rather variable. Apart from the differences in the brain's
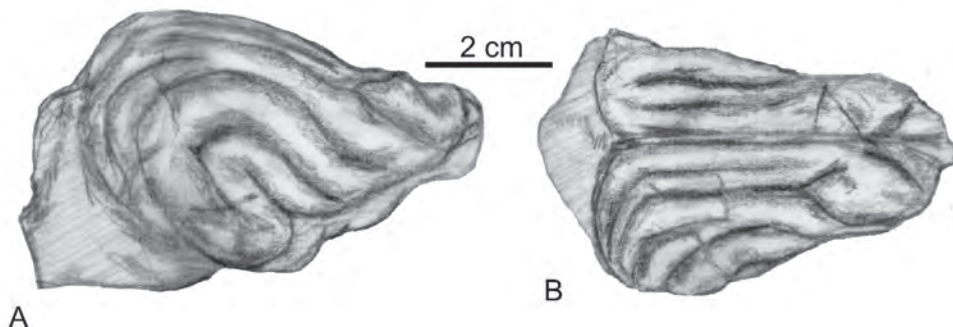

Fig. 37. Endocranial cast of Pleistocene *Lycalopex culpaeus* AMNH 27904 (endocranial cast NNM RGM 195227), (A) lateral and (B) dorsal views.

overall morphology, the most important variations are in the cortex medial to the coronal sulci and anterior to the presylvian sulcus. The coronal sulci of *Lycalopex culpaeus* form a heart-shaped outline on the dorsal side of the cerebrum, similar to that of *Cerdocyon*. In the remaining *Lycalopex* species and *Dusicyon australis*, the coronal sulci form a parenthesis-like outline. In the genera *Atelocynus* and *Speothos*, the sigmoid gyri expand very abruptly. This creates an orthogonal or oblong outline of the ansate and coronal sulci on the dorsal surface of the cerebrum. In *Chrysocyon brachyurus* the posterior sigmoid gyri expand laterally more than the anterior sigmoid gyri.
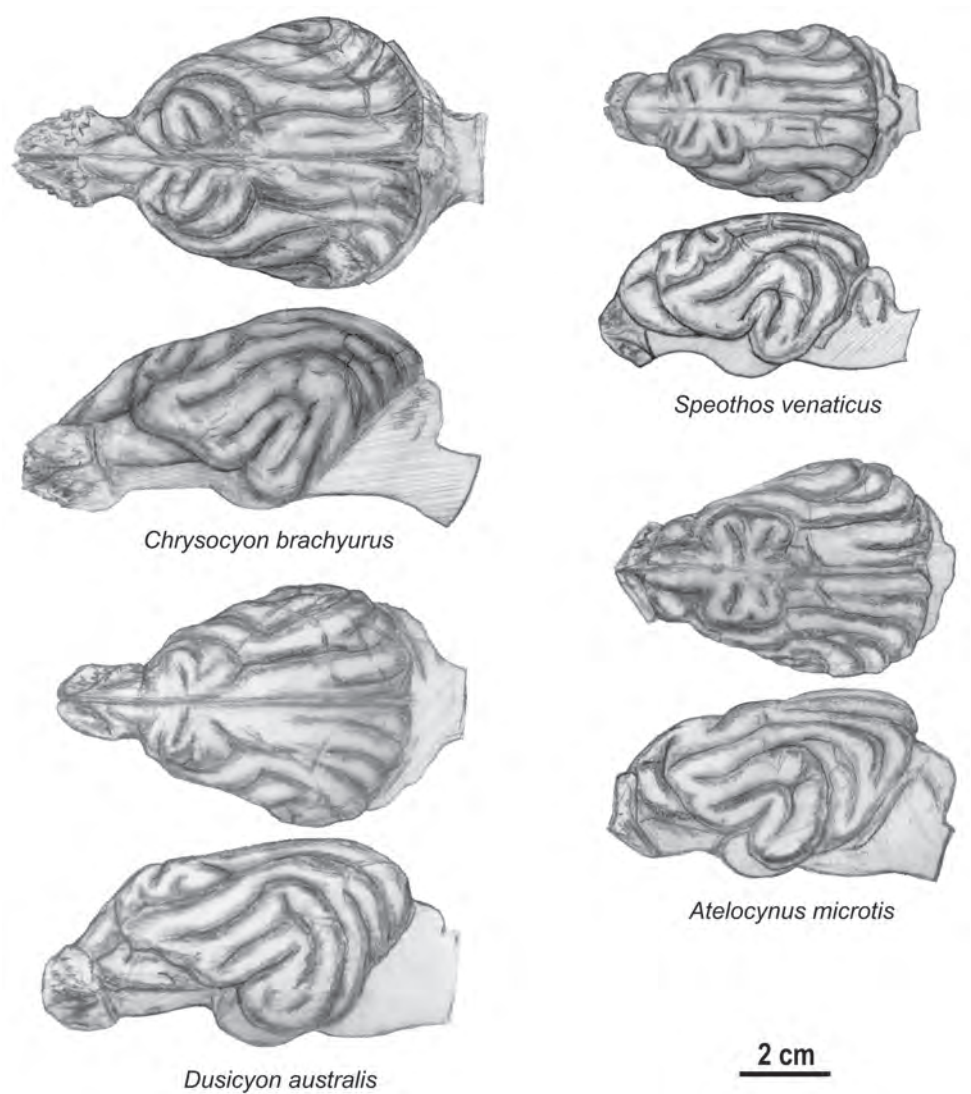

Fig. 38. Endocranial casts from living and recently extinct (*D. australis*) South American Caninae (from Lyras & Van der Geer, 2003).
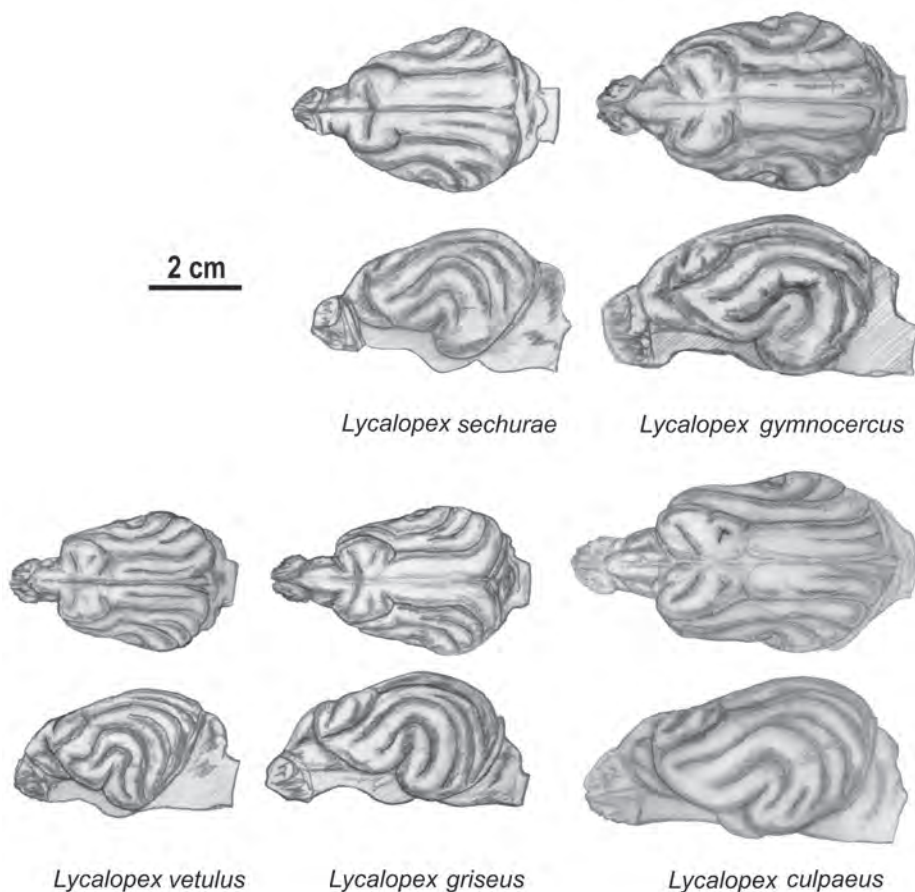
Fig. 39. Endocranial casts from living South American Caninae (from Lyras & Van der Geer, 2003).

All specimens in which the anterior part of the brain is preserved have a proreal gyrus that is relatively long and bilaterally constricted compared to that of most foxes. Its exact proportions are variable. *Lycalopex vetulus* has the shortest proreal gyrus. *Chrysocyon* and the rest of the living *Lycalopex* spp. have a much longer and bilaterally constricted gyrus. In *Atelocynus* and *Speothos* the proreal gyrus is shorter and considerably thicker. The orbital gyri of *Chrysocyon* and *Lycalopex* have only one sulcus (the proreal sulcus) which separates the proreal and orbital gyri. The two specimens of *Dusicyon australis* examined as part of this study, have three sulci in that region, that is the proreal sulcus, the intraorbital sulcus and a third sulcus, not found in the domestic dog, which form the dorsal boundary of the anterior portion of the orbital gyrus (Lyras & Van der Geer, 2003).

Speothos venaticus has relatively high frontal lobes, a feature related to the short rostrum of this species. As noted in other canids whose muzzles became shorter during evolution (such as *Enhydrocyon stenocephalus*, *Borophagus dudleyi*, *Nyctereutes procyonoides*), the broader or higher rostral part of the brain is the result of a packing rearrangement
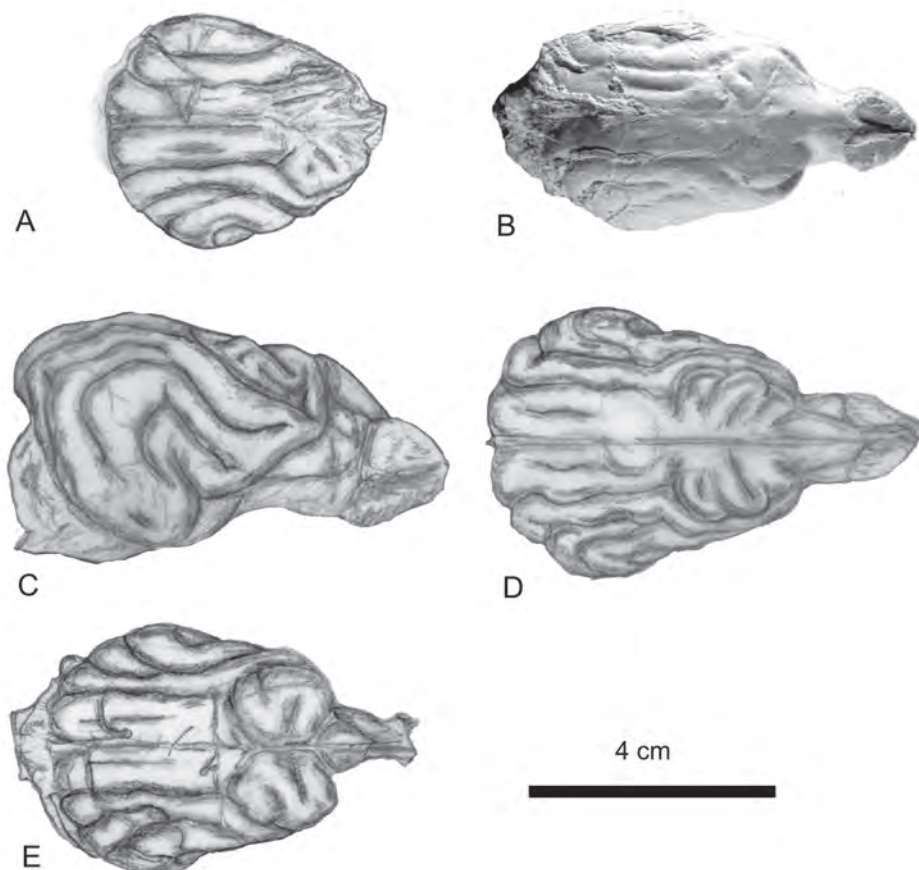
Fig. 40. Endocranial casts from Pleistocene *Canis.* (A) Dorsal view of *Canis lepophagus* WT 760 (endocranial cast AMNH 104782) (from Lyras & Van der Geer, 2003); (B) dorsal view of *Canis edwardii* F:AM 63100; (C) lateral and (D) dorsal views of *Xenocyon lycaonoides* GIN 3722-144 (endocranial cast NNM RGM 195206) (from Lyras & Van der Geer, 2003); (E) dorsal view of *Cynotherium sardous* SASN CB 84-8022 (from Lyras, 2001).

of the skull due to the backward movement of the caudal palatine border and the cribriform plate.

Pliocene - Holocene: *Canis, Xenocyon, Cynotherium, Lycaon* and *Cuon*

Phylogenetic position — This group includes wolves, jackals, the dhole, the Cape hunting dog and their fossil relatives. The earliest record of the genus *Canis* is from the late Miocene of North America (Rook, 1993; Miller & Carranza-Castañeda, 1998). During the Early Blancan (Early Pliocene) the diversity of the genus increased with the appearance a series of jackal-sized species (such as *C. ferox, C. edwardii, C. lepophagus*) (Nowak, 1979). *Canis* entered the Old World in the Early Pliocene (Flynn *et al.*, 1991), where it underwent an extensive radiation (Hunt, 1996; Wang *et al.*, 2004). During the

mid Pliocene *Canis* entered Africa (Werdelin & Lewis, 2005) and, at the latest Pliocene-Early Pleistocene, Europe (Rook & Torre, 1996). The genus *Canis* is also known from the Pleistocene of South America (Berta, 1988).

The grey wolf (*Canis lupus*) appeared in the Late Pleistocene. The jackals (*Canis aureus*, *C. mesomelas* and *C. adustus*) are believed to be of African origin (Rook, 1993). Of North American origin are the coyote (*Canis latrans*), and the extinct *Canis dirus* and *Canis armbrusteri*.

The Cape hunting dog, *Lycaon pictus*, is a canid phylogenetically related to some hypercarnivorous species of Late Pliocene-Middle Pleistocene. Martínez-Navarro & Rook (2003) suggested *Xenocyon lycaonoides* as its possible ancestor. A canid related to *Xenocyon* is *Cynotherium sardous*, an insular mammal from the islands of Sardinia and Corsica (Lyras *et al.*, 2006). Another hypercarnivorous member of this group is *Cuon*. Today this animal lives only in south and southeast Asia, but *Cuon* occupied large parts of Eurasia and North America during the Pleistocene.

Material — *Canis lepophagus* AMNH 104782 (cast of WT 760) - Late Blancan (Late Pliocene) of N. Cita Canyon, Texas, U.S.A. Complete skull with mandible, from which a nearly complete endocast has been prepared (Fig. 40). The endocast was figured and described by Lyras *et al.* (2001) and Lyras & Van der Geer (2003).

Canis edwardii F:AM 63100 - Late Blancan (Late Pliocene) of Dry Mountain, Graham County, South Arizona, U.S.A. Nearly complete skull with mandible from which a partial latex endocranial cast has been prepared (F:AM 63100) (Fig. 40). The endocast does not preserve the cerebellum and the posterior part of the cerebrum.

Canis mosbachensis IQW 1982/18052 (mei 17572) - Middle Pleistocene of Untermassfeld, Thüringen, Germany. Partial skull. Due to the fragmentary nature of the specimen, it was not possible to prepare an endocast. Therefore, the anatomy of the brain was inferred simply by studing the impressions of the sulci on the internal side of the neurocranium (Fig. 41).

Xenocyon lycaonoides GIN 3722-144 - Middle Pleistocene of Kolyma, North Siberia, Russia. Complete skull from which a complete endocast (RGM.195206) has been pre-
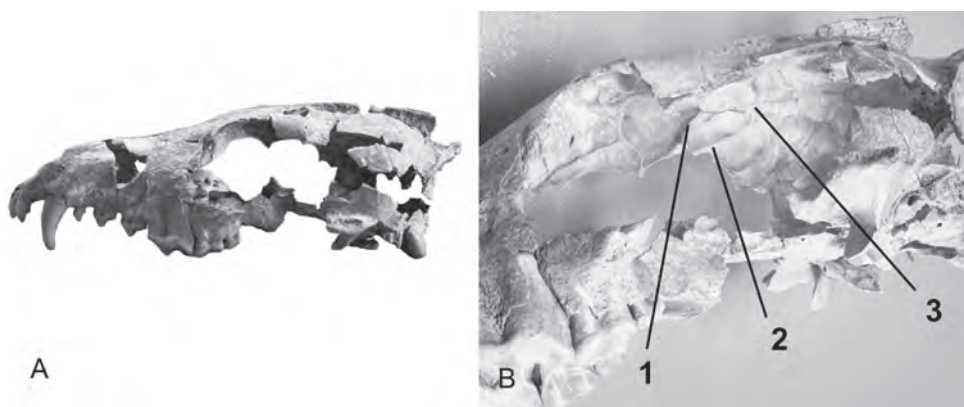

Fig. 41. Skull of *Canis mosbachensis* IQW 1982/18052 (mei 17572). (A) Lateral view and (B) detail of the internal walls of the neurocranium. Imprints of the sulci on the neurocranium walls, 1: cruciate sulcus; 2: coronal sulcus; 3: ansate sulcus.

pared (Fig. 40C, D). The endocast was figured and described by Lyras *et al.* (2001) and Lyras & Van der Geer (2003).

Canis armbrusteri F:AM 67286 - Irvingtonian (Pleistocene) of Mcleod Lime Rock Mine, Levy County, Florida, U.S.A. Nearly complete skull from which an almost complete endocast has been prepared (Fig. 42). Only the olfactory bulbs are missing from this specimen.

Canis dirus FMNH PM 394 - Rancholabrean (Late Pleistocene), Rancho la Brea, Los Angeles County, California, U.S.A. Isolated neurocranium that was split in two, in order to prepare a plaster endocast (Fig. 42). The endocast was figured and described by Moodie (1922).

Cynotherium sardous SASN-CB-84-8022 - Late Pleistocene, Corbeddu Cave, Lanito Valey, Nuoro, Sardinia, Italy. Nearly complete skull with mandible, from which a latex
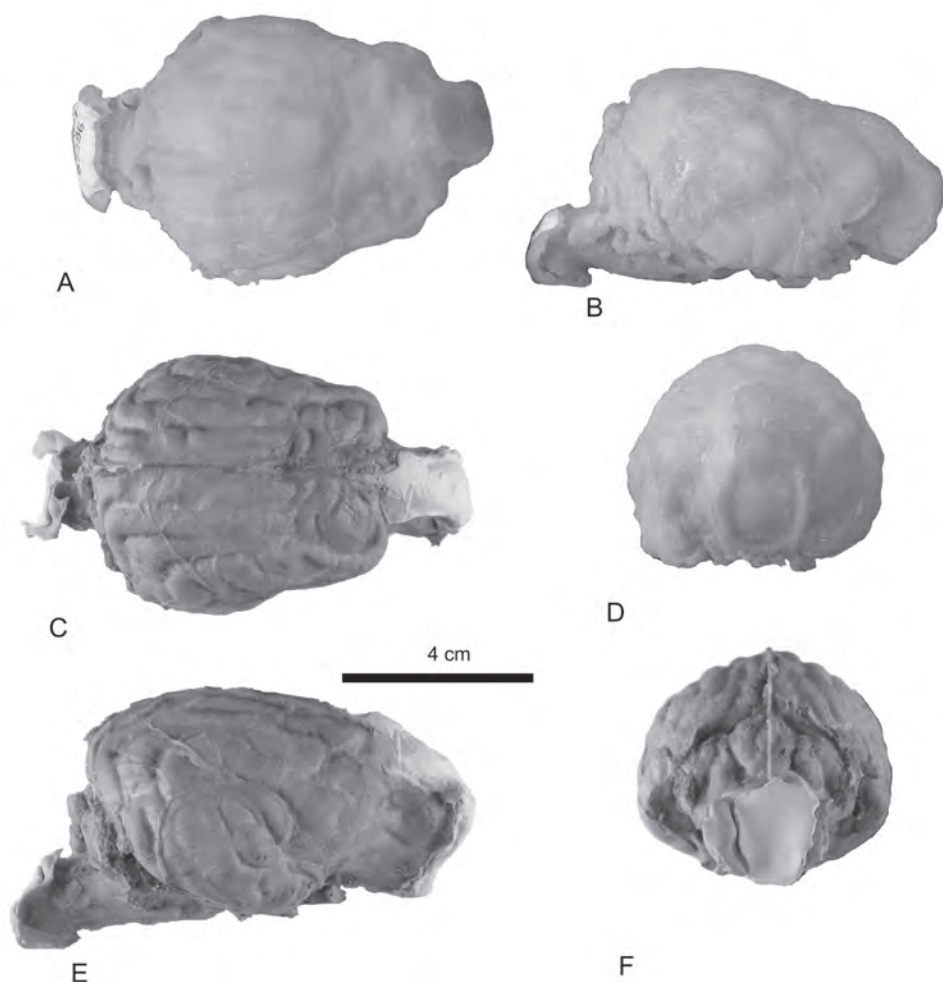

Fig. 42. Endocranial casts from Pleistocene *Canis.* (A) Dorsal, (B) lateral and (D) anterior views of *Canis armbrusteri* F:AM 67286; (C) dorsal, (E) lateral and (F) posterior views of *Canis dirus* FMNH PM 394.

endocast has been prepared. The specimen was figured and described by Lyras (2001) and Lyras *et al.* (2006).

Living species of the genera *Canis, Lycaon* and *Cuon* (Figs. 43, 44)*: Canis lupus* (NNM RMNH cat. no. l. and FMNH 7619), *Canis mesomelas* (NNM RMNH reg. no. 25891, NNM RMNH cat. no. l, AMNH(M) 2288, FMNH 85508), *Canis aureus* (NNM RMNH cat. ost. b, NNHM-Z 11597/378/3), *Canis latrans* (NNM RMNH cat. no. c)*, Canis rufus* (AMNH 112), *Canis adustus* (NNM RMNH cat. no. h, FMNH 97857), *Canis sinensis* (NNM RMNH cat. no. b, FMNH 146291), *Lycaon pictus* (NNM RMNH cat. no. c, AMNH(M) 24218) and *Cuon alpinus* (NNM RMNH reg. no. 1546, FMNH 91246). Endocasts from the skulls of those Recent canids were taken.

Description and comparisons — In all *Canis*-like species, the cerebral hemispheres widen out abruptly immediately posterior to the presylvian sulci, and the proreal gyrus is very long and bilaterally constricted, more than in any other member of the family Canidae. Additionally, the sigmoid gyri expand very abruptly in these species. This creates an orthogonal or oblong outline of the ansate and coronal sulci on the dorsal surface of the cerebrum (the only exception is *Canis edwardii,* see below).

The earliest *Canis* species available for study is *C. lepophagus* (WT 760, cast, AMNH 104782). Its proreal gyrus is not completely preserved, yet it clearly has a development similar to that of the living *Canis* species. The sigmoid gyri are more expanded than in *Eucyon davisi*, but not as much as in *Canis latrans* (the coyote), that once was thought to be its descendant (e.g., Kurtén, 1974).

A later member of this group is *Canis edwardii* (F:AM 63100). Its brain is unlike all the other *Canis*-like species studied herein. The coronal sulci form a parenthesis outline on the dorsal surface of the cerebrum similar to that of most South American canids and *Nyctereutes*. It should be noted that in two living jackals, *C. aureus* and *C. adustus*, the oblong pattern is also not very clear (Lyras & Van der Geer, 2003), yet it is more distinct than in *C. edwardii*. Further, its brain is rather elongated for *Canis*, but that might be simply the result of its cranial anatomy.

The Middle Pleistocene *Canis mosbachensis* and *Xenocyon lycaonoides* have an endocranial anatomy similar to that of modern, similarly-sized *Canis*-like species. The endocasts of the Late Pleistocene, large *C. armbrusteri* and *C. dirus* are of similar morphology. *Canis dirus,* in particular, has the most fissured brain of all canids studied, a feature that was already noted by Moodie (1922).

From all the living *Canis* species, *C. lupus*, *C. rufus* and *C. simensis* have relatively the narrowest proreal gyrus (Lyras & Van der Geer, 2003). *Cuon alpinus* and *Lycaon pictus* have a considerably broader proreal gyrus. Some additional details of the sulcal pattern of the living species have been described by Radinsky (1973) and Lyras & Van der Geer (2003). According to them, *Canis 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 into two parts (Radinsky, 1973). The orbital gyri of *C. aureus*, *C. adustus* and *C. mesomelas* have only one sulcus (the proreal sulcus), which separates the proreal and orbital gyri. *Canis latrans*, *Cuon alpinus* and *Lycaon pictus* have an additional sulcus, the intraorbital sulcus, which extends parallel to the lower section of the presylvian sulcus. *Canis simensis, C. lupus* and *C. rufus* have three sulci in that region, the proreal, intraorbital and a third sulci, not found in the domestic dog, that forms the dorsal boundary of the anterior part of the orbital gyrus (Lyras & Van der Geer, 2003).

Fig. 43. Endocranial casts from living species of *Canis* (from Lyras & Van der Geer, 2003).

Canis latrans

Canis lupus

Canis aureus

4 cm

Canis simensis

Fig. 44. Endocranial casts from living species of *Canis, Cuon* and *Lycaon* (from Lyras & Van der Geer, 2003).

Cynotherium was an island species, endemic to Sardinia and Corsica, and differs from all the other canids included in this study with the exeption of the recently extinct *Dusicyon australis*. The external brain anatomy of *Cynotherium* is typical of the members of the *Canis*-like species (Lyras *et al.*, 2006). A more interesting point concerning *Cynotherium* is its relative brain size. As noted in the introduction, the subject of relative brain

size has been covered extensively by previous authors and, therefore, this aspect of the brain is beyond the scope of the present study. However, in contrast to the impressive literature on the brain size of mainland species, only a few papers have been published on the brain of insular mammals (Dechaseaux, 1961, and Köhler & Moyà-Solà, 2004, on *Myotragus*; Accordi & Palombo, 1971, and Palombo & Giovinazzo, 2005, on *Elephas falconeri*; Willemsen, 1980, on *Lutrogale cretensis*; Palombo & Giovinazzo, 2004, on *Cynotherium*, Falk *et al.*, 2005, on *Homo floresiensis*). Dechaseaux (1961) noted that *Myotragus* had an extensive neocortex and a large frontal lobe, while Köhler & Moyà-Solà (2004) stated that it underwent a significant reduction in relative brain size. Falk *et al.* (2005) reported that the brain size of *Homo floresiensis* is considerably smaller than that of late *Homo* spp. The opposite result, a relativly larger brain, has been reported in the case of the dwarf elephant of Sicily, *E. falconeri* (Accordi & Palombo, 1971; Palombo & Giovinazzo, 2005). Palombo & Giovinazzo (2004) suggested that the brain of *Cynotherium* from Dragonara Cave was not relatively larger than that of *Canis lupus* or *Canis mesomelas*. So, in contrast to the well established patterns of relative brain size evolution in mainland mammals, only a few and contradictory results have been published about the brain of insular forms.

The relatively large neurocranium of *Cynotherium* (Malatesta, 1970; Lyras *et al.*, 2006; Lyras & Van der Geer, 2006) raises the question as to whether its brain was equally large. In order to answer this question I followed Radinsky's (1967) method of comparing the brain size with the area of the foramen magnum. The volume of the endocast of *Cynotherium* SASN -CB-84-8022 is 84 cm^3. The width of the foramen magnum is 1.270 cm and its height is 1.804 cm. Using these values in Radinsky's (1973) equation – log (endocranial volume) = 1.54 + 1.48 log (foramen magnum area) – we see that the endocranial volume of *Cynotherium* (log 84 = 1.924) is very close to the expected endocranial volume (1.54 + 1.48 log 1.804 = 1.919). In other words, *Cynotherium* has the brain size of living mainland canids of comparable body mass.

Summary and conclusions concerning the brain of Caninae

Remarks — The Caninae appeared in the Oligocene with the genus *Leptocyon*, but the earliest available endocast is much younger, from the Early Miocene. The external brain anatomy of this early *Leptocyon* is comparable to that of *Hesperocyon* and *Archaeocyon*: the frontal lobes are very low; the overlap of the cerebellum is small; and there are only two main sulci, the coronolateral, which runs almost parallel to the longitudinal fissure, and the suprasylvian, which forms a wide vertical arch on the lateral side of the brain. This early *Leptocyon* has a small presylvian sulcus and a small rostral part of the coronolateral sulcus, which is clearly separated from the occipital part by a small inward turn of the sulcus.

The next Caninae endocast is from Late Miocene *Leptocyon.* Its brain has a more overlapped cerebellum and a more twisted cerebellar vermis than any canid of its time or earlier. Its sulcal pattern is, in general, similar to that of modern Caninae. The most important distinction from later Caninae is that the region medial to the coronal sulci is very narrow.

During the Mio-Pliocene Caninae radiation, the evolution of the cerebrum took place mainly in the region medial to the coronal sulci, in the form of different sulcal patterns, and in the region rostral to presylvian sulcus, in the shape and relative size of

the proreal gyrus. During the radiation, several sulcal patterns and types of proreal gyri evolved.

One early outcome of this radiation was the genus *Vulpes*. Its earliest known species, *Vulpes stenognathus*, has a brain comparable to that of modern *Vulpes*. In all living *Vulpes* species, the coronal sulci form a pentagonal outline on the dorsal surface of the cerebrum and the proreal gyrus is short. The arctic fox, *Vulpes lagopus*, differs somewhat from the other foxes in that the frontal lobes are higher and the proreal gyrus is better developed than in any other fox. The coronal sulci of two other foxes, *Urocyon cinereoargenteus* and *Otocyon megalotis*, form a heart-shaped outline. The proreal gyrus in *Urocyon* species is small and similar to the one seen in *Vulpes*. In *Otocyon* the length of the cruciate sulcus, and the length and the bilateral constriction of the proreal gyrus, are variable.

Another outcome of this radiation was the dog-like species (Canini). The brain of their earliest representative, *Eucyon davisi*, is more primitive than that of *Canis* and in some aspects comparable to that of *Vulpes*. The proreal gyrus is bilaterally constricted, but it is shorter than the one in similar-sized living *Canis*. The expansion of the sigmoid gyri is comparable to that of *Vulpes*, the pyriform lobe is more exposed than in jackals, the ectolateral sulcus is not connected with the suprasylvian sulcus and there is no or only a very shallow endolateral sulcus.

The genus *Nyctereutes* appeared in Eurasia during the Pliocene. The endocranial casts of Pliocene *Nyctereutes* have a long and narrow proreal gyrus, and the coronal sulci form a heart-shaped outline on the dorsal surface of the cerebrum. These two features of *Nyctereutes* resemble *Cerdocyon* and give further support to the phylogenetic schemes that consider the two taxa to be related.

During the Pleistocene the evolutionary history of *Nyctereutes* was characterized by a reduction in size. However, living *Nyctereutes* differs not only in size from its Pliocene ancestors, but also in certain cranial and neural features. The most important distinction in its external brain anatomy is the form of the proreal gyrus, which is broader and lower in the living species than in the Pliocene forms. Also, the skull of the living raccoon dogs has a shorter rostrum and the caudal palatine border extends further caudally than in its Pliocene relatives. Since similar changes occur in the brain of other canids with short rostra (including *Lycaon*, *Enhydrocyon*, *Borophagus* and *Speothos*), it is possible that these changes in the form of the proreal gyrus of *Nyctereutes* are due to the shortening of their rostrum.

There is a considerable variation in the general shape of the brain of the South American Caninae. This is due to the general shape of the skulls, which are equally variable. Apart from these differences, all South American canids have well developed proreal gyri (although the exact shape and size shows a considerable variation) and three basic outlines of the sulcal patterns of the coronal and ansate sulsi: heart-shaped (*Lycalopex culpaeus*), parenthesis-like outline (the rest of the living *Lycalopex* species and *Dusicyon australis*) or orthogonal (*Atelocynus* and *Speothos*). In *Chrysocyon brachyurus*, the posterior sigmoid gyrus extents laterally more than the anterior sigmoid gyrus.

The cerebral hemispheres of all *Canis*-like species (members of *Canis*, *Cuon*, *Cynotherium*, *Lycaon* and *Xenocyon*) expand abruptly behind the presylvian sulcus. The proreal gyrus is long and bilaterally constricted, more so than in any other canid group. Additionally, in these species the sigmoid gyri expand very abruptly (with the exception of *Canis edwardii*). This creates an orthogonal or oblong outline of the ansate and coronal

sulci on the dorsal surface of the cerebrum. This expansion is smaller in the Pliocene *Canis lepophagus*, while the Early and Middle Pleistocene *Canis* had brains with the modern morphology.

The external brain anatomy of the dwarf *Cynotherium sardous* (the only known fossil insular canid) is comparable to that of its mainland relatives. So, despite the fact that this canid evolved in an isolated island environment for more than 700,000 years (Lyras & Van der Geer, 2006), its brain did not change as the rest of its body did (whose size and relative proportions were considerably modified).

Brain evolution and craniodental specialization

Brain and skull specialization — There is a common belief that species with larger or more complex brains are generally more intelligent and thus more successful. This idea was promoted by early authors (such as Marsh, 1879) and, despite negative criticisms (Edinger, 1962; Radinsky, 1982), it is still a widespread idea (Jerison, 1973; Colbert & Morales, 1991; Hone & Benton, 2005). There are many studies that show that species with larger brains perform better on intelligence tests (for example, Glickman & Sroges, 1966; Ehrlich *et al.*, 1976; Riddell & Corl, 1977). However, there is no work that clearly indicates that increased intelligence leads to increased fitness.

The present study compares the specialization of the brain (as it is revealed in the endocasts) with the craniodental specialization of canids. The purpose of this comparison is to determine if there is any correlation between the rates of brain and craniodental evolution. Of course, it is not only the skull and teeth that evolve. Important modifications also take place in the rest of the body. However, due to the lack of a good fossil record of postcranial elements, it is necessary to focus on the skull. Therefore, the modifications of the skull and teeth should be considered as the minimum adaptations that can be measured, as in many cases the addition of postcranial adaptations would have increased the calculated specialization.

Since the main goal of this comparison is to investigate evolutionary processes, it will focus on a few genera that represent actual phylogenetic lineages. This approach considerably limits the amount of the available material since it is restricted not only to species from which complete endocasts are available (of which there are not many), but also to species that belong to the same evolving lineages. I have followed the common approach of comparing heterogeneous groups formed by animals that lived in successive geochronological time intervals. That increases the amount of available material; however, successive assemblages do not necessarily sample the same evolving lineages (Radinsky, 1975).

Principal component analysis of craniodental characters in canids — Van Valkenburgh & Koepfli (1993) took 30 craniodental measurements on 27 species of modern canids and used them to produce a set of ratios that reflect three aspects of craniodental function: relative tooth size or shape; jaw muscle leverage; and relative rigidity of the dentary. A discriminant analysis of these ratios easily separated hypercarnivores as having relatively deep jaws, large canine and incisor teeth, reduced molar grinding areas and longer shearing blades on their lower carnassials (Van Valkenburgh & Koepfli, 1993). Later, Van Valkenburgh *et al.* (2003) compared the craniodental morphology of living canines,

living hyaenids and borophagines. Their comparison was based on the results of a principal component analysis that was performed on a combination of the ratio data from the above-mentioned paper and new ones produced in a similar way from the two other groups. In a more recent paper, Van Valkenburgh *et al.* (2004) undertook a similar analysis in Borophaginae and Hesperocyoninae, but, due to the fragmentary and incomplete character of most fossil specimens, they focused on only three indices that were more simplified.

In the present study, a principal components analysis was performed with 13 out of the 16 ratios originally developed by Van Valkenburgh & Koepfli (1993) (see Table 1). The other three ratios were not used because complete specimens are rare in the fossil record. The results of the analysis are similar to that of Van Valkenburgh *et al.* (2003), although there are slight diferences in the importance of the factor scores and variances, mainly due to the addition of species (Hesperocyoninae, some Borophaginae and fossil Caninae).

The first principal component (PC1) represents 58 % of the total variance. The most significant variables of the first component are relative incisor size (I3), relative rostral breath (C1C1), jaw rigidity (IxP4) and the length of the m1 trigonid (M1BS). The second axis (PC2) accounts for another 14 % of the total variance, with the most important variables being the relative upper molar grinding area (RUGA) and the relative size of m2 (M2S).

The first principal component (PC1) can be used to infer hypercarnivorous adaptation. Species with relatively larger incisors, broader muzzles, deeper jaws and longer m1 trigonid have high positive scores on this component, whereas those with less hypercarnivorous features have low negative scores on this axis and positive scores on the second (Fig. 45).
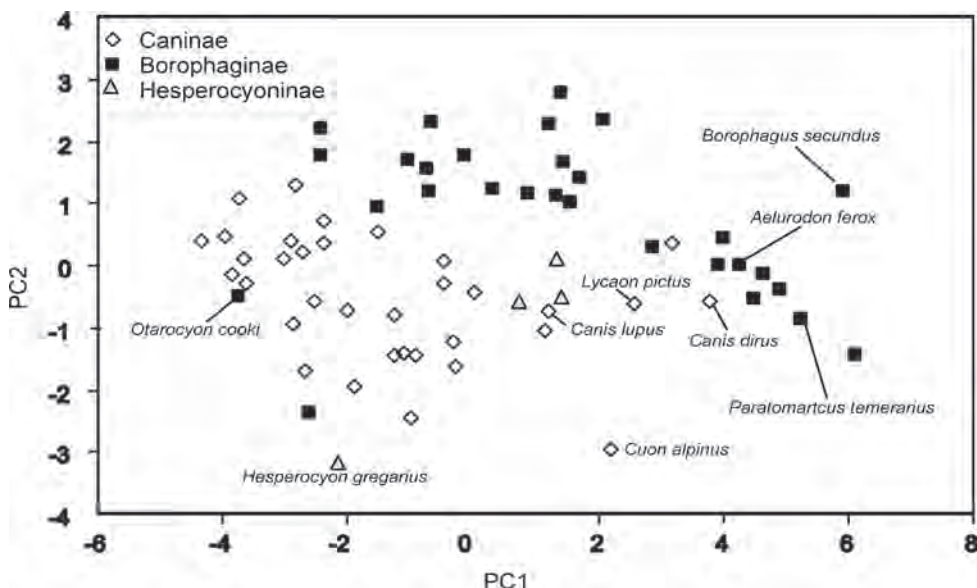

Fig. 45. Scatter diagram of the first two principal components of canids (for further details see Appendix 4.2).

Brain and skull evolution in canids — The first canid group that evolved towards hypercarnivory was the Hesperocyoninae. The trend towards hypercarnivory can be best seen in a hypothesized lineage from *Mesocyon* to *Cynodesmus* and then to *Enhydrocyon* (for more details, see the phylogenetic analysis of Wang, 1994). Of these genera, endocranial material is known from *Mesocyon coryphaeus*, *Cynodesmus thooides* and *Enhydrocyon stenocephalus*. Unfortunately, there is no complete mandible known of *E. stenocephalus*, so it cannot be included in the principal component analysis. However, considering its overall morphology (Fig. 14), it is obvious that *Enhydrocyon* was more adapted towards hypercarnivory than either *Mesocyon* or *Cynodesmus*.
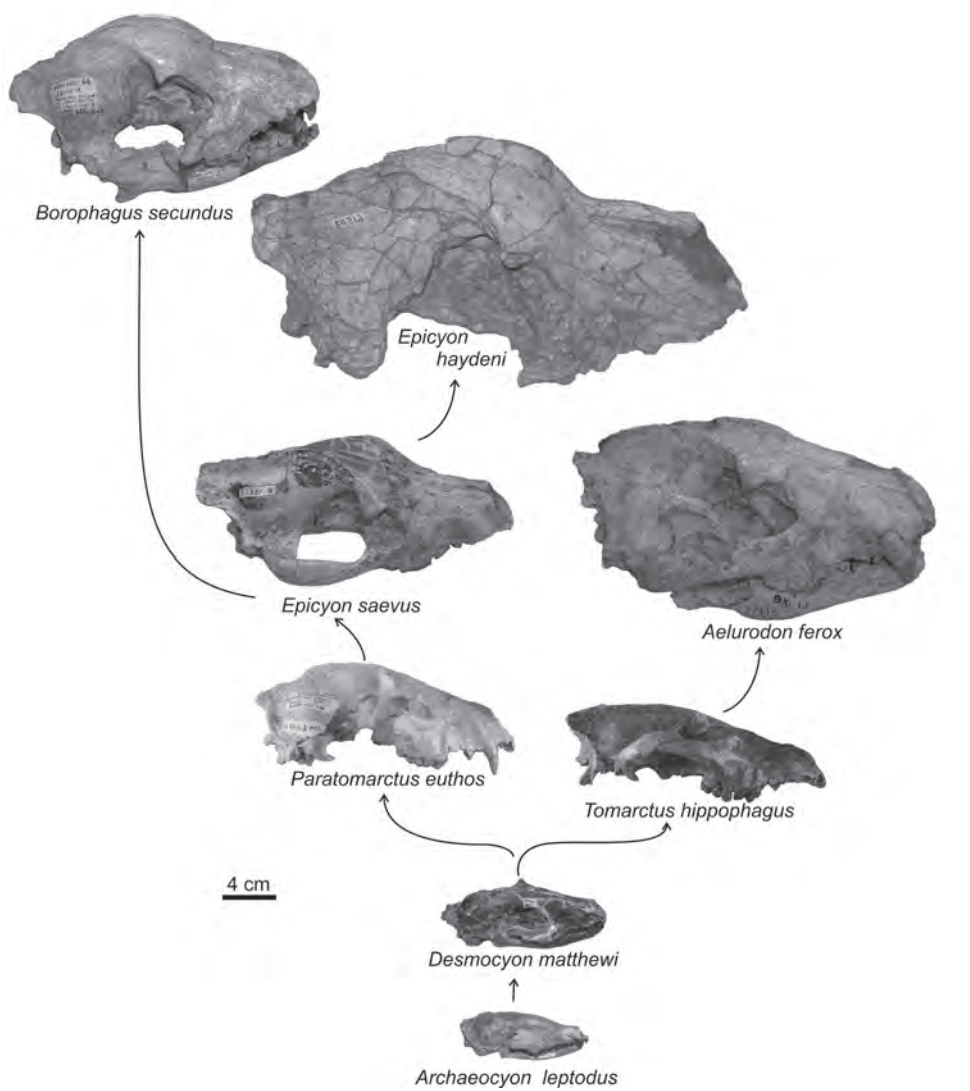

Fig. 46. Simplified phylogenetic diagram of two Borophaginae clades (Aelurodontina and Borophagina), based of the analysis of Wang *et al.* (1999).

The brain of *Enhydrocyon stenocephalus* is not more fissurated than that of *Mesocyon* or *Cynodesmus* (see above). The sulcal length index of *E. stenocephalus* is practically the same as that of *Mesocyon*. There are some differences between the brains of *Mesocyon* and *Enhydrocyon*, but they have to do with general shape (the brain of *E. stenocephalus* is more compressed anteroposteriorly) and are related to packing problems due to shortening of the skull (Fig 14).

The second canid group is the Borophaginae, that is adequately represented by both endocasts and skulls, and therefore can be explored in more detail. A series of endocasts and skulls from *Archaeocyon* to *Desmocyon,* and then to *Tomarctus-Aelurodon*, *Paratomarctus-Borophagus* and *Paracynarctus*, illustrates the increase in the degree of cortical folding and the craniodental specialization in Borophaginae (Figs. 16-25, 46). *Desmocyon matthewi* has the same sulci as *Archaeocyon leptodus*, yet they are longer and there is also a small lateral expansion of the rostral part of the coronolateral sulcus. As a result, the gyral length index of *Desmocyon matthewi* is almost twice that of in *Archaeocyon leptodus*.

The later Borophaginae are represented by *Paracynarctus sinclairi, Tomarctus hippophagus* and *Paratomarctus temerarius.* Their brains show greater development of the sigmoid gyri and an even greater lateral expansion of the coronal sulci. The somatic-sensory and motor-control cortical areas of living carnivores are located on the sigmoid gyri (Welker & Campos, 1963). Therefore, it is possible that the expansion of the sigmoid gyri is related to the development of better sensorimotor control abilities in those species (Radinsky, 1973). The development of this cortical area, which took place rather quickly, just after the end of Hemingfordian (16 Ma), was an important step towards the greater complexity of the Borophaginae brain. As a result of this expansion, the total sulcal length was increased and the later canids are located further to the right in Figure 47.
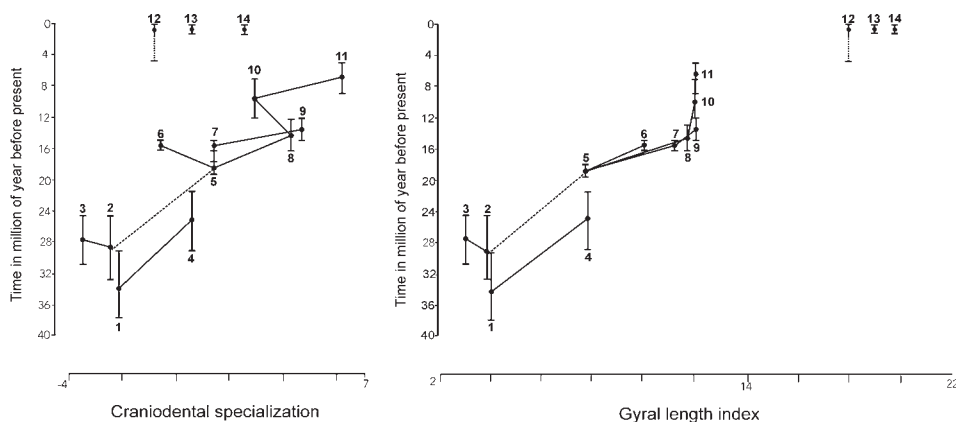

Fig. 47. Craniodental specialization (as it is expressed by the first principal component - PC1 - of the analysis) and gyral length index (the ratio between the total length of the superficially exposed gyri and the cubic root of the endocast volume) plotted against the species temporal distribution. The solid lines conect species which are phylogenticaly related, the dotted line indicates a more distant relationship. 1, *Hesperocyon gregarius*; 2, *Archaeocyon leptodus*; 3, *Otarocyon cooki*; 4, *Mesocyon* sp.; 5, *Desmocyon matthewi*; 6, *Paracynarctus sinclairi*; 7 *Tomarctus hippophagus*; 8, *Paratomartus temerarius*; 9, *Aelurodon ferox*, 10, *Epicyon saevus*; 11, *Borophagus secundus*; 12, *Vulpes vulpes*; *Canis lupus*; 14, *Lycaon pictus*. See Appendix 4.2 for data and specimens used for the PC1 and Appendix 3 for the gyral length index.

Tomarctus is phylogeneticaly related to *Aelurodon,* and *Paratomarctus* is phylogeneticaly related to *Epicyon* and *Borophagus*. These two lineages of large-sized hypercarnivorous canids have brains that are not more convoluted than their ancestors. Thus, although there was a leap forward from *Desmocyon* to the later borophagines, very few changes took place in the brain after that point.

The last canid group is Caninae, in which brain is relatively larger and more fissurated than that of the other two groups (Fig. 47). There is the even more lateral expansion of the sigmoid gyri and the development of the cortex anterior to the presylvian sulcus. The Caninae are represented by relatively unspecialized members. The only examples toward hypercarnivory are some large sized *Canis* spp., *Lycaon*, *Xenocyon*, *Speothos* and *Ducicyon*. Their brains are not more convoluted than their less specialized relatives.

The importance of brain in carnivore evolution — Based on the data presented above, the degree of cortical folding evolved in a punctuated manner. Brains become more fissurated with the expansion of particular areas, such as the sigmoid gyri and the prefrontal cortex. According to the model of Uylings & Van Eden (1990), particular cortical fields rapidly became more developed and better separated (Fig. 48). It is reasonable to assume that the addition of new areas can be beneficial for the establishment and evolution of a species. However, it is not possible to say if such development of the brain is more crucial than any other development such as of the teeth. What can be demonstrated is that such brain development took place twice in canids, in Borophaginae during the Middle Miocene and in the Caninae during the Late Miocene – Pliocene. In both cases, it coincides with a successful establishment of the group as evidenced by their extensive radiation. It should be noted, however, that the more complex brains did not prevent the Borophaginae from going extinct, nor other groups, like the Nimravidae (which had a rather complex brain for their time, see Radinsky 1975).

An interesting case is the stasis in brain evolution during the development of hypercarnivorous dietary adaptations. Such cases are seen in the presumable transitions from *Mesocyon* to *Enhydrocyon*, from *Paratomarctus* to *Borophagus*, from *Tomarctus* to *Aelurodon.* A possible explanation for this phenomenon could be that this stasis is related to energetic constraints.

Among living terrestrial carnivores, half of species larger than about 21 kg prey on taxa as large or larger than themselves, whereas smaller carnivores can subsist on much smaller prey, such as invertebrates and rodents (Carbone *et al.*, 1999). Further, during the transition to taking larger prey, carnivores evolve larger size and specific craniodental adaptations. These trends led Van Valkenburgh *et al.* (2004) to suggest that evolution towards hypercarnivory reflects energetic constraints imposed by tradeoffs

lower mammals   higher mammals

Fig. 48. Schematic diagram of the evolution of cerebral cortex redrawn from Uylings & Van Eden (1990). Squares represent cortical fields. In the "primitive" mammals the cortical fields are smaller and have a considerable overlap. In the "higher" mammals the cortical fields are larger and are better separated. According to this model, during cortical evolution there is an expansion and, at the same time, a better separation of cortical fields.

between foraging effort and food acquired. Nervous tissue is one of the most energetically costly tissues in terms of both development and maintenance (Armstrong *et al.*, 1995; Kaas, 2000; Köhler & Moyà-Solà, 2004). Because hunting large prey requires more energy (Carbone *et al.*, 2007), it contradicts the development of more complicated and, therefore, energetically more expensive brains.

Conversely, larger or more complicated brains have many advantages, including greater efficiency of the sensory organs and better motor control. However, in the cases presented above, what was obviously more important was the development of craniodental adaptations rather than the development of the brain. Therefore, although there is a general selective pressure towards the common development of complex brains (Jerison, 1973, 1990, 1991; Radinsky, 1978b), in these examples development occurred primarily in the teeth and skulls.

Summary — Evolution within some canid clades shows a clear tendency towards hypercarnivory, which means that they increased the percentage of meat in their diet. The representatives of these evolutionary lineages evolved craniodental characters - deep jaws, large canine and incisor teeth, reduced molar grinding areas - that were related to the general tendency of hypercarnivores to prey on large-bodied animals.

During the transition to hypercarnivory there was stasis in brain evolution in Canidae, from *Mesocyon* to *Enhydrocyon*, from *Paratomarctus* to *Borophagus* and from *Tomarctus* to *Aelurodon*. Previous work concluded that the development of hypercarnivorous craniodental characters is related to energetic constraints. Alternately, some studies indicate that the neural tissue is energetically one of the most expensive. Therefore, based on these conclusions and on the data of the present study, it might very well be possible that the stasis in brain evolution is due to energetic constraints. In other words, evolution favours the development of the skull and teeth (in order to facilitate the predation on larger animals) more than the development of brain.

Conclusions

In order to investigate the evolution of the canid brain, casts of the brain cavity (endocranial casts or endocasts) from Recent and fossil species were studied. The study of fossil brains is limited to their external anatomy. However, cortical folding, although just an external feature, can be used to infer internal differences between brains.

The examination of brain morphology is focused on cortical folding, which was studied descriptively (the sulcal pattern) and quantitatively (the length of the superficially exposed gyri). Further, the degree of cortical folding was compared with some particular craniodental parameters that are informative to infer dietary adaptations.

The evolution of general brain morphology and sulcal pattern — Canid brain evolution followed three independent, yet convergent paths. This occurred because the evolutionary history of the family is characterized by an early tripartite separation, which gave rise to three independent evolutionary radiations. Each group began with a simple brain, which had pear-shaped cerebral hemispheres, small temporal and frontal lobes, a widely exposed cerebellum and a straight cerebellar vermis. The evolution of the three subfamilies led to the development of brains with similar morphology and

sulcal pattern. The extent to which these evolutionary changes took place is different in the three subfamilies. The brain of the Hesperocyoninae (the first to radiate and also the first to go extinct) did not evolve so much as that of Borophaginae (the second group that radiated) and Borophaginae did not reach the evolutionary stage seen in Caninae today (Caninae started to radiate relatively recently).

Prohesperocyon — The evolutionary history of canids began with *Prohesperocyon*, a form that was transitional from Miacidae to Canidae. The cerebral cortex of this genus had only two sulci (coronolateral and suprasylvian) and the cerebellum, which was widely exposed, had a straight cerebellar vermis and small cerebellar hemisphere.

Hesperocyoninae — The oldest member of the subfamily is *Hesperocyon.* Its brain is similar to that of *Prohesperocyon.* The most important difference is that *Hesperocyon* had more globular cerebral hemispheres, something that is related to differences in their cranial proportions (*Hesperocyon* is more brachycephalic).

The cerebral hemispheres of the later Hesperocyoninae, *Mesocyon, Cynodesmus* and *Enhydrocyon,* had a more extensive cerebral cortex. *Cynodesmus* had one additional sulcus (the ectosylvian), *Mesocyon* had yet another (the ectolateral) and *Enhydrocyon* had four sulci (coronolateral, suprasylvian, ectosylvian and presylvian).

Osbornodon fricki was one of the last Hesperocyoninae. Its brain was far more advanced than that of any earlier member of the family, as it had a small sylvian sulcus and the rostral part of the coronolateral sulci bow out laterally, indicating a separation between the coronal and lateral parts. Early signs of such an arrangement can be seen in *Mesocyon* and *Cynodesmus* and even in a few *Hesperocyon* specimens; however, it is in *O. fricki* that it becomes distinct.

Borophaginae — Early members of this subfamily (*Archaeocyon, Otarocyon, Rhizocyon*) had brains similar to that of *Hesperocyon.* An important change took place in two later Borophaginae, *Phlaocyon* and *Desmocyon,* which developed three major sulci (coronolateral, ectolateral and ectosylvian).

Desmocyon gave rise to all later Borophaginae, including *Paracynarctus, Tomarctus* and *Paratomarctus.* The genus *Paracynarctus* had five major sulci (the coronolateral, ectolateral, suprasylvian, ectosylvian and presylvian), a very well formed orbital gyrus and possibly a small Sylvian sulcus. *Tomarctus* and *Paratomarcus* had, in addition to the sulci mentioned above, a cruciate sulcus and a very well formed Sylvian sulcus. The cruciate sulcus, and commonly the cortex around that sulcus, was better developed in *Paratomarctus* than in *Tomarctus.* These two genera gave rise to two evolutionary lineages of hypercarnivorous canids of large size (such as *Aelurodon, Epicyon* and *Borophagus*). The evolution of the brain continued in these lineages without any radical innovations.

Caninae — As in the case of the other two subfamilies, the earliest Caninae had a relatively simple brain. The major evolutionary radiation of the subfamily began in the Late Miocene-Pliocene, when the first representatives of the basic Caninae lineages appeared. During this period, the evolution of the cerebral hemispheres took place mainly in the cortex medial to the coronal sulci (sigmoid gyri) and rostral to the presylvian sulci (proreal and orbital gyri). The expansion of these gyri coincided with the beginning of the Caninae adaptive radiation. Thus, different sulcal patterns appeared in each major evolutionary line of the subfamily.

Vulpes has a short proreal gyrus and small expansion of the sigmoid gyri; the coronal sulci form a pentagonal outline on the dorsal surface of the cerebrum. *Urocyon* has

a short proreal gyrus and the coronal sulci form a heart-shaped outline. The lateral expansion of the sigmoid gyri in *Eucyon* is also very small; however, the proreal gyrus is longer. The species of *Canis, Cuon, Cynotherium, Lycaon* and *Xenocyon* have a long and bilaterally constricted proreal gyrus, and the sigmoid gyri expanded very abruptly. In these genera the coronal and ansate sulci form an orthogonal outline on the dorsal surface of the cerebrum; the only exception is *Canis edwardii*, in which the coronal sulci form a parenthesis outline. All the South American Caninae have a relatively long proreal gyrus (although its exact size and form presents a considerable variation) and three basic patterns of the coronal sulcal outline, a parenthesis, heart-shaped and orthogonal. The Pliocene *Nyctereutes* have a long and bilaterally constricted proreal gyrus and the coronal sulci forming a heart-shaped outline on the dorsal surface of the cerebrum. The outline of the coronal sulci is the same in the living *Nyctereutes;* however, the proreal gyrus is broader and lower than that of its Pliocene ancestors. This is related with the shortening of its skull length during the last 2 million years.

Relation between brain shape and length of the rostrum — The brains of species with short rostra have massive frontal lobes. In these species the posterior border of the palate extends more caudally than that of their close relatives with long rostra. The posterior position of the posterior palatine border affects the position of the cribriform plate, which also moves backwards. As a result, the olfactory bulbs (which are housed behind the cribriform plate) are pushed caudally, thereby causing the anterodorsal compression of the anterior lobes of the brain. In most cases, the shortening of the face is related to adaptation towards hypercarnivory in order to prey on larger animals (such as in *Enhydrocyon, Borophagus* and *Speothos*). In one case, that of *Nyctereutes*, the shortening of the rostrum took place without adaptation to a more carnivorous diet. However, in this case as well, the shortening of the rostrum had an effect on the shape of the anterior part of the brain.

Parallel evolution of the sulcal pattern — The similar sulcal patterns seen in living carnivore families evolved independently in each family. A more extensive study of the evolutionary history of the brain in Canidae shows that the same phenomenon took place in independent lineages within the family. The cruciate sulcus appeared independently four times within Canidae; once in Hesperocyoninae (in *Osbornodon*), twice in Borophaginae (in *Phlaocyon* and *Tomarctus*) and once in Caninae (in *Leptocyon*). A similar parallel development occurred in the Sylvian, endolateral, ectolateral and ectosylvian sulci (three times within the family).

Cortical folding and craniodental specialisation — Some canid lineages evolved large size and particular craniodental characters, such as deep jaws, large canine and incisor teeth and reduced molar grinding areas, which allowed them to prey on large-bodied animals. In these cases there is stasis in brain evolution. A possible explanation for this phenomenon may be that carnivores that prey on large animals expend relatively more energy during predation. Since neural tissue is energetically one of the most expensive tissues, the evolution of the brain may be too costly to occur. Therefore, despite the general trend towards larger and more complicated brains, and despite the obvious advantages of a more complex brain, in these particular cases the evolution of the teeth and skulls was of greater importance than that of the brain.

Acknowledgements

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Appendix 1

Studied endocasts from fossil canids and the reference on which the attribution of the taxon was based.

Species	Number of skull	Number of endocast	Stratigraphic position	Region	Reference
Aelurodon ferox	F:AM 61746	FMNH PM 58965	Middle Miocene	Nebraska, U.S.A.	Wang et al. (1999)
Aelurodon ferox	F:AM 25230	FMNH PM 58951	Middle Miocene	Nebraska, U.S.A.	Wang et al. (1999)
Aelurodon taxoides	UNSM 25933	FMNH PM 58969	Middle Miocene	Nebraska, U.S.A.	Wang et al. (1999)
Aelurodon taxoides	F:AM 67015	FMNH PM 58971	Middle Miocene	Nebraska, U.S.A.	Wang et al. (1999)
Archaeocyon leptodus	F:AM 49031	–	Late Oligocene	Wyoming, U.S.A.	Wang et al. (1999)
Archaeocyon leptodus	F:AM 49033	–	Late Oligocene	Wyoming, U.S.A.	Wang et al. (1999)
Borophagus dudleyi	MCZ 3688	FMNH PM 58963	Late Miocene	Florida, U.S.A.	Wang et al. (1999)
Borophagus secundus	F:AM 61649	FMNH PM 58954	Late Miocene	Kansas, U.S.A.	Wang et al. (1999)
Canis armbrusteri	F:AM 67286	F:AM 67286	Pleistocene	Florida, U.S.A.	AMNH catalogue
Canis dirus	FMNH PM 394	FMNH PM 394	Pleistocene	California, U.S.A.	FMNH catalogue
Canis edwardii	F:AM 63100	F:AM 63100	Pliocene	Arizona, U.S.A.	AMNH catalogue
Canis lepophagus	WT 760	AMNH 104782	Pliocene	Texas, U.S.A.	AMNH catalogue
Canis mosbachensis	IQW 1982/180512 (mei 17572)	-	Early Pleistocene	Thuringia, Germany	Sotnikova (2001)
Carpocyon webbi	F:AM 61328	FMNH PM 58964	Middle Miocene	Nebraska, U.S.A.	Wang et al. (1999)
Cynodesmus thooides	YPM-PU 10412	–	Late Oligocene	Montana, U.S.A.	Wang (1994)
Cynodesmus thooides	F:AM 63373	–	Late Oligocene	South Dakota, U.S.A.	Wang (1994)
Cynotherium sardous	SASN CB-84-8022	SASN CB-84-8022	Late Pleistocene	Sardinia, Italy	Lyras et al. (2006)
Desmocyon matthewi	F:AM 61300	FMNH PM 58983	Late Miocene	Nebraska, U.S.A.	Wang et al. (1999)
Enhydrocyon stenocephalus	FMNH PM 59036	USNM 7745	Late Oligocene	Oregon, U.S.A.	Wang (1994)
Epicyon haydeni	F:AM 61476A	FMNH PM 58968	Late Miocene	Kansas, U.S.A.	Wang et al. (1999)
Epicyon haydeni	F:AM 61474	FMNH PM 58976	Late Miocene	Kansas, U.S.A.	Wang et al. (1999)
Epicyon saevus	F:AM 67331	FMNH PM 58970	Middle Miocene	Nebraska, U.S.A.	Wang et al. (1999)
Eucyon davisi	F:AM 63005	NNM RGM 195215	Late Miocene	Arizona, U.S.A.	Tedford (pers. comm. 2004)
Eucyon davisi	F:AM 97057	-	Early Pliocene	Shanxi, China	Tedford & Qiu (1996)
Hesperocyon gregarius	F:AM 50277	-	L. Eocene - E. Oligocene	Wyoming, U.S.A.	Wang (1994)
Hesperocyon gregarius	F:AM 76518	-	Early Oligocene	Nebraska, U.S.A.	Wang (1994)
Hesperocyon gregarius	F:AM 76520	-	Early Oligocene	Nebraska, U.S.A.	Wang (1994)
Hesperocyon gregarius	AMNH 1408	-	Early Oligocene	South Dakota, U.S.A.	Wang (1994)

Species			Epoch	Location	Reference
Hesperocyon gregarius	AMNH 85888	-	Early Oligocene	Nebraska, U.S.A.	Wang (1994)
Hesperocyon gregarius	F:AM 76166	-	Early Oligocene	Wyoming, U.S.A.	Wang (1994)
Hesperocyon gregarius	YPM 10067	-	Early Oligocene	South Dakota, U.S.A.	Wang (1994)
Hesperocyon sp.	AMNH 39476	-	Early Oligocene	South Dakota, U.S.A.	Present work
Hesperocyon sp.	AMNH 129176	-	Early Oligocene	Wyoming, U.S.A.	Present work
Hesperocyon sp.	AMNH 9766	-	Early Oligocene	South Dakota, U.S.A.	Present work
Leptocyon gregorii	F:AM 49063	FMNH PM 58961	Late Miocene	Wyoming, U.S.A.	Tedford (pers. comm. 2004)
Leptocyon sp.	F:AM 49433	NNMRGM 195222	Late Miocene	South Dakota, U.S.A.	Tedford (pers. comm. 2004)
Mesocyon coryphaeus	AMNH 6920	AMNH 6920	Oligocene	Oregon, U.S.A.	Wang (1994)
Mesocyon sp.	–	AMNH 6946	Late Oligocene	Oregon, U.S.A.	Radinsky (1973)
Microtomarctus confertus	F:AM 27534	FMNH PM 58967	Middle Miocene	California, U.S.A.	Wang et al. (1999)
Nyctereutes megamastoides	GIN	NNM RGM 195220	Late Pliocene	Beregovaya, Russia	Sotnikova (pers. comm. 2004)
Nyctereutes megamastoides	AMPG(V)-Σ 384	NNM RGM 195221	Late Pliocene	Thessaly, Greece	Athanassiou (1998)
Nyctereutes megamastoides	AUT DFN 17	-	Late Pliocene	Macedonia, Greece	Koufos (1993)
Nyctereutes sinensis	F:AM 96750	NNM RGM 195223	Late Pliocene	Shanxi, China	Tedford (pers. comm. 2004)
Nyctereutes sinensis	F:AM 96792	NNM RGM 195218	Late Pliocene	Shansi, China	Tedford (pers. comm. 2004)
Nyctereutes sinensis	F:AM 22336	NNM RGM 195219	Late Pliocene	Shansi, China	Tedford (pers. comm. 2004)
Nyctereutes tingi	F:AM 96757	NNM RGM 195216	Late Pliocene	Shansi, China	Tedford & Qiu (1991)
Nyctereutes tingi	AUT MEL-1	-	Late Pliocene	Macedonia, Greece	Koufos (1997)
Osbornodon fricki	F:AM 67098	FMNH PM 58964	Early Miocene	Nebraska, U.S.A.	Wang (1994)
Otarocyon cooki	F:AM 49043	FMNH PM 58987	Late Oligocene	Wyoming, U.S.A.	Wang et al. (1999)
Paracynarctus sinclairi	F:AM 61009	FMNH PM 58973	Middle Miocene	Nebraska, U.S.A.	Wang et al. (1999)
Paratomarctus sp.	–	CSCLA 207	Middle Miocene	California, U.S.A.	Present work
Paratomarctus temerarius	F:AM 61070	FMNH PM 58958	Middle Miocene	Nebraska, U.S.A.	Wang et al. (1999)
Phlaocyon marslandensis	UNSM 26153	FMNH PM 58977	Early Miocene	Arizona, U.S.A.	Wang et al. (1999)
Prohesperocyon wilsoni	AMNH 127172	TMM 40504-126	Late Eocene	Texas, U.S.A.	Wang (1994)
Lycalopex culpaeus	AMNH 27904	NNM RGM 195227	Pleistocene	Equador	Tedford (pers. comm. 2004)
Rhizocyon oregonensis	AMNH 6879	–	Late Oligocene	Oregon, U.S.A.	Wang et al. (1999)
Tomarctus brevirostris	F:AM 61179C	FMNH PM 58957	Middle Miocene	Arizona, U.S.A.	Wang et al. (1999)
Tomarctus hippophagus	F:AM 61179A	NNM RGM 195225	Middle Miocene	Arizona, U.S.A.	Wang et al. (1999)
Tomarctus hippophagus	F:AM 61179B	FMNH PM 58959	Middle Miocene	Arizona, U.S.A.	Wang et al. (1999)
Vulpes stenognathus	F:AM 49284	FMNH PM	Late Miocene	Nevada, U.S.A.	Tedford (pers. comm. 2004)
Xenocyon lycaonoides	GIN 3722-144	NNM RGM 195206	Middle Pleistocene	Siberia, Russia	Sotnikova (pers. comm. 1998)

Appendix 2

Studied endocasts from living and recently extinct canids. See materials and methods section for institutional abbreviations.

Species	Number
Atelocynus microtis	AMNH(M) 76579
Canis aureus	NNM RMNH cat. ost. no. b.
Canis aureus	NNHM-Z 11597/378/3
Canis adustus	NNM RMNH cat. no. h.
Canis latrans	NNM RMNH cat. no. c.
Canis lupus	NNM RMNH cat. no. l.
Canis lupus	FMNH 7619
Canis mesomelas	NNM RMNH reg. no. 25891
Canis mesomelas	NNM RMNH cat. no. l.
Canis mesomelas	FMNH 85508
Canis mesomelas	FMNH 146290
Canis rufus	AMNH 112
Canis simensis	NNM RMNH cat. no. b.
Canis simensis	FMNH 146291
Cerdocyon thous	NNM RMNH cat. no. b.
Cerdocyon thous	AMNH(M) 14853
Chrysocyon brachyurus	NNM RMNH cat. no. a.
Chrysocyon brachyurus	FMNH 146295
Chrysocyon brachyurus	FMNH 146296
Cuon alpinus	NNM RMNH reg. no. 1546
Cuon alpinus	FMNH 91246
Dusicyon australis	NNM RMNH reg. no. 19111
Dusicyon australis	NNM RMNH reg. no. 19112
Leopardus pardalis	FMNH 90023
Leptailurus serval	FMNH 90022
Lycaon pictus	NNM RMNH cat. no. c.
Lycaon pictus	FMNH 146299
Nyctereutes procyonoides	NNM RMNH cat. no. d.
Nyctereutes procyonoides	NNM RMNH cat. no. h.
Nyctereutes procyonoides	NNHM-P 6433
Nyctereutes procyonoides	NNHM-P 6434
Otocyon megalotis	NNM RMNH cat. no. a.
Otocyon megalotis	FMNH 146303
Otocyon megalotis	FMNH 146301
Lycalopex culpaeus	NNM RMNH reg. no. 620
Lycalopex culpaeus	AMNH(M) 67088
Lycalopex griseus	AMNH(M) 41509
Lycalopex griseus	NNM RMNH cat. no. a.
Lycalopex gymnocercus	AMNH(M) 205782
Lycalopex sechurae	NNM RMNH reg. no. 2381
Lycalopex vetulus	NNM RMNH cat. ost. no. a
Lycalopex vetulus	AMNH(M) 13398
Speothos venaticus	NNM RMNH reg. no. 3224
Urocyon cinereoargenteus	AMNH(M) 68527
Urocyon cinereoargenteus	NNM RMNH reg. no. 626
Vulpes bengalensis	NNM RMNH cat. no. c.

Vulpes bengalensis	NNM RMNH cat. no. b.
Vulpes chama	NNM RMNH reg. no. 25900
Vulpes corsac	NNHM-Z 11616/527/4
Vulpes corsac	NNHM-Z 11614/383/2
Vulpes lagopus	NNM RMNH cat. no. c.
Vulpes lagopus	NNM RMNH cat. no. d.
Vulpes lagopus	NNM RMNH cat. no. h.
Vulpes lagopus	FMNH 74070
Vulpes lagopus	FMNH 146276
Vulpes rueppelli	NNM RMNH cat. no. b.
Vulpes vulpes	NNM RMNH cat. no. b.
Vulpes vulpes	NNM RMNH reg. no. 932
Vulpes vulpes	NNHM-P 6419
Vulpes vulpes	FMNH 67413
Vulpes zerda	NNM RMNH cat. no. c.
Vulpes zerda	FMNH 90369
Vulpes zerda	FMNH 91743
Vulpes zerda	FMNH 91748

Appendix 3

Endocast measurements. Asterisks indicate estimates.

Species	Specimens	Brain volume (in cm³)	Length of super-ficially exposed gyri (in cm)
Aelurodon ferox	FMNH PM 58951, FMNH PM 58965	137.5	63.8
Aelurodon taxoides	FMNH PM 58969	150*	64
Archaeocyon leptodus	FAM 49031	17	9.6
Borophagus dudleyi	FMNH PM 58963	200	82
Borophagus secundus	FMNH PM 58954	114*	52
Canis armbrusteri	FAM 67286	190*	98
Canis dirus	FMNH PM 394	210*	131
Canis lupus	FMNH 7619	154	92
Canis mesomelas	FMNH 85508, FMNH 146290	55	64
Canis simensis	FMNH 146291	112	86.2
Carpocyon webbi	FMNH PM 58964	118	60
Chrysocyon brachyurus	FMNH 146295, FMNH 146296	116	83.5
Cuon alpinus	FMNH 91246	125	79.6
Desmocyon matthewi	FMNH PM 58983	26*	22.6
Enhydrocyon stenocephalus	FMNH PM 59036	64*	32
Epicyon saevus	FMNH PM 58978	125	59.6
Eucyon davisi	FAM 97057	61	66
Hesperocyon gregarius	AMNH 9766, AMNH 39476	14	10
Leptocyon gregorii	FMNH PM 58961	14	11.4
Lycaon pictus	FMNH 146299	148	104
Mesocyon sp.	AMNH 6946	45	28
Nyctereutes megamastoides	AUT-DFN 17	48	62
Nyctereutes tingi	AUT-MEL 1	56	66
Osbornodon fricki	FMNH PM 58964	80	47
Otarocyon cooki	FMNH PM 58987	14	7
Otocyon megalotis	FMNH 146303, FMNH 146301	30	46.5
Paracynarctus sinclairi	FMNH PM 58973	57	38
Paratomarctus temerarius	FMNH PM 58958	48	40
Lycalopex culpaeus	AMNH (M) 67088	48	74
Tomarctus hippophagus	NNM RGM 195225	60	23
Vulpes lagopus	FMNH 74070, FMNH 146276	36	62
Vulpes vulpes	FMNH 67413	56	69
Vulpes zerda	FMNH 91743, FMNH 90369, FMNH 91748	15.5	39.5
Xenocyon lycaonoides	NNM RGM 195206	100	108

Appendix 4.1

Factor scores of the first four principal components.

	PC1	PC2	PC3	PC4
% of the total variance	58.8182	13.5375	8.6125	5.6042
Accumulative % of the total variance	58.8182	72.3557	80.9682	86.5724
RBL	0.27795	-0.10137	-0.39553	0.03201
RLGA	-0.25906	0.31204	0.38731	0.27662
RUGA	-0.22948	0.52317	0.03579	-0.03827
M1BS	0.30186	-0.03157	-0.34321	0.41230
M2S	0.6271	0.50887	-0.54273	0.19890
IxP4	0.31316	0.16798	0.22650	0.27300
IxM2	0.30382	0.21688	0.26427	0.20598
I2	0.29994	0.05329	0.12608	-0.35611
I3	0.32735	0.02070	0.19539	-0.24034
C1	0.27545	0.19694	-0.13690	-0.46412
C1C1	0.31872	0.14647	0.13746	-0.18212
UM2/1	-0.22406	0.42574	-0.13481	-0. 33588
DIA	0.30184	0.19446	0.22126	0.22027

Appendix 4.2

Values of the first two principal components used in the diagram of Figure 45.

Species	PC1	PC2	Species	PC1	PC2
Aelurodon asthenostylus	4.321264	-0.07102	*Hesperocyon gregarious*	-2.16182	-3.2342
Aelurodon ferox	4.693064	-0.28722	*Lycalopex culpaeus*	-1.98175	-0.73171
Aelurodon mcgrewi	5.295836	-1.01961	*Lycalopex griseus*	-2.69085	0.208096
Aelurodon stitroni	6.151641	-1.54571	*Lycalopex gymnocerus*	-3.00064	0.095951
Aelurodon taxoides	1.604644	0.882939	*Lycalopex sechurae*	-3.7021	1.072165
Vulpes lagopus	-0.2287	-1.61637	*Lycaon pictus*	2.607451	-0.61914
Archaeocyon leptodus	-2.57642	-2.51018	*Mesocyon coryphaeus*	0.759777	-0.784
Arhaeocyon pavidus	-2.38739	1.661108	*Microtomarctus confertus*	-0.68577	1.478766
Borophagus secundus	5.97471	1.087941	*Nyctereutes procyonoides*	-1.48115	0.516047
"Canis" adoxus	-1.22277	-1.48579	*Nycterutes sinensis*	-2.34197	0.348217
Canis adustus	-2.35413	0.755722	*Osbornodon fricki*	1.344351	0.099881
Canis armbrusteri	1.183482	-1.19638	*Otarocyon cooki*	-3.65615	-0.56502
Canis aureus	-0.40595	0.094934	*Paracynarctus sinclairi*	-0.58055	2.249594
Canis cf. falconeri	3.223789	0.319066	*Paratomarctus euthos*	3.995637	-0.11311
Canis dirus	3.82048	-0.66053	*Paratomarctus temerarious*	4.956372	-0.49396
Canis latrans	-0.29367	-1.23268	*Phlaocyon leucosteus*	-2.36631	2.150336
Canis lepophagus	-1.9269	0.800612	*Protepicyon raki*	0.930422	1.09066
Canis lupus	1.261422	-0.75972	*Protomarctus optatus*	2.157738	2.296578
Canis mesomelas	-0.41785	-0.28914	*Psalidocyon marianae*	0.360714	1.128324
Canis simensis	-2.50217	-0.58321	*Rhizocyon oregonensis*	-1.46243	0.869906
Carpocyon compressus	1.503145	1.55432	*Speothos venaticus*	0.049585	-0.54497
Carpocyon webbi	4.095577	0.345011	*Tomarctus brevirostris*	1.785226	1.388706
Cerdocyon thous	-2.77591	1.287615	*Tomarctus hippophagus*	1.372006	1.090238
Chrysocyon brachyurus	-2.8884	0.333544	*Urocyon cinereoargenteus*	-3.61626	0.104398
Cormocyon copei	-0.97924	1.640537	*Urocyon littoralis*	-3.92996	0.44976
Cormocyon haydeni	1.467733	2.722645	*Vulpes bengalensis*	-4.31343	0.324953
Cuon alpinus	2.259305	-3.03614	*Vulpes cana*	-1.89006	-2.08282
Cynarctus galushai	-0.64376	1.106643	*Vulpes chama*	-3.83698	-0.24237
Cynodesmus thooides	1.476422	-0.60123	*Vulpes corsac*	-0.97332	-2.56863
Desmocyon matthewi	1.280858	2.200653	*Vulpes macrotis*	-2.65265	-1.73793
Desmocyon thomsoni	-0.07282	1.703607	*Vulpes rueppellii*	-2.87233	-1.0166
Epicyon haydeni	4.572163	-0.6678	*Vulpes vulpes*	-0.88754	-1.47682
Epicyon saevus	2.914288	0.090141	*Vulpes zerda*	-3.59031	-0.34193
Eucyon davisi	-1.06867	-1.4337			

Appendix 4.3

Specimens used in the PCA and the values of their morphometric ratios.

Species	Speci-mens	RBL	RLGA	RUGA	MIBS	M2E	IXP4	IXM2	I2	I3	C1	C1C1	UM2/1	DIA
Archaeocyon leptodus	(1)	0.655	0.919	0.927	0.096	0.027	0.055	0.059	0.017	0.024	0.008	0.145	0.610	0.693
"Canis" adoxus	(2)	0.688	0.807	0.962	0.094	0.045	0.046	0.057	0.024	0.028	0.024	0.145	0.628	0.794
Canis armbrusteri	(3)	0.694	0.675	0.860	0.119	0.05	0.055	0.068	0.018	0.030	0.059	0.174	0.584	0.770
Canis cf. falconeri	(4)	0.716	0.702	0.862	0.120	0.076	0.060	0.071	0.031	0.034	0.062	0.217	0.578	0.841
Canis dirus	(5)	0.705	0.683	0.743	0.126	0.065	0.064	0.073	0.026	0.039	0.068	0.217	0.543	0.858
Canis lepophagus	(6)	0.631	0.890	1.246	0.093	0.063	0.051	0.062	0.020	0.025	0.026	0.167	0.608	0.795
Cynodesmus thooides	(7)	0.664	0.816	0.897	0.097	0.039	0.066	0.076	0.023	0.035	0.046	0.206	0.609	0.873
Eucyon davisi	(8)	0.655	0.929	0.932	0.088	0.043	0.047	0.054	0.022	0.029	0.027	0.188	0.573	0.816
Hesperocyon gregarius	(9)	0.673	0.886	0.868	0.102	0.032	0.056	0.041	0.017	0.025	0.014	0.099	0.542	0.819
Mesocyon coryphaeus	(10)	0.714	0.688	0.937	0.104	0.036	0.067	0.071	0.018	0.025	0.042	0.207	0.679	0.848
Nyctereutes sinensis	(11)	0.575	1.021	1.086	0.091	0.052	0.046	0.063	0.019	0.028	0.035	0.156	0.638	0.790
Osbornodon fricki	(12)	0.695	0.697	1.073	0.078	0.034	0.050	0.058	0.027	0.037	0.084	0.212	0.670	0.893
Otarocyon cooki	(13)	0.527	1.325	1.007	0.071	0.021	0.060	0.070	0.016	0.024	0.008	0.171	0.614	0.810
Paracynarcuus singlairi	(14)	0.658	0.914	1.264	0.080	0.049	0.066	0.072	0.023	0.036	0.039	0.207	0.776	0.833

Specimens used: (1) FAM 49045 –(2) BMN Rss 45 –(3) AMNH 104765 (cast of USNM 11885), AMNH 104766 (cast of USNM 11886), AMNH 104777 (cast of USNM 11882) –(4) FAM 97052–(5) AMNH 15867 –(6) AMNH 104782 (cast of WY 760) –(7) AMNH123531, PU10412 –(8) FAM 97058, FAM 49294, AMNH 129013– (9) FAM 39096 –(10) AMNH 6860 –(11) FAM 22336, FAM 9675, FAM 9678 –(12) AMNH 27363 –(13) FAM 49020, FAM 38986, FAM 49042 –(14) FAM 61008A, FAM 61040, FAM 61009.

Values of *Canis lupus, Cuon alpinus, Lycaon pictus, Speothos venaticus, Canis simensis, Canis aureus, Canis mesomelas, Canis latrans,Vulpes vulpes, Canis adustus, Cerdocyon thous, Chrysocyon brachyurus, Lycalopex culpaeus, Lycalopex griseus, Lycalopex gymnocerus, Lycalopex sechurae, Vulpes zerda, Nyctereutes procyonoides, Urocyon cinereoargenteus, Urocyon litoralis, Vulpes bengalensis, Vulpes cana, Vulpes chama, Vulpes corsac, Vulpes macrotis, Vulpes lagopus, Vulpes rueppelli* are from Van Valkenburgh & Koepfli (1993).

Values of *Archaeocyon pavidus, Rhizocyon oregonensis, Cormocyon haydeni, Cormocyon copei, Phlaocyon leucosteus, Desmocyon thomsoni, Desmocyon matthewi, Microtomarctus confertus, Tephrocyon optatus, Cynarctus galushai, Psalidocyon marianae, Tomarctus hippophagus, Tomarctus brevirostris, Aelurodon asthenostylus, Aelurodon mcgrevi, Aelurodon stironi, Aelurodon ferox, Paratomarctus temerarius, Carpocyon compressus, Carpocyon webbi, Protepicyon raki, Aelurodon taxoides, Paratomarctus euthos, Epicyon saevus, Epicyon haydeni, Borophagus secundus* are from Van Valkenburgh *et al.* (2003).