The phylogenetic position of raccoon dogs: Implications of their neuroanatomy

Dermitzakis M.D.[1], Van Der Geer A.A.E.[2] & Lyras G.A.[3]

[1,3]Department of Geology, National and Kapodistrian University of Athens, Panepistimiopolis GR-157 84, Zografos, Greece, [1]mdermi@geol.uoa.gr, [3]glyras@geol.uoa.gr
[2]IIAS, University of Leiden, Nonnensteeg 1-3, PO Box 9515, 2300 RA Leiden, The Netherlands, A.A.E.van.der.Geer@umail.LeidenUniv.NL

Keywords: *Nyctereutes, Cerdocyon*, Canidae, Pliocene, brain, endocast

Introduction

Raccoon dog is the common name of *Nyctereutes procyonoides*, an unlikely looking canid whose facial marks resemble that of a raccoon, hence its name. The geologically speaking oldest *Nyctereutes* dates from the Late Miocene of Spain (Soría and Aguirre, 1976). During the Pliocene the genus was spread all over Eurasia with three species in Europe (*N. donnezani, N. tingi* and *N. megamastoides*) and two in Asia (*N. tingi* and *N. sinensis*). *Nyctereutes* became extinct in Europe already before the beginning of the Pleistocene, while in Asia they persisted till the present day with the living species *N. procyonoides*. This species is believed to originate from *N. sinensis* (Soría and Aguirre, 1976; Tedford and Qiu, 1991). During the 20th century individuals were introduced for their fur into western Russia, and following this, the species has again spread though most of eastern Europe.

Although there are many studies on the living species and a lot of data have been collected concerning their craniodental evolution, the temporal range and the geographic distribution of fossil raccoon dogs (e.g. Viret, 1954; Soría and Aguirre, 1976; Tedford and Qiu, 1991), their phylogenetic position remained uncertain. Already more than hundred years ago, Huxley (1880) in his pioneer work on the craniodental anatomy of living Canidae, expressed these uncertainties by noting that *Nyctereutes* is "*essentially a low Thooid of the South-American type*". Two recent works, one using morphological data (Tedford, Taylor and Wang, 1995) and the other based upon a combination of morphological and molecular data (Wayne *et all*., 1997), present major differences in their conclusions about the phylogenetic position of *Nyctereutes*. Tedford *et al.* (1995) consider *Nyctereutes* a sister taxon of *Cerdocyon*, the crab-eating fox of South America. Wayne *et al.* (1997) on the other hand cannot find a relation between *Nyctereutes* and any of the living canids. Previous works on this subject treat *Nyctereutes* as a sister taxon of the foxes of the genus *Vulpes* (Wayne *et al.,* 1987a; Wayne *et al.* 1987b), of the zorros of the South American genus *Pseudalopex* (Clutton-Brock *et al*., 1976), or as a clade on its own (Wayne and O'Brien, 1987; Clutton-Brock *et al*., 1976).

The aim of this contribution is to present neuroanatomical data and to compare them with cranial characters in order to solve this problem.

Neuroanatomical data

The overall shape and proportions of the brain is similar in all living wild canids (Radinsky, 1973). The same is true for the basic sulcal pattern of the cerebrum, which is characterised by a uniformity (Atkins, 1978), with the exception of two features: (1) the length and bilateral constriction of the proreal gyrus, which is long and bilaterally constricted in the dogs (fig.1) and short in the foxes (Radinsky, 1973), and (2) the cortex medial to the coronal sulci (Lyras, Van Der Geer & Dermitzakis, 2001; Lyras & Van Der Geer, 2003), in which four different pat-

terns are recognised (fig. 2).

These features developed during the Plio-Pleistocene (Lyras, 2001; Lyras & Van der Geer, 2003), coinciding with the time during which the major radiation in the subfamily of the Caninae took place. The remainder of external brain features appear to have been already established in the Middle Miocene and remained unchanged during further evolution of the subfamily (fig. 3).

In the living *Cerdocyon*, the crab-eating fox, the cerebral hemispheres widen out abruptly immediately behind the presylvian sulci, and the proreal gyrus is long and bilaterally constricted. The coronal sulci diverge rostrally, creating a heart-shaped outline (fig. 4a).

In *Nyctereutes procyonoides* the proreal gyrus is broad and low with hardly any bilateral constriction and its length is smaller than is the case in *Cerdocyon*. The coronal sulci create a heart-like outline, similar to that of *Cerdocyon* (fig. 4b).

An interesting observation is that in three fossil brain endocasts of *Nyctereutes* from the Pliocene of China (one of *N. tingi* F:AM 96757, and two of *N. sinensis*: F:AM 96750, F:AM 96792), the coronal sulci create a heart-shaped pattern on the dorsal part of the cerebrum which is strikingly similar to that found in the living *Nyctereutes* and *Cerdocyon* (fig. 4c). At the same time, however, the proreal gyrus in the Pliocene *Nyctereutes* is long and bilaterally constricted, resembling in this way the proreal gyrus of the living crab-eating fox *Cerdocyon*, and not that of the living raccoon dog *Nyctereutes*, which is remarkable.

Thus, we have to conclude that the brain of the living *Nyctereutes* is similar to that of *Cerdocyon,* with the exception of the proreal gyrus, while such a difference appears not to exist if we compare the Pliocene *Nyctereutes* with the living *Cerdocyon.*

Discussion

In this contribution features of external brain anatomy are used to clarify phylogenetic problems that could not sufficiently be solved by the use of osteological and dental features alone. From this it appears that indeed external brain anatomy confirms these other data, and can thus contribute to taxonomy.

The similarities in external brain anatomy between the living crab-eating fox *Cerdocyon* and the fossil raccoon dogs *Nyctereutes tingi* and *N. sinensis* confirm Tedford's *et alli's* (1995) conclusion, based upon osteological and dental features, that *Nyctereutes* should be considered a sister taxon of *Cerdocyon.* In first instance, this sounds like a geographic paradox, as *Cerdocyon thous* is a typical South American canid, while *Nyctereutes procyonoides* is an Eurasian species. However, fossil remains of *Cerdocyon* from the Late Miocene-Early Pliocene of Central America (Torres & Ferrusquia, 1981) and of North America (McKenna & Bell, 1997; R.H. Tedford, pers. comm. 2002) narrow this temporal and geographic gap.

Actually, the fossil *Nyctereutes* appears to be closer to the living *Cerdocyon* than to the living *Nyctereutes*. Similarities in cranial anatomy are more evident between the living *Cerdocyon thous* and *Nyctereutes tingi* than between the former and the fossil *Nyctereutes* species *N. sinensis* and *N. megamastoides*. The latter two differ from *N. tingi* in having a larger subangular lobe, tabular postorbital process, highly elevated parasaggital crest, multicuspidate talonid and a smaller frontal sinus. *N. procyonoides* is even more distinct from *N. tingi* in having an even greater postorbital constriction, smaller frontal sinus, extended hypoconulid shelf of m1 the talonid basin and parasagital crests joining at the frontal-parietal suture (Tedford and Qiu, 1991). So here, too, data from brain endocasts confirm osteological data.

In conclusion, based upon osteological, dental, and cerebral data, the raccoon dog *Nyctereutes* should be considered a sister taxon of the crab-eating fox *Cerdocyon*.

Abbreviations: AMNH: American Museum of Natural History; F:AM: Frick collection, American Museum; NNML: Nationaal Natuurhistorisch Museum, Leiden.

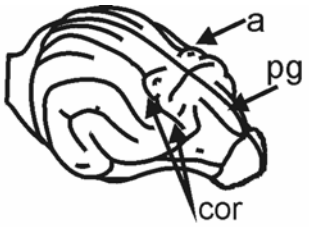


Fig. 1. Anterodorsolateral view of a *Canis* sp. endocranial cast.
pg: proreal gyrus
cor: cororonal sulcus
a: ansate sulcus

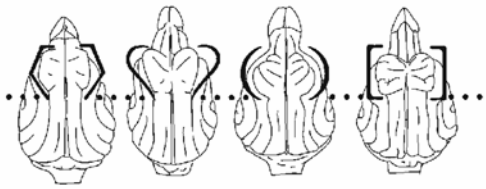
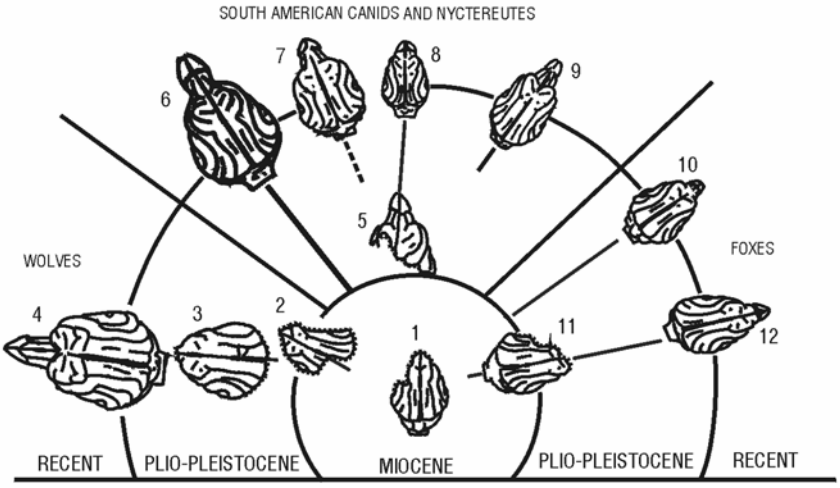


Fig. 2. Different types of outlines that are created by the coronal and ansate sulci. Redrawn from Lyras & Van der Geer (2003)



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. 3. Adaptive radiation of the Caninae brain

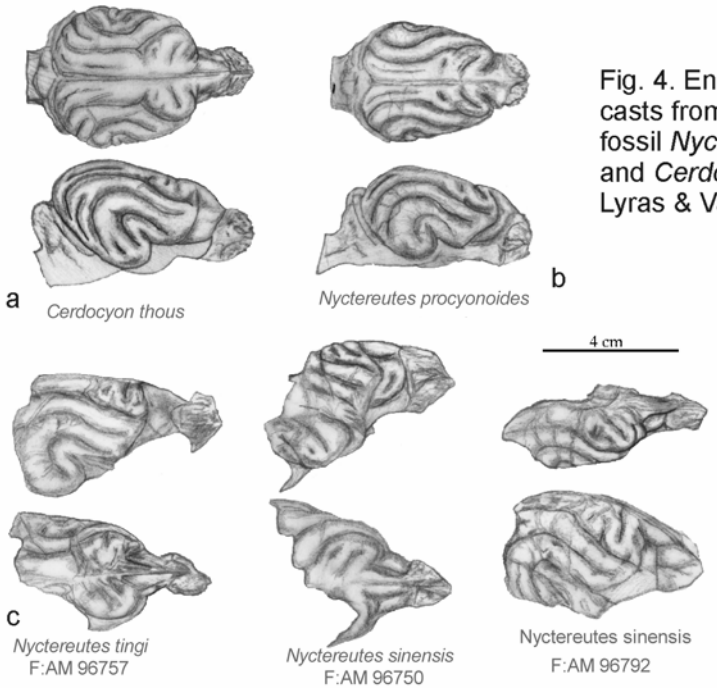


Fig. 4. Endocranial casts from living and fossil *Nyctereutes* and *Cerdocyon.* From Lyras & Van der Geer (2003)

Acknowledgments

We thank Richard Tedford (American Museum of Natural History, New York, USA), Dmitri Ivanoff (National Museum of Natural History of Ukraine, Kiev, Ukrain), John de Vos and Chris Smeenk (Nationaal Natuurhistorisch Museum, Leiden, the Netherlands) for their permission to make endocasts from specimens in their charge. The interpretation of the cortical sulcal maps was done with the help of G. Papadopoulos (Aristotelian University of Thessaloniki, Greece).

References

Atkins D.L. (1978). Evolution and morphology of the Coyote brain, *In:* Bekoff M. *(ed.), Coyotes, New York: Academic Press,* 17-35.

Clutton-Brock J., Corbert G.B. & Hills M. (1976). A review of the family Canidae, with a classification by numerical methods, *Bulletin of the British Museum (Natural History), Zoology*, 29, 119-199.

Huxley T.H. (1880). On the cranial and dental characters of the Canidae. *Proceedings of the Zoological Society of London,* 1880, 238-288.

Lyras G.A. (2001). Adaptive radiation of the brain of the Caninae (Carnivora:Canidae), *Proceedings of the 16th Congress of the Hellenic Society for Neuroscience,* October 19-21, Thessaloniki, 86.

Lyras G.A., Van Der Geer A.A.E. & Dermitzakis M.D. (2001). Evolution of the brain of Plio-Pleistocene wolves, *Cranium,* 18(2), 30-40.

Lyras G.A. & Van Der Geer A.A.E. (2003). External brain anatomy in relation to the phylogeny of Caninae (Carnivora: Canidae), *Zoological Journal of the Linnean Society,* 138, 505-522.

McKenna M.C. & Bell S.K. (1997). Classification of mammals above the species level, *New York: Columbia University Press.*

Radinsky L.B. (1973). Evolution of the canid brain, *Brain, Behavior and Evolution,* 7, 169-202.

Soría D. & Aguirre E. (1976). El cánido de Layna: revisión de los *Nyctereutes* fósiles, *Trabajos sobre Neógeno- Cuaternario,* 5, 83-116.

Tedford R.H. Taylor B.E. & Wang X. (1995). Phylogeny of the Caninae (Carnivora: Canidae): the living taxa, *American Museum Novitates,* 3146, 1-37.

Tedford R.H. & Qiu Z. (1991). Pliocene *Nyctereutes* (Carnivora: Canidae) from Yushe, Shanxi, with comments on Chinese fossil raccoon-dogs, *Vertebrata PalAsiatica,* 29(3), 179-189.

Torres R.V. & Ferrusquia I. (1981). *Cerdocyon* sp. nov. A (Mammalia, Carnivora) en Mexico y su significacion evolutiva y zoogeografica en relacion a los canidos sudamericanos, *Anais II Congreso Latino-Americano de Paleontologia, Porto Alegre* 2 , 709-719.

Viret J. (1954). Le Loess a bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères Villafranchiens, *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon,* 4, 1-200.

Wayne R.K., Nash W.G. & O'Brien S.J. (1987a). Chromosomal evolution of the Canidae, I. Species with high diploid numbers, *Cytogenetics Cell Genetics,* 44, 123-133.

Wayne R.K., Nash W.G. & O'Brien S.J. (1987b). Chromosomal evolution of the Canidae, II. Divergence from the primitive carnivore karyotype, *Cytogenetics Cell Genetics,* 44, 134-141.

Wayne R.K. & O'Brien S.J. (1987). Allozyme divergence within the Canidae, *Systematic Zoology,* 36, 339-355.

Wayne R.K., Geffen E., Girman D.J., Koepfi K.P., Lau L.M. & Marshall C.R. (1997). Molecular systematics of the Canidae, *Systematic Biology,* 46(4), 622-653.