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

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

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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. donnez-ani, 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 (Soria 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 Thoid 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 al., 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 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 & Demitzakis, 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 parasagittal 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 parasagittal 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.


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

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

Fig. 3. Adaptive radiation of the Caninae brain

Fig. 4. Endocranial casts from living and fossil Nyctereutes and Cerdacyon. From Lytras & Van der Geer (2003)

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