UNIVERSITY OF SOUTH BOHEMIA, FACULTY OF SCIENCES

Paleoecology of fossil species of canids (Canidae, Carnivora, Mammalia)

Master thesis

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Annotation:

There were reconstructed phylogeny of recent and fossil species of subfamily Caninae in this study. Resulting phylogeny was used for examining possible causes of cooperative behaviour in Caninae. The study tried tu explain evolution of social behavior in canids.

Declaration:

I hereby declare that I have worked on my master thesis independently and used only the sources listed in the bibliography.

I hereby declare that, in accordance with Article 47b of Act No. 111/1998 in the valid wording, I agree with the publication of my master thesis in electronic form in publicly accessible part of the STAG database operated by the University of South Bohemia accessible through its web pages.

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In České Budějovice, 13. December 2013

Bc. Isabela Okřinová

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1 INTRODUCTION

1.1 Why are *Canidae* so interesting?

The family Canidae includes 36 extant (Nowak 1999) and many fossil species (in the subfamilies Caninae, Hesperocyoninae, and Borophaginae: approximately 70, 27 and 66 fossils are comprised respectively) (Wang et Tedford 1994, Wang et al. 1999, 2004, 2008). Representatives of the family inhabit nearly all terrestrial areas of the world except e.g. Australia, Madagascar, Antarctica, islands of Indonesia etc. (Nowak 1999). Canids can be omnivorous (*Cerdocyon thous*), hypercarnivorous (*Lycaon pictus*) and insectivorous (*Otocyon megalotis*) (Nowak 1999, Sillero-Zubiri et al. 2004). Canids represent a very unique group among mammals because of their unusual behavioral and reproductive traits. Monogamy with paternal care, the typical mating system of Canidae, is found in less than three percent of mammalian species (Kleiman 1977, Asa et Valdespino 1998). Female reproduction is limited to one estrus per one reproductive season and it´s typically suppressed in subordinate individuals (Asa et Valdespino 1998). Subordinate females have rarely their own offspring and they usually take care of pups born to a dominante female (Moehlman 1986, 1989). The subordinate females have concentrations of hormones similar to pregnant individual and are also able to nurse puppies from their groups (Moehlman et Hofer 1997, Asa et Valdespino 1998). Moreover, subadults of some species join the social group for very long time (Scott 1967). It usually happens that some of these indivuals (so called helpers) stay in a pack for whole life and take care of puppies (Nowak 1999). These traits seem to be adaptive for social hunting species. However, the present phylogenetical studies (Tedford et al. 1995, Zrzavý et Řičánková 2004, Tedford et al. 2009) suggest that basal canids are solitary hunters and social hunting is a derived feature. A suitable outgroup is needed for better understanding of these phenomenon. Since the subfamily Canidae is a basal clade of Caniformia, all current outgroups for canids are overly distant, which hinders the interpretations of results. So, the evolution of social hunting in canids and it´s adaptive value still remains unclear. Incorporation of fossil species into a complete phylogeny of Canidae could solve for this problem. Behavioural and ecological characteristics of recent canids are well known. But, how to recognize behavioural traits within fossil species?

1.2 Indicative characters of social hunters

1.2.1 Hypercarnivory

Fortunatelly, characteristics of foraging ecology can be determined according to morphology of dentition and skull (Van Valkenburgh 1989, Van Valkenburgh et Koepfli 1993, Holliday and Steppan 2004). Animals hunting prey larger than themselves have specific adaptations. The hunters of large prey share morphological traits on dentition and skull, which are different from traits of omnivorous species or consumers of small prey (Van Valkenburgh et Koepfli 1993). Short and deep jaws, stronger bite and a very robust skull are typical for manipulation with large prey (Slater et al. 2009). This complex set of adaptations deals with a high pressure on the skull, which results from handling of large prey (Wang et al. 2008). The recent canid hunters of large prey exhibit considerable reduction of grinding area of their molars, larger canines and incisors and broader snouts (Van Valkenburgh and Koepfli 1993). Shortening of jaws is associated with widened palate, compression of premolars and loss of posterior molars (Tedford et al. 1995). Shortening of the jaws contributes to effective and strong bite, as it moves canines closer to mandibule joint (Wang et al. 2008). These characters are connected with so-called hypercarnivory. Changes in dentition involve reduction or loss of the second and third lower molars (see: Fig. 1 – 2 in Appendix) and adaptation of the first and second upper molars for grinding (Van Valkenburgh, 1989). Van Valkenburgh (1991) claims that hypercarnivory is the best way of manipulation with a large prey. It has been proposed that the complex of hypercarnivorous traits is a possible indicator of pack-hunting, which supposedly represents yet another adaptation for hunting of larger animals (Van Valkenburgh 1989, Holliday and Steppan 2004).

1.2.2 Body size

Body size is considered as another indicator of social hunting. Carbone et al. (1999) proposed that body size of carnivores does not depend only on the size of prey, but also on the energy acquired from diet. Large predators have to consume enough energy-rich food to cover their daily energy demands (Van Valkenburgh et al. 2004). Since social predators are able to use broader size range of prey than predators hunting alone (Earle 1987), there seems to be an evolutionary trend toward increased body size. There were two periods, when representatives of the Borophaginae and Caninae distinctively enlarged their body. These events correlate with the occurrence of morphological adaptations for hypercarnivory and extensive diversification occured in these two subfamillies. It seems that hypercarnivory specialization as well as increase in body size was associated with colonization of new or vacant ecological niches (Van Valkenburgh 1991, Finarelli 2007). Replacement of Borophaginae by Caninae was not due to a competition as larger canins evolved after the decline of the borophagine diversity (Van Valkenburgh 1999, Finarelli 2007). Similarly, distinctively large hypercarnivores occured after the extinction of Hesperocyoninae (Van Valkenburgh 2004, Wesley-Hunt 2005, Finarelli 2007). Thus, there is a link between body size and hypercarnivorous dentition. This type of dentition allows for the easiest handling of a large prey (Van Valkenburgh 1991). However, the presence of hypercarnivorous dentition in small-sized *Speothos pacivorus* (Tedford et al. 1995) does not support this hypothesis. The large body size may be also response to climatic and enviromental changes. Herbivores were shown to increase their body size during Pleistocene glacial cycles (Wang et al. 2008). Also the biggest member of Caninae, Pleistocene *Canis dirus* lived had larger *musculus temporalis* compare to contemporary wolf, *C. lupus* and could therefore exert a greater bite force (Anyonge et Baker 2005) in order to better handle contemporary megafauna.

1.2.3 Brain size

A connection between a social hunting and size of a brain can be found as well. Dunbar´s hypothesis (1998) on a so-called “social brain” implies that size of a brain increased during evolution along with occurrence of social behaviour. Recent canids, including basal solitary hunters, exhibit apparent enlargement of the brain. Relative enlargement of the brain in proportion to body size is a synapomorphy for subfamily Caninae. Borophaginae and Hesperocyoninae do not exhibit this trait. A significant increase in a brain size occurred already within the genus *Leptocyon*, which represents a basal lineage of the clade Caninae (Finarelli 2008). This phenomenon can be explained in two ways. If the large brain was an adaptation for social hunting, the cooperative hunting would have arisen twice in the evolution of Caninae. However, the larger brain could be an attendant of the other process leading to sociality. According to Schultz and Dunbar (2007), the higher brain size is associated with pair bonding, which is typical for all the recent canids. Moreover, the fact that members of Felinae have smaller brain than Canidae (Radinsky 1978) supports the hypothesis on relation between cooperative hunting and brain size, because most of the cats are solitary predators. There is also interesting relation between the brain size and hypercarnivory. Lyras (2009) suggested that evolution probably prefferred the hypercarnivorous dentition to the increase in the brain size. However, Van Valkenburgh et al. (2004), argued that it is a due to a trade off between energy benefits and costs. Hunting large prey requires more energy and therefore development of a tissue with really high energetic costs, such as a brain, is really demanding. However, a well-developed brain provides many sensoric and motor advantages in hunt. However, according Lyras (2009) it´s obvious that development of useful craniodental characters was more important in the evolution of canids. Radinsky (1969, 1973) and also Andersson 2005 suggested that *prorean gyrus*, the structure in the frontal part of brain (Wang et al. 2008), could associated with evolution of the pack-hunting in canids. For instance, no enlarged *prorean gyrus* was found in members of Borophaginae (Radinsky 1973). Based on this argument, borophagines should not be social hunters. On the contrary, fossil members of genus *Nyctereutes* had an expanded *prorean gyrus* (Lyras et Van der Geer 2003). However, recent *Nyctereutes* certainly does not hunt in group. Thus it can be concluded that external brain morphology is not a proper indicator for social behaviour in canids (Van Valkenburgh et al. 2003).

1.3 Canidae

The family Canidae comprises the extant subfamily Caninae and two completely extinct subfamilies Hesperocyoninae, and Borophaginae (Wang et al. 2008). Borophaginae is a sister group of Caninae (Tedford et al. 2009). Borophaginae were a diverse subfamily with seven genera of large dogs (Wang et al. 1999). Representatives of the subfamily Hesperocyoninae are the most basal and oldest members of Canidae (Wang 1994).

The centre of origin of the Canidae is North America. The oldest canid fossil, *Hesperocyon gregarious* of the subfamily Hesperocyoninae, come from the Eocene (40 Mya) sediments (Wang et al. 2008). Early hesperocyonins were small omnivorous species, which could occasionally climb the trees (Van Valkenburgh 1999). However, the first remarkable diversification of Canidae occurred in the late Oligocene (Wang et al. 2008). During the late Miocene members of the subfamily Caninae crossed the Beringia land bridge and reached Eurasia (Wang et al. 2004). This event was followed by extensive radiation, which gave rise to modern canids in the Old World, including wolves, jackals etc. (Martin 1989). These types of canids came back to the North America at the end of Miocene (Wang et al. 2008). The oldest known evidence for canids in Africa is a fossil record of *Vulpes riffautae* from the late Miocene (de Bonis et al. 2007). During the Pliocene, after the emergence of Isthmus of Panama, members of Caninae spread to the South American continent (Perini et al. 2009), where they underwent substantial radiation (Berta 1987, Wang et al. 2008, Rook 2009).

1.4 Major lineages of Caninae

1.4.1 SUBFAMILY CANINAE Fischer de Waldheim, 1817

As mentioned above the subfamily Caninae comprises all extant canid species and their closest fossil relatives (Tedford et al. 2009). Sister clade of this group is the extinct subfamily Borophaginae (Wang et al. 1999, 2008). Caninae share with their sister clade so-called bicuspid talonid (see: Fig. 3 in Appendix) - modification of lower carnassial for better function in mastication (Tedford et al. 2009). The first representatives of this group appeared in early Oligocene in the North American continent (Wang et al. 2004). This basal fox-like species exhibited very limited cladogenesis toward the end of the medial Miocene (Tedford et al. 2009). The phylogenetic analysis of the North American Caninae the extant Caninae divides the extant species into two groups: fox-like Vulpini and Canini, which comprisees wolf-like canids and South American canins) (Tedford et al. 1995). Molecular (Bardeleben et al. 2005) and combined (Zrzavý et Řičánková 2004) analyses consider *Urocyon* as a basal taxon of Caninae However, the position of *Otocyon-Nyctereutes* group is still unclear (Bardeleben et al. 2005, Perini 2009, Zrzavý et Řičánková 2004).

Genus *Leptocyon* Matthew, 1918

The earliest recognized member of the subfamily Caninae was a small fox-sized species of genus *Leptocyon*. This genus includes 11 species (Wang et al. 2008).

Distribution: From the early Oligocene until the late Miocene (Wang et al. 1999, Wang et al. 2008) in the southwest regions of North America (Wang et al. 2004, Tedford et al. 2009).

Phylogenetic relationship: According to the phylogeny by Tedford et al. (1995, 2009), *Leptocyon* is the basal taxon of Caninae and *L. matthewi* is the most closely related species to other Caninae (Tedford et al. 2009).

Monophyly: Tedford et al (2009) suggested that the *Leptocyon* is paraphyletic.

Type species: *Leptocyon vafer* (Leidy, 1858) – from the Miocene until the Late Miocene in North America (Wang et al. 2008)

Anatomy and morphology: Typical anatomic traits were long and shallow jaws, slender premolars separated by gaps, narrow rostrum, nuchal crest and more cursorial legs (Wang et al. 2008). *Leptocyon* species weighted about 3-4 kg (Finarelli et Flynn 2009). Representatives of this genus were small fox-like canids very similar to the first borophagines (Wang et al. 2008).

Ecology: *Leptocyon* canids were omnivores, which usually foraged small vertebrates and vegetation (Wang et al. 2008). The longer rostrum was advantageous for foraging of insects and better sniffing. It was also a good adaptation for cold and arid environment as it allowed better thermoregulation. Moreover, due to the presence of nuchal crest and higher cursoriality, they were able to search for prey even at a relatively long distance by smelling with a bowed head, which is another great advantage for cold and arid environment. At the same time as the *Leptocyon* canines, the representatives of borophagine canids, mainly species of the genus *Tomarctus* have lived in North America (Munthe 1989, Voorhies 2008, Wang et al. 2008). Nonetheless, there was not any distinctive competition between borophagines and first representatives of *Caninae*. *Tomarctus* species were larger and less, which is why they probably inhabited the more bushy edges of grasslands (Webb 1977). On the contrary, small fox-like *Leptocyon* species, preferred the more open landscape due to their cursorial adaptations (Voorhies 2008, Webb 1977, Munthe 1989). Both *Leptocyon* and early borophagines were small omnivorous species. At the same time American grasslands were inhabited by the more hypercarnivorous representatives of *Hesperocyoninae*, which hunted contemporary herbivores (Wang et al. 2008).

TRIBE VULPINI Hemprich and Ehrenberg, 1932

According to the Tedford study (1995) and the phylogeny suggested by Wang et al. (1994, 1999) the Vulpini group includes three extant genera: *Vulpes*, *Urocyon* and *Otocyon* and one fossil genus: *Metalopex* (Wang et al. 2008). According to the several studies (Bardeleben et al. 2005, Perini 2009, Zrzavý et Řičánková 2004), *Nyctereutes* also could be a part of this tribe.

Monophyly: It is supported by Tedford et al. (1995). Monophyly of the Vulpini after inclusion of *Nyctereutes* has also been suggested by a molecular analysis by Bardeleben et al. 2005. On the contrary, Perini et al´s (2009) combined analysis indicates the monophyly of the tribe without *Nyctereutes*. However, Zrzavý et Řičánková (2004) as well as one molecular study (Lindblad-Toh et al. 2005) suggested that *Urocyon* is a basal recent canine, and thus the monophyly of Vulpini is not supported in this case. According to the Prevosti (2009), the tribe is not monophyletic as two fossil species of *Cerdocyon* could belong to the Vulpini.

Genus *Metalopex* Tedford and Wang, 2008

The first members of the tribe Vulpini were the representatives of the genus *Metalopex* (Tedford et al. 2009, Wang et al. 2008), which comprises three extinct species (Wang et al. 2008).

Distribution: From the late Miocene till the beginning of the Pliocene (Wang et al. 2008, Tedford et al. 2009) in the southern region of North America (Tedford et al. 2009).

Phylogenetic relationship: According to Tedford et Wang (2008), the sister taxon of this genus is extant genus *Urocyon*.

Monophyly: According to the only study including this fossil genus (Tedford et al. 2009) it is supported.

Type species: ***Metalopex merriami*** Tedford and Wang, 2008 – from the late Miocene until the beginning of Pliocene (Wang et al. 2008, Tedford et al. 2008)

Anatomy and morphology: Species of the genus *Metalopex* were typical fox-sized hypocarnivores. There are many characters, which can distinguish between this genus and genus *Vulpes*. The most distinctive are mastoid process, more quadrate shape of first two upper molars and isolation of second lower premolar by longer diastemata (Tedford et al. 2009).

Ecology: It was contemporary species with the latest representatives of Boropohaginae (e.g. *Borophagus*) and with the earliest members of Canini (Wang et al. 2008). They were probably omnivores also coexisting with the first representatives of mesocarnivorous *Vulpes* (Tedford et al. 2009).

Genus *Urocyon* Baird, 1858

This genus comprises five extinct and two extant species (Tedford et al. 2009).

Distribution: from the late Miocene in North America until recent in northern regions of South America and in Central America (Tedford et al. 2009)

Phylogenetic relationship: Species allied in the genus *Vulpes*, descendants of *Leptocyon*, were joined by species of the fossil genus *Metalopex*, allied to the living gray fox, *Urocyon* (Wang et al. 2008). According to the combined analysis (Zrzavý et Řičánková 2004) as well as according the one molecular analysis (Lindblad-Toh et al. 2005), *Urocyon* is the most basal extant canid. However, Bardeleben et al´s (2005) Bayesian analysis of combined nuclear and mitochondrial dataset suggested that *Urocyon* is a basal taxon of fox-like canids. Nevertheless, the ML analysis of mitochondrial dataset showed *Urocyon* as a sister taxon of *Nyctereutes* within Vulpini. The combined analysis by Perini et al. (2009) placed *Urocyon* as a sister taxon of *Vulpes*.

Monophyly: It is supported by Tedford et al. (2009).

Type species: ***Urocyon cinereoargenteus*** (Schreber, 1775) – from the Pleistocene until recent times (Wang et al. 2008).

Anatomy and morphology: Hypocarnivorous dentition with distinctive complex lower molars. The most derived species have prominent subangular lobe (Tedford et al. 2009).

Ecology: The *Urocyon* species preferred more wooded areas (Wang et al. 2004) and mainly fed on vegetation and insects (Wang et al. 2008). The *Urocyon* species never distinctively spread from southern North American range, which is accord with distribution of extant species *U. cinereoargenteus* and *U. littoralis* (Tedford et al. 2009).

Genus *Vulpes* Frisch, 1754

The genus *Vulpes* includes 10 extinct species, including the former separate genera *Fennecus* and *Alopex*, and 12 recent representatives (Wang et al. 2008). The first members of this genus coexisted with first members of the genus *Urocyon* during the latest Miocene after the extinction of small borophagines (Wang et al. 2004).

Distribution: from the latest Miocene until recent times (Wang et al. 2008). The oldest *Vulpes* records are fossils of red fox-like *V. stenognatus* and swift fox-like *V. kernensis* from North America (Tedford et al. 2009). There was extensive diversification of *Vulpes* species (*V.praeglacialis, V. beihaiensis etc.*) following collonizations in Eurasia in the Pliocene (Qiu et Tedford 1990). Members of the extant taxa *V. vulpes* and *V. lagopus* came back to the New World in the Pliocene during the last glacial cycle (Kurtén et Anderson 1980). Species of *Vulpes* also live in Africa with the first fossil record of *Vulpes riffautae* dating to the late Miocene (de Bonis 2007).

Phylogenetic relationship: Based on the phylogeny by Wang et al. (2008), the genus *Vulpes* is a sister taxon of the genera *Metalopex* and *Urocyon*. The morphological study by Tedford et al. (1995) indicates that *Vulpes* forms a clade with *Urocyon* and *Otocyon* group. Perini et al´s. analysis of combined dataset (2009) shows the sister group relationship between *Vulpes* and *Urocyon*. According to the molecular study (Lindblad-Toh et al. 2005), *Otocyon megalotis* is the most closely related to *Vulpes.* Bardeleben et al´s study (2005) exhibits sister group relationship between *Vulpes* and monophyletic group *Nyctereutes-Otocyon* (for nuclear and combined dataset). One of the combined analyses (Zrzavý et Řičánková 2004) indicates unresolved relationship of *Vulpes* and other taxa.

Monophyly: It is supported (Zrzavý et Řičánková 2004, Bardeleben et al. 2005, Lindblad-Toh et al. 2005, Perini et al. 2009, Tedford et al. 2009).

Type species: ***Vulpes vulpes*** (Linnaeus, 1758) – from the Pleistocene until the recent times (Wang et al. 2008)

Anatomy and morphology: This genus usually does not have distinctive frontal sinus. It has long, low body and narrow muzzle (Nowak 1999). It is not very diversified genus with hypocarnivory dentition (Tedford et al. 2009).

Ecology: Representatives of this genus occupy wide range of habitats from desert (*V. zerda*, *V. rueppellii, V. chama)* through savannahs (*V. pallida, V. velox*), steppes (*V. cana, V. corsac*) and forests (*V. vulpes*) to arctic tundra (*V. lagopus*) (Nowak, 1999). Most of the members of the genus *Vulpes* are mesocarnivorous (Tedford et al. 2009) solitary hunters (Nowak, 1999).

TRIBE CANINI Fischer de Waldheim, 1817

This sister tribe of Vulpini contains fossil and extant species of several wolf-like genera (subtribe Canina) such as *Eucyon, Canis, Cuon, Lycaon* and also members of South American lineage (subtribe Cerdocyonina) – *Chrysocyon, Speothos, Theriodictis, Lycalopex* and *Dusicyon*. Morphological analysis placed also phylogenetically unresolved genus *Nyctereutes* in this tribe (Tedford et al. 1995). However, molecular and combined studies do not support this claim (Bardeleben et al. 2005, Zrzavý et Řičánková 2004). First members of tribe Canini appeared during the second half of the Miocene in North America (Tedford et al. 2009, Wang et al. 2008).

Monophyly: It is supported by Zrzavý et Řičánková (2004) Lindblad-Toh et al. (2005) and Perini et al. (2009). According to the morphological study by Tedford et al. 1995, the monophyly is disrupted by position of *Nyctereutes* within this tribe. However, Prevosti´s phylogeny (2009) suggests that *Nyctereutes* forms, together with *Otocyon*, a sister clade of the monophyletic Canini.

SUBTRIBE CERDOCYONINA Tedford, Wang and Taylor 2009

South American tribe is a highly diverse group of small to medium-sized omnivores, which comprises also some extinct large hypercanivorous species (Prevosti 2009). This subtribe is represented by 28 species classified in 10 genera (Berta 1987). Phylogenetically unresolved genus *Nyctereutes* is sometimes placed into this subtribe (Tedford 1995, Wang et al. 2008). The most primitive genus of tribe Canini, the genus *Cerdocyon* from the earliest Pliocene, is a part of this lineage. The ancestors of South American canid fauna occurred in North America before the rise of the Panama Isthmus (Perini et al. 2009, Tedford et al. 2009).

Monophyly: It is supported by Bardeleben et al. (2005), Lindblad-Toh et al. (2005) and Perini et al. (2009). The position of *Nyctereutes* within Cerdocyonina based on the morphological analyses (Tedford et al. 2005, Wang et al. 2008), remains problematic. Combined analysis by Zrzavý et Řičánková (2004) shows uncertain position of the *Speothos-Chrysocyon* clade within South American canids, because the trees based on various characters shows various results.

Genus *Protocyon* Giebel 1855

Distribution: from the late Pliocene until the second half of Pleistocene in South America (Wang et al. 2008). Records of representatives of the genus *Protocyon* were the oldest among *Cerdocyonina* (Perini et al. 2009).

Phylogenetic relationship: This taxon is, together with other South American fossils (*Theriodictis spp.* and "*Canis*" gezi), most closely related to the extant *Chrysocyon* and *Speothos* (Prevosti 2009). Berta (1988) proposed close relationship between *Theriodictis-Protocyon*, *Dusicyon* and *Lycalopex*.

Monophyly: Prevosti (2009) supports monophyly of *Protocyon*. However, Perini et al´s study (2009) suggested that *Theriodictis platensis* is an internal group of *Protocyon.*

Type species: *Protocyon troglodytes* (Lund, 1838)

Anatomy and morphology: Representatives of this genus have large frontal sinus. However it does not penetrate into the postorbital process and extends posteriorly to the fronto-parietal suture as in *Canis*. Moreover, it has wide palates, absent hypoconid on first and second upper molars and reduced or absent protocone on fourth lower premolar. They were middle-sized hypercarnivorous canids weighting around 20 kg (Berta 1988, Van Valkenburgh 1991).

Ecology: Canids from genus *Protocyon* were able to hunt large mammals (camelids, equids etc.) in open landscape during the Pleistocene (Prevosti et al. 2005).

Genus *Theriodictis* Mercerat 1891

This genus includes 3 extinct species (Berta 1988, Prevosti 2009).

Distribution: during the Pleistocene in South America (Wang et al. 2008).

Phylogenetic relationship: This genus is a paraphyletic taxon most closely related to the extant genera *Speothos* and *Chrysocyon* (Perini et al. 2009, Prevosti 2009).

Monophyly: It is not supported. According to the Prevosti (2009), *T. floridanus* is the most closely related to *Chrysocyon brachyurus*, whereas remaining *Theriodictis* species are related to *Protocyon.*

Type species: ***Theriodictis platensis*** Mercerat, 1891 - during the Pleistocene in South America (Wang et al. 2008).

Anatomy and morphology: Species of this genus exhibit wide palate, deep zygomata with wide masseteric scar, reduced hypocone on first two upper molars, anteroposteriorly broad and dorsoventrally low coronoid process and large frontal sinus penetrating postorbital process and extending posteriorly to the fronto-parietal suture (Berta 1988).

Ecology: They were large hypercarnivory canids with average weight around 35 kg (Van Valkenburgh 1991), which were able to utilize carcasses of large prey (Berta 1988). They also probably hunted large cervids and camelids, which lived in the South American grasslands during the Pleistocene (Prevosti et Vizcaíno 2006).

Genus Speothos Lund, 1839

This genus includes one fossil and one extant species (Wang et al. 2008).

Distribution: from the late Pleistocene until recent times in South America (Wang et al. 2008).

Phylogenetic relationships: *Speothos venaticus* is most closely related to another South American genus *Chrysocyon* (Bardeleben et al. 2005, Lindblad-Toh et al. 2005, Perini et al. 2009, Zrzavý et Řičánková 2004). According to the combined study (Prevosti 2009), *Speothos venaticus* is closely related to the *Theriodictis-Protocyon* clade. Another combined study (Perini et al. 2009) suggests that fossil *Speothos pacivorus* is the sister taxon of *Protocyon- Theriodictis* lineage. Tedford et al´s morphological study (1995) suggested that *Speothos venaticus* is a sister taxon of *Atelocynus microtis*.

Monophyly: It is not supported. According to the Perini et al.´s phylogeny (2009), *Speothos venaticus*, followed by fossil *Speothos pacivorus*, is the most related to *Chrysocyon brachyurus.*

Type species: ***Speothos venaticus***, (Lund, 1842) - from the late Pleistocene until recent times in South America (Wang et al. 2008).

Anatomy and morphology: It is a small canid weighting around 6 kg (Nowak 1999). Berta (1984) mentioned that the fossil species *S. pacivorus* was larger. Lack and recuction of molars is typical for the *Speothos* dentition. *S. venaticus* usually has only one upper molar. It also has wide palate, short rostrum and small frontal sinus not penetrating the postorbital process (Berta 1984).

Ecology: These hypercarnivory canids were highly social. They lived in wet forests of South America and hunted in packs (Nowak 1999).

Genus *Chrysocyon* Smith, 1839

Into this genus belongs only one known extant species *Chrysocyon brachyurus* (Berta 1988). Tedford et al. (2009) and (Prevosti 2009) also mentioned a one new fossil species *Chrysocyon nearcticus*.

Distribution: from the early Pliocene in North America (Berta 1987) until recent times in South America (Berta 1987, Wang et al. 2008).

Phylogenetic relationships: Several studies (Bardeleben et al. 2005, Lindblad-Toh et al. 2005, Perini et al. 2009, Zrzavý et Řičánková 2004) suggest *Speothos venaticus* as the most closely related species to *Chrysocyon*. The newest molecular phylogeny indicated that the Falkland Island dogs (*Dusicyon*) are a sister taxa of *Chrysocyon* followed by *Speothos venaticus* (Austin et al. 2013). According to Tedford et al. (1995), *Chrysocyon* has unresolved relationship within South American clade.

Monophyly: It is not supported. According to the Prevosti´s phylogeny (2009), *C. nearcticus* is a sister taxon to *Lycalopex fulvipes* and *C. brachyurus* is most closely related to *Theriodictis floridanus*.

Type species: *Chrysocyon brachyurus* (Illiger, 1815) – from the early Pliocene until recent times in South America (Berta 1987).

Anatomy and morphology: Canids of genus *Chrysocyon* exhibit large frontal sinus penetrating the postorbital process, dorsoventrally narrow and anteroposteriorly high coronoid process, and very broad first two upper molars (Berta 1988). The upper carnassials are reduced in comparison with representatives of genus *Canis*. Genus *Chrysocyon* can be distinguished from other South American canids by the sagittal crest forming a prominent ridge (Dietz 1985).

Ecology: This omnivorous canid, which usually eats small mammals, birds, fruits and insects, lives in grasslands and savannahs of South America (Nowak 1999). It does not have typical chasing hunting strategy as many other canids, but rather pounce on its prey as foxes (Kleiman 1972).

Genus *Lycalopex* Burmeister, 1854

Genus *Lycalopex* is comprised of five extant species and one fossil species (Wang et al. 2008).

Distribution: From the Pleistocene until recent times in South America (Wang et al. 2008).

Phylogenetic relationships: According to molecular phylogenetic studies (Bardeleben et al. 2005, Lindblad-Toh et al. 2005) as well as Perini et al´s (2009) combined analysis, *Cerdocyon* and *Atelocynus* are the most closely related to *Lycalopex*. As suggested by both phylogenies of South American canids (Perini 2009, Prevosti 2009) and Tedford et al. (1995), *Dusicyon* is related to *Lycalopex*. However, the newest molecular phylogeny placed *Dusicyon* as a sister taxon of *Chrysocyon* (Austin et al. 2013).

Monophyly: According to the latest molecular phylogeny (Austin et al. 2013), the monophyly is supported. However, three combined studies (Perini et al. 2009, Prevosti 2009, Zrzavý et Řičánková 2004) indicated *Dusicyon* as an ingroup of *Lycalopex*. Prevosti (2009) further added *C. nearcticus* as a sister taxon of *L. fulvipes*.

Type species: ***Lycalopex culpaeus*** (Molina, 1782)

Anatomy and morphology: Species of this genus have simple canines and premolars (Clutton-Brock et al. 1976). The weight of these canids ranges from 4 to 13 kg. The largest member is *Lycalopex culpaeus*, the smallest is *Lycalopex sechurae* (Nowak 1999).

Ecology: All species are omnivorous inhabitants of rather dry and open landscapes (Nowak 1999).

Genus *Dusicyon* Smith, 1839

This genus of Falkland Islands dogs includes one extinct a one recent (but eliminated) species (Berta 1987).

Distribution: from the late Pliocene until the 20th century in South America and Falkland Islands (Wozencraft 2005, Wang et al. 2008).

Phylogenetic relationship: According to the newest molecular study (Austin et al. 2013), *Dusicyon* is the most closely related to the maned wolf (*Chrysocyon brachyurus*). Other analyses (Perini 2009, Prevosti 2009) suggested close relationship with *Lycalopex*. Tedford et al. (1995) indicated sister group relationship between *Dusicyon* and *Lycalopex*.

Monophyly: The latest molecular (Austin et al. 2013) and combined (Prevosti 2009) phylogenies supported the monophyly of this genus.

Type species: *Dusicyon australis* (Kerr, 1792)

Anatomy and morphology: They have broad muzzle and large skull with inflated frontal sinus (Nowak 1999). Adult males of *Dusicyon* weighted on average 10-15 kg (Prevosti et Vizcaíno 2006).

Ecology: It usually hunted birds on the Falkland Islands (Nowak 1999).

Genus *Nyctereutes* Temminck, 1839

This problematic genus comprises of one extant and 7 fossil species (Wang et al. 2008, Geraads et al. 2010).

Distribution: from the late Miocene until recent times. The common ancestor of this genus probably originates in *Cerdocyon-Nyctereutes* lineage in North America. Important lineage (*N. sinensis, N. megamastoides*) became widespread in Eurasia. It probably gave rise to the extant species *N. procyonoides*. There were also African *Nyctereutes* species (*N. abdeslani, N. terblanchei*) (Wang et al. 2008).

Phylogenetic relationship: Genus *Nyctereutes* is placed as a sister taxon to South American genus *Cerdocyon* according to the phylogeny by Tedford et al. (1995). However molecular (Lindblad-Toh et al. 2005) and combined (Zrzavý et Řičánková 2004) approach placed this genus as the basal lineage of Vulpini. Bardeleben et al. (2005) molecular phylogeny placed *Nyctereutes* as closely related to *Vulpes.* The Prevosti´s combined analysis (2009) indicated that *Nyctereutes* and *Otocyon* form a monophyletic group related to Canini.

Monophyly: non tested

Type species: ***Nyctereutes procyonoides*** (Gray, 1834) – from the Pliocene until recent times (Wang et al. 2008).

Anatomy and morphology: It exhibits short narrow muzzle, distinct rounded subangular lobe (Ward et Wurster-Hill 1990) and reduced blades of carnassials (Ewer 1998). It´s a small canid weighting around 4-6 kg (Nowak 1999).

Ecology: *Nyctereutes procyonoides* is an omnivorous forest species with rather nocturnal activity (Nowak 1999).

SUBTRIBE CANINA Fisher de Waldheim, 1817

This subtribe includes five genera with around 40 extant and fossil species (Wang et al. 2008). The oldest genus of this subtribe is a genus *Eucyon* (Wang et al. 2008, Tedford et al. 2009). Two morphological synapomorphies characterize this subtribe: dorsoventrally strongly arched zygoma and presence of second posterior cusp on p4 (Tedford et al. 2009).

Monophyly: It is supported by Bardelen et al. 2005, Lindblad-Toh et al. 2005, Perini et al. 2009, Prevosti 2009, Tedford et al. 1995, 2009 and Zrzavý et Řičánková 2004.

Genus *Eucyon* Tedford and Qui, 1996

This fossil genus is comprised of six species (Wang et al. 2008).

Distribution: from the late Miocene until the middle Pliocene (Wang et al. 2008). In the late Miocene, the genus *Eucyon* expanded to the Old World, which is designated as the "*Eucyon* event" (Sotnikova and Rook 2010). This expansion occurred despite the high sea level, during the warm period via the Beringia land bridge affected by repeated uplift.

Phylogenetic relationship: According to Tedford et al. (2009) and Prevosti (2009), *Eucyon* is a most related taxon to *Canis ferox.*

Monophyly: non tested

Type species: ***Eucyon davisi*** (Merriam, 1911) - from the late Miocene until the beginning of Pliocene in North America (Tedford et al. 2009).

Anatomy and morphology: This genus exhibits a typical evolutionary trend toward enlargement of the frontal sinus of skull (Wang et al. 2008), which was, however, still smaller than frontal sinus of the representatives of the genus *Canis* (Tedford et al. 2009). This is related to foraging adaptations. Frontal sinus provides protection of skull against the pressure exerted during the processing of food. Most of the representatives were coyote-size canids weighting around 15 kg (Wang et al. 2008).

Ecology: Species of the genus *Eucyon* occurred during the late Miocene, when the latest borophagines were already in decline (Finarelli 2007, Wang et al. 2008). The first species of *Eucyon* occurred, when open grasslands extended in North America. They were more cursorial than borophagines, which enables them to chase and catch omnipresent herbivores in grasslands (Wang et al. 2008).

Genus *Canis* Linnaeus, 1758

The genus *Canis* includes 28 fossil and extant species (Wang et al. 2008). The first two species of *Canis* (*C. ferox* and *C. lepophagus*) appeared in North America, representing the initial cladogenesis within the genus. *Eucyon davisi* was their direct ancestor (Wang et al 2008).

Distribution: from the late Miocene until recent times (Wang et al. 2008). It orriginated in North America and dispersed to Eurasia, Africa and South America, where it became extinct during the latest Pleistocene (Macdonald et Sillero-Zubiri 2004). Large species of the genus *Canis*, which resembled wolves, had their origins in Eurasia (Tedford et al. 2009). At the beginning of the Pleistocene the genus *Canis* underwent another expansion,which was connected with the rise of steppe biomes in North America (Wang et al. 2008).

Phylogenetic relationship: Several studies (Lindblad-Toh et al. 2005, Perini et al. 2009, Prevosti 2009, Tedford et al. 2009, Zrzavý et Řičánková 2004) claim that *Lycaon* and *Cuon* belong to *Canis*, rendering the latter genus paraphyletic. The basalmost extant species (*C. adustus* and *C. mesomelas*) were consequently, proposed to be reclassified as a separate genus *Lupulella* (Zrzavý et Řičánková 2004).

Monophyly: According to the combined (Zrzavý et Řičánková 2004, Perini et al. 2009, Prevosti 2009) and morphological (Tedford et al. 2009) phylogenies, *Lycaon* and *Cuon* are internal group of *Canis*, which refutes it monophyly. Moreover, Tedford et al. (2009) placed *Xenocyon* within the genus *Canis*. The Bayesian analysis of combined nuclear and mitochondrial dataset thus provided the only support for the monophyly of *Canis* (Bardeleben et al´s study 2005)

Type species: *Canis lupus* Linnaeus, 1758 - The oldest record of *Canis lupus* originates from Beringia areas in the early-medial Pleistocene. Wolves reached the mid-latitude areas of North America together with large ungulates during the last glacial cycle (Tedford et al. 2009).

Anatomy and morphology: There are several synapomorphies, which link genera *Canis, Lycaon, Cuon* and *Lycaon*. The most important is large frontal sinus, which penetrates the postorbital process and intrudes posteriorly into the frontoparietal suture. Typical anatomic traits of dentition in this genus are second posterior cusp on fourth lower premolar and linking between entoconid and hypoconid on first lower molar by cristids (Tedford et al 2009).

Ecology: The first representatives (*C. ferox*, *C.thooides*, *C. lepophagus)* were small rather hypocarnivory species (Wang et al. 2008). The first large canid in North America was *Canis armbrusteri*, which exhibited hypercarnivorous adaptations (Tedford et al. 2009). This species appeared after the extinction of large borophagines and emergence of the open grasslands (Wang et al. 2008), therefore the *Canis* species had wide range of empty niches. The following huge species *C. dirus* was an important predator of megafauna in North America during the Pleistocene. These largest representatives of *Canis* weighted around 60 kg and their shoulder height was around 75 cm (Wang et al. 2008). Dentition of this species was distinctively stronger than dentition of other species of genus *Canis* (Wang et al. 2008). According to the osteological study (Van Valkenburgh et Hertel 1993), dire wolves very often and systematically fed on carcasses and they probably competed with saber-toothed cats and lions.

Genus *Xenocyon* Kretzoi, 1938

According to the Tedford (2009), this genus includes two fossil species.

Distribution: From the medial Pliocene until the late Pleistocene in Eurasia. In the Pleistocene *Xenocyon* also reached the North American continent (Tedford et al. 2009).

Phylogenetic relationships: The Tedford et al. (2009) suggested the close phyletic relationship between *Xenocyon* and *Lycaon-Cuon* lineage.

Monophyly: non tested

Type species: *Xenocyon lycanoides* Kretzoi, 1938 – from the medial Pliocene until the late Pleistocene (Tedford et al. 2009).

Anatomy and morphology: The genus was hypercarnivorous with a deep and robust horizontal ramus. Unlike the *Lycaon* and *Cuon*, this genus did not lack the third lower molar (Tedford et al. 2009).

Ecology: The oldest records came from the eastern China from the medial Pliocene. In the same time the species of genus *Canis* were widespread in Eurasia. Species of *Xenocyon* were markedly larger than Canis (Tedford et al. 2009), even larger than modern African hunting dog (Hemmer 2000). *Xenocyon* could have been the great predator of Eurasian Pliocene fauna.

Genus *Lycaon* Brookes, 1827

This African genus is comprises of one extant and one or two fossil species (Wang et al. 2008, Hartstone-Rose et al. 2010).

Distribution: From the late Pliocene until recent times in Africa (Wang et al. 2008, Hartstone-Rose et al. 2010).

Phylogenetic relationships: According to the latest studies (Zrzavý et Řičánková 2004, Tedford et al. 1995, 2009), *Lycaon* is the sister taxon of the Eurasian genus *Cuon.* However, the molecular studies (Bardeleben et al. 2005, Lindblad-Toh et al. 2005) and also one combined study (Perini et al. 2009) do not indicate sister relationship between them. The sister taxon of extant African hunting dog could be a Plio-Pleistocene species *Lycaon sekowei* (Hartstone-Rose et al. 2010), but it has not yet been supported by any phylogenetic analysis yet.

Monophyly: non tested

Type species: *Lycaon pictus* (Temninck, 1820) **–** from the late Pleistocene until recent times (Wang et al. 2008).

Anatomy and morphology: African hunting dog has extremely hypercarnivorous dentition: sharp blades of carnassials, lack of lower and upper third molars (Hillson 2005), trenchant heel (large hypoconid on centrall position) on lower first molar (Van Valkenburgh 1991) and massive and strong skull (Wang et al. 2008). The average weight of this canid is 28 kg (Clutton-Brock et al. 1976).

Ecology: *Lycaon pictus* is a species of open African landscape living in packs, which are capable to hunt wildebeest, kudu and other great antelopes (Ewer 1998).

Genus *Cuon* Hodgson, 1838

This genus comprises one extant (Wang et al. 2008) and one fossil species (Pocock 1936).

Distribution: from the Pleistocene until recent times in Eurasia (Wang et al. 2008).

Phylogenetic relationship: According to the morphological (Tedford et al. 1995, 2009) and combined (Zrzavý et Řičánková 2004) study, *Cuon* is the sister taxon of Afrotropical *Lycaon.* However, the recent molecular (Bardeleben et al. 2005, Lindblad-Toh et al. 2005) and combined (Perini et al. 2009) studies do not support a sister group relationship between these two taxa.

Monophyly: non tested

Type species: ***Cuon alpinus*** (Pallas, 1811)

Anatomy and morphology: Dhole has broader and shorter rostrum in comparison with species from the genus *Canis* (Wang et al. 2008). With *Lycaon* it shares similar traits of hypercarnivorous dentition: lack of third upper and lower molars, sharp blades of carnassials (Hillson 2005) and trenchant heel on first lower molar (Van Valkenburgh 1991). The average weight of adult males is 16 kg (Clutton-Brock et al. 1976).

Ecology: Dholes are pack-hunters of large prey, such as deer, wild pigs, antelopes etc. These canids inhabit many types of habitats, but avoid desert (Nowak 1999).

1.5 Aims of the study

1. Reconstruct phylogeny of recent and fossil species of Caninae
2. To examine possible causes of the evolution of cooperative behavior in Caninae

2 METHODS

2.1 Species and characters in matrix

The original matrix comes from my bachelor thesis (Okřinová 2010) and is based on the data obtained from phylogenetic study of recent species of canids (Zrzavý et Řičánková 2004). It contained 81 fossil representatives of the family Canidae: 57 Caninae and 27 Hesperocyoninae, which have been characterized by 85 morphological traits acquired from literature. This matrix (Okřinová 2010) was supplemented, adjusted and then used for the present phylogenetic analysis.

Altogether 196 species of the extant and extinct carnivorans were selected for the present analysis. They included 189 canids (27 hesperocyonines, 66 borophagines, 69 canines) and 5 non-canid outgroups, namely, *Ailuropoda melanoleuca*, *Mustela* sp., *Procyon lotor*, *Ursus* sp. and *Miacis pacivorus*. Morphological characteristics of these outgroups were filled into the matrix according data available from literature. The tribe and genus-level classification was adopted from Wang (1994), McKenna and Bell (1997), Wang et al. (1999), and Tedford et al. (2009). All species of the recent Canidae were included in the present analysis as 'operational taxonomic units', except for the problematic *Canis lycaon*/*C. rufus* complex (Reich et al. 1999, Wilson et al. 2000, Mech and Federoff 2002, Nowak 2002), which is represented by three nominal species (*C. lupus*, *C. rufus*, *C. latrans*) probably underrepresenting the real diversity of North American „wolves". The Falkland Islands wolf (*Dusicyon australis*), which was exterminated as recently as 1876 was treated as a Recent species here.

Current matrix is comprised of 17092 morphological (212), reproduction, ontogenetic, ecological, behavioural (77), cytogenetic (12) and genomic (16790) characters obtained from literature (see: List 1 in Appendix). Nucleotide sequences of 21 nuclear protein-coding (APOBE29S1, APOBE29S2, BDNF, BRAC1S1, BRACS2, CHST12, CMKOR1, RAG1, TMEM20, VANGL2, VWF, Ch14, Ch21, Ch24, FGFR, CHRNA1, CYPIA1, FES, GHR, VTN, TRSP) and 3 mitochondrial genes (cyt b, COI and COII - "MOL" hereinafter) were obtained from Genbank (see Bardeleben et al. 2005, Lindblad-Toh et al. 2005) and aligned using multiple alignment program MAAFT 7 (Katoh and Standley 2013).

2.2 Phylogenetic analysis

The maximum-parsimony (MP) analysis was applied to MOR, molecular, and combined data matrices (NONA version 2.0, Goloboff 1999: heuristics, option ‘hold 10000 mult* 100 hold/100’unconstrained search strategy with TBR branch swapping). For Recent species (see ‘complete-species analysis’ below) Bayesian analyses were performed as well, using MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) and j model test 0.1.1 (Posada 2008).

To investigate the topological changes caused by different species samples, several experimental cladistic analyses were performed. The different data partitions to be combined in simultaneous analyses covered different species spectra (192 species for MOR, 35 for MOL). We performed (i) separate analyses for individual data partitions; (ii) combined analyses of all morphological characters and sequences of all the 192 recent and fossil taxa, introducing missing values for the absent sequences (“all-species analysis”); (iii) combined analyses of all character partitions and the 35 recent species for which both MOR and MOL data are available (“complete-species analysis”).

In addition, three ‘experimental’ maximum-parsimony analyses were performed in context of combined dataset.

(1) The modified ‘slow-fast’ (SF) method (Brinkmann and Philippe 1999) was used to remove MOR characters that were supposedly responsible for stochastic information noise. New datasets were constructed, in which only characters with no observed variability within one of the five well-supported clades were included. The analysed clades included *Urocyon*, *Vulpes*, *Lycalopex*, *Lupullella* (*Canis adustus-C. mesomelas*) and *Canis* s.str. (*C. simensis*, *C. aureus*, *C. latrans*, *C. rufus*, *C. lupus*).

(2) In the ‘congruence analysis’ (compare Gaubert *et al*. 2005), all MOR characters‘ retention indices (*ri*) were computed for the „complete-species“ morphological, combined, and molecular trees (ri_{MOR}, ri_{COMB}, and ri_{MOL}, respectively). The MOR characters were then classified as (i) ‘congruent’ with the molecular ones ($ri_{\mathrm{MOR}} < ri_{\mathrm{COMB}}$ or $ri_{\mathrm{COMB}} < ri_{\mathrm{MOL}}$), (ii) ‘constant’, or context-independent ($ri_{\mathrm{MOR}} = ri_{\mathrm{COMB}} = ri_{\mathrm{MOL}}$), and (iii) ‘convergent’, or conflicting with the molecular information ($ri_{\mathrm{MOR}} > ri_{\mathrm{COMB}}$ or $ri_{\mathrm{COMB}} > ri_{\mathrm{MOL}}$). Consequently, all “convergent” MOR characters were excluded from the analysis.

(3) All MOR characters either hypothesized as linked with the "hypercarnivory" or shared exclusively by *Speothos, Lycaon* and *Cuon* were excluded.

Finally, the four MOR datasets (all characters, SF, non-convergent and non-hypercanivorous) were compared with results of the purely molecular (unrooted) analysis, using the incongruence length difference (= ILD; NONA) metrics. The SF MOR dataset was found to be best congruent with the MOR tree topology and together with the original all-character dataset the SF dataset were used for all further combined analyses including also fossil species.

The species whose position was highly unstable, and/or whose presence/absence caused important topological changes were identified (all fossil species, plus a few poorly known Recent species, namely, *Vulpes ferrilata*, *V. bengalensis* and *V. pallida*, and recently extinct *Dusicyon australis*). Topological effects of including/removing the species identified as 'problematic' were tested by constructing an unrooted 'backbone tree' that included only the 'unproblematic species', to which individual 'problematic" species were appended in one-by-one manner (Siddall and Whiting 1999).

2.3 Trees used for ancestral reconstructions

For the following analysis, I used the topology of weighted tree (Mor:Mol = 1:100) in two modifications. 1) Complete phylogeny of Canidae with topology of Borophaginae and Hesperocyoninae taken from literature (Wang 1994, Wang et al. 1999) was used for ancestral recostrucion of discrete traits (i.e. osteological characters). The adjusted tree including only species with available values for continuous traits (brain volume and body size). This modified tree was transformed into a phylogeny scaled to geologic in programme Mesquite 2.75 (Maddison et Maddison 2011). The data about the time of origin and the time of extinction for species from all subfamillies were taken from previous phylogenetic studies (for Caninae: Perini et al. 2009, Tedford et al. 2009, for Borophaginae: Wang et a. 1999, for Hesperocyoninae: Wang 1994). As a result, we obtain a tree for ancestral reconstruction including the branch lengths (see Fig. 6 in Appendix). The branch lengths were estimated as a distance between the time of the extinction particular species and time of the origin it´s ancestor or as a distance between the times of origin of two close lineages.

2.4 Characters used for ancestral reconstructions

For the traits, which are not available for fossil species, the best correlated osteological indicators were used based on the principal component analysis (see: List 2 in Appendix). Evolutionary relationship between selected indicators with significant phylogenetic signal and behavioural traits (cooperative hunting and hunting of large prey) was examined tracing the character history onto the phylogeny of recent Caninae (see the List 4 in Appendix). The osteological indicators with the evident evolutionary connection were used for the ancestral reconstruction of the examined trait. The changes in evolution of brain and body size were observed by the parallel tracing these on the cladogram of Canidae. I used the values of brain volume and body size by Finarelli et Flynn (2009) and Damasceno et al. (2013). The category 26-38,5 kg was used for indicating a real large canids, because the the lower category (13-25,5kg) may also include quite small species. Brain and body size values reconstructed at each node were used for estimation of encephalization quotient. The selected osteological correlates of a particular foraging strategy (see: Table 11 in Appendix) were used for tracing on the cladogram of Canidae, where the evolution of brain size was marked.

2.5 Methods used for evolutionary analyses

2.5.1 Principal component analysis

Selected characters with a minimum of missing data were put into the matrix with 17 recent species of *Canidae* (see: Table 9 in Appendix), which was used for following analysis. Only limited number of recent species was used, because the PCA can not work with the missing data in matrix. The resulting matrix included 17 samples and 64 variables (see: List 2 in Appendix). For the analysis with encephalization quotient, the matrix with 13 samples (see: Table 10 in Appendix) and 30 variables (see: List 3 in Appendix) was used. Multivariate data were analysed by PCA method in Canoco for Windows (ter Braak et Šmilauer 1998) and then visualized by Canodraw programme (Šmilauer 1992).

2.5.2 Randomization test (Abouheif 1999)

I used the randomization test (Abouheif 1999) for testing phylogenetic conservatism of discrete traits. The values gained from this analysis were compared with the real numbers of parsimony steps for each character by the percentile analysis (95% credibility intervals) (Antonelli 2009). The programme Mesquite 2.75 (Maddison et Maddison 2011) was used for the analysis of seven traits selected from the principal component analysis (see: List 4 in Appendix).

2.5.3 Lambda method and K statistics in R (package phytools)

I tested the phylogenetic signal for continuous traits (brain volume and body size) in programme R 3.0.1 using the package phytools (Revell, 2012). This package is able to compute phylogenetic signal by the Pagel (1999) lambda method and K statistics (Blomberg et al. 2003). Lambda is a correlation factor, which indicates the value of similarity among species characters relative to values expected under Brownian motion (λ=1 shows that the phylogeny suitably predict the character similarity of species, dependence among species traits corresponds with the expectation, λ=0 means the independent relation between phylogeny and the similarity of characters among species) (Pagel 1999, Freckleton et al. 2002). K-value statistical test is based on the pattern of character similarity relative to a null model of variation. Brownian motion is also expectation for this statistics. In case that K is not significant, the evolution of traits was not influenced by phylogeny. The value of K=1 means that the evolution of particular trait correspond with phylogeny. (Blomberg et al. 2003). When K is lower than 1, closely-related species are resembled each other less than expected by Brownian model of evolution. This phenomenon could be caused by measurement error, adaptive evolution leading to homoplasy in distant lineages of the phylogeny or as result of strong stabilizing selection to a unique adaptive peak (Revell et al. 2008). On the other hand, when the K is higher than 1 closely-related species are more similar than expected by a Brownian model of evolution. This cause is interpreted as phylogenetic conservatism (Blomberg et al. 2003).

2.5.4 Parsimony ancestral states

For mapping the discrete traits on the acquired phylogeny I used the parsimony ancestral reconstruction with unordered parsimony model in Mesquite 2.75 (Maddison et Maddison 2011).

2.5.5 Squared-change parsimony

For tracing the continuous traits on phylogenetic tree I used the squared-change parsimony algorithm in programme Mesquite 2.75 (Maddison et Maddison 2011). This method is based on the minimizing the sum of squared changes on a tree and the lengths of branches are taken into account (Maddison 1991).

2.5.6 Encephalization quotient

For better interpretation of the results brain volume and body size optimization, I computed the encephalization quotient (EQ) as a ratio between observed and expected brain volume (see: Table 12 in Appendix), according to the Radinky´s (1977) equation: $EQ = \text{brain volume}/0{,}12\ (\text{body size})^{0{,}67}$.

3 RESULTS

3.1 Phylogenetic analysis of Caninae

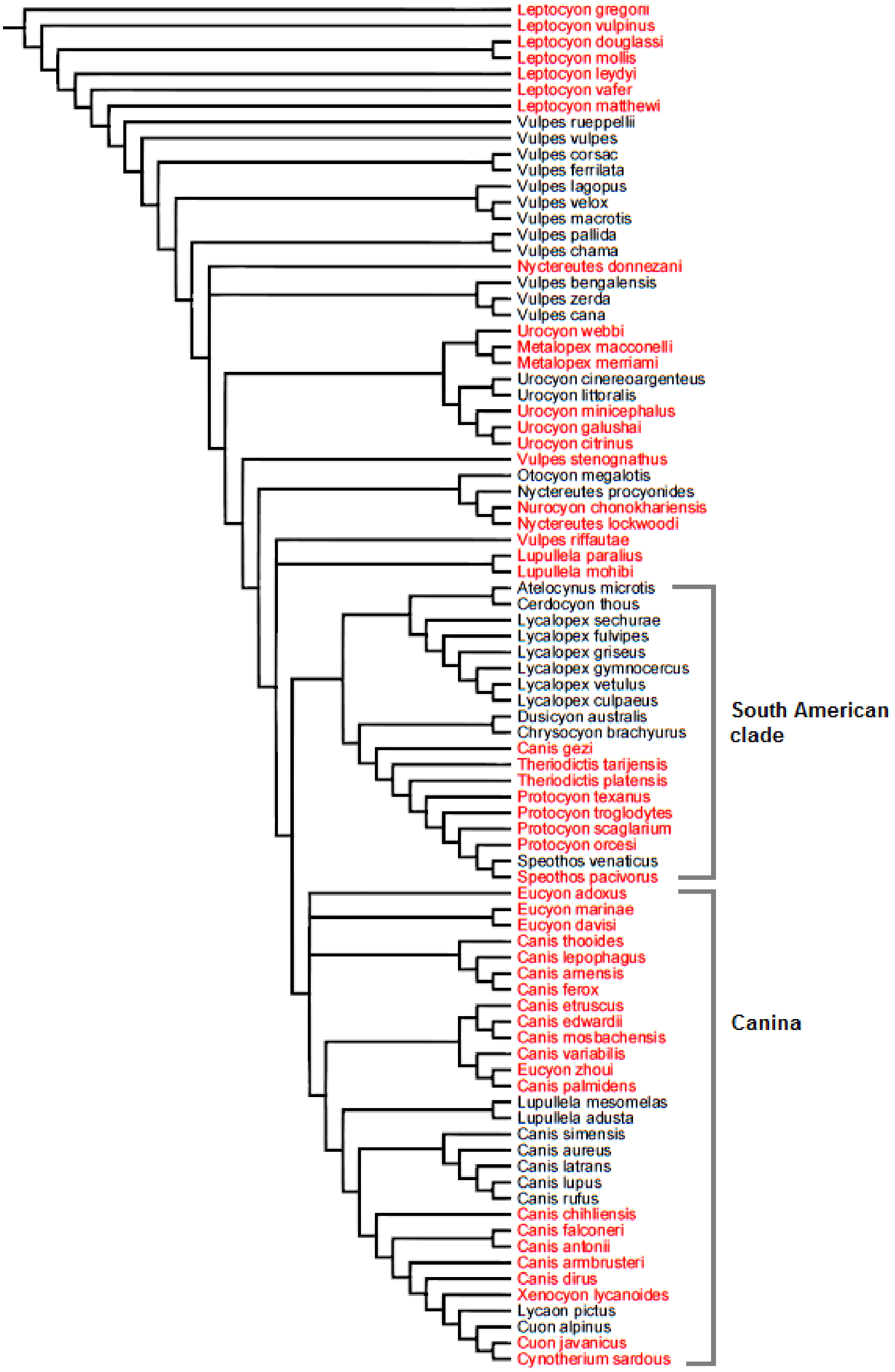

Fig.1. Phylogeny of Caninae. Majority-rule consensus from MP analysis on combined morphological and molecular characters, unweighted over transitions. (red names – fossil species).

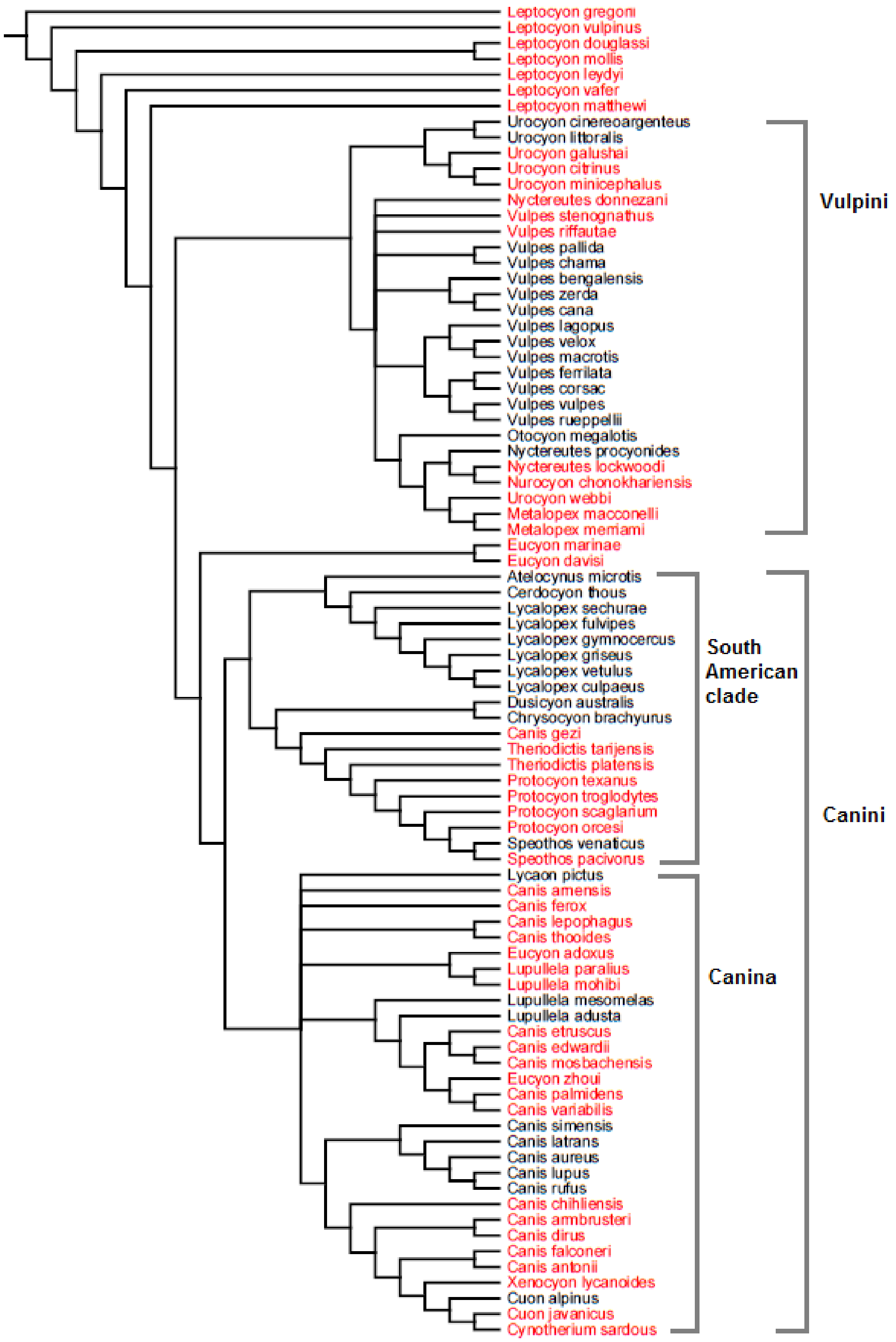

Fig.2. Phylogeny of Caninae. Majority-rule consensus from MP analysis on combined morphological and molecular characters, weighted over transitions (Mor:Mol = 1:100). (red names – fossil species).

3.1.1 *The unweighted tree*

The tree (see: Fig 1) indicates that the base of subfamily Caninae is formed by paraphyletic group including *Leptocyon* and *Vulpes*. There is no evidence for the monophyly of *Vulpes* and also for the whole Vulpini. Moreover, division of the Caninae into the fox-like (Vulpini) and dog-like (Canini) is not evident in the present tree owing to possible (but weakly supported) position of *Vulpes riffautae* at the base Canini. On the other hand, the main subclades (South American canids and Afro-Holarctic wolf-like species) of Canini are monophyletic and well-supported. Monophyly of *Urocyon* is uncertain as *Metalopex* seems to be nested within the former genus (as a sister group of *U. webbi*). The traditionally problematic genera *Otocyon* and *Nyctereutes* exhibit sister-group relation in this tree; however, *Nuroyon chonokhariensis* is nested within *Nyctereutes* (a sister species of *N. lockwoodi*), and *N. donnezani* groups within paraphyletic *Vulpes.* The *Otocyon-Nyctereutes-Nurocyon* group is then a sister group of the dog-like clade. South American group is divided in two subclades: the first is formed by large fossil species (*Theriodictis* and *Protocyon*) together with *Speothos* and by the *Dusicyon-Chrysocyon* group (*Canis gezi*, the only putative representative of *Canis* in South American canid fauna, belongs here as well, i.e. it is not closely related to the other *Canis* species). The second South American subclade includes *Lycalopex* with the crab-eating and short-eared dogs. This tree does not confirm monophyly of *Canis* as *Eucyon*, *Lycaon*, *Cuon*, *Cynotherium*, and *Xenocyon* are nested within *Canis s.lat.* (*Eucyon* is basal, the other genera forming a clade together with large and hypercarnivorous fossil *Canis* species).

3.1.2 *Differences of weighted tree (Mor:Mol = 1:100) compared to the weighted tree (see: Fig 2)*

Except of the paraphyletic basal lineage formed by species of *Leptocyon*, all fox-like canids form a clade (*Vulpini*), further split into *Urocyon* and *Vulpes-Otocyon-Nyctereutes* subclades (with *Nurocyon* and *U. webbi-Metalopex* belonging into the *Otocyon-Nyctereutes* group). Within the dog-like clade *Eucyon marinae-E. davisi* subclade predates the South American–Afroholarctic split and *Lycaon* is not a member of the group of large-bodied hypercarnivorous species (including e.g. *Canis dirus, C. armbrusteri, Xenocyon, Cynotherium* and *Cuon*).

3.2 Principal component analysis

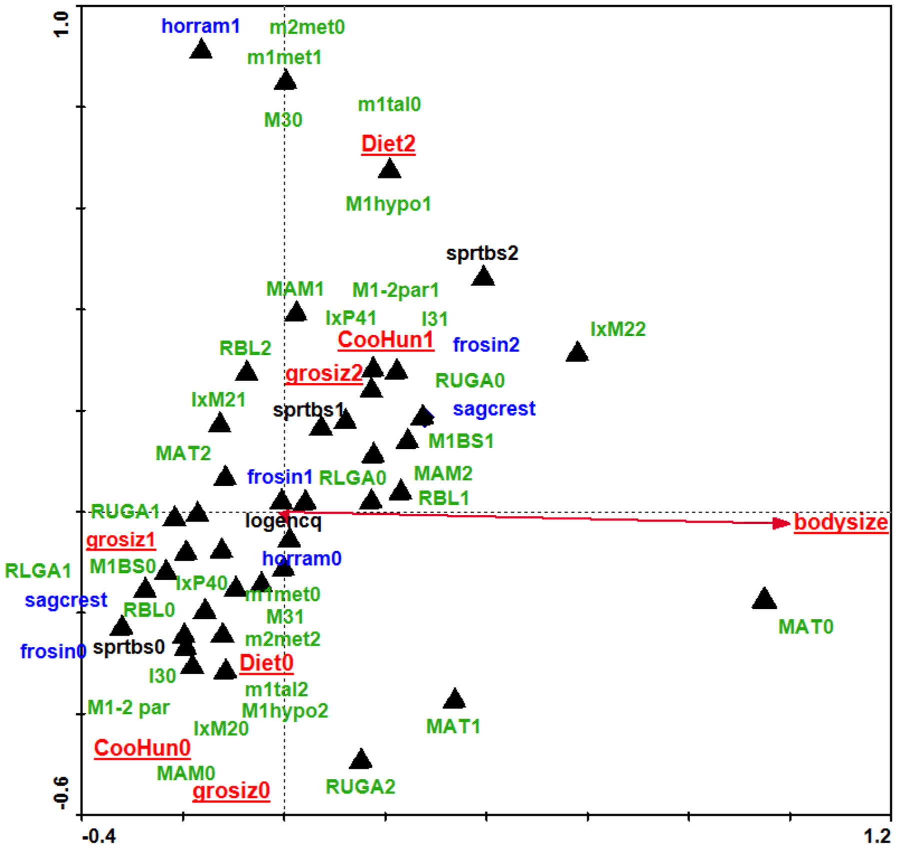

Fig. 3. Correlates for cooperative hunting and large prey hunting (PCA analysis). (green – traits on dentition, blue – traits on skull, red – important indicating traits, black – the others). (The first two axes describe 93% of variance).

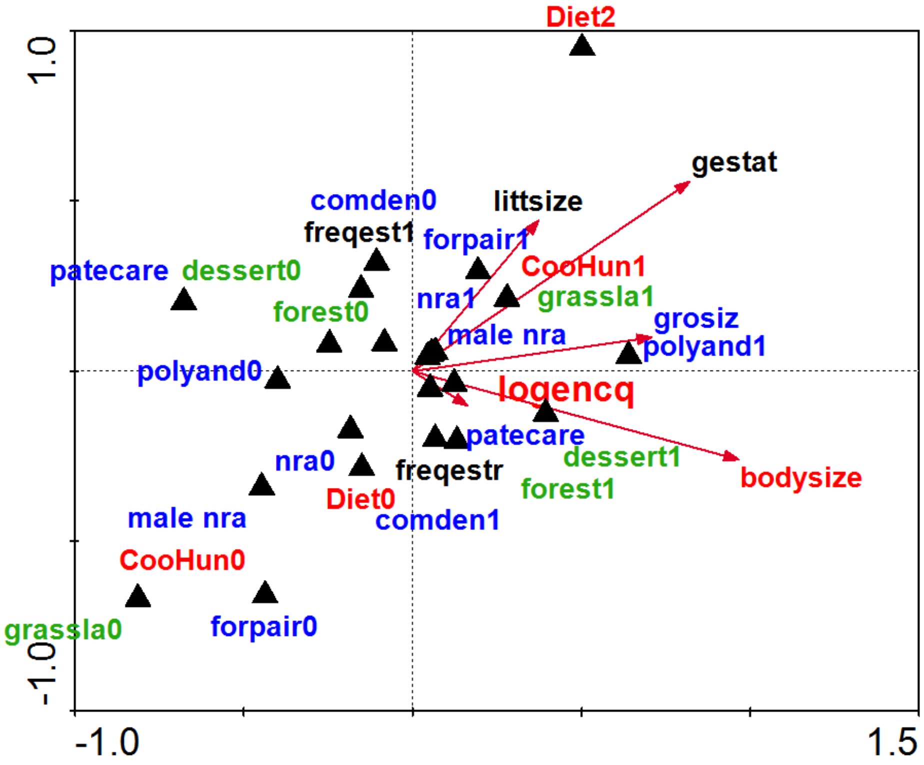

Fig. 4. Ecological, reproductive and etological correlates for log encephalization quotient (PCA analysis). (green – habitat, blue – etological traits, red – important indicating traits, black – reproductive characteristics). (The first two axes describe 90,5 % of variance).

The principal component analysis indicates the best correlates of cooperative hunting and hunting of larger sized prey (see: Fig 3). According to the results, the social hunters have mainly larger incisives (**I31**). They have an enlarged paracone compare to metacone on the first upper molar (**M1-2 par1**) and a small hypocone on the first upper molar (**M1hypo1**). A greatly reduced or absent metaconid on the first and second lower molar (**m1met1 and m2met0**) correlates with the hunting of larger prey as well. Figure 3 also shows that the larger species hunt for larger prey (**sprtbs2**). Cooperative hunters have higher relative resistance of the dentary to bending in the parasagittal plane **(IxP41).** Hunters of larger prey have a fully trenchant talonid on the first lower molar (**m1tal0**). The „**MAM1**“ indicates that canids hunting larger prey have better mechanical function of *musculus masseter* for effective handling of meat. The large frontal sinus penetrating the postorbital process (**frosin2**) is also significantly associated with larger prey hunting.

Moreover, according the PCA, solitary hunters of smaller prey have typically a bicuspid talonid (**m1tal2**) and an enlarged hypocone on the first upper molar (**M1hypo2**). They also have the lower relative resistance of dentary to bending (**IxM20**). Unlike cooperative hunters, the solitary hunters exhibit the lower relative resistance of the dentary to bending in the parasagittal plane (**IxP40**).

However, the analysis does not provide significant support to two characters previously considered as indicators of cooperative hunting, trait describing the proportion of jaws (**horram**) and an absence of the third upper molar (**M30**).

So, seven traits, namely I3, M1-2 paracones, m1 metaconid, m2 metaconid, m1 talonid, frontal sinus, and M1 hypocone (see: Fig 4 – 5 in Appendix) were selected as appropriate osteological indicators for tracing of parallel evolution of cooperative hunting. Other suitable indicators (IxP4 and MAM) were not used, because there is no data for them in fossil species. There is no evident correlate between socio-etological and ecological characteristics for encephalization quotient (see: Fig. 4).

3.3 Randomization test

The randomization test for phylogenetic conservatism (Abouheif 1999) found a significant phylogenetic signal for 3 discrete traits: M 1 - 2 paracones, m1 talonid and frontal sinus. Regarding the remaining characters, none of them exhibits fewer steps than the red line on the left part of the chart, which is the indicator of significant phylogenetic signal.

3.4 Lambda and K statistics in R

Table 1. Values of K and lambda computed in R (phytools) for both traits.

trait	lambda	p	K	p
brain volume	0.9834564	< 0,0001	0.2677961	0.001
body size	0.9320064	< 0,0001	0.2275439	0.007

According to the Pagel´s lambda test, both continuous traits show significant phylogenetic signal. Values of lambda close to 1 mean that these characters evolved in accordance with the Brownian motion model of evolution. These high values of phylogenetic signal could be also interpreted as a phylogenetic conservatism. The significant results for K < 1 in both traits mean that the closely-related species are less similar than is expected by the Brownian motion model of evolution.

3.5 Suitable indicators for ancestral reconstructions

According to the tracing the evolution of cooperative hunting and its osteological correlates, the best indicator of pack-hunting is an enlargement of paracones relative to the metacones on the first two upper molars (see: Fig. 7-8 in Appendix). This character was mapped on the cladogram of Canidae, where the proces of the body size evolution was marked. A fully trenchant talonid on the first lower molar (m1 talonid) and a small hypocone on the first upper molar (M1 hypocone) came out as the best indicator of hypercarnivory from the optimization of cooperative hunting and its osteological correlates on the phylogenetic tree of recent Caninae (see: Fig. 9-10 in Appendix).

3.6 Ancestral reconstructions

3.6.1 Testing of evolutionary relationship between cooperative hunting and body size

The cooperative hunting evolved three times in the evolution of Caninae: 1) Speothos-Protocyon-Theriodictis lineage + *Canis gezi*, 2) lineage of medium to larger size Afro-holarctic wolf-like species, and 3) *Lycaon pictus*. The first case corresponds to the weight category between 26-38,5 kg, and weight category assigned to the cases 2 and 3 is 0,5 – 12,5kg. On contrary, the large canids (category 26-38,5 kg and more) among Caninae emerged five times in Caninae (see: Fig 11 in Appendix), namely in: 1) Speothos-Protocyon-Theriodictis lineage + *Canis gezi*. 2) *Canis ferox*, 3) *Canis edwardi, C. mosbachensis*, 4) *Canis lupus*, 5) *Canis dirus, C. armbrusteri, C. falconeri, C. antonii, Xenocyon lycanoides.*

3.6.2 Testing of the evolutionary relationship between cooperative hunting and hypercarnivory

The parsimony reconstruction method performed on the phylogenetic tree of Canidae, with indicated evolution evolution of the M1 – 2 paracones (osteological indicator of cooperative hunting), suggested that the cooperative hunting originated before the occurrence of hypercarnivory specialization (see Fig. 12 in Appendix.). It shows that a fully trenchant talonid (indicator of hypercarnivory) occured four times during the evolution of Caninae in: 1) *Protocyon troglodytes-Speothos lineage,* 2) *Lycaon pictus*, 3) *Canis dirus*, 4) *Xenocyon lycanoides, Cuon alpinus, C. javanicus, Cynotherium sardous*. The smal M1 hypocone (indicator of hypercarnivory) also emerged four times: 1) *Protocyn-Speothos* lineage, 2) *Lycaon pictus*, 3) *Canis dirus*, 4) *Xenocyon lycanoides, Cuon alpinus, Cuon javanicus*.

3.6.3 Reconstruction of a brain volume and body size evolution

Table 2. The relevant changes of brain a volume, brain size and EQ values during the Canidae evolution.

node number change	**brain volume (ml) change**	**body size (kg) change**	**EQ change**	**Period**
1. 73 → 75	14,2 → 21,2	19 → 25	0,75 → 0,93	30 Mya
2. 113 → 119	54,9 → 67,3	15 → 22,8	0,73 → 0,67	25 Mya
3. 75 → 79	21,2 → 31,8	2,5 → 5	0,93 → 0,88	24 Mya
4. 88 → 96	69,5 → 83,3	17,1 → 24,7	0,84 → 0,79	15 Mya
5. 4 → 6	16,8 → 32,3	2,9 → 5	0,67 → 0,89	14 Mya
6. 96 → 101	83,3 → 113,9	24,7 → 35,3	0,79 → 0,85	12 Mya
7. 6 → 8	32,3 → 46,4	5 → 7,3	0,89 → 1	9,5 Mya
8. 8 → 9	46,4 → 41,6	7,3 → 6	1 → 1,02	8,5 Mya
9. 58 → 66	99,7 → 127,5	21,3 → 32,6	1,05 → 1	3,5 Mya
10. 34 → 35	77,2 → 54,1	14,4 → 8	1,05 → 1,09	2,5 Mya

The first evident change in EQ values (**ad.1**. see: Table 2 and Fig. 13 in Appendix) was recorded during the evolution of Borophaginae (30 Mya). In this case all three values (brain volume, body size and EQ) increased. The second change occured 25 Mya (**ad. 2.** see: Table 2**)** within Hesperocyoninae, when the brain volume and body size increased, but the EQ value decreased. The evolution of Borophaginae is typical by continuous enlargement of a brain volume and body size. In several cases (**ad. 3,4** see: Table 2), this phenomenon was accompanied by lowering of EQ values in periods 24 and 15 Mya. The increase of EQ values together with the brain volume and body size has occured 12 Mya (**ad. 6,** see: Table 2) during the evolution of Borophaginae. The big shift in the brain volume and body size accompanied by relatively great increase of EQ values is evident between *Leptocyon gregorii* and *L. vafer* (**ad. 5** see: Table 2). Distinctive increase of EQ values also occured around 9,5 Mya (**ad. 7** see: Table 2) which corresponds to the origin of the modern Caninae. However, there were two cases (**ad.8 and 10,** see: Table 2**)**, typical by decreasing of the brain volume and body size with increasing EQ values. This phenomenon was related to evolution of group Vulpini and also the emergence of South American canids (except the species *Ch. brachyurus* and *S. venaticus*). Special case of pronounced increase in the brain volume and body with considerable decrease of EQ is evident in evolution of large hypercarnivorous canids *C. dirus* and *C. armbrusteri* (**ad. 9,** see: Table 2).

3.6.4 Testing of the evolutionary relationship between brain size and foraging strategy

The optimization foraging strategy indicators on the Canidae tree (see: Fig 15 in Appendix) revealed a parallel change in foraging strategy and EQ just in one case (node 8 – origin of modern Caninae). During this event canids became more mesocarnivorous, but only according to optimization of the m1 talonid trait. M1 hypocone does not show any important change at this point. There are two evident phenomena, regarding the inclination to hypercarnivory. On one hand, *Speothos venaticus* and *Canis dirus* exhibit decrease in EQ, which coincide with the origin of hypercarnivory. On the other hand, *Lycaon pictus* and *Cuon alpinus* show the increase in EQ.

3.6.5 Ancestral reconstruction of the origin of Canidae and Caninae

According to the parsimony reconstruction method, ancestors of both Canidae and Caninae were quite small omnivorous solitary hunter (see: Table 3). The Canidae ancestor was larger than the ancestor of Caninae.

Table 3. Reconstruction of the Canidae and Caninae ancestor.

Ancestor	Brain size	Body size	EQ	M1-2 paracones	m1 talonid	M1 hypocone
Canidae	23,92 ml	4,9 kg	0,67	not enlarged	fully trenchant bicuspid basined	small enlarged
Caninae	16,8 ml	2,9 kg	0,67	not enlarged	fully trenchant bicuspid basined	enlarged

3.6.6 Optimization of all characters

There is no relationship between change of body size and occurrence of hypercarnivorous traits in all subfamilies (see: Fig. 14-15 in Appendix). Hypercarnivory occurred in some species smaller than 20 kg and consequently, not all large canids had adaptations to hypercarnivory. Transition from hypocarnivory to mesocarnivory in Caninae (9,5 Mya) corresponds with the increase in EQ. There is also evident that hypercarnivorous canid is only special cause of cooperative hunter within Caninae. The results not show any link between cooperative hunting and increase in EQ. Caninae evolution is typical by a continuous increase in EQ, while the two fossil subfamillies show rather opposite process. The increase in EQ within Borohaginae and Hesperocyoninae were ofte replaced by a periods of a EQ decrease. The first increasing of body size occurred in the evolution of canids much later (9 Mya) than the increasing of EQ (14 Mya). A distinctive decrease in EQ emerged within the evolution of Caninae only in two cases, namely *Otocyon-Nyctereutes* clade and *C. dirus-C. armbrusteri* group.

4 DISCUSSION

4.1 Phylogeny of Caninae

The results of the presented analysis of combined (morphological, cytogenetic, ethological, ontogenetic, ecological and molecular) data confirm several previous statements about phylogeny of Caninae.

Position of *Leptocyon*

The basal position of *Leptocyon* has been suggested by Tedford et al. (2009), the only phylogenetic analysis of the Caninae, which includes this fossil genus. Both this analysis and Tedford et al. (2009) suggested that *Leptocyon* is not a monophyletic group. Inadequate amount and various types of *Leptocyon* fossil records could cause this paraphyly. However, the results of this study are in accordance with the stratigraphy of this genus (Tedford et al. 2009).

Vulpini and Canini

Split of Caninae in fox-like and dog-like clades, which likely occured some 10 Mya, was suggested by both morphological (Tedford et al. 1995, 2009) and molecular (Bardeleben et al. 2005) studies. The weighted tree inferred in this analysis supports this hypothesis. However, another purely molecular study (Lindblad-Toh et al. 2005) indicated *Urocyon* as the basalmost Recent genus of Caninae rather than a part of Vulpini, which was further supported by the analysis of combined data by Zrzavý et Řičánková (2004). In agreement with previous studies based on morphological (Tedford et al. 1995), combined (Zrzavý et Řičánková 2004), and molecular data (Bardeleben et al. 2005, Lindblad-Toh et al. 2005), the presented analysis divides the dog-like group Canini into the Afro-Holarctic and South American clades.

Urocyon

As mentioned above, the combined study by Zrzavý et Řičánková (2004) as well as one of the molecular studies (Lindblad-Toh et al. 2005) showed that *Urocyon* is the basalmost Recent canine. Another molecular study (Bardeleben et al. 2005) exhibited various results depending on the methods and datasets used. According to the ML analysis of the mitochondrial DNA, *Urocyon* belongs to Vulpini as a sister taxon of *Nyctereutes*. Bayesian analysis of the combined nuclear and mitochondrial datasets supported the basal position of *Urocyon* within the remaining fox-like canids (including also *Nyctereutes* and *Otocyon*). This study covering several extinct and Recent species of *Urocyon* confirmed the basal position of *Urocyon* only in case of weighted analysis (except *U. webbi*, which grouped with *Metalopex*). However, none of the inferred trees supported monophyly of *Urocyon* with all fossil species included.

Otocyon and *Nyctereutes*

The present analysis also tries to resolve two problematic genera: *Otocyon* and *Nyctereutes*.These taxa are sisters in the unweighted tree and together with fossil *Nurocyon chonokhariensis,* they form a sister group to the dog-like clade. In the weighted tree, both genera together form a sister lineage to the *Urocyon webbi-Metalopex* group within Vulpini. The Bayesian analysis of the combined mitochondrial and nuclear dataset as well as ML of the nuclear dataset (Bardeleben et al. 2005) suggested that *Otocyon-Nyctereutes* clade forms a sister taxon to *Vulpes*. However, the ML analysis of the mitochondrial dataset (Bardeleben et al. 2005) supported the sister relationship between *Nyctereutes* and *Urocyon,* and suggested *Otocyon* as a basal member of Vulpini. This is in contrast with morphological studies (Tedford et al. 1995, Wang et al. 2008), which consider *Otocyon* a sister taxon to *Urocyon* and place *Nyctereutes procyonoides* within the South American clade, or with combined analysis (Prevosti 2009) in which *Otocyon-Nyctereutes* clade represents basal branch of the dog-like group. The molecular phylogenetic analysis (Lindblad-Toh et al. 2005) indicates *Otocyon* and *Nyctereutes* are closely related to *Vulpes*. Two studies analysing combined datasets (Zrzavý et Řičánková 2004, Perini 2009) showed unstable position of these problematic taxa. In general, the problematic position of *Nyctereutes* in morphological studies could be caused by its morphological similarities with *Cerdocyon* (Tedford et al. 2009), which is the basal genus of the South American clade. One of the fossil species, *Nyctereutes donnezani,* has unclear position in present canid phylogeny. For instance, Tedford and Qui (1996) found that *N. donnezani* belongs to *Eucyon*. However, this study rather suggested its relation with *Vulpes*.

South American clade

The topology of the South American clade obtained in this analysis provides similar results as Perini's combined study focused on the South American canids (Perini 2009), which included several fossil species. Both trees inferred in this analysis suggested that *Atelocynus* and *Cerdocyon* form a clade with *Lycalopex*. Close relationship between *Atelocynus* and *Cerdocyon* is further supported by Perini´s combined (2009) and Bardeleben et al.´s (2005) molecular studies. However, according to Lindblad-Toh et al. (2005), *Cerdocyon* is a sister group to *Lycalopex* while *Atelocynus* is more basal. In the Perini´s phylogeny (2009) *Dusicyon* is sister to *Lycalopex*. However, the most recent molecular study (Austin et al. 2013) suggests that *Dusicyon* is the most closely related to the maned wolf. According to this study, *Dusicyon* actually belongs to the group including *Chrysocyon, Speothos, "Canis" gezi*, *Theriodictis* and *Protocyon*.

Canis and *Eucyon*

In agreement with the previous combined studies (Zrzavý et Řičánková 2004, Perini et al. 2009, Prevosti 2009), this phylogenetic analysis did not support the monophylyof Recent *Canis*. However, its monophyly was suggested by molecular study based on the Bayesian analysis of combined mitochondrial and nuclear dataset (Bardeleben et al. 2005). Also Lindblad-Toh et al. (2005) did not support the monophyly of Recent representatives of *Canis* because of unclear position of *C. adustus* and *C. mesomelas*. Moreover, the position of *Eucyon* species seems to be problematic as well. In the unweighted tree, representatives of the genus *Eucyon* are scattered within Afro-Holarctic wolf-like canids. In the weighted tree, two species (*E. marinae* and *E. davisi*) form the basal group of Canini as a whole, while the remaining *Eucyon* species are scattered within the Afro-Holarctic wolf-like canids. The Tedford et al´s phylogeny (2009) suggested *Eucyon* as a sister group to *Canis* rather than as a basal taxon of Canini. The unclear position of *Eucyon* may be caused by wide range of morphological synapomorphies shared between *Eucyon* species and individual species of Canina (Tedford et al. 2009).

Cuon and *Lycaon*

The *Lycaon*-*Cuon* clade is well supported by morphological (Tedford et al. 2009) and combined analyses (Zrzavý et Řičánková 2004, this study). However, the presented weighted tree along with the molecular studies (Bardeleben et al. 2005, Lindblad-Toh et al. 2005) did not support this clade. In these analyses, *Lycaon* is placed in the unresolved group at the base of Canina, while *Cuon* is more closely related to the recent *Canis s.str.* and to fossil hypercarnivores (i.e. *Xenocyon lycanoides*). The results of the unweighted analysis performed in this study agree with the phylogeny of Tedford et al. (2009). This contradiction could stem from the hypercarnivory-related morphological and behavioural traits, which are shared between *Cuon* and *Lycaon*, and could be only a result of convergent evolution. The morphological connection of *Cuon*, *Lycaon* and *Xenocyon* is based mainly on characters on the first lower molar (Tedford et al. 2009).

4.2 Evolution of cooperative behaviour in Caninae

The results of this study revealed that the origin of unusual behavioural and reproductive canid traits is not linked to the evolution of social hunting, increasing body size or occurrence of hypercarnivory adaptations. A common ancestor of modern Caninae was relatively small solitary hunter and social hunting represents a derived feature. Observed increase in relative brain size coupled with shift to more carnivorous diet occurred at the base of modern Caninae about 10 Mya during a period of pronounced climate cooling. These changes could be associated with emergence of common traits of the recent canids, such as social monogamy, biparental care, presence of helpers, and monoestrus, which served as a preadaptation for further evolution of pack –hunting and living in large societies (Macdonald et Sillero-Zubiri 2004).

This study confirmed the Finarelli´s (2008) hypothesis that the brain evolution in Caninae is unlike in the other fossil subfamilies, characterized by continuous enlargement of the brain volume in comparison to the body size. This enlargement occurred also in other groups of Caniformia at approximately the same time as in Caninae (8-10 Mya), which suggests great influence of environmental changes and potential impact of intra-guild competition on the Caniform brain size (Finarelli et Flynn 2007). The cooling event occurred during the second half of Miocene in North America, when the open grasslands became a dominant habitat (Edwards et al. 2010, Strömberg et McInerney 2011). Species diversity radically decreased as many species, including large prey, became extinct. Stem group of Caninae, the genus Leptocyon, was adaptated for cursorial hunting and catching of small, quickly moving prey (Wang et al. 2008). The ancestor of recent Caninae took advantage of these characters in novel environment and responded to the pronounced seasonality of environment and change in the food supply by increase in relative brain size, shift to more carnivorous diet and possibly also by emergence of monogamous behaviour, cooperative breeding and monoestrus.

Increase in relative brain size is tightly correlated to increased longevity and carnivorous diet in comparison with insectivory and omnivory (Gonzales–Lagos et al. 2010). Longer life span may compensate for the restricted number of breeding opportunities per lifetime imposed by restriction of breeding to one estrus per season (Asa et Valdespino 1998). According to Sol et al. (2008), mammals with a larger brain better cope with new environmental conditions. Schultz and Dunbar (2007) proposed a direct relationship between increasing brain size and occurrence of social monogamy, which is common to all present-day canids (so-called “social brain hypothesis”). Moreover, the increase in relative brain size occurred earlier in the evolution of Canidae than increase in body size, which means that evolution of these two characteristics is probably influenced by different selection pressures.

Body mass has been considered the best correlate of canid behavior and ecology and causal relationship between evolution of cooperative hunting and increase of body size has been suggested (Carbone et al. 1999, Macdonald et Sillero-Zubiri 2004). However, evolution of body size seems to be more a consequence of climate and food supply than cooperative behaviour.

According to the presented analyses of osteological indicators of cooperative hunting and hypercarnivory, both foraging adaptations evolved several times during the canid evolution and represent derived traits.

Parallel occurrence of larger body mass, hypercarnivorous dentition and cooperative hunting was recorded within South American canids around 2,5 Mya. On the contrary, cooperative hunting predates increase in body size and hypercarnivorous adaptations in Afro-Holarctic canids. It evolved 4,5 Mya, which corresponds to the distinctive Pliocene cooling (Ravelo et al. 2004) and spread of arid grasslands (e.g. Hernandéz Fernandéz et Vrba 2006, Edward et al. 2010). Since herbivores adapted for these types of grasslands were more cursorial, hunting in pack was, in general, more advantageous for both large and small canids in these vast grasslands. The occurrence of cooperative hunting in Afro-Holarctic canids corresponds to species weighting between 0,5-12,5 kg. This is in contrast with the previous hypothesis by Carbone et al. (1999), who suggested that, the predator bigger than 21 kg have to forage larger prey. It is due to the higher energetic demands of large predators (Carbone et al. 1999, Van Valkenburgh 2004).

The results show that the hypercarnivorous predator is just a special diverse form of cooperative hunter. In both cases (South American and Afro-Holarctic region), the hypercarnivory occurred within Caninae at the Plio-Pleistocene boundary (around 2,5 Mya). This time period is characterized by high number of large herbivores (Alberdi et al. 1993). So the shift into the strict hypercarnivory specialization could be the consequence of this large-bodied food supply at the Plio-Pleistocene boundary and during the Pleistocene.

This study allows a new view on the evolutionary forces behind specialized aspects of canid behaviour, which could not have been explained without more complete phylogeny of Caninae including fossil species and the extinct subfamilies Borophaginae and Hesperocyoninae. Further research could focus on proper identification of relevant changes in brain size and other life-history characters, using other methods better suited for tracking shifts in character evolution than parsimony. Application of these methods to the final cladogram will help us to fully understand the origin of unusual canid behavioural and reproductive traits.

5 CONCLUSIONS

The phylogenetic hypothesis of Caninae was inferred from combined morphological and molecular dataset comprising fossil species. The results confirmed paraphyly of the genus Leptocyon, but did not provide support for monophyly of the genus Canis. The position of the Otocyon-Nyctereutes lineage remains unresolved.

The ancestor of recent canids was small, mesocarnivorous, solitary hunter with relatively large brain. Cooperative hunting, large body size, and hypercarnivorous adaptations represent derived traits within Caninae. The evolution of unique behavioral and reproductive characters (monogamy, biparental care, reproductive supression, monoestrus) is probably associated with climate cooling and increase in relative brain size. These traits represent possible preadaptations for further evolution of cooperative hunting.

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7 APPENDIX:

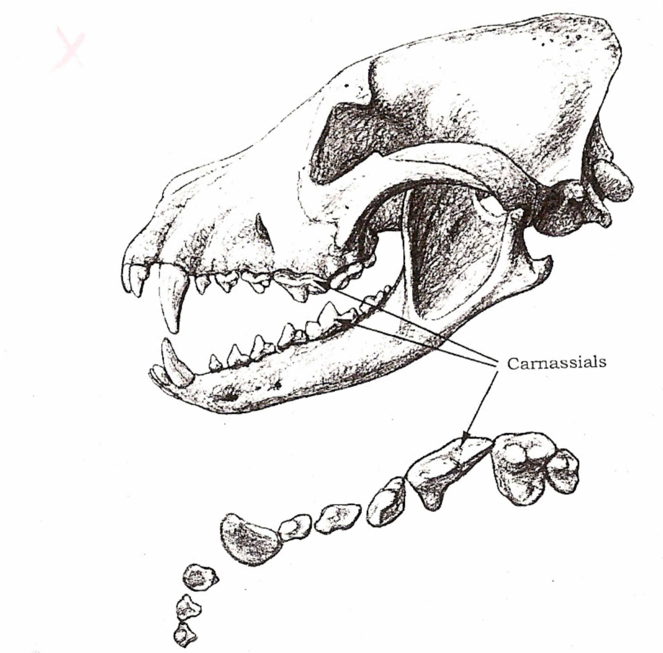


Fig. 1. Typical skull and dentition proportions of hypercarnivory canid – *Lycaon pictus*, emphasizing the appearance and position of carnassials (taken from: Wang et al. 2008).

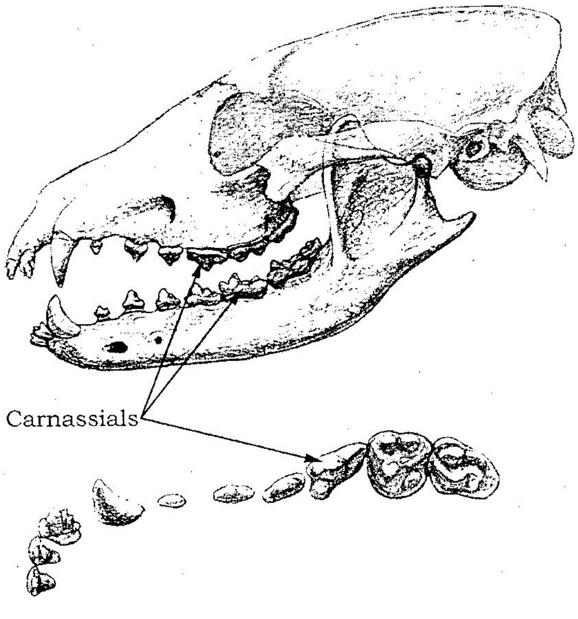


Fig. 2. Typical skull and dentition proportions of hypocarnivory canid – *Cynarctus*, emphasizing the appearance and position of carnassials (taken from: Wang et al. 2008).

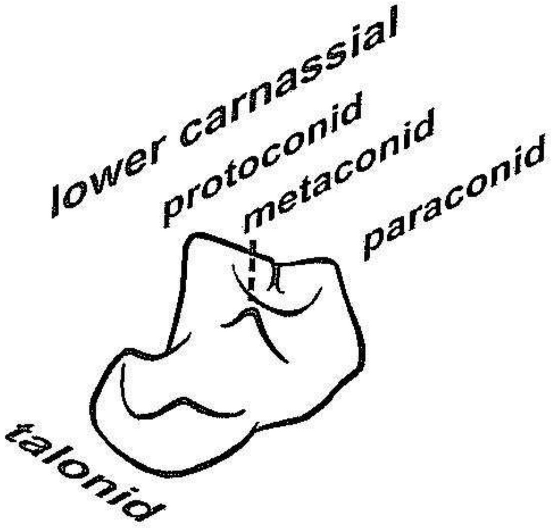


Fig.3. Bicuspid talonid (taken from: Hillson 2005).

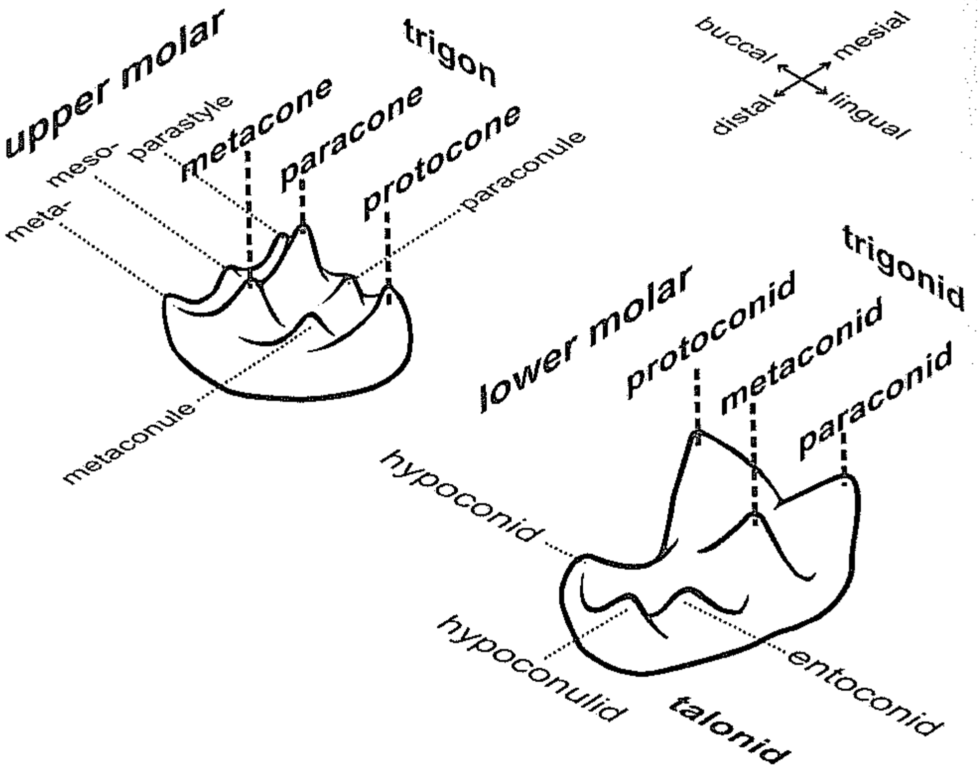


Fig. 4. Basic description of dental morphology (taken from: Hillson 2005).

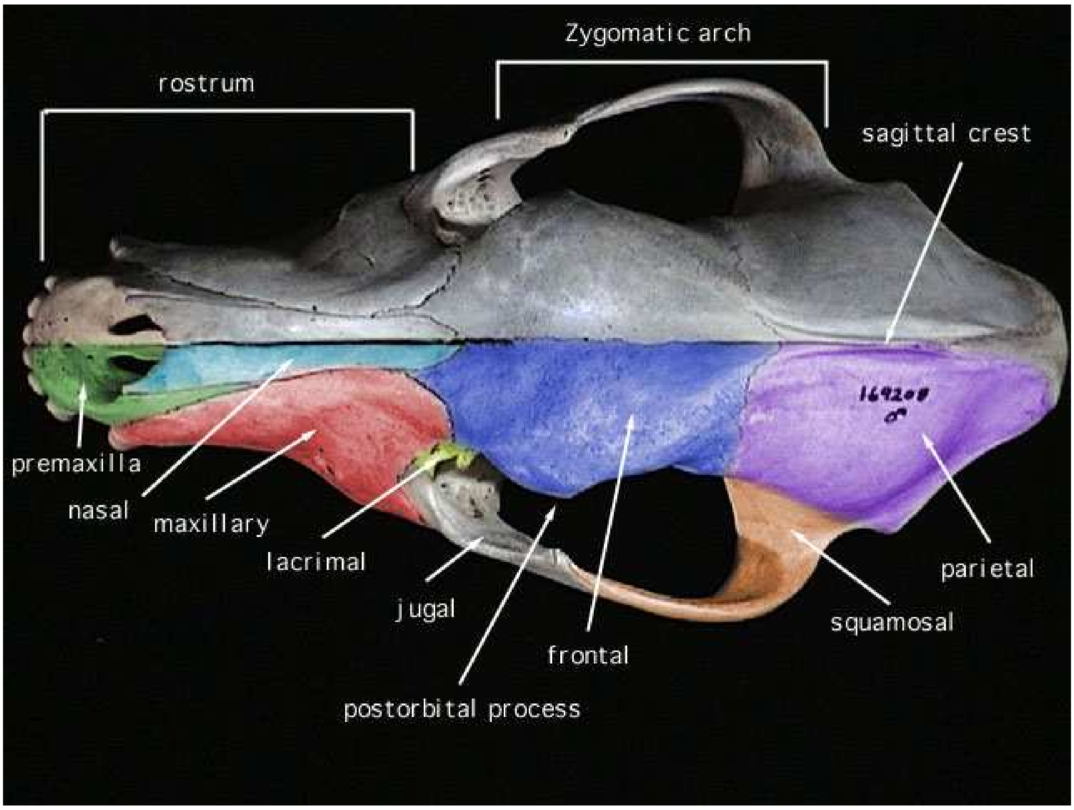


Fig. 5. Dorsal anatomy of canid skull (taken from: www.anatomy.wikispaces.com).

Table 1: The list of Caninae species and representation (O = present, X = absent) of particular categories of characters in matrix (part 1).

Species	**1.Brain**	**2.Skull**	**3. Dentition**	**4. Postcranial**
Leptocyon gregorii	O	O	O	O
Leptocyon vulpinus	X	O	O	O
Leptocyon douglassi	X	O	O	O
Leptocyon mollis	O	O	O	O
Leptocyon leidyi	X	O	O	O
Leptocyon matthewi	O	O	O	O
Vulpes rueppellii	O	O	O	O
Vulpes vulpes	O	O	O	O
Vulpes corsac	O	O	O	O
Vulpes ferrilata	O	O	O	O
Vulpes lagopus	O	O	O	O
Vulpes macrotis	O	O	O	O
Vulpes velox	O	O	O	O
Vulpes bengalensis	O	O	O	O
Vulpes cana	O	O	O	O
Vulpes zerda	O	O	O	O
Vulpes chama	O	O	O	O
Vulpes pallida	O	O	O	O
Vulpes stenognathus	O	O	O	O
Vulpes praeglacialis	X	O	O	O
Vulpes hassani	X	O	O	O
Vulpes beihaiensis	X	O	O	O

Vulpes riffautae	X	O	O	O
Nyctereutes tingi	X	O	O	O
Nyctereutes donnezani	X	O	O	O
Nyctereutes procyonides	O	O	O	O
Nyctereutes lockwoodi	X	O	O	O
Otocyon megalotis	O	O	O	O
Nurocyon chonokhariensis	X	O	O	O
Urocyon progressus	X	O	O	O
Urocyon cinereoargenteus	O	O	O	O
Urocyon littoralis	O	O	O	O
Urocyon citrinus	X	O	O	O
Urocyon galushai	X	O	O	O
Urocyon webbi	X	O	O	O
Urocyon minicephalus	O	O	O	O
Metalopex macconnelli	O	O	O	O
Metalopex merriami	O	O	O	O
Atelocynus microtis	O	O	O	O
Cerdocyon thous	O	O	O	O
Lycalopex fulvipes	X	O	O	O
Lycalopex griseus	O	O	O	O
Lycalopex culpaeus	O	O	O	O
Lycalopex gymnocercus	O	O	O	O
Lycalopex sechurae	O	O	O	O
Lycalopex vetulus	O	O	O	O

Dusicyon australis	O	O	O	O
Chrysocyon brachyurus	O	O	O	O
Theriodictis tarijensis	X	O	O	O
Theriodictis platensis	X	O	O	O
Protocyon texanus	X	O	O	O
Protocyon troglodytes	X	O	O	O
Protocyon scaglarium	X	O	O	O
Protocyon orcesi	X	O	O	O
Speothos venaticus	O	O	O	O
Speothos pacivorus	X	O	O	O
Canis gezi	X	O	O	O
Canis accitanus	X	O	O	O
Canis cipio	X	O	O	O
Canis aureus	O	O	O	O
Canis latrans	O	O	O	O
Canis lupus	O	O	O	O
Canis simensis	O	O	O	O
Canis rufus	O	O	O	O
Canis falconeri	X	O	O	O
Canis antonii	O	O	O	O
Canis armbrusteri	O	O	O	O
Canis arnensis	O	O	O	O
Canis chihliensis	O	O	O	O
Canis dirus	O	O	O	O

Canis edwardi	O	O	O	O
Canis etruscus	O	O	O	O
Canis ferox	O	O	O	O
Canis lepophagus	O	O	O	O
Canis mosbachensis	O	O	O	O
Canis palmidens	O	O	O	O
Canis thooides	X	O	O	O
Canis variabilis	O	O	O	O
Eucyon adoxus	X	O	O	O
Eucyon debonisi	X	O	O	O
Eucyon monticinensis	X	O	O	O
Eucyon zhoui	X	O	O	O
Eucyon marinae	X	O	O	O
Eucyon davisi	O	O	O	O
Lupullela paralius	X	O	O	O
Lupullela mohibi	X	O	O	O
Lupullela adusta	O	O	O	O
Lupullela mesomelas	O	O	O	O
Cynotherium sardous	O	O	O	O
Xenocyon lycanoides	O	O	O	O
Lycaon pictus	O	O	O	O
Lycaon sekowei	X	O	O	O
Cuon alpinus	O	O	O	O
Cuon javanicus	O	O	O	O

Table 2. The list of Caninae species and representation ((O = present, X = absent) of particular categories of characters in matrix (part 2).

Species	**5. Other morphology**	**6. Reproduction and development**	**7. Ecology and behavior**	**8. Cytogenetic**
Leptocyon gregorii	O	X	O	X
Leptocyon vulpinus	O	X	O	X
Leptocyon douglassi	O	X	O	X
Leptocyon mollis	O	X	O	X
Leptocyon leidyi	O	X	O	X
Leptocyon matthewi	O	X	O	X
Vulpes rueppellii	O	O	O	X
Vulpes vulpes	O	O	O	O
Vulpes corsac	O	O	O	O
Vulpes ferrilata	O	O	O	O
Vulpes lagopus	O	O	O	O
Vulpes macrotis	O	O	O	O
Vulpes velox	O	O	O	O
Vulpes bengalensis	O	O	O	X
Vulpe cana	O	O	O	X
Vulpes zerda	O	O	O	O
Vulpes chama	O	O	O	X
Vulpes pallida	O	O	O	X
Vulpes stenognathus	O	O	O	X
Vulpes praeglacialis	O	X	O	X
Vulpes hassani	O	X	X	X

Vulpes beihaiensis	O	X	O	X
Vulpes riffautae	O	X	O	X
Nyctereutes tingi	O	X	O	X
Nyctereutes donnezani	O	X	O	X
Nyctereutes procyonides	O	O	O	O
Nyctereutes lockwoodi	O	X	O	X
Otocyon megalotis	O	O	O	O
Nurocyon chonokhariensis	O	X	X	O
Urocyon progressus	O	X	O	X
Urocyon cinereoargenteus	O	O	O	O
Urocyon littoralis	O	O	O	O
Urocyon citrinus	O	X	O	X
Urocyon galushai	O	X	O	X
Urocyon webbi	O	X	O	X
Urocyon minicephalus	O	X	O	X
Metalopex macconnelli	O	X	O	X
Metalopex merriami	O	X	O	X
Atelocynus microtis	O	O	O	O
Cerdocyon thous	O	O	O	O
Lycalopex fulvipes	O	O	O	O
Lycalopex griseus	O	O	O	O
Lycalopex culpaeus	O	O	O	O
Lycalopex gymnocercus	O	O	O	O
Lycalopex sechurae	O	O	O	O

Lycalopex vetulus	O	O	O	O
Dusicyon australis	O	O	O	X
Chrysocyon brachyurus	O	O	O	O
Theriodictis tarijensis	O	X	O	X
Theriodictis platensis	O	X	O	X
Protocyon texanus	O	X	O	X
Protocyon troglodytes	O	X	O	X
Protocyon scaglarium	O	X	O	X
Protocyon orcesi	O	X	O	X
Speothos venaticus	O	X	O	O
Speothos pacivorus	O	O	O	X
Canis gezi	O	X	O	X
Canis accitanus	O	X	O	X
Canis cipio	O	X	O	X
Canis aureus	O	O	O	O
Canis latrans	O	O	O	O
Canis lupus	O	O	O	O
Canis simensis	O	O	O	X
Canis rufus	O	O	O	O
Canis falconeri	O	X	O	X
Canis antonii	O	X	O	X
Canis armbrusteri	O	X	O	X
Canis arnensis	O	X	O	X
Canis chihliensis	O	X	O	X

Canis dirus	O	X	O	X
Canis edwardi	O	X	O	X
Canis etruscus	O	X	O	X
Canis ferox	O	X	O	X
Canis lepophagus	O	X	O	X
Canis mosbachensis	O	X	O	X
Canis palmidens	O	X	O	X
Canis thooides	O	X	O	X
Canis variabilis	O	X	O	X
Eucyon adoxus	O	X	O	X
Eucyon debonisi	O	X	O	X
Eucyon monticinensis	O	X	O	X
Eucyon zhoui	O	X	O	X
Eucyon marinae	O	X	O	X
Eucyon davisi	O	X	O	X
Lupullela paralius	O	X	X	X
Lupullela mohibi	O	X	X	X
Lupullela adusta	O	X	O	X
Lupullela mesomelas	O	X	O	O
Cynotherium sardous	O	X	O	X
Xenocyon lycanoides	O	X	O	X
Lycaon pictus	O	O	O	O
Lycaon sekowei	O	X	O	X
Cuon alpinus	O	O	O	O

Cuon javanicus	O	X	O	X

Table 3. The list of Hesperocyoninae species and representation (O = present, X = absent) of particular categories of characters in matrix (part 1)

Species	1.Brain	2.Skull	3.Dentition	4.Postcranial
Caedocyon tedfordi	O	O	O	O
Cynodesmus martini	O	O	O	O
Cynodesmus thooides	O	O	O	O
Ectopocynus antiquus	O	O	O	O
Ectopocynus entermedius	O	O	O	O
Ectopocynus simplicidens	O	O	O	O
Enhydrocyon basilatus	O	O	O	O
Enhydrocyon crassidens	O	O	O	O
Enhydrocyon pahisintewakpa	O	O	O	O
Enhydrocyon stenocephalus	O	O	O	O
Hesperocyon coloradensis	O	O	O	O
Hesperocyon gregarius	O	O	O	O
Hesperocyon pavidus	O	O	O	O
Mesocyon brachyops	O	O	O	O
Mesocyon coryphaeus	O	O	O	O
Mesocyon temnodon	O	O	O	O
Osbornodon brachypus	O	O	O	O
Osbornodon fricki	O	O	O	O
Osbornodon iamonensis	O	O	O	O
Osbornodon renijei	O	O	O	O
Osbornodon sesnoni	O	O	O	O
Paraenhydrocyon josephi	O	O	O	O

Paraenhydrocyon robustus	O	O	O	O
Paraenhydrocyon wallovianus	O	O	O	O
Philotrox condoni	O	O	O	O
Prohesperocyon wilsoni	O	O	O	O
Sukahetanka geringensis	O	O	O	O

Table 4. The list of Hesperocyoninae species and representation (O = present, X = absent) of particular categories of characters in matrix (part 2)

Species	**5.Other morphology**	**6. Reproduction and development**	**7.Ecology and behavior**	**8.Cytogenetic**
Caedocyon tedfordi	O	X	O	X
Cynodesmus martini	O	X	O	X
Cynodesmus thooides	O	X	O	X
Ectopocynus antiquus	O	X	O	X
Ectopocynus entermedius	O	X	O	X
Ectopocynus simplicidens	O	X	O	X
Enhydrocyon basilatus	O	X	O	X
Enhydrocyon crassidens	O	X	O	X
Enhydrocyon pahisintewakpa	O	X	O	X
Enhydrocyon stenocephalus	O	X	O	X
Hesperocyon coloradensis	O	X	O	X
Hesperocyon gregarius	O	X	O	X
Hesperocyon pavidus	O	X	O	X
Mesocyon brachyops	O	X	O	X
Mesocyon coryphaeus	O	X	O	X
Mesocyon temnodon	O	X	O	X
Osbornodon brachypus	O	X	O	X
Osbornodon fricki	O	X	O	X
Osbornodon iamonensis	O	X	O	X
Osbornodon renijei	O	X	O	X
Osbornodon sesnoni	O	X	O	X

Paraenhydrocyon josephi	O	X	O	X
Paraenhydrocyon robustus	O	X	O	X
Paraenhydrocyon wallovianus	O	X	O	X
Philotrox condoni	O	X	O	X
Prohesperocyon wilsoni	O	X	O	X
Sukahetanka geringensis	O	X	O	X

Table 5. The list of Borophaginae species and representation (O = present, X = absent) of particular categories of characters in matrix (part 1)

Species	1. Brain	2. Skull	3. Dentition	4. Postcranial
Archaeoxcyon falkenbachi	O	O	O	O
Borophagus dudleyi	O	O	O	O
Borophagus hilli	O	O	O	O
Borophagus orc	O	O	O	O
Carpocyon limosus	O	O	O	O
Cynarctoides emryi	O	O	O	O
Cynarctoides harlowi	O	O	O	O
Cynarctoides roii	O	O	O	O
Cynarctus marylandica	O	O	O	O
Cynarctus voorhiesi	O	O	O	O
Epicyon aelurodontoides	O	O	O	O
Otarocyon macdonaldi	O	O	O	O
Euoplocyon spissidens	O	O	O	O
Oxetocyon cuspidatus	O	O	O	O
Phlaocyon achoros	O	O	O	O
Phlaocyon annectens	O	O	O	O
Phlaocyon mariae	O	O	O	O
Phlaocyon multicuspus	O	O	O	O
Phlaocyon yatkolai	O	O	O	O
Aelurodon asthenostylus	O	O	O	O
Aelurodon ferox	O	O	O	O
Aelurodon mcgrewi	O	O	O	O

Aelurodon stirtoni	O	O	O	O
Aelurodon taxoides	O	O	O	O
Archaeocyon leptodus	O	O	O	O
Archaeocyon pavidus	O	O	O	O
Borophagus diversidens	O	O	O	O
Borophagus littoralis	O	O	O	O
Borophagus parvus	O	O	O	O
Borophagus pugnator	O	O	O	O
Borophagus secundus	O	O	O	O
Carpocyon compressus	O	O	O	O
Carpocyon robustus	O	O	O	O
Carpocyon webbi	O	O	O	O
Cormocyon copei	O	O	O	O
Cormocyon haydeni	O	O	O	O
Cynarctoides acridens	O	O	O	O
Cynarctoides gawnae	O	O	O	O
Cynarctoides lemur	O	O	O	O
Cynarctoides luskensis	O	O	O	O
Cynarctus crucidens	O	O	O	O
Cynarctus galushai	O	O	O	O
Cynarctus saxatilis	O	O	O	O
Desmocyon matthewi	O	O	O	O
Desmocyon thomsoni	O	O	O	O
Epicyon haydeni	O	O	O	O

Epicyon saevus	O	O	O	O
Euoplocyon brachygnathus	O	O	O	O
Metatomarctus canavus	O	O	O	O
Microtomarctus conferta	O	O	O	O
Otarocyon cooki	O	O	O	O
Otarocyon macdonaldi	O	O	O	O
Paracynarctus kelloggi	O	O	O	O
Paracynarctus sinclairi	O	O	O	O
Paratomarctus euthos	O	O	O	O
Paratomarctus temerarius	O	O	O	O
Phlaocyon latidens	O	O	O	O
Phlaocyon leucosteus	O	O	O	O
Phlaocyon marslandensis	O	O	O	O
Phlaocyon minor	O	O	O	O
Proepicyon raki	O	O	O	O
Protomarctus optatus	O	O	O	O
Psalidocyon marianae	O	O	O	O
Rhizocyon oregonensis	O	O	O	O
Tephrocyon rurestris	O	O	O	O
Tomarctus brevirostris	O	O	O	O
Tomarctus hippophaga	O	O	O	O

Table 6. The list of Borophaginae species and representation (O = present, X = absent) of particular categories of characters in matrix (part 2)

Species	**5. Other morphology**	**6. Reproduction and development**	**7. Ecology and behavior**	**8. Cytogenetic**
Archaecyon falkenbachi	O	X	O	X
Borophagus dudleyi	O	X	O	X
Borophagus hilli	O	X	O	X
Borophagus orc	O	X	O	X
Carpocyon limosus	O	X	O	X
Cynarctoides emryi	O	X	O	X
Cynarctoides harlowi	O	X	O	X
Cynarctoides roii	O	X	O	X
Cynarctus marylandica	O	X	O	X
Cynarctus voorhiesi	O	X	O	X
Epicyon aelurodontoides	O	X	O	X
Otarocyon macdonaldi	O	X	O	X
Euoplocyon spissidens	O	X	O	X
Oxetocyon cuspidatus	O	X	O	X
Phlaocyon achoros	O	X	O	X
Phlaocyon annectens	O	X	O	X
Phlaocyon mariae	O	X	O	X
Phlaocyon multicuspus	O	X	O	X
Phlaocyon yatkolai	O	X	O	X
Aelurodon asthenostylus	O	X	O	X
Aelurodon ferox	O	X	O	X
Aelurodon mcgrewi	O	X	O	X

Aelurodon stirtoni	O	X	O	X
Aelurodon taxoides	O	X	O	X
Archaeocyon leptodus	O	X	O	X
Archaeocyon pavidus	O	X	O	X
Borophagus diversidens	O	X	O	X
Borophagus littoralis	O	X	O	X
Borophagus parvus	O	X	O	X
Borophagus pugnator	O	X	O	X
Borophagus secundus	O	X	O	X
Carpocyon compressus	O	X	O	X
Carpocyon robustus	O	X	O	X
Carpocyon webbi	O	X	O	X
Cormocyon copei	O	X	O	X
Cormocyon haydeni	O	X	O	X
Cynarctoides acridens	O	X	O	X
Cynarctoides gawnae	O	X	O	X
Cynarctoides lemur	O	X	O	X
Cynarctoides luskensis	O	X	O	X
Cynarctus crucidens	O	X	O	X
Cynarctus galushai	O	X	O	X
Cynarctus saxatilis	O	X	O	X
Desmocyon matthewi	O	X	O	X
Desmocyon thomsoni	O	X	O	X
Epicyon haydeni	O	X	O	X

Epicyon saevus	O	X	O	X
Euoplocyon brachygnathus	O	X	O	X
Metatomarctus canavus	O	X	O	X
Microtomarctus conferta	O	X	O	X
Otarocyon cooki	O	X	O	X
Otarocyon macdonaldi	O	X	O	X
Paracynarctus kelloggi	O	X	O	X
Paracynarctus sinclairi	O	X	O	X
Paratomarctus euthos	O	X	O	X
Paratomarctus temerarius	O	X	O	X
Phlaocyon latidens	O	X	O	X
Phlaocyon leucosteus	O	X	O	X
Phlaocyon marslandensis	O	X	O	X
Phlaocyon minor	O	X	O	X
Proepicyon raki	O	X	O	X
Protomarctus optatus	O	X	O	X
Psalidocyon marianae	O	X	O	X
Rhizocyon oregonensis	O	X	O	X
Tephrocyon rurestris	O	X	O	X
Tomarctus brevirostris	O	X	O	X
Tomarctus hippophaga	O	X	O	X

Table 7. The list of outgroups and representation (O = present, X = absent) of particular categories of characters in matrix (part 1).

Species	1.Brain	2.Skull	3.Dentition	4.Postcranial
Miacis pacivorus	X	O	O	O
Ursus sp.	X	O	O	O
Ailuropoda melanoleuca	X	O	O	O
Mirounga angustirostris	X	X	O	X
Mustela sp.	X	O	O	O
Odobenus rosmarus	X	X	O	X
Procyon lotor	X	O	O	O

Table 8. The list of outgroups and representation (O = present, X = present) of particular categories of characters in matrix (part 2).

Species	5.Other morphology	6.Reproduction and development	7.Ecology and behavior	8.Cytogenetic
Miacis pacivorus	O	X	X	X
Ursus sp.	O	O	O	O
Ailuropoda melanoleuca	O	O	O	O
Mirounga angustirostris	X	X	X	X
Mustela sp.	O	O	O	O
Odobenus rosmarus	X	X	X	X
Procyon lotor	O	O	O	O

List 1. The list of characters in matrix

I. Brain

0. **log encephalization quocient** (0) 0,436 – 0,16, (1) 0,155 – 0,004, (2) -0,001 - -0,183, (3) -0,201 - -0,471, (4) -0,472 - -0,71 (Finarelli 2008)
1. **posteroventral septum of IS** (0) absent, (1) very rare, (2) occasional, (3) frequent, (4) constantly present, (5) fused (Ivanoff 2007)
2. **proreal gyrus of cerebrum** (0) elongated, bilaterally compressed, (1) small, (2) wide low (Lyras, Van der Geer 2003)
3. **orbital gyri sulci** (0) one, (1) two, (2) three (Lyras, Van der Geer 2003)
4. **intrabullar septum** (0) absent, (1) less developed, (2) well developed, (3) complete invariably uninterrupted (Ivanoff 2007)
5. **anteroventral septum of IS** (0) absent, (1) present, (2) fused (Ivanoff 2007)
6. **coronal and ansate sulci cerebral pattern** (0) pentagonal, (1) heartshaped, (2) parenthesislike, (3) orthogonal (Lyras, Van der Geer 2003)
7. **ratio of neocortex volume to the rest of brain (total brain volume minus neocortex volume)** (0) 1,22 – 1,31, (1) 1,40 – 1,62, (2) 1,66 – 1,83 (Clutton – Brock et al. 1976, Zrzavý and Řičánková 2004)
8. **cerebellum, dorsal exposure** (0) dorsoposteriorly between cerebrum and lambdoidal crest, (1) completely overlapped by cerebrum not exposed dorsoposteriorly (Tedford et al. 2009)

II. Skull

9. **skull proportion** (0) normal proportioned, (1) slightly brachycephalic, (2) further shortening of skull (Wang et al. 1999)
10. **ossification of entotympanic bulla** (0) absent, (1) present (Wang, Tedford 1994)
11. **ectotympanic ring** (0) incomplete, (1) ectotympanic forming a full ring (Wang et al. 1999)
12. **paroccipital process location** (0) posteriorly directed, free from bulla except at base, (1) ventrally directed, fused with bulla through most of its lenght (Tedford et al. 2009)

13. **height of masseteric fossa** (0) masseteric fossa low, (1) masseteric fossa high (Wang et al. 1999)
14. **temporal crest** (0) single-crested, (1) double-crested, often lyrate, (2) strong, widely separated (Wang et al. 1999)
15. **sagittal crest location** (0) confined to parietal, (1) extends onto fronta (Tedford et al. 2009)
16. **sagittal crest** (0) uniformly high-strongly compressed, well defined temporal ridges, (1) low-temporal ridges weakly developed (Berta 1988)
17. **sagittal crest profile** (0) dorsally arched or straight, (1) concave (Wang et al. 1999)
18. **infraorbital foramen** (0) positioned above the anterior root of P4, (1) positioned above the posterior root of P3, (2) positioned above the anterior root of P3 (Berta 1988)
19. **tympanic bullae** (0) relatively large, inflated, (1) small, strongly inflated, (2) relatively small, narrow (Berta 1988)
20. **postparietal foramen** (0) present, (1) absent (Tedford et al. 2009)
21. **suprameatal fossa** (0) shallow or absent, (1) enlarged (Wang et al. 1999)
22. **external auditory meatus very short and of a small diameter** (0) absent, (1) present (Berta 1987, Zrzavý and Řičánková 2004)
23. **opening of auditory meatus** (0) external auditory meatus with large opening, (1) small opening of the external auditory meatus (Wang et al. 1999)
24. **interparietal crest** (0) absent, (1) developed, (2) well developed (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)
25. **parietal bones rugosity** (0) smooth, (1) little rugose, (2) distinctly rugose (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)
26. **postorbital processes convexity** (0) concave, (1) flat, (2) strongly convex (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)
27. **subangular lobe of mandible** (0) absent (1) present (Tedford et al. 2009)
28. **premaxillary meeting frontal** (0) premaxillary does not meet frontal, (1) premaxillary just meets frontal, (2) widened contact between premaxillary and frontal (Wang et al. 1999)
29. **condylobasal length** (0) 90-139, (1) 144-188, (2) 213-226 (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)
30. **mandibular condyle** (0) low, (1) elevated above toothrow (Feldhammer 2007)

31. **palate, greatest width as % of length of palate** (0) 49-57, (1) 58-67, (2) 70-76 (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)
32. **rostrum, width as % of length of palate** (0) 24-31, (1) 32-36, (2) 40-47 (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)
33. **rostrum, width as % of width of palate** (0) 45-49, (1) 50-53, (2) 54-57, (3) 59-62 (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)
34. **premaxillae, anterior palatine length as % of width of rostrum** (0) 61-82, (1) 83-98, (2) 115-124 (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)
35. **zygomatic width as % of condylobasal length** (0) 51-56, (1) 57-59, (2) 61-68 (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)
36. **horizontal ramus** (0) deep and thick, (1) shallow and thin (Tedford et al. 1995, Zrzavý a Řičánková 2004)
37. **symphyseal flange on ramus of mandible** (0) ramus without a flange, (1) ramus with a symphyseal flange (Wang et al. 1999)
38. **paroccipital process width** (0) narrow mediolaterally, (1) broad, closely appressed to bulla, short free tip turned laterally, rarely extends below body of process (Tedford et al. 1995, Zrzavý a Řičánková 2004)
39. **nasal length** (0) long, usually extending posteriorly beyond maxillary-frontal suture, (1) short, rarely extend to level of most posterior position of maxillary-frontal suture (Tedford et al 1995, Zrzavý a Řičánková 2004)
40. **paroccipital process posterior expansion** (0) no or little expansion, (1) expanded posteriorly from bulla, usually with prominent free tip, (2) large, greater posterolateral expansion (Tedford et al. 1995, Zrzavý a Řičánková 2004)
41. **frontal sinus** (0) absent, presence of a depression on dorsal surface of postorbital process, (1) present, lacks a depression on dorsal surface of postorbital process, (2) present, large, penetrates postorbital process and expands posteriorly toward the frontal-parietal suture, (3) reached frontoparietal suture (Tedford et al. 1995, Tedford et al. 2009, Zrzavý a Řičánková 2004)
42. **frontal shield** (0) narrow, (1) widened (Wang et al. 1999)
43. **mastoid process** (0) small, crestlike, (1) enlarged, knob- or ridgelike (Tedford et al. 1995, Zrzavý a Řičánková 2004)
44. **Zygomatic arch** (0) nearly flat or moderately arched,(1) strongly arched dorsoventrally (Tedford et al. 2009)

45. **anterior excavation of masseteric fossa** (0) not excavated, (1) excavated anteriorly (Wang et al. 1999)
46. **scars of medial masseteric muscle** (0) narrow and uniform width on zygomatic arch and on lateral surface of angular process, (1) wide on zygomatic arch and enlarged on mandible (Tedford et al. 1995, Zrzavý and Řičánková 2004)
47. **coronoid process** (0) short at base relative to dorsoventral height, (1) long at base relative to dorsoventral height (Tedford et al. 1995, Zrzavý and Řičánková 2004)
48. **angular process** (0) slender, attenuated, with dorsal hook, inferior pterygoid fossa not expanded, (1) large, usually blunt without dorsal hook, fossa for interior branch of medial pterygoid muscle expanded, (2) deep, short process, fossae for the pterygoid muscle are expanded (Tedford et al. 1995, Zrzavý and Řičánková 2004)
49. **palate** (0) not widened, (1) widened (Tedford et al. 1995, Zrzavý a Řičánková 2004)
50. **angular process, superior fossa** (0) not expanded, (1) expanded with large fossa for superior branch of medial pterygoid muscle (Tedford et al. 1995, Zrzavý a Řičánková 2004)
51. **palatine length** (0) extends posteriorly to or just anterior to end of tooth row, (1) extends beyond end of tooth row (Tedford et al. 1995, Zrzavý a Řičánková 2004)
52. **strongly arched zygoma with inverted jugals** (0) absent, (1) present (Berta 1987)
53. **mandibular condyle above level of alveolar border of cheekteeth** (0) absent, (1) present (Berta 1987)
54. **supraoccipital shield** (0) rectangular or fan-shaped in posterior view, inion may not overhang condyles, (1) triangular in shape, inion usually pointed and overhangs condyles (Tedford et al. 1995, Zrzavý and Řičánková 2004)
55. **nuchal crest expansion** (0) not expanded, (1) extended posteriorly beyond occipital condyle (Wang et al. 1999)
56. **lambdoidal crest narrowing** (0) not constricted, (1) laterally constricted (Wang et al. 1999)
57. **average height of olfactory bulb (mm)** (0) 1,10 – 1,46, (1) 1,53 – 1,80, (2) 1,94 – 2,33 (Gittleman 1991)
58. **average width of olfactory bulb (mm)** (0) 0,83 – 1,20, (1) 1,21 – 1,56, (2) 1,67 – 2,12 (Gittleman 1991)

III. Dentition

59. **Hunter-Schreger bands in enamel ulstrastructure** (0) undulating, (1) zigzag (Stefen 1999)
60. **bite-force at canines (in Newtons)** (0) 32-100, (1) 113-237, (2) 435-743 (Christiansen and Adolfssen 2005)
61. **bite-force at carnassials (in Newtons)** (0) 55-205, (1) 272-1262 (Christiansen and Adolfssen 2005)
62. **m3** (0) with two trigonid cusp, (1) with a single, centrally placed trigonid cusp, (2) posterior shelf of trigonid enlarged, (3) absent (Tedford et al. 2009)
63. **c1 lateral groove** (0) without lateral groove, (1) with a lateral groove (Wang et al. 1999)
64. **recurved c1** (0) not recurved, (1) recurved (Wang et al. 1999)
65. **m1 talonid** (0) fully trenchant or no talonid, (1) moderately trenchant, (2) bicuspid, (3) basined talonid (Van Valkenburgh 1991)
66. **m1 talonid width** (0) width subequal to that of trigonid, (1) widened relative to trigonid, (2) narrow relative to trigonid (Wang et al. 1999)
67. **p3** (0) 2 posterior cusplet behind principal cusp, (1) 1 small posterior cusplet behind principal cusp (Berta 1988)
68. **M1 parastyle** (0) large and salient, united, well developed preparacrista, (1) subdued, remains united with preparacrista, (2) preparacrista directed more anteriorly, lingual parastyle (Tedford et al. 2009)
69. **M1 labial cingulum at metacone** (0) M1 labial cingulum present at metacone, (1) cingulum absent lateral to the metacone (Wang et al. 1999)
70. **M1 labial cingulum at paracone** (0) present at paracone, (1) absent lateral to the paracone (Wang et al. 1999)
71. **reduction of p1** (0) p1 present, (1) p1 absent (Wang et al. 1999)
72. **anterior premolars low-crowned** (0) premolars unshortened, (1) shortened (Wang et al. 1999)
73. **premolar shape** (0) broad and short, (1) narrow and elongate (Tedford et al. 2009)
74. **premolar diastemata** (0) closed premolar row, (1) premolars separated by diastemata (Tedford et al. 2009)
75. **premolars shortened** (0) unshortened, (1) shortened (Wang et al. 1999)
76. **premolars slender** (0) not slender, (1) slender (Wang et al. 1999)

77. **m2 paraconid** (0) present, (1) very weak or absent (Tedford et al. 2009)
78. **m2 talonid length** (0) talonid longer than trigonid (90 %), (1) trigonid (90%) longer than talonid (Tedford et al. 2009)
79. **m2 enlargement** (0) not enlarged, (1) enlarged, (2) extremely enlarged (Wang et al. 1999)
80. **m2 reduction** (0) not reduced, (1) reduced, (2) further reduced (Wang et al. 1999)
81. **m2 anterobuccal cingulum** (0) small, (1) large (Tedford et al. 1995)
82. **M2 posterior cingulum** (0) absent or weakly developed, (1) well developed (Wang et al. 1999)
83. **M2 metacone** (0) present, (1) very reduced or absent (Wang et al. 1999)
84. **M2 metaconule** (0) present, (1) very weak or absent (Tedford et al. 2009)
85. **p2-p4 anterior cingular cusps** (0) present, (1) present only on P4, (2) very weak or absent (Tedford et al. 2009)
86. **M2 postprotocrista** (0) present, (1) incomplete or absent (Tedford et al. 2009)
87. **m2 anterolabial cingulum** (0) weak, (1) well developed,often reaching labial side of protoconid (Tedford et al. 2009)
88. **m1-m2 selenodont** (0) lower molars not selenodont, (1) lower molars selenodont (Wang et al. 1999)
89. **m1 hypoconulid shelf** (0) absent, (1) present (Tedford et al. 2009)
90. **m1 trigonid elongation** (0) m1 trigonid short, (1) m1 trigonid elongated and open (Wang et al. 1999)
91. **m1 trigonid shortening** (0) not shortened, (1) shortened (Wang et al. 1999)
92. **p3, height principal cusp vs p2,p4** (0) forms ascending series with p2,p4 or is at same height, (1) lies below p2 and p4 (Tedford et al. 2009)
93. **p4 unworn principal cusp** (0) equals or exceeds height of m1 paraconid, (1) lower than m1 paraconid (Tedford et al. 2009)
94. **M1 lingual cingulum** (0) well developed, extends across protocone, (1) very weak, max be discontinuous across protocone (Tedford et al. 2009)
95. **m1 hypoconid** (0) situated laterally on talonid, (1) situated centrally on talonid (Tedford et al. 2009)
96. **M1 posterior border** (0) slightly curved, (1) sharply concave (Wang et al. 1999)
97. **M1 metaconule** (0) present, (1) very weak or absent (Tedford et al. 2009)
98. **M1 paraconule** (0) absent or weakly developed, (1) enlarged (Wang et al. 1999)

99. **m1, anterior edge of paraconid** (0) nearly linear and vertical, (1) nclined posteriorly and may be curved (Tedford et al. 2009)

100. **lingual cingulae on upper molars** (0) presence of complete lingual cingulum on upper molars, (1) reduction or loss of anterior segment of internal cingulum (Wang, Tedford 1994)

101. **DP^3 protocone developed as a cusp** (0) absent, (1) present (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)

102. **DP^4 posterior border concave, so that metacone appears as a separate lobe** (0) absent, (1) present (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)

103. **P^4 (carnassial), length as % of condylobasal length** (0) 5-8, (1) 9, (2) 10-11 (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)

104. **M^2, greatest width as % of condylobasal length** (0) 4-5, (1) 6, (2) 7-8 (Clutton-Brock et al. 1976, Zrzavý and Řičánková 2004)

105. **M1 hypocone** (0) absent, (1) small, (2) enlarged (Tedford et al. 2009)

106. **m1 entoconid** (0) entoconid is a low crest on the lingual border of talonid, (1) conical or crestlike as discrete cusp, (2) conical cusp, enlarged, may coalesce with base of hypoconid to block talonid basin, (3) joined to hypoconid with cristids that form a transverse crest, (4) reduce relative to hypoconid, but retains cristid, (5) greatly reduced and lacks cristid (Tedford et al. 2009)

107. **m2 metaconid** (0) greatly reduced or lost, (1) equal or lower than protoconid, (2) enlarged than protoconid (Tedford et al. 1995, Zrzavý and Řičánková 2004)

108. **I1-3 medial cusplets** (0) present, (1) cusplet in I3 absent, (2) cusplet in I1-2 weak or absent (Tedford et al. 1995, Zrzavý a Řičánková 2004)

109. **Crown height of premolars** (0) low-crowned, (1) high-crowned (Tedford et al. 1995, Zrzavý a Řičánková 2004)

110. **p2 position** (0) not isolated, (1) isolated by relatively larger diastemata than other premolars (Tedford et al. 1995, Zrzavý a Řičánková 2004)

111. **Canine shape** (0) long, slender with recurved crown, (1) short, slender, crown not recurved (Tedford et al. 1995, Zrzavý a Řičánková 2004)

112. **m2 protostylid** (0) absent, (1) buccal cingulum bears protostylid (Tedford et al. 1995, Zrzavý a Řičánková 2004)

113. **m1 protostylid** (0) absent, (1) present (Tedford et al. 1995, Zrzavý and Řičánková 2004)

114. **M1-2 shape** (0) transversely wide for their labial length, (1) narrow for their labial length (Tedford et al. 1995, Zrzavý and Řičánková 2004)

115. **p4 second posterior cusplet** (0) absent, (1) undifferentiated from cingulum, (2) present (Tedford et al. 1995, Zrzavý a Řičánková 2004)

116. **p4 posterior accesory cusp position** (0) located along midline of tooth, (1) shifted lateraly (Wang et al. 1999)

117. **P4 parastyle** (0) no p4 parastyle on the anterior cingulum, (1) parastyle originating from the anterior cingulum separate from the anterir ridge of paracone, (2) strong ridge on anterior face of paracone, (3) a distinct parastyl as delineated by a notch on the anterior ridge of paracone, (4) parastyle prominently enlarged (Wang et al. 1999)

118. **P4 lingual cingulum or hypocone** (0) internal cingulum week or absent, (1) cingulum thickened, (2) cingulum raised to become a hypocone (Wang et al. 1999)

119. **P4 protocone and parastyle connection** (0) protocone not connected to parastyle by a ridge, (1) protocone connected to parastyle (Wang et al. 1999)

120. **relative size of P4 vs M1-M2** (0) upper molars reduced relative to P4, (1) normally proportioned P4 and upper molars, (2) upper molars enlarged relative to P4 (Wang et al. 1999)

121. **P4 protocone** (0) salient, located medial to anterior border of paracone, (1) reduced, (2) further reduced or absent, located posterior to anterior border of paracone (Tedford et al. 1995, Zrzavý a Řičánková 2004)

122. **m1 metaconid** (0) not reduced, (1) greatly reduced or absent (Tedford et al. 1995, Zrzavý a Řičánková 2004)

123. **m2 metaconid and entoconid** (0) not reduced, (1) greatly reduced or absent (Tedford et al. 1995, Zrzavý a Řičánková 2004)

124. **M1-2 hypocones** (0) not reduced, (1) greatly reduced or absent (Tedford et al. 1995, Zrzavý a Řičánková 2004)

125. **M1-2 paracones** (0) not enlarged, (1) enlarged relative to metacone (Tedford et al. 1995, Zrzavý a Řičánková 2004)

126. **M2** (0) triple-rooted, (1) double-rooted, or M2 absent (Tedford et al. 1995, Zrzavý a Řičánková 2004)

127. **I3** (0) small crown extending to or just below level of I1-2, posteromedial cingulum weak or absent, (1) large crown extending markedly below level of I1-2,

cingulum enlarged, medial crest of I1-2 present merges with cingulum (Tedford et al. 1995, Zrzavý a Řičánková 2004)

128. **I3 lateral cusp** (0) without lateral cusp, (1) one lateral cusp, (2) two lateral cusp, (3) three lateral cusp (Wang et al. 1999)

129. **P3 and p2-3 posterior cusplets** (0) present, (1) weak or absent (Tedford et al. 1995, Zrzavý a Řičánková 2004)

130. **m1-2 with mesoconid** (0) absent, (1) present (Berta 1987)

131. **m2 with strong paracristid** (0) absent (1) present (Berta 1987, Zrzavý a Řičánková 2004)

132. **canines small relative to cheekteeth** (0) absent, (1) present (Berta 1987, Zrzavý a Řičánková 2004)

133. **carnassials small relative to cheekteeth** (0) absent, (1) present (Berta 1987, Zrzavý a Řičánková 2004)

134. **carnassials well differentiated** (0) absent, (1) present (Ewer 1998, Wang et al. 2008)

135. **Bladelike cheekteeth** (0) not bladelike, (1) bladelike (Wang et al. 1999)

136. **Upper incisor row** (0) curved, (1) straight (Wang et al. 1999)

137. **Third upper molar** (0) absent, (1) present (Wozencraft 1996)

138. **RBL** - Relative blade length of lower first molar (m1 carnassial) measured as the ratio of trigonid length to total anteroposterior legth of m1 (0) 0.565 - 0.623, (1) 0.624 – 0.68, (2) 0.681 -0.738 (Van Valkenburgh et Koepfli 1993,Friscia et al. 2007)

139. **RLGA -** Relative lower grinding area, measured as the square root of the summed areas of the m1 talonid and m2 divided by the length of the m1 trigonid (0) 0.604 – 0.923, (1) 0.924 – 1.243 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

140. **RUGA -** Relative upper grinding area, measured as the square root of the summed areas of M1 and M2 divided by the anteroposterior length of P4 (upper carnassial) (0) 0.836 – 0.987, (1) 0.988 – 1.139, (2) 1.14- 1.29 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

141. **M1BS -** m1 blade size relative to dentary length, measured as the length of the trigonid of m1 (carnassial) divided by dentary length (0) 0.068 – 0.0925, (1) 0.093 – 0.117 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

142. **M2S -** m2 size relative to dentary length, measured as the square root of m2 area divided by dentary length (0) 0.035 – 0.0515, (1) 0.0516 – 0.068 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

143. **IXP4 -** Second moment of area of the dentary at the interdental gap between the third and fourth lower premolars relative to dentary length (0) 0.039 – 0.05, (1) 0.051 – 0.061 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

144. **IXM2 -** Estimate of resistance of dentary to bending, as measured by the second moment of area at the interdental gap between the first and second molars (or posterior to the first molar if no second molar was present) (0) 0.041 – 0.053, (1) 0.054 – 0.065 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

145. **MAT -** Mechanical advantage of the temporalis muscle, measured as the distance from the mandibular condyle to the apex of the coronoid process divided by dentary length (0) 0.023 – 0.0855, (1) 0.148-0.2105, (2) 0.2106 – 0.273 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

146. **MAM** Mechanical advantage of the masseter muscle, measured as the distance from the mandibular condyle to the ventral border of the mandibular angle divided by dentary length (0) 014- 0.1993, (1) 0.1994 – 0.259, (2) 0.318 – 0.377 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

147. **C1 -** Relative size of the upper canine, measured by the square root of the basal area of C1 divided by square root of the size of the lower first molar (carnassial) (0) 0.387 – 0.545, (1) 0.546 – 0.704 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

148. **P4P -** Relative size of the protocone of the upper fourth premolar (carnassial) (0) 0.398 – 0.473, (1) 0.474 – 0.548, (2) 0.549 – 0.623 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

149. **UM21 -** Square root of upper second molar area divided by square root of upper first molar area (0) 0.570 – 0.701, (1) 0.702 – 0.833 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)

150. **P4S -** Lower fourth premolar shape, measured as maximum width of p4 divided by its maximum legth (0) 0.263 – 0.337, (1) 0.338 – 0.411, (2) 0.412 – 0.485 (, Friscia et al. 2007)

151. **PMZ** Relative total length of premolars (0) 0.144 – 0.166, (1) 0.167 – 0.188 (Friscia et al. 2007)

152. **P4Z** - Relative legth of fourth lower premolar, measured as the maximum length of p4 divided by rejtary legth (measured as in M1BS) (Friscia et al. 2007)

IV. Postcranial

153. **gape angle (in degress)** (0) less than 61, (1) more than 62 (Friscia et al. 2007)
154. **scapula, shape of *teres major* muscle scar on posterior angle** (0) on posterior border only, with plane at right angles to lateral face, (1) intermediate, (2) whole scar on lateral face (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
155. **scapula, extent of scar of *serratus magnus* muscle on medial side** (0) small, (1) large (Clutton-Brock *et al*. 1976, Zrzavý a Řičánková 2004)
156. **number of thoracic vertebrae** (0) more than 14, (1) 13 (Gilbert 1990)
157. **baculum anterior end bifurcate** (0) absent, (1) present (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
158. **baculum, length as % of condylobasal length** (0) 34-41, (1) 43-49, (2) 50-58 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
159. **cylindrical baculum** (0) absent, (1) present (Weber, 1852-1937)
160. **tail, length as % of length of head and body** (0) 22-38, (1) 41-59, (2) 60-76 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
161. **hind feet, length as % of length of head and body** (0) 17-19, (1) 20-22, (2) 23-26 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
162. **fore legs, length as % of length of body spine (cervical to lumbal vertebrae)** (0) 52-62, (1) 63-71, (2) 92 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
163. **hind legs, length as % of length of body spine (cervical to lumbal vertebrae)** (0) 58-70, (1) 73-83, (2) 103 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
164. **neck, length of cervical vertebrae as % of combined length of thoracic and lumbar vertebrae** (0) 34-38, (1) 39-42, (2) 43-47 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
165. **pelvis, width as % of length** (0) 53-63, (1) 67-77 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

166. **femur, length as % of length of tibia** (0) 80-89, (1) 93-97, (2) 100-108 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

167. **femur, minimum width of shaft as % of length** (0) 6, (1) 7, (2) 8 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

168. **third metatarsal, length as % of length of femur** (0) 37-42, (1) 43-46, (2) 48-53 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

169. **metatarsal I** (0) present, with phalanges, (1) reduced to rudiment, lacking phalanges (Tedford et al. 2009)

170. **humerus, entepicondylar foramen** (0) present, (1) absent (Tedford et al. 2009)

171. **relative length of fore- to hindlimbs** (0) short, radius/tibia ratio <90%, (1) long, radius/tibia ratio >90% (Tedford et al. 1995, Zrzavý a Řičánková 2004)

172. **forelimb (humerus-radius)** (0) longer than 30% of head-body length, (1) less than 30% of head-body length (Tedford et al. 1995, Zrzavý a Řičánková 2004)

173. **reciprocal arm translocation** (0) absent, (1) present (Wayne *et al*. 1987a, b)

174. **rotation of forearm** (0) absent, (1) present (Wang et al. 2008)

V. The other morphological characters

175. **muzzle** (0) light, (1) dark (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

176. **facial mask between nose and eye** (0) absent, (1) present (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

177. **facial mask behind and below eye** (0) absent, (1) present (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

178. **mystacial vibrissae, length and thickness** (0) low, (1) medium, (2) high (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

179. **neck and back** (0) no crest, (1) crest, (2) mane (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

180. **back dark longitudinal band** (0) absent, (1) narrow stripe, (2) wide stripe, (3) saddle (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

181. **guard hairs' coarseness** (0) soft, (1) medium, (2) coarse (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

182. **dorsal guard hairs, length in relation to body size** (0) short, (1) medium, (2) long (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

183. **dorsal guard hairs banded (agouti)** (0) present, (1) absent (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

184. **underfur, density** (0) low, (1) medium, (2) high (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

185. **ear pinnae** (0) pointed, (1) rounded (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

186. **ear pinnae** (0) light, (1) dark (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

187. **ear pinna dark rim** (0) absent, (1) present (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

188. **tail bushiness** (0) low, (1) medium, (2) high (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

189. **tail dark patch on dorsal surface** (0) absent, (1) short, (2) long (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

190. **tail tip** (0) white, (1) same as rest of tail, (2) black (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

191. **fore legs** (0) light, (1) entirely dark (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

192. **fore legs with black line on front** (0) absent, (1) present (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

193. **hind legs** (0) light, (1) dark (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

194. **hind feet, dark plantar surface** (0) absent, (1) present (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

195. **skin darkly pigmented** (0) light, (1) medium, (2) dark (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)

196. **face contrasting** (0) absent, (1) present (Ortolani & Caro 1989, Zrzavý a Řičánková 2004)

197. **face** (0) darker, (1) unicolour, (2) lighter (Ortolani & Caro 1989, Zrzavý a Řičánková 2004)

198. **eye contour** (0) dark around, (1) unicolour, (2) light ring (Ortolani & Caro 1989, Zrzavý a Řičánková 2004)

199. **throat and neck** (0) darker, (1) unicolour, (2) lighter, (3) white (Ortolani & Caro 1989, Zrzavý a Řičánková 2004)
200. **below eyes** (0) unicolour, (1) dark patch (Ortolani & Caro 1989, Zrzavý a Řičánková 2004)
201. **overall colour, intensity of black pigment** (0) absent, (1) grey or banded hairs, (2) general appearance dark (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
202. **overall colour, intensity of red pigment** (0) absent, (1) present as yellow or red underfur, (2) general appearance reddish or tan, (3) extensive red colour (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
203. **eye pupil** (0) elliptic, (1) circular (Nowak 1999, Zrzavý a Řičánková 2004)
204. **ears, length as a % of length of head and body** (0) 7-13, (1) 14-18, (2) 20-25 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
205. **body size** (0) 0,5-12,5, (1) 13-25,5, (2) 26-38,5, (3) 39-51,5, (4) 52-64,5, (5) 65-72 (Wang et al. 2008, Tedford et al. 2009)
206. **digitigrade** (0) absent, (1) present (Wang et al. 2008)
207. **glandulae vasis deferentis** (0) absent, (1) present (Weber, 1852-1937)
208. **prostata** (0) not rudimental, (1) rudimental (Weber, 1852-1937)
209. **caecum** (0) absent, (1) present (Berta 1984, Nowak 1999)
210. **number of mammae** (0) 4-7, (1) 8, (2) 10-14 (Clutton-Brock et al. 1976, Zrzavý a Řičánková 2004)
211. **five toes on hindfeet** (0) absent, (1) (Nowak 1999)

VI. Reproduction and developmental characters

212. **delayed implantation** (0) absent, (1) present (Nowak 1999)
213. **induced ovulation** (0) absent, (1) present (Nowak 1999)
214. **basal metabolic rate kJ/d** (0) less than 400, (1) 480-1000, (2) more than 1000 (Mun˜oz-Garcia and Williams 2005.)
215. **endocranial volume** (0) <52 ml, (1) >62 ml (Finarelli 2006)
216. **Female body mass** (0) < 5 kg, (1) 6-9 kg, (2) 10-12 kg, (3) 13-16 kg, (4) > 20 kg (Moehlman & Hofer 1997)
217. **Sexual dimorphism (M/F)** (0) < 1 or equal, (1) > 1 (Moehlman & Hofer 1997)

218. **Frequency of oestrus phases** (0) once a year, (1) aseasonal (Clutton-Brock *et al*. 1976)

219. **Estrus duration from** (0) short to (2) long (Estes 1991; Asa & Valdespino 1998; Nowak 1999)

220. **Gestation time** (0) 50-58 days, (1) 60-65 days, (2) > 67 days (Hayssen *et al*. 1993; Moehlman & Hofer 1997)

221. **Neonate mass** (0) 25-150 g, (1) 160-350 g, (2) more than 350 g (Hayssen *et al*. 1993; Moehlman & Hofer 1997)

222. **litter size** (0) less than 4, (1) 4 to 6, (2) more than 6 (Moehlman & Hofer 1997, Sillero – Zubiri et al. 2004)

223. **litter weight** (0) less than 200, (1) 200 to 700, (2) 700 to 2000, (3) more than 2000 (Moehlman & Hofer 1997, Sillero – Zubiri et al. 2004)

224. **age when eyes open** (0) 5-8 days, (1) 9-12 days, (2) more than 13 days (Moehlman & Hofer 1997)

225. **age when teeth erupt** (0) 7-11 days, (1) 12-15 days, (2) more than 21 days (Moehlman & Hofer 1997)

226. **age when eating first solids** (0) 17-21 days, (1) 24-28 days, (2) 32-40 days (Moehlman & Hofer 1997)

227. **age at weaning** (0) 49-63 days, (1) 90-120 days (Moehlman & Hofer 1997)

228. **age when reaching adult body mass** (0) 90-190 days, (1) more than 200 days (Moehlman & Hofer 1997)

229. **age at sexual maturity** (0) 240-270 days, (1) 285-330 days, (2) 360-365 days (Hayssen *et al*. 1993; Moehlman & Hofer 1997)

230. **life span** (0) 40-80 months, (1) 100-155 months, (2) more than 165 months (Hayssen *et al*. 1993; Moehlman & Hofer 1997)

VII. Ecological and behavioural characters

231. **communal denning and nursing** (0) absent, (1) present (Moehlman & Hofer 1997)

232. **polygyny** (0) absent (monogamy), (1) present (Moehlman & Hofer 1997)

233. **multiple pairs breeding** (0) absent, (1) present (Moehlman & Hofer 1997)

234. **polyandry** (0) absent (monogamy), (1) present (Moehlman & Hofer 1997)

235. **territorial behaviour** (0) absent, (1) present (Moehlman & Hofer 1997)

236. **multiple litters** (0) absent, (1) present (Moehlman & Hofer 1997)

237. **solitary during breeding season** (0) absent, (1) present (Moehlman & Hofer 1997, Sillero – Zubiri et al. 2004)

238. **close contact (resting in heaps)** (0) absent, (1) present (Estes 1991, Macdonald 1996)

239. **regurgitation** (0) absent, (1) present (see, e. g., Estes 1991)

240. **submissive grin** (0) less developed, (1) well developed, (2) extremely developed (Fox 1970)

241. **raising lip to show fangs as a threat behaviour** (0) absent (merely opening their mouths slightly), (1) present (Fox 1970; see Clutton-Brock *et al*. 1976)

242. **low level of food caching** (0) absent, (1) present (Macdonald 1996)

243. **handstand urination** (0) absent, (1) present (see Estes 1991)

244. **Scratching ground before or after urination** (0) absent, (1) present (see Estes 1991)

245. **laying during submissive display (belly crawl)** (0) absent, (1) present (Estes 1991; Hudakova 1998)

246. **licking during greeting ceremony** (0) absent, (1) present (see Fox 1970)

247. **tucking tail between hindlegs as a subordination posture** (0) absent, (1) present (see, e. g., Estes 1991; Hudáková 1998)

248. **size of prey relative to body size from** (0) small to (2) large (Clutton-Brock *et al*. 1976)

249. **social grooming** (0) rare and only between pairs, (1) well developed (Clutton-Brock *et al*. 1976)

250. **howling** (0) absent or only as long-distance contact call, (1) present but no physical contact, (2) close contact call, social howling in unison [unordered] (Clutton-Brock *et al*. 1976)

251. **defecation at specific sites** (0) absent, (1) present (Clutton-Brock *et al*. 1976)

252. **tail posture in dominant animals** (0) no distinct posture, (1) straight and horizontal, (2) raised in a J-shape, (3) inverted U-shape [unordered] (Clutton-Brock *et al*. 1976)

253. **frequency of tail-wagging in submissive posture from** (0) low to (2) high (Clutton-Brock *et al*. 1976)

254. **duration of copulatory tie from** (0) short to (2) long (see Estes 1991; Alderton 1998; Nowak 1999)

255. **average number of adults per group during breeding season from** (0) low to (2) high (Moehlman & Hofer 1997; Muñoz-Durán (2002)

256. **treatment of prey** (0) aggressive defense of all food, (1) sharing of some foods, (2) sharing of most or all foods (Biben 1982b)

257. **treatment of play object** (0) aggressive competition (playmates discouraged), (1) mock competition (playmates encouraged), (2) sharing without competition (Biben 1982a)

258. **diet** (0) opportunist, (1) specialised to small prey, (2) specialised to large prey [unordered] (see, e. g,. Estes 1991; Malcolm 1986; Kauhala 1996; Nowak 1999; Juarez & Marinho 2002)

259. **ontogeny of the aggressivity over food** (0) aggressive, (1) youngsters more aggressive than adults, (2) non-aggressive (Biben 1982a, 1983)

260. **age of first killing and eating of the prey** (0) less that 35 days, (1) more than 50 days (Fox 1969a; Biben 1983)

261. **age of first social interactions (pawing, licking, monting)** (0) less than 15 days, (1) more than 20 days (Biben 1983; Fox 1970)

262. **age of first roll over as a submissive expression** (0) less than 23 days, (1) 26-35 days (Fox 1969b)

263. **jaw wrestling** (0) absent or rare, (1) common (see Fox 1969b, 1970)

264. **age of first jaw wrestling** (0) 14 days, (1) 22-23 days, (2) 35-45 days (see Fox 1969b, 1970; Biben 1983)

265. **period of fighting begins at age** (0) 24 days, (1) 30-32 days, (2) 40-45 days (Fox 1969b; Biben 1983)

266. **play bow (a posture with lowered forequaters and elevated hindquaters)** (0) absent or rare, (1) common (Fox 1970)

267. **adults initiate interactions by assuming a submissive posture** (0) absent, (1) present (see, e. g., Estes 1991)

268. **male urinary behaviour is related to dominance** (0) absent, (1) present (in social species the top male marks most often; see Estes 1991)

269. **orientation of attack during agonistic interactions** (0) towards the scruff of the neck, (1) towards cheeks, muzzle or lower jaw (Fox 1969b)

270. **scruff bite intention or scruff-biting associated with mating** (0) absent, (1) present (Fox 1969b)

271. **dead shake movements** (0) absent, (1) present (Fox 1969a)

272. **play with prey terminated when a conspecific attempted to take the prey from its owner** (0) absent, (1) present (Fox 1969b**,** 1970)

273. **playing together at the same time with one object (‘tugs-of-war’)** (0) rare, (1) common (see, e. g., Estes 1991; Macdonald 1996)

274. **gape (facial expression with the opened mouth)** (0) absent, (1) less developed, (2) well developed (Fox 1970)

275. **cut off" response during higher level of the intraspecific conflict (facial expression used to stop aggressive behaviour)** (0) absent, (1) present (Fox 1970)

276. **head turning and avoidance of eye contact as a submissive response** (0) absent, (1) present (Fox 1970)

277. **back arching resemble feline pattern as defensive threat display** (0) absent, (1) present (Fox 1969, 1970)

278. **T-position standing over (dominance)** (0) absent, (1) present (Fox 1969)

279. **ability to climb on trees or cliffs** (0) absent, (1) present(Sillero – Zubiri et al. 2004)

280. **nonreproductive adults** (0) absent, (1) present (Moehlman & Hofer 1997, Sillero – Zubiri et al. 2004)

281. **helpers** (0) absent, (1) present (Moehlman & Hofer 1997, Sillero – Zubiri et al. 2004)

282. **nonreproductive males** (0) absent, (1) present (Moehlman & Hofer 1997, Sillero – Zubiri et al. 2004)

283. **breeding male spent more time with pups that female** (0) absent, (1) present (Sillero – Zubiri et al. 2004)

284. **paternal care equal or more than maternal (male feeding)** (0) absent, (1) present (Sillero – Zubiri et al. 2004)

285. **cooperative hunting** 0) absent, (1) present (Estes 1991; Sillero-Zubiri & Gottelli 1995; Macdonald & Courtenay 1996; Nowak 1999, Sillero – Zubiri et al. 2004)

286. **foraging in pairs or groups without direct cooperation** (0) absent, (1) present (see, e. g., Estes 1991; Sillero-Zubiri & Gottelli 1995; Macdonald & Courtenay 1996; Nowak 1999, (Sillero – Zubiri et al. 2004)

287. **habitat** (0) desert semidesert, (1) savannah and shrubland, (2) forest (Sillero – Zubiri et al. 2004)

288. **arboreal (semiarboreal)** (0) absent, (1) present (Nowak 1999)

289. **diet** (0) large vertebrates, (1) small vertebrates, (2) invertebrates and plants (Sillero – Zubiri et al. 2004)

VIII. Cytogenetic characters

290. **chromosome diploid number** (0) less than 74, (1) 74, (2) 76, (3) 78 [unordered] (Wayne *et al*. 1987a, b)

291. **acrocentric chromosomes** (0) present, (1) absent (Wayne *et al*. 1987a, b)

292. **metacentric chromosomes** (0) present, (1) rare, (2) absent [unordered] (Wayne *et al*. 1987a, b)

293. **chromosome 40** (0) absent, (1) present (Wayne *et al*. 1987a, b)

294. **chromosome 34** (0) absent, (1) present (Wayne *et al*. 1987a, b)

295. **chromosome 36** (0) absent, (1) present (Wayne *et al*. 1987a, b)

296. **chromosome 28** (0) present, (1) absent (Wayne *et al*. 1987a, b)

297. **chromosome 22** (0) present, (1) absent (Wayne *et al*. 1987a, b)

298. **terminal segments added to chromosomes** 12, 18, 24, and 30 (0) absent, (1) present (Wayne *et al*. 1987a, b)

299. **chromosome 31** (0) present, (1) absent (Wayne *et al*. 1987a, b)

300. **chromosome 37** (0) present, (1) absent (Wayne *et al*. 1987a, b)

301. **chromosome 38** (0) absent, (1) present (Wayne *et al*. 1987a, b)

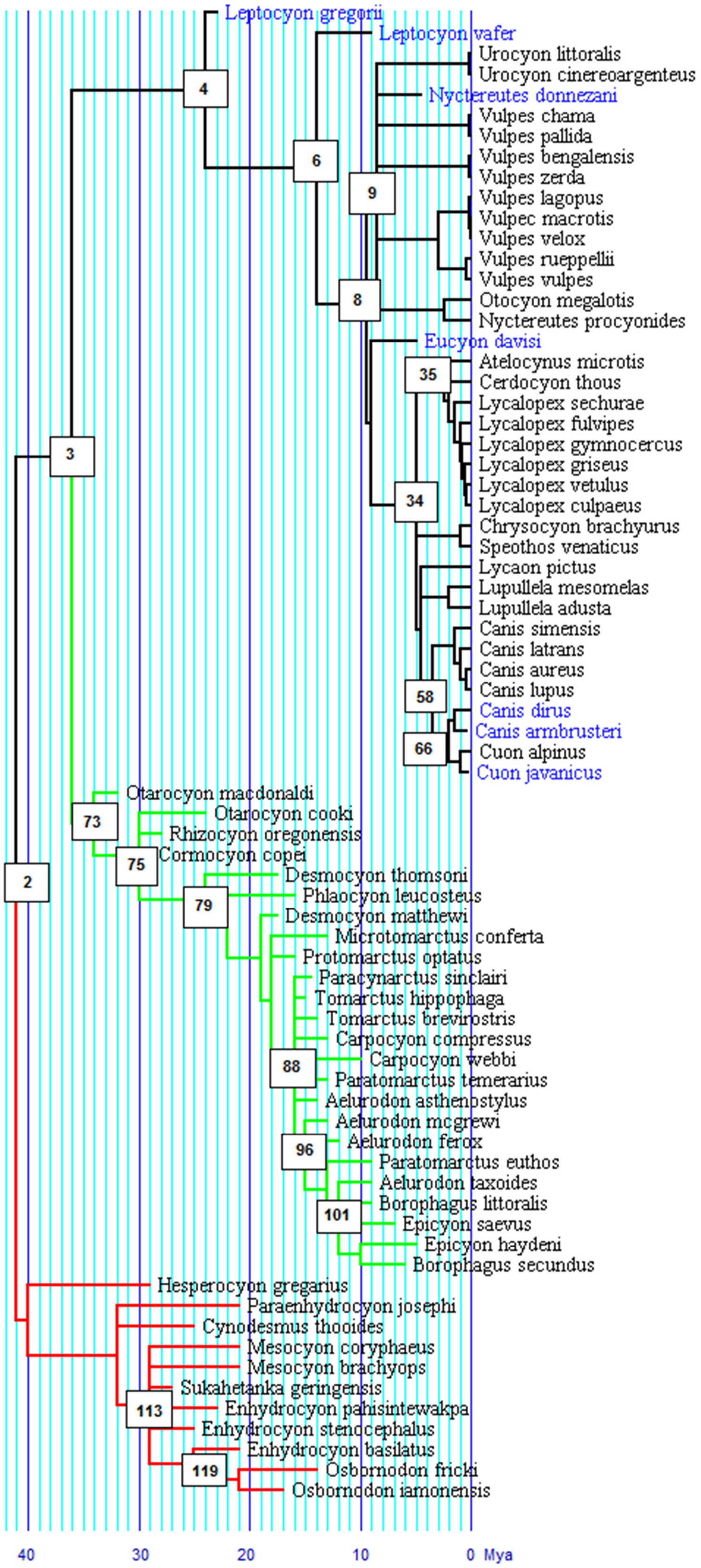


Fig. 6. Phylogeny of Canidae with timescale used for analyses (red line – Hesperocyoninae, green line – Borophaginae, blue names – fossil Caninae). (numbers in squares = node numbers)

List 2. The list of characters for 1. PCA analysis:

- **log encephalization quotient (logencq) –** log-transformed quotient expressing allometric relation between body mass and brain volume (Finarelli et Flynn, 2007)
- **body size (bodysize)** – body size of canids in kilograms (Finarelli et Flynn, 2009)
- **group size (grosiz)** – number of adults during breeding season (Sillero-Zubiri et al. 2004)
- **horizontal ramus (horram)** – (0) deep and thick, (1) shallow and thin (Tedford et al. 1995, Zrzavý et Řičánková 2004)
- **sagittal crest (sagcrest) –** (0) uniformly high-strongly compressed-well defined temporal ridges, (1) low-temporal ridges weakly developed (Berta 1988)
- **frontal sinus (frosin) –** (0) absent, presence of a depression on dorsal surface of postorbital process, (1) present, lacks a depression on dorsal surface of postorbital process, (2) present, large, penetrates postorbital process and expands posteriorly toward the frontal-parietal suture, (3) reached frontoparietal suture (Tedford et al. 1995, Tedford et al. 2009, Zrzavý etŘičánková 2004)
- **m1 talonid (m1tal)** – (0) fully trenchant or no talonid, (1) moderately trenchant, (2) bicuspid, (3) basined talonid (Van Valkenburgh 1991)
- **M3 (M3) –** (0) absent, (1) present (Clutton-Brock et al. 1976, Zrzavý et Řičánková 2004)
- **M1 hypocone (M1hypo) –** (0) absent, (1) present, (2) enlarged (Tedford et al. 2009)
- **m2 metaconid (m2met) –** (0) greatly reduced or lost, (1) equal to or lower than protoconid, (2) enlarged, taller than protoconid (Tedford et al. 1995, Zrzavý et Řičánková 2004)
- **m1 metaconid (m1met)–** (0) not reduced, (1) greatly reduced or absent (Tedford et al. 1995, Zrzavý etŘičánková 2004)
- **M1-2 paracones (M1-2par) –** (0) not enlarged, (1) enlarged relative to metacone (Tedford et al. 1995, Zrzavý etŘičánková 2004)
- **I3 (I3) –** (0) small crown exntending to or just below level of I1-2, posteromedial cingulum weak or absent, (1) large crown exntending markedly below level of I1-2, cingulum enlarged, medial crest of I1-2 present merges with cingulum (Tedford et al. 1995, Zrzavý et Řičánková 2004)

- **RBL (RBL) -** Relative blade length of lower first molar (m1 carnassial) measured as the ratio of trigonid length to total anteroposterior length of m1: (0) 0.565 - 0.623, (1) 0.624 – 0.68, (2) 0.681 -0.738 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)
- **RLGA (RLGA) -** Relative lower grinding area, measured as the square root of the summed areas of the m1 talonid and m2 divided by the length of the m1 trigonid: (0) 0.604 – 0.923, (1) 0.924 – 1.243 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)
- **RUGA (RUGA) -** Relative upper grinding area, measured as the square root of the summed areas of M1 and M2 divided by the anteroposterior length of P4 (upper carnassial): (0) 0.836 – 0.987, (1) 0.988 – 1.139, (2) 1.14- 1.29 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)
- **M1BS (M1BS) -** m1 blade size relative to dentary length, measured as the length of the trigonid of m1 (carnassial) divided by dentary length: (0) 0.068 – 0.0925, (1) 0.093 – 0.117 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)
- **IXP4 (IXP4) –** Relative resistance of the dentary to bending in the parasagittal plane as estimated by second moment of area of the dentary at the interdental gap between the third and fourth lower premolars relative to dentary length: (0) 0.039 – 0.05, (1) 0.051 – 0.061 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)
- **IXM2 (IXM2) -** Estimate of resistance of dentary to bending, as measured by the second moment of area at the interdental gap between the first and second molars (or posterior to the first molar if no second molar was present): (0) 0.041 – 0.053, (1) 0.054 – 0.065 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)
- **MAT (MAT) -** Mechanical advantage of the temporalis muscle, measured as the distance from the mandibular condyle to the apex of the coronoid process divided by dentary length: (0) 0.023 – 0.0855, (1) 0.148-0.2105, (2) 0.2106 – 0.273 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)
- **MAM (MAM) -** Mechanical advantage of the masseter muscle, measured as the distance from the mandibular condyle to the ventral border of the mandibular angle divided by dentary length (0) 014- 0.1993, (1) 0.1994 – 0.259, (2) 0.318 – 0.377 (Van Valkenburgh et Koepfli 1993, Friscia et al. 2007)
- **Size of prey relative to body size (sprtbs) -** from (0) small to (2) large (Clutton-Brock et al. 1976)

- **Diet (Diet) -** (0) opportunist, (1) specialised to small prey, (2) specialised to large prey (e. g. Estes 1991, Kauhala 1996, Nowak 1999, Juarez et Marinho 2002)
- **Cooperative hunting (CooHun) –** (0) absent, (1) present (e. g. Estes 1991, Sillero-Zubiri et Gottelli 1995, Nowak 1999, Sillero – Zubiri et al. 2004).

Table 9. The list of the species in the matrix for the 1. PCA analysis.

SPECIES	VERNACULAR NAME
Urocyon cinereoargenteus	Gray fox
Urocyon littoralis	Island fox
Vulpes lagopus	Arctic fox
Vulpes bengalensis	Bengal fox
Vulpes chama	Cape fox
Nyctereutes procyonoides	Raccoon dog
Chrysocyon brachyurus	Maned wolf
Speothos venaticus	Bush dog
Cerdocyon thous	Crab-eating fox
Canis adustus	Side-striped jackal
Canis mesomelas	Black-backed jackal
Lycaon pictus	African wild dog
Cuon alpinus	Dhole
Canis simensis	Ethiopian wolf
Canis latrans	coyote
Canis lupus	Grey wolf

List 3. The list of characters for 2. PCA analysis.

- **Log encephalization quotient (logencq) –**log-transformed quotient expressing allometric relation between body mass and brain volume (Finarelli et Flynn, 2007)
- **Body size (bodysize) –** body size of canids in kilograms (Finarelli et Flynn, 2009)
- **Group size (grosiz) –** number of adults during breeding season (Sillero-Zubiri et al. 2004)
- **Diet (Diet) -** (0) opportunist, (1) specialised to small prey, (2) specialised to large prey (e. g. Estes 1991, Kauhala 1996, Nowak 1999, Juarez et Marinho 2002)
- **Cooperative hunting (CooHun) –** (0) absent, (1) present (e. g. Estes 1991, Sillero-Zubiri et Gottelli 1995, Nowak 1999, Sillero – Zubiri et al. 2004)
- **Gestation period (gestat) –** duration of gestation in days (Moehlman & Hofer 1997)
- **Litter size (littsize) –** size of litter (Moehlman & Hofer 1997, Sillero – Zubiri et al. 2004)
- **Desert & semidesert (desert) –** occupying of desert habitat (0) absent, (1) present (Sillero – Zubiri et al. 2004)
- **Grassland & shrublands (grassla) –** occupying of grassland habitat (0) absent, (1) present (Sillero – Zubiri et al. 2004)
- **Forest –** occupying of forest habitat (0) absent, (1) present (Sillero – Zubiri et al. 2004)
- **Nonreproductive adults (nra) –** nonreproductive adults in group (0) absent, (1) present (Moehlman & Hofer 1997, Sillero – Zubiri et al. 2004)
- **Nonreproductive males (male nra) –** nonreproductive males in group (0) absent, (1) present (Moehlman & Hofer 1997, Sillero – Zubiri et al. 2004)
- **Paternal care (patecare) –** paternal care for puppies (0) absent, (1) present (Sillero – Zubiri et al. 2004)
- **Polyandry (polyand) –** polyandry (0) absent, (1) present (Moehlman & Hofer 1997)
- **Communal denning (comden) –** communal denning (0) absent, (1) present (Moehlman & Hofer 1997)
- **Frequency of oestrus phases (freqestr) –** presence of oestrus (0) once a year, (1) aseasonal (Clutton-Brock *et al.* 1976)

Foraging in pairs or groups without direct cooperation (forpair) – foraging in pairs or groups without direct cooperation (0) absent, (1) present (see, e. g., Estes 1991; Sillero-Zubiri & Gottelli 1995; Macdonald & Courtenay 1996; Nowak 1999)

Table 10. The list of the species in the matrix for the 2. PCA analysis.

SPECIES	VERNACULAR NAME
Urocyon cinereoargenteus	Gray fox
Vulpes lagopus	Arctic fox
Vulpes bengalensis	Bengal fox
Nyctereutes procyonoides	Raccoon dog
Chrysocyon brachyurus	Maned wolf
Speothos venaticus	Bush dog
Cerdocyon thous	Crab-eating fox
Canis mesomelas	Black-backed jackal
Lycaon pictus	African wild dog
Cuon alpinus	Dhole
Canis simensis	Ethiopian wolf
Canis latrans	coyote
Canis lupus	Grey wolf

List 4. The list of discrete traits used in randomization test.

- **I3 (I3) –** (0) small crown exntending to or just below level of I1-2, posteromedial cingulum weak or absent, (1) large crown exntending markedly below level of I1-2, cingulum enlarged, medial crest of I1-2 present merges with cingulum (Tedford et al. 1995, Zrzavý et Řičánková 2004)
- **M1-2 paracones (M1-2par) –** (0) not enlarged, (1) enlarged relative to metacone (Tedford et al. 1995, Zrzavý etŘičánková 2004)
- **m1 metaconid (m1met)–** (0) not reduced, (1) greatly reduced or absent (Tedford et al. 1995, Zrzavý etŘičánková 2004)
- **m2 metaconid (m2met) –** (0) greatly reduced or lost, (1) equal to or lower than protoconid, (2) enlarged, taller than protoconid (Tedford et al. 1995, Zrzavý et Řičánková 2004)
- **m1 talonid (m1tal)** – (0) fully trenchant or no talonid, (1) moderately trenchant, (2) bicuspid, (3) basined talonid (Van Valkenburgh 1991)
- **frontal sinus (frosin) –** (0) absent, presence of a depression on dorsal surface of postorbital process, (1) present, lacks a depression on dorsal surface of postorbital process, (2) present, large, penetrates postorbital process and expands posteriorly toward the frontal-parietal suture, (3) reached frontoparietal suture (Tedford et al. 1995, Tedford et al. 2009, Zrzavý etŘičánková 2004)
- **M1 hypocone (M1hypo) –** (0) absent, (1) present, (2) enlarged (Tedford et al. 2009)

Table 11. Foraging strategies and states of correlated osteological characters.

Foraging strategy	**m1 talonid**	**M1 hypocone**
hypercarnivory	fully trenchant	small
hypocarnivory	bicuspid or basined	enlarged
mesocarnivory	bicuspid	enlarged

Table 12. The list of the species used for ancestral reconstruction and their values of brain volume, body size and EQ.

Species	Brain volume (ml)	Body size (kg)	EQ	Subfamily
Leptocyon gregorii	15.27	2.7	0.64	Caninae
Leptocyon vafer	24.21	3.62	0.83	Caninae
Vulpes rueppellii	24.29	3.25	0.90	Caninae
Vulpes vulpes	43.38	5.6	1.11	Caninae
Vulpes lagopus	35.52	4.87	1.00	Caninae
Vulpes velox	32.14	2.2	1.54	Caninae
Vulpes chama	33.5	2.96	1.32	Caninae
Vulpes pallida	25.03	2.8	1.02	Caninae
Vulpes macrotis	30.76	2.25	1.45	Caninae
Nyctereutes donnezani	53.45	8.0	1.08	Caninae
Vulpes bengalensis	25.8	2.73	1.07	Caninae
Vulpes zerda	17.29	1.1	1.32	Caninae
Urocyon cinereoargenteus	40.85	3.83	1.35	Caninae
Urocyon littoralis	27.66	1.9	1.46	Caninae

Otocyon megalotis	26.84	4.15	0.84	Caninae
Nyctereutes procyonoides	28.5	4.04	0.91	Caninae
Atelocynus microtis	62.18	7.75	1.28	Caninae
Cerdocyon thous	41.8	5.24	1.12	Caninae
Lycalopex gymnocercus	40.0	4.69	1.16	Caninae
Lycalopex culpaeus	51.5	9.83	0.91	Caninae
Lycalopex fulvipes	34.41	2.85	1.39	Caninae
Lycalopex vetulus	37.77	3.3	1.38	Caninae
Lycalopex griseus	41.76	4.0	1.34	Caninae
Lycalopex sechurae	34.66	?	?	Caninae
Chrysocyon brachyurus	120.3	23.25	1.19	Caninae
Speothos venaticus	40.45	6.0	0.99	Caninae
Eucyon davisi	55.68	9.0	1.04	Caninae
Lupullela adusta	51.94	10.25	0.89	Caninae
Lupullela mesomelas	51.42	8.5	1.00	Caninae
Canis simensis	80.67	10.0	1.40	Caninae

Canis aureus	72.24	10.35	1.23	Caninae
Cani latrans	88.23	13.41	1.26	Caninae
Canis lupus	131.6	29.0	1.12	Caninae
Canis armbrusteri	153.43	47.46	0.94	Caninae
Canis dirus	177.66	63.37	0.90	Caninae
Lycaon pictus	129.0	22.05	1.32	Caninae
Cuon alpinus	95.0	12.76	1.40	Caninae
Cuon javanicus	117.19	18.41	1.35	Caninae
Osbornodon fricki	101.22	38.31	0.72	Hesperocyoninae
Osbornodon iamonensis	63.36	15.62	0.82	Hesperocyoninae
Cynodesmus thooides	37.77	9.05	0.70	Hesperocyoninae
Enhydrocyon basilatus	73.68	29.99	0.61	Hesperocyoninae
Enhydrocyon pahisintewakpa	54.12	18.71	0.62	Hesperocyoninae
Enhydrocyon stenocephalus	69.11	20.74	0.74	Hesperocyoninae
Hesperocyon gregarius	14.88	2.3	0.69	Hesperocyoninae
Mesocyon brachyops	39.35	7.29	0.85	Hesperocyoninae

Mesocyon coryphaeus	48.17	10.42	0.82	Hesperocyoninae
Paraenhydrocyon josephi	40.04	6.93	0.90	Hesperocyoninae
Sukahetanka geringensis	54.69	12.6	0.82	Hesperocyoninae
Cormocyon copei	24.9	3.0	0.97	Hesperocyoninae
Desmocyon matthewi	38.62	6.05	0.94	Hesperocyoninae
Desmocyon thompsoni	36.76	5.19	0.99	Hesperocyoninae
Rhizocyon oregonensis	17.27	1.69	0.99	Borophaginae
Otarocyon cooki	11.04	0.81	1.03	Borophaginae
Otarocyon macdonaldi	7.87	0.7	0.81	Borophaginae
Phlaocyon leucosteus	18.97	2.81	0.77	Borophaginae
Paracynarctus sinclairi	59.59	8.51	1.15	Borophaginae
Microtomarctus conferta	34.93	6.71	0.79	Borophaginae
Protomarctus optatus	54.78	10.33	0.93	Borophaginae
Tomarctus hippophaga	68.05	13.96	0.95	Borophaginae
Paratomarctus euthos	59.94	13.73	0.84	Borophaginae
Paratomarctus temerarius	53.99	9.94	0.94	Borophaginae

Carpocyon compressus	71.62	15.42	0.93	Borophaginae
Carpocyon webbi	100.8	24.8	0.95	Borophaginae
Tomarctus brevirostris	51.3	19.39	0.57	Borophaginae
Aelurodon asthenostylus	92.31	27.01	0.82	Borophaginae
Aelurodon ferox	134.4	35.75	1.00	Borophaginae
Aelurodon taxoides	148.65	42.98	0.97	Borophaginae
Aelurodon mcgrewi	62.59	28.1	0.54	Borophaginae
Epicyon haydeni	131.27	71.86	0.61	Borophaginae
Epicyon saevus	104.11	39.3	0.72	Borophaginae
Borophagus littoralis	127.02	32.04	1.01	Borophaginae
Borophagus secundus	119.17	34.77	0.90	Borophaginae

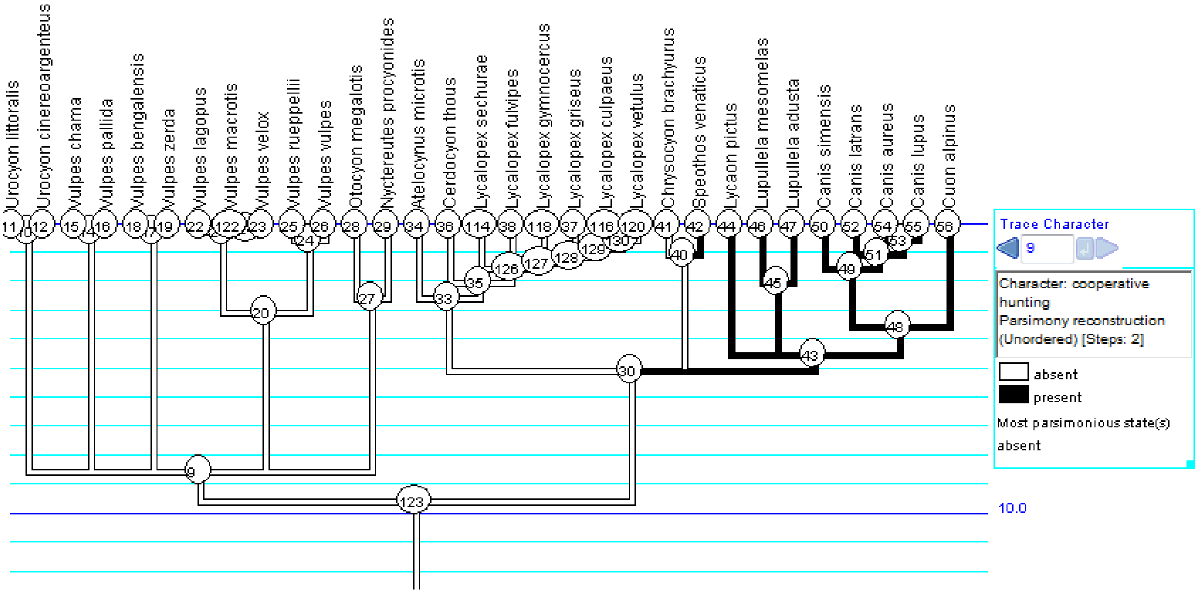


Fig. 7. Parsimony reconstruction of cooperative hunting within recent Caninae. (numbers in circles = node numbers)

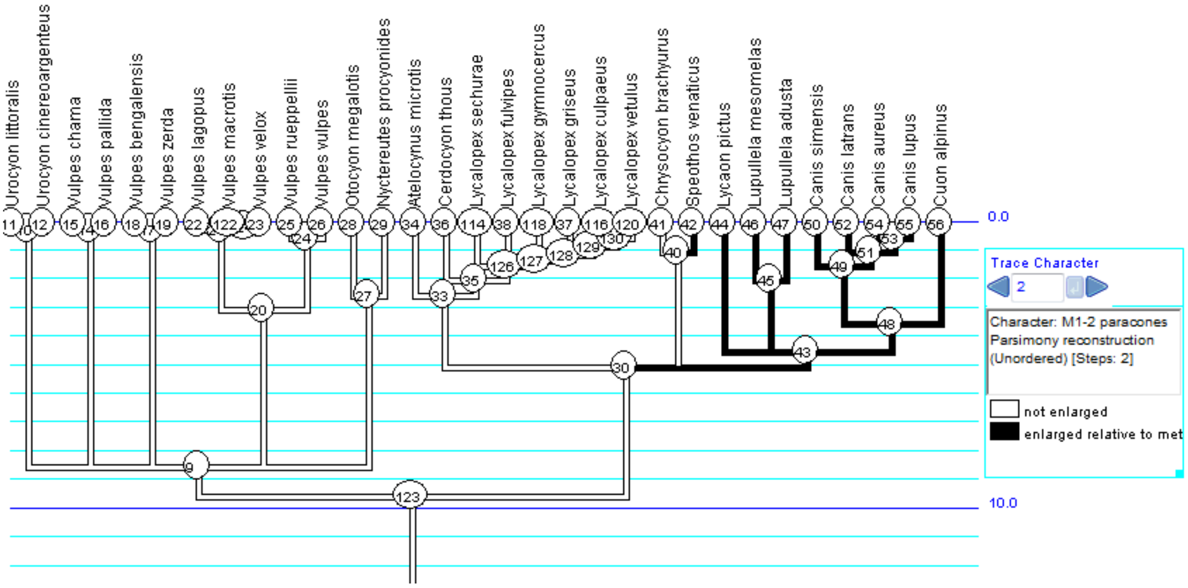
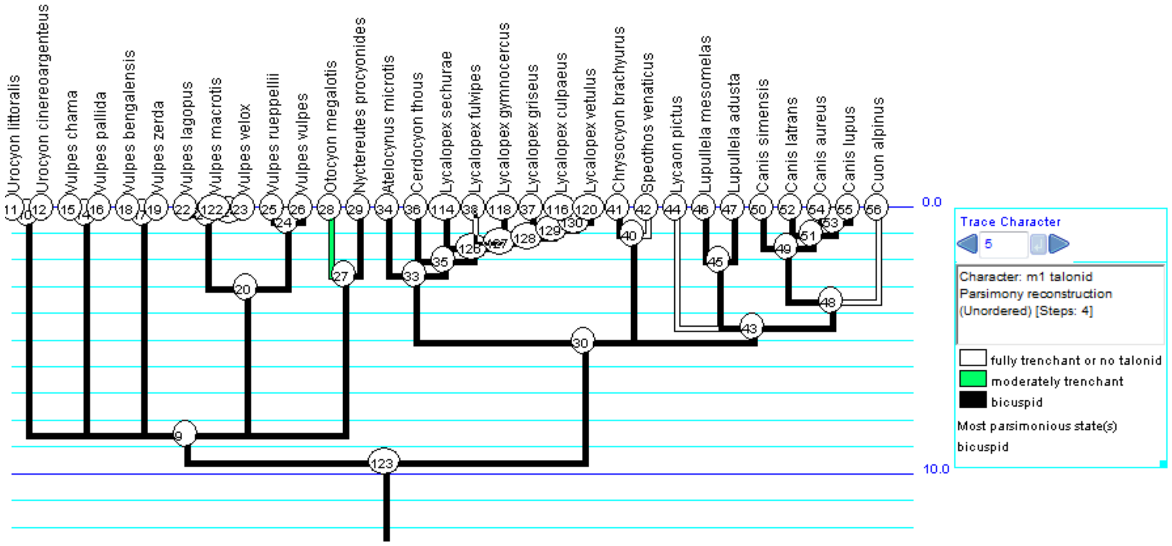


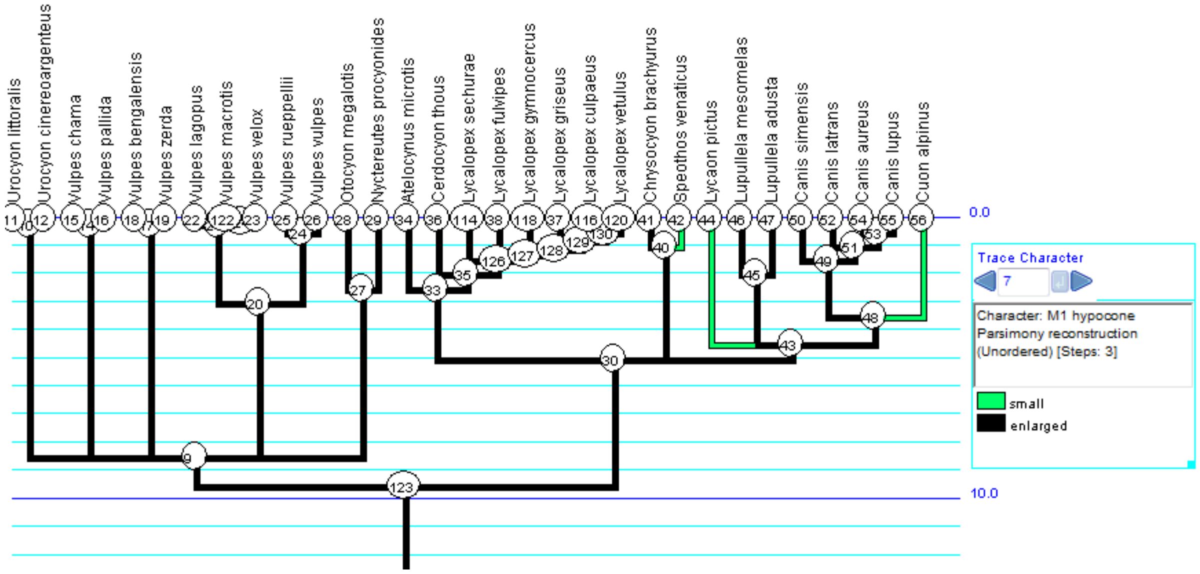
Fig. 8. Parsimony reconstruction of trait M1-2 paracones within recent Caninae. (numbers in circles = node numbers)



Character: m1 talonid
Parsimony reconstruction
(Unordered) [Steps: 4]

Most parsimonious state(s)
bicuspid

Fig. 9. Parsimony reconstruction of trait m1 talonid within recent Caninae. (numbers in circles = node numbers)



Character: M1 hypocone
Parsimony reconstruction
(Unordered) [Steps: 3]

Fig 10. Parsimony reconstruction of trait M1 hypocone within the recent Caninae. (numbers in circles = node numbers)

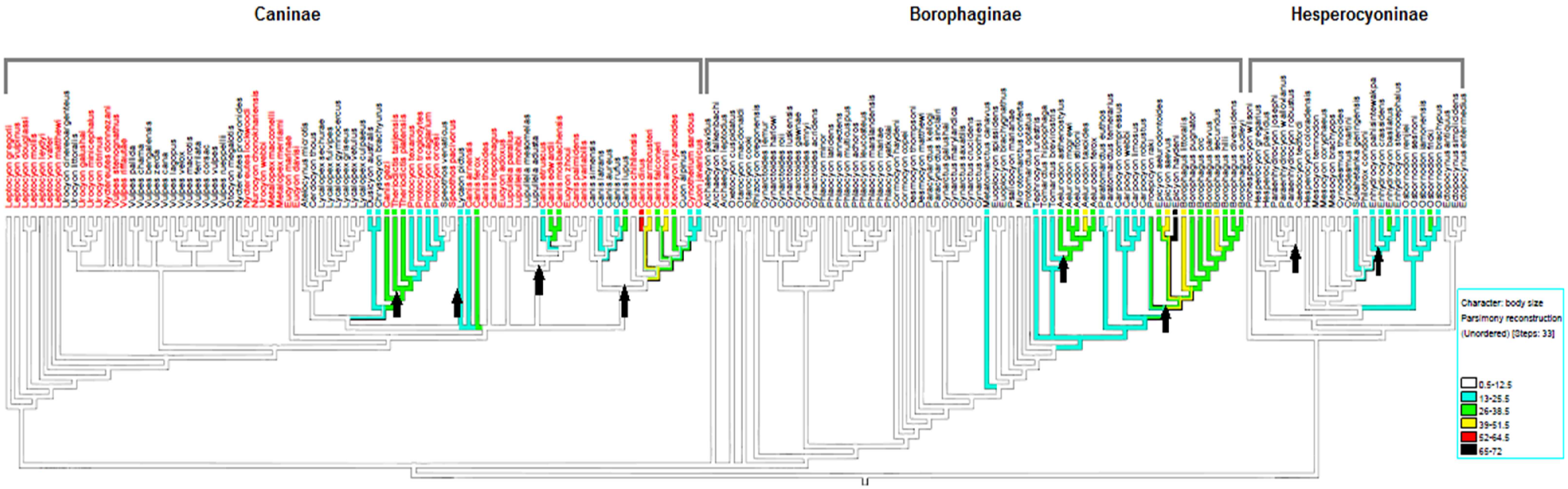


Fig. 11. Parsimony optimization of the osteological indicator of cooperative hunting (M1-2 paracones**)** on the tree, where the body is mapped (black arrow – occurence of M1-2 paracones, CI = 0,11, RI = 0,64). (red names: fossil species of Caninae)

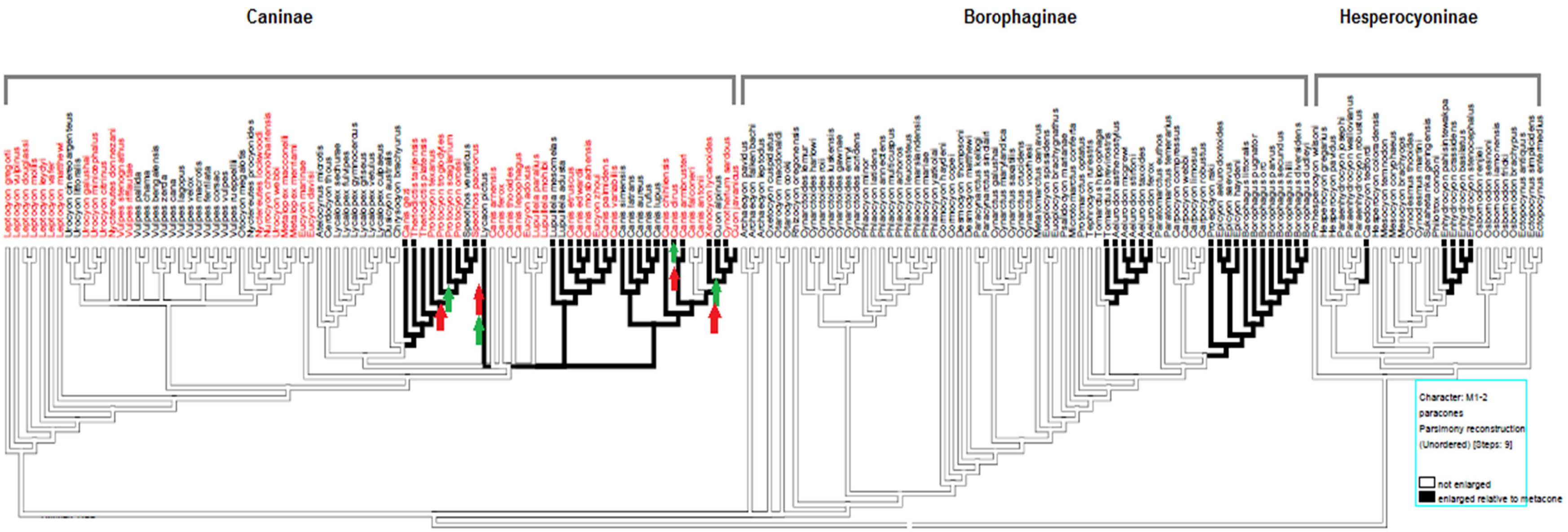


Fig. 12. Parsimony optimization by two indicators of hypercarnivory (green arrow – m1 talonid, red arrow – M1 hypocone) on the tree, where the osteological indicator of cooperative hunting (M1-2 paracones) is mapped. (for m1 talonid: CI = 0,37, RI = 0,87, for M1 hypocone: CI = 0,2, RI = 0,66). (red names: fossil species of Caninae).

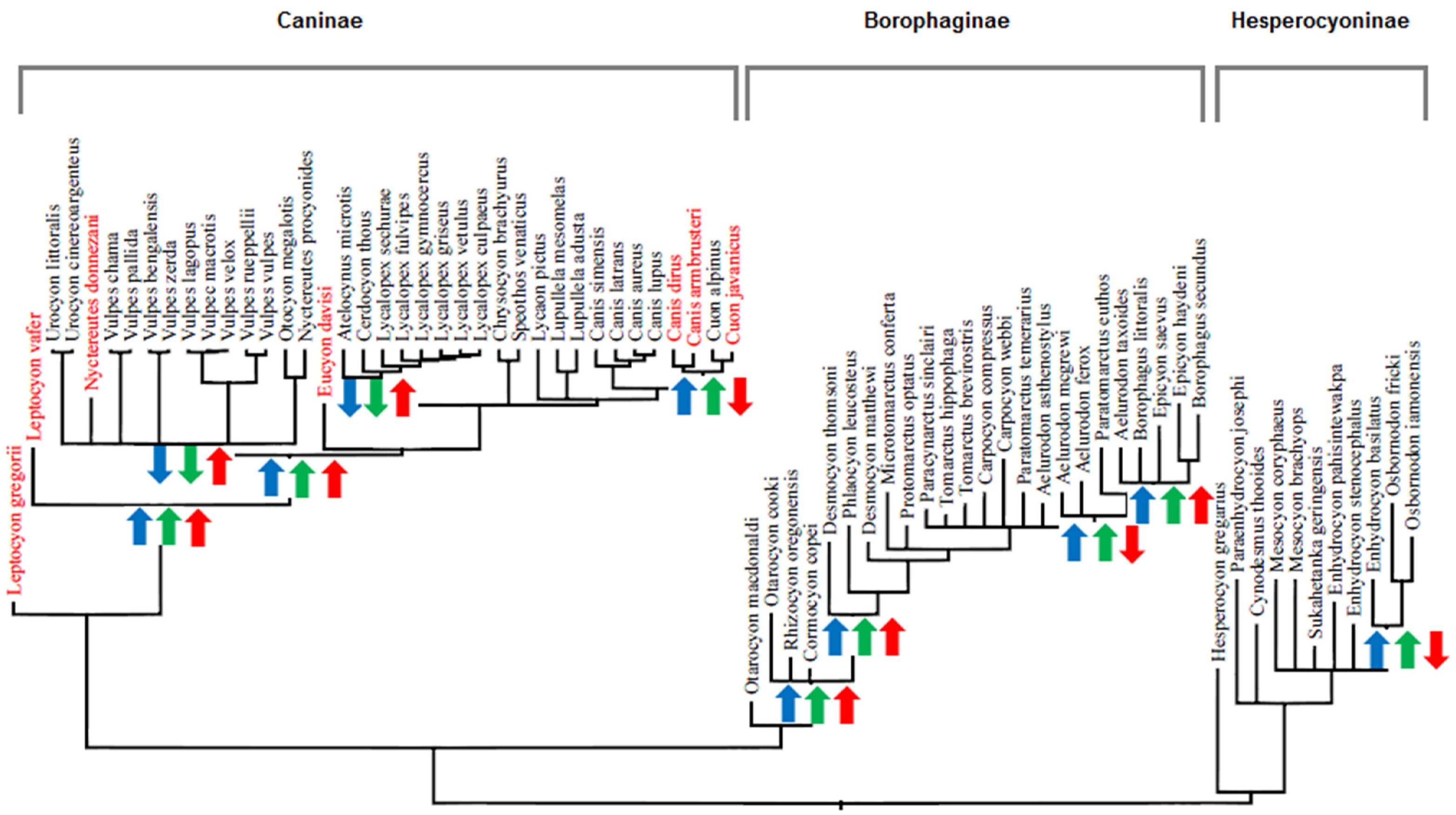


Fig. 13. Ancestral reconstruction of brain volume, body size and encephalization quotient (EQ). (blue – brain volume, green – body size, red – EQ).

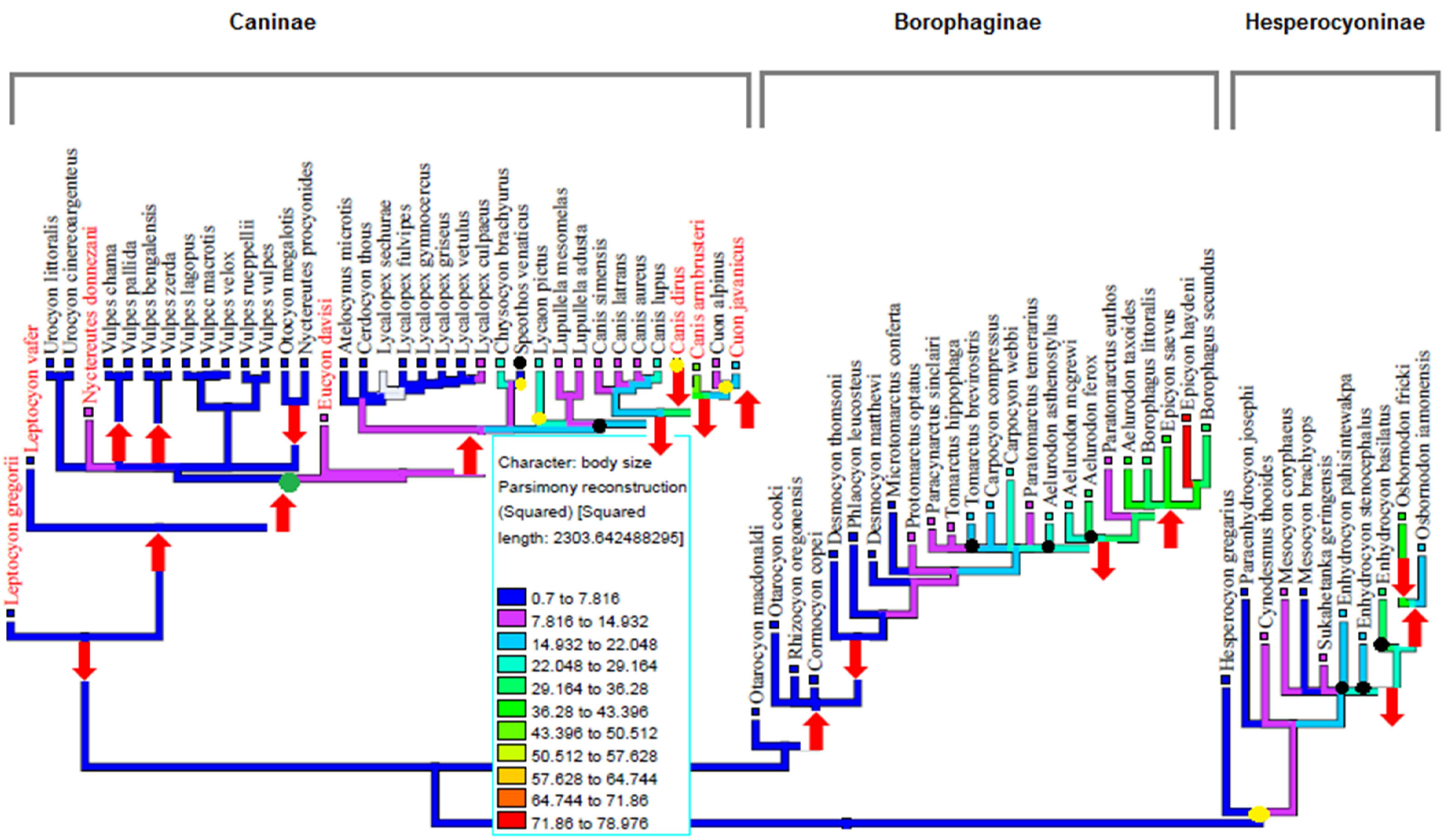


Fig. 14. Parsimony optimization of all characters on the Caninae tree, where the body size is mapped. (red arrows – increasing/decreasing of EQ, green spot – occurence of mesocarnivory, black spot – occurence of cooperative hunting, yellow spot – occurence of hypercarnivory, blue names: fossil species of Caninae).

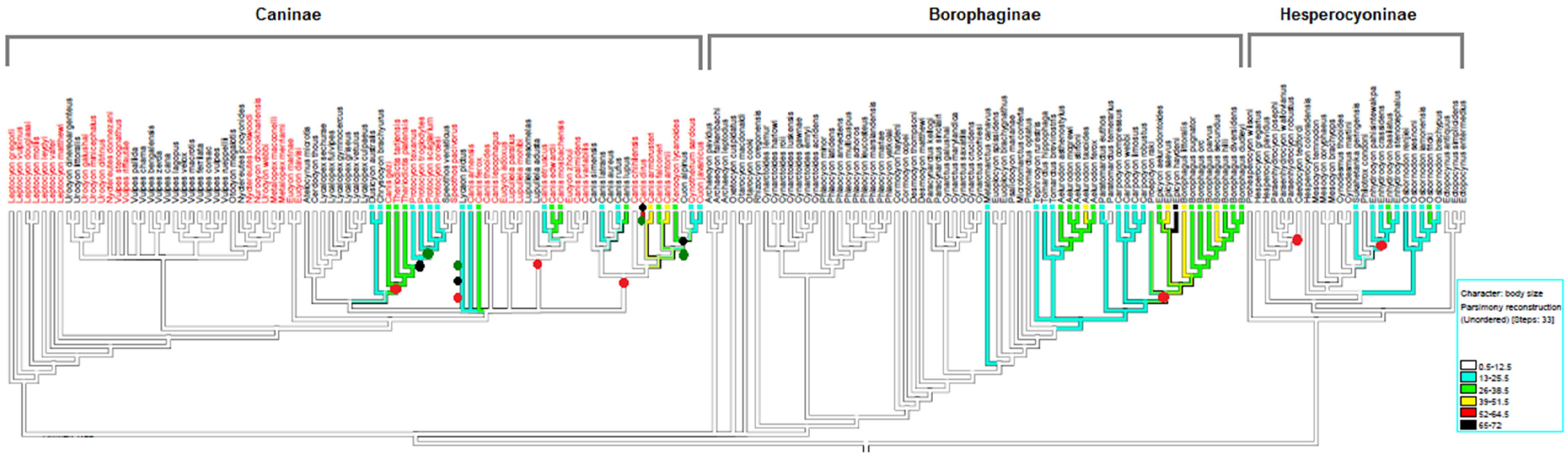


Fig. 15. Parsimony optimization of all osteological characters on the Canidae tree, where the body size is mapped. (red spot – occurence of cooperative hunting, black and green spot – occurence of hypercarnivory, red names – fossil species of Caninae)

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