

## Deer Inquiry: Evolution Why have red deer and elk diverged?

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# Phylogenetic History of Deer (Cervids)

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- Cervidae originated in Asia (8.5 mya)
  - Diverged after the final uplift of the northern Tibetan mountains
  - forests receding
  - grasslands expanding
- North American lineage diverged about 7.8 mya
  - Ancestors of white-tailed deer and caribou
    - Female caribou gained antlers
  - Ancestors of South American lineages
    - Lost antlers
    - Decline in body size
    - Adaptation to the tropics/Andes mountain uplift
- Cervus diverged from Dama (fallow deer; about 3 mya)
  - Divergence of 4 cervus species occurred during ice ages (1.5 mya)
  - Elk crossed the Beringia land bridge to North America

Sources: Gilbert et al. 2006, Cap et al. 2008

# Phylogenetic History of Deer (Gilbert et al. 2006)

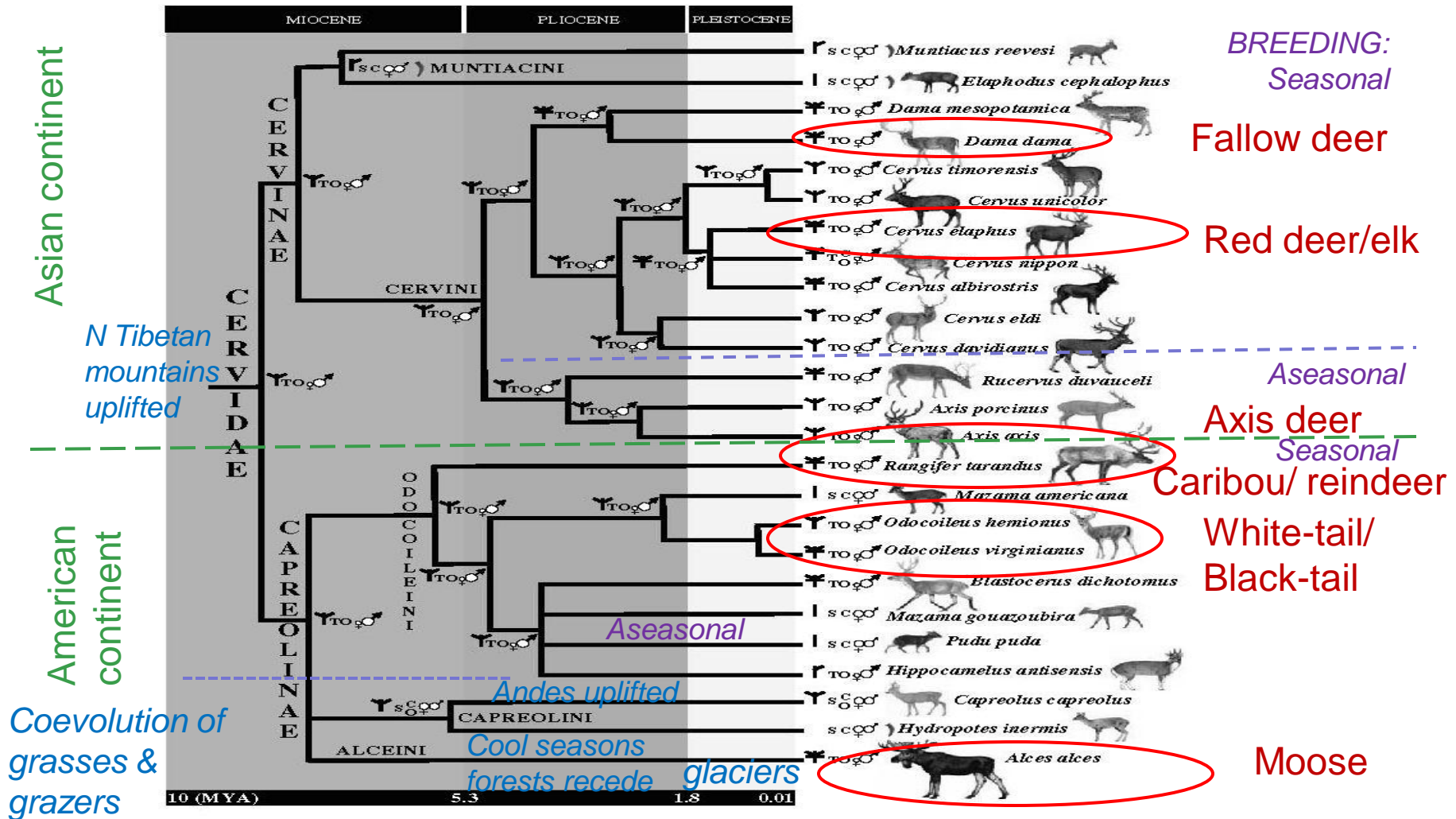


Fig. 4. Synthetic tree of the family Cervidae. The tree is a consensus derived from the Bayesian and maximum likelihood analyses of the matrix combining all four markers (*CO2*, *Cyb*, *αLAIb* and *PRKCI*). The nodes supported by a Bootstrap value below 70 in the combined analysis are not represented. The date estimates were calculated by using the tree shown in Fig. 2 and are detailed in Table 2. The time scale comes from the Geological Society of America (1999, available at <http://www.geosociety.org/science/timescale/timescl.pdf>). The symbols indicate the distributions of different character states corresponding to antlers (I = one tine; II = two tines; III = three tines; IV = four tines or more), > = tusk-like upper canines, body size (S = Small, or minimum shoulder size <650 mm; T = Tall or minimum shoulder size >650 mm), sexual dimorphism in weight (♂ = monomorphism; ♀ = dimorphism), and habitat type (O = open; C = closed). As detailed in Section 2, the evolution of these characters was inferred using PAUP 4.0b10 (Swofford, 2003).

# Rutting call: comparison of structure across species

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H. Cap et al. / *Cladistics* 24 (2008) 917–931

Source: Cap et al. 2008

## Rutting call

|                                  |   |
|----------------------------------|---|
| <i>Ovis gmelini</i>              | absent (Gonzalez, pers. comm.)            |
| <i>Moschus moschiferus</i>       | absent (Flerov 1952, Green 1985)          |
| <i>Hydropotes inermis</i>        | whistle (Cook and Farrel 1998)            |
| <i>Capreolus capreolus</i>       | rasping grunt (Danilkin and Hewison 1996) |
| <i>Alces alces</i>               | grunt (Geist 1999)                        |
| <i>Odocoileus virginianus</i>    | complex grunt (Atkeson et al., 1988)      |
| <i>Rangifer tarandus</i>         | grunts (Lent 1975)                        |
| <i>Muntiacus muntjak</i>         | cackling (Dubost, 1971)                   |
| <i>Dama dama</i>                 | groan (Reby 1998)                         |
| <i>Cervus elaphus elaphus</i>    | roars (Reby and McComb 2003a)             |
| <i>Cervus elaphus corsicanus</i> | roars (Reby and McComb 2003b)             |
| <i>Cervus nippon</i>             | moan (Minami and Kawamishi, 1992)         |
| <i>Cervus canadensis</i>         | bugle (Feighny et al. 2006)               |

ancestral →

Diverged during Pleistocene ice ages

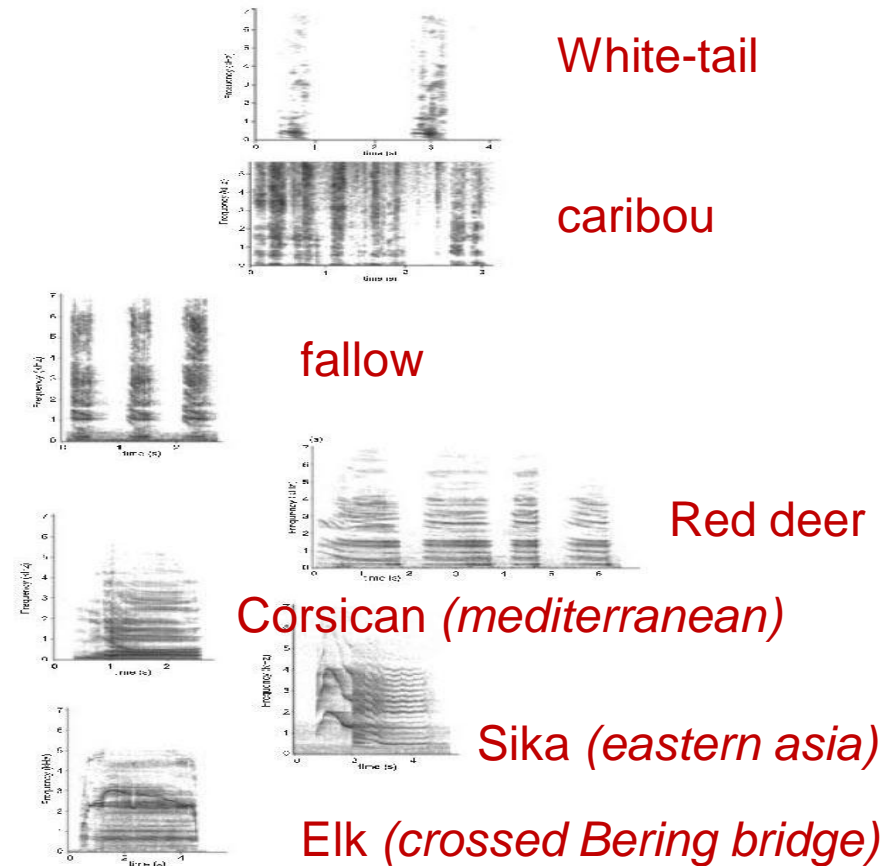


Fig. 2. Spectrograms of the rutting calls for 7 of the 13 taxa.

# Phylogenetic similarity: combined genetic & behavior traits

926

H. Cap et al. | *Cladistics* 24 (2008) 917-931

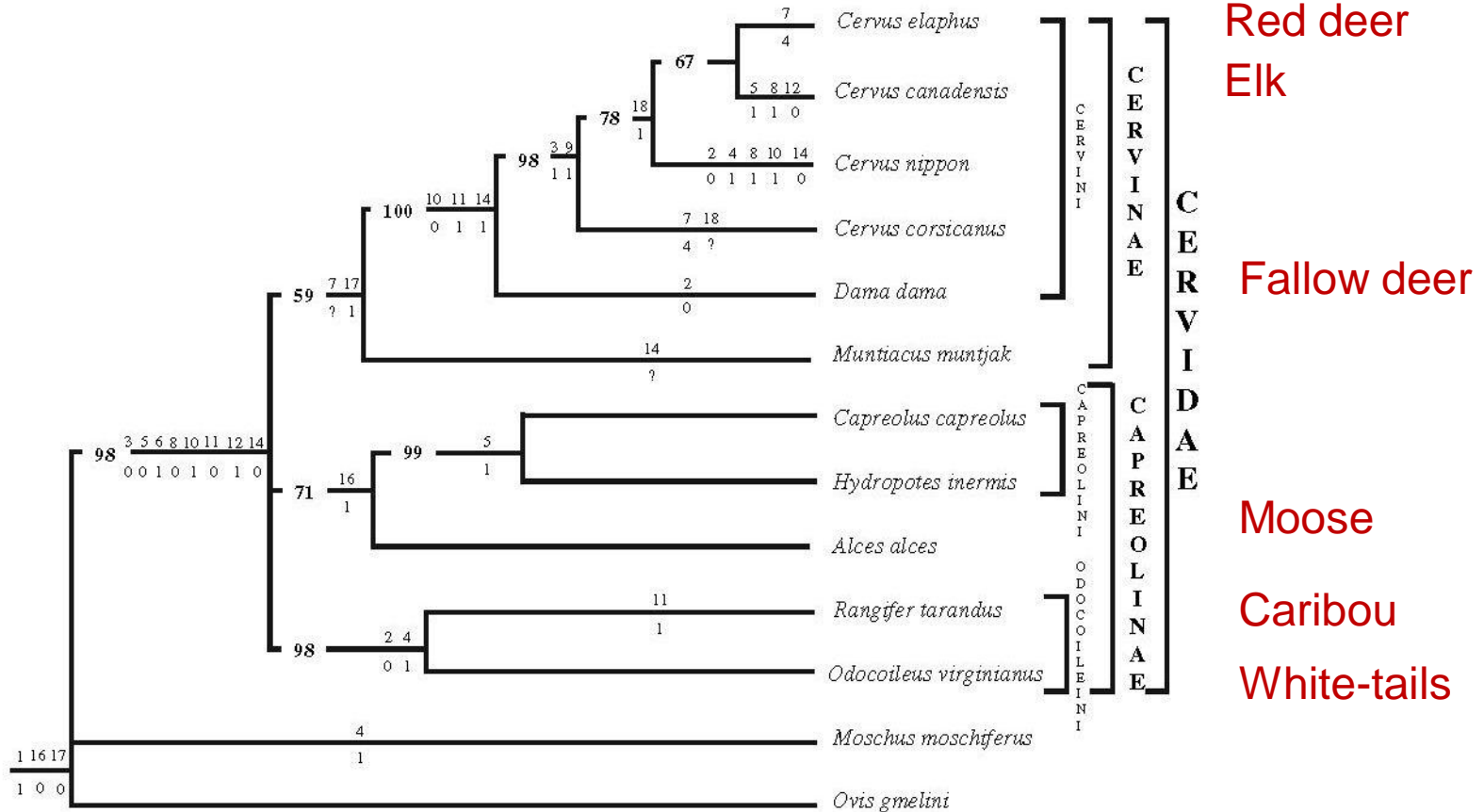


Fig. 3. Cladogram supported by vocal and molecular data (simultaneous parsimony analysis). Bold numbers on branches indicate bootstrap values. Vocal synapomorphies (except for ambiguous characters 13 and 15, see text) are indicated with character number (above branches) and character state number (below), referring to character descriptions and data matrix (Tables 2 and 3).

# Rutting call: Hypotheses about long-term Functions

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- ▶ **Long term “priming” (weeks, i.e. reproductive hormones)**
- ▶ **Synchronizes (speeds up) ovulation cycles in females**
  - H1: synchronized calving is an anti-predator adaptation
  - H2: calves born earlier in the spring grow larger by fall (survive winter)
  - H3: larger female groups less vulnerable to predators (female calls)
  - H4: avoid harassment by intruders (cost to asynchronous females)
- ▶ **Elevates testosterone in older males (audience effect)**
  - H5: higher rate of calling by males is more attractive to females
  - H6: lower formant frequencies are more intimidating to males
  - H7: older, stronger males defend territories with better resources
  - H8: younger, less experienced males stay in bachelor herds where they practice sparring and avoid injury as they mature
  - H9: “good genes” survival to an older age is correlated with other traits influencing overall health (of father and sons)
  - H10: physical sound structure=> lower pitch=> sound carries further in dense vegetation (Geist 1972)

# Rutting call: Hypotheses about short-term Functions

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- ▶ **Short term “releaser” (seconds/minutes, i.e. neurotransmitters)**
- ▶ **High pitch (fundamental frequency) attracts attention of females**
  - H1: short distance function of cow calls (sound blocked by trees)
  - H2: females that chose higher pitched roars had more competitive “sneaky sons” (Reby et al. 2010)
- ▶ **Low pitch (fundamental frequency) intimidates male intruders**
  - H3: motivational structure rules; predicts escalation (Feighny et al. 2006)
  - H4: in the ancestral form (fallow deer) low pitch was an honest indicator of male dominance (Vannoni & McElligott 2008)
- ▶ **Resonance (formant frequency/dispersion)=> dual function**
  - H5: Corsican deer are smaller, shorter vocal tract, higher resonance but lower fundamental frequency (Kidjo et al. 2008)
  - H6: females avoid harassment by sub-adults (Charlton et al. 2008)
  - H7: females distinguish between individuals, i.e. harem master & intruders (Reby et al. 2001, Reby et al. 2006, Charlton et al. 2007)
  - H8: “size exaggeration” by dropping larynx (McElligott et al. 2006)

# Function of “Switching” between De-escalation & Escalation

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- **Youngsters that escalated fights more likely died when mismatched**
  - Young non-breeders inexperienced at winning fights
  - Those that de-escalated when very young would have survived longer, potentially gaining a territory at prime breeding age
- **Those prime-age males that escalated were more likely to have taken over a breeding territory from an older, weaker individual**
  - “Mismatch”: older males likely were in worse body condition at end of rutting season, compared to prime-age males
  - Older “past prime” breeders have already contributed “switcher” genotypes to the gene pool (when they were younger, they de-escalated)
  - “Switcher” genotypes would have controlled access to food resources attractive to those females that were most successful at raising calves
- **“Switching” had few benefits in monogamous, monomorphic, small-bodied species adapted to forests (eat high quality shoots & leaves)**
  - Duikers (Africa) and muntjacs (Asia)
  - Brouwer's deer (South America)



# Phylogenetic Similarity of Deer Species (Cap et al. 2008)

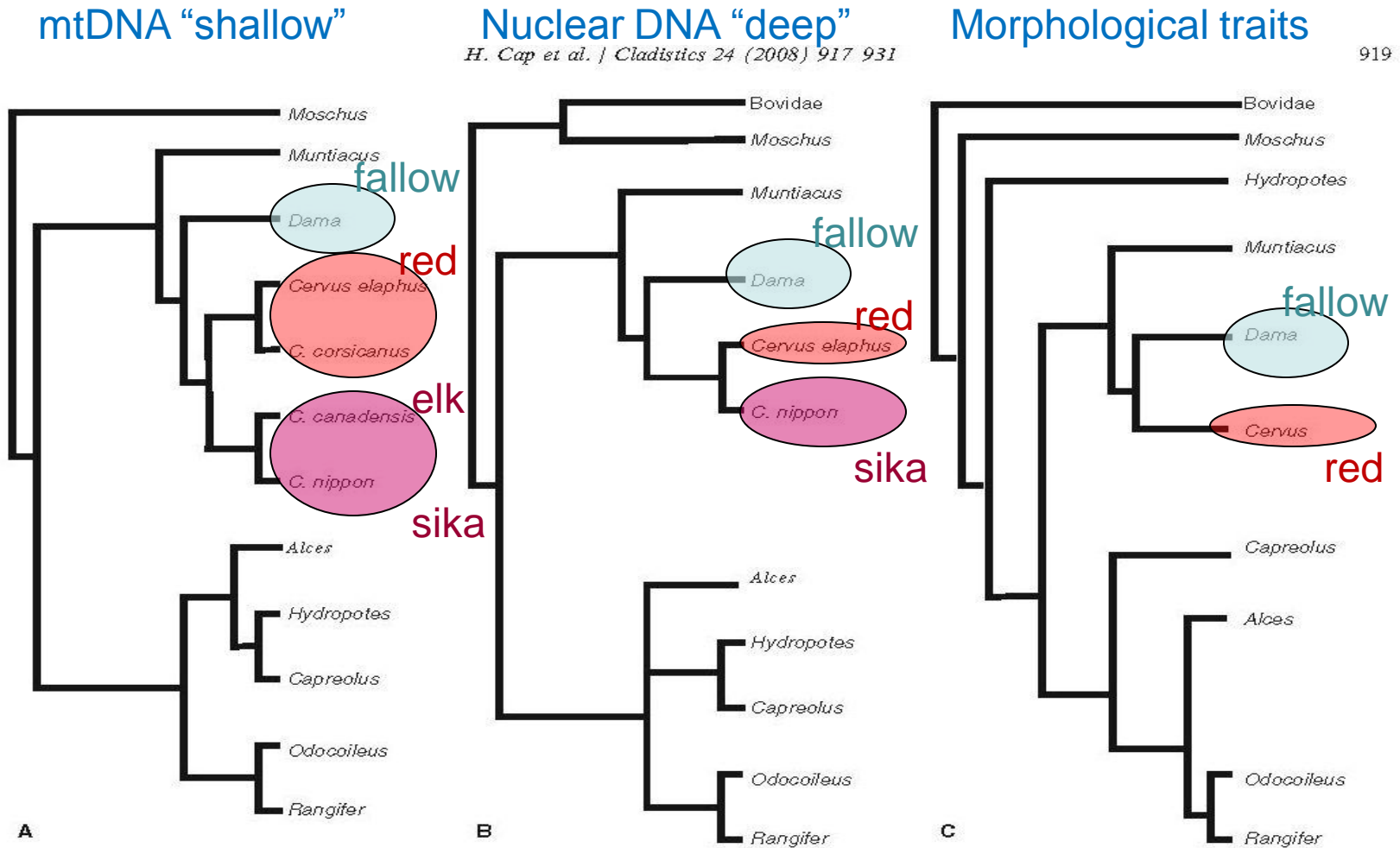


Fig. 1. Cladograms (maximum parsimony) of Cervids phylogenetic relationships based on: (A) *Cytochrome b* mtDNA gene data (Randi et al., 1998; Pitra et al., 2004); (B) *Cytochrome b* and *CO2* mtDNA and nuclear fragments: exon 2 of *alpha-lactalbumin* and intron 1 of the gene encoding *protein kinase C iota* data (Gilbert et al., 2006); (C) morphological data (Groves and Grubb, 1987).

# SUMMARY

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- ▶ **H1. The smaller body size and lesser ability to drop the larynx was the ancestral form (elk more similar to ancestors)**
  - Advantage to large body size in foraging for grass
  - Sexual selection for baritones (dropped larynx)
- ▶ **H2. The larger body size and greater ability to drop the larynx was ancestral (red deer more similar to ancestors)**
  - Elk lost large body size
  - Elk lost ability to drop larynx
- ▶ **H3. Both elk and red deer diverged from an ancestor intermediate in character traits**

## Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): Systematics, morphology, and biogeography

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### Abstract

The family Cervidae includes 40 species of deer distributed throughout the northern hemisphere, as well as in South America and Southeast Asia. Here, we examine the phylogeny of this family by analyzing two mitochondrial protein-coding genes and two nuclear introns for 25 species of deer representing most of the taxonomic diversity of the family. Our results provide strong support for intergeneric relationships. To reconcile taxonomy and phylogeny, we propose a new classification where the family Cervidae is divided in two subfamilies and five tribes. The subfamily Cervinae is composed of two tribes: the tribe Cervini groups the genera *Cervus*, *Axis*, *Dama*, and *Rucervus*, with the Père David's deer (*Elaphurus davidianus*) included in the genus *Cervus*, and the swamp deer (*Cervus duvaucelti*) placed in the genus *Rucervus*; the tribe Muntiacini contains *Muntiacus* and *Elaphodus*. The subfamily Capreolinae consists of the tribes Capreolini (*Capreolus* and *Hydropotes*), Alceini (*Alces*), and Odocoileini (*Rangifer* + American genera). Deer endemic to the New World fall in two biogeographic lineages: the first one groups *Odocoileus* and *Mazama americana* and is distributed in North, Central, and South America, whereas the second one is composed of South American species only and includes *Mazama gouazoubira*. This implies that the genus *Mazama* is not a valid taxon. Molecular dating suggests that the family originated and radiated in central Asia during the Late Miocene, and that Odocoileini dispersed to North America during the Miocene/Pliocene boundary, and underwent an adaptive radiation in South America after their Pliocene dispersal across the Isthmus of Panama. Our phylogenetic inferences show that the evolution of secondary sexual characters (antlers, tusk-like upper canines, and body size) has been strongly influenced by changes in habitat and behaviour.

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**Keywords:** Cervidae; Ruminantia; Phylogeny; Taxonomy; Evolution; Biogeography; Sexual dimorphism; Mitochondrial DNA; Nuclear DNA

## Male vocal behavior and phylogeny in deer

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### Abstract

The phylogenetic relationships among 11 species of the Cervidae family were inferred from an analysis of male vocalizations. Eighteen characters, including call types (e.g. antipredator barks, mating loudcalls) and acoustic characteristics (call composition, fundamental frequency and formant frequencies), were used for phylogeny inference. The resulting topology and the phylogenetic consistency of behavioral characters were compared with those of current molecular phylogenies of Cervidae and with separate and simultaneous parsimony analyses of molecular and behavioral data. Our results indicate that male vocalizations constitute plausible phylogenetic characters in this taxon. Evolutionary scenarios for the vocal characters are discussed in relation with associated behaviors.

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