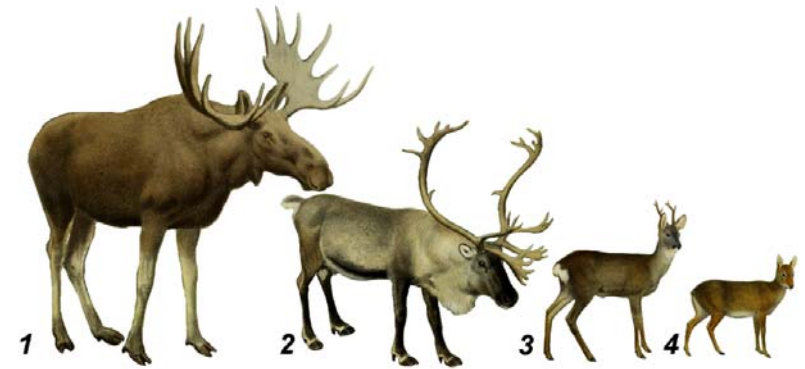


# Phylogeny, evolution, and diversity of Old World telemetacarpal deer (Capreolinae, Cervidae, Mammalia)

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## introduction



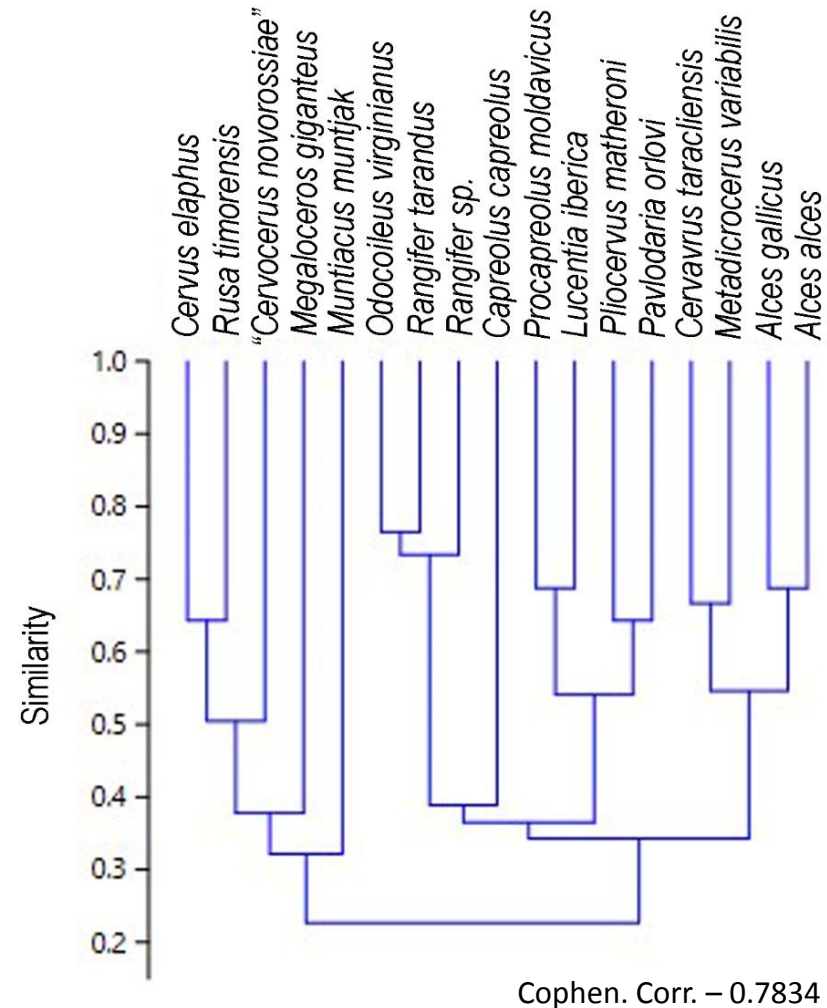
- Modern telemetacarpal deer (subfamily **Capreolinae**) are represented by few very specialized Old World forms (**1**, *Alces alces*; **2**, *Rangifer tarandus*; **3**, *Capreolus capreolus*; **4**, *Hydropotes inermis*) and a diversified radiation of New World telemetacarpal deer. The known paleontological record of Capreolinae in Eurasia is rather scarce and for some genera (*Procapreolus*) is traced from the Late Miocene, while other lineages appear only in the Early Pleistocene and already represented by very specialized forms (*Alces*). Some poor Pliocene remains of *Capreolus* and of a form similar to *Alces* are reported by Vislobokova et al. (1995) from the Late Pliocene of Baikal Area. Another interesting recent finding is *Rangifer sp.* from the Early Pleistocene of Western Siberia that maintains the primitive orientation of pedicles (Bondarev et al., 2017). Those sparse findings suggest that Capreolines continuously were present in the middle latitudes of Eurasia, but their fossil remains apparently are misunderstood.
- The Miocene record of Capreolinae is insufficiently known and many of cervid forms and species are poorly understood. This is the case of *Metadicrocerus variabilis*, *Cervavitus tarakliensis*, and *Pliocervus matheroni* (traditionally are placed in the tribe **Pliocervini** of the subfamily Cervinae) that are believed to have the intermediate phylogenetic position between modern Cervinae (plesiometacarpal deer) and archaic “muntjac-like” deer. The present study proposes a new look on the Late Miocene “Pliocervines” and focus attention upon their possible relationships with Capreolinae.

# material and methods

- A multivariate cluster analysis of the diagnostic cranial, dental, and antler characters was carried out in order to estimate the taxonomic value of the selected characters and to find support for the systematic position of the Late Miocene – Pliocene deer the middle latitudes of Eurasia (genera *Lucentia*, *Procapreolus*, *Cervavitus*, *Pliocervus*, *Pavlodaria*, etc.) and modern telemetacarpal cervid species included in the present study.
- The cluster analysis is based on postcranial (tele- and plesiometacarpality) and craniodental characters (including antler morphology) that are used as taxonomic criteria at family, genus, and species level.
- In some cases, the hypothesized assumption of missing characters (telemetacarpality, upper canines development, etc.) is accepted.
- The hierarchical clustering paired group algorithm UPGMA was computed using the Jaccard Similarity Index for presence-absence data (PAST-3 application: Hammer et al., 2001). The cophenetic correlation coefficient is computed in order to estimate how faithfully a dendrogram preserves the pairwise distances among the original, unmodeled data points (Farris, 1969).
- The fossil and modern osteological material used in the present study is stored in the National Museum of Natural History, Paris (France); the National Museum of Natural History, Kiev (Ukraine); the Paleontological Institute, Moscow (Russia); the Palaeontological Museum of the University of Bucharest (Romania); the Institute of Zoology of the University of Wroclaw (Poland).
- A part of analysed morphological data are adapted from Teilhard de Chardin & Trassaert (1937); Flerov (1952), Azanza (2000), Azanza & Montoya (1995), Vislobokova (1980), Vislobokova et al. (1995), Bondarev et al. (2017).

## results

- The puzzling holometacarpal “*Cervocerus novorossiae*” (Teilhard de Chardin & Trassaert, 1937) from the Late Tertiary of China is nested within plesiometacarpal Cervinae.
- *Rangifer sp.* from the Pliocene of Isakovka-4 (Omsk, Russia) is grouped with modern *R. tarandus* and *Odocoileus virginianus*. The loss of *Palaeomeryx* fold is the most peculiar characteristic of this group.
- *Pliocervus* is closely associated with *Pavlodaria* from the Pliocene of Kazakhstan. In their turn, they are grouped with primitive “muntjac-like” capreoline genera *Procapreolus* and *Lucentia*.
- Modern *Capreolus* is quite distant from *Procapreolus* and is placed closer to the *Rangifer-Odocoileus* group, apparently, because of the similar with Pliocene *Rangifer* parallel position of pedicles and the loss of *Palaeomeryx* fold.
- The *Alces/Cervavitus/Metadicrocerus* group is opposed to the groups of primitive capreolinae, *Capreolus* and *Rangifer-Odocoileus*. This group is distinguished by moderate-to-strong divergence of pedicles and a peculiar direction in antler evolution that evolve supernumerary antler prongs.

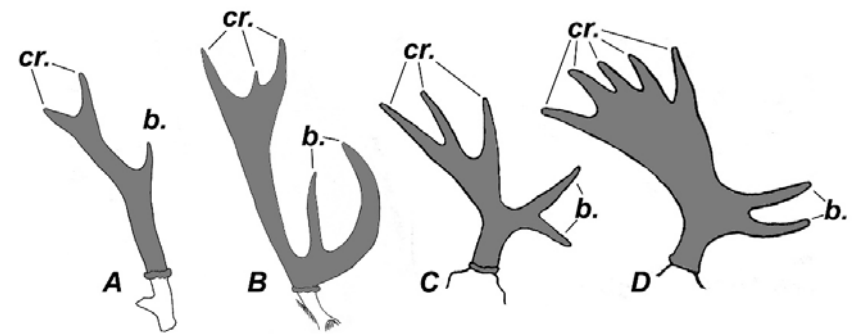


## discussion

Despite the extreme evolutionary specialization of modern and fossil Capreolinae, practically all of them maintain the basic antler bauplan found, for example, in *Capreolus*: a three-pointed antler with a high position of first ramification (*b.*, basal tine) and a distal fork formed by a posterior crown tine (*cr.*). Exactly the same antler bauplan is characteristic of *Procapreolus* (A), while, for instance, in *Metadicrocerus* (B) and *Alces* (C-D) antler are complicated by addition of crown tines and bifurcation of basal tine.

The development of *Palaeomeryx* fold in lower molars and protoconal fold in upper molars is another specific feature of the early “confirmed” Capreolinae (*Procapreolus*, *Pavlodaria*, *Alces gallicus*). *Pliocervus matheroni* from the Late Miocene of Cucuron (France) shows the same antler and molar morphology as *Pavlodaria orlovi*, with exception of primitive P<sub>4</sub>. This affinity between geographically distant forms (France and Kazakhstan) is confirmed by the present cluster analysis.

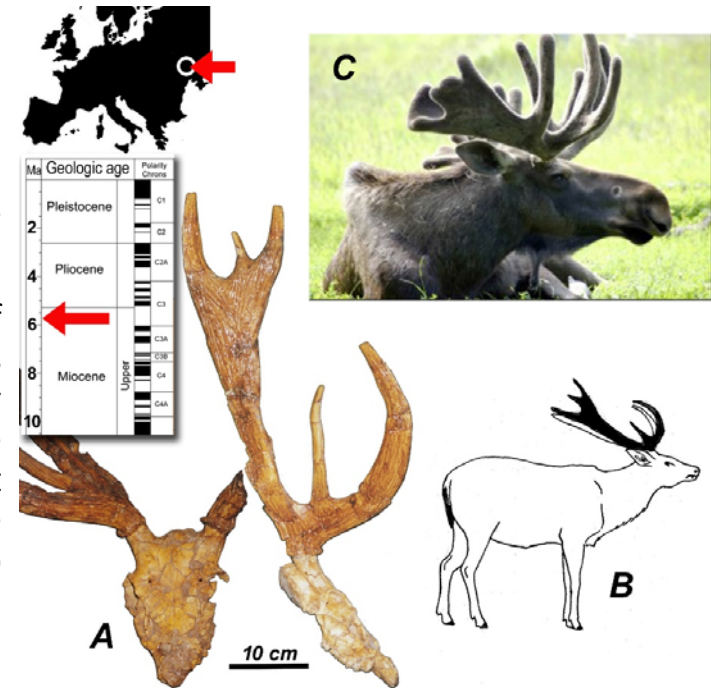
*Lucentia* from the Late Miocene of Iberia is characterized by simple two-tined antlers, its upper molars show the emerging protoconal fold, while lower molars are supplemented with a *Palaeomeryx* fold. Apparently, *Lucentia* is the most primitive Capreolinae deer and its association with “muntjac-like” *Procapreolus* confirms this assumption.



Antler bauplan in the Old World deer of the subfamily Capreolinae: A, *Procapreolus cusanus*; B, *Metadicrocerus variabilis*; C-D, *Alces alces*.

# conclusions

- Modern Eurasian Capreolinae represent a modest remnant of the Late Miocene radiation. The evolutionary radiation of capreolines took place in the middle latitudes of Eurasia and was significantly depleted during the subsequent climate changes.
- The multivariate cluster analysis demonstrated that such Late Miocene and Pliocene genera as *Cervavitus*, *Pliocervus*, and *Lucentia* represent the diversified evolutionary radiation of the subfamily Capreolinae in the past.
- *Lucentia* represents primitive two-pointed stage of antler evolution of Capreolinae and possibly belongs to the phylogenetic branch that includes *Procapreolus* and *Pliocervus*. The *Capreolus/Rangifer/Odocoileus* phylogenetic branch has a more distant phylogenetic relationship with the *Lucentia/Procapreolus/Pliocervus* group. The cluster analysis shows that modern *Capreolus* may represent an early evolutionary off-shoot of the *Rangifer/Odocoileus* lineage. The *Cervavitus/Metadicrocerus/Alces* group (see figure) is the most detached phylogenetic branch of Capreolinae. According to the present study, holometacarpal "*Cervavitus tarakliensis*" from the Late Miocene of China is associated with the subfamily Cervinae.
- Among the diagnostic plesiomorphic craniodental characters of Capreolinae should be mentioned the parallel and sloped backwards long pedicles, the *Palaeomeryx* fold in lower molars, the protoconal fold in upper molars, the high position of the first antler ramification, and the strong development of upper canines.



**A)** *Metadicrocerus variabilis* (= *Cervavitus variabilis*) from the Late Miocene of Eastern Europe; **B)** reconstruction of *Metadicrocerus variabilis*; **C)** antlers of modern *Alces alces*.